# PLS 002: BOTANY AND PHYSIOLOGY OF CULTIVATED PLANTS



*Tom Buckley*
University of California Davis

LibreTexts™

# PLS 002: Botany & Physiology of Cultivated Plants

Tom Buckley

University of California, Davis

This text is disseminated via the Open Education Resource (OER) LibreTexts Project (https://LibreTexts.org) and like the thousands of other texts available within this powerful platform, it is freely available for reading, printing, and "consuming."

The LibreTexts mission is to bring together students, faculty, and scholars in a collaborative effort to provide an accessible, and comprehensive platform that empowers our community to develop, curate, adapt, and adopt openly licensed resources and technologies; through these efforts we can reduce the financial burden born from traditional educational resource costs, ensuring education is more accessible for students and communities worldwide.

Most, but not all, pages in the library have licenses that may allow individuals to make changes, save, and print this book. Carefully consult the applicable license(s) before pursuing such effects. Instructors can adopt existing LibreTexts texts or Remix them to quickly build course-specific resources to meet the needs of their students. Unlike traditional textbooks, LibreTexts' web based origins allow powerful integration of advanced features and new technologies to support learning.




LibreTexts is the adaptable, user-friendly non-profit open education resource platform that educators trust for creating, customizing, and sharing accessible, interactive textbooks, adaptive homework, and ancillary materials. We collaborate with individuals and organizations to champion open education initiatives, support institutional publishing programs, drive curriculum development projects, and more.

The LibreTexts libraries are Powered by NICE CXone Expert and was supported by the Department of Education Open Textbook Pilot Project, the California Education Learning Lab, the UC Davis Office of the Provost, the UC Davis Library, the California State University Affordable Learning Solutions Program, and Merlot. This material is based upon work supported by the National Science Foundation under Grant No. 1246120, 1525057, and 1413739.

Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation nor the US Department of Education.

Have questions or comments? For information about adoptions or adaptions contact info@LibreTexts.org or visit our main website at https://LibreTexts.org.

This text was compiled on 03/04/2026

# TABLE OF CONTENTS


Licensing

## 1: Intro - what is life

- 1.1: Potential Energy in Biology

## 2: Plant structure

- 2.1: Cells and Tissues
  - 2.1.1: Introduction to Cells
  - 2.1.2: Plant Cell Structure
  - 2.1.3: Plant Tissues
  - 2.1.4: Chapter Summary
- 2.2: Roots
  - 2.2.1: Organs and Organ Systems
  - 2.2.2: External Root Structure
  - 2.2.3: Internal Root Structure
  - 2.2.4: Root Modifications
  - 2.2.5: Chapter Summary
- 2.3: Stems
  - 2.3.1: Stem Morphology (External Structure)
  - 2.3.2: Internal Anatomy of the Primary Stem
  - 2.3.3: Secondary Stem
  - 2.3.4: Stem Modifications
  - 2.3.5: Chapter Summary
- 2.4: Leaves
  - 2.4.1: External Structure of Leaves
  - 2.4.2: Internal Leaf Structure
  - 2.4.3: Leaf Modifications
  - 2.4.4: Chapter Summary
- 2.5: Meristems

## 3: Origin and evolution of land plants

- 3.1: A Brief History of Life on Earth
  - 3.1.1: A Brief History of Life on Earth
- 3.2: Biodiversity (Organismal Groups)
  - 3.2.1: Systematics
    - 3.2.1.1: Introduction
    - 3.2.1.2: Organizing Life on Earth
    - 3.2.1.3: Determining Evolutionary Relationships
    - 3.2.1.4: Perspectives on the Phylogenetic Tree
    - 3.2.1.5: Chapter Summary
  - 3.2.2: Early Land Plants
    - 3.2.2.1: Introduction to Early Land Plants
    - 3.2.2.2: Bryophytes

- 3.2.2.2: Bryophytes
  - 3.2.2.2.1: Anthocerotophyta
  - 3.2.2.2.2: Marchantiophyta
  - 3.2.2.2.3: Bryophyta
- 3.2.2.3: Seedless Vascular Plants
  - 3.2.2.3.1: Lycopodiopsida
  - 3.2.2.3.2: Polypodiopsida
- 3.2.2.4: Chapter Summary
- 3.2.3: Seed Plants
  - 3.2.3.1: Introduction to Seed Plants
  - 3.2.3.2: Gymnosperms
    - 3.2.3.2.1: Cycads and Ginkos
    - 3.2.3.2.2: Conifers and Gnetophytes
  - 3.2.3.3: Angiosperms
    - 3.2.3.3.1: Flowers
    - 3.2.3.3.2: Angiosperm Life Cycle
  - 3.2.3.4: Chapter Summary
- 3.2.4: Angiosperm Diversity
  - 3.2.4.1: Monocots and Eudicots
  - 3.2.4.2: Pollination Syndromes
  - 3.2.4.3: Fruits and Dispersal
  - 3.2.4.4: Angiosperm Families
  - 3.2.4.5: Chapter Summary
- 3.3: Life Cycles
- 3.4: The Origins of Crop Plants

## 4: Asexual reproduction

- 4.1: Asexual Reproduction
- 4.2: Grafting
  - 4.2.1: Grafts and Wounds
  - 4.2.2: Unique Storage Organs
  - 4.2.3: Terms

## 5: Sexual reproduction

- 5.1: Reproductive Development and Structure
- 5.2: Pollination and Fertilization

## 6: Plant genetics and breeding

- 6.1: The Early History of Genetics
- 6.2: Cataloging, Classification, and Deliberate Hybridizations
- 6.3: Plant Breeding
- 6.4: Genetic Improvement in Cereal Crops and the Green Revolution

## 7: Biotechnology

- 7.1: Genetically Engineered Crops
- 7.2: Genetic Modification
  - 7.2.1: Introduction

- 7.2.2: GMO Food (Activity)
- 7.3: GMOs

## 8: Basic chemistry and biochemistry

- 8.1: The Chemical Foundation of Life
  - 8.1.1: Prelude to The Chemical Foundation of Life
  - 8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
  - 8.1.3: Water
  - 8.1.4: Carbon
  - 8.1.E: The Chemical Foundation of Life (Exercises)
- 8.2: Biological Macromolecules
  - 8.2.1: Prelude to Biological Macromolecules
  - 8.2.2: Synthesis of Biological Macromolecules
  - 8.2.3: Carbohydrates
  - 8.2.4: Lipids
  - 8.2.5: Proteins
  - 8.2.6: Nucleic Acids
  - 8.2.E: Biological Macromolecules (Exercises)
- 8.3: Unit I- The Chemistry of Life

## 9: Photosynthesis - carbon reactions

- 9.1: Discovery of Photosynthesis
- 9.2: Photosynthesis Overview and Equation
- 9.3: Light-independent Reactions

## 10: Photosynthesis - light reactions

- 10.1: Energy and ATP
- 10.2: The Light-dependent Reactions

## 11: Plant water relations

- 11.1: Water Potential
- 11.2: Transpiration
  - 11.2.1: Adaptations to Reduce Transpiration
  - 11.2.2: Stomatal Opening and Closure
- 11.3: Cohesion-Tension Theory
- 11.4: Water Absorption
- 11.5: Water Transport
- 11.6: Transport of Water and Solutes in Plants

## 12: Photosynthetic adaptations

- 12.1: Photorespiration and Photosynthetic Pathways
- 12.2: CO2 uptake - C4 and CAM Pathways

## 13: Respiration and metabolism

- 13.1: Aerobic Cellular Respiration

## 14: Mineral nutrition

- 14.1: Prelude to Soil and Plant Nutrition
- 14.2: Nutritional Requirements of Plants
- 14.3: The Soil
- 14.4: Nutritional Adaptations of Plants
- 14.E: Soil and Plant Nutrition (Exercises)

## 15: Functional morphology and anatomy

- 15.1: Translocation (Assimilate Transport)

## 16: Environmental plant biology

- 16.1: Environmental Responses
  - 16.1.1: Tropisms
  - 16.1.2: Flowering
  - 16.1.3: Photoperiodism
  - 16.1.4: Etiolation and Shade Avoidance
  - 16.1.5: Dormancy
  - 16.1.6: Chapter Summary
- 16.2: Plant Sensory Systems and Responses

## 17: Measuring and analyzing plants

## 18: Predicting plants

## 19: Biotic interactions

- 19.1: Industrial Agriculture
- 19.2: Sustainable Agriculture

## 20: Climate change and plants

- 20.1: Earth's Energy Budget
- 20.2: The Greenhouse Effect
- 20.3: Climate and the Effects of Global Climate Change
- 20.4: Soil and Water Conservation

## Index

## Glossary

## Detailed Licensing



## Detailed Licensing

# Licensing

*A detailed breakdown of this resource's licensing can be found in **Back Matter/Detailed Licensing**.*

# CHAPTER OVERVIEW

## 1: Intro - what is life

1.1: Potential Energy in Biology

This page titled 1: Intro - what is life is shared under a not declared license and was authored, remixed, and/or curated by Tom Buckley.

# Matter and Energy in Biology

## Matter and Energy

The concepts of matter and energy are essential to all scientific disciplines. Yet, while ubiquitous and fundamental, these concepts are often amongst the most confounding for students. Take the concept of energy. The term is used in a variety of contexts in everyday life - “Can we move the couch tomorrow? I don’t have the energy.” “Hey dude! Turn the light off. We need to conserve energy.” “This is a great energy drink.” In many sciences classes, students are told that energy comes in different forms (i.e. kinetic, thermal, electrical, potential, etc.), making it difficult to understand exactly what energy “is”. In class, the concept of energy is also associated with myriad different equations, each with different variables, but that somehow all seem to end up having units of work. Hold on! Work? I thought we were talking about energy?! Given all the different contexts and sometimes seemingly contradictory treatments and definitions, it’s not hard to understand why these topics seem challenging for many students and in some cases end up turning them off of the fields that make heavy use of these ideas. While the concepts of matter and energy are most often associated with chemistry and physics, they are nevertheless central ideas in biology and we don’t shy away from this in BIS2A. Our instructional goals, however, are to help students develop a conceptual framework that will help them use the concepts of matter and energy to:

- successfully describe biological reactions and transformations;
- create models and hypotheses for “how things work” in biology that explicitly include matter and energy and;
- be scientifically correct and transferable to new problems and to other disciplines.

While there may be a couple of energy-related equations to learn and use in BIS2A, the main focus of the course will be on the robust development of the concepts of energy and matter and their use in the interpretation of biological phenomena.

## Motivation for Learning About Matter and Energy

Discussions about matter and energy make many, but not all, BIS2A students a little apprehensive. After all, aren’t these topics that belong in chemistry or physics? However, the transformations of matter and energy transfer are not phenomena reserved for the chemists and physicists or even scientists and engineers more generally. Understanding, conceptualizing, and doing some basic accounting of transformations of matter and transfers of energy are fundamental skills regardless of occupation or academic training. The scientist may need more rigorous and systematic descriptions of these transformations than the artist but both make use of these skills at various points of their personal and or professional lives. Take the following examples:

### Example 1: Matter and Energy Transformation in Global Warming

Let us for a moment consider a topic that affects us all, global warming. At its core lies a relatively simple model that is based on our understanding of energy in solar radiation, the transfer of this energy with matter on the Earth, and the role and cycling of key carbon containing gases in the Earth's atmosphere. In simple terms solar energy hits the earth and transfers energy to its surface, heating it. Some of this energy is transferred back into space. However, depending on the concentration of carbon dioxide (and other so-called greenhouse gases) different amounts of this energy may become “trapped” in the Earth’s atmosphere. Too little carbon dioxide and relatively little energy/heat is trapped - the Earth freezes and becomes inhospitable for life. Too much carbon dioxide and too much heat is trapped - the Earth overheats and becomes inhospitable for life. It stands to reason, therefore, that mechanisms (biological or other) that influence the levels of carbon dioxide in the atmosphere may be important to consider in the story of global warming and that developing a good understanding of global warming phenomena requires one to trace the flow of the carbon through its different forms and the mechanisms by which energy is transferred to and from different components of the system.

### Example 2: Muscle Contraction

Let us now consider a more personal example, the flexing of an arm starting from an extended position and ending in a flexed position. Like most processes, this one can be described and understood at various levels of detail: from the anatomical point of view where the system consists of muscles, skin, and bones to the molecular where the system is composed of individual interacting biomolecules. At whatever level of detail, if we want to create a story describing this process we know that: (a) the description must include an accounting for what happened to the matter in the system (this includes the change in position of the molecules making up the various parts of the arm and the fuel “burned” to move it) and (b) that some fuel was burned to initiate the movement and therefore, that any description of the process must also include an accounting change in the energy of the system. In simpler terms, this is really just saying that if you want to describe a process where something has happened, you need to describe what happened to the “stuff” in the system and what happened to the energy in the system to make the process happen.

We can't possibly cover all examples of matter and energy transfer in BIS2A. But, we will explore these issues often and practice describing transformations that happen in Nature with a structured and explicit attention to what is happening to the matter and energy in a system as it changes. We will do this exercise across different structural levels in biology, from the molecular level (like a single chemical reaction) to more large-scale and abstracted models like nutrient cycling in the environment. We will practice this skill by using a pedagogical tool we call “The Energy Story”. Be prepared to participate!

# The Energy Story

## Overview of the Energy Story

Whether we know it or not, we tell stories that involve matter and energy everyday, we just don’t often use terminology associated with scientific discussions of matter and energy.

### Example 1

*The setup: a simple statement with implicit details*

You tell your roommate a story about how you got to campus by saying, "I biked to campus today". In this simple statement are several assumptions that are instructive to unpack, even if they may not seem very critical to include explicitly in a casual conversation between friends over transportation choices!

*An outsider's reinterpretation of the process*

To illustrate this, imagine an external observer, for instance an alien, watching the comings and goings of humans on earth. Without the benefit of knowing much of the implied meanings and reasonable assumptions that are buried in our language, the alien's description of the morning cycling trip would be quite different than your own. What you described efficiently as "biking to campus" might be more specifically described by the alien as a change in location of a human body and its bicycle from one location (the apartment, termed position A) to a different location (the university, termed position B). The alien might be even more abstract and describe the bike trip as the movement of matter (the human body and its bike) between an initial state (at location A) to a final state (at location B). Furthermore, from the alien's standpoint what you'd call "biking" might be more specifically described as the use of a two-wheeled tool that couples the transfer of energy from the electric fields in chemical compounds to the acceleration of the two-wheeled tool-person combo and heat in its environment. Finally, buried within the simple statement describing how we got to work is also the tacit understanding that the mass of the body and bike were conserved in the process (with some important caveats we’ll look at in future lectures) and that some energy was converted to enable the movement of the body from position A to position B.

#### Possible discussion:

Details are important. What if you owned a fully electric bike and the person you were talking with didn’t know that? What important details might this change about the “everyday” story you told that the more detailed description would have cleared up? How would the alien’s story have changed? In what scenarios might these changes be relevant?

As this simple story illustrates, irrespective of many factors, the act of creating a full description of a process includes some accounting of what happened to the matter, what happened to the energy and almost always some description of a mechanism that describes how changes in matter and energy of a system were brought about.

To practice this skill, in BIS2A we will make use of something we like to call "The Energy Story". You may be asked to tell an "energy story" in class and to use the concept on your exams. In this section, we focus primarily on introducing the concept of an energy story and explaining how to tell one. It is worth noting that the term "energy story" is used almost exclusively in BIS2A (and has a specific meaning in this class). This precise term will not appear in other courses at UC Davis (at least in the short term) or if it appears, is not likely be used in the same manner. You can think of “The Energy Story” as a systematic approach creating a statement or story describing a biological process or event.

## Definition 1: Energy Story

An energy story is a narrative describing a process or event. The critical elements of this narrative are:

1. Identifying at least two states (e.g. start and end, aka, initial and final states) in the process.
2. Identifying and listing the **matter** in the system and its state at the start and end of the process.
3. Describing the **transformation of the matte**r that occurs during the process.
4. Accounting for the location and form of energy in the system at the start and end of the process.
5. Describing the transfer of energy that happens during the process.
6. Identifying and describing mechanism(s) responsible for mediating the transformation of matter and transfer of energy.

A complete energy story will include a description of the initial reactants and their energetic states as well as a description of the final products and their energetic states after the process or reaction is completed.

### Possible discussion:

We argue that the energy story can be used to communicate all of the useful details that are required to describe nearly any process. Can you think of a process that cannot be adequately described by an energy story? If so, describe such a process.

### Example 2: Energy Story Example

Let us suppose that we are talking about the process of driving a car from "Point A" to "Point B" (see the figure).

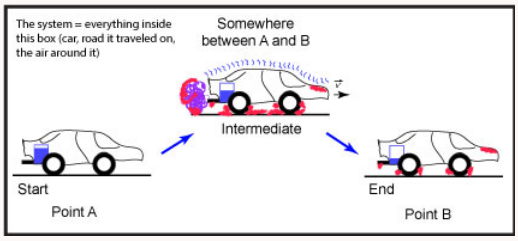



*Figure 1: A schematic of a car moving at the start from position "Point A" to position "Point B" at the end. The blue rectangle depicted in the back of the car represents the level of gasoline, the purple squiggly line near the exhaust pipe represents the exhaust, squiggly blue lines on top of the car represent sound vibrations and the red shading represents areas that are hotter that at the start. Source: Created by Marc T. Facciotti (Own work) A Car Moves from Point A to Point B*

Let's step through the Energy Story rubric:

**1. Identifying at least two states (e.g. start and end) in the process.**
In this example we can easily identify two states. The initial state is the non-moving car at "Point A", the start of the trip. The finalond state, after the process is done, is the non-moving car at "Point B".

**2. Identifying and listing the matter in the system and its state at the start and end of the process.**
In this case we first note that the "system" includes everything in the figure - the car, the road, the air around the car etc.

It is important to understand the we are going to apply the physical law of conservation of matter. That is, in any of the processes that we will discuss, matter is neither created or destroyed. It might change form, but one should be able to account for everything at the end of a process that was there at the beginning.

At the beginning of the process, the matter in the system consists of:
1. The car and all the stuff in it
2. The fuel in the car (a special thing in the car)
3. The air (including oxygen) around the car.
4. The road
5. The driver

At the end of the process, the matter in the system is distributed as follows:
1. The car and all the stuff in it is in a new place (lets assume, aside from the fuel and position, that nothing else changed)
2. There is less fuel in the car and it too is in a new place
3. The air has changed - it now has less molecular oxygen, more carbon dioxide and more water vapor.
4. The road (let's assume it didn't change - other than a few pebbles moved around)
5. The driver (let's assume she didn't change - though we'll see by the end of the term we'll know that she did, a little). But the driver is now in a different place.

**3. Describing the transformation of the matter that occurs during the process.**

What happened to the matter in this process? Thanks to a lot of simplifying assumptions, we see that two big things happened. First, the car and its driver changed positions - they went from "Point A" to "Point B". Second, we note that some of the molecules in the fuel, which used to be in the car as a liquid have changed forms and are now mostly in the form of carbon dioxide and water vapor (purple blob coming out the tailpipe). Some of the oxygen molecules that used to be in the air are now also in a new place as part of the carbon dioxide and water that left the car.

**4. Accounting for the “location” of energy in the system at the start and end of the process.**
It is again important to understand that we are going to invoke the physical law of conservation of energy. That is, we stipulate that the energy in the system cannot be created or destroyed and therefore the energy that is in the system at the start of the process must still be there at the end of the process. It may have been redistributed but you should be able to account for all the energy.

At the beginning of the process, the energy in the system is distributed as follows:
1. The energy tied up in the associations between atoms that make up the matter of the car.
2. The energy tied up in the associations between atoms that make up the fuel.
3. The energy tied up in the associations between atoms that make up the air.
4. The energy tied up in the associations between atoms that make up the road.
5. The energy tied up in the associations between atoms that make up the driver.
6. For all things above we can also say that there is energy in the molecular motions of the atoms that make up the stuff.

At the end of the process, the energy in the system is distributed as follows:
1. The energy tied up in the associations between atoms that make up the matter of the car.
2. The energy tied up in the associations between atoms that make up the fuel.
3. The energy tied up in the associations between atoms that make up the air.
4. The energy tied up in the associations between atoms that make up the road.
5. The energy tied up in the associations between atoms that make up the driver.
6. For all things above we can also say that there is energy in the molecular motions of the atoms that make up the stuff.

This is interesting in some sense because the lists are the same. We know that the amount of energy stored in the car has decreased because there is less fuel. Something must have happened.

**5. Describing the transfer of energy that happens during the process.**
In the particular example it is the transfer of energy among the components of the system that is most interesting. As we mentioned, there is less energy stored in the gas tank of the car at the end of the trip because there is now less fuel. We also know intuitively (from our real life experience) that the transfer of energy from the fuel to something else was instrumental in moving the car from "Point A" to "Point B". So, where did this energy go? Remember, it didn't just disappear. It must have moved somewhere else in the system.

Well we know that there is more carbon dioxide and water vapor in the system after the process. There is energy in the associations between those atoms (atoms that used to be in the fuel and air). So some of the energy that was in the fuel is now in the exhaust. Let's also draw from our real life experience again and state that we know that parts of our car have gotten hot by the end of the trip (e.g. the engine, transmission, wheels/tires, exhaust etc.). For the moment we'll just tap our intuition and say that we understand that making something hot involves some transfer of energy. So we can reasonably postulate that some of the energy in the fuel went (directly or indirectly) into heating the car, parts of the road, the exhaust and thus the environment around the car. An amount of energy also went into accelerating the car from zero velocity to whatever speed it traveled, but most of that eventually went into heat when the car came to a stop.

The main point is that we should be able to add all the energy at of the system at the beginning of the process (in all the places it is found) and at the end of the process (in all the places it is found) and those two values should be the same. Our actually examples in class will be simpler than this, but this example provides you with an opportunity to think about these in a well-understood context. Our goal here is to instill an intuitive sense of the nature of energy transfers. Our examples from Biology, mostly involving molecules that you cannot see, are more abstract, and so not the easiest to grasp intuitively. Hopefully by the end of the quarter you will have developed an "intuitive feel" about the energetics of these chemical changes.

**6. Identifying and describing mechanism(s) responsible for mediating the transformation of matter and transfer of energy.**

Finally, it is useful to understand how those transformations of matter and transfers of energy might have been facilitated. For the sake of brevity, in this example we might just say that there was a complicated mechanical device (the engine) that helped facilitate the conversion of matter and transfer of energy about the system and coupled this to the change in position of the car. Someone interested in engines would, of course, give a more detailed explanation.

In this example we made a bunch of simplifying assumptions to highlight the process and to focus on the transformation of the fuel. But that's fine. The more you understand about the processes the finer details you can add. Note that you can use the Energy Story rubric for describing your understanding (or looking for holes in your understanding) of nearly any process (certainly in biology). In BIS2A we'll use the Energy Story to get an understanding of processes as varied as biochemical reactions, DNA replication, the function of molecular motors, etc.

Important:

First: We will be working many examples of the energy story throughout the course - do not feel that you need to have mastery over this topic today.

Second: Nevertheless, while it is tempting to think all this is superfluous or not germane to your study of biology in BIS2a, let this serve as a reminder that your instructors (those creating the course midterm and final assessments) view it as core material. We will revisit this topic often throughout the course but you'll need to become familiar with some of the basic concepts now.

This is important material and an important skill to develop - do not put off studying it because it doesn't "look" like Biology to you today. The academic term moves VERY quickly and it will be difficult to catch up later if you don't give this some thought now.

# Energy

Energy is a central concept in all sciences. Energy is a property of a system. While energy can be neither created nor destroyed, understanding the transfer of energy around physical systems is a key component of understanding how and why things change. In this following sections we are going to explore some basic concepts associated with common transformations in biology and chemistry - the solubility of various biomolecules, the making and breaking of chemical bonds, the transfer of electrons, the transfer of energy to and from light, and the transfer of energy as heat. In class, many of the discussions will happen in the context of the Energy Story rubric, so when we consider a reaction or transformation, we will be interested in defining the system in question and trying to account for all the various transfers of energy that occur within the system, making sure that we abide by the **Law of conservation of energy**.

There are plenty of examples where we use the concept of energy in our everyday lives to describe processes. A bicyclist can bike to get to campus for class. The act of moving herself and her bicycle from point A to point B can be explained to some degree by examining the transfers energy that take place. We can look at this example through a variety of lenses, but as biologists we more than likely want to understand the series of events that explain how energy is transferred from molecules of food, to the connected coordinated activity of biomolecules in her flexing muscle, and how this can finally be connected to moving the bike to get her from point A to point B. To do this we need to be able to talk about various ways in which energy can be transferred between parts of a system and where it is stored or transferred out of the system. In the next section, we will also see the need to consider how that energy is distributed among the many microstates (molecular states) of the system and its surroundings.

## How We will Approach Conceptualizing Energy

In BIS2A we will think about energy with a "stuff" metaphor. Note, however, that energy is **NOT** a substance, it is rather a **property** of a system. But we will think of it in some sense as property that can be stored in a part of a physical system and transferred or "moved" from one storage place to another. This in turn also encourages us to make sure that energy always has a home and that we account for all of the energy in a system before and after a transformation, it is not just "made" or "lost" (both ideas in contradiction of the Law of Conservation of Energy). When energy is being transferred we therefore must identify where it is coming from and where it is going - all of it! Again, we can't just have some getting lost (though it may be present in a less useable form).

When energy is transferred, there must be some mechanism associated with that transfer. Let's think about that to help us explain some of the phenomena we're interested in. That mechanism is part of the "how" that we are often interested in understanding. Finally, if we talk about transfer, we must realize that both components, the part of the physical system that gave up energy and the part of the system that received that energy are changed from their initial states. We should make sure that we are looking at all of the components of a system for changes in energy when examining a transformation.

- **"Lost" energy**: While "conservation of mass" seems clear enough, the concept of "conservation of energy" seems counterintuitive. In our daily life, we "run out of gas", metaphorically or literally, all the time! So where is that energy- the energy present in gasoline, that we used to commute to class- going? What new form does it take? Could any of that that "waste energy" be used to do something useful?

## Energy Sources

The source of energy for many processes, including biological processes, occurring on the earth's surface comes from solar radiation. But as we will see Life has been very clever at tapping a variety of forms of energy to construct and maintain living beings. As we move through this course we will explore a variety of energy sources and the ways which Life has devised to harvest energy from these fuels.

# Energy in Chemical Reactions

Chemical reactions involve a redistribution of energy within the reacting chemicals and with their environment. So, like it or not, we need to develop some models that can help us describe where energy is in a system (perhaps how it is "stored"/distributed) and how it can be moved around in a reaction. The models we develop will not be overly detailed - in the sense that they would not satisfy a hard-core chemist or physicist with technical detail - but we expect that they should still be technically correct and not form incorrect mental models that will make it difficult to get the "refinements" down later. We'll discuss the transfer and storage of energy between different parts of a system and thus think about energy as a property that can get redistributed. That'll hopefully make the accounting easier.

**CAUTION:**

If we are going to think about transferring energy from one part of a system to another, we also need to be careful about **NOT** treating energy like a substance that moves like a fluid or substance. Rather, we need to appreciate energy simply as a property of a system that can be measured and reorganized.

Since we are will often be dealing with transformations of biomolecules we can start by thinking about where energy can be found/stored in these systems. We'll start with a couple of ideas and add more to them later.

Let us propose that one place that energy can be stored is in the motion of matter. We'll give the energy stored in motion a name: **kinetic energy**. Molecules in biology are in constant motion and therefore have a certain amount of kinetic energy (energy stored in motion) associated with them.

Let us also propose that there is a certain amount of energy stored in the biomolecules themselves and that the amount of energy stored in those molecules is associated with the types and numbers of atoms in the molecules and the their organization (the number and types of bonds between them). The discussion of exactly where the energy is stored in the molecules is beyond the scope of this class but we can approximate it by suggesting that a good proxy is in the **bonds**. Different types of bonds may be associated with storing different amounts of energy. In some contexts this type of energy storage could be labeled **potential energy** or more specifically **chemical energy**. With this view, one of the things that happens during the making and breaking of bonds in a chemical reaction is that the energy is transferred about the system into different types of bonds. In the context of an Energy Story one could theoretically count the amount of energy stored in the bonds and motion of the reactants and the energy stored in the bonds and energy of the products.

In some cases you might find that when you compare the energy stored in the products and the energy stored in the reactants these sums are not equal. If the energy in the reactants is greater than the products where did this energy go? It had to get transferred to something else. Some will certainly have moved into other parts of the system, stored in the motion of other molecules (warming the environment) or perhaps in the energy associated with photons of light. One good real life example is the chemical reaction between wood and oxygen (reactants) and it's conversion to carbon dioxide and water (products). At the beginning, the energy in the system is largely in the molecular bonds of oxygen and the wood (reactants). There is still energy left in the carbon dioxide and water (products), but less than at the beginning. We all appreciate that some of that energy was transferred to the energy in light and heat. This reaction where heat is transferred to the environment- like the burning of wood- is termed **exothermic**. By contrast, in some spontaneous reactions heat will transfer in from the environment- as in the melting of ice. These reactions are called **endothermic**.

A third, perhaps less intuitive place to store potential energy is in the concentration of molecules. We'll discuss this more later.

The transfer of energy in or out of the reaction from the environment is NOT the only thing that determines whether a reaction will be spontaneous or not (as described above, for melting of ice). We'll discuss that soon. For the moment, it is important to get comfortable with the idea that energy can be transferred between different components of a system during a reaction and that you should be able to track it.

# Thermodynamics

Thermodynamics is concerned with describing the changes in systems before and after a change. This usually involves a discussion about the energy transfers and its dispersion within the system. In nearly all practical cases, these analyses require that the system and its surroundings be completely described. For instance, when discussing the heating of a pot of water on the stove, the system may includes the stove, the pot, and the water and the environment or surroundings may include everything else. Biological organisms are what are called **open systems**; energy is transferred between them and their surroundings.

## 1st Law of Thermodynamics

The first law of thermodynamics deals with the total amount of energy in the universe. It states that this total amount of energy is constant. In other words, there has always been, and always will be, exactly the same amount of energy in the universe. According to the first law of thermodynamics, energy may be transferred from place to place, but it cannot be created or destroyed. The transfers of energy take place around us all the time. Light bulbs transfer energy from an electrical power station into heat and photons of light. Gas stoves transfer energy stored in the bonds of chemical compounds into heat and light. Heat, by the way, is the amount of energy transferred from one system to another because of a temperature difference. Plants perform one of the most biologically useful energy transfers on earth: they transfer energy in the photons of sunlight into the chemical bonds of organic molecules. In every one of these cases energy is neither made nor destroyed and we must try to account for all of the energy when we examine some of these reactions.

## 1st Law and the Energy Story

The first law of thermodynamics is deceptively simple. Students often understand that energy cannot be created or destroyed. Yet, when describing an energy story of a process they (and their professors) often make the mistake of saying things such as "energy is produced from the transfer of electrons from atom A to atom B". While most of us understand the point the speaker is trying to make, the wrong words are being used. Energy is not made or produced, it is simply transferred. To be consistent with the first law, when telling an energy story, make sure that you try to explicitly track all of the places that ALL of the energy in the system at the start of a process goes by the end of a process.

## 2nd Law of Thermodynamics

An important concept in physical systems is that of *entropy*. Entropy is related to the with the ways in which energy can be distributed or dispersed within the particles of a system. The 2nd Law of Thermodynamics states that entropy is always increasing in an isolated system. (Please use this link to understand what an isolated system is- the universe *may* be an isolated system, but a plant, or a planet, is not). This idea helps explain the directionality of natural phenomena. In general, the notion is that the directionality comes from the tendency for energy in a system to move towards a state of maximal dispersion (as opposed to concentration). The 2nd law, therefore, means that in any transformation we should look for an overall increase in entropy (or dispersion of energy), *somewhere*. An idea that is associated with increased dispersion of energy in a system and/or its surroundings is that as dispersion increases, the ability of the energy to be directed towards work decreases.

There will be many examples of where the entropy of a system decreases (things become more organized, rather than more random). Life routinely organizes matter into a specific form! To be consistent with the second law, however, we must try to find something else (likely a closely connected system in the surroundings) that must compensate for the "local" decrease in entropy with an equal or greater increase in entropy... somewhere.

The entropy of a system can increase when: (a) it increases in temperature (but in this class, we will stay at constant temperature) (b) a change of state occurs from solid to liquid to gas (but in this class, we will always discuss molecules dissolved in liquid water) (c) mixing or dilution of a given number of particles occurs (very relevant here!) (d) the number of particles increases during a reaction (for example, a large molecule is broken down into several smaller ones- again, quite relevant here).

**Possible discussion**

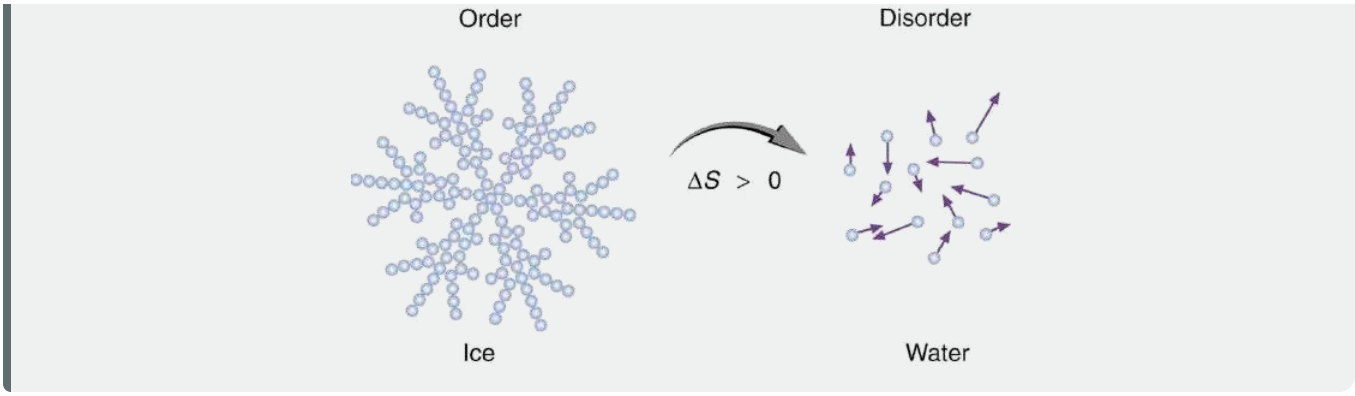
Does the second law say that entropy is conserved?

**Possible discussion**

Biological systems, on the surface, see to defy the Second Law of Thermodynamics. They don't. Why? Hint: You might want to employ the terms "isolated system" vs. "closed system" vs. "open system" in your answer.

**Possible discussion**

A fine point. The figure below mentions order and disorder and shows that this is somehow related to a change in entropy ($\Delta S$). It is common to describe entropy as a measure of disorder as a way to simplify the more concrete description relating entropy to the number of states in which energy can be dispersed in a system. While the idea of measuring disorder to define entropy has some flaws, it is sometimes a useful, if imperfect, proxy. Consider the figure below. Here order serves as a good proxy for approximating the number of ways to distribute energy in the system. Can you describe why this is the case?




# Free Energy

If we want to describe transformations, it is useful to have a measure of (a) how much energy is in a system and (b) the dispersal of that energy within the system and, of course, (c) how these change between the start and end of a process. The concept of ***free energy***, often referred to as Gibbs free energy (abbreviated with the letter G), in some sense, does just that. Gibbs free energy can be defined in several interconvertible ways, but a frequently encountered, and conceptually useful, one is the enthalpy (internal energy) of a system minus the entropy of the system scaled by the temperature. The difference in free energy when a process takes place is often reported in terms of the change (Δ) of enthalpy (internal energy) denoted H, minus the temperature scaled change (Δ) in entropy, denoted S. See the equation below.

$$[\Delta G=\Delta H-T\Delta S]$$

Where ΔG = the free energy of the final state minus the free energy of the initial state of the physical matter under consideration. If this equation makes you nervous, don't worry, we will not be working with it. However, you might *play* with it a bit to see whether, for example, a system that undergoes a change that results in increased entropy would have more, or less, free energy after that change. The term "enthalpy" is tricky as the definition "internal energy" covers a lot of ground. In most of what we discuss in this class, we will mean the energy inherent in the structure of a particular molecule or set of molecules. Gibbs free energy is often interpreted as the amount of energy available to do useful work. We'll refer to this quite often as **potential energy**. With a bit of hand waving we can interpret this equation by invoking the idea presented in the section on entropy that states that the dispersion of energy (required by the Second Law) associated with a positive change in entropy somehow renders some of the energy that is transferred less useful to do work. This is reflected in part in the TΔS term of the Gibbs equation. Thus ΔG would be better regarded as the theoretical upper limit of the energy available to do work- the "potential" Potential energy.

To provide a basis for fair comparisons of changes in Gibbs free energy amongst different biochemical reactions, the free energy change of a reaction is measured under a set of common standard experimental conditions. The resulting **standard free energy change** of a biochemical reaction is expressed as an amount of energy per mole of the reaction product generated (expressed either in kilojoules or kilocalories, kJ/mol or kcal/mol; 1 kJ = 0.239 kcal) when measured at a biologically "standard" pH, temperature, and pressure conditions. Biological standard pH, temperature, and pressure conditions are generally calculated at pH 7.0, 25˚ Celsius, 1 molar concentration of reactants and products, in an aqueous solution, and 100 kilopascals (1 atm) pressure. It is important to note that cellular conditions can vary considerably from these standard conditions (particularly in terms of concentration!), and so *actual* ΔG of a reaction inside a cell will differ considerably from that calculated under standard conditions. Note also, that *biological* "standard ΔG", written **ΔG˚'**, is not the same as a *chemist's* standard ΔG, written **ΔG˚**. The chemist's standard conditions are very non-biological.

# Endergonic and Exergonic Reactions

Reactions that have a ΔG < 0 means that the products of the reaction have less free energy than the reactants. Since ΔG is the difference between the enthalpy and entropy changes in a reaction a net negative ΔG can arise in different ways- enthalpy could drop (in our case, bonds between atoms could be rearranged to a less energy-rich structure), entropy could rise (perhaps because the reaction turns 1 molecule into two, and two molecules have more possible states than one), or some combination of the two effects

could (and probably does) occur. In our examples, the temperature of the system- a living organism- will not change, so we don't need to worry about that.

**Possible discussion**

Most of the ongoing chemical reactions that occur in living things- for example, a goldfish- are exothermic. Why then would we think that they do not produce an increase in the temperature of the goldfish?

Reactions that have a negative ΔG are termed **exergonic reactions**. These reactions are said to occur "spontaneously". Understanding which chemical reactions are spontaneous is extremely useful for biologists that are trying to understand whether a reaction is likely to "go" or not.

It is important to note that the term "spontaneous" - in the context of thermodynamics - does NOT imply anything about how fast the reaction proceeds. In fact, this term is a little misleading- it would be simpler and more correct to say a reaction with a negative ΔG "will proceed as written (R->P), eventually." The change in free energy only describes the difference in potential energy between reactants and products- NOT how long that transition takes. This is somewhat contrary to the everyday use of the term "spontaneous" which usually carries the implicit understanding that something happens quickly. As an example, the oxidation/rusting of iron is a spontaneous reaction. However, an iron nail exposed to air does not rust instantly - it may take years.

A chemical reaction with a positive ΔG means that the products of the reaction have a higher free energy than the reactants. These chemical reactions are called **endergonic reactions**, and they are NOT spontaneous. An endergonic reaction will not take place, in biology, without coupling to some sort of second reaction that is exergonic. We'll see specific examples soon.

In future readings we will discuss:

1. Why exergonic reactions do not always proceed quickly
2. The effects of concentration on ΔG
3. How Life maintains many products and reactants at steady-state (but non-equilibrium) concentrations in order to drive the reaction in the desired direction
4. How Life regulates reaction rate

---

This page titled 1.1: Potential Energy in Biology is shared under a not declared license and was authored, remixed, and/or curated by Tom Buckley.

- **1.6: Potential Energy in Biology** has no license indicated.

# CHAPTER OVERVIEW

## 2: Plant structure

Plants cells are complex structures with several organelles lacking in animal cells. Among these are the cell wall, central vacuole, and plastids (the most familiar of which are chloroplasts). There are three main tissue types, called epidermal, ground, and vascular tissue. Each tissue type consists of specialized cells adapted for unique functions. Plants have two organ systems: the root system and the shoot system (figure **2.a**). The root system is typically belowground and consists of roots, which specialized in water and nutrient absorption. The shoot system consists of stems and leaves and is typically aboveground. Stems function in supporting the plant and transporting materials (conduction), and leaves function in photosynthesis. This unit will explore these structure at the macroscopic and microscopic level.



Figure **2.1**: The shoot system consists of the stems and leaves, and the root system is the fibrous mat embedded in the soil. Image by Maria Morrow (CC-BY-NC).


2.1: Cells and Tissues

- 2.1.1: Introduction to Cells
- 2.1.2: Plant Cell Structure
- 2.1.3: Plant Tissues
- 2.1.4: Chapter Summary

2.2: Roots

- 2.2.1: Organs and Organ Systems
- 2.2.2: External Root Structure
- 2.2.3: Internal Root Structure
- 2.2.4: Root Modifications
- 2.2.5: Chapter Summary

2.3: Stems

- 2.3.1: Stem Morphology (External Structure)
- 2.3.2: Internal Anatomy of the Primary Stem
- 2.3.3: Secondary Stem
- 2.3.4: Stem Modifications
- 2.3.5: Chapter Summary

2.4: Leaves
2.4.1: External Structure of Leaves
2.4.2: Internal Leaf Structure
2.4.3: Leaf Modifications
2.4.4: Chapter Summary
2.5: Meristems

---

This page titled 2: Plant structure is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

# SECTION OVERVIEW

## 2.1: Cells and Tissues

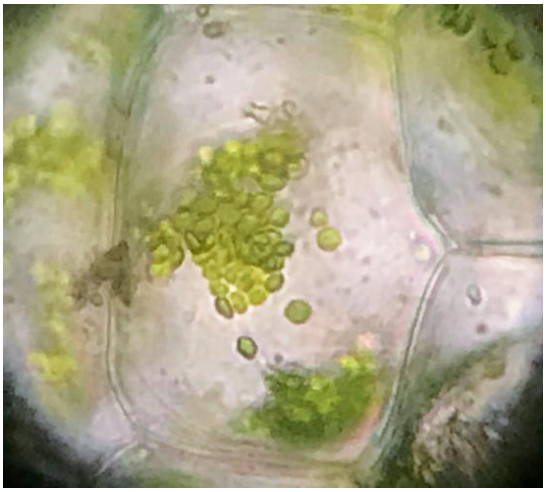


Figure **2.1.1**: An *Elodea* cell and green chloroplasts, Credit: Kammy Algiers (CC-BY)

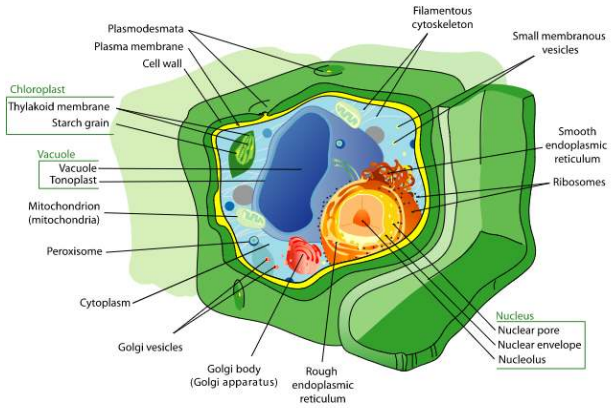



Figure **2.1.2**: A typical plant cell Credit: Mariana Ruiz Villarreal (public domain).

Plants are multicellular organisms composed of eukaryotic cells. Cells are the basic building blocks of the organism. Plants are autotrophic and thus many of their cells contain large amounts of chloroplast, the organelle for photosynthesis (Figure **2.1.1**). The green color of leaves are due to the large amounts of chloroplast within the cells. Plant cells obtain many other organelles, which we will study in this chapter (Figure **2.1.2**). Cells with similar functions are arranged in tissues, which are arranged into plant organs such as roots, stems, and leaves. Together, these organs and their associated organ systems form the plant organism.


### 2.1.1: Introduction to Cells

### 2.1.2: Plant Cell Structure

### 2.1.3: Plant Tissues

### 2.1.4: Chapter Summary

## Attribution

Kammy Algiers (CC-BY-NC)

---

This page titled 2.1: Cells and Tissues is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

# 2.1.1: Introduction to Cells

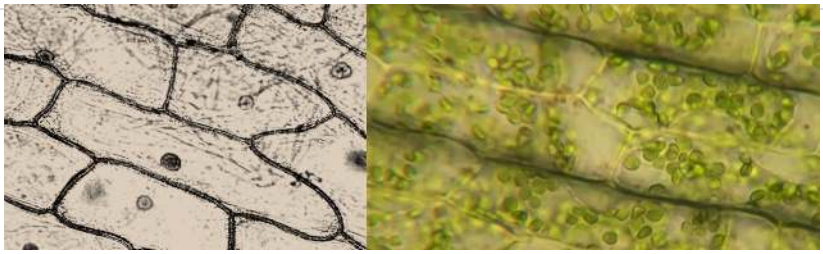


Figure **2.1.1.1**:(a) onion cells, and (b) *Elodea* cells, both viewed with a light microscope. Credit: Kammy Algiers (CC-BY).

## Learning Objectives

- Describe the role of cells in organisms.
- Summarize cell theory.
- Address the significance of cell size.

A cell is the smallest unit of a living thing. Whether comprised of one cell (like bacteria) or many cells (like a plant, Figure **2.1.1.1**), we call it an organism. Thus, cells are the basic building blocks of all organisms.

Several plant cells of one kind that interconnect with each other and perform a shared function form tissues. An example of a plant tissue would be the epithelial tissue found on the surface of a leaf. These tissues combine to form an organ, such as a leaf. and several organs comprise an organ system (in this case, the shoot system). Two two plant organ systems, the shoot and root system, make up the plant. Here, we will examine the structure and function of cells.

## Cell Theory

In 1665, Robert Hooke looked at cork under a microscope and saw multiple chambers which he called “cells”. In 1838, Schleidern and Schwann stated that (1) all plants and animals are composed of cells and that (2) cell is the most basic unit (“atom”) of life. In 1858, Virchow stated that (3) all cells arise by reproduction from previous cells (“Omnis cellula e cellula” in Latin). These three statements became the base of the **cell theory**.

## Cell Size

At 0.1 to 5.0 µm in diameter, prokaryotic cells are significantly smaller than eukaryotic cells, which have diameters ranging from 10 to 100 µm (Figure **2.1.1.2**. The prokaryotes' small size allows ions and organic molecules that enter them to quickly diffuse to other parts of the cell. Similarly, any wastes produced within a prokaryotic cell can quickly diffuse. This is not the case in eukaryotic cells, which have developed different structural adaptations to enhance intracellular transport.

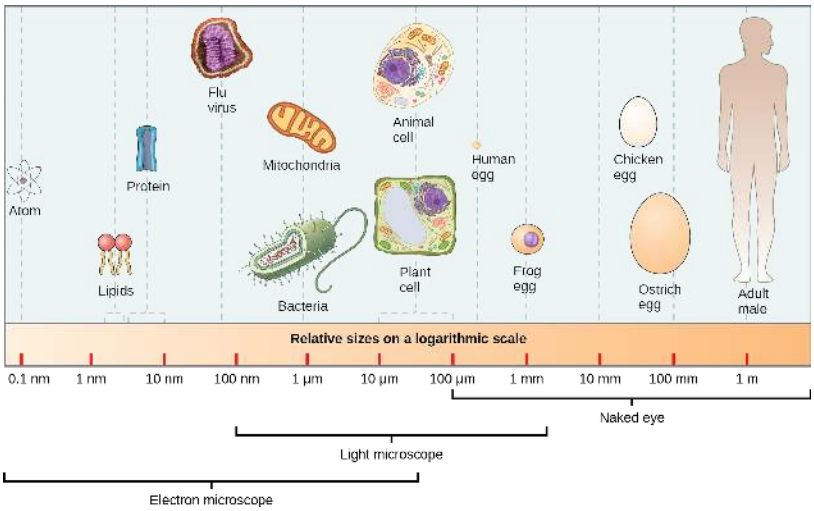
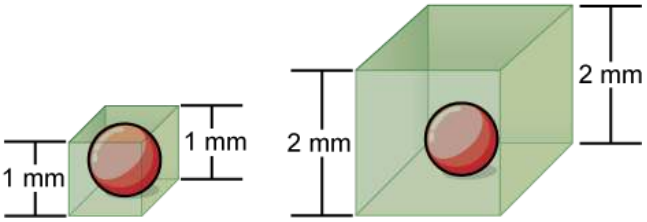



Figure **2.1.1.2**): This figure shows relative sizes of microbes on a logarithmic scale (recall that each unit of increase in a logarithmic scale represents a 10-fold increase in the quantity measured). Note that the smallest object is an atom, about 1 nm in size while the largest is a human, at approximately 1m tall.

Small size, in general, is necessary for all cells, whether prokaryotic or eukaryotic. Let's examine why that is so. First, we'll consider the area and volume of a typical cell. Not all cells are spherical in shape, but most tend to approximate a sphere. You may remember from your high school geometry course that the formula for the surface area of a sphere is $4\pi r^2$, while the formula for its volume is $4\pi r^3/3$. Thus, as the radius of a cell increases, its surface area increases as the square of its radius, but its volume increases as the cube of its radius (much more rapidly). Therefore, as a cell increases in size, its surface area-to-volume ratio decreases. This same principle would apply if the cell had a cube shape (Figure **2.1.1.3**). If the cell grows too large, the plasma membrane will not have sufficient surface area to support the rate of diffusion required for the increased volume. In other words, as a cell grows, it becomes less efficient. One way to become more efficient is to divide. Other ways are to increase surface area by foldings of the cell membrane, become flat or thin and elongated, or develop organelles that perform specific tasks. These adaptations lead to developing more sophisticated cells, which we call eukaryotic cells.

## Visual connection




**(Figure 2.1.1.3)**: Notice that as a cell increases in size, its surface area-to-volume ratio decreases. When there is insufficient surface area to support a cell's increasing volume, a cell will either divide or die. The cell on the left has a volume of 1 $mm^3$ and a surface area of 6 $mm^2$, with a surface area-to-volume ratio of 6 to 1; whereas, the cell on the right has a volume of 8 $mm^3$ and a surface area of 24 $mm^2$, with a surface area-to-volume ratio of 3 to 1.

## Attributions

Curate and authored by Kammy Algiers using the following sources:

- 4.1 Studying Cells from *Biology2e* by OpenStax (licensed CC-BY). Access for free at openstax.org.
- 2.1 Introduction to Cells from *Introduction to Botany* by Alexey Shipunov (public domain)

This page titled 2.1.1: Introduction to Cells is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **3.1.1: Introduction to Cells** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC 4.0.

# 2.1.2: Plant Cell Structure

**Learning Objectives**

- Describe the structures that all cells share in common.
- State the role of the plasma membrane.
- Describe the structures of eukaryotic cells.
- Summarize the functions of the major cell organelles.

## Components of All Cells

All cells contain these same four components: 1. **plasma** (**cell**) **membrane**, a phospholipid bilayer with a mosaic of proteins, which functions as a barrier between the cell and its environment. 2. **cytoplasm**, the region between the region of DNA and plasma membrane, and the **cytosol**, a fluid, jelly-like region inside the cell where chemical reactions take place. 3. **DNA**, the heredity information of cells, which can be found in a nucleus of eukaryotic cells and the a nucleoid region of prokaryotic cell. 4. **ribosomes**, or protein-synthesizing structures composed of ribosomes and proteins. These structures can be found on the image of the plant cell (Figure **2.1.2.1**).

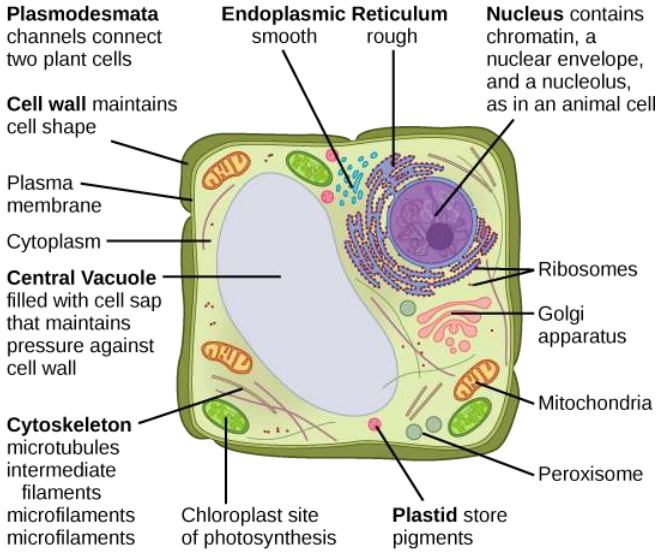
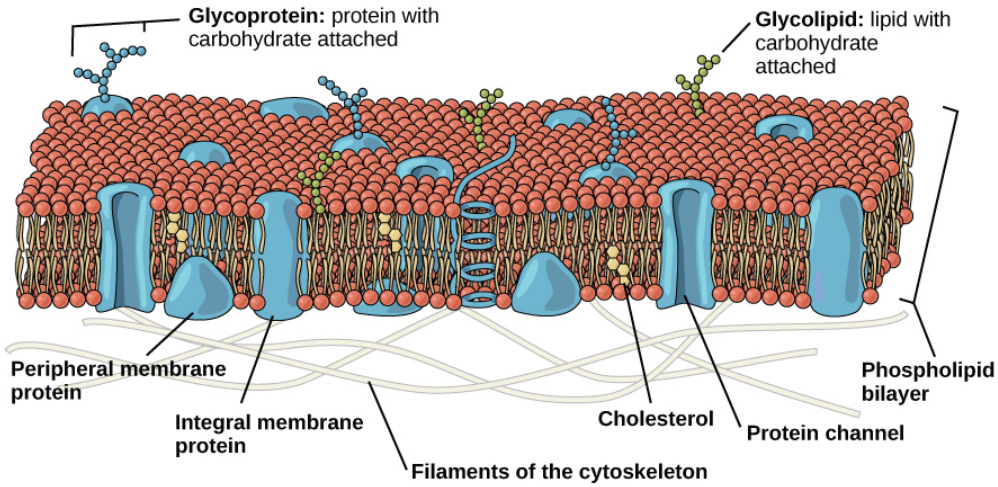



Figure **2.1.2.1**): This figure show the major organelles and other cell components of a typical eukaryotic plant cell. The plant cell has a cell wall, chloroplasts, plastids, and a central vacuole—structures not in animal cells. Most cells do not have lysosomes or centrosomes.

### The Plasma Membrane

Both prokaryotic and eukaryotic cells have a plasma membrane (Figure **2.1.2.2**), a phospholipid bilayer with embedded proteins that separates the internal contents of the cell from its surrounding environment. A phospholipid is a lipid molecule with two fatty acid chains and a phosphate-containing group. The plasma membrane controls the passage of organic molecules, ions, water, and oxygen into and out of the cell. Wastes (such as carbon dioxide and ammonia) also leave the cell by passing through the plasma membrane. The plasma membrane are semi-permeable and allow small and/or non-polar molecules to pass through. Water, being small, can pass through the membrane and will move from an area of low solute concentration to an area of high solute concentration by the process of **osmosis**.



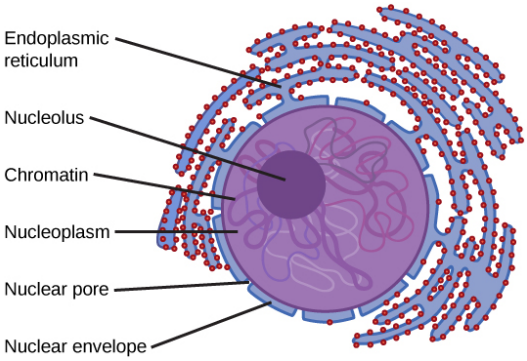

(Figure 2.1.2.2): The eukaryotic plasma membrane is a phospholipid bilayer with proteins and cholesterol embedded in it.

### The Cytoplasm

The cytoplasm is the cell's entire region between the plasma membrane and the nuclear envelope (a structure we will discuss shortly). It is comprised of organelles suspended in the gel-like cytosol, the cytoskeleton, and various chemicals (Figure 2.1.2.1). Even though the cytoplasm consists of 70 to 80 percent water, it has a semi-solid consistency, which comes from the proteins within it. However, proteins are not the only organic molecules in the cytoplasm. Glucose and other simple sugars, polysaccharides, amino acids, nucleic acids, fatty acids, and derivatives of glycerol are also there. Ions of sodium, potassium, calcium, and many other elements also dissolve in the cytoplasm. Many metabolic reactions, including protein synthesis, take place in the cytoplasm.

### DNA

In eukaryotic cells, the DNA is typically housed in a nucleus (plural = nuclei), the most prominent organelle in a cell (Figure 2.1.2.1. This organelle directs the synthesis of ribosomes and proteins. Let's look at it in more detail (Figure 2.1.2.3).




(Figure 2.1.2.3): The nucleus stores chromatin (DNA plus proteins) in a gel-like substance called the nucleoplasm. The nucleolus is a condensed chromatin region where ribosome synthesis occurs. We call the nucleus' boundary the nuclear envelope. It consists of two phospholipid bilayers: an outer and an inner membrane. The nuclear membrane is continuous with the endoplasmic reticulum. Nuclear pores allow substances to enter and exit the nucleus.

### The Nuclear Envelope

The **nuclear envelope** is a double-membrane structure that constitutes the nucleus' outermost portion (Figure 2.1.2.3. Both the nuclear envelope's inner and outer membranes are phospholipid bilayers.

The nuclear envelope is punctuated with pores that control the passage of ions, molecules, and RNA between the nucleoplasm and cytoplasm. The **nucleoplasm** is the semi-solid fluid inside the nucleus, where we find the chromatin and the nucleolus.

## Chromatin and Chromosomes

To understand chromatin, it is helpful to first explore **chromosomes**, structures within the nucleus that are made up of DNA, the hereditary material. You may remember that in prokaryotes, DNA is organized into a single circular chromosome. In eukaryotes, chromosomes are linear structures. Every eukaryotic species has a specific number of chromosomes in the nucleus of each cell. For example, in humans, the chromosome number is 46, while in fruit flies, it is eight. Chromosomes are only visible and distinguishable from one another when the cell is getting ready to divide. When the cell is in the growth and maintenance phases of its life cycle, proteins attach to chromosomes, and they resemble an unwound, jumbled bunch of threads. We call these unwound protein-chromosome complexes **chromatin** (Figure **2.1.2.4**. Chromatin describes the material that makes up the chromosomes both when condensed and decondensed.

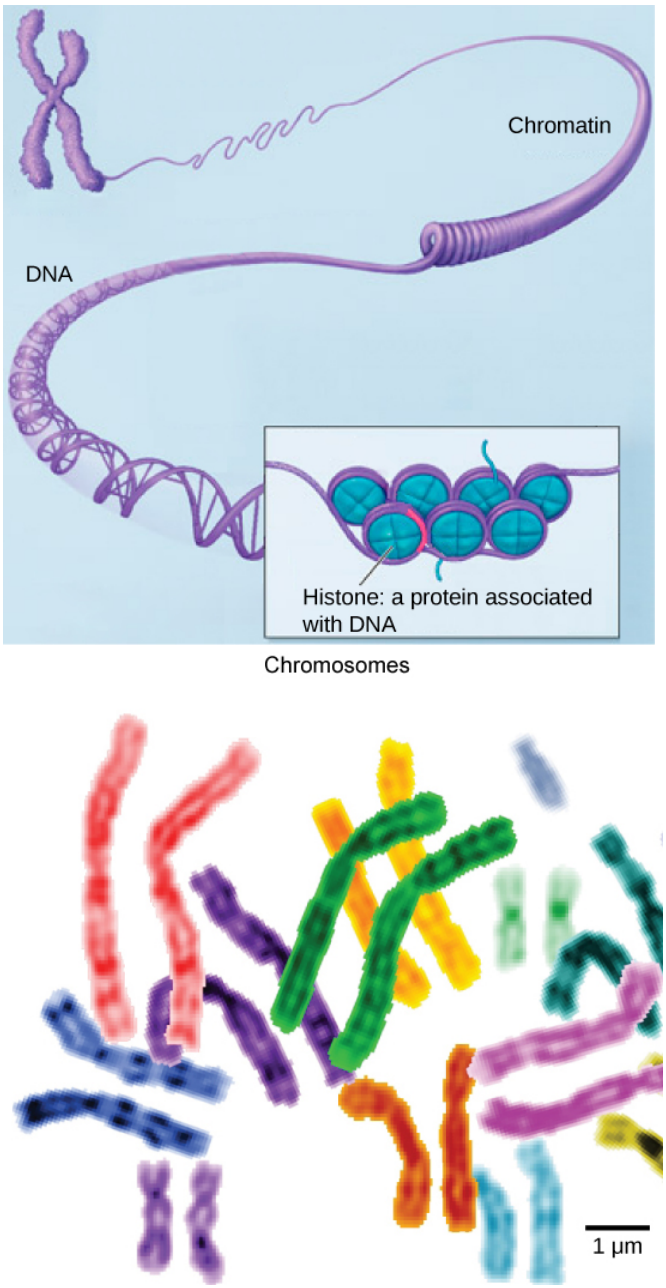



Figure **2.1.2.4**: (a) This image shows various levels of chromatin's organization, DNA tightly coiled into two thick cylinders and DNA coiled around proteins called histones. (b) Paired chromosomes, colored as pairs. Notice individuals of each pair are the same size to one another. (credit b: modification of work by NIH; scale-bar data from Matt Russell)

### The Nucleolus

We already know that the nucleus directs the synthesis of ribosomes, but how does it do this? Some chromosomes have sections of DNA that encode ribosomal RNA. A darkly staining area within the nucleus called the **nucleolus** (plural = nucleoli) aggregates the ribosomal RNA with associated proteins to assemble the ribosomal subunits that are then transported out through the pores in the nuclear envelope to the cytoplasm.

### Ribosomes

**Ribosomes** are the cellular structures responsible for protein synthesis. They are not organelles. They can be small dot-like structures that float freely in the cytoplasm (known as free ribosomes) or they may be attached to the plasma membrane's cytoplasmic side or the endoplasmic reticulum's cytoplasmic side and the nuclear envelope's outer membrane, and called attached ribosomes (Figure **2.1.2.1**). Ribosomes are large protein and RNA complexes consisting of two subunits, a large and a small (Figure **2.1.2.5**. Ribosomes receive their "orders" for protein synthesis from the nucleus where the DNA transcribes into messenger RNA (mRNA). The mRNA travels to the ribosomes, which translate the code provided by the sequence of the nitrogenous bases in the mRNA into a specific order of amino acids in a protein. Amino acids are the building blocks of proteins.

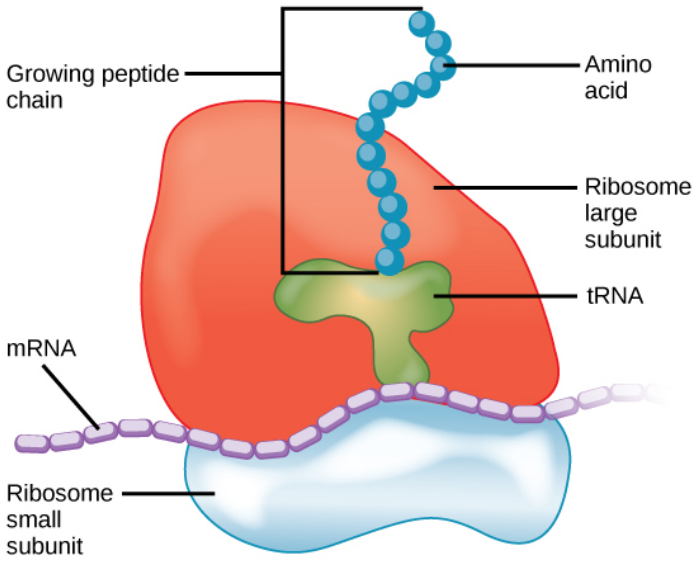



Figure **2.1.2.5**: A large subunit (top) and a small subunit (bottom) comprise ribosomes. Note that the large subunit sits on top of the small subunit. During protein synthesis, ribosomes assemble amino acids into proteins using information from a chain of mRNA. The tRNA carries amino acids to the ribosome, where the arrangement is made.

Because protein synthesis is an essential function of all cells (including enzymes, hormones, antibodies, pigments, structural components, and surface receptors), there are ribosomes in practically every cell. Ribosomes are particularly abundant in cells that synthesize large amounts of protein. For example, the pancreas is responsible for creating several digestive enzymes and the cells that produce these enzymes contain many ribosomes. Thus, we see another example of form following function.

## Components Unique to Eukaryotic Cells

All cells contain DNA, as described above. However, plant cells, which are eukaryotic, contain organelles and a nucleus while prokaryotic cells do not possess organelles or a membrane bound nucleus. We will start by going over the structures that are unique to all eukaryotic. Next, we will go over structures unique to plant cells.

### Endomembrane System

The endomembrane system (endo = "within") is a group of membranes and organelles (Figure **2.1.2.6**) in eukaryotic cells that works together to modify, package, and transport lipids and proteins. It includes the nuclear envelope, lysosomes, and vesicles, the tonoplast (see below), and the endoplasmic reticulum and Golgi apparatus. Although not technically *within* the cell, the plasma membrane is included in the endomembrane system because, as you will see, it interacts with the other endomembranous organelles. The endomembrane system does not include either mitochondria or chloroplast membranes.

# Visual Connection

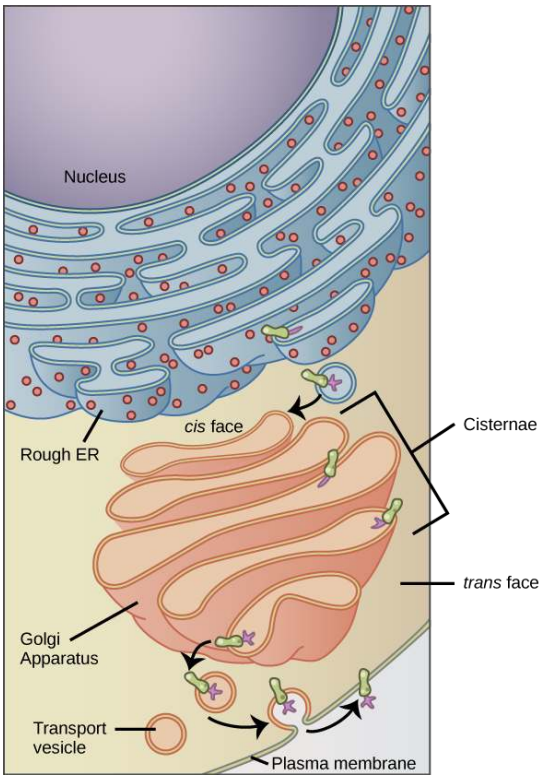



Figure 2.1.2.6Membrane and secretory proteins are synthesized in the rough endoplasmic reticulum (RER). The RER also sometimes modifies proteins. In this illustration, an attachment of a (purple) carbohydrate modifies a (green) integral membrane protein in the ER. Vesicles with the integral protein bud from the ER and fuse with the Golgi apparatus' cis face. As the protein passes along the Golgi's cisternae, the addition of more carbohydrates further modifies it. After its synthesis is complete, it exits as an integral membrane protein of the vesicle that buds from the Golgi's **trans** face. When the vesicle fuses with the cell membrane, the protein becomes an integral portion of that cell membrane. (credit: modification of work by Magnus Manske)

If a peripheral membrane protein were synthesized in the lumen (inside) of the ER, would it end up on the inside or outside of the plasma membrane?

## The Endoplasmic Reticulum

The **endoplasmic reticulum (ER)** (Figure 2.1.2.6) is a series of interconnected membranous sacs and tubules that collectively modifies proteins and synthesizes lipids. They are formed as an extension of the nuclear membrane and fold out towards the cytoplasm. The two functions of the ER take place in separate areas: the rough ER and the smooth ER, respectively.

The **rough endoplasmic reticulum** (RER) can be found has ribosomes along its surface, and the proteins they create are either secreted or incorporated into membranes in the cell. The **smooth endoplasmic reticulum (SER)** is continuous with the RER but has few or no ribosomes on its cytoplasmic surface (Figure 2.1.2.6). SER functions include synthesis of carbohydrates, lipids, and steroid hormones; detoxification of medications and poisons; and storing calcium ions.

## Vesicles

Transport vesicles, composed of endomembrane system material, bud off the from the RER, carrying material into the Golgi Apparatus, the next component of the endomembrane system.

## Golgi Apparatus

The lipids or proteins within the transport vesicles still need sorting, packaging, and tagging so that they end up in the right place. Sorting, tagging, packaging, and distributing lipids and proteins takes place in the **Golgi apparatus** (also called the Golgi body), a series of flattened membranes (Figure 2.1.2.6).

We call the side of the Golgi apparatus that is closer to the ER the *cis* face. The opposite side. closer to the plasma membrane, is the *trans* face. The transport vesicles that formed from the ER travel to the *cis* face of the Golgi, fuse with it, and empty their contents into the Golgi apparatus' lumen. As the proteins and lipids travel through the Golgi, they undergo further modifications that allow them to be sorted. The most frequent modification is adding short sugar molecule chains. These newly modified proteins and lipids then tag with phosphate groups or other small molecules in order to travel to their proper destinations.

Finally, the modified and tagged proteins are packaged into secretory vesicles that bud from the Golgi's *trans* face. While some of these vesicles deposit their contents into other cell parts where they will be used, other secretory vesicles fuse with the plasma membrane and release their contents outside the cell.

In plant cells, the Golgi apparatus has the additional role of synthesizing polysaccharides, some of which are incorporated into the cell wall and some of which other cell parts use.

### Cytoskeleton

The cellular skeleton is a collection of protein filaments within the cytoplasm. **Microtubules** are key organelles in cell division, they form the basis for cilia and flagella. Plant cells do not have cilia, which are short projections from the cell that function in movement, but the sperm cells of early diverging plants, like bryophytes and seedless vascular plants, have **flagella**. These are long projections that function in movement. Microtubules are also are guides for the construction of the cell wall, and cellulose fibers are parallel due to the microtubules. The movement in microtubules is based on tubulin-kinesin interactions. In contrast, the movement of **microfilaments** is based on actin-myosin interactions. Microfilaments guide the movement of organelles within the cell.

### Mitochondria

Mitochondria (singular = mitochondrion) are often called the “powerhouses” or “energy factories” of a cell because they are responsible for making a nucleic acid called adenosine triphosphate (ATP), the cell’s main energy-carrying molecule. ATP represents the short-term stored energy of the cell. Cellular respiration is the process of making ATP using the chemical energy found in glucose and other nutrients. In mitochondria, this process uses oxygen and produces carbon dioxide as a waste product. In fact, the carbon dioxide that you exhale with every breath comes from the cellular reactions that produce carbon dioxide as a byproduct.

In keeping with our theme of form following function, it is important to point out that muscle cells have a very high concentration of mitochondria that produce ATP. Your muscle cells need a lot of energy to keep your body moving. When your cells don’t get enough oxygen, they do not make a lot of ATP. Instead, the small amount of ATP they make in the absence of oxygen is accompanied by the production of lactic acid.

Mitochondria are oval-shaped, double membrane organelles (Figure **2.1.2.7**) that have their own ribosomes and DNA. Each membrane is a phospholipid bilayer embedded with proteins. The inner layer has folds called cristae. The area surrounded by the folds is called the mitochondrial matrix. The cristae and the matrix have different roles in cellular respiration.

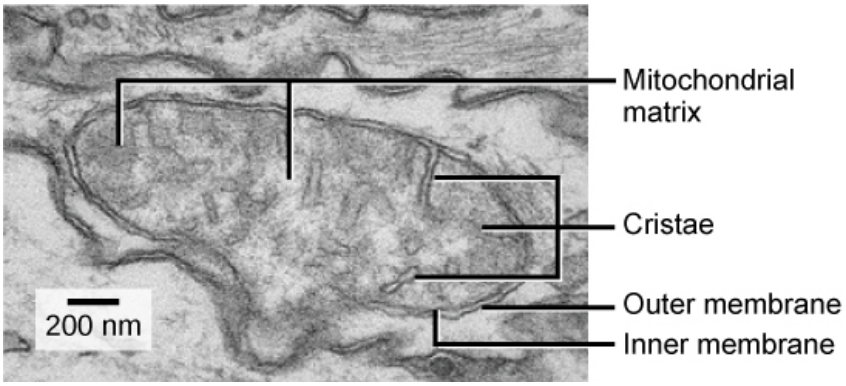



Figure **2.1.2.7**: This electron micrograph shows a mitochondrion as viewed with a transmission electron microscope. This organelle has an outer membrane and an inner membrane. The inner membrane contains folds, called cristae, which increase its surface area. The space between the two membranes is called the intermembrane space, and the space inside the inner membrane is called the mitochondrial matrix. ATP synthesis takes place on the inner membrane. (credit: modification of work by Matthew Britton; scale-bar data from Matt Russell)

### Peroxisomes

Eukaryotic cells frequently have smaller vesicles including **peroxisomes** which, among other functions, help in photosynthesis in plant cells. In addition, many plant cells accumulate lipids as oil drops located directly in cytoplasm. Peroxisomes are small, round organelles enclosed by single membranes. They carry out oxidation reactions that break down fatty acids and amino acids. They also detoxify many poisons that may enter the body. (Many of these oxidation reactions release hydrogen peroxide, $H_2O_2$, which would be damaging to cells; however, when these reactions are confined to peroxisomes, enzymes safely break down the $H_2O_2$ into oxygen and water.) For example, alcohol is detoxified by peroxisomes in liver cells. Glyoxysomes, which are specialized peroxisomes in plants, are responsible for converting stored fats into sugars.

## Components Unique to Plant Cells

The following structures are found exclusively in plant cells and are absent in animal cells.

### Cell wall

Though a **cell wall** is commonly found in prokaryotes and fungi as well as plants, their diversity is due to convergent evolution, not common ancestry, when it comes to these three groups of organisms. Plant cell walls are composed of cellulose are an excretion found outside the plasma membrane. They serve as a covering that provides structural support and gives shape to the cell.

### Central Vacuole

The **central vacuole** is a large, membrane-bound structure that fills much of the plant cell. The membrane surrounding the central vacuole is called the **tonoplast**. The central vacuole plays a key role in regulating the cell's concentration of water in changing environmental conditions. Have you ever noticed that if you forget to water a plant for a few days, it wilts? That's because as the water concentration in the soil becomes lower than the water concentration in the plant, water moves out of the central vacuoles and cytoplasm (Figure **2.1.2.8**). As the central vacuole shrinks, it leaves the cell wall unsupported. This loss of support to the plant's cell walls results in the wilted appearance. The central vacuole also supports the cell's expansion. When the central vacuole holds more water, the cell becomes larger without having to invest considerable energy in synthesizing new cytoplasm. Lastly, central vacuoles store nutrients, accumulate ions, or become a place to store wastes.

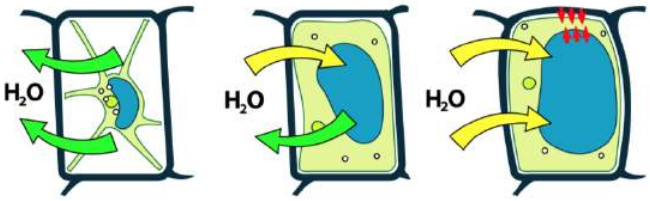



Figure **2.1.2.8** Osmosis (from left to right) in a hypertonic environment (high salt), an isotonic environment, and a hypotonic (low salt) environment. Blue color is for the vacuole. Red arrows on the right image show turgor—combined pressure of the vacuole and the cell wall.

### Plastids

Plastids are a group of storage organelle found in plants and algae. **Chloroplasts** are a type of plastid that store chlorophyll and other pigments for photosynthesis. **Chromoplasts** are plastids that store orange or yellow pigments, found in plants and fruit such as bell peppers. They are rich in carotenes and xanthophyls. **Amyloplasts** store starch and can be found in plants such as potato tubers, carrot roots, sweet potato roots, and grass seeds.

Chloroplasts store their pigments in interconnected sacs called **thylakoids** (Figure **2.1.2.9**). These sacs are often found in stacks called **grana** (singular **granum**). The fluid portion of the double membraned chloroplast is called the **stroma**. Because the thylakoid stores chlorophyll a, b, and accessory pigments, it is the main region for the first reaction of photosynthesis, where sunlight is used to create molecular energy. In the stroma, the products of the first reaction are used to produce organic molecules such as glucose. The combination of these reactions allow these autotrophic organisms to produce their own organic food.

The chloroplast, like the mitochondria, contains its own DNA, ribosomes, and is double membraned.

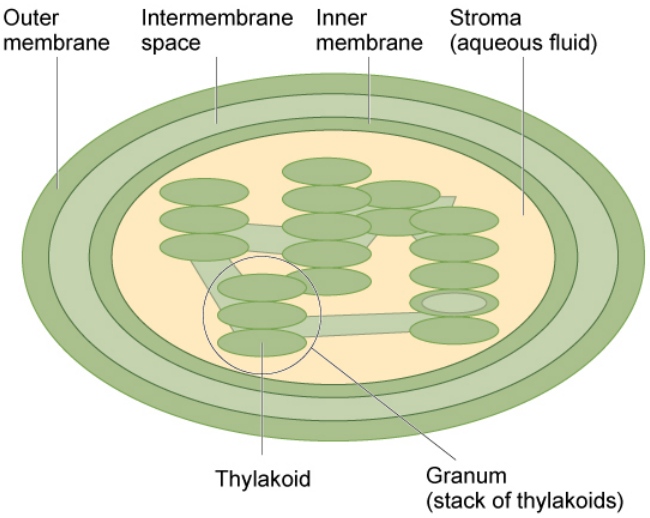



Figure **2.1.2.9**: The chloroplast has an outer membrane, an inner membrane, and membrane structures called thylakoids that are stacked into grana. The space inside the thylakoid membranes is called the thylakoid space. The light harvesting reactions take place in the thylakoid membranes, and the synthesis of sugar takes place in the fluid inside the inner membrane, which is called the stroma. Chloroplasts also have their own genome, which is contained on a single circular chromosome.

## Evolution Connection- Endosymbiosis

We have mentioned that both mitochondria and chloroplasts contain DNA and ribosomes. Have you wondered why an organelle would have its own DNA and ribomosome?

The Endosymbiosis Theory explains:

Symbiosis is a relationship in which organisms from two separate species depend on each other for their survival. Endosymbiosis (endo- = "within") is a mutually beneficial relationship in which one organism lives inside the other. Endosymbiotic relationships abound in nature. For example, there are microbes that produce vitamin K living inside the human gut. This relationship is beneficial for us because we are unable to synthesize vitamin K. It is also beneficial for the microbes because they are protected from other organisms and from drying out, and they receive abundant food from the environment of the large intestine.

Scientists have long noticed that bacteria, mitochondria, and chloroplasts are similar in size. We also know that bacteria have DNA and ribosomes, just as mitochondria and chloroplasts do. Scientists believe that host cells and bacteria formed an endosymbiotic relationship when the host cells ingested both aerobic and autotrophic bacteria (cyanobacteria) but did not destroy them. Through many millions of years of evolution, these ingested bacteria became more specialized in their functions, with the aerobic bacteria becoming mitochondria and the autotrophic bacteria becoming chloroplasts.

## Attributions

Curated and authored by Kammy Algiers using the following sources:

- 4.1 Studying Cells and 4.3 Eukaryotic cells from *Biology 2e* by OpenStax (licensed CC-BY). Access for free at openstax.org.
- 2.2 Mitochondria and Chloroplasts, 2.3 Cell wall, Vacuoles, and Plasmodesmata, and 2.4 Other Parts of the Cellfrom *Introduction to Botany* by Alexey Shipunov (public domain)

This page titled 2.1.2: Plant Cell Structure is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **3.1.2: Plant Cell Structure** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC 4.0.

# 2.1.3: Plant Tissues

**Learning Objectives**

- Describe the difference between meristematic and non-meristematic tissues.
- Compare and contrast dermal, ground, and vascular tissue.

Plants are multicellular eukaryotes with tissue systems made of various cell types that carry out specific functions. Plant tissues are composed of cells that are similar and perform a specific function. Together, tissue types combine to form organs. Each organ itself is also specific for a particular function.

Plant tissue systems fall into one of two general types: meristematic tissue, and permanent (or non-meristematic) tissue. Cells of the meristematic tissue are found in **meristems**, which are plant regions of continuous cell division and growth. Meristematic tissue cells are either undifferentiated or incompletely differentiated, and they continue to divide and contribute to the growth of the plant. In contrast, permanent tissue consists of plant cells that are no longer actively dividing.

Meristematic tissues consist of three types, based on their location in the plant. **Apical meristems** contain meristematic tissue located at the tips of stems and roots, which enable a plant to extend in length. **Lateral meristems** facilitate growth in thickness or girth in a maturing plant. **Intercalary meristems** occur only in monocots, at the bases of leaf blades and at nodes (the areas where leaves attach to a stem). This tissue enables the monocot leaf blade to increase in length from the leaf base; for example, it allows lawn grass leaves to elongate even after repeated mowing.

Meristems produce cells that quickly differentiate, or specialize, and become permanent tissue. Such cells take on specific roles and lose their ability to divide further. They differentiate into three main types: dermal, vascular, and ground tissue. Dermal tissue covers and protects the plant. The ground tissue serves as a site for photosynthesis, provides a supporting matrix for the vascular tissue, and helps to store water and sugars. The vascular tissue transports water, minerals, and sugars to different parts of the plant. Ground tissue is a **simple tissue**, meaning that each ground tissue consists of only one cell type. Dermal and vascular tissues are **complex tissues** because they consist of multiple cell types.

## Dermal Tissue

Dermal tissue covers the plant and can be found on the outer layer of roots, stems and leaves. Its main functions are *transpiration, gas exchange and defense*. The epidermis is an example of dermal tissue (Figure **2.1.3.1**). It is composed of a single layer of epidermis cells. It may contains stomata and guard cells that allow gas exchange. It may contain root hairs that increase surface area or or trichomes used in transpiration or defense. It may contain a waxy cuticle if found on the upper surface of leaves, to aid with lowering transpiration.

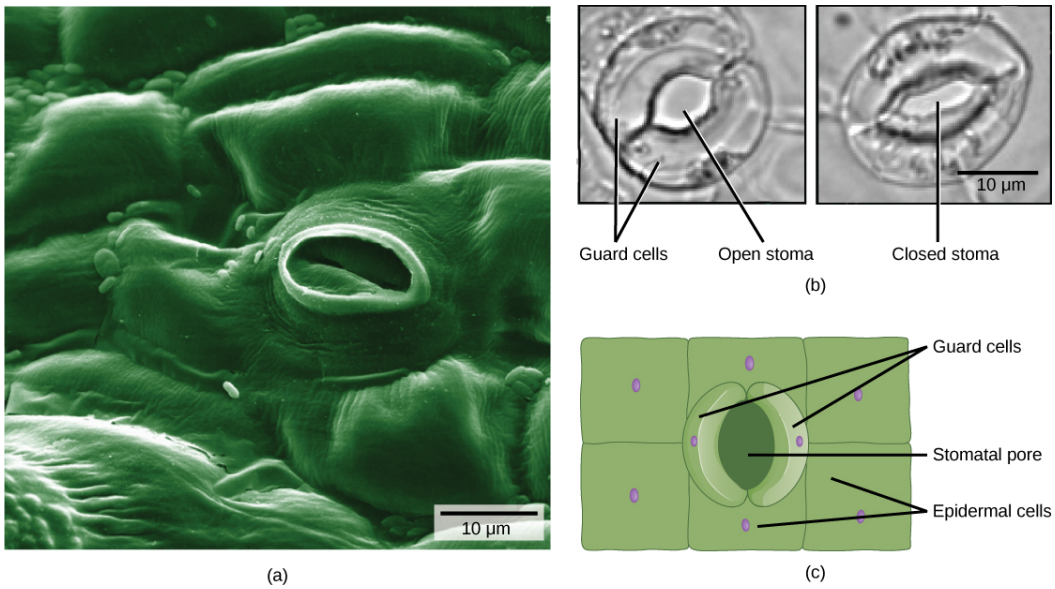



Figure **2.1.3.1**: Openings called stomata (singular: stoma) allow a plant to take up carbon dioxide and release oxygen and water vapor. The (a) colorized scanning-electron micrograph shows a closed stoma of a eudicot. Each stoma is flanked by two guard cells that regulate its (b) opening and closing. The guard cells are more curved when the stoma is open compared to when it is closed. The (c) guard cells sit within the layer of epidermal cells (credit a: modification of work by Louisa Howard, Rippel Electron Microscope Facility, Dartmouth College; credit b: modification of work by June Kwak, University of Maryland; scale-bar data from Matt Russell)

In woody plants, the epidermis breaks apart into a thick **periderm** as secondary growth allows the plant to grow in girth. The cork cambium, which makes cork cells, the cork cells (which are dead at maturity), and the phelloderm (parenchyma cells on the inside of the cork cambium) together make up the periderm (Figure **2.1.3.2**). The periderm functions as the first line of defense for the plant, protecting it from fire or heat injury, dehydration, freezing conditions, and/or disease.

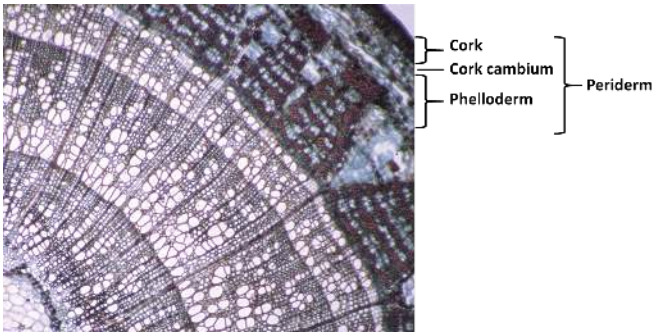



Figure **2.1.3.2**: Cross section of a woody stem. The periderm is composed of the cork cambium, cork cells, and phelloderm. Credit: Kammy Algiers (CC-BY).

## Ground Tissue

Often times, tissues that are not considered dermal or vascular tissue are noted as ground tissue. These cells store molecules (such as starch), photosynthesize (such as mesophyll cells), or support the plant. There are three types of ground tissue: collenchyma, sclerenchyma, and parenchyma.

**Collenchyma** (Figures **2.1.3.3 – 4**) is living supportive tissue that has elongated cells and an unevenly thickened primary cell wall. Its main function is the mechanical support of young stems and leaves via turgor.

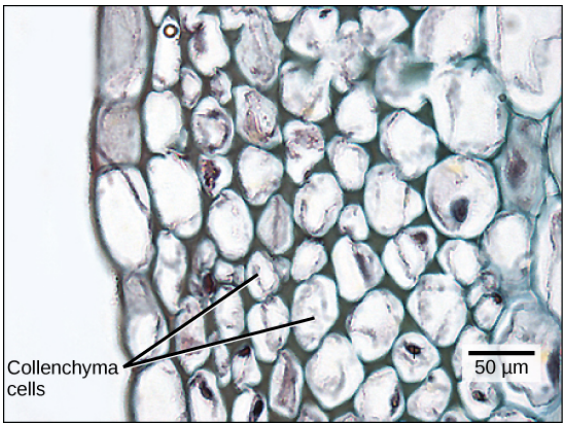



Figure **2.1.3.3**: Collenchyma cell walls are uneven in thickness, as seen in this light micrograph. They provide support to plant structures. (credit: modification of work by Carl Szczerski; scale-bar data from Matt Russell)

**Sclerenchyma** is a dead supportive tissue that consists of long **sclerenchyma fibers** (Figure **2.1.3.4**) or short, crystal-like cells (**sclereids**; Figure **2.1.3.5**). Sclerenchyma fibers occur in groups (bundles). Sclereids may be branched or not and occur individually or in small clusters. Each cell has a uniformly thick *secondary wall* that is rich in lignin. Its main function is a support of older plant organs, and also hardening different parts of plants (for example, make fruit inedible before ripeness so no one will take the fruit before seeds are ready to be distributed). Without sclerenchyma, if a plant isn't watered, the leaves will droop because the vacuoles will decrease in size which lowers the turgor. Fibers inside phloem (see below) are sometimes regarded as a separate sclerenchyma.

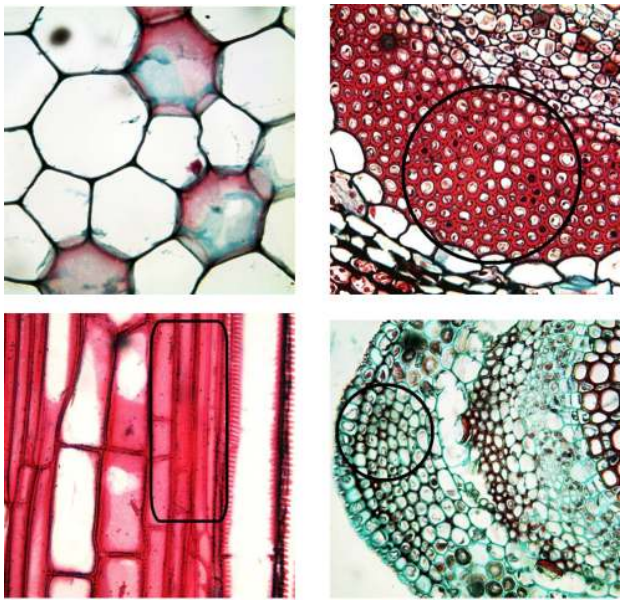


Figure **2.1.3.4**: Left to right, top to bottom: parenchyma, sclerenchyma (cross- and longitudinal sections) and collenchyma. First three photos from the stem of *Helianthus*, fourth from *Medicago* stem. Magnification ×400.

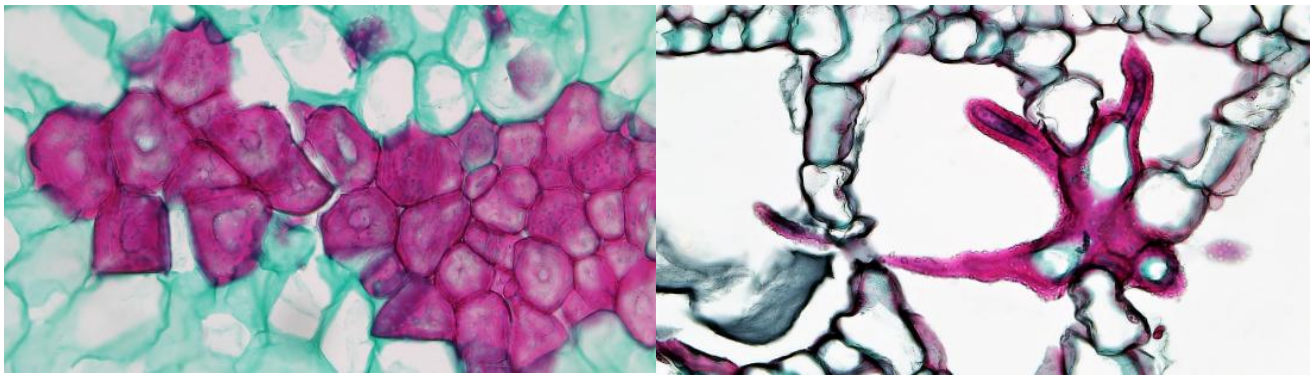


Figure **2.1.3.5**: The grainy texture of pears (*Pyrus*) is due to clusters of stone cells (sclereids), the thick-walled cells that stained pink (left, magnification = 400X). Water lily (*Nymphea*) leaves contains single, branched sclereids (right, magnification = 400X). Left and right image by Berkshire Community College Bioscience Image Library (public domain).

**Parenchyma** (Figure **2.1.3.4**) are spherical, elongated cells with a thin primary cell wall. It is a main component of young plant organs. The basic functions of parenchyma are *photosynthesis and storage*. They are also important in regeneration because they are **totipotent** (capable of differentiating into any cell type). Parenchyma cells are widespread in plant body. They fill the leaf, frequent in stem cortex and pith and is a component of complex vascular tissues (see below).

## Vascular Tissue

Vascular tissue is the plumbing system of the plant. It allows water, minerals, and dissolved sugars from photosynthesis to pass through roots, stems, leaves, and other parts of the plant. It is primary composed of two types of conducting tissue: xylem and phloem. The veins on leaves are an example of vascular tissue, moving material through the plant in the same manner that our blood vessels carry nutrients through our body. The xylem and phloem always lie adjacent to each other (Figure **2.1.3.6**). In stems, the xylem and the phloem form a structure called a vascular bundle; in roots, this is termed the vascular stele or vascular cylinder.

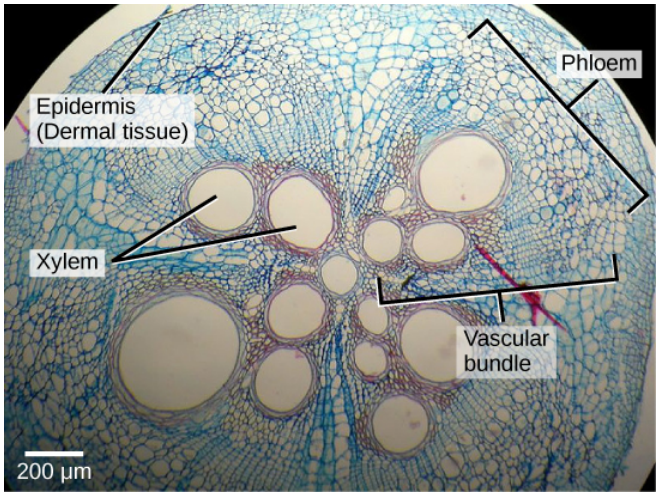



Figure **2.1.3.6**: This light micrograph shows a cross section of a squash (*Curcurbita maxima*) stem. Each teardrop-shaped vascular bundle consists of large xylem vessels toward the inside and smaller phloem cells toward the outside. Xylem cells, which transport water and nutrients from the roots to the rest of the plant, are dead at functional maturity. Phloem cells, which transport sugars and other organic compounds from photosynthetic tissue to the rest of the plant, are living. The vascular bundles are encased in ground tissue and surrounded by dermal tissue. (credit: modification of work by "(biophotos)"/Flickr; scale-bar data from Matt Russell)

**Xylem tissue** transports water and minerals from the roots to different parts of the plant. The conducting cells of the xylem are called **tracheary elements**. Parenchyma cells are also found in the xylem, and sclerenchyma fibers and sclereids are sometimes present.

There are two type of tracheary elements: **vessel elements** and **tracheids** (Figure **2.1.3.7**). Both cell types that are dead at maturity and have thickened secondary cell walls. These cells connect to one another and allow water to be transported through them. Structurally, the vessel elements are wider than tracheids and contain **perforation plates** between adjacent vessel elements (Figure

2.1.3.7 – 8). Wide openings (slits or pores) in perforation plates allow water to flow vertically between vessel elements, forming a continuous tube. Both types of tracheary elements contain **pits**, gaps in their secondary cell walls. Adjacent cells have pits in the same locations, forming **pit pairs**, which allow water and minerals to flow between adjacent cells through the **pit membrane** (the remaining, thin primary cell walls in these regions; Figure 2.1.3.9 – 10). Therefore, water flows through both perforation plates and pit pairs in vessel elements but only through pit pairs in tracheids. While water can move more quickly through vessel elements, they are more susceptible to air bubbles. An air bubble disrupts cohesion in the column of water moving up the tube of vessel elements preventing use of that particular pathway. In tracheids, an air bubble would only decommission a single tracheid rather than an entire column of vessel elements. Vessel elements are found only in angiosperms, but tracheids are found in both angiosperms and gymnosperms.

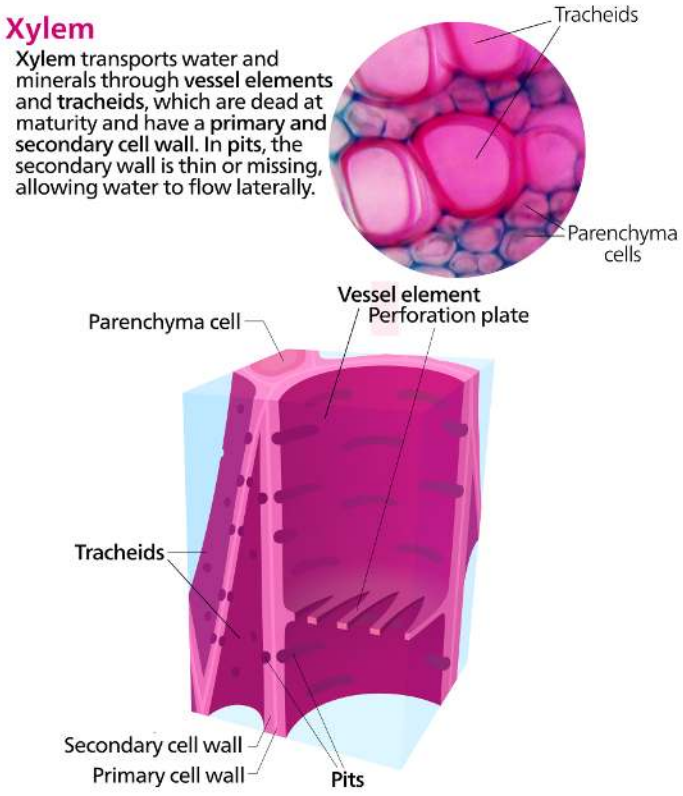



Figure 2.1.3.7: Xylem transports water and minerals through vessel elements and tracheids, which are dead at maturity and have a thin primary and thick secondary cell wall internal to the primary cell wall. In pits, the secondary wall is thin or missing, allowing water to flow laterally. The xylem of angiosperms contains both types of tracheary elements: vessel elements, and tracheids. Vessel elements are stacked up top of each other and contain perforation plates in between cells. Tracheids are thinner and lack performation plates. Pits are thinned regions in the cell wall that allow movement of water between adjacent tracheary elements. Image modified from Kelvinsong (CC-BY-SA).

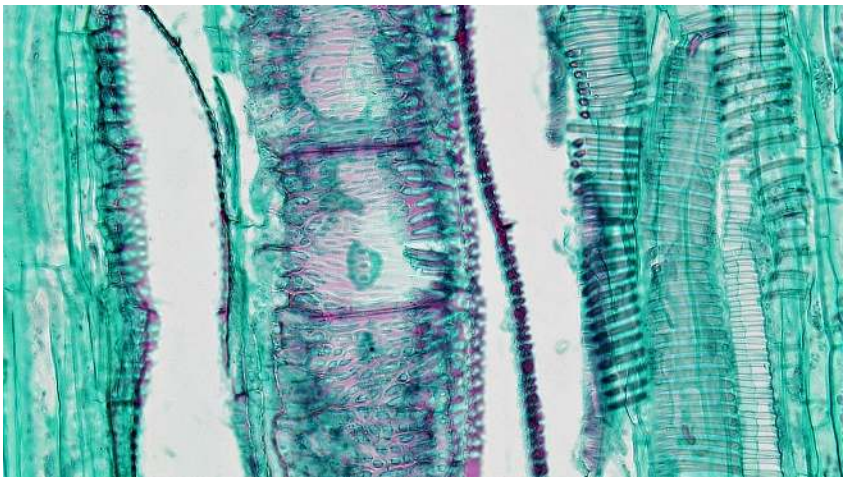


Figure **2.1.3.8**: Longitudinal section of vessel elements in a *Cucurbita* (squash) stem (magnification = 400X). Horizontal purple lines represent perforation plates between cells in a column. The rings around the cells are annular cell wall thickenings. Image by Berkshire Community College Bioscience Image Library (public domain).

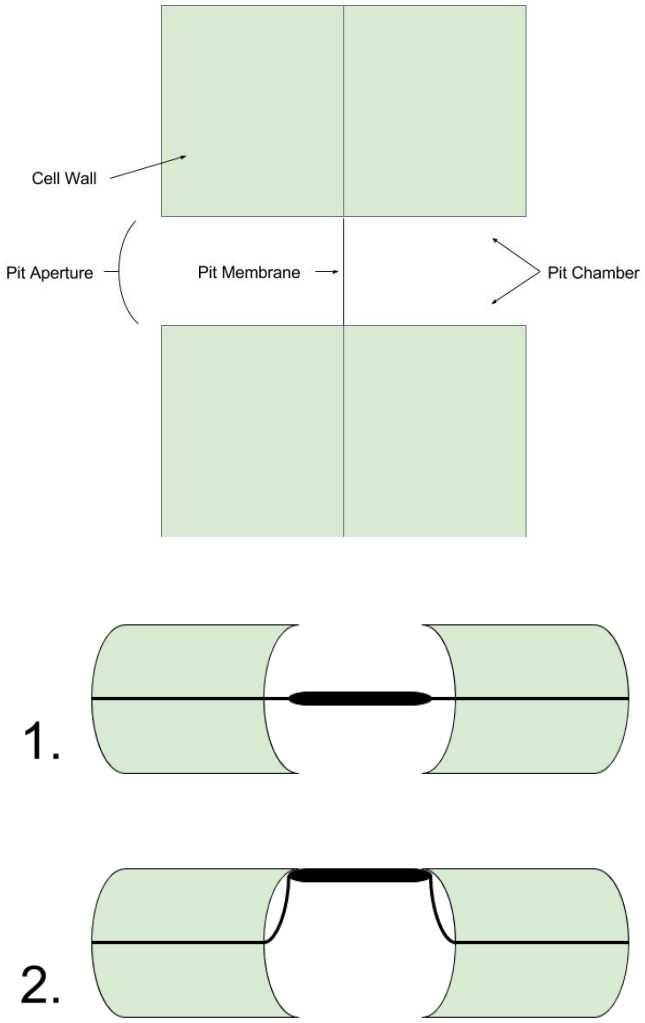



Figure 2.1.3.9: Pits are thinned regions of the cell wall (left). Pits of adjacent cells together form pit pairs separated by a pit membrane. On either side of the pit membrane is a pit chamber. The pit aperature is the opening to the pit chamber. The pit membranes of gymnosperms have a thickened central region called the torus (right). 1: The margo is the part of the membrane surrounding the torus. 2: The torus can block the pit opening (aperture) as needed to prevent air bubbles from spreading throughout the xylem. Left and right image by Pagliaccious (CC-BY-SA).

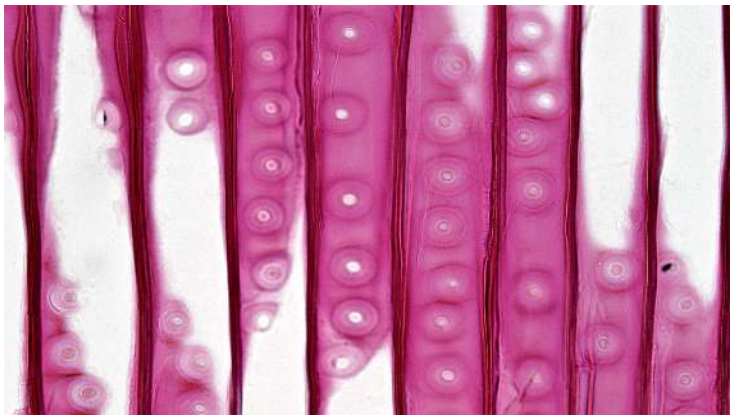


Figure 2.1.3.10: Bordered pits in tracheids of pine (*Pinus*) wood appear as bulls eyes. Pit pairs of some species have thickened outer regions (borders). Inside of this is a thinned membrane (margo) and a thickened central portion (torus). Image by Berkshire Community College Bioscience Image Library (public domain).

**Phloem tissue** transports organic compounds such as sugars from the site of photosynthesis to rest of the plant (Figure 2.1.3.11 – 12). The conducting cells of the phloem are called **sieve elements**. In comparison to tracheary elements, sieve elements have only primary cell walls (and thus thinner cell walls overall) and are alive at maturity; however, they lack certain organelles, including a nucleus. **Sieve-tube elements** are the sieve elements found only in angiosperms while **sieve cells** are found only in gymnosperms while. Both types of sieve elements have pores in their cell walls (**sieve areas**) that allow transfer of materials between adjacent cells, but these are concentrated at **sieve plates** in sieve-tube elements and evenly distributed in sieve cells. Because they lack essential organelles, sieve elements rely on specialized parenchyma cells to support them. **Companion cells** support sieve-tube elements in angiosperms, and **albuminous cells** support sieve cells in gymnosperms. Additionally parenchyma cells and sclerenchyma cells (phloem fibers) are also found in the phloem.

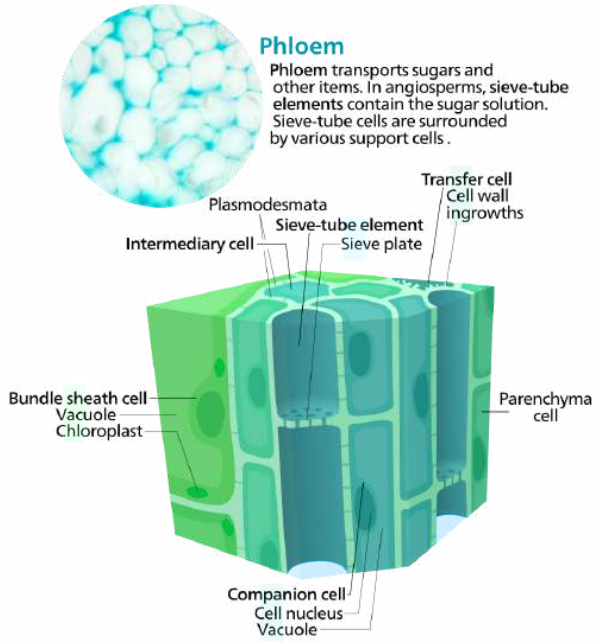



Figure 2.1.3.11: Phloem transports sugars and other items. In angiosperms, sieve-tube elements contain the sugar solution. Sieve-tube elements are the conducting cells of the phloem in angiosperms. Sieve plates allow sieve-tube elements stacked on top of each other to connect. Sieve-tube cells are surrounded by various support cells. Companion cells are narrower than sieve-tube elements and each contain a nucleus. They are connected to sieve-tube elements via plasmodesmata and provide them with the molecules they need to function (energy molecules, proteins, etc.) Some companion cells are specialized as intermediary cells, which are between the bundle sheath (see below) and sieve-tube element. Transfer cells are parenchyma cells with cell wall ingrowths, which increase surface area for transport. The bundle sheath cells form the bundle sheath, which surrounds vascular bundles (where the xylem and phloem are located). Within the bundle sheath cell are oval chloroplasts, a nucleus (not labeled), and the central vacuole, which fills most of the cell. Image by Kelvinsong (CC-BY-SA).

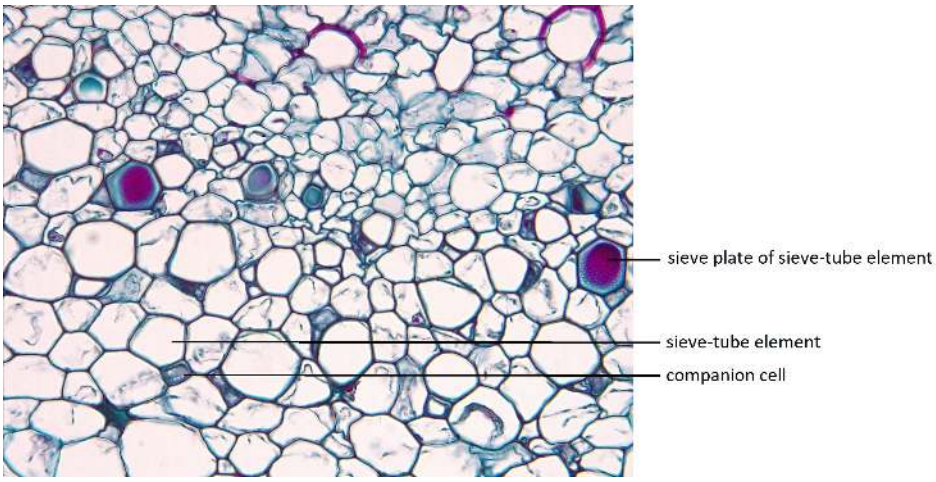



Figure **2.1.3.12**: Phloem in a cross section of a *Cucurbita* (squash) stem, magnified at 400X. Each wide sieve-tube cell has a small, dark companion cell associated with it. (The companion cells are dark because each contains a nucleus.) The cross section cut exactly in between two sieve tube elements in some cases, revealing the sieve plate. Image by Melissa Ha (CC-BY).

The table below summarizes differences between xylem and phloem:

| | Xylem | Phloem |
|---|---|---|
| Contains mostly | Dead cells | Living cells |
| Transports | Water & Minerals | Sugar |
| Direction | Up | Up and Down |
| Biomass | Big | Small |

## Meristematic Tissue

Meristems produce cells that quickly differentiate, or specialize, and become permanent tissue. Such cells take on specific roles and lose their ability to divide further. They differentiate into three main types: dermal, vascular, and ground tissue. Dermal tissue covers and protects the plant, and vascular tissue transports water, minerals, and sugars to different parts of the plant. Ground tissue serves as a site for photosynthesis, provides a supporting matrix for the vascular tissue, and helps to store water and sugars.

## Attributions

Curated and authored by Kammy Algiers and Melissa Ha using the following sources:

- 30.1 The Plant Body and 30.2 Stems from Biology 2e by OpenStax (licensed CC-BY). Access for free at openstax.org.
- 5.1 Tissues from *Introduction to Botany* by Alexey Shipunov (public domain)

---

This page titled 2.1.3: Plant Tissues is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **3.1.3: Plant Tissues** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-SA 4.0.

# 2.1.4: Chapter Summary

A **cell i**s the smallest unit of a living thing. Whether comprised of one cell (like bacteria) or many cells (like a plant), we call it an organism. Thus, cells are the basic building blocks of all organisms. Eukaryotic cells are generally around 10 to 100 µm in size. As a cell increases in size, its surface area-to-volume ratio decreases, decreasing the efficiency of transport. If the cell grows too large, the plasma membrane will not have sufficient surface area to support the rate of diffusion required for the increased volume. All cells contain these same four components: 1. **plasma (cell) membrane**, 2. **cytoplasm** and the fluid region, **cytosol**, 3. DNA, and 4. **ribosomes**. Eukaryotic cells contain **organelles** and a membrane-bound **nucleus** that is attached to an endomembrane system. The main structures that comprise the **endomembrane system** are the **endoplasmic reticulum**, **vesicles**, and the **Golgi body**. Furthermore, eukaryotic cells contain **cytoskeleton** and a **mitochondria**. Plant cells contain some structures animal cells don't possess: a **cell wall**, **central vacuole**, **peroxisomes**, and **plastids**, most notably **chloroplasts**. The mitochondria and chloroplast have evolved via the **Endosymbiosis Theory**.

Several plant cells of one kind that interconnect with each other and perform a shared function form tissues. Plant tissue systems fall into one of two general types: **meristematic tissue**, and **permanent** (or non-meristematic) tissue. **Dermal tissue** covers the plant and can be found on the outer layer of roots, stems and leaves. **Vascular tissue** is the plumbing system of the plant. It allows water, minerals, and dissolved sugars from photosynthesis to pass through roots, stems, leaves, and other parts of the plant. It is primary composed of two types of conducting tissue: **xylem** and **phloem**. Tissues that are not considered dermal or vascular tissue are noted as **ground tissue**. These cells store molecules (such as starch), photosynthesize (such as mesophyll cells), or support the plant. Ground tissue is often divided into three cell types: **collenchyma**, **sclerenchyma**, and **parenchyma**.

**After completing this chapter, you should be able to...**

- Describe the role of cells in organisms.
- Summarize cell theory.
- Address the significance of cell size.
- Describe the structures that all cells share in common.
- State the role of the plasma membrane.
- Describe the structures of eukaryotic cells.
- Summarize the functions of the major cell organelles.
- Describe the difference between meristematic and non-meristematic tissues.
- Compare and contrast dermal, ground, and vascular tissue.

## Attribution

Curated and authored by Kammy Algiers using 4.1 Studying Cells and 4.3 Eukaryotic cells from *Biology 2e* by OpenStax (licensed CC-BY). Access for free at openstax.org.

This page titled 2.1.4: Chapter Summary is shared under a CC BY 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **3.1.4: Chapter Summary** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY 4.0.

# SECTION OVERVIEW

## 2.2: Roots



Figure 2.2.1: Based on the type of substrate, roots can sometimes become visible on the ground. Credit: SKsiddhartthan (CC-BY-SA-4.0)

Roots are plant organs that are usually found underground. They not only anchor the plant, but also transport water, minerals, and sugars. In many plants, carbohydrates are stored in the roots so they can be used when needed. Roots can be very deep, and spread out very far. Some roots are as deep as the tree is high. Roots can also spread far beyond the canopy of the tree. However, being underground, they are often gone unnoticed.

**Roots**


2.2.1: Organs and Organ Systems

2.2.2: External Root Structure

2.2.3: Internal Root Structure

2.2.4: Root Modifications

2.2.5: Chapter Summary


### Attribution

Kammy Algiers (CC BY-NC)


This page titled 2.2: Roots is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

# 2.2.1: Organs and Organ Systems

## Learning Objectives

- Describe the types of organs and organ systems in plants.
- Describe the function of roots.

Plant tissues form **organs** (such as leaves, stems, or roots), each of which perform a specific set of functions. Together, organs often work to form organ systems. Vascular plants have two distinct organ systems: a shoot system, and a root system. The **shoot system** consists of two portions: the vegetative (non-reproductive) parts of the plant, such as the leaves and the stems, and the reproductive parts of the plant, which include flowers and fruits. The shoot system generally grows above ground, where it absorbs the light needed for photosynthesis. The **root system**, which anchors the plant into the ground, absorbs water and minerals, and serves as a storage site for food is usually underground. (Figure **2.2.1.1**) shows the organ systems of a typical plant.

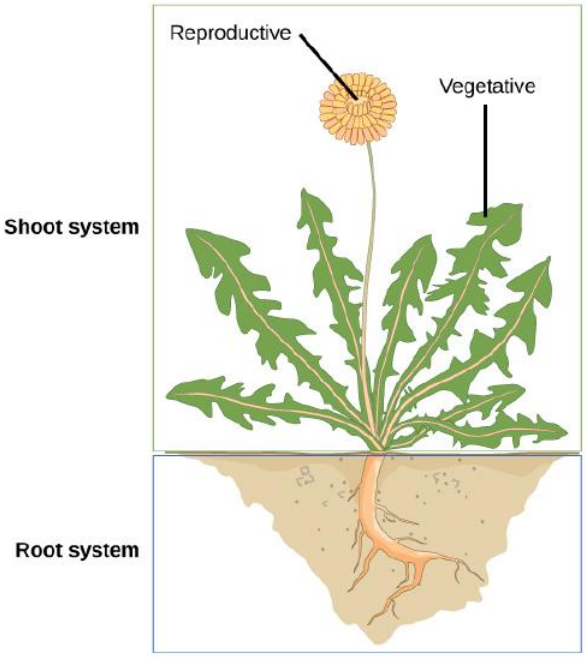



Figure **2.2.1.1**: The shoot system of a plant consists of leaves, stems, flowers, and fruits. The root system anchors the plant while absorbing water and minerals from the soil. The dandelion root system consists of a single, thick root that branches into smaller roots.

## Attribution

Curated and authored by Kammy Algiers using 30.3 Roots from *Biology 2e* by OpenStax (licensed CC-BY). Access for free at openstax.org.

This page titled 2.2.1: Organs and Organ Systems is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **3.2.1: Organs and Organ Systems** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC 4.0.

# 2.2.2: External Root Structure

**Learning Objective**

Identify the types of root systems found in plants.

There are two types of root systems. The first is a **fibrous root system** which has multiple big roots that branch and form a dense mass which does not have a visible primary root (“grass-like”). The other is the **tap root system** which has one main root that has branching into lateral roots (“carrot-like”).

Root systems are mainly of two types (Figure 2.2.2.1). Eudicots have a tap root system, while monocots have a fibrous root system. A tap root system has a main root that grows down vertically, and from which many smaller lateral roots arise. Dandelions are a good example; their tap roots usually break off when trying to pull these weeds, and they can regrow another shoot from the remaining root). A tap root system penetrates deep into the soil. In contrast, a fibrous root system is located closer to the soil surface, and forms a dense network of roots that also helps prevent soil erosion (lawn grasses are a good example, as are wheat, rice, and corn). Some plants have a combination of tap roots and fibrous roots. Plants that grow in dry areas often have deep root systems, whereas plants growing in areas with abundant water are likely to have shallower root systems.




Figure 2.2.2.1: (a) Tap root systems have a main root that grows down, while (b) fibrous root systems consist of many small roots. (credit b: modification of work by “Austen Squarepants”/Flickr)

Along with having different systems, there are **primary root** that originated from the root of the seedling (Figure 2.2.2.2*a*) and **secondary (lateral) roots** originate from the primary roots, and **adventitious roots** originate on stems or leaves, rather than from the base of the embryo. Adventitious roots can grow if plant cuttings are placed in water (Figure 2.2.2.2*b*).



Figure **2.2.2.2**: a) Mung bean tap root (eudicot) and wheat bean fibrous root (monocot) from sprouts. b) Jade plant cutting, showing adventitious roots growing from stem after being placed in water. Credit: Kammy Algiers (CC-BY).

## Attribution

Curated and authored by Kammy Algiers using 5.5 The Root from *Introduction to Botany* by Alexey Shipunov (public domain)

---

This page titled 2.2.2: External Root Structure is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **3.2.2: External Root Structure** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC 4.0.

# 2.2.3: Internal Root Structure

**Learning Objectives**

- Describe the different structures and zones of a root.
- Compare and contrast a monocot root to a eudicot root.
- Describe secondary root growth and the function of vascular and cork cambium.

## Root Anatomy

Root growth begins with seed germination. When the plant embryo emerges from the seed, the **radicle** of the embryo begins to grow downward and forms the root system. As the root system grows, various structures begin to appear.

## Longitudinal Section

If you were to cut a root down longitudinally, you would see the various layers inside. The tip of the root is protected by the **root cap**, a structure exclusive to roots and unlike any other plant structure. The root cap is continuously replaced because it gets damaged easily as the root pushes through soil. The root tip can be divided into three zones: a **zone of cell division**, a **zone of elongation**, and a **zone of maturation and differentiation** (Figure **2.2.3.1**). The zone of cell division is a continuation of the root cap; it is made up of the actively dividing cells of the root meristem. The zone of elongation is where the newly formed cells begin to increase in length, thereby lengthening the root. They are older than cells at the zone of cell division. Beginning at the first root hair is the zone of cell maturation where the root cells begin to differentiate into special cell types. The root has an outer layer of cells called the epidermis, which surrounds areas of ground tissue and vascular tissue. The epidermis provides protection and helps in absorption. **Root hairs**, which are extensions of root epidermal cells, increase the surface area of the root, greatly contributing to the absorption of water and minerals. All three zones are in the first centimeter or so of the root tip.

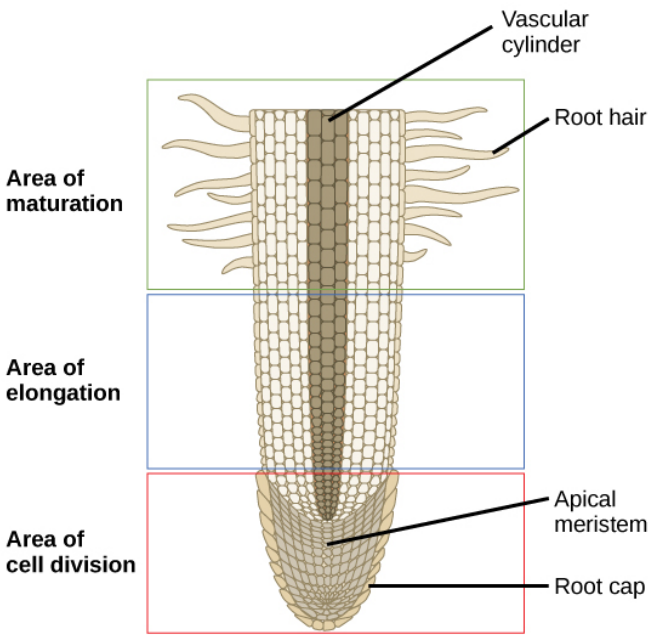


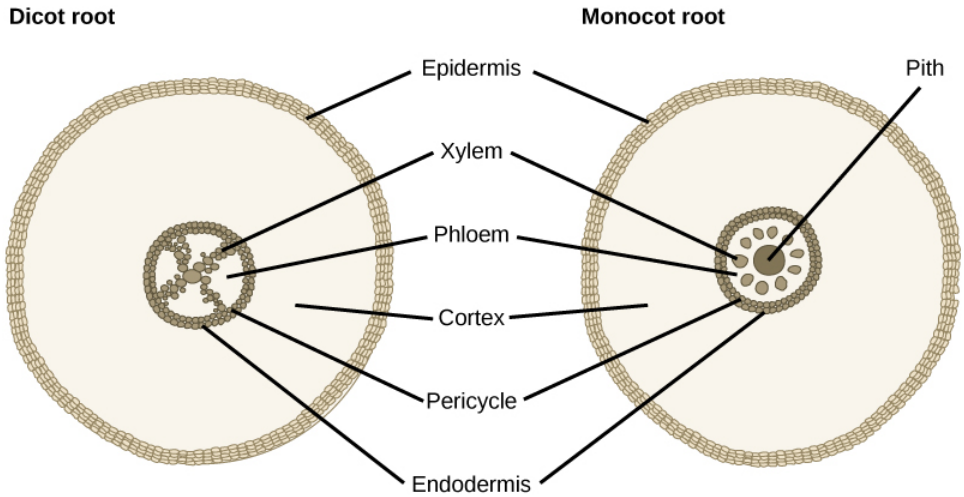

Figure **2.2.3.1**: A longitudinal view of the root reveals the zones of cell division, elongation, and maturation. Cell division occurs in the apical meristem.

## Cross Section

If you were to cut a cross section of the leaf, you could see other features that are not as obvious in the longitudinal section. Inside the root, the ground tissue may form two regions: the **cortex** and the **pith** (Figure **2.2.3.2**). When comparing roots to stems, roots have much more cortex and very little pith. Whereas eudicot roots have no central pith, monocots have a small pith. Both cortex

and pith include cells that store photosynthetic products. The cortex is between the epidermis and the vascular tissue, whereas the pith lies between the vascular tissue and the center of the root.

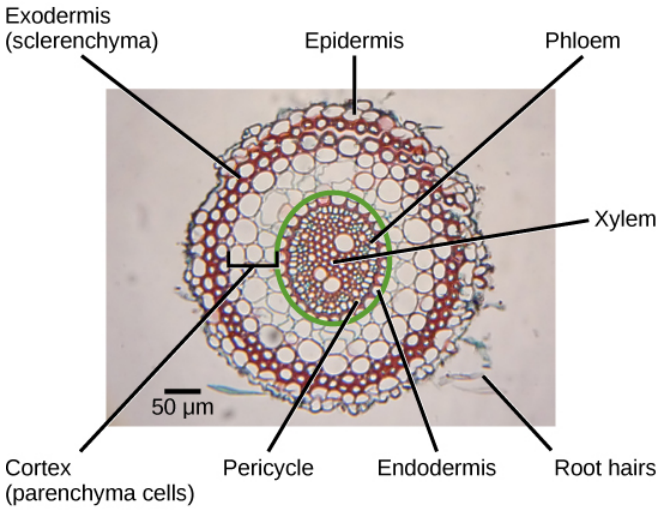
The inner portion of the root contains the vascular tissue (xylem and phloem). This area is called the **stele**. A layer of cells known as the **endodermis** borders the stele (Figure 2.2.3.2) and is considered the innermost layer of the cortex. The endodermis is exclusive to roots, and serves as a checkpoint for materials entering the root's vascular system. A waxy substance called suberin is present on the walls of the endodermal cells. This waxy region, known as the **Casparian strip**, forces water and solutes to cross the plasma membranes of endodermal cells instead of slipping between the cells. This ensures that only materials required by the root pass through the endodermis, while toxic substances and pathogens are generally excluded. The outermost cell layer of the root's vascular tissue is the **pericycle**, an area that can give rise to lateral roots.




(Figure 2.2.3.2): In (left) typical eudicots, the vascular tissue forms an X shape in the center of the root. In (right) typical monocots, the phloem cells and the larger xylem cells form a characteristic ring around the central pith.

## Monocots

Note that the size of the stele in the monocot cross section is large (everything inside the green ring (Figure 2.2.3.3). The vascular tissue is arranged in a ring around the pith. This arrangement is called a **siphonostele**. The cortex surrounds the stele. The **endodermis** is the innermost layer of the cortex, and the **exodermis** is the outermost layer of the cortex. The exodermis controls the flow of water, ions, and nutrients. The outermost layer of the root (external to the cortex) is the epidermis, which covers the root and aids in absorption.




(Figure **2.2.3.3**): Staining reveals different cell types in this light micrograph of a wheat (*Triticum*) root cross section. Sclerenchyma cells of the exodermis and xylem cells stain red, and phloem cells stain blue. Other cell types stain black. The stele, or vascular tissue, is the area inside endodermis (indicated by a green ring). Root hairs are visible outside the epidermis. (credit: scale-bar data from Matt Russell)

## Eudicots

In eudicot roots, the vascular tissue fills the center of the root, and there is no pith. This arrangment is called a **protostele**. The xylem and phloem of the stele are arranged alternately in an X shape (Figure **2.2.3.4**). Most of the root is composed of cortex tissue, and the **endodermis**, the innermost layer of the cortex, borders the stele. The outer layer of the root (external to the cortex) is the epidermis.



Figure **2.2.3.4**: Eudicot root cross section. From center out, the xylem (in red) make an X, and the side tissues (green) make up the phloem.. The endodermis separates the stele from the cortex, which is the largest tissue. The last layer of cells on the edge is the epidermis layer. (Credit: Wikimedia)

## Secondary Root Growth

Many roots have secondary growth as well as primary growth (figures **2.2.3.5 – 6**). This occurs by the production of two types of meristemic tissue, the **vascular cambium** and the **cork cambium**. The cork cambium is responsible for the girth or growth in the diameter of the root. This occurs by the cork cambium adding vascular tissue to the root. Cells of the pericycle and procambium (the meristematic tissue between the primary phloem and xylem) begin division, and form a vascular cambium around the primary xylem. The vascular cambium then divides to form secondary xylem on the inside and secondary phloem on the outside.

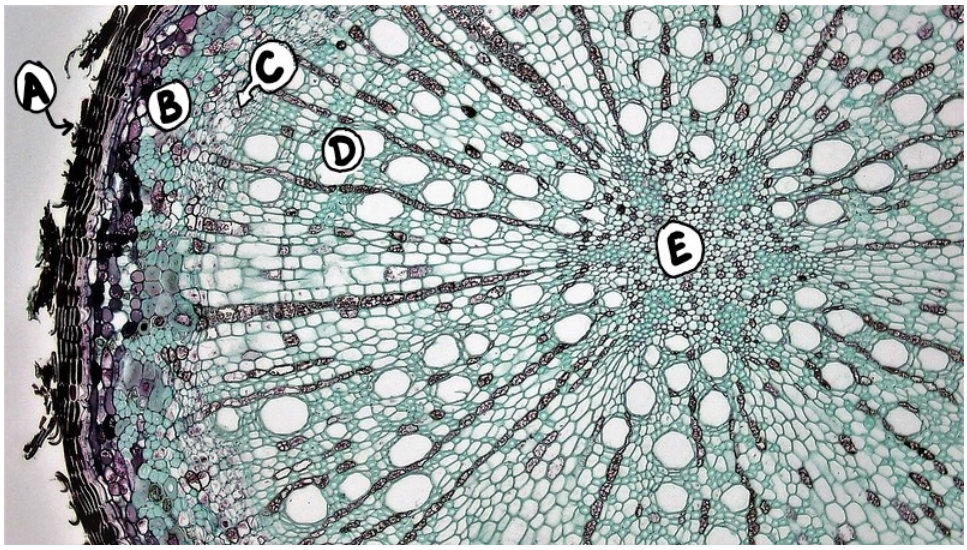



Figure **2.2.3.5**: A labeled cross section through an older *Quercus* root, 100x. A=Periderms, B=Seconary Phloem, C=Vascular Cambium, D=Secondary Xylem, E=Primary xylem. Image from Berkshire Community College Bioscience Image Library (public domain). Labels added by Maria Morrow.

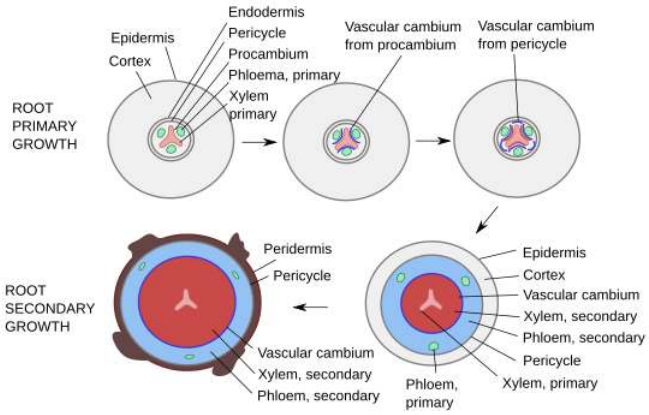



Figure **2.2.3.6**: The process of secondary growth in roots begins when the vascular cambium (dark blue ring) arises from the pericycle and embryonic tissue called the procambium. The vascular cambium produces secondary xylem (dark red) internally and secondary phloem (light blue) externally. Additionally, the cork cambium arises from the pericycle and produces cork and phelloderm, forming the periderm (dark brown outer layer). Image from Atlas of Plant and Animal Histology (CC-BY-NC-SA)

Some roots with secondary growth may form a periderm (a protective layer, replacing the epidermis). This occurs by the formation of a cork cambium which originate from the pericycle. The cork cambium produces parenchyma tissues called phelloderm to the inside of the root and the cork on the outside of the root. Cork cells (phellem) are dead at maturity. They are hollow and the addition of air space in the tissue functions as a protective layer. They also produce a waxy substance called **suberin**. This wax functions to aid in water loss. It also makes the root more resistant to bacterial and fungal infections. The three layers 1. phelloderm 2. cork cambium and 3. cork cells are collectively known as the periderm.

## Attributions

Curated and authored by Kammy Algiers and Melissa Ha from the following sources

- 11.2 Secondary Growth from *A Photographic Atlas for Botany* by Maria Morrow (CC-BY-NC).
- 30.3 Roots from *General Biology* by OpenStax (CC-BY).

---

This page titled 2.2.3: Internal Root Structure is shared under a CC BY 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **3.2.3: Internal Root Structure** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY 4.0.

# 2.2.4: Root Modifications

**Learning Objective**

Describe the types of modified roots and their functions.

Root structures may be modified for specific purposes. For example, some roots are bulbous and store starch. Tap roots in plants such as carrots, turnips, and beets, are examples of roots that are modified for food storage (Figure **2.2.4.1**).



Figure **2.2.4.1**: Many vegetables are modified roots.

Aerial roots are forms of aboveground roots that provide additional support to anchor the plant. **Epiphytic roots** are a type of aerial root that enable a plant to grow on another plant. For example, the epiphytic roots of orchids develop a spongy tissue to absorb moisture. The banyan tree (*Ficus* sp.) begins as an epiphyte, germinating in the branches of a host tree. The plant's aerial roots develop from the branches and eventually reach the ground, providing additional support (Figure **2.2.4.2**). In screwpine (*Pandanus* sp.), a palm-like tree that grows in sandy tropical soils. Plants which grow on sand have another problem: their substrate constantly disappears. To avoid this, plants developed **contractile roots** which may shorten and pull plant body deeper into the sand.



(a) (b)

Figure **2.2.4.2**: The (a) banyan tree, also known as the strangler fig, begins life as an epiphyte in a host tree. Aerial roots extend to the ground and support the growing plant, which eventually strangles the host tree. The (b) screwpine develops aboveground roots that help support the plant in sandy soils. (credit a: modification of work by "psyberartist"/Flickr; credit b: modification of work by David Eikhoff)

Plants growing in ocean coastal swamps need additional specializations. Roots of mangroves are frequently modified into supportive aerial roots called **stilt roots.** Stilt roots are adventitious and grow from lateral branches. Swamp plants are often flooded and need additional adaptations for respiration. **Pneumatophores** are specialized roots that grow upward and allow oxygen and carbon dioxide exchange from the plant's root system. They passively catch the air via multiple pores (Figure **2.2.4.3**).



Figure **2.2.4.3**: Mangrove pneumatophores in Sulawesi. (Credit: Wikimedia CC BY_SA 3.0)

Some aerial roots will function as photosynthetic organs as well. Though rare, you can see green photosynthetic roots in some plants such as epiphytic orchids (Figure **2.2.4.4**). In some cases, the plant is leaf-less so all the photosynthesis is done by the aerial roots. In other plants, the aerial roots aid in photosynthesis.



Figure **2.2.4.4**: Photosynthetic roots of leafless orchid *Chiloschista segawai*.

**Root nodules** present on the roots of nitrogen-fixing plants, they contain bacteria capable to deoxidize atmospheric nitrogen into ammonia: $N_2 \rightarrow NH_3$. Root nodules contain also hemoglobin-like proteins which facilitate nitrogen fixation by keeping oxygen concentration low. Nitrogen-fixing plants are especially frequent among *faboid rosids*: legumes (Leguminosae family) and many other genera (like alder, *Alnus*, or *Shepherdia*, buffaloberry) have root nodules with bacteria. Some other plants (mosquito fern, *Azolla* and dinosaur plant, *Gunnera*) employ cyanobacteria for the same purpose.

**Mycorrhiza** is a root modification started when fungus penetrates root and makes it more efficient in mineral and water absorption: it will exchange these for organic compounds. In addition to mycorrhizal fungi, **endophytic fungi** inhabit other plant organs and tissues.

## Attributions

Curated and authored by Kammy Algiers using 30.3 Roots from *Biology 2e* by OpenStax (licensed CC-BY). Access for free at openstax.org.

---

This page titled 2.2.4: Root Modifications is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **3.2.4: Root Modifications** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-SA 4.0.

# 2.2.5: Chapter Summary

Roots help to anchor a plant, absorb water and minerals, and serve as storage sites for food. **Taproots** and **fibrous roots** are the two main types of root systems. In a taproot system, a main root grows vertically downward with a few **lateral roots**. Fibrous root systems arise at the base of the stem, where a cluster of roots forms a dense network that is shallower than a taproot. The growing root tip is protected by a **root cap**. The **root tip** has three main zones: a **zone of cell division** (cells are actively dividing), a **zone of elongation** (cells increase in length), and a **zone of maturation** (cells differentiate to form different kinds of cells). The root's ground tissue contains **cortex** and **pith** while its vascular tissue contains xylem and phloem. Monocots and eudicots have different organization of their vascular tissues, with the monocot vascular tissue organized into a characteristic ring around the central pith while the eudicot vascular tissue forms an "X" shape in the center of the root and lacks a pith. Many roots have **secondary growth** as well as primary growth. Secondary growth occurs by the production of two types of meristemic tissue, the **vascular cambium** and the **cork cambium**.

In some habitats, the roots of certain plants may be modified and adapted for various environments. Some examples of these modifications result in **storage roots**, **aerial roots**, **epiphytic roots**, **contractile roots**, **stilt roots**, **penumatophores**, and **photosynthetic roots**. **Root nodules** and **mycorrhizae** are root adaptations that increase the efficiency of nutrient uptake.

**After completing this chapter, you should be able to ...**

- Describe the types of organs and organ systems in plants.
- Describe the function of roots.
- Identify the types of root systems found in plants.
- Describe the different strictures and zones of a root.
- Compare and contrast a monocot root to a eudicot root.
- Describe secondary root growth and the function of vascular and cork cambium.
- Describe the types of modified roots and their functions.

## Glossary

**adventitious root**

**Casparian strip**

**endodermis**

**fibrous root system**

**pericycle**

**root cap**

**root hair**

**stele**

**tap root system**

This page titled 2.2.5: Chapter Summary is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **3.2.5: Chapter Summary** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC 4.0.

# SECTION OVERVIEW

## 2.3: Stems

The shoot system of a plant consists of stems and leaves (Figure **2.3.1**). Stems may range in length from a few millimeters to hundreds of meters, and also vary in diameter, depending on the plant type. Stems are usually aboveground, although the modified stems of some plants, such as the potato, also grow underground. Stems may be herbaceous (soft) or woody in nature. A stem may be unbranched, like that of a palm tree, or it may be highly branched, like that of a magnolia tree.



Figure **2.3.1**: The shoot system of bamboo plants. Image by RanaAnees (CC-BY-SA).

The stem of the plant functions in support, conduction, photosynthesis, and storage. Stems support leaves, flowers, and buds. They connect the roots to the leaves, helping to transport absorbed water and minerals to different parts of the plant. It also helps to transport the products of photosynthesis, namely sugars, from the leaves to the rest of the plant. Stems also store food for the plant, mainly in the form of starch.

### Attributions

Curated and authored by Melissa Ha using the following sources:

- 5.4 The Stem from *Introduction to Botany* by Alexey Shipunov (public domain)
- 30.2 Stems from *Biology 2e* by OpenStax (licensed CC-BY). Access for free at openstax.org.

**Stems**


2.3.1: Stem Morphology (External Structure)

2.3.2: Internal Anatomy of the Primary Stem

2.3.3: Secondary Stem

2.3.4: Stem Modifications

2.3.5: Chapter Summary


This page titled 2.3: Stems is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

# 2.3.1: Stem Morphology (External Structure)

**Learning Objective**

Identify the main external structures of the shoot system, including the nodes, internodes, leaves, axillary buds, and axillary shoots.

Plant stems, whether above or below ground, are characterized by the presence of nodes and internodes (Figure **2.3.1.1**). **Nodes** are points of attachment for leaves. Leaves often consist of a thin region that attaches to the stem (the **petiole**) and a broader **blade** (see Leaves). The stem region between two nodes is called an **internode**. An **axillary bud** is usually found in the **axil**—the area between the base of a leaf and the stem—where it can give rise to a branch called an **axillary shoot** (Figure **2.3.1.2**). The **shoot apex** at the tip shoot contains the **shoot apical meristem** surrounded by developing leaves called **leaf primordia** (see Meristems).

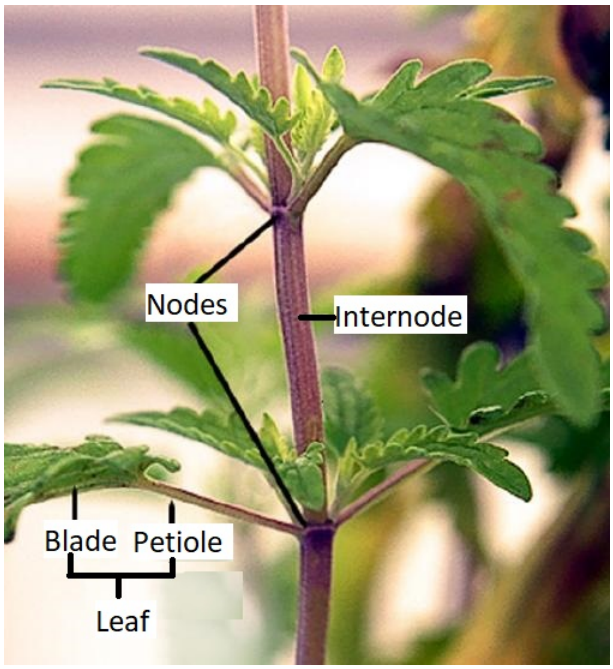



Figure **2.3.1.1**: Leaves are attached to the plant stem at areas called nodes. An internode is the stem region between two nodes. The smaller leaves just above the nodes are the beginning of axillary shoots, which arose from axillary buds. Image modified from OpenStax (CC-BY)



Figure **2.3.1.2**: Axillary buds of sweet granadilla (*Passiflora ligularis*). One of the axillary buds is labeled with an arrow. Image modified from Eiku (CC-BY-SA).

## Attributions

Curated and authored by Melissa Ha from 30.2 Stems from *Biology 2e* by OpenStax (licensed CC-BY)

---

This page titled 2.3.1: Stem Morphology (External Structure) is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **3.3.1: Stem Morphology (External Structure)** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-SA 4.0.

# 2.3.2: Internal Anatomy of the Primary Stem

## Learning Objectives

- Identify the structures representing each of the three tissue systems in stems.
- Compare the structure of solenosteles, eusteles, and atactosteles.
- Explain the arrangement of leaf traces, leaf trace gaps, branch traces, and branch trace gaps.

The primary stem refers to the herbaceous (non-woody) stem, which has not undergone secondary growth (the growth that produces bark and wood). Some species (all monocots and some eudicots) remain herbaceous for their entire lives, maintaining the primary stem. Other species of eudicots initially form a primary stem but later become woody, replacing the primary stem with the secondary stem. The anatomy of the stem (internal structure) can be examined through longitudinal sections (cutting the stem lengthwise) or in cross sections (cutting a slice of the stem perpendicular to the length).

All three tissue types are represented in the primary stem. The **epidermis** is the dermal tissue that surrounds and protects the stem. The epidermis typically consists of one layer of cells. A waxy cuticle on the outside of these cells limits water loss. Epidermal cells are the most numerous and least differentiated of the cells in the epidermis. Pores in the epidermis called **stomata** (singular: stoma) allow for gas exchange. Each stoma is bordered by a pair of **guard cells**, which regulate stomatal opening. While stomata are present in stems, they occur at higher densities in leaves. Trichomes are hair-like structures on the epidermal surface. They help to reduce transpiration (the loss of water by aboveground plant parts), increase solar reflectance, and store compounds that defend the leaves against predation by herbivores (Figure **2.3.2.1**).



Figure **2.3.2.1**: Trichomes extend from the epidermis of this *Datrua inoxia* stem. Image by Silk666 (CC-BY-SA).

Ground tissue fills much of the stem, forming the **cortex** directly within the epidermis and the **pith** (if present) in the center. The outermost portion of the cortex is usually a few layers of collenchyma cells. The remainder of the cortex and pith consist of parenchyma cells. The arrangement of vascular tissue in the stem depends on the species (see below).

Cross sections reveal three possible arrangements of vascular tissue (**steles**) in the stem. The first arrangement (**solenostele**) is present in a few eudicots, such as basswood (*Tilia*). In the solenostele, the vascular tissue appears as a continuous ring (**vascular cylinder**; Figure **2.3.2.2**). The **interfascicular regions** (pith rays) of parenchyma cells that separate vascular tissue are thus extremely narrow. The second arrangement (**eustele**) is present in most eudicots such as sunflower (*Helianthus*) and buttercup (*Ranunculus*). In the eustele, vascular tissue is clustered into distinct **vascular bundles** arranged in a ring, allowing for thicker interfascicular regions in between them (Figure **2.3.2.3 – 4**). In these solenosteles and eusteles, the vascular tissue separates ground tissue into an outer cortex and central pith. The third arrangement (**atactostele**) is present in most monocots, such as corn (*Zea mays*) and a few eudicots. In the atactostele, vascular bundles are scattered throughout the stem (Figure **2.3.2.3,**). While vascular bundles near the outside of the stem are packed more densely in this third arrangement, their distribution is somewhat disorderly. There is no distinction between the cortex and pith in the third arrangement.

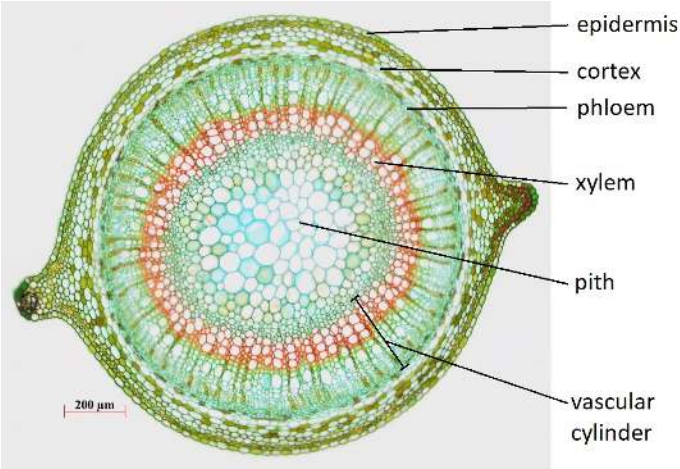



Figure **2.3.2.2**: Cross section of a common St. John's Wort (*Hypericum perforatum*) stem, illustrating a solenostele. The epidermis borders the entire root. The central pith (greenish-blue, in the center) and peripheral cortex (narrow zone 3–5 cells thick just inside the epidermis) are composed of parenchyma cells. Vascular tissue, forming the vascular cylinder, is composed of xylem (red) and phloem tissue (green, between the xylem and cortex) surrounds the pith. Image by RolfDieterMueller (CC-BY)

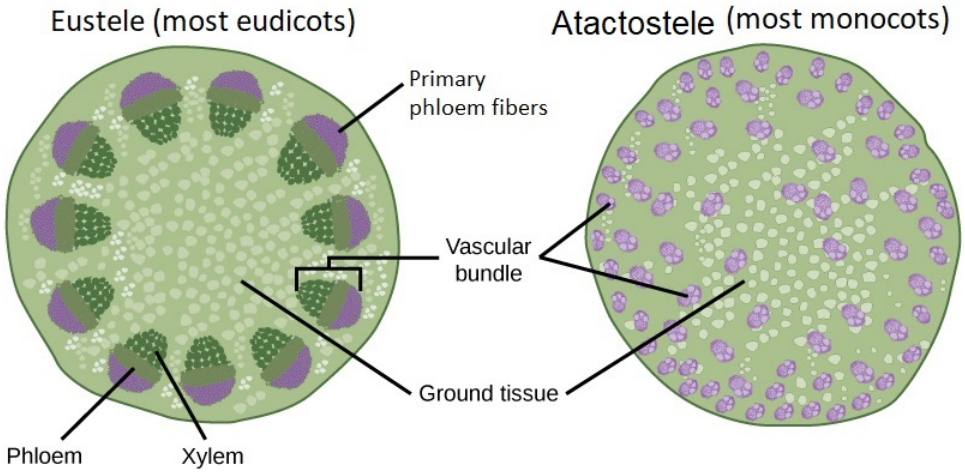



Figure **2.3.2.3**: In eusteles (left), vascular bundles are arranged around the periphery of the ground tissue. The xylem tissue is located toward the interior of the vascular bundle, and phloem is located toward the exterior. Primary phloem fibers cap the vascular bundles. In atactosteles (right), vascular bundles composed of xylem and phloem tissues are scattered throughout the ground tissue.

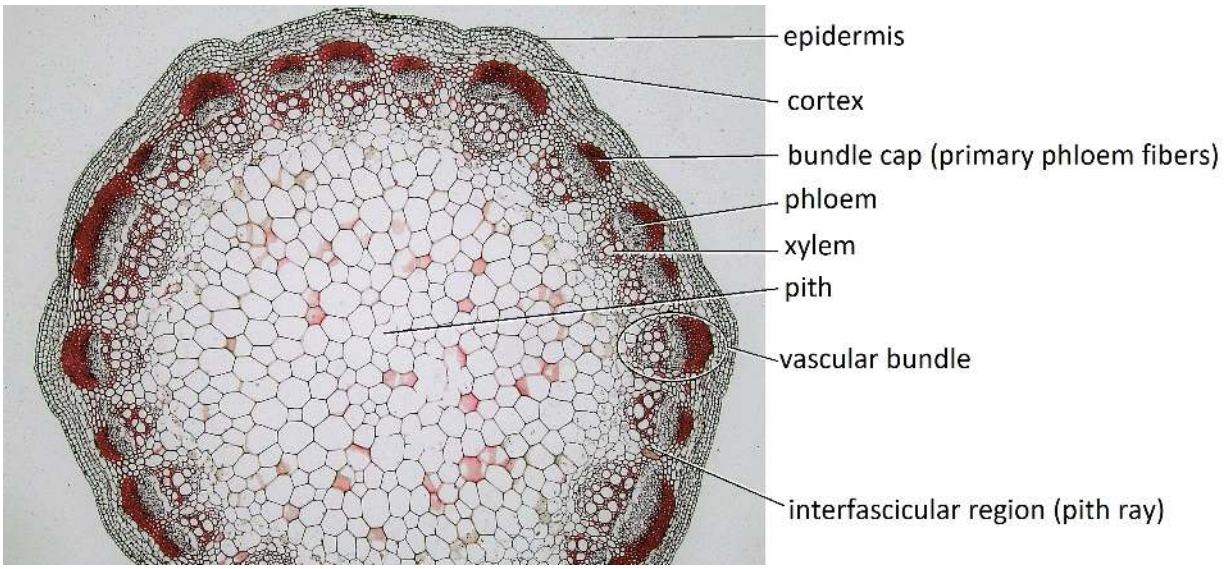



Figure **2.3.2.4**: Cross section of a sunflower (*Helianthus*) stem, illustrating a eustele. Vascular bundles are arranged in a ring. The interfascicular regions between the vascular bundles are thick compared to the solenostele, where they were too thin to be visible. The ground tissue is separated into an outer cortex and a central pith. The epidermis borders the entire stem. Image labeled from Berkshire Community College Bioscience Image Library (public domain)

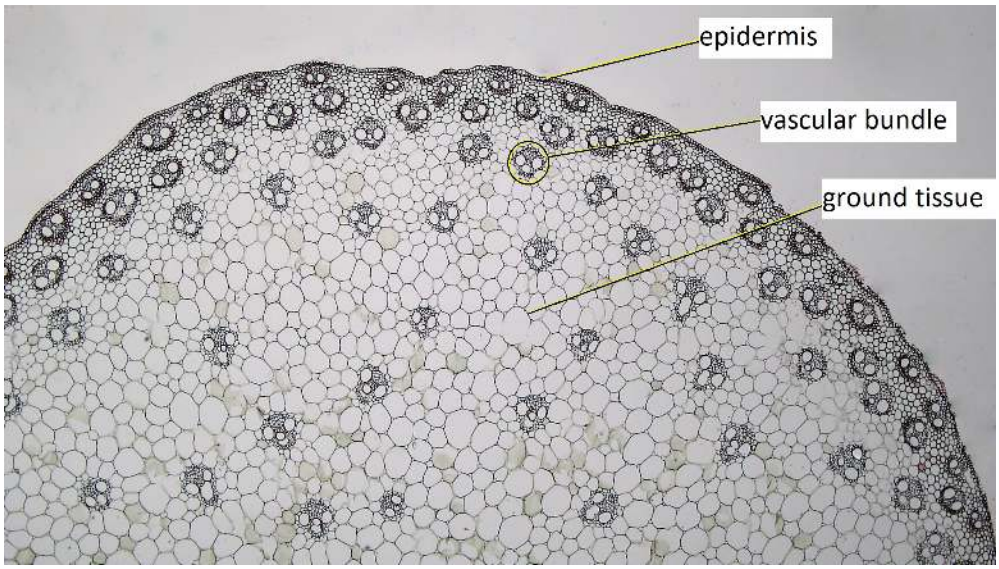



Figure **2.3.2.5**: Cross section of a corn (*Zea mays*) stem, an example of an atactostele, at 40X magnification. Vascular bundles are scattered but are at a higher density near the outside of the stem. In contrast to solenosteles and eusteles, the ground tissue is not separated into a pith and cortex. The epidermis borders the entire stem. Image labeled from Berkshire Community College Bioscience Image Library (public domain)

The cells of embryonic tissue called the **procambium** (see Meristems) divides to produce primary xylem internally and primary phloem externally. In some vascular bundles, some procambial cells remain and form the **fascicular cambium** in the center of the vascular bundle. Once the stem has finished lengthening, sclerenchyma fibers called **primary phloem fibers** are produced just outside of the primary phloem. The primary phloem fibers of each vascular bundle are sometimes called phloem caps (bundle caps). If primary phloem fibers surrounded the entire vascular bundle, they form a **bundle sheath** (Figure **2.3.2.6**).

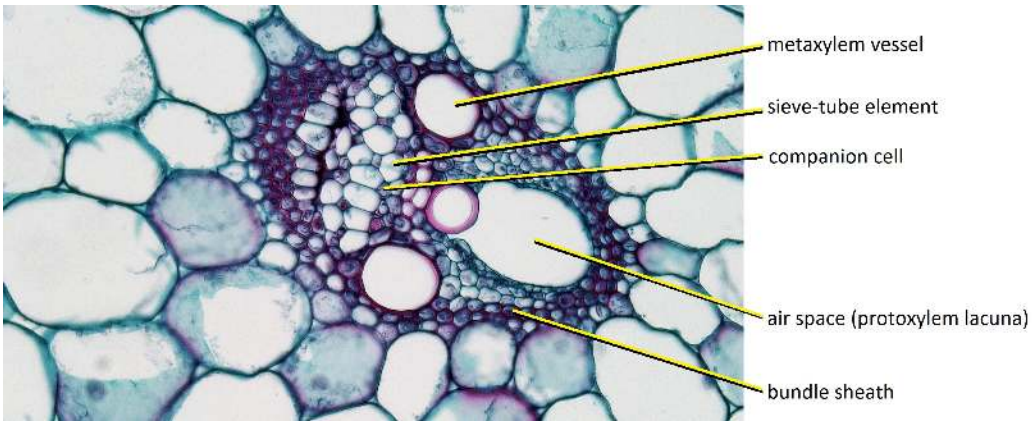



Figure **2.3.2.6**: A vascular bundle in the stem of corn (*Zea mays*) at 400X magnification. The protoxylem vessel element matured prior to the metaxylem vessel elements of the xylem. At maturity, the protoxylem vessel breaks, leaving an air space. The sieve-tube elements and companion cells form the phloem. The **bundle sheath** consists of primary phloem fibers (sclerenchyma fibers) that surround the vascular bundle. Image labeled from Berkshire Community College Bioscience Image Library (public domain)

Vascular bundles connect leaves and stems. The strands of vascular tissue that connect the leaves to the stem are called **leaf traces**. Just above leaf traces are portions of stem without vascular tissue called **leaf trace gaps**. Similarly, **branch traces** connect axillary shoots to the main stem, leaving **branch trace gaps** just above them (Figure **2.3.2.7 – 8**).

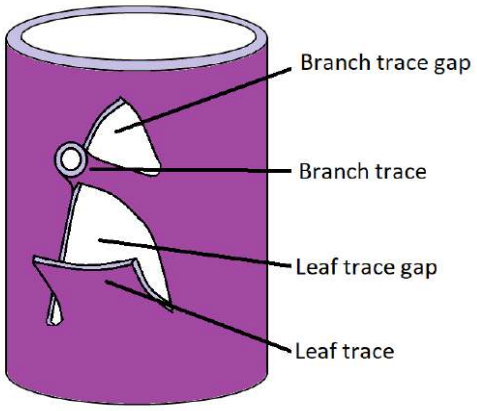



Figure **2.3.2.7**: The purple cylinder represents the vascular tissue in a stem. Vascular tissue leaves the stem to enter the leaf, forming a **leaf trace**. The space without vascular tissue just above the leaf trace is the **leaf trace gap**. The **branch trace** likewise produces a **branch trace gap**. Image by Melissa Ha (CC-BY).

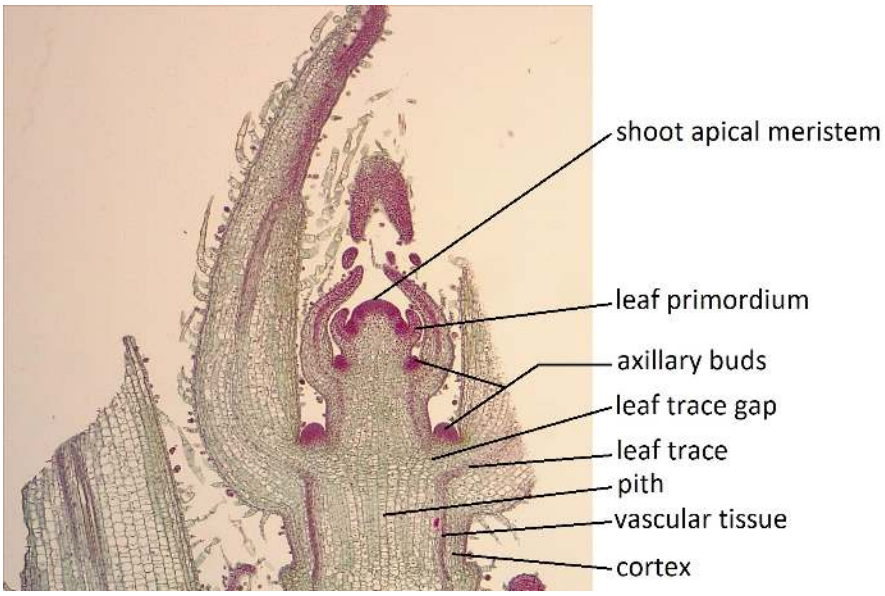



Figure **2.3.2.8**: A longitudinal section of a *Coleus* shoot tip. The **leaf trace gaps** are spaces without vascular tissue just above the **leaf traces**, which are strands of vascular tissue moving from the stem to the leaf. The three tissue system in this stem are represented by the epidermis (outer layer of dermal tissue, not labeled), pith and cortex (ground tissue), and vascular tissue between the pith and cortex. At the upper tip is the shoot apical meristem. Youong leaves (leaf primordia) emerge from either side. Axillary buds emerge just above where each leaf or leaf primordium meets the stem. Image by Melissa Ha (CC-BY).

## Attributions

Curated and authored by Melissa Ha from the following sources:

- From 5.4: The Stem from *Introduction to Botany* by Alexey Shipunov (public domain)
- From 30.2 Stems from *Biology 2e* by OpenStax (licensed CC-BY)

---

This page titled 2.3.2: Internal Anatomy of the Primary Stem is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **3.3.2: Internal Anatomy of the Primary Stem** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-SA 4.0.

# 2.3.3: Secondary Stem

## Learning Objectives

- Compare the origin and function of the vascular cambium and cork cambium.
- Define bark and distinguish between inner and outer bark.
- Explain the production of wood and relate this to annual rings.
- Distinguish between heartwood and sapwood.
- Distinguish between softwood and hardwood.
- Identify the external features of winter twigs.

**Primary growth** occurs as a stem increases in length as a result of cell division in the shoot apical meristem. **Secondary growth** is characterized by an increase in thickness or girth of the plant, and is caused by cell division secondary meristems. Herbaceous plants mostly undergo primary growth, with hardly any secondary growth or increase in thickness. Secondary growth or "wood" is noticeable in woody plants; it occurs in some eudicots, but occurs very rarely in monocots.

## Secondary Meristems (Lateral Meristems)

Two **secondary meristems** (**lateral meristems**) are responsible for secondary growth: the vascular cambium and cork cambium (Figure 2.3.3.1).

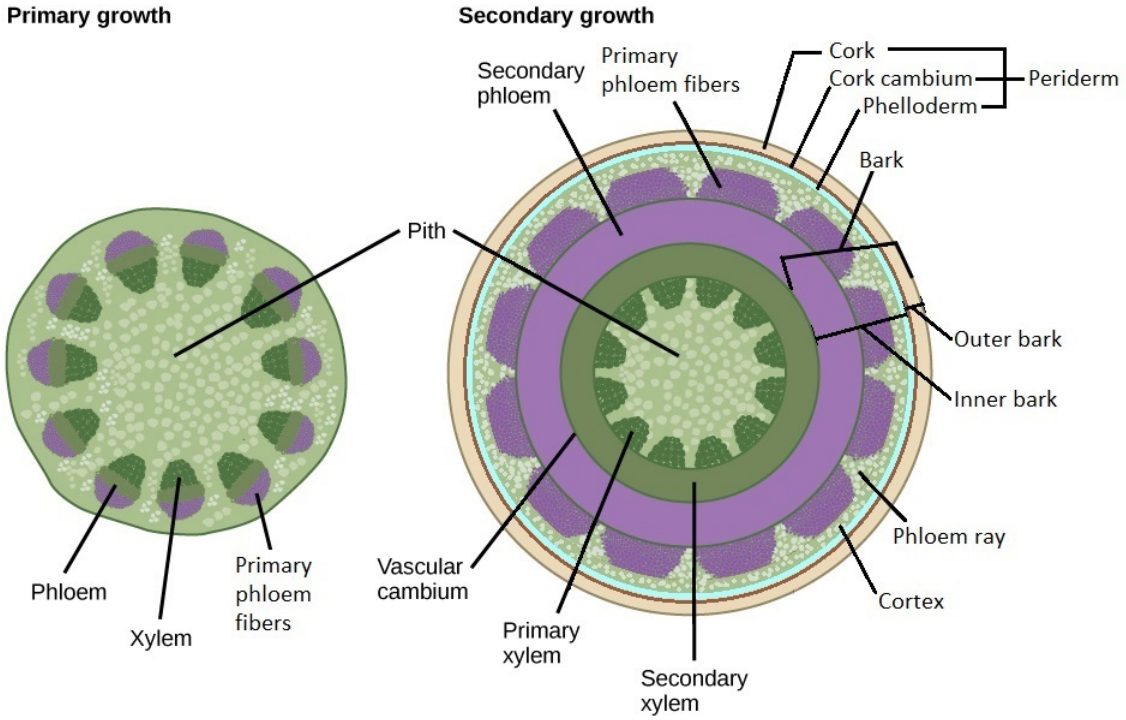



Figure 2.3.3.1: In woody plants, primary growth (left) is followed by secondary growth (right), which allows the plant stem to increase in thickness or girth. Secondary vascular tissue is added by the vascular cambium, and the cork cambium generates the periderm. In the primary stem, vascular bundles surround a central pith. Each vascular bundle has xylem on the inside, phloem on the outside, and primary phloem fibers external to the phloem. In the secondary stem, the pith, primary xylem, primary phloem fibers, and cortex remain. The vascular cambium, which is between the primary xylem and primary phloem fibers, has deposited secondary xylem internally and secondary phloem externally. The periderm is external to the cortex and consists of the phelloderm, cork cambium, and cork (from inside to outside). All tissue layers external to the vascular cambium form the bark. The cork cambium and cork form the outer bark, and the inner bark is everything between the vascular cambium and cork cambium.

The **vascular cambium** produces secondary vascular tissue. The **fusiform initials** are the cells of the vascular cambium that divide to produce secondary xylem internally and secondary phloem externally. The **ray initials** are the cells of the vascular cambium that produce **vascular rays** (xylem rays and phloem rays). These are bands of parenchyma that are perpendicular to the concentric layers of xylem and phloem (Figure 2.3.3.2). They function in storage, producing secondary compounds (molecules used by the

plant that are not essential parts of metabolism), and transporting materials between the xylem and phloem. As the secondary stem thickens, the phloem rays thicken externally (becoming wedge-shaped) to accommodate the increasing diameter. While the vascular cambium is technically only a single layer cell layer, it looks similar to the layers of cells that surround it (that it recently divided to produce), and this entire region is sometimes called the vascular cambium as a result.

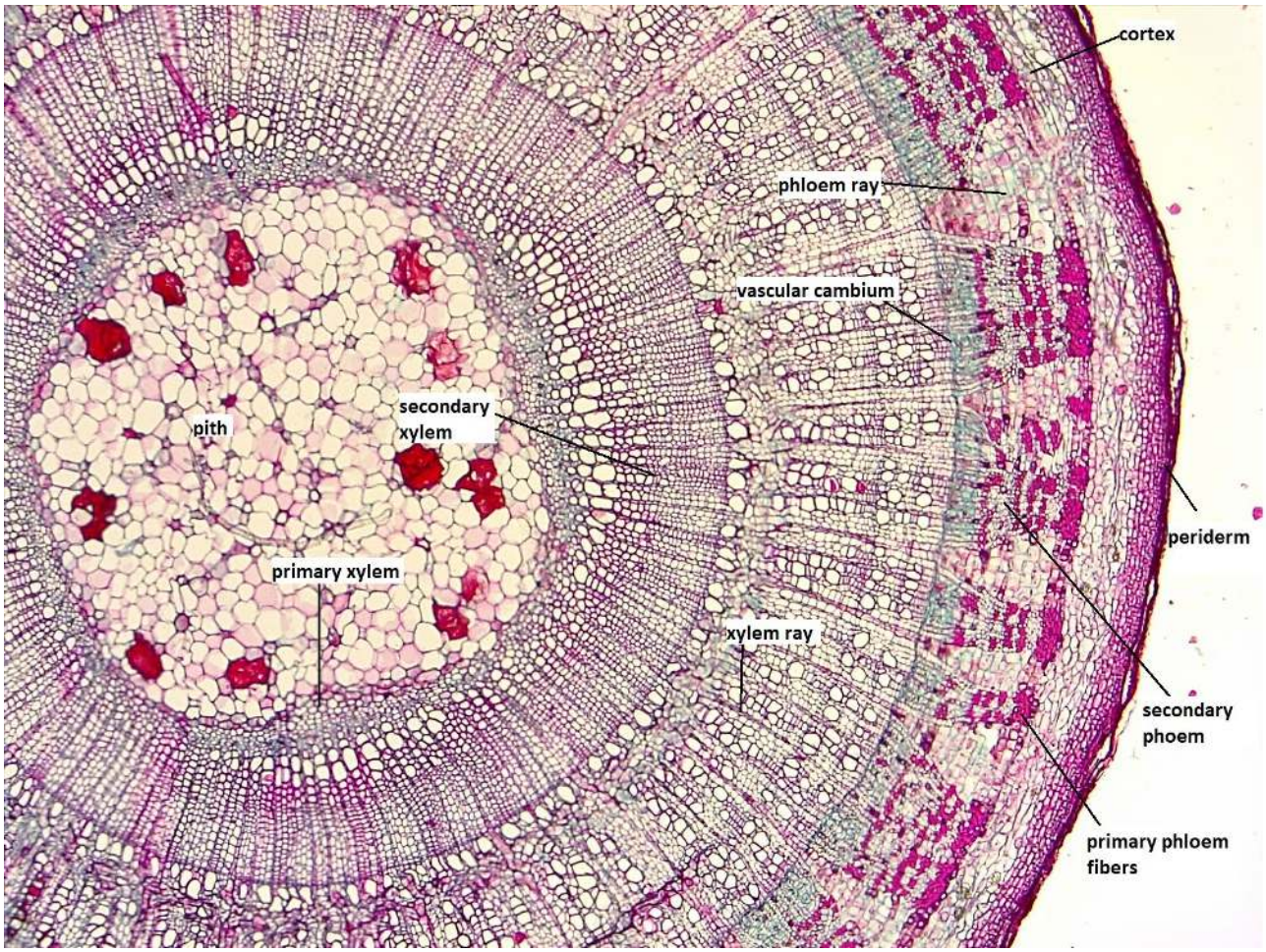



Figure **2.3.3.2**: Cross section of a basswood (*Tilia*) stem magnified at 400X. The periderm is the outermost layer and has thin, dark layers. Some appear to be peeling. Within this is the cortex. Next, is are clusters of primary phloem fibers, narrow, thick-walled sclerenchyma cells, which stained bright pink. Within this is the secondary phloem. It alternates with wedge-shaped phloem rays. The phloem rays consist of plump, thin-walled parenchyma cells. Within the secondary phloem is the thin vascular cambium, which divides to produce secondary phloem externally and secondary xylem internally. Next are several thick layers of secondary xylem, which contain wide, thick-walled vessel elements. There are five concentric layers in the secondary xylem, and each is annual ring. The inner portion of each annual ring has the widest vessel elements. This is the spring (early) wood. The outer portion of each annual ring has narrower conducting cells of the summer (late wood). Thin, xylem rays pass through the secondary xylem like spokes of a wheel. Some align with the phloem rays. Within the secondary xylem is the primary xylem. In the center is the pith, which contains plump, thin-walled, white parenchyma cells. Image by Melissa Ha (CC-BY-NC).

The vascular cambium arises from stem cells within and between the vascular bundles in some silenosteles and eusteles. Within vascular bundles, such stem cells (specifically, procambial cells) form the **fascicular cambium**. In the interfascicular regions between vascular bundles is **interfascicular cambium** (Figure **2.3.3.3**). The fascicular cambium and interfascicular cambium ultimately form the vascular cambium. In contrast, the vascular cambium in roots arises from the procambium and pericycle.

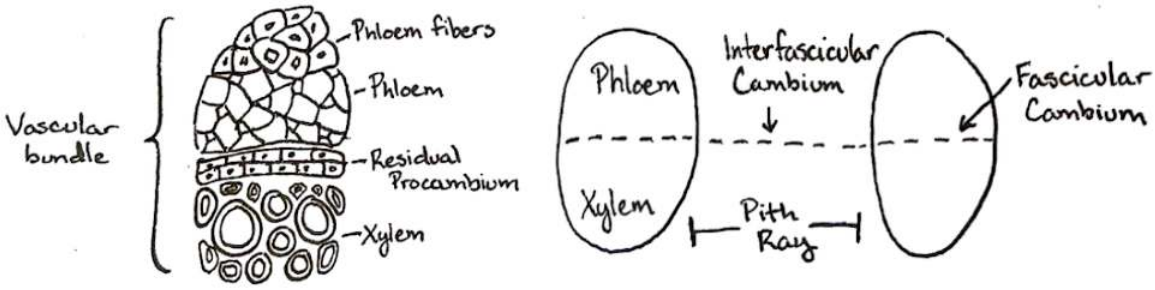



Figure **2.3.3.3**: The vascular bundle of a eustele (left) and two vascular bundles with the interfascicular region (pith ray) between them. The vascular bundle consists of narrow, thick-walled phloem fibers, phloem, residual procambium, and thick-walled xylem. The interfascicular cambium and fascicular cambium (from the residual procambium) form the vascular cambium. Image by Maria Morrow (CC-BY).

The **cork cambium** divides to produce phelloderm internally and cork externally. Together, the phelloderm, cork cambium, and cork form the **periderm**, the dermal tissue of the secondary plant body (figure **2.3.3.4**). The first cork cambium produced by a stem arises from the cortex, but subsequent cork cambia are produced by the parenchyma cells of the secondary phloem. (In contrast, the cork cambium arises from the pericycle in roots.)

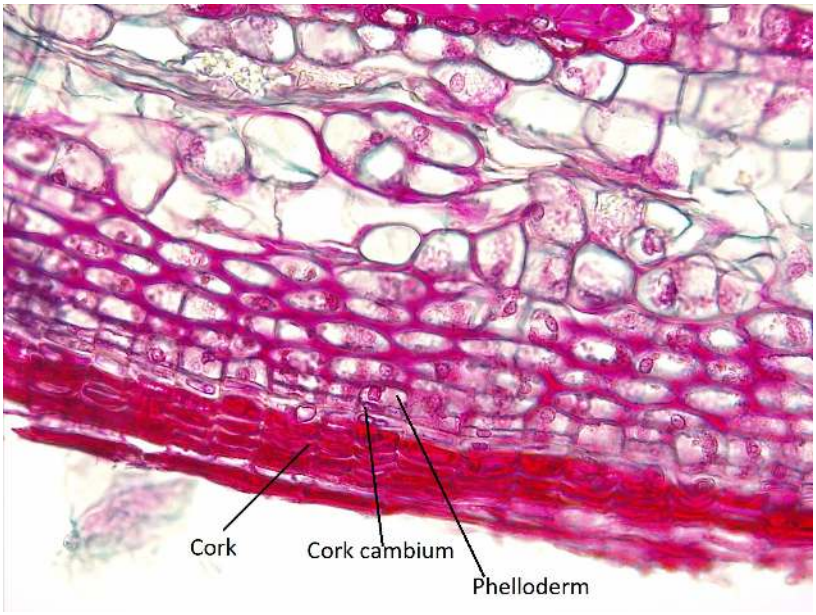



Figure **2.3.3.4**: Cross section of a basswood (*Tilia*) stem magnified at 400X. The three layers of the periderm are labeled. From outside to inside they are the cork, cork cambium, and phelloderm. Image by Melissa Ha (CC-BY-NC).

Palm trees, which are monocots, do not have secondary meristems and true wood. Some thickening does occur in a palm but this happens at the base of the tree, as a result of adventitious roots growing. Palms may also have diffuse secondary growth which is division and enlargement of some parenchyma cells. These processes do not compensate the overall growth of plant, and palms frequently are thicker on the top than on the bottom. Another monocot, dragon blood tree (*Dracaena*), has **anomalous secondary growth**, which employs cambium but this cambium does not form the stable ring.

## Periderm and Bark

At the end of the secondary stem's first year of growth, the periderm replaces the epidermis, but the cortex and pith are retained. In contrast, roots that undergo secondary growth do not have piths to begin with, and the cortex is lost during secondary growth. Like the epidermis, most of the periderm is not permeable to water vapor, carbon dioxide, and gaseous oxygen. This is due to the waxy suberin that fills the cork cells, which are dead at maturity. However, gas exchange with the environment is possible at **lenticels**, elevated regions of the periderm with many intercellular air spaces (Figure **2.3.3.5 – 6**). To produce lenticels, some cork cambium cells divide and grow much faster, which will finally break the periderm open. Woody stems do not do regular gas exchange as

primary stems do by opening and closing stomata, but woody plants still have leaves with high densities of stomata to regulate gas exchange.



Figure **2.3.3.5**: Lenticels on the bark of this cherry tree enable the woody stem to exchange gases with the surrounding atmosphere. (credit: Roger Griffith)

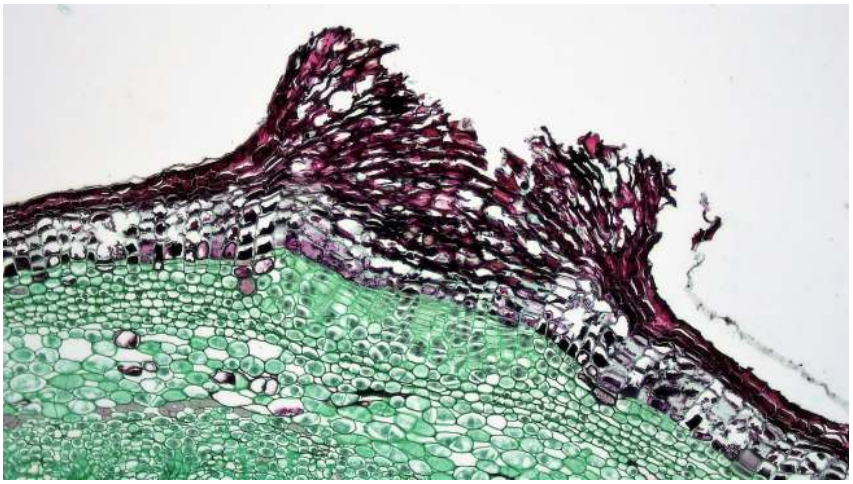


Figure **2.3.3.6**: A cross section of an elderberry (*Sambucus*) secondary stem showing a lenticel. (Magnification = 100X). Image by Berkshire Community College Bioscience Image Library (public domain).

**Bark** consists of all of the tissue layers external to the vascular cambium. It protects the plant against physical damage and helps reduce water loss. In a one-year stem from inside to outside, this would be the secondary phloem, primary phloem fibers, cortex, phelloderm, cork cambium, and cork. The cork cambium divides the inner and outer bark. The **inner bark** is everything within the cork cambium. The **outer bark** is the cork cambium and everything external to it (Figure **2.3.3.7**).

A secondary stem ultimately produces multiple layers of periderm. The inner bark in an older stem thus consists of the newest secondary phloem and the newest phelloderm. Only the **conducting phloem** of the inner bark contains live cells and transports materials while the **nonconducting phloem** of the inner bark contains dead cells that are used for storage. As the secondary stem ages, the old layers of the secondary phloem are pushed externally and crushed, with the exception of the phloem fibers, which have thickened cell walls. The outer bark in an older stem would be the newest cork cambium, newest cork, and concentric layers of old phloem and old periderm. If the multiple periderms form perfect circles, the bark is smooth. More often, multiple periderm do not overlap evenly, resulting in rough bark with scales.

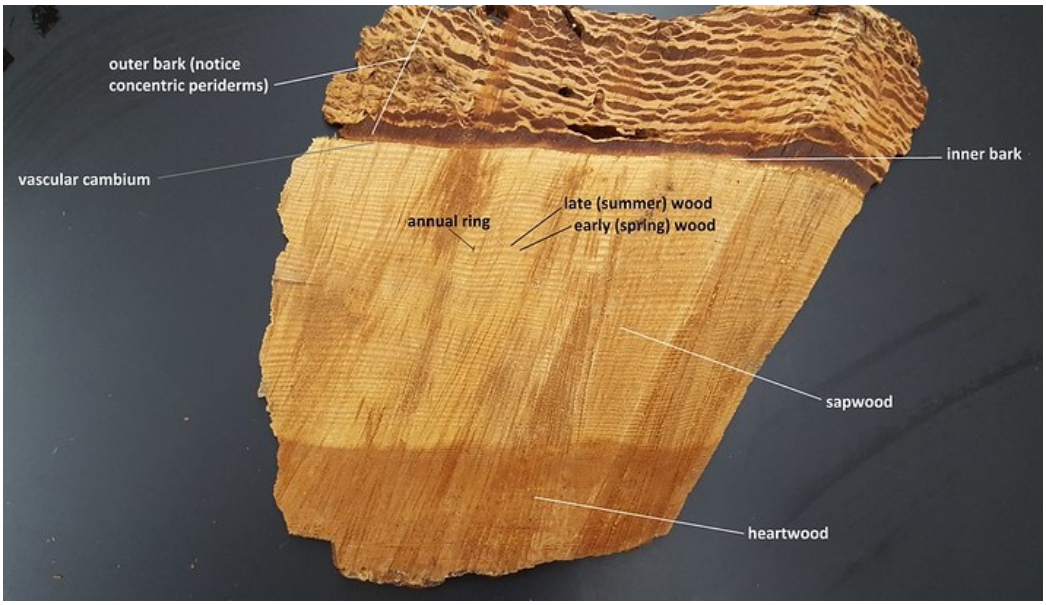



Figure **2.3.3.7**: A cross section of a Douglas fir trunk reveals outer bark and a thin layer of inner bark. The outer bark has distinct, wavy stripes, representing concentric periderms. Everything external to the vascular cambium (both the inner and outer bark) form the bark. The sapwood is the conducting (living) portion of the xylem and is lighter than the heartwood. Each annual ring contains a band of light early wood and an outer band of dark late wood. Image by Melissa Ha (CC-BY-NC).

## Wood (Secondary Xylem)

**Wood** consists of the secondary xylem produce by the vascular cambium (Figure **2.3.3.8**). In contrast to the phloem, old layers of secondary xylem are retained and are not easily crushed. However, the oldest secondary xylem (close to the center of the secondary stem) no longer conducts water. This is the **heartwood**, which stores various compounds and appears darker than the surrounding wood. To block the flow of water in the heartwood, plants use tylosesvessel element “stoppers”, which also help control winter functioning of vessels. A tylose forms when a cell wall of parenchyma grows into the tracheary element; they look like bubbles. The **sapwood** surrounds the heartwood, is lighter in color, and consists of the conducting xylem, which was more recently produced (Figure **2.3.3.7**).

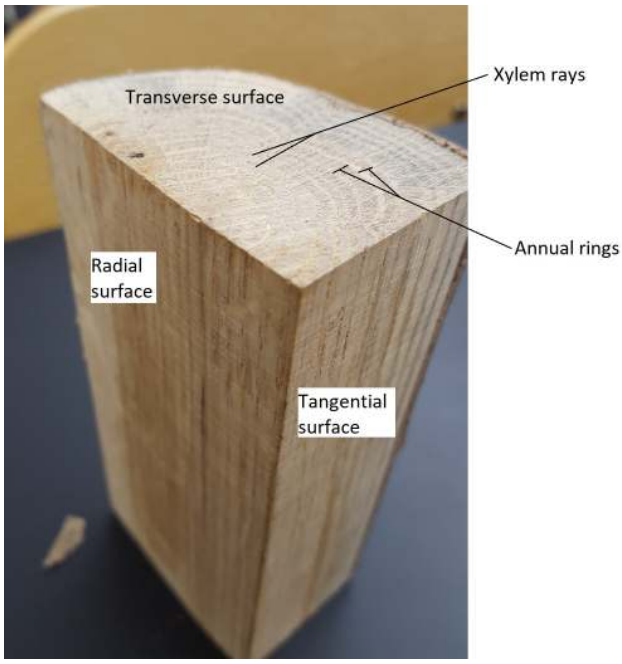



Figure **2.3.3.8**: Wood can be examined through three different sections. A cross section reveals the **transverse surface**. In this view, annual rings are concentric circles, and xylem rays intersect them like the spokes of a wheel. Cutting from the periphery to the center (like cutting a slice of pie) reveals the **radial surface**. In this view, the annual rings appear as vertical lines. Cutting along the outside of the stem (tangential to it) reveals the **tangential surface** (oblique surface). In this view, annual rings more spaced apart and unevenly so. Image by Melissa Ha (CC-BY-NC).

In the spring of temperate regions, the vascular cambium produces wide tracheary elements (the conducting cells of the xylem, either vessel elements or tracheids). These transport large volumes of water, which is abundant due to spring rains. During the summer, the vascular cambium produces narrow tracheary elements as a result of lower water availability. In the winter, the vascular cambium's activity is low. It resumes the next spring by again producing the wide tracheary elements of **early wood** (spring wood), which distinctly contrast with the adjacent **late wood** (summer wood) from the previous year. Early wood appears lighter and is less dense than late wood. Each year of wood production is thus visible in a cross section of a woody stem because it consists of a light layer and a dark layer. These are called **annual rings** (tree rings; Figure **2.3.3.9 – 10**) and can be used to determine the age of a tree or branch through the study of **dendrochronology**. Furthermore, thick annual rings indicate wet years, and thin annual rings indicate dry years.

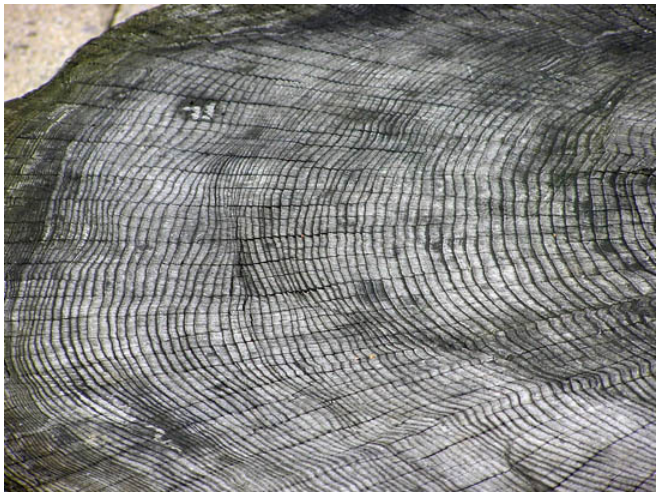


Figure **2.3.3.9**: The rate of wood growth increases in summer and decreases in winter, producing a characteristic ring for each year of growth. Seasonal changes in weather patterns can also affect the growth rate—note how the rings vary in thickness. (credit: Adrian Pingstone)

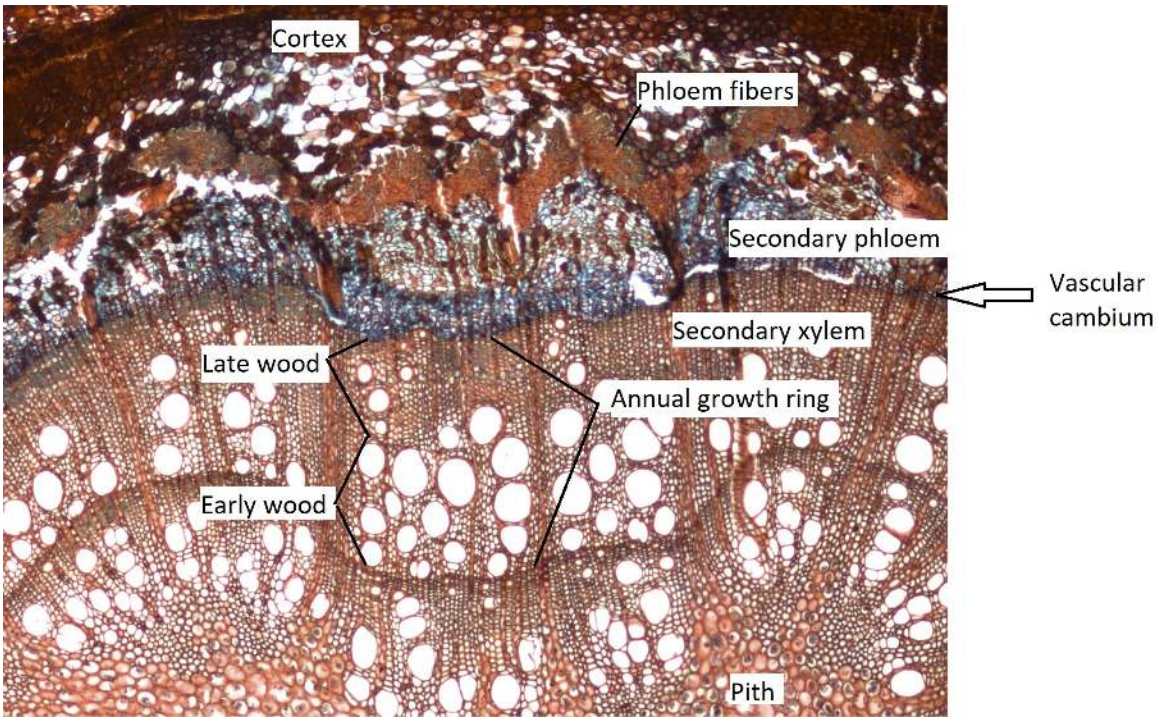



Figure **2.3.3.10**: In this cross section of a two-year-old oak stem, the inner portion of each annual ring contains early wood, which consists of wide tracheary elements. The outer part of each annual ring contains of late wood, which consists of narrow tracheary elements. The pith is inside the wood. The vascular cambium is just outside the wood. Next, is the secondary phloem, the phloem fibers (which consist of narrow, thick-walled cells), and the cortex. Image by Maria Morrow (CC-BY-NC).

Some trees (like oaks, *Quercus*) have large vessel elements are found primarily in early wood; this pattern is known as **ring porous** (Figure **2.3.3.10**). Large vessel elements of other trees (like elm, *Ulmus*) occur more evenly in both early and late wood. This pattern is known as **diffuse porous** wood: with large vessel elements in both early and late wood. (Diffuse porous species still produce annual rings due to differences in tracheid size.) Trees growing in climates without well-expressed seasons, such as the tropical rainforest, will not make annual rings at all.

**Hardwoods** are produced by angiosperms and contain both vessel elements and tracheids (figure **2.3.3.10**). **Softwoods** are produced by conifer trees (in the gymnosperm phylum Coniferophyta) and contain only tracheids (Figure **2.3.3.11**). These terms are misnomers to an extent, however, because hardwoods are not always denser than softwoods. Xylem rays tend to occupy a greater volume in hardwoods relative to softwoods. Additionally, the arrangement of cells appears more disorderly in hardwoods due to the large size of vessel elements. Finally, softwoods contain **resin ducts** (Figure **2.3.3.11**), which contain a thick substance (resin) important in defense and response to injury.

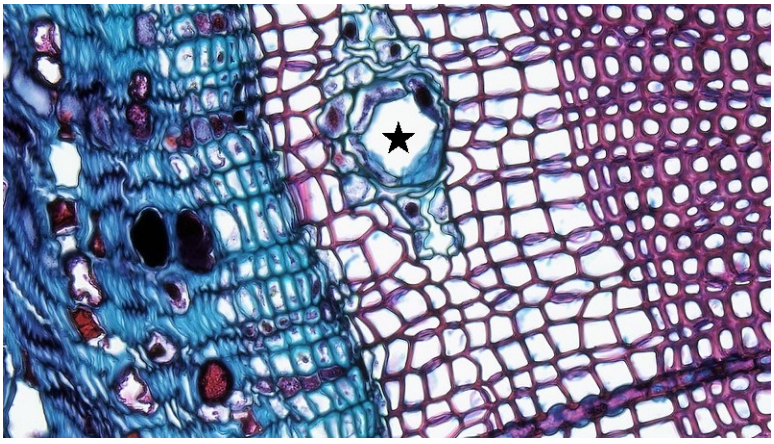


Figure **2.3.3.11**: A cross section of a five-year-old pine (*Pinus*) stem magnified at 400X. The black star marks a resin duct. It is surrounded by the parenchyma cells that produce resin. Image by Berkshire Community College Bioscience Image Library (public domain).

## Winter Twigs

Winter deciduous trees and shrubs in temperate regions become dormant in winter. The twigs of these species have the basic external features of a stem (axillary buds, nodes, etc.), but they are modified to facilitate dormancy in the winter and resumption of growth in the spring. At the end of a winter twig is the **terminal bud**, which contains a shoot apex surrounded by protective structures called **bud scales**. When the terminal bud resumes growth, the bud scales fall off and leave marks called terminal bud-scale scars. These form a ring around the twig, marking the winter of each year. **Lateral buds** are similar in structure to terminal buds, but they are found at each node. Just below the lateral buds are **leaf scars**, where the leaves were formerly attached. Within the leaf scars are **bundle scars**, marking leaf traces (consisting of vascular bundles) that moved from the stem to the leaf (Figure 2.3.3.12).

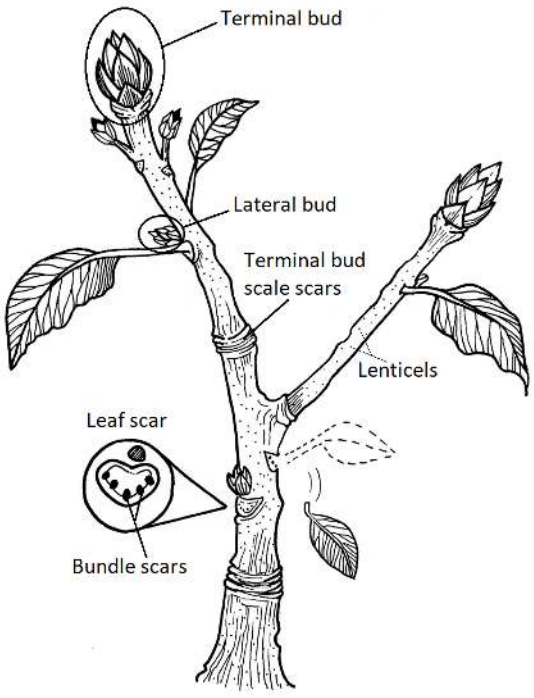



Figure 2.3.3.12: Winter twigs contain terminal buds at the ends and lateral buds at each node. Below each lateral bud is a leaf scar containing bundle scars. Lenticels are raised portions in the periderm and appear as dots in the bark from a distance. Terminal bud scale scars resemble rings of indentations around the twig and are formed after a terminal bud resumes growth. Image labeled from Nikki Harris (CC-BY-NC).

## Attributions

Curated and authored by Melissa Ha from the following sources:

- From 5.4: The Stem from *Introduction to Botany* by Alexey Shipunov (public domain)
- From 30.2 Stems from *Biology 2e* by OpenStax (licensed CC-BY)

---

This page titled 2.3.3: Secondary Stem is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **3.3.3: Secondary Stem** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC 4.0.

# 2.3.4: Stem Modifications

**Learning Objective**

Define and provide examples of the major stem and shoot modifications.

Stems (or entire shoots) of some species deviate in structure and function from a typical stem. These are called **stem modifications** (**shoot modifications**). While leaves are part of the shoot, modifications involving just the leaf are discussed separately (see Leaf Modifications).

Rhizomes and stolons are horizontal stems that function in propagation (Figure 2.3.4.1). **Rhizomes** are belowground stems that burrow into the ground just below the soil surface. They have short internodes and usually have small, scale-like leaves that are not photosynthetic. Buds from the axils of the leaves make new branches that will grow to become aboveground shoots. Ginger (*Zingiber*) and Johnson grass (*Sorghum halepense*) form rhizomes. **Stolons** (runners) are aboveground horizontal shoots, which sprout and produce a new plants. Compared to rhizomes, stolons have long internodes. Examples include strawberry (*Fragaria*), spider plants (*Chlorophytum*), and Bermuda grass (*Cynodon dactylon*).



Figure 2.3.4.1: Examples of horizontal stems. Ginger rhizomes are thick and belowground (top), and stolons of this spider plant are aboveground with long internodes (bottom). Leaves and roots emerge from the end of a stolon, forming a smaller plant. Top image by Sengai Podhuvan (CC-BY-SA), and bottom image by Eptalon (CC-BY-SA).

Tubers, corms, and bulbs are modified for starch storage. **Tubers**, such as potatoes, are thick, belowground stems found at the tips of rhizomes or stolons (figure 2.3.4.2). The “eyes” of potato are actually lateral buds, and the tuber body is comprised of many parenchyma cells that contain amyloplasts with starch. Corms and bulbs are modified shoots. A **corm** is a short, thick underground storage stem with thin scaly leaves (for example, *Gladiolus* and *Crocus*; Figure 2.3.4.3; Video 2.3.4.1). A **bulb**, such as an onion, differs from a corm in the fact that it stores its nutrients in its fleshy leaves (Figure 2.3.4.3). Lilies and tulips also form bulbs.



Figure 2.3.4.2: Potato tubers are expanded, belowground stems modified for starch storage. Image by pxhere (public domain).

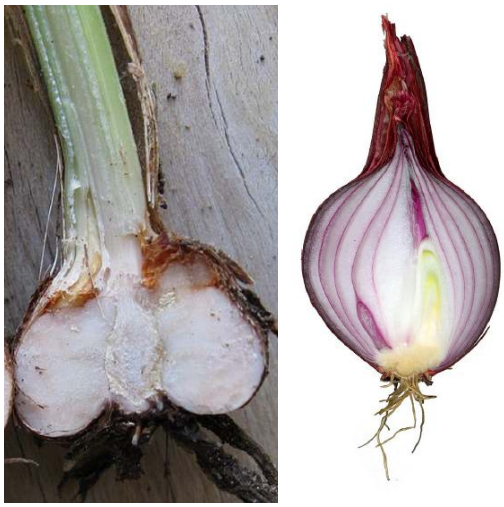


Figure **2.3.4.3**: Both corms (left) and bulbs (right) are shoots modified for starch storage. The *Crocosmia* corm has a thick, expanded stem stores starch, and the leaves that surround it are non-photosynthetic and papery. The onion bulb has a relatively small stem surrounded by thick, fleshy leaves. Left image by JonRichfield (CC-BY-SA), and right image by Amada44 (CC-BY-SA).

Some plants have sharp, generally narrow projections that function in defense against herbivores. Such structures are called **thorns** when they arise from an entire stem. Hawthorn (*Crataegus*) and *Bougainvillea* produce thorns. In contrast, **prickles** form from the surface tissues (epidermis and cortex) of the stem rather than the whole organ (figure **2.3.4.4**). Rose (*Rosa*) and blackberry (*Rubus*) produce prickles. **Spines** are similar structures derived from leaves (see Leaf Modifications).



Figure **2.3.4.4**: Thorns (left) and prickles (right). The thorns of the hawthorn are derived from the whole stem. They arise from axillary buds in the axils just above the leaves. The sharp projections on the rose stem are technically classified as prickles because they are derived from only the surface tissues of the stem. Left image by Rasbak (CC-BY-SA), and right image by Ingrid Taylar (CC-BY).

Tendrils are thin, string-like structures that allow the shoot to attach to other surfaces to access light. Tendrils can be derived from stems, leaves, or leaflets, and they are common in vines. Morning glory and sweet potato (*Ipomoea*), grapes (*Vitis*), and many members of the cucumber family (Cucurbitaceae) such as cucumbers, pumpkin, and squash have tendrils that arise from stems (Figure **2.3.4.5**).



Figure **2.3.4.5**: The thin, pale tendrils of the wild cucumber plant arise from stems and coil around surrounding structures. Image by erwin66as (public domain)

**Cladophylls** (cladodes) are stems that resemble leaves in function and appearance, arise from the axils of a shoot, and have determinate growth (stop growth after reaching a certain size). They may be cylindrical (*Asparagus;* Figure **2.3.4.6**) or flattened (butcher's broom, *Ruscus;* figure **2.3.4.7**). **Phylloclades** are flattened stems that resemble leaves that can continue growing indeterminately (Figure **2.3.4.8**). They are subtended by reduced, scale-like leaves. Examples include prickly pear cactus (*Opuntia*), Christmas cactus (*Schlumbergera*), and ribbon plant, *Homalocladium.* **Phyllodes** are similar are similar to cladophylls and phylloclades, but they are modified petioles (see Leaf Modifications).



Figure **2.3.4.6**: Cladophylls in *Asparagus* (left) and actual leaves of young asparagus marked by arrows (right). Left image by DenesFeri (CC-BY-SA), and right image by Sam Saunders (CC-BY-SA).



Figure **2.3.4.7**: Cladophylls in butchers broom (*Ruscus*) are flattened like leaves. A flower arises from a node within the cladophyll. Image by Rosser1954 (CC-BY-SA).



Figure **2.3.4.8**: Phylloclades in Christmas cactus. Image by Mokkie (CC-BY-SA).

Some shoots are modified as **insect traps** are used by some carnivorous plants, such as bladderwort (*Utricularia*; Video **2.3.4.1**).



Video **2.3.4.1**: This video shows a waterflea caught in a bladderwort insect trap. This video has no sound. Here is a description of what occurs during the video: Bladderwort and water fleas. Taken through a Leica microscope 60X objective- standard microscope lighting. The water fleas are tiny crustaceans, and they are swimming around in slow motion. At 3:50, one water flea is about to get caught. It swims into the cup-shaped leaf and escapes. A slow-motion replay of that moment shows the leaf close around the water flea temporarily before it escapes.

## Attributions

Curated and authored by Melissa Ha using 7.4: Modified Shoot from *Introduction to Botany* by Alexey Shipunov (public domain)

---

This page titled 2.3.4: Stem Modifications is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **3.3.4: Stem Modifications** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-SA 4.0.

# 2.3.5: Chapter Summary

The stem of a plant bears leaves, flowers, and fruits. Stems are characterized by the presence of **nodes** (the points of attachment for leaves or branches) and **internodes** (regions between nodes).

All three tissue systems can be found in stems. In the primary stem, dermal tissue is represented by the epidermis, the outer covering of the plant. The cortex and pith (if present) represent ground tissue, and vascular tissue is found in the vascular cylinder or vascular bundles. Vascular tissue may be arranged in a continuous ring (**silenostele**), in vascular bundles forming a ring (**eustele**), or in scattered vascular bundles (**ataktostele**).

Primary growth occurs at the tips of roots and shoots, causing an increase in length. Woody plants may also exhibit **secondary growth**, or increase in thickness. **Secondary meristems** (lateral meristems) are responsible for secondary growth. The **vascular cambium** produces secondary phloem externally and secondary xylem internally, and the **cork cambium** produces cork externally and phelloderm internally. The cork, cork cambium, and phelloderm form the **periderm**, the secondary dermal tissue. **Bark** consists of all the tissue layers external to the vascular cambium, and **wood** consists of secondary xylem. **Annual rings** in wood reflect differences in growth due to changing water availability throughout the year.

Some plant species have **modified stems** or **modified shoots** that help to propagate new plants, store food, or deter herbivores. Examples of such modifications are rhizomes, stolons, tubers, corms, bulbs, tendrils, and thorns.

**After completing this chapter, you should be able to...**

- Identify the main external structures of the shoot system, including the nodes, internodes, leaves, axillary buds, and axillary shoots.
- Identify the structures representing each of the three tissue systems in stems.
- Compare the structure of silenosteles, eusteles, and ataktosteles.
- Explain the arrangement of leaf traces, leaf trace gaps, branch traces, and branch trace gaps.
- Compare the origin and function of the vascular cambium and cork cambium.
- Define bark and distinguish between inner and outer bark.
- Explain the production of wood and relate this to annual rings.
- Distinguish between heartwood and sapwood.
- Distinguish between softwood and hardwood.
- Identify the external features of winter twigs.
- Define and provide examples of the major stem and shoot modifications.

## Attribution

Curated and authored by Melissa Ha using 30.2 Stems from *Biology 2e* by OpenStax (licensed CC-BY)

This page titled 2.3.5: Chapter Summary is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **3.3.5: Chapter Summary** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC 4.0.
- **3.3.3: Secondary Stem** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC 4.0.

# SECTION OVERVIEW

## 2.4: Leaves

Leaves are specialized organs of the shoot for performing photosynthesis. A leaf is often a relatively large, flat surface used to optimize sunlight capture. Most leaves have **determinate growth**, meaning that growth stops once the leaf reaches a certain size. This is in contrast to the overall plant body, which grows **indeterminately**. Leaves arise from the shoot apical meristem through **leaf primordia**.

Usually, true leaves are easily distinguishable, but in some species, modified stems (cladophylls and phyloclades) or leaflets (parts of leaves) superficially appear like whole leaves. True leaves subtend an axillary bud in the axil and are lateral (rather than at the tip, or apex of the shoot; Figure **2.4.1**). New shoots and leaves do not arise from true leaves.

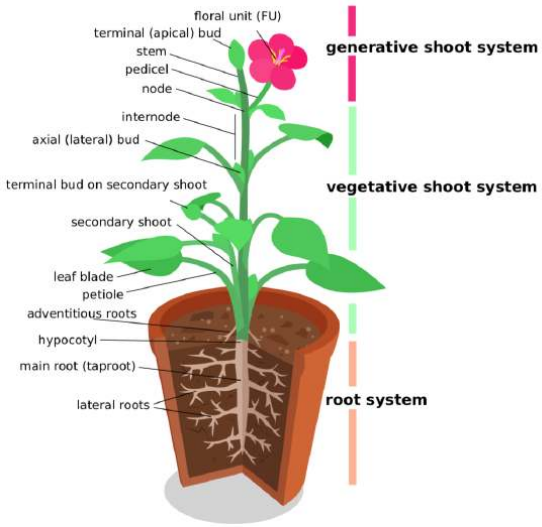



Figure **2.4.1**: Leaves are lateral structures of the shoot system. The plant here is divided into a generative shoot system, vegetative shoot system, and root system. The generative shoot system consists of the floral unit, which is supported by the pedicel. The vegetative shoot system consists of stems and leaves. Leaves attach at nodes on the main stem. Stem segments between nodes are internodes. Leaves consist of a flattened blade and stalklike petiole, and they subtend axillary buds (labeled axial bud here). Some axillary buds have developed into secondary shoots. Terminal (apical) buds are found at the end of stems. In the root system, lateral roots arise from the main root (taproot). Adventitious roots arise from the stem. At the base of the main stem, just before it transitions to the main root is the hypocotyl.

Most leaves are usually green, due to the presence of chlorophyll in the chloroplasts of their cells. However, some leaves may have different colors, caused by other plant pigments that mask the green chlorophyll. The thickness, shape, and size of leaves are adapted to the environment. Each variation helps a plant species maximize its chances of survival in a particular habitat.

### Attributions

Curated and authored by Melissa Ha using the following sources:

- 30.4 Leaves from *Biology 2e* by OpenStax (licensed CC-BY). Access for free at openstax.org.
- 5.3 The Leaf from *Introduction to Botany* by Alexey Shipunov (public domain).
- 9.2 Introduction to Leaf Anatomy from *Botany Lab Manual* by Maria Morrow (licensed CC-BY)

**Leaves**

2.4.1: External Structure of Leaves

2.4.2: Internal Leaf Structure

2.4.3: Leaf Modifications

2.4.4: Chapter Summary

---

This page titled 2.4: Leaves is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

# 2.4.1: External Structure of Leaves

## Learning Objectives

- Identify the main parts of a leaf.
- Compare petiolate and sessile leaves.
- Distinguish among alternate, opposite, and whorled phyllotaxes.
- Compare simple, pinnately compound, and palmately compound leaves.
- Compare parallel, pinnate, and palmate venation in leaves.
- Recognize common leaf margins and shapes.

Each leaf typically has a flat, wide portion called the **blade** (lamina), which is also the widest part of the leaf (Figure **2.4.1.1**). Some leaves are attached to the plant stem by a stalklike petiole and are called **petiolate leaves** (Figure **2.4.1.2**). Although petioles are narrow and often resemble stems, they are considered part of the leaf. A petiolate leaf thus consists of the blade and the petiole. Petioles usually attach at to the **margin** (edge) of the blade along the base, but in **peltate** leaves, the petiole is attached underneath the blade (Figure **2.4.1.3**). Leaves that do not have a petiole and are directly attached to the plant stem are called **sessile** (apetiolate) leaves (Figure **2.4.1.4**). In a special type of sessile leaves called **perfoliate** leaves, the stem passes through the center of the blade (Figure **2.4.1.4**). Many leaves have a **midrib**, which travels the length along the center of the leaf. The midrib contains the **main vein** (primary vein) of the leaf as well as supportive ground tissue (collenchyma or sclerenchyma).

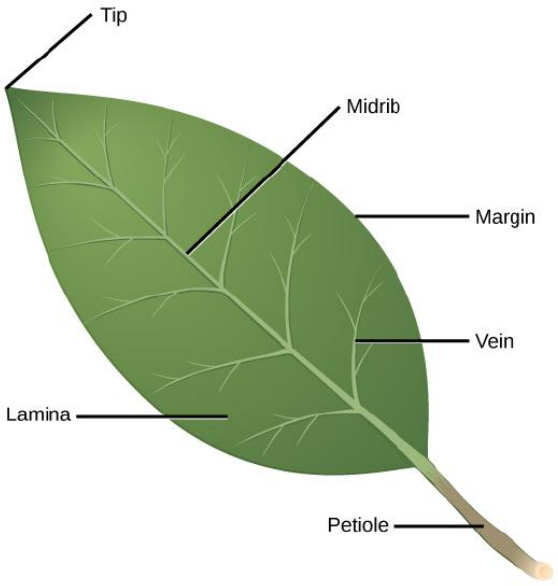



Figure **2.4.1.1**: A typical eudicot leaf. Many leaves consist of a stalk-like petiole and a wide, flat blade (lamina). The midrib extends from the petiole to the leaf tip and contains the main vein. Additional veins branch from the midvein. The margin is the edge of the leaf.



Figure 2.4.1.2: The petiolate leaves of the geranium consist of a petiole and blade (lamina). The wide lamina is attached to the stalk-like petiole. In the sessile leaves of *Aster amellus*, the blade is attached directly to the stem. Left image by Melissa Ha (CC-BY), and right image by Enrico Blasutto (CC-BY-SA).



Figure 2.4.1.3: In the peltate leaves of nasturtium, petioles attach underneath the leaf blade, similar to an umbrella. Image by Melissa Ha (CC-BY).



Figure 2.4.1.4: The stem runs through the center of the blade in the perfoliate leaves of miner's lettuce. Image by Wikimediaimages/Pixabay (Pixabay license).

Small, green appendages usually found at the base of the petiole are known as **stipules** (Figure 2.4.1.5). Other structures located near leaf base **sheath** (typical for grasses, lilies, and related species) and **ocrea** (typical for buckwheat family, Polygonaceae).

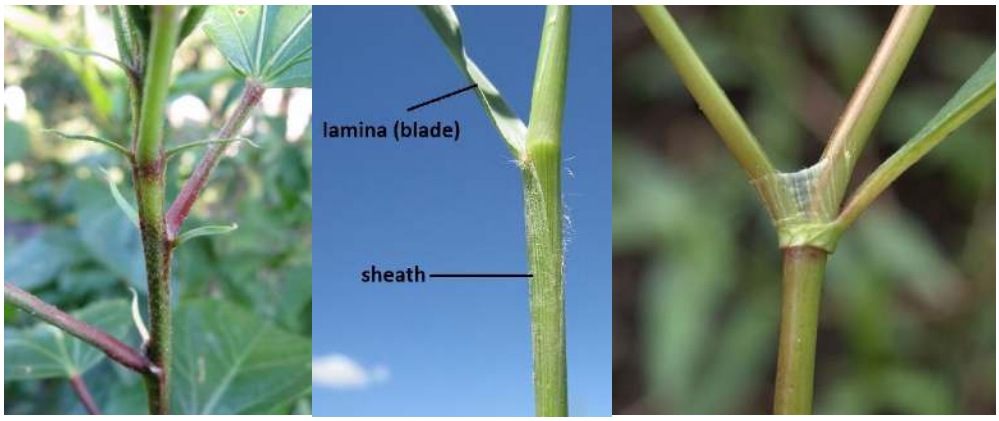



Figure 2.4.1.5: Left: In *Hibiscus*, two small, narrow, green stipules emerge at the base of each petiole. Middle: This grass blade (lamina) is attached to a sheath, which wraps around the stem. Right: The ocrea of *Persicaria maculosa* from the buckwheat family is constructed of fused stipules. Left image by Nadiatalent (CC-BY-SA), middle image by Harry Rose (CC-BY), and right image by Martin Olsson (CC-BY-SA).

## Phyllotaxy

The arrangement of leaves on a stem is known as **phyllotaxy**. The number and placement of a plant's leaves will vary depending on the species, with each species exhibiting a characteristic leaf arrangement. Leaves arrangements are classified as either alternate, opposite, or whorled (Figure 2.4.1.6). Plants that have only one leaf per node have leaves that are said to be **alternate**, and alternate leaves often spiral up the stem. In an **opposite** leaf arrangement, two leaves arise at the node (with the leaves usually connecting opposite each other along the branch). Pairs of opposite leaves may face all in the same direction, or each pair can rotate at 90° (**decussate**). If there are three or more leaves connected at a node, the leaf arrangement is classified as **whorled,** and each whorl can also rotate. Each type of spiral phyllotaxis has its own angle of divergence.

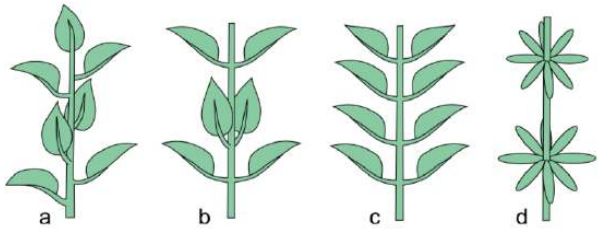



Figure 2.4.1.6: Types of phyllotaxis (leaf arrangement): (a) alternate— with only one leaf attaching to each node, (b) and (c) opposite— with two leaves attaching at each node, and (d) whorled— with more than two leaves attached at each node. While both (b) and (c) illustrate opposite arrangements, leaf pairs are perpendicular to each other in (b) and aligned in (c).

## Simple and Compound Leaves

Leaves may be simple or compound (Figure 2.4.1.7). In a **simple** leaf, the blade is either completely undivided (Figures 2.4.1.8,)— or it has lobes, but the separation does not reach the midrib, as in the maple leaf. In a **compound** leaf, the leaf blade is completely divided, forming **leaflets**, as in the locust tree. Each leaflet may have its own stalk but is attached to the rachis. A **palmately compound** leaf resembles the palm of a hand, with leaflets radiating outwards from one point (Figure 2.4.1.8). Examples include the leaves of poison ivy, the buckeye tree, or the familiar houseplant *Schefflera* sp. (common name "umbrella plant"). **Pinnately compound** leaves take their name from their feather-like appearance; the leaflets are arranged along the midrib, as in rose leaves (*Rosa* sp.), or the leaves of hickory, pecan, ash, or walnut trees (Figure 2.4.1.8). **Trifoliate** leaves, such as in clover or strawberry, have only three leaflets (Figure 2.4.1.9)

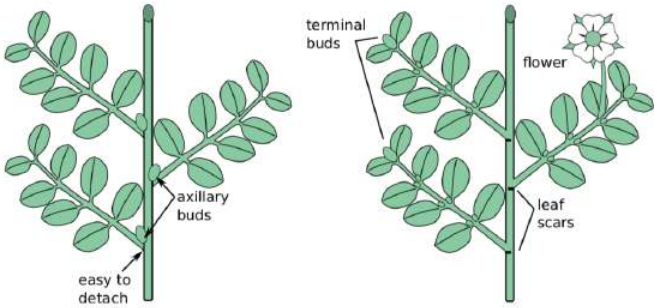



Figure **2.4.1.7**: Compound leaves (left) and simple leaves (right). While these plants appear similar, each true leaf has an axillary bud above. On the left, the axillary bud is above each compound leaf (but not each leaflet). On the right, each leaf has a bud above it, identifying them as leaves rather than leaflets. Leaflets are always on the same plane with in a leaf (such that the leaf is flat), but this is not the case for multiple simple leaves on the same branch.



(a) Simple




(b) Palmately compound



(c) Pinnately compound



(d) Doubly compound

Figure **2.4.1.8**: Leaves may be simple or compound. In simple leaves, the blade is continuous. The (a) banana plant (*Musa* sp.) has simple leaves. In compound leaves, the blade is separated into leaflets. Compound leaves may be palmate or pinnate. In (b) palmately compound leaves, such as those of the horse chestnut (*Aesculus hippocastanum*), the leaflets branch from the petiole. In (c) pinnately compound leaves, the leaflets branch from the midrib (rachis), as on a scrub hickory (*Carya floridana*). The (d) honey locust has double compound leaves, in which leaflets branch from the veins. (credit a: modification of work by "BazzaDaRambler"/Flickr; credit b: modification of work by Roberto Verzo; credit c: modification of work by Eric Dion; credit d: modification of work by Valerie Lykes)



Figure 2.4.1.9: The trifoliate leaves of strawberry each consist of three leaflets. Each leaflet has a dentate margin, consisting of symmetrical teeth. Image by Melissa Ha (CC-BY).

Simple leaves have just one level of hierarchy whereas compound leaves have two or more levels of hierarchy (Figure 2.4.1.10). Pinnately compound leaves with two levels of hierarchy are **unipinnate**. Those with three levels of hierarchy are called **bipinnate** (twice pinnate; doubly compound), and those with four levels of hierarchy are **tripinnate**. For compound leaves, a botanist could describe characteristics of the leaf overall as well as the shape, margin, and venation (see below) of the leaflets.

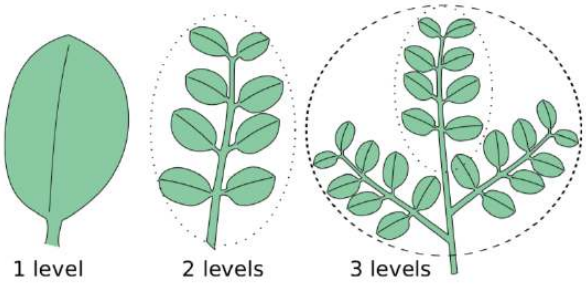



Figure 2.4.1.10: Leaves with one (simple), two (unipinnate), and three (bipinnate) levels of hierarchy. The blade of the simple leaf is continuous. In the unipinnate leaf, the blade is divided into leaflets, which attach on either side of the midrib (rachis). In the bipinnate leaf, each leaflet is further subdivided. The dotted lines indicate the shape of each level, which is not necessarily the same for each level.

## Venation

Leaf veins are vascular bundles coming to the leaf from stem. The arrangement of veins in a leaf is called the venation pattern. Frequently, there is one or more **main vein** (primary vein) and **secondary veins** that branch from it. **Tertiary veins** branch from secondary veins (Figure 2.4.1.11).

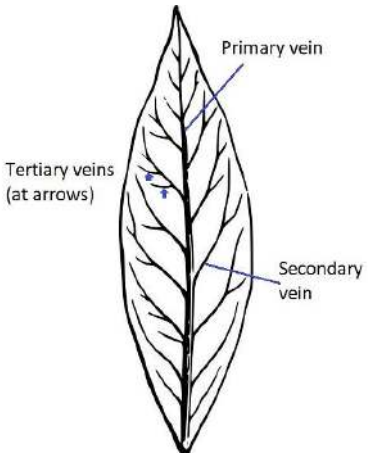



Figure 2.4.1.11: The main (primary) vein of this leaf is the largest, central vein. Secondary veins emerge from the primary vein. Tertiary veins (at arrows) emerge from the secondary veins. Image modified from freesvg (public domain).

There are three main arrangements of the most prominent (major) of the leaf. They may all run longitudinally (**parallel venation**, Figure 2.4.1.12), they may branch from a single midvein (**pinnate venation**, Figure 2.4.1.8*a*,), or they may arise from a single point at the base of the leaf (**palmate venation**; Figure 2.4.1.13). Parallel venation is found in monocots, and pinnate and palmate venation is common in eudicots. The maidenhair tree, ginkgo (*Ginkgo biloba*), has a unique venation pattern in which each vein divides into two similar parts. This is known as **dichotomous venation** (Figure 2.4.1.12).

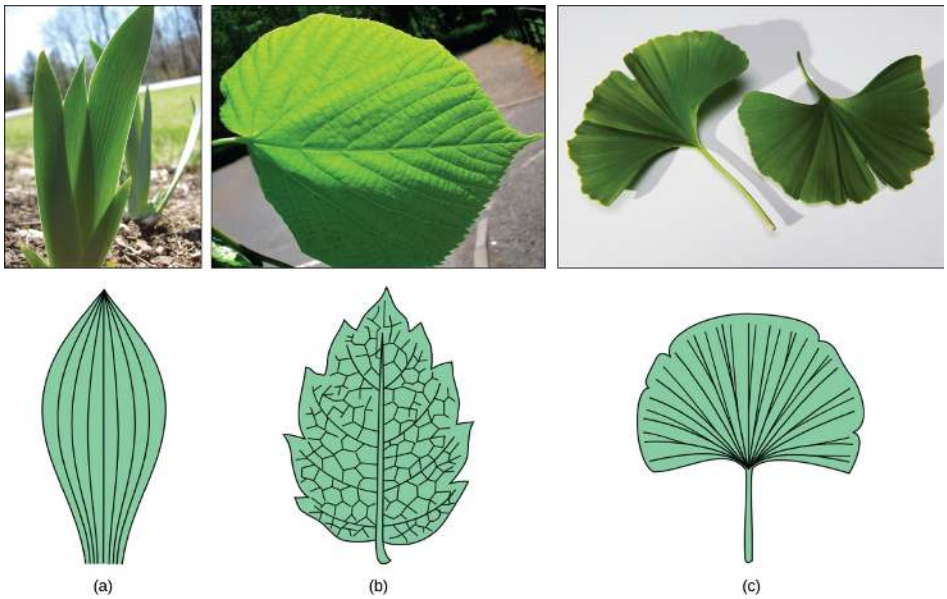



Figure 2.4.1.12: (a) Tulip (*Tulipa*), a monocot, has leaves with parallel venation, with veins running up the leaves in the same direction. They do not intersect. (b) Linden (*Tilia cordata*) is a eudicot with pinnate and reticulate venation. Veins radiate out from the midrib, and smaller veins radiate out from these.The (c) *Ginkgo biloba* tree has dichotomous venation with veins radiating out from the petiole. Each of these veins branches into two veins. (credit a photo: modification of work by “Drewboy64”/Wikimedia Commons; credit b photo: modification of work by Roger Griffith; credit c photo: modification of work by "geishaboy500"/Flickr; credit abc illustrations: modification of work by Agnieszka Kwiecień)



Figure 2.4.1.13: In leaves with palmate venation, multiple main veins branch from a central point, which is near the base of the leaf, similarly to how the fingers radiate from the palm of a hand. Left image cropped from Maksim (CC-BY-SA), and right image by Maksim (CC-BY-SA).

The less prominent (minor) veins of a leaf may form a branching, netlike pattern, which is called **reticulate venation** (Figure 2.4.1.14). In contrast, the minor veins are arranged neatly, forming a ladderlike structure in **percurrent venation**.

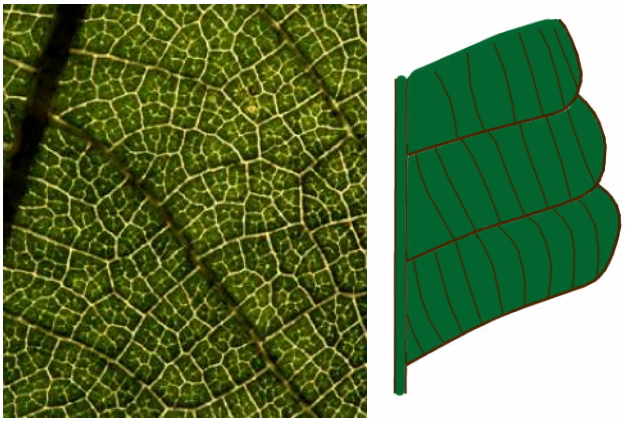


Figure 2.4.1.14: Minor veins may demonstrate reticulate venation (left) or percurrent (right). Left image cropped from Katifori E, Magnasco MO (2012) Quantifying Loopy Network Architectures. PLoS ONE 7(6): e37994 (CC-BY), and right image by RoRo (public domain).

## Margins

The margin describes the outline of a simple leaf or leaflet (Figure 2.4.1.15). Leaves with smooth margins are called **entire**. Those with irregularly wavy margins are **undulate**. **Lobate** (lobed) leaves may be **palmately lobate** (with lobes outlining the palmate venation pattern of veins arising from a single point at the base of the leaf) or **pinnately lobate** (with lobes outlining the pinnate venation pattern of secondary veins branching from a midvein; Figure 2.4.1.16). Toothed leaves have small projections (teeth) and indentations that do not align with the venation. For **serrate** leaves, the sharp teeth point forward, like a serrated knife. For **dentate** leaves, sharp teeth are symmetrical, like equilateral triangles. For **crennate** leaves, the teeth are rounded rather than sharp.

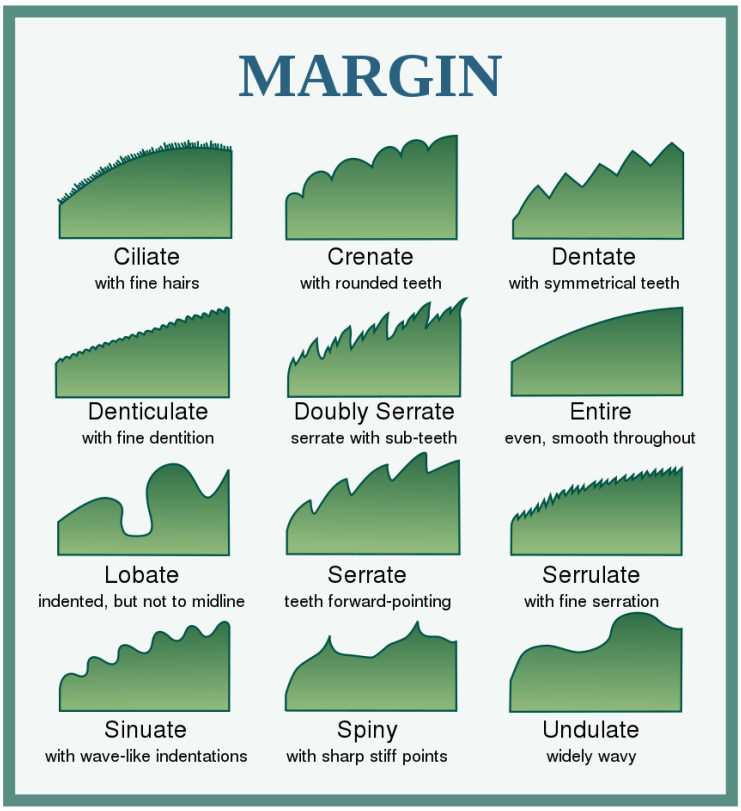



Figure **2.4.1.15**: Examples of leaf margins. Ciliate margins have fine hairs. Crenate margins have rounded teeth, dentate margins have symmetrical teeth, and denticulate margins have fine dentition (small teeth). Serrate margins have forward-facing teeth, like a serrated knife. Doubly serrate margins are serrate with sub-teeth. Entire margins are smooth. Lobate margins are indented, but not to the midline. Serrulate margins have fine serration. Sinuate margins have wave-like indentations. Spiny margins have sharp, stiff points, and undulate leaf margins are widely, irregularly wavy. Image cropped from McSush/Debivort (CC-BY-SA).



Figure **2.4.1.16**: Lobed leaves have indentations that match the venation pattern. Oak leaves (left) are pinnately lobate. The leaves on the right are palmately lobate. Images by Melissa Ha (CC-BY).

## Shape

There are several general leaf shapes (Figure **2.4.1.17**). The widest part of **ovate** leaves is near the based whereas the widest portion of **obovate** leaves is near the apex (tip). If the widest portion of the leaves is equidistant form the apex and base, the leaf may be elliptic or oblong. In **elliptic** leaves, a single wide middle portion tapers as it approaches the apex or base. **Oblong** leaves are similarly, but there is a longer section in the middle of these leaves that is uniformly wide. **Linear** leaves are long and thin. **Lanceolate** leaves are lance-shaped and somewhat intermediate between ovate and linear.

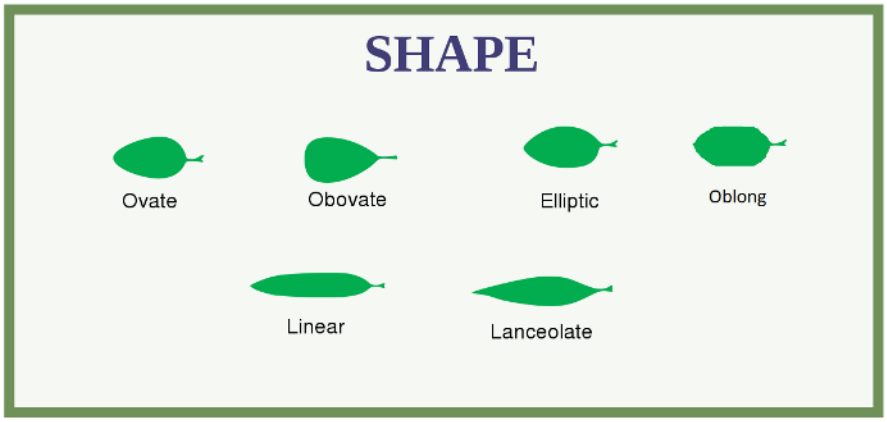



Figure **2.4.1.17**: Six main leaf shapes. Ovate leaves are egg-shaped, but the base is the widest portion. Obovate are egg-shaped, but the base is the narrowest portion. Elliptic leaves have a wide center and taper at the base and tip. Oblong leaves are elongated. Linear leaves are long, and lanceolate leaves are lance-shaped. Image modified from McSush/Debivort (CC-BY-SA).

The leaf shape can be described in further detail using specific terminology that applies to the leaf apex (Figure **2.4.1.18**) and leaf base (Figure **2.4.1.19**). The leaf apex could be **rounded**, **acute** (forming an angle less than 90º), **obtuse** (forming an angle greater than 90º), **attenuate** (tapering to a point), or **acuminate** (dramatically curving inward to a narrow point). The base of the leaf blade could be **rounded**, **acute**, **obtuse**, **truncate** (straight), **cuneate** (wedge-shaped or triangular), or **cordate** (indented in the center, like an upside-down heart).

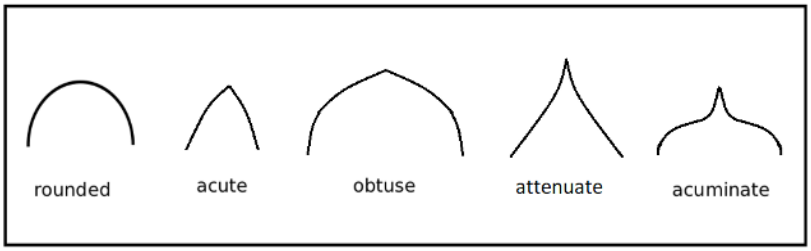



Figure **2.4.1.18**: Five leaf apex shapes. The leaf apex could be rounded, acute (forming an angle less than 90º), obtuse (forming an angle greater than 90º), attenuate (tapering to a point), or acuminate (dramatically curving inward to a narrow point). Image modified by Melissa Ha (CC-BY) from Shipunov (public domain).

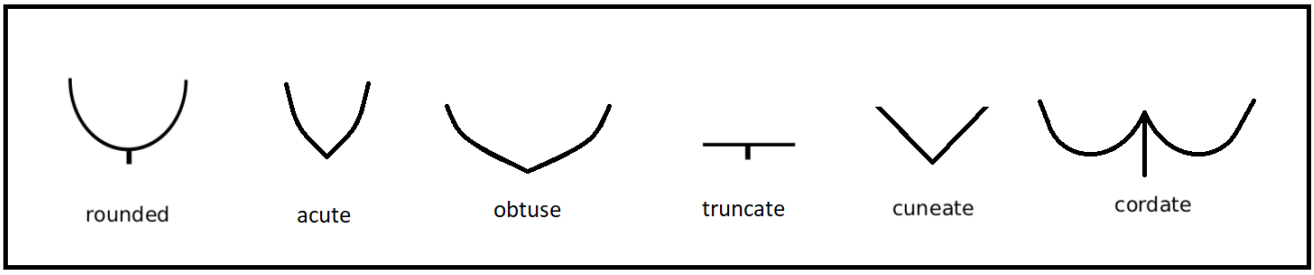



Figure **2.4.1.19**: Six leaf base shapes. The base of the leaf blade could be rounded, acute (forming an angle less than 90º), obtuse (forming an angle greater than 90º), truncate (straight), cuneate (wedge-shaped or triangular), or cordate (indented in the center, like an upside-down heart). Image modified by Melissa Ha (CC-BY) from Shipunov (public domain).

## Hetrophylly

**Heterophylly** refers to a plant having more than one kind of leaf. A plant can have both juvenile leaves and adult leaves, water leaves and air leaves, or sun leaves and shade leaves. In California live oak, leaves growing closely to the ground have sharp teeth, presumably to deter herbivores such as deer. Leaves at the top of the plant are too high for herbivores to reach and have entire margins. California sycamore has both palmately lobed leaves and small, perfoliate leaves (Figure **2.4.1.20**).



Figure 2.4.1.20: The California sycamore exhibits heterophylly because it has two different leaf types. The stem pierces a small, circular perfoliate leaf in the center of the image. The other larger leaves are palmately lobate. Image by Melissa Ha (CC-BY).

## Attributions

Curated and authored by Melissa Ha using the following sources:

- 30.4 Leaves from *Biology 2e* by OpenStax (licensed CC-BY). Access for free at openstax.org.
- 5.3 The Leaf from *Introduction to Botany* by Alexey Shipunov (public domain).
- 9.2 Introduction to Leaf Anatomy from *Botany Lab Manual* by Maria Morrow (licensed CC-BY)

---

This page titled 2.4.1: External Structure of Leaves is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **3.4.1: External Structure of Leaves** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-SA 4.0.
- **3.4: Leaves** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC 4.0.

# 2.4.2: Internal Leaf Structure

## Learning Objectives

- Describe the microscope internal structure of leaves, including the epidermis, mesophyll, and vascular bundles.
- Compare the adaptations of mesophytic, hydrophytic, and xerophytic leaves.
- Identify the unique features of pine and corn leaves.
- Compare the structures of sun and shade leaves.

## Tissue Organization in Leaves

All three tissue types are represented in leaves. The epidermis represents the dermal tissue, the mesophyll that fills the leaf is ground tissue, and the vascular bundles that form the leaf veins represent vascular tissue (Figure **2.4.2.1**). These three tissues will be discussed using a eudicot leaf that is adapted to a moderate amount of water (mesophytic leaf). Variations in leaf structure are discussed later on this page.

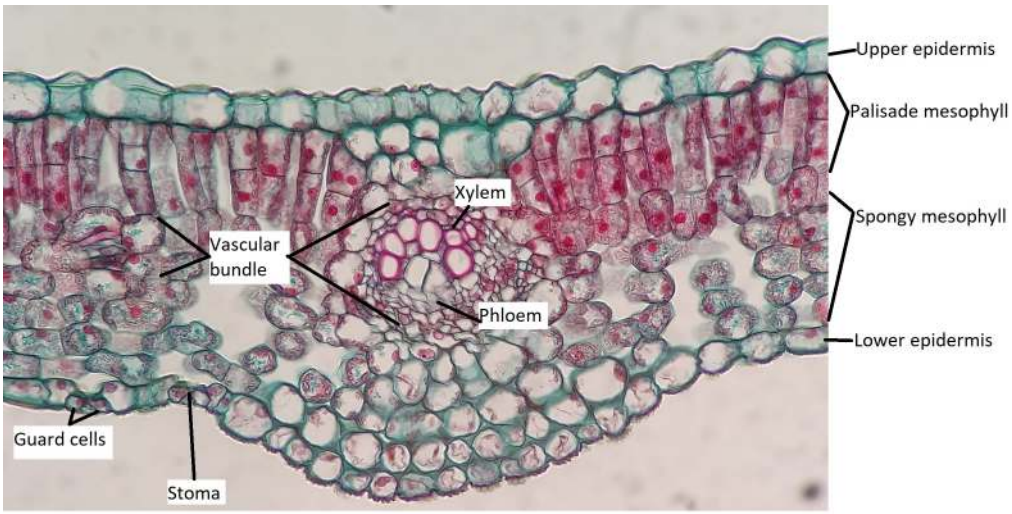



Figure **2.4.2.1**: A cross section through a eudicot leaf. The upper epidermis is a single layer of parenchyma cells. There are no stomata present in the upper epidermis of this leaf. Below the epidermis, cells (appearing pink due to staining of the nuclei and chloroplasts) are arranged in columns, forming the palisade mesophyll. Beneath the palisade mesophyll is the spongy mesophyll. The cells are approximately the same size as the palisade mesophyll, but there are large intercellular spaces between them. The lower epidermis is another single layer of parenchyma cells, but several stomata (flanked by guard cells) are visible in this epidermal layer. A large vascular bundle is in the center of the leaf. The xylem (stained pink) is on the top and the phloem is on the bottom. Image by Maria Morrow (CC-BY-NC).

### Epidermis

The outermost layer of the leaf is the **epidermis**; it is present on both sides of the leaf and is called the upper and lower epidermis, respectively. Botanists call the upper side the adaxial surface (or adaxis) and the lower side the abaxial surface (or abaxis). The epidermis helps in the regulation of gas exchange. It contains **stomata** (singular = stoma; Figure **2.4.2.2**), openings through which the exchange of gases takes place. Two **guard cells** surround each stoma, regulating its opening and closing, and the guard cells are sometimes flanked by **subsidiary cells**. Guard cells are the only epidermal cells to contain chloroplasts. In most cases, the lower epidermis contains more stomata than the upper epidermis because the bottom of the leaf is cooler and less prone to water loss.

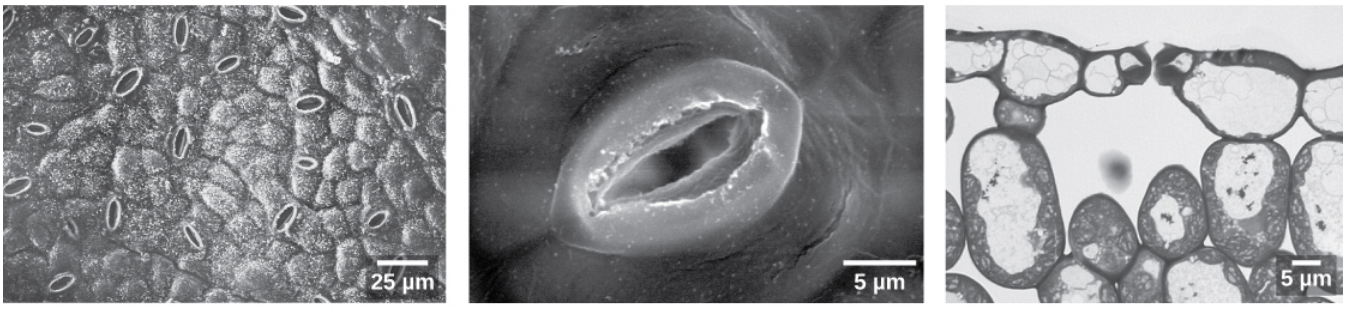



Figure **2.4.2.2**: Visualized at 500x with a scanning electron microscope, several stomata are clearly visible on (a) the surface of this sumac (*Rhus glabra*) leaf. The small, oval-like stomata are scattered on the bumpy surface of the leaf. At 5,000x magnification, the thick lip-like guard cells of (b) a single stoma from lyre-leaved sand cress (*Arabidopsis lyrata*) have the appearance of lips that surround the opening. In this (c) light micrograph cross-section of an *A. lyrata* leaf, the guard cell pair is visible along with the large, substomatal air space in the leaf. The other cells in the leaf (mesophyll cells) are egg-shaped. (credit: modification of work by Robert R. Wise; part c scale-bar data from Matt Russell)

The epidermis is usually one cell layer thick; however, in plants that grow in very hot or very cold conditions, the epidermis may be several layers thick to protect against excessive water loss from transpiration. A protective layer called the **cuticle** covers surface of the epidermal cells (Figure **2.4.2.3**). The cuticle is rich in lignin (which lends some rigidity) and waxes (which function in waterproofing). The cuticle reduces the rate of water loss from the leaf surface. Other leaves may have small hairs (**trichomes**) on the leaf surface. Trichomes help to deter herbivory by restricting insect movements, or by storing toxic or bad-tasting compounds; they can also reduce water loss by blocking air flow across the leaf surface (Figure **2.4.2.4**). For this reason, trichomes (like stomata) are frequently denser on the lower side of the leaf.

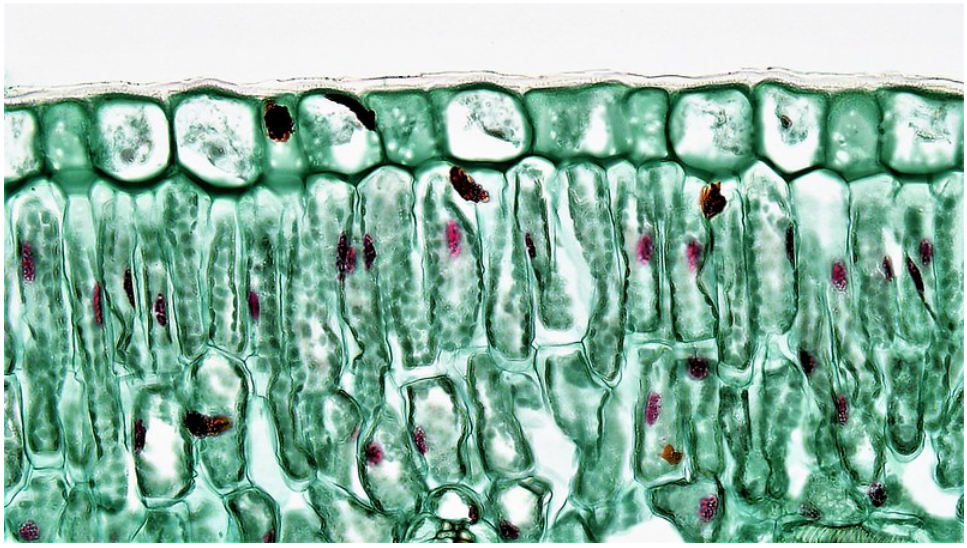
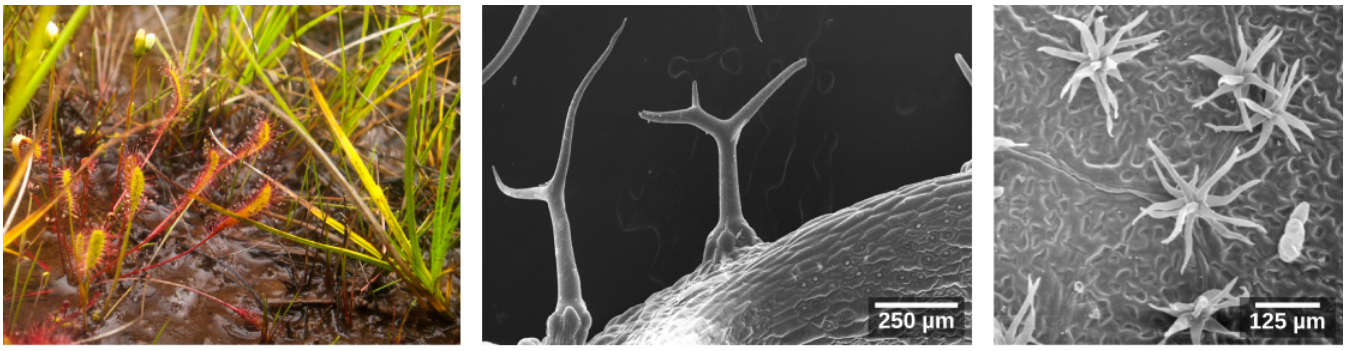


Figure **2.4.2.3**: A cross section through the upper epidermis and the upper portion of the mesophyll (palisade mesophyll). On top of the upper epidermis of this leaf, a transparent layer of cuticle is visible, sealing the top of the leaf. Image by Berkshire Community College Bioscience Image Library (public domain).

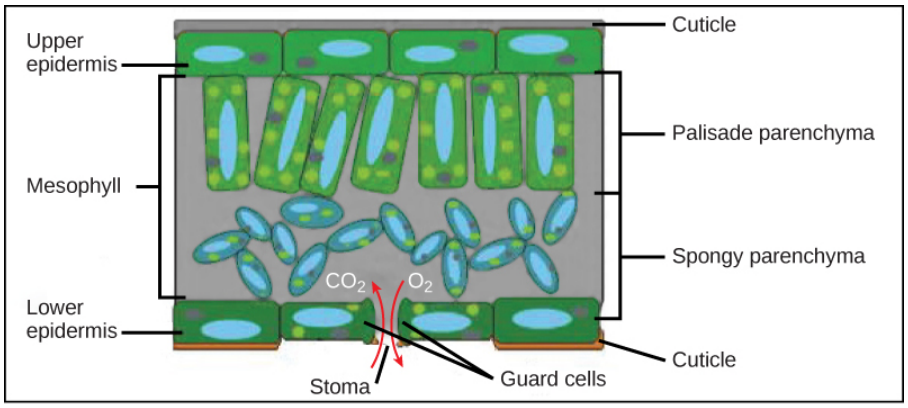



(a) (b) (c)

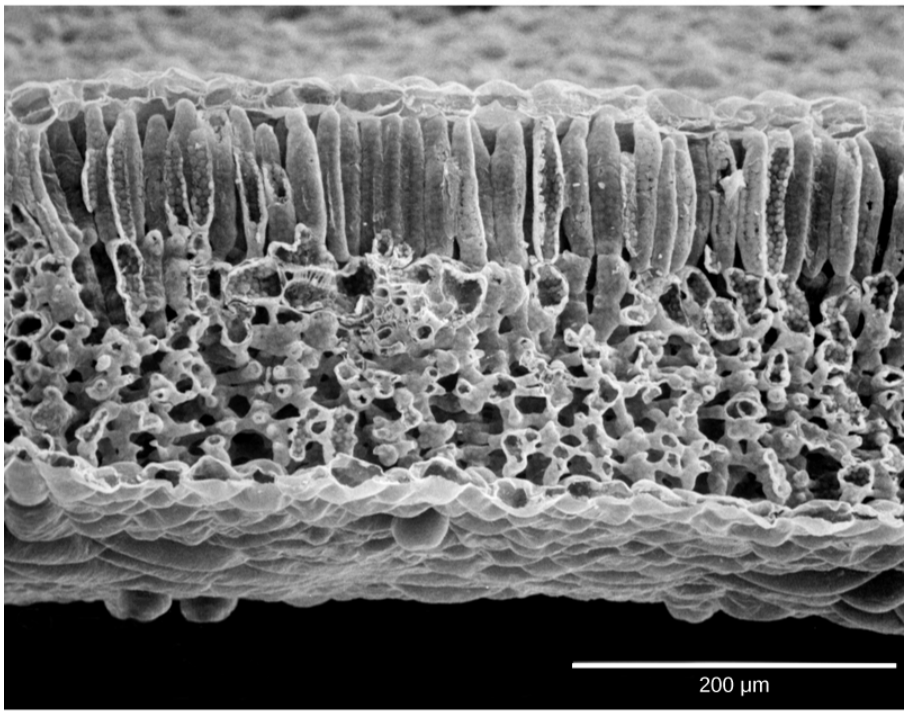
Figure 2.4.2.4: Trichomes give leaves a fuzzy appearance as in this (a) sundew (Drosera sp.). Scanning electron micrographs of (b) branched, tree-like trichomes on the leaf of *Arabidopsis lyrata* and (c) multibranched trichomes, which resemble sea anenomes, on a mature *Quercus marilandica* leaf. (credit a: John Freeland; credit b, c: modification of work by Robert R. Wise; scale-bar data from Matt Russell)

## Mesophyll

Below the epidermis are layers of cells known as the **mesophyll**, or "middle leaf." Mesophyll cells contain many chloroplasts and specialize in photosynthesis. The mesophyll of most leaves typically contains two arrangements of parenchyma cells: the **palisade parenchyma** and **spongy parenchyma** (Figure 2.4.2.5). The palisade parenchyma (also called the palisade mesophyll) has column-shaped and may be present in one, two, or three layers. The palisade cells specialize in capturing incoming sunlight (including slanted sun rays), rotating chloroplasts to the top of the leaf and then allowing them to regenerate by cycling them toward the leaf's center. They also decrease the intensity of sunlight for the spongy mesophyll. Although palisade cells may appear tightly packed in a cross section because there are many rows of cells behind those in the foreground, there is actually ample space (**intercellular air spaces**) between them. Below the palisade parenchyma are seemingly loosely arranged cells of an irregular shape. These are the cells of the **spongy parenchyma** (or spongy mesophyll). The intercellular air spaces found between mesophyll cells facilitate gaseous exchange.




(a)




(b)

Figure 2.4.2.5: The meosphyll often consists of palisade and spongy parenchyma. Part A is a leaf cross section illustration. A flat layer of rectangular cells make up the upper and lower epidermis. A cuticle layer protects the outside of both epidermal layers. A stoma in the lower epidermis allows carbon dioxide to enter and oxygen to leave. Oval guard cells surround the pore. Sandwiched between the upper and lower epidermis is the mesophyll. The upper part of the mesophyll is comprised of columnar cells called palisade parenchyma. The lower part of the mesophyll is made up of loosely packed spongy parenchyma. Part B is a scanning electron micrograph of a leaf in which all the layers described above are visible. Palisade cells are about 50 microns tall and 10 microns wide and contain tiny bumps, which are the chloroplasts. Spongy cells smaller and irregularly shaped. (credit b: modification of work by Robert R. Wise)

## Vascular Bundles (Veins)

Like the stem, the leaf contains vascular bundles composed of xylem and phloem (Figure 2.4.2.6 – 7). When a typical stem vascular bundle (which has xylem internal to the phloem) enters the leaf, xylem usually faces upwards, whereas phloem faces downwards. The conducting cells of the xylem (tracheids and vessel elements) transport water and minerals to the leaves. The sieve-tube elements of the phloem transports the photosynthetic products from the leaf to the other parts of the plant. The phloem is typically supported by a cluster of fibers (sclerenchyma) that increase structural support for the veins. A single vascular bundle, no matter how large or small, always contains both xylem and phloem tissues.

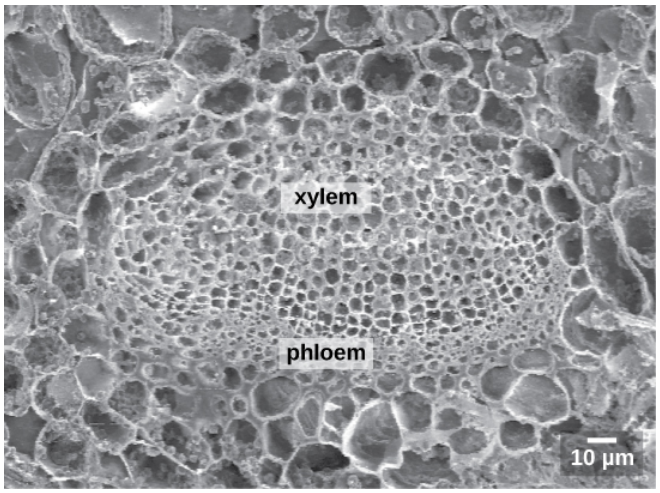



Figure **2.4.2.6**: This scanning electron micrograph shows xylem (larger cells on top) and phloem (smaller cells on bottom) in the leaf vascular bundle from the lyre-leaved sand cress (*Arabidopsis lyrata*). (credit: modification of work by Robert R. Wise; scale-bar data from Matt Russell)

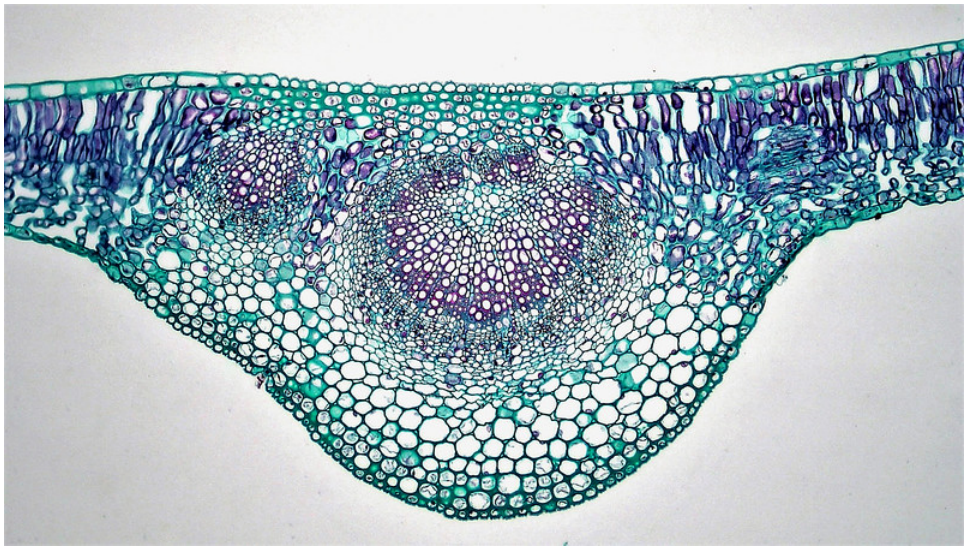


Figure **2.4.2.7**: A cross section through the midvein of a eudicot leaf. The xylem tissue within the large vascular bundle is arranged in an arcing semi-circle, with phloem tissue in an arc traveling just below it. The thick cell walls of the large xylem vessels stain reddish, while the cells of the phloem are smaller with thin cell walls and stain blue. There are layers of collenchyma cells under the epidermis both above and below the midvein. The vascular bundle just to the left of the midrib is coming more or less straight at us, so it is easy to distinguish the tissues. In contrast, the vascular bundle to the right of the midrib was moving diagonally and so was caught in an oblique section and looks more like a smear. Image by Berkshire Community College Bioscience Image Library (public domain).

## Leaf Adaptations

The broad, flat shape of most leaves increases surface area relative to volume, which helps it capture sunlight; however this also provides more opportunity for water loss. The anatomy of a leaf has everything to do with achieving the balance between photosynthesis and water loss in the environment in which the plant grows. Plants that grow in moist areas can grow large, flat leaves to absorb sunlight like solar panels because sunlight is likely more limiting than water. Plants in dry areas must prevent water loss and adapt a variety of leaf shapes and orientations to accomplish the duel tasks of water retention and sunlight absorption. In general, leaves adapted to dry environments are small and thick with a much lower surface area-to-volume ratio.

In regards to water, there are three main types of plants: mesophytes, hydrophytes, and xerophytes. **Mesophytes** are typical plants which adapt to moderate amounts of water ("meso" means middle, and "phyte" means plant). Many familiar plants are mesophytes, such as lilac, *Ranunculus* (buttercup), roses, etc. **Hydrophytes** grow in water ("hydro" refers to water). Their leaf blades are frequently highly dissected (deeply lobed) to access gases dissolved in water, and their petioles and stems have air canals to supply

underwater organs with gases. Hygrophytes (not discussed further) live in constantly wet environment, their leaves adapted to rapidly release water through the stomata. They sometimes even excrete of water drops through the leaf margins (guttation). **Xerophytes** are adapted to the scarce water ("xero" refers to dryness). Xerophytes are found in deserts and Mediterranean climates (such as in much of California), where summers are hot and dry. The leaves of mesophytes are called mesophytic, hydrophyte leaves are called hydrophytic, and so on. The structure of mesophytic leaves was already described (Figure **2.4.2.1**). Adaptaions in hydrophytic and xerophytic leaves and discussed below in more detail.

## Hydrophytic Leaves

The structure of a hydrophytic leaf differs from a mesophytic leaf due to selective pressures in the environment -- water is plentiful, so the plant is more concerned with staying afloat and preventing herbivory. Hydrophytic leaves have a thin epidermal layer and the absence of stomata in the lower epidermis (Figure **2.4.2.8**). In the spongy mesophyll, there are large pockets where air can be trapped, helping the leaf float. This type of parenchyma tissue, specialized for trapping gases, is called **aerenchyma**. Sharp, branched sclereids (astrosclereids) traverse the mesophyll of a hydrophytic leaf. These provide the leaf structural support, as well as prevention of herbivory. Vascular tissue is somewhat reduced in hydrophytic leaves.

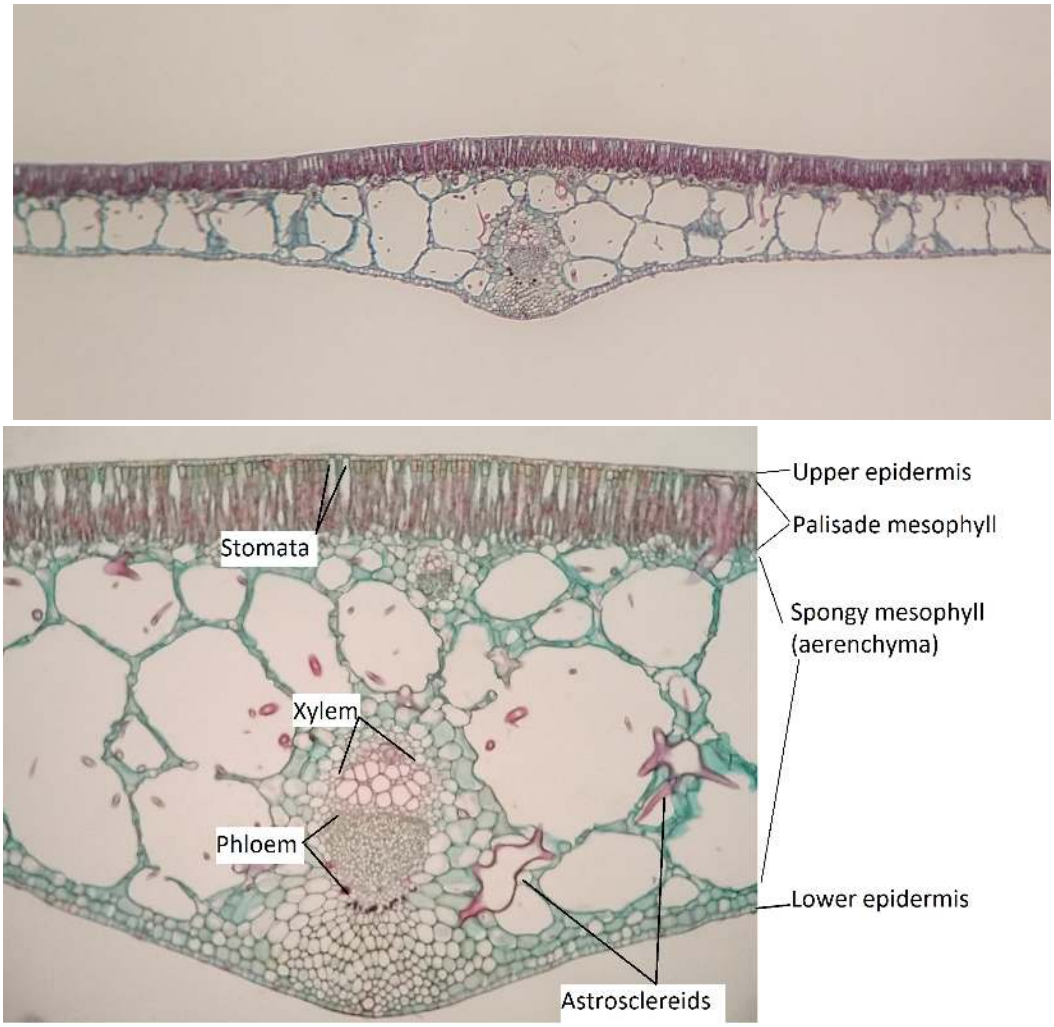



Figure **2.4.2.8**: Cross sections through a hydrophytic leaf from *Nymphaea* (water lily) at two magnifications. The upper epidermis is a thin layer of parenchyma with many stomata. Below each stoma, there is a chamber of air located within the palisade mesophyll (this makes them easier to find). Under the palisade mesophyll is a much larger region of spongy mesophyll than in the mesophytic leaf. Most of the space is taken up by large air pockets, making this tissue aerenchyma. The lower epidermis has no stomata. Within the mesophyll, there are spiky, pink-stained astrosclereids that have been sectioned at different angles during slide preparation. These stain pink due to the lignin in their thick secondary cell walls. Images by Maria Morrow (CC-BY-NC).

## Xerophytic Leaves

Xerophytic leaves (Figure **2.4.2.9**) have thick cuticles to limit water loss, especially on the upper epidermis (Figure **2.4.2.10**). Both the upper and lower epidermis consists of several layers (multiple epidermis). Sometimes the additional layers are called the **hypodermis** ("hypo" meaning under; "dermis" meaning skin). Depressions in the lower epidermis creates a pockets that are lined with trichomes, and the stomata are located at the base of these pockets (called **stomatal crypts;** figure **2.4.2.10**). The trichomes help capture evaporating moisture and maintain a relatively humid environment around the stomata. These stomatal crypts are located only on the underside of the leaves, where they experience less sun exposure and therefore less water loss. The upper epidermis is free from stomata.

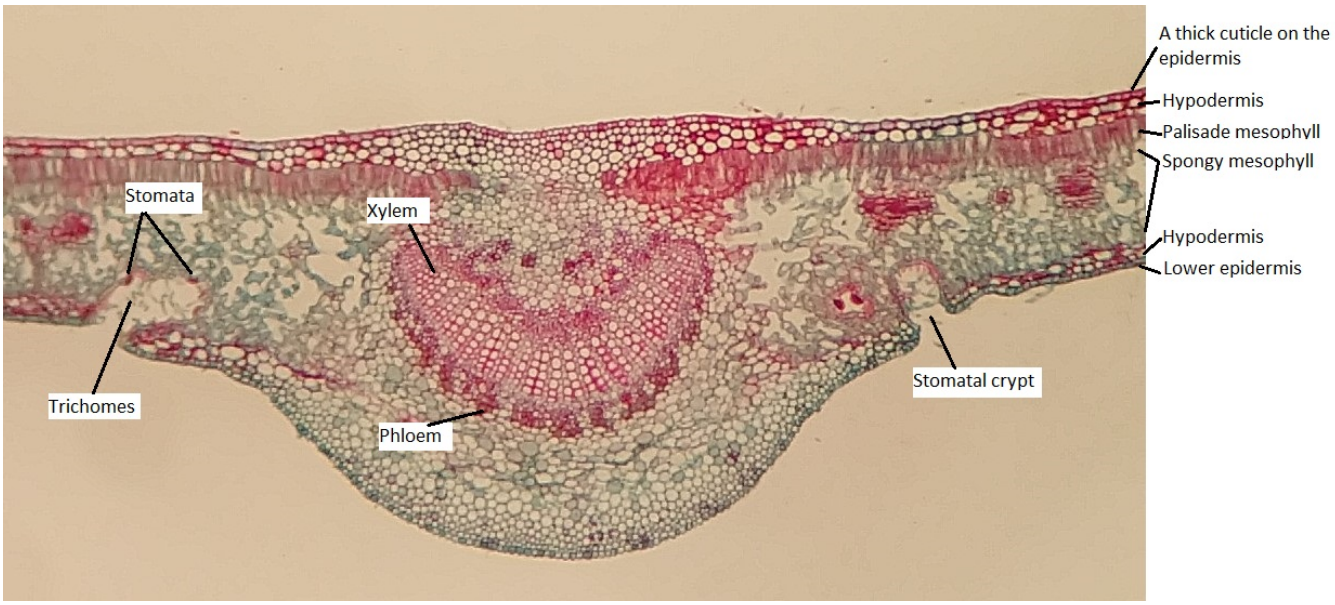



Figure **2.4.2.9**: Tissue organization through the xerophytic leaf of oleander (*Nerium*). On the right side of the image, the layers of tissue are labeled from the upper surface of the leaf to the lower. The upper epidermis of the leaf is sealed by a thick, waxy cuticle. There are no stomata present in the upper epidermis. Just below the epidermis are several layers of tightly packed cells called the hypodermis. Beneath the hypodermis, the palisade and spongy mesophylls are arranged as in a mesophytic leaf. There are more layers of hypodermis between the spongy mesophyll and the lower epidermis. There are invaginations in the lower epidermis called stomatal crypts. Stomata are located within these, surrounded by trichomes. Image by Maria Morrow (CC-BY-NC).

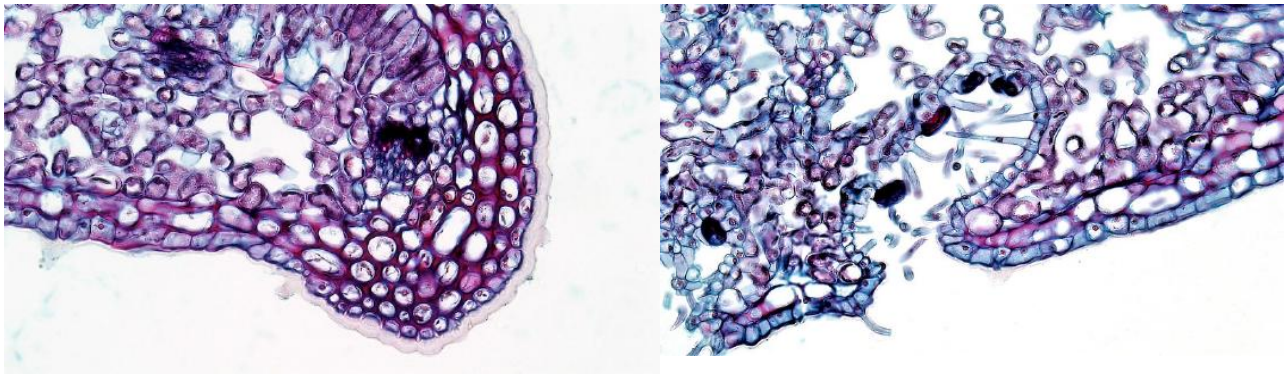


Figure **2.4.2.10**: The margin of the xerophytic leaf of oleander (*Nerium*). Left: There is a thick cuticle on the upper epidermis (it looks like a transparent skin). The cuticle gets thinner as it transitions to the lower epidermis. Right: A stomatal crypt on the lower epidermis is filled with trichomes. Several closed stomata are visible; they are bordered by dark guard cells. Images from Berkshire Community College Bioscience Image Library (public domain).

## Pine Leaves

Pines evolved during a period in Earth's history when conditions were becoming increasingly dry, and pine needles have many adaptations to deal with these conditions. Many of these adaptations are similar the xerophytic leaves of some angiosperms (described above) because pines themselves are xerophytes.

The epidermis of the leaf seems to be more than one cell layer thick (figure **2.4.2.11**). These subsequent layers of epidermis-like tissue under the single, outer layer of true epidermis are called the **hypodermis** , which offers a thicker barrier and helps prevent water loss. The epidermis itself is coated on the outside by a thick layer of wax called the **cuticle**. Because waxes are hydrophobic, this also helps prevent water loss through the epidermis. The stomata are typically sunken, occurring within the hypodermis instead of the epidermis. **Sunken stomata** create a pocket of air that is protected from the airflow across the leaf and can aid in maintaining a higher moisture content (figure **2.4.2.12**).

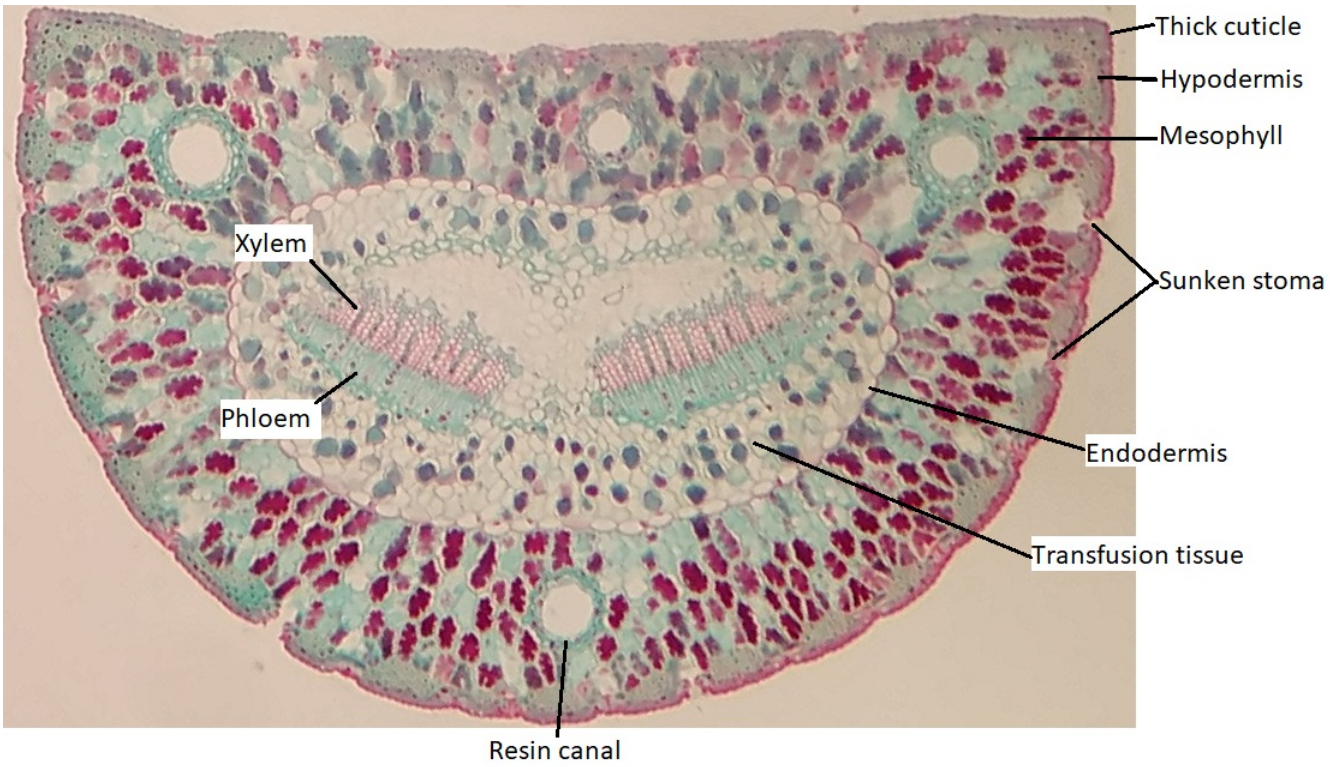



Figure **2.4.2.11**: Cross section of a pine leaf (needle). Much like the *Nerium* leaf, this leaf is coated in a thick cuticle and there is a hypodermis below the epidermis (because this leaf is so round, there is not really a distinct 'upper' and 'lower'). There are no stomatal crypts, but the stomata are sunken, located in the hypodermis. The leaf has a low surface area to volume ratio (more volume, less surface area), which decreases water loss. In the center of the leaf, There is a large region surrounded by an suberized endodermis (much look in a root). There are two vascular bundles within this region, surrounded by transfusion tissue. Image and caption (modifed) by Maria Morrow (CC-BY-NC).

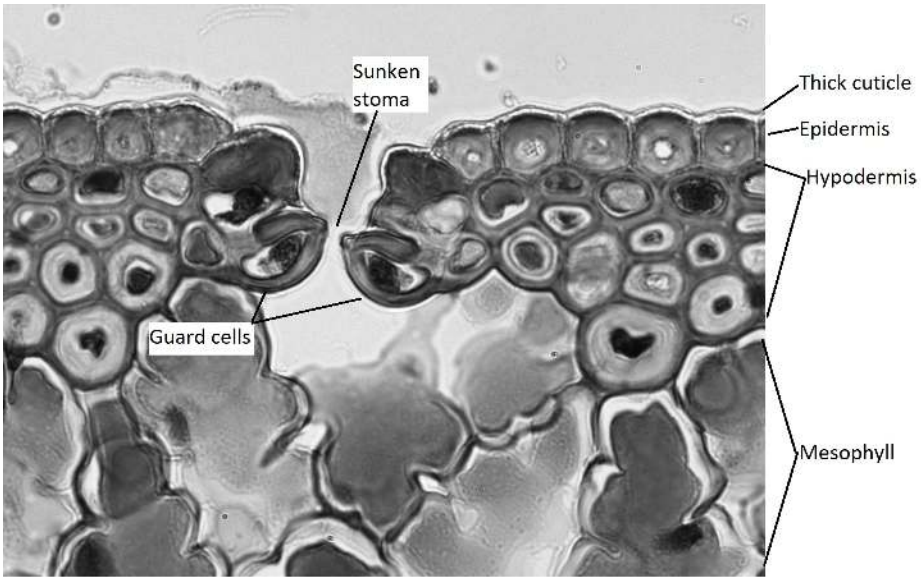



Figure 2.4.2.12: A closer view of a sunken stoma and the outermost layers of the pine needle. The thick cuticle is visible as a transparent layer coating the small epidermal cells. Each of the epidermal cells has a thick cell wall. The hypodermis is composed of 3-4 layers of small, tightly packed cells that also have thick walls (sclerenchyma). The guard cells of the stoma are located about three layers below the epidermis, and the cuticle can be seen extending down over them. The stoma is open in this image. Below the stoma, there is a gap of air space, then highly invaginated mesophyll cells. Image by Maria Morrow (CC-BY-NC).

Within the mesophyll, there are several canals that appear as large, open circles in the cross section of the leaf. These are **resin canals**. The cells lining them secrete resin (the sticky stuff that coniferous trees exude, often called pitch), which contains compounds that are toxic to insects and bacteria. When pines evolved, not only was the Earth becoming drier, but insects were evolving and proliferating. These resin canals are not features that help the plant survive dry conditions, but they do help prevent herbivory. In addition to prevention of herbivory, resin can aid in closing wounds and preventing infection at wound sites.

There are two bundles of vascular tissue embedded within a region of cells called **transfusion tissue**, which functions in transporting materials to and from the mesophyll cells. The transfusion tissue and vascular bundles are surrounded by a distinct layer of cells called the **endodermis**. This is similar to the tissue of the same name in the root, but the cells are not impregnated with the water-repelling compound suberin.

Finally, the overall shape of the leaf allows for as little water loss as possible by decreasing the relative surface area, taking a rounder shape as opposed to a flatter one. This **low surface area-to-volume ratio** is characteristic of xerophytes.

## Corn Leaves

The model organism for monocots in botany is usually corn (*Zea mays*). In corn, there are approximately the same number of stomata on both the upper and lower epidermis. The mesophyll is not divided into two distinct types. The vascular bundles all face the same directly (appearing circular in cross section) because they run parallel to each other.

Corn is not necessarily a xerophyte, but it is adapted to deal with high temperatures. One of these adaptations, $C_4$ type photosynthesis is discussed in Photorespiration and Photosynthetic Pathways and results in a cell arrangement called **Kranz anatomy**. The vascular bundles are surrounded by obviously inflated parenchyma cells that form a structure called a **bundle sheath**, and these are packed with chloroplasts (Figure 2.4.2.13). (Bundle sheaths surround vascular bundles of other types of leaves as well, but the bundle sheath cells are much smaller). Mesophyll cells encircle the bundle sheath cells. In $C_4$ photosynthesis, carbon dioxide is first gathered by the mesophyll cells and temporarily stored as a four-carbon sugar. This four-carbon sugar is transferred to the bundle sheath cells, where it is broken down to release carbon dioxide. It is in the bundle sheath cells where a process called the Calvin cycle, and glucose is ultimately produced. $C_4$ photosynthesis concentrates carbon dioxide inside the bundle sheath cells, reducing the need to frequently open stomata for gas exchange. This helps conserve water.

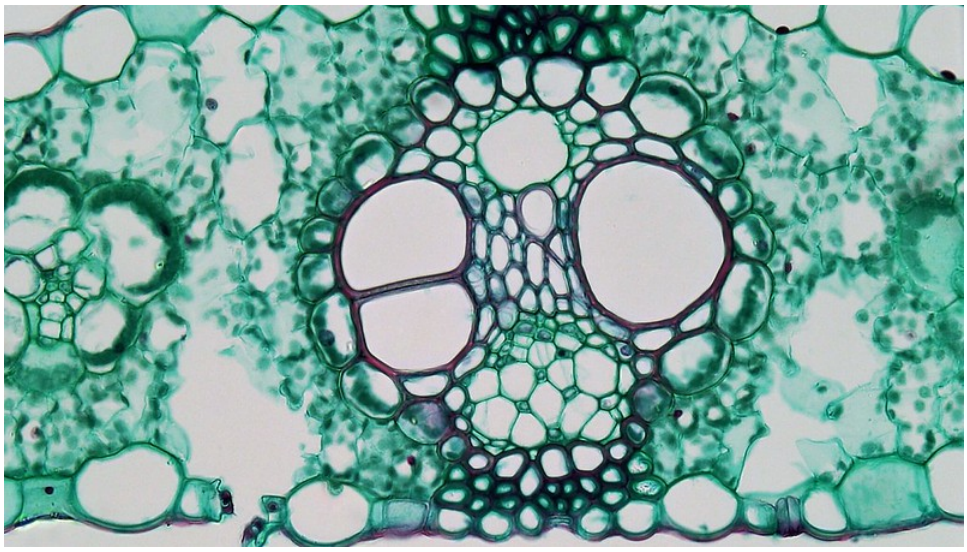


Figure **2.4.2.13**: A vascular bundle of a corn (*Zea mays*) leaf. There are two vascular bundles in this image. The one on the left is difficult to distinguish and most of what you see are the enlarged bundle sheath cells. The larger vascular bundle on the right has less prominent bundle sheath cells, though they still form a distinct border between the vascular tissue and the mesophyll. The xylem tissue is located closer to the upper epidermis. You can locate it by searching for the large, open cells (vessel elements) with red-stained secondary walls. Below the xylem is the phloem tissue, which encompasses a smaller area. The larger cells in the phloem are sieve-tube elements, and the smaller ones are companion cells. Images from Berkshire Community College Bioscience Image Library (public domain).

When moisture is plentiful, the corn leaves are fully expanded and able to maximize photosynthesis. When moisture is limited, the leaves roll inward, limiting both moisture loss and photosynthetic capacity. This is accomplished by the presence of **bulliform cells** in the upper epidermis (Figure **2.4.2.14**). These clusters of enlarged cells are swollen with water when there is abundant water available. As the water content in the plant decreases, these cells shrivel, causing the upper epidermis to curl or fold inward at these points. This adaptation to sun exposure can be found in many other grasses, as well (corn is a member of the Poaceae, the grass family).

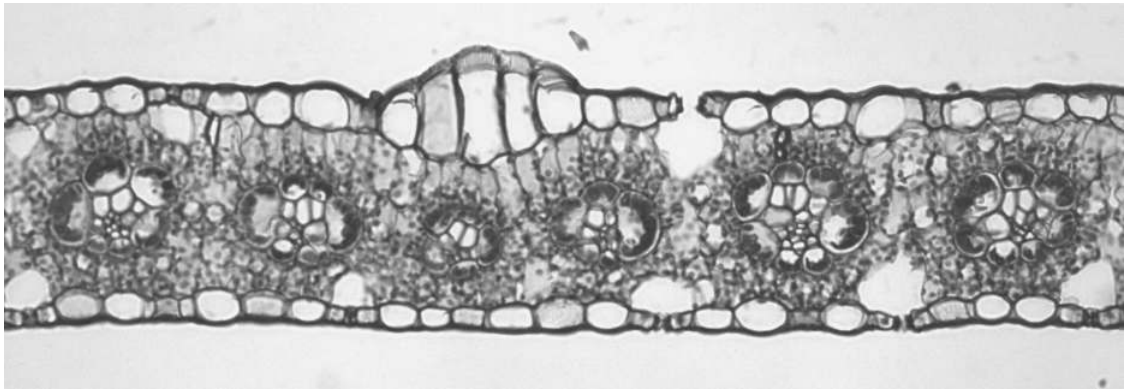


Figure **2.4.2.14**: Cross section of *Zea mays* (corn). The bulliform cells of are the group of tall cells along the upper epidermis, just to the left of the opening (stoma).

## Sun and Shade Leaves

The light intensity experienced by a developing leaf influences its structure. Leaves that develop when consistently exposed to direct sunlight (sun leaves) thus differ from leaves exposed to low light intensities (shade leaves) in several ways (Figure **2.4.2.15**). Relative to shade leaves, sun leaves are smaller and thicker. This reduces surface area relative to volume, conserving water, which would otherwise be easily lost under bright sunlight and resultantly warmer temperatures. In contrast, the broad, thin shape of shade leaves helps capture sufficient light when light intensity is low. The thicker cuticle of sun leaves also limits water loss. They have more palisade parenchyma and more vascular tissue. Sun leaves can maintain a high photosynthetic rate at high light intensities, but shade leaves cannot.

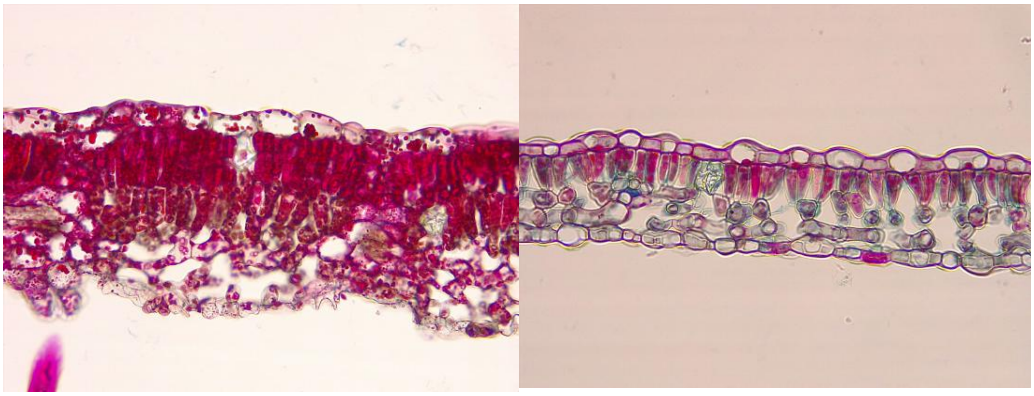


Figure **2.4.2.15**: Cross sections of a sun leaf (left) and shade leaf (right). The palisade parenchyma of the sun leaf consists of several layers, but there is only a single layer in the shade leaf. The chloroplasts (red dots) are also packed more densely in both the palisade and spongy mesophyll cells of the sun leaf compared to the shade leaf. The sun leaf is overall thicker. Images by Melissa Ha (CC-BY).

## Attributions

Curated and authored by Melissa Ha using the following sources:

- 30.2 Stems and 30.4 Leaves from *Biology 2e* by OpenStax (licensed CC-BY). Access for free at openstax.org.
- 5.3 The Leaf from *Introduction to Botany* by Alexey Shipunov (public domain).
- 9.2 Introduction to Leaf Anatomy and 9.3 Leaf Anatomy from *Botany Lab Manual* by Maria Morrow (licensed CC-BY)
- 13 Leaves from *A Photographic Atlas for Botany* by Maria Morrow (licensed CC-BY-NC).

---

This page titled 2.4.2: Internal Leaf Structure is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **3.4.2: Internal Leaf Structure** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC 4.0.

# 2.4.3: Leaf Modifications

**Learning Objective**

Identify common leaf modifications and their functions, including storage leaves, succulent leaves, spines, tendrils, phyllodes, showy bracts, plantlets, and insect traps.

The structure and function of a leaf can be modified over the course of evolution as a plant adapts to a particular environment (Figure **2.4.3.1**). When function of the leaf blade is no longer primarily photosynthesis, some other plant part is usually modified to take its place. **Storage leaves** are thick leaves underground that store starch (as with a bulb; see Stem Modifications). **Succulent leaves** are also thickened leaves, but they are found above ground, still conduct photosynthesis, and function primarily in water storage (Figure **2.4.3.2**).

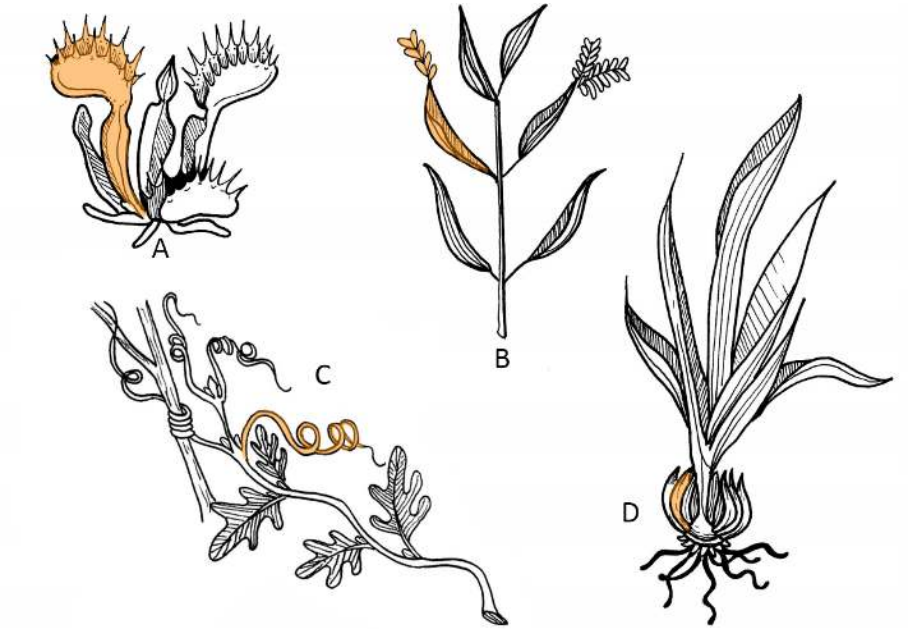



Figure **2.4.3.1**: A diagram of leaf modifications. In each plant (A-D), one leaf has been shaded with orange. In A, the blade has been modified for a trap, the petiole is flattened into a phyllode. In B, the blade is a compound leaf and the petiole is flattened into a phyllode. In C, some of the leaves are thin, coiling tendrils (emerging below axillary buds). In D, the basal leaves are thick and fleshy with a short stem (a bulb). Diagram by Nikki Harris (CC-BY) with labels and color added by Maria Morrow.



Figure **2.4.3.2**: Succulent leaves are thickened for water storage. Left photo by Simon Burchell (CC-BY-SA), and right image by Melissa Ha (CC-BY).

**Spines** are sharp projections derived from leaves that function in plant defense. Almost all cacti (in the plant family Cactaceae) have spines (Figure **2.4.3.3**). Other examples include barberry and some *Acacia* species, in which large spines house mutualist ants. Spines can also be formed from stipules (stipular spines) or bud scales. Recall from Stem Modifications that thorns and prickles have the same function, but they are derived from whole stems or the outer tissue layers of stems, respectively.



Figure **2.4.3.3**: Cactus spines are not stems, but modified leaves. These spines have a thick cuticle and stomata can be seen as darker green areas within the pale white cuticle. Photo by André Karwath (CC-BY-SA).

**Tendrils** are another structure that can originate from multiple structures, including stems, leaves, or leaflets. These are narrow, coiling structures that climbing plants attach to nearby structures for support (Figure **2.4.3.4**).



Figure **2.4.3.4**: Left: The tips of the leaves of glory lily are modified as tendrils. Right: some of the leaflets in the compound leaves of pea plants are modified as tendrils. Left image by Krishna satya 333 (CC BY-SA), and right image by Melissa Ha (CC-BY).

A **phyllode** resembles cladodes and phylloclades but refers to a flattened petiole that resembles a leaf blade (rather than a narrow stalk). The Australian acacias (*Acacia*) have phyllodes (Figure **2.4.3.5**).



Figure 2.4.3.5: Acacia koa with a flat phyllode between the branch and the pinnately compound leaf blades. Image and caption from Wmpearl (public domain).

**Showy bracts** are brightly colored leaves function in attracting pollinators. From a distance, showy bracts often appear like the petals of a flower. However, the actual flowers are typically small and in a cluster surrounded by the bracts (Figure 2.4.3.6).



Figure 2.4.3.6: Showy bracts are brightly colored leaves modified to attract pollinators in *Bougainvillea* (left) and dogwood (right). Although bracts superficially look like petals, the actual petals are part of tiny flowers at the central point where the bracts meet. Images by Melissa Ha (CC-BY).

**Plantlets** are mini plants that grow on the main plant and then fall off and grow into new plants. In *Kalanchoë* , mitosis at meristems along the leaf margins produce tiny plantlets that fall off and grow independently into mature plants. This is a form of asexual reproduction (Figure 2.4.3.7).



Figure 2.4.3.7: Plantlets on the leaf margins of *Kalanchoë.* Plantlets that fall and land on the soil can grow into full-sized plants. Note that this species is also an example of succulent leaves. Image by Melissa Ha (CC-BY).

Carnivorous plants grow in bogs where the soil is low in nitrogen, and their leaves are adapted to help them to survive this nutrient-poor environment. In these plants, leaves are modified as **traps** to capture insects. While they still conduct photosynthesis to capture energy and synthesize sugars (and are thus autotrophs), they rely on insect-capturing leaves as a supplementary source of much-needed nitrogen, similar to fertilizer. Several examples of carnivorous plants are the cobra lily (*Darlingtonia*), various pitcher plants (*Nepenthes* [Figure **2.4.3.8**], *Cephalotus*, *Sarracenia*), the butterwort (*Utricularia*), the sundew (*Drosera*; Figure **2.4.3.9**), and the best known, the Venus flytrap (*Dionaea;* Figure **2.4.3.*h***).




(a) (b)

Figure **2.4.3.8**: The (a) Venus flytrap has modified leaves that can capture insects. When an unlucky insect touches the trigger hairs inside the leaf, the trap suddenly closes. The opening of the (b) pitcher plant is lined with a slippery wax. Insects crawling on the lip slip and fall into a pool of water in the bottom of the pitcher, where they are digested by bacteria. The plant then absorbs the smaller molecules. Top two photos by Maria Morrow (CC-BY). Bottom photos are modification of work by Peter Shanks; credit b: modification of work by Tim Mansfield.

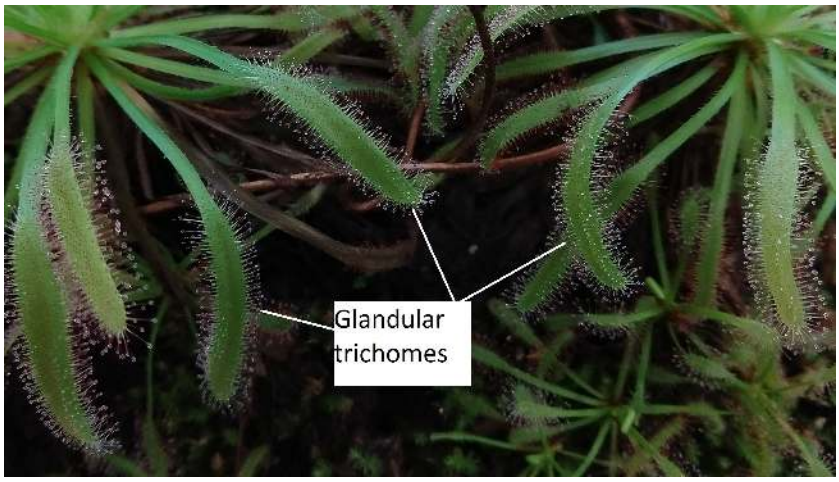



Figure 2.4.3.9: The ends of sundew (*Drosera* sp.) leaves are covered with glandular trichomes. Each trichome has a blob of sticky fluid at the tip. Insects are attracted to the fluid, becoming trapped in it, as the plant slowly digests their bodies for the mineral nutrients that are lacking in their environment. Image by Maria Morrow (CC-BY).

## Attributions

Modified by Melissa Ha from the following sources:

- Leaves from *General Biology* by OpenStax (CC-BY). Access for free at openstax.org.
- Modified Stem and The Leaf from *Introduction to Botany* by Alexey Shipunov (public domain)
- Modified Leaves from *A Photographic Atlas for Botany* by Maria Morrow (CC-BY).
- Asexual Reproduction in Plants from *Biology* by John W. Kimball (CC-BY)

---

This page titled 2.4.3: Leaf Modifications is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **3.4.3: Leaf Modifications** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-SA 4.0.

# 2.4.4: Chapter Summary

Leaves are the main site of photosynthesis. A typical leaf consists of a **blade** (the broad part of the leaf, also called the lamina) and a **petiole** (the stalk that attaches the leaf to a stem). The arrangement of leaves on a stem, known as **phyllotaxy**, enables maximum exposure to sunlight. Each plant species has a characteristic leaf arrangement and form. The pattern of leaf arrangement may be alternate, opposite, or whorled, while leaf form may be **simple** or **compound** (consisting of multiple leaflets). Leaves also differ in the venation patterns, **margins** (edges), and shape.

Leaf tissue consists of the **epidermis**, which forms the outermost cell layer, and **mesophyll** and **vascular bundles** (veins), which make up the inner portion of the leaf. Leaves may be **mesophytic** (adapted to moderate water availability), **hydrophytic** (adapted to on water), or **xerophytic** (adapted for dry conditions). Pine leaves share some characteristics with other xerophytic leaves. The leaves of corn, a monocot, are characterized by **Kranz anatomy**, parallel vascular bundles, and **bulliform cells**. Leaves that develop in the sun tend to be thicker, have a thicker cuticle, and have more palisade mesphyll than those that develop in the shade.

In some plant species, leaf form is modified for functions other than photosynthesis, form structures such as tendrils, spines, or bracts.

**After completing this chapter, you should be able to...**

- Identify the main parts of a leaf.
- Compare petiolate and sessile leaves.
- Distinguish among alternate, opposite, and whorled phyllotaxes.
- Compare simple, pinnately compound, and palmately compound leaves.
- Compare parallel, pinnate, and palmate venation in leaves.
- Recognize common leaf margins and shapes.
- Describe the microscope internal structure of leaves, including the epidermis, mesophyll, and vascular bundles.
- Compare the adaptations of mesophytic, hydrophytic, and xerophytic leaves.
- Identify the unique features of pine and corn leaves.
- Compare the structures of sun and shade leaves.
- Identify common leaf modifications and their functions, including storage leaves, succulent leaves, spines, tendrils, phyllodes, showy bracts, plantlets, and insect traps.

## Attribution

Curated and authored by Melissa Ha using 30.4 Leaves from *Biology 2e* by OpenStax (licensed CC-BY). Access for free at openstax.org.

This page titled 2.4.4: Chapter Summary is shared under a not declared license and was authored, remixed, and/or curated by Tom Buckley.

- **3.4.4: Chapter Summary** by Melissa Ha, Maria Morrow, & Kammy Algiers has no license indicated.

# 2.5: Meristems

**Learning Objective**

Define and locate the two apical meristems and the three primary meristems.

**Meristems** are centers of cell division and growth. In animals, **totipotent** stem cells, which can differentiate into any tissue type are only found early in development; however, plants contains such embryonic tissues throughout their lives.

**Apical meristems** are located on the very ends of shoots (**shoot apical meristem**; SAM; Figure 2.5.1) and roots (**root apical meristem**; RAM; Figure 2.5.2). They produce three types **primary meristems**: the protoderm, ground meristem, and procambium. The **protoderm** gives rise to epidermis, which surrounds the plant. The **ground meristem** gives rise to ground tissue, a group of tissues with generalized functions such as photosynthesis, storage, and support. Finally, the **procambium** gives rise to the vascular tissue, which functions in transport. The three primary meristems first appear in the embryo proper, with the protoderm on the outside, the procambium in the center, and the ground meristem in between them.

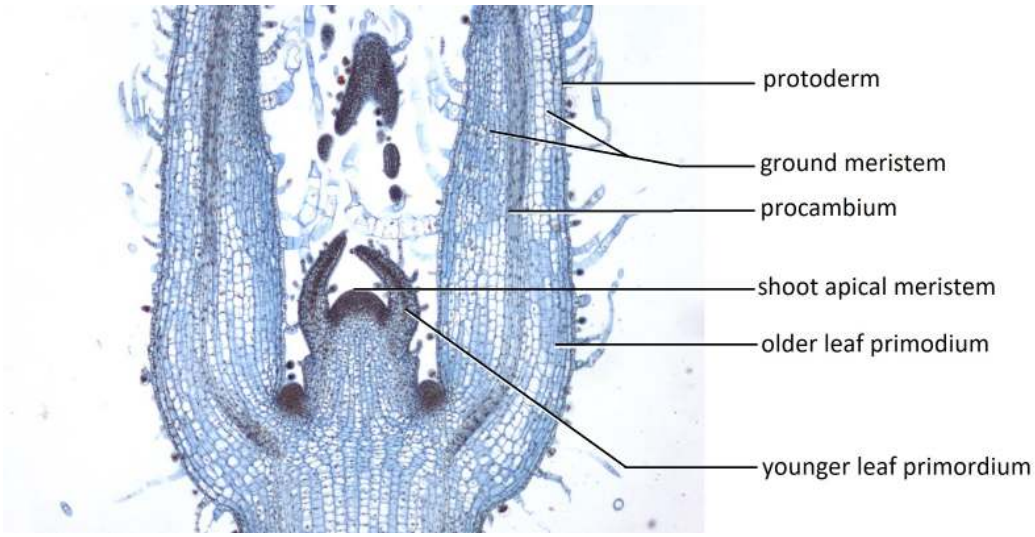



Figure 2.5.1: A longitudinal section of the shoot apex of *Coleus* includes the **shoot apical meristem** and the developing leaves (leaf primoridia) that surround it. The three **primary meristems** are visible in the leaf primordia. The **protoderm** surrounds the leaf primoridum, the **procambium** appears as a line running through the center, and the ground meristem fills the rest of the leaf primodium. Smaller, younger leaf primordia are closer to the shoot apical meristem than older leaf primordia are. Image labeled from Maria Morrow (CC-BY-NC).

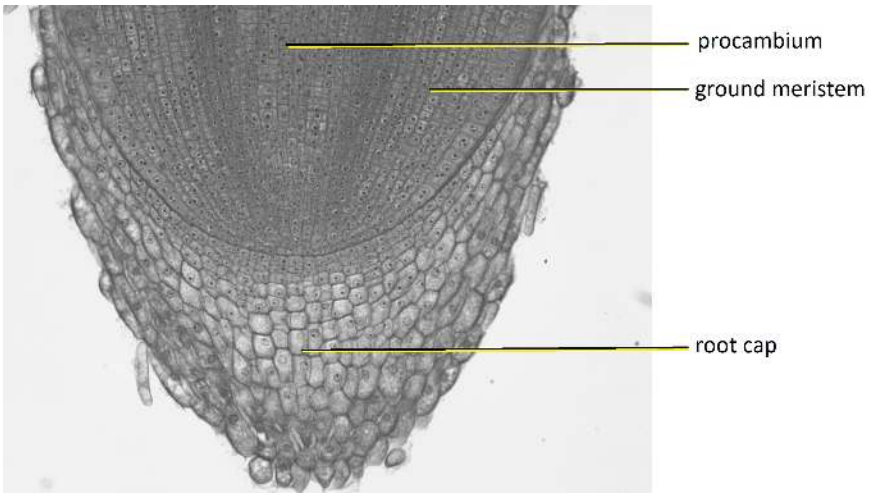



Figure **2.5.2**: A longitudinal section of the root tip of corn (*Zea mays*). The large, lighter cells at the bottom form the protective root cap. The remaining visible portion of the root tip (above the root cap) is the **root apical meristem** (zone of cell division). It gives rise to the central **procambium** and the **ground meristem**, which is external to the procambium. The third primary meristem (**protoderm**) is not visible here. It would be the outer layer of the root tip, just above the current view. Image labeled from Maria Morrow (CC-BY-NC).

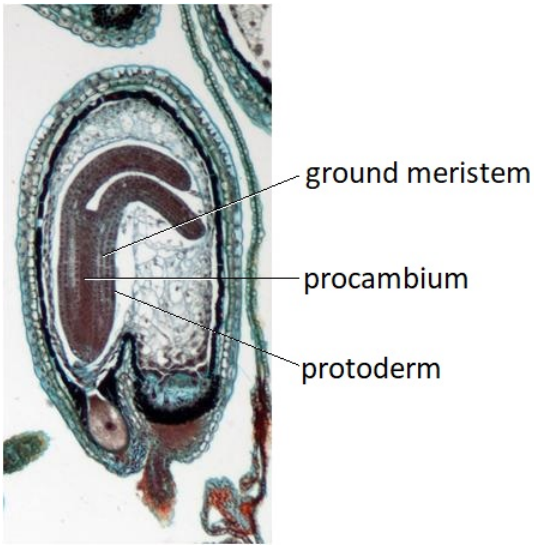



Figure **2.5.3**: The torpedo stage of the *Capsella busra-pastoris* embryo proper showing the three primary meristems. Image labeled from Wisewire (CC-BY).

**Secondary meristems** (lateral meristems) result in secondary growth, a woody increase in girth. These include the vascular cambium and cork cambium. The **vascular cambium** arises from from the procambium and pericycle in roots. In stems, it arises from procambium cells of the vascular bundles (fascicular cambium) and parenchyma cells between vascular bundles (interfascicular cambium). The vascular cambium gives rise to secondary phloem (part of the bark) and secondary xylem (wood; Figures **2.5.4 – 5**).

The **cork cambium** arises from the pericycle in roots and the parenchyma cells of the cortex in stems, both of which arise from the ground meristem. The cork cambium produces periderm, secondary dermal tissue that is also a component of bark. (See Roots and Secondary Stem for more details; Figures **2.5.4 – 5**).)

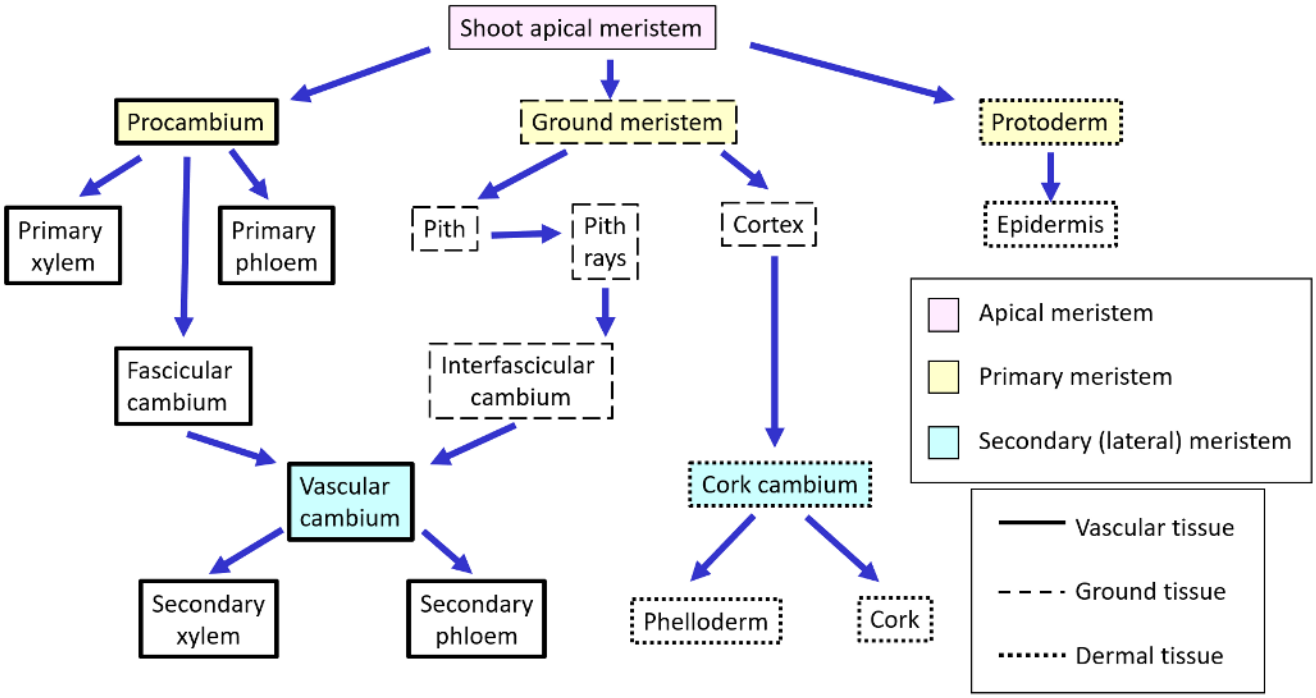



Figure **2.5.4**: Tissue development in stems. The **shoot apical meristem** produces the three **primary meristems**: **procambium**, **ground meristem**, and **protoderm**. The procambium produces vascular tissues. The primary xylem, fascicular cambium, and primary phloem arise from the procambium. The ground meristem produces the pith and cortex, which are ground tissues. The pith generates pith rays, which give rise to the interfascicular cambium.The protoderm produces the epidermis, a dermal tissue. The **secondary meristems** (lateral meristems) are the **vascular cambium** and **cork cambium**. The vascular cambium arises from the procambial cells of the fascicular cambium and the interfascicular cambium. The secondary xylem and secondary phloem arise from the vascular cambium. The cortex gives rise to the cork cambium. The cork cambium and tissues it produces (phelloderm and cork) are dermal tissues. Image by Melissa Ha based on diagram from Maria Morrow (CC-BY).

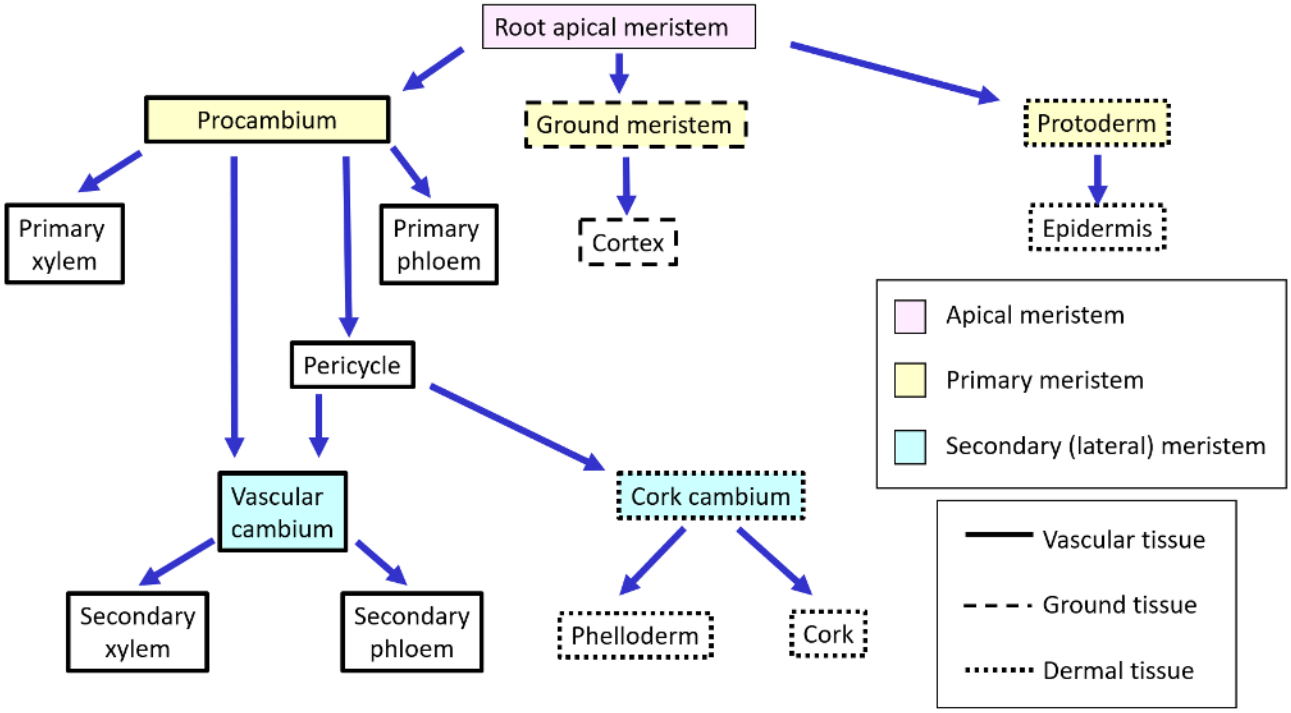



Figure **2.5.5**: Tissue development in roots. The **root apical meristem** produces the three primary meristems: **procambium**, **ground meristem**, and **protoderm**. The procambium gives rise to vascular tissues, including the primary xylem and primary phloem. The ground meristem produces the cortex, a ground tissue. The protoderm produces the epidermis, a dermal tissue. The **secondary meristems** (lateral meristems) are the **vascular cambium** and **cork cambium**. The vascular cambium arises from the procambium and pericycle (which arose from the procambium). The vascular cambium produces secondary xylem and secondary phloem (both vascular tissues). The pericycle also produces the cork cambium, which gives rise to the phelloderm and cork (all dermal tissues). Image by Melissa Ha (CC-BY-NC).

Other meristems include **intercalary meristems** which elongate stems from the "middle" (in between nodes) and **marginal meristems**, which are located along leaf edges and are responsible for leaf development.

## Attribution

Curated and authored by Melissa Ha using 5.1 Tissues from *Introduction to Botany* by Alexey Shipunov (public domain)

---

This page titled 2.5: Meristems is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **4.6.2: Meristems** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC 4.0.

# CHAPTER OVERVIEW

## 3: Origin and evolution of land plants


- 3.1: A Brief History of Life on Earth
  - 3.1.1: A Brief History of Life on Earth
- 3.2: Biodiversity (Organismal Groups)
  - 3.2.1: Systematics
    - 3.2.1.1: Introduction
    - 3.2.1.2: Organizing Life on Earth
    - 3.2.1.3: Determining Evolutionary Relationships
    - 3.2.1.4: Perspectives on the Phylogenetic Tree
    - 3.2.1.5: Chapter Summary
  - 3.2.2: Early Land Plants
    - 3.2.2.1: Introduction to Early Land Plants
    - 3.2.2.2: Bryophytes
      - 3.2.2.2.1: Anthocerotophyta
      - 3.2.2.2.2: Marchantiophyta
      - 3.2.2.2.3: Bryophyta
    - 3.2.2.3: Seedless Vascular Plants
      - 3.2.2.3.1: Lycopodiopsida
      - 3.2.2.3.2: Polypodiopsida
    - 3.2.2.4: Chapter Summary
  - 3.2.3: Seed Plants
    - 3.2.3.1: Introduction to Seed Plants
    - 3.2.3.2: Gymnosperms
      - 3.2.3.2.1: Cycads and Ginkos
      - 3.2.3.2.2: Conifers and Gnetophytes
    - 3.2.3.3: Angiosperms
      - 3.2.3.3.1: Flowers
      - 3.2.3.3.2: Angiosperm Life Cycle
    - 3.2.3.4: Chapter Summary
  - 3.2.4: Angiosperm Diversity
    - 3.2.4.1: Monocots and Eudicots
    - 3.2.4.2: Pollination Syndromes
    - 3.2.4.3: Fruits and Dispersal
    - 3.2.4.4: Angiosperm Families
    - 3.2.4.5: Chapter Summary
- 3.3: Life Cycles
- 3.4: The Origins of Crop Plants


This page titled 3: Origin and evolution of land plants is shared under a not declared license and was authored, remixed, and/or curated by Tom Buckley.

# 3.1: A Brief History of Life on Earth

The diversity of species, ecosystems and landscapes that surround us today are the product of perhaps 3.7 billion (i.e., 3.7×1093.7×109) to 3.85 billion years of evolution of life on Earth (Mojzsis et al., 1996; Fedo and Whitehouse, 2002). Life may have first evolved under harsh conditions, perhaps comparable to the deep-sea thermal vents where chemo-autotrophic bacteria are currently found (these are organisms that obtain their energy only from inorganic, chemical sources).

A subterranean evolution of life has also been suggested. Rock layers deep below the continents and ocean floors, that were previously thought to be too poor in nutrients to sustain life, have now been found to support thousands of strains of microorganisms. Types of bacteria have been collected from rock samples almost 2 miles below the surface, at temperatures up to 75 degrees Celsius. These chemo-autotrophic microorganisms derive their nutrients from chemicals such as carbon, hydrogen, iron and sulphur. Deep subterranean communities could have evolved underground or originated on the surface and become buried or otherwise transported down into subsurface rock strata, where they have subsequently evolved in isolation. Either way, these appear to be very old communities, and it is possible that these subterranean bacteria may have been responsible for shaping many geological processes during the history of the Earth (e.g., the conversion of minerals from one form to another, and the erosion of rocks) (Fredrickson and Onstott, 1996).

The earliest evidence for photosynthetic bacteria - suspected to be cyanobacteria - is dated at sometime between 3.5 and 2.75 billion years ago (Schopf, 1993; Brasier et al., 2002; Hayes, 2002). These first photosynthetic organisms would have been responsible for releasing oxygen into the atmosphere. (Photosynthesis is the formation of carbohydrates from carbon dioxide and water, through the action of light energy on a light-sensitive pigment, such as chlorophyll, and usually resulting in the production of oxygen). Prior to this, the atmosphere was mainly composed of carbon dioxide, with other gases such as nitrogen, carbon monoxide, methane, hydrogen and sulphur gases present in smaller quantities.

It probably took over 2 billion years, from the initial advent of photosynthesis for the oxygen concentration in the atmosphere to reach the level it is at today (Hayes, 2002). As oxygen levels rose, some of the early anaerobic species probably became extinct, and others probably became restricted to habitats that remained free of oxygen. Some assumed a lifestyle permanently lodged inside aerobic cells. The anaerobic cells might, initially, have been incorporated into the aerobic cells after those aerobes had engulfed them as food. Alternatively, the anaerobes might have invaded the aerobic hosts and become parasites within them. Either way, a more intimate symbiotic relationship subsequently evolved between these aerobic and anaerobic cells. In these cases the survival of each cell was dependent on the function of the other cell.

The evolution of this symbiotic relationship was an extremely important step in the evolution of more complex cells that have a nucleus, which is a characteristic of the Eucarya or eucaryotes (eu = good, or true; and karyon = kernel, or nucleus). Recent studies of rocks from Western Australia have suggested that the earliest forms of single-celled eucaryotes might be at least 2.7 billion years old (Anon, 2001). According to contemporary theories, there has been sufficient time, over those 2.7 billion years, for some of the genes of the invading anaerobe to have been lost, or even transferred to the nucleus of the host aerobe cell. As a result, the genomes of the ancestral invader and ancestral host have become mingled and the two entities can now be considered as one from a genetic standpoint.

The evolutionary history of the Eucarya is described in various standard references and so is not covered in detail here. Briefly, eucaryotes constitute three well known groups - the Viridiplantae or green plants, the Fungi, and the Metazoa or animals. There are also many basal groups of eucaryotes that are extremely diverse - and many of which are evolutionarily ancient. For example, the Rhodophyta, or red algae, which might be the sister-group to the Viridiplantae, includes fossil representatives dating from the Precambrian, 1025 billion years ago. The Stramenopiles includes small, single-celled organisms such as diatoms, fungus-like species of water moulds and downy mildews, and extremely large, multicellular brown seaweeds such as kelps.

The earliest known green plants are green algae, dating from the Cambrian, at least 500 million years ago. By the end of the Devonian, 360 million years ago, plants had become quite diverse and included representatives similar to modern plants. Green plants have been extremely important in shaping the environment. Fueled by sunlight, they are the primary producers of carbohydrates, sugars that are essential food resources for herbivores that are then prey to predatory carnivores. The evolution and ecology of pollinating insects is closely associated with the evolution of the Angiosperms, or flowering plants, since the Jurassic and Cretaceous periods.

Fungi, which date back to the Precambrian times about 650 to 540 million years ago, are also important in shaping and sustaining biodiversity. By breaking down dead organic material and using this for their growth, they recycle nutrients back through ecosystems. Fungi are also responsible for causing several plant and animal diseases. Fungi also form symbiotic relationships with tree species, often in nutrient-poor soils such as are found in the humid tropics, allowing their symbiont trees the ability to flourish in what would otherwise be a difficult environment.

Metazoa, which date to over 500 million years ago have also been responsible for shaping many ecosystems, from the specialized tubeworms of deep sea, hydrothermal vent communities of the ocean floor, to the birds living in the high altitudes of the Himalayas, such as the impeyan pheasant and Tibetan snow cock. Many species of animals are parasitic on other species and can significantly affect the behavior and life-cycles of their hosts.

Thus, the evolutionary history of Earth has physically and biologically shaped our contemporary environment. Many existing landscapes are based on the remains of earlier life forms. For example, some existing large rock formations are the remains of ancient reefs formed 360 to 440 million years ago by communities of algae and invertebrates (Veron, 2000).

## Glossary

**Photosynthesis**

the formation of carbohydrates from carbon dioxide and water, through the action of light energy on a light-sensitive pigment, such as chlorophyll, and usually resulting in the production of oxygen

---

This page titled 3.1: A Brief History of Life on Earth is shared under a CC BY 3.0 license and was authored, remixed, and/or curated by Tom Buckley via source content that was edited to the style and standards of the LibreTexts platform.

- **10: A Brief History of Life on Earth** by Nora Bynum is licensed CC BY 3.0. Original source: https://cnx.org/contents/AK5sUWpu1.1:GNNbYBSX1.

# 3.1.1: A Brief History of Life on Earth

The diversity of species, ecosystems and landscapes that surround us today are the product of perhaps 3.7 billion (i.e., 3.7×1093.7×109) to 3.85 billion years of evolution of life on Earth (Mojzsis et al., 1996; Fedo and Whitehouse, 2002). Life may have first evolved under harsh conditions, perhaps comparable to the deep-sea thermal vents where chemo-autotrophic bacteria are currently found (these are organisms that obtain their energy only from inorganic, chemical sources).

A subterranean evolution of life has also been suggested. Rock layers deep below the continents and ocean floors, that were previously thought to be too poor in nutrients to sustain life, have now been found to support thousands of strains of microorganisms. Types of bacteria have been collected from rock samples almost 2 miles below the surface, at temperatures up to 75 degrees Celsius. These chemo-autotrophic microorganisms derive their nutrients from chemicals such as carbon, hydrogen, iron and sulphur. Deep subterranean communities could have evolved underground or originated on the surface and become buried or otherwise transported down into subsurface rock strata, where they have subsequently evolved in isolation. Either way, these appear to be very old communities, and it is possible that these subterranean bacteria may have been responsible for shaping many geological processes during the history of the Earth (e.g., the conversion of minerals from one form to another, and the erosion of rocks) (Fredrickson and Onstott, 1996).

The earliest evidence for photosynthetic bacteria - suspected to be cyanobacteria - is dated at sometime between 3.5 and 2.75 billion years ago (Schopf, 1993; Brasier et al., 2002; Hayes, 2002). These first photosynthetic organisms would have been responsible for releasing oxygen into the atmosphere. (Photosynthesis is the formation of carbohydrates from carbon dioxide and water, through the action of light energy on a light-sensitive pigment, such as chlorophyll, and usually resulting in the production of oxygen). Prior to this, the atmosphere was mainly composed of carbon dioxide, with other gases such as nitrogen, carbon monoxide, methane, hydrogen and sulphur gases present in smaller quantities.

It probably took over 2 billion years, from the initial advent of photosynthesis for the oxygen concentration in the atmosphere to reach the level it is at today (Hayes, 2002). As oxygen levels rose, some of the early anaerobic species probably became extinct, and others probably became restricted to habitats that remained free of oxygen. Some assumed a lifestyle permanently lodged inside aerobic cells. The anaerobic cells might, initially, have been incorporated into the aerobic cells after those aerobes had engulfed them as food. Alternatively, the anaerobes might have invaded the aerobic hosts and become parasites within them. Either way, a more intimate symbiotic relationship subsequently evolved between these aerobic and anaerobic cells. In these cases the survival of each cell was dependent on the function of the other cell.

The evolution of this symbiotic relationship was an extremely important step in the evolution of more complex cells that have a nucleus, which is a characteristic of the Eucarya or eucaryotes (eu = good, or true; and karyon = kernel, or nucleus). Recent studies of rocks from Western Australia have suggested that the earliest forms of single-celled eucaryotes might be at least 2.7 billion years old (Anon, 2001). According to contemporary theories, there has been sufficient time, over those 2.7 billion years, for some of the genes of the invading anaerobe to have been lost, or even transferred to the nucleus of the host aerobe cell. As a result, the genomes of the ancestral invader and ancestral host have become mingled and the two entities can now be considered as one from a genetic standpoint.

The evolutionary history of the Eucarya is described in various standard references and so is not covered in detail here. Briefly, eucaryotes constitute three well known groups - the Viridiplantae or green plants, the Fungi, and the Metazoa or animals. There are also many basal groups of eucaryotes that are extremely diverse - and many of which are evolutionarily ancient. For example, the Rhodophyta, or red algae, which might be the sister-group to the Viridiplantae, includes fossil representatives dating from the Precambrian, 1025 billion years ago. The Stramenopiles includes small, single-celled organisms such as diatoms, fungus-like species of water moulds and downy mildews, and extremely large, multicellular brown seaweeds such as kelps.

The earliest known green plants are green algae, dating from the Cambrian, at least 500 million years ago. By the end of the Devonian, 360 million years ago, plants had become quite diverse and included representatives similar to modern plants. Green plants have been extremely important in shaping the environment. Fueled by sunlight, they are the primary producers of carbohydrates, sugars that are essential food resources for herbivores that are then prey to predatory carnivores. The evolution and ecology of pollinating insects is closely associated with the evolution of the Angiosperms, or flowering plants, since the Jurassic and Cretaceous periods.

Fungi, which date back to the Precambrian times about 650 to 540 million years ago, are also important in shaping and sustaining biodiversity. By breaking down dead organic material and using this for their growth, they recycle nutrients back through ecosystems. Fungi are also responsible for causing several plant and animal diseases. Fungi also form symbiotic relationships with tree species, often in nutrient-poor soils such as are found in the humid tropics, allowing their symbiont trees the ability to flourish in what would otherwise be a difficult environment.

Metazoa, which date to over 500 million years ago have also been responsible for shaping many ecosystems, from the specialized tubeworms of deep sea, hydrothermal vent communities of the ocean floor, to the birds living in the high altitudes of the Himalayas, such as the impeyan pheasant and Tibetan snow cock. Many species of animals are parasitic on other species and can significantly affect the behavior and life-cycles of their hosts.

Thus, the evolutionary history of Earth has physically and biologically shaped our contemporary environment. Many existing landscapes are based on the remains of earlier life forms. For example, some existing large rock formations are the remains of ancient reefs formed 360 to 440 million years ago by communities of algae and invertebrates (Veron, 2000).

## Glossary

**Photosynthesis**

the formation of carbohydrates from carbon dioxide and water, through the action of light energy on a light-sensitive pigment, such as chlorophyll, and usually resulting in the production of oxygen

---

This page titled 3.1.1: A Brief History of Life on Earth is shared under a CC BY 3.0 license and was authored, remixed, and/or curated by Tom Buckley via source content that was edited to the style and standards of the LibreTexts platform.

- **10: A Brief History of Life on Earth** by Nora Bynum is licensed CC BY 3.0. Original source: https://cnx.org/contents/AK5sUWpu1.1:GNNbYBSX1.

# SECTION OVERVIEW

## 3.2: Biodiversity (Organismal Groups)

Biodiversity refers to the diversity of living organisms. Botany, rather than strictly plant biology, includes the study of many different groups of organisms. This section begins by discussing the organization (**classification**) and naming (**taxonomy**) of these groups based on their evolutionary history and genetic relatedness. The following chapters explore the wealth of diversity, beginning with the unicellular **prokaryotes** and acellular **viruses**. The other chapters cover eukaryotic groups that are often distinguished based on life cycles, morphology, nutritional mode, and cellular composition.

**Fungi**, officially classified in the same group as plants until 1969, are heterotrophic eukaryotes more closely related to animals. Other heterotrophic organisms once thought to be fungi, including the **slime molds** and **water molds**, are discussed in the Protists chapter. Protists include an unrelated assemblage of eukaryotes that simply don't fit in as plants, fungi, or animals. Some of these lineages engulfed photosynthetic organisms and gained chloroplasts. These include the **brown algae** and **diatoms** from one engulfing event, and the **red algae** and **green aglae** from another.

The red and green algae share their ancestors with **land plants**. These terrestrial, multicellular organisms can be divided into four major groups based on important evolutionary adaptations: **bryophytes**, **seedless vascular plants**, **gymnosperms**, and **angiosperms**. The angiosperms are the most diverse and most recent lineage, containing nearly 90% of all plant species. Unlike other plants, angiosperms make flowers and fruits.



Figure **3.2.1**: This photo includes many of the organisms mentioned above. The central mushrooms are part of a lichen relationship, *Lichenomphalia umbellifera*, which includes a fungus and a green alga. The mushrooms are surrounded by mosses (of the bryophytes), ferns (from the seedless vascular plants), and a branch from a conifer (belonging to the gymnosperms) lays across them. Among the mosses, microscopic diatoms can likely be found living epiphytically, as well as free-living cyanobacteria. Uncharacteristically, one of the few lineages not pictured here is angiosperms. Perhaps they are all growing upon a fallen tanoak or some other hardwood tree. Photo Credit: Richard Tehan, CC BY-NC.

### 3.2.1: Systematics


3.2.1.1: Introduction

3.2.1.2: Organizing Life on Earth

3.2.1.3: Determining Evolutionary Relationships

3.2.1.4: Perspectives on the Phylogenetic Tree

3.2.1.5: Chapter Summary

## 3.2.2: Early Land Plants

3.2.2.1: Introduction to Early Land Plants
3.2.2.2: Bryophytes
3.2.2.2.1: Anthocerotophyta
3.2.2.2.2: Marchantiophyta
3.2.2.2.3: Bryophyta
3.2.2.3: Seedless Vascular Plants
3.2.2.3.1: Lycopodiopsida
3.2.2.3.2: Polypodiopsida
3.2.2.4: Chapter Summary

## 3.2.3: Seed Plants

3.2.3.1: Introduction to Seed Plants
3.2.3.2: Gymnosperms
3.2.3.2.1: Cycads and Ginkos
3.2.3.2.2: Conifers and Gnetophytes
3.2.3.3: Angiosperms
3.2.3.3.1: Flowers
3.2.3.3.2: Angiosperm Life Cycle
3.2.3.4: Chapter Summary

## 3.2.4: Angiosperm Diversity

3.2.4.1: Monocots and Eudicots
3.2.4.2: Pollination Syndromes
3.2.4.3: Fruits and Dispersal
3.2.4.4: Angiosperm Families
3.2.4.5: Chapter Summary


## Attribution

Content by Maria Morrow, CC BY-NC


This page titled 3.2: Biodiversity (Organismal Groups) is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

# SECTION OVERVIEW

## 3.2.1: Systematics


### 3.2.1.1: Introduction

### 3.2.1.2: Organizing Life on Earth

### 3.2.1.3: Determining Evolutionary Relationships

### 3.2.1.4: Perspectives on the Phylogenetic Tree

### 3.2.1.5: Chapter Summary


### Contributors and Attributions

- Chapter thumbnail by Pengo, Public domain, via Wikimedia Commons.


This page titled 3.2.1: Systematics is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

# 3.2.1.1: Introduction

The history of life on earth goes back more than 3.5 billion years, with all life evolving from a common ancestor and diversifying to what we currently see on earth today. The evolutionary history of a group of species is referred to as a **phylogeny**. The process of reconstructing a phylogeny is part of the science of **systematics** (the scientific study of biological diversity and its classification). **Taxonomy** is the science of classification (categorizing) and nomenclature (naming). Biologists prefer a system of classification that indicates evolutionary relationships among organisms. **Cladistics** is a method of classification in which organisms are categorized in groups (or clades) based on the most recent common ancestor. This methodology produces a phylogenetic tree that is a testable representation of the theoretical true phylogeny. Cladistics differs from historical methods of classification by relying on shared derived characters (a character shared by closely related organisms because they inherited it from their closest ancestor and which is not present in more distant ancestors) rather than overall similarity.



Figure **3.2.1.1.1**: The life of a bee is very different from the life of a flower, but the two organisms are related. Both are members the domain Eukarya and have cells containing many similar organelles, genes, and proteins. (credit: modification of work by John Beetham)

## Contributors and Attributions

- Curated and authored by Kammy Algiers, CC BY-NC
- Figure from General Biology, OpenStax (20.0)

This page titled 3.2.1.1: Introduction is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **2.1.1: Introduction** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC 4.0.

# 3.2.1.2: Organizing Life on Earth

**Learning Objectives**

- Discuss the components and purpose of a phylogenetic tree.
- Interpret relationships between organisms using a phylogenetic tree.
- Correctly order the different levels of taxonomic classification.
- Discuss the benefits of having a comprehensive classification system.

The evolutionary history of a group of species is referred to as a **phylogeny**. Phylogeny describes the relationships of the group within the context of related organisms. Though phylogenetic relationships provide information on shared ancestry, they don't necessarily address how organisms are similar or different.

## Phylogenetic Trees

Scientists use a tool called a phylogenetic tree to show the evolutionary pathways and connections among organisms. A phylogenetic tree is a diagram used to reflect evolutionary relationships among organisms or groups of organisms. Scientists consider phylogenetic trees to be a hypothesis of the evolutionary past since one cannot go back to confirm the proposed relationships. In other words, a “tree of life” can be constructed to illustrate when different organisms evolved and to show the relationships among different organisms (Figure **3.2.1.2.1**).

Unlike a taxonomic classification diagram, a phylogenetic tree can be read like a map of evolutionary history. Many phylogenetic trees have a single lineage at the base representing a **common ancestor**. Scientists call such trees **rooted**, which means there is a single ancestral lineage (typically drawn from the bottom or left) to which all organisms represented in the diagram relate. Notice in the rooted phylogenetic tree that the three domains— Bacteria, Archaea, and Eukarya—diverge from a single point and branch off. The small branch that plants and animals (indicated with a "you are here" star in Figure **3.2.1.2.1**) occupy in this diagram shows how recent and miniscule these groups are compared with other organisms. **Unrooted** trees don’t predict a common ancestor but do show relationships among species.

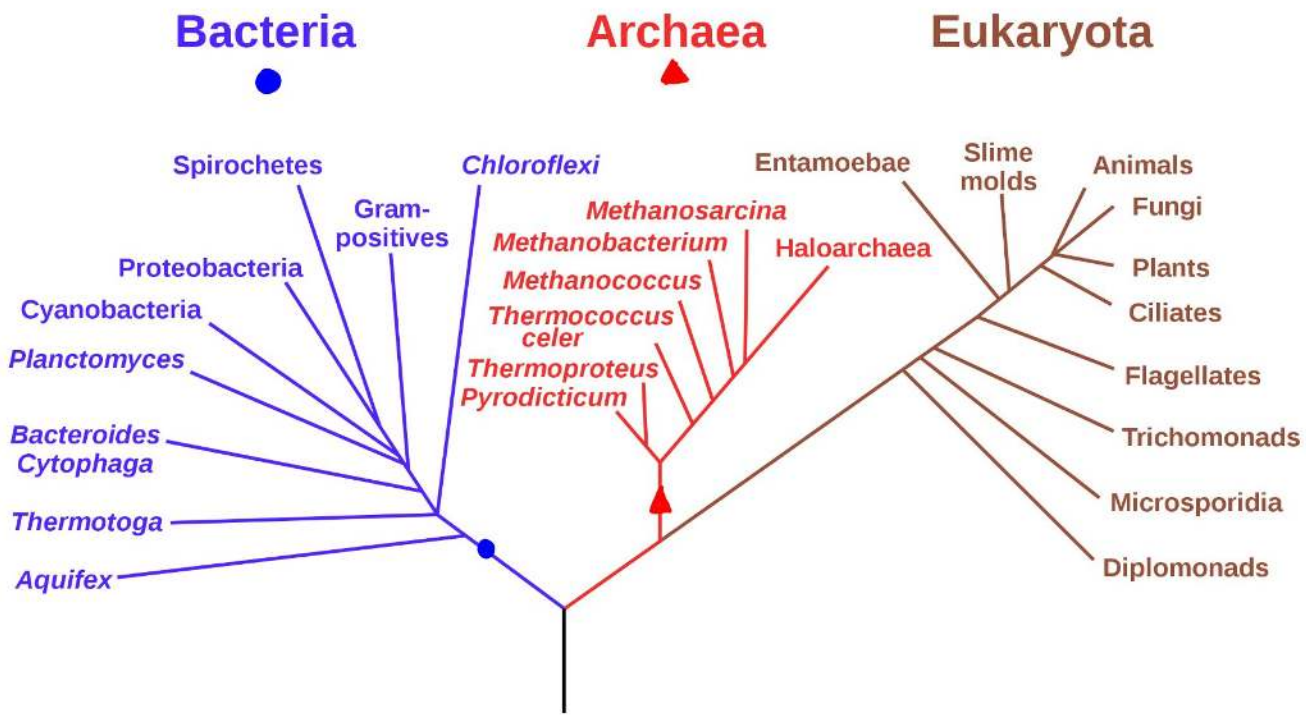



Figure **3.2.1.2.1**: The phylogenetic tree in part a is rooted and resembles a living tree, with a common ancestor indicated as the base of the trunk. Two branches form from the trunk. The left branch leads to the domain Bacteria. The right branch branches again, giving rise to Archaea and Eukarya. Smaller branches within each domain indicate the groups present in that domain. The phylogenetic tree in part B is unrooted. It does not resemble a living tree; rather, groups of organisms within the Archaea, Eukarya, and Bacteria domains are arranged in a circle. Lines connect the groups within each domain. The groups within Archaea and Eukarya are then connected together. A line from the Archaea/Eukarya domains, and another from the Bacteria meet in the center of the circle. There is no root, and therefore no indication of which domain arose first. Both of these phylogenetic trees shows the relationship of the three domains of life—Bacteria, Archaea, and Eukarya—but the (a) rooted tree attempts to identify when various species diverged from a common ancestor while the (b) unrooted tree does not. (credit a: modification of work by Eric Gaba)

In a rooted tree, the branching indicates evolutionary relationships (see Figure **3.2.1.2.2**). The point where a split occurs, called a **branch point** or node, represents where a single lineage evolved into a distinct new one. A lineage that evolved early from the root and remains unbranched is called a **basal taxon**. When two lineages stem from the same branch point, they are called **sister taxa**. A branch with more than two lineages is called a **polytomy** and serves to illustrate where scientists have not definitively determined all of the relationships. It is important to note that although sister taxa and polytomy do share an ancestor, it does not mean that the groups of organisms split or evolved from each other. Organisms in two taxa may have split apart at a specific branch point, but neither taxa gave rise to the other.

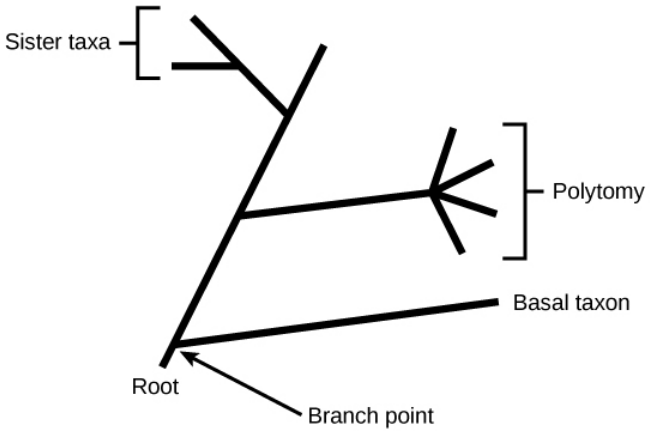



Figure **3.2.1.2.2**: The root of a phylogenetic tree indicates that an ancestral lineage gave rise to all organisms on the tree. A branch point indicates where two lineages diverged. A lineage that evolved early and remains unbranched is a basal taxon. When two lineages stem from the same branch point, they are sister taxa. A branch with more than two lineages is a polytomy. Descriptive text: A phylogenetic tree that starts at a root, indicating that all organisms on the tree share a common ancestor. Shortly after the root, the tree branches out. One branch gives rise to a single, basal lineage (basal taxon), and the other gives rise to all other organisms on the tree. The next branch forks at one point into four different lineages, an example of polytomy. The final branch gives rise to two lineages, an example of sister taxa.

The diagrams above can serve as a pathway to understanding evolutionary history. The pathway can be traced from the origin of life to any individual species by navigating through the evolutionary branches between the two points. By starting with a single species and tracing back towards the "trunk" of the tree, one can discover that species' ancestors, as well as where lineages share a common ancestry. In addition, the tree can be used to study entire groups of organisms.

Another point to mention on phylogenetic tree structure is that rotation at branch points does not change the information. For example, if a branch point was rotated and the taxon order changed, this would not alter the information because the evolution of each taxon from the branch point was independent of the other.

Many disciplines within the study of biology contribute to understanding how past and present life evolved over time; these disciplines together contribute to building, updating, and maintaining the “tree of life.” Information is used to organize and classify organisms based on evolutionary relationships in a scientific field called systematics. Data may be collected from fossils, from studying the structure of body parts or molecules used by an organism, and by DNA analysis. By combining data from many sources, scientists can put together the phylogeny of an organism; since phylogenetic trees are hypotheses, they will continue to change as new types of life are discovered and new information is learned.

## Examples of Simple Trees

In Figure **3.2.1.2.3** and Figure **3.2.1.2.4**, some example trees are drawn to show how to interpret the structure of a phylogenetic tree.

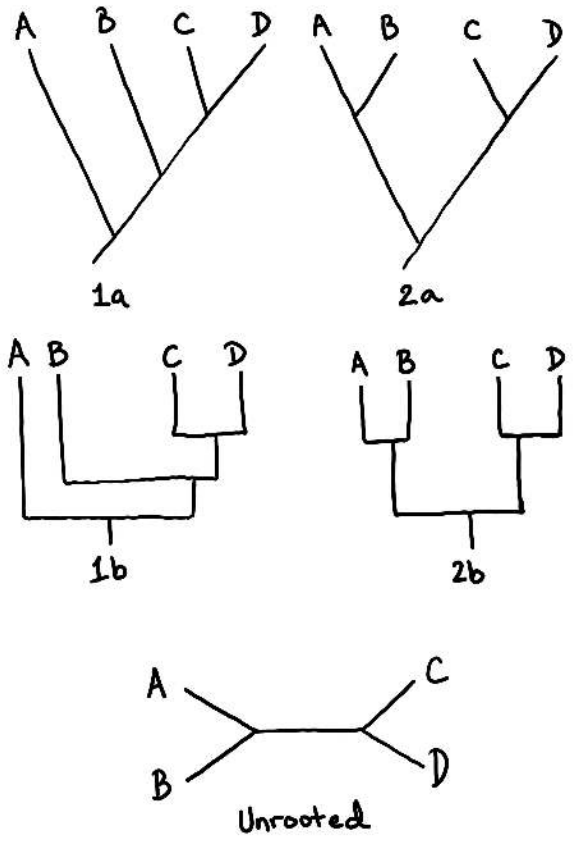



Figure **3.2.1.2.3**: These diagrams show hypotheses for four different taxa: A, B, C, and D. These taxa could represent individuals, different species, or any other level of classification. Trees 1a and 1b are drawn differently but represent the same hypothesis: C and D are most closely related (sister taxa) and A is the most ancestral lineage. Trees 2a and 2b represent a slightly different hypothesis: C and D are sister taxa, but A and B are also sister taxa; neither lineage is depicted as "older" than the other. This last relationship is also represented in the "Unrooted" tree: there is no hypothesis in this tree for which group is most ancestral (no "root"). Images drawn by Maria Morrow, CC-BY-NC.

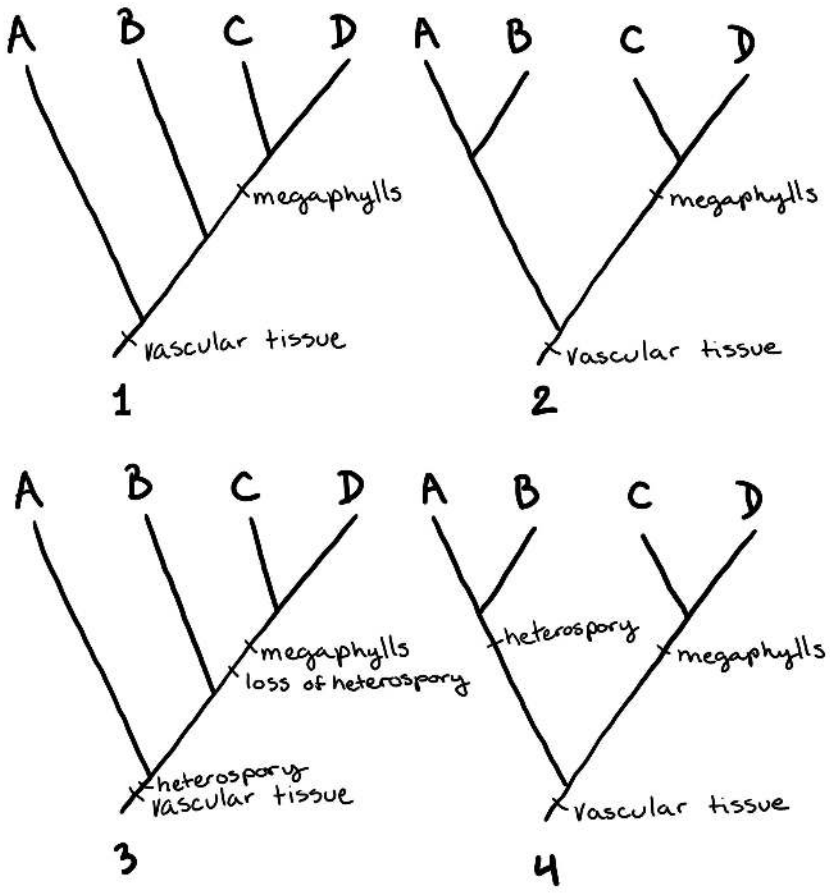



Figure **3.2.1.2.4**. Vascular tissue appears on the root of the trees as an ancestral trait. This means that A, B, C, and D all have vascular tissue. Megaphylls appears in both trees as a shared derived characteristic (synapomorphy) of C and D. This means C and D have megaphylls, but A and B do not. Both tree 1 and tree 2 are equally parsimonious. In trees 3 and 4, a third trait has been added: heterospory. In addition to the information from trees 1 & 2, we now see that A and B are heterosporous, while C and D are not. In tree 3, heterospory appears as an ancestral trait which is lost in C and D. In tree 4, heterospory is a synapomorphy of A and B. Tree 3 has four changes, while tree 4 only has three. This means that tree 4 is more parsimonious and therefore more likely (though not necessarily correct!). Images drawn by Maria Morrow, CC-BY-NC.

## The Levels of Classification

**Taxonomy** (which literally means “arrangement law”) is the science of classifying organisms to construct internationally shared classification systems with each organism placed into more and more inclusive groupings. Think about how a grocery store is organized. One large space is divided into departments, such as produce, dairy, and meats. Then each department further divides into aisles, then each aisle into categories and brands, and then finally a single product. This organization from larger to smaller, more specific categories is called a hierarchical system.

The taxonomic classification system (also called the Linnaean system after its inventor, Carl Linnaeus, a Swedish botanist, zoologist, and physician) uses a hierarchical model. Moving from the point of origin, the groups become more specific, until one branch ends as a single species. As you saw in Figure **3.2.1.2.1**, scientists divide organisms into three large categories called **domains**: Bacteria, Archaea, and Eukarya. Within each domain is a second category called a **kingdom**. Each domain might encompass many kingdoms. For example, kingdom Plantae, kingdom Animalia, and kingdom Fungi represent three of the many kingdoms contained within domain Eukarya. After kingdoms, the subsequent categories of increasing specificity are: **phylum, class, order, family, genus,** and **species** (Figure **3.2.1.2.5**).

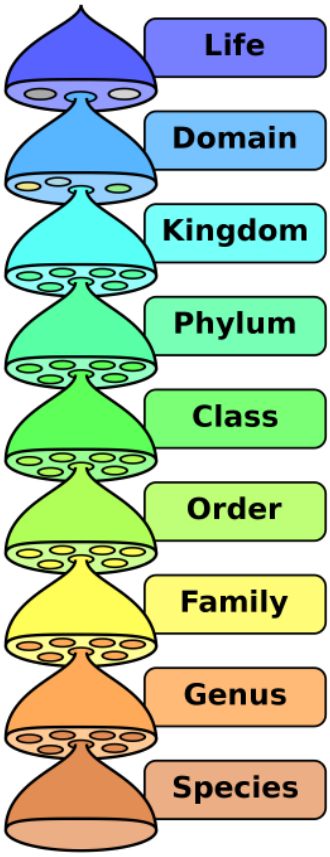



Figure 3.2.1.2.5: The taxonomic classification system uses a hierarchical model to organize living organisms into increasingly specific categories. Within what we have currently described as life, there are three domains. Within each domain, there are kingdoms. Within each kingdom, there are phyla. Within phyla there are classes, within classes there are orders, within orders there are families, within families there are genera, and within genera there are species. Diagram by Pengo, Public domain, via Wikimedia Commons.

The kingdom Plantae stems from the Eukarya domain. For the shore pine (*Pinus contorta var. contorta*), the classification levels would be as shown in Figure 3.2.1.2.6. Therefore, the full name of an organism technically has multiple terms associated. For the shore pine, it is: Eukarya, Plantae, Pinophyta, Pinopsida, Pinales, Pinaceae, *Pinus*, *Pinus contorta*, and var. *contorta*. Notice that each name is capitalized except for the specific epithet (contorta), and the genus and species names are italicized. Notice also the underlined endings of the words. In plant taxonomy, the underlined portion is always used for those taxonomic levels: phyla end in -phyta, classes end in -opsida, orders end in -ales, and families end in -aceae.

The scientific name for an organism usually refers to the species name, a two-word scientific name that includes the genus name (e.g. *Pinus*) and specific epithet (e.g. *contorta*). This two word naming system is called **binomial nomenclature**. The name at each level is also called a taxon. In other words, pines are in order Pinales. Pinales is the name of the taxon at the order level; Pinaceae is the taxon at the family level, and so forth. Organisms also have a common name that people typically use, in this case, shore pine. Note that the shore pine is additionally a subspecies or variety: the second "*contorta*" in *Pinus contorta* var. *contorta.* Subspecies are members of the same species that are capable of mating and reproducing viable offspring, but they are considered separate subspecies due to geographic or behavioral isolation or other factors. Shore pines are coastal (hence the common name) and tend to grow in scraggly, twisted shapes (hence the scientific name). Lodgepole pines (*Pinus contorta* var. *latifolia)* typically have a straight trunk and grow in the mountains.

Figure 3.2.1.2.6 shows how the levels move toward specificity with other organisms. Notice how the shore pine (leftmost image) shares a domain with the widest diversity of organisms, including plants, fungi, algae, and animals. At each sublevel, the organisms become more similar because they are more closely related. Historically, scientists grouped similar organisms using characteristics, but as DNA technology developed, more precise relationships have been determined.

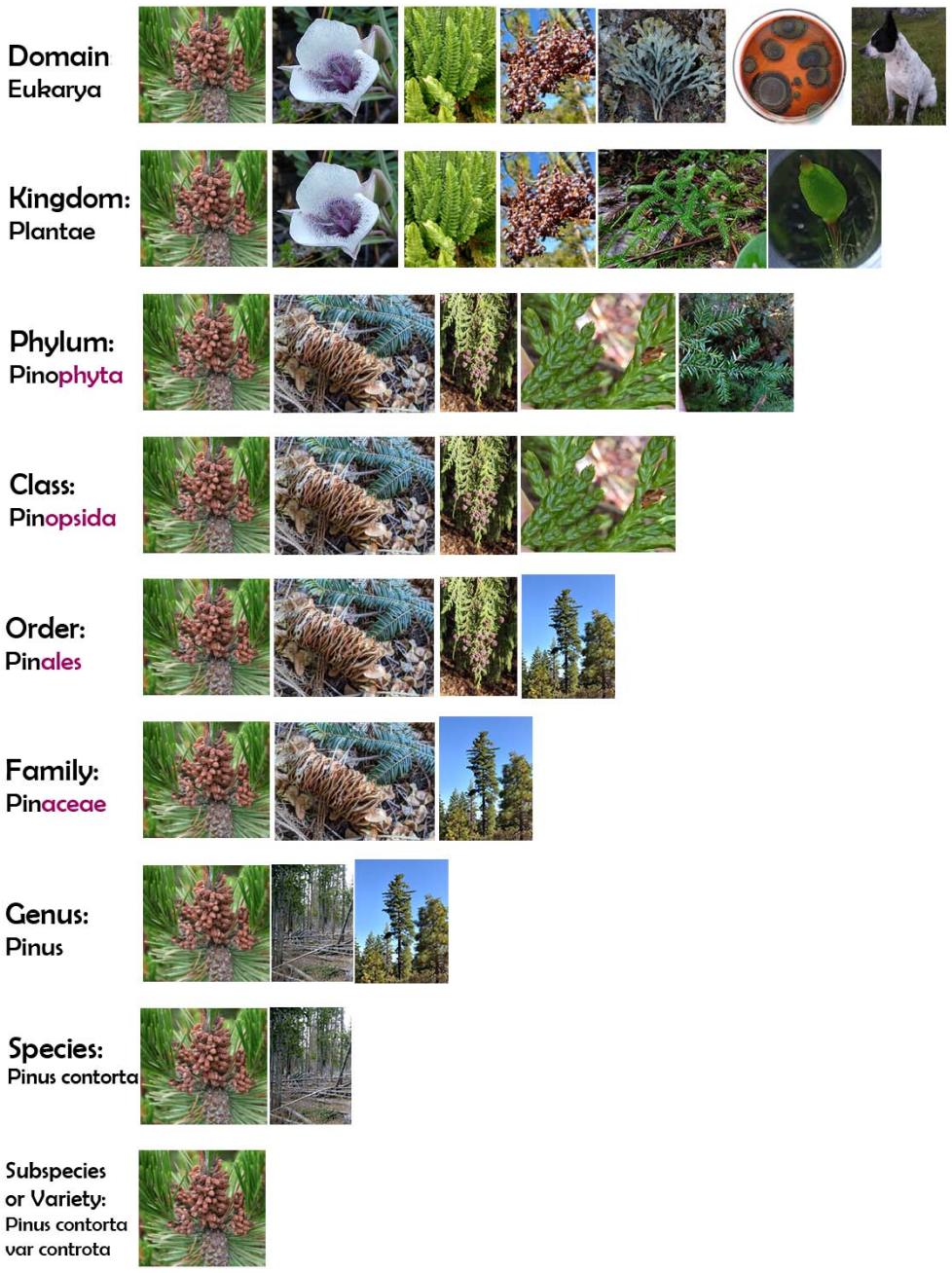



Figure 3.2.1.2.6: At each sublevel in the taxonomic classification system, organisms become more similar. Author's note: The reduction is slightly artificial in this diagram, as Pinales is the only order within Pinopsida. Figure and images by Maria Morrow, CC-BY-NC, except: the lodgepole pine, which comes from the public domain in the Wikimedia Commons, retrieved from the following page [1] of the Yellowstone Digital Slide Files archives; the *Pinus contorta* var *contorta* image, by Janice S, CC-BY-NC.

Recent genetic analysis and other advancements have found that some earlier phylogenetic classifications do not align with the evolutionary past; therefore, changes and updates must be made as new discoveries occur. Recall that phylogenetic trees are hypotheses and are modified as data becomes available. In addition, classification historically has focused on grouping organisms mainly by shared characteristics and does not necessarily illustrate how the various groups relate to each other from an evolutionary perspective. For example, despite the fact that a hippopotamus resembles a pig more than a whale, the hippopotamus may be the closest living relative of the whale.

## Summary

Scientists continually gain new information that helps understand the evolutionary history of life on Earth. Each group of organisms went through its own evolutionary journey, called its phylogeny. Each organism shares relatedness with others, and based on morphologic and genetic evidence, scientists attempt to map the evolutionary pathways of all life on Earth. Historically, organisms were organized into a taxonomic classification system. However, today many scientists build phylogenetic trees to illustrate evolutionary relationships.

## Contributors and Attributions

Curated and authored by Maria Morrow using the following sources:

- 20.1 Organizing Life on Earth from *Biology* by OpenStax (licensed CC-BY). Access for free at openstax.org.

---

This page titled 3.2.1.2: Organizing Life on Earth is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **2.1.2: Organizing Life on Earth** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC 4.0.

# 3.2.1.3: Determining Evolutionary Relationships

**Learning Objectives**

- Compare homologous and analogous traits.
- Discuss the purpose of cladistics.
- Describe the concept of maximum parsimony.

Scientists must collect accurate information that allows them to make evolutionary connections among organisms. Similar to detective work, scientists must use evidence to uncover the facts. In the case of phylogenies, evolutionary investigations focus on two types of evidence: morphologic (form and function) and genetic.

## Two Options for Similarities

In general, organisms that share similar physical features and genomes tend to be more closely related than those that do not. Such features that overlap both morphologically (in form) and genetically are referred to as **homologous structures** and stem from developmental similarities that are based on evolution. For example, the bones in the wings of bats and birds have homologous structures (Figure 3.2.1.3.1), as do the leaves of monocots and eudicots (Figure 3.2.1.3.2).

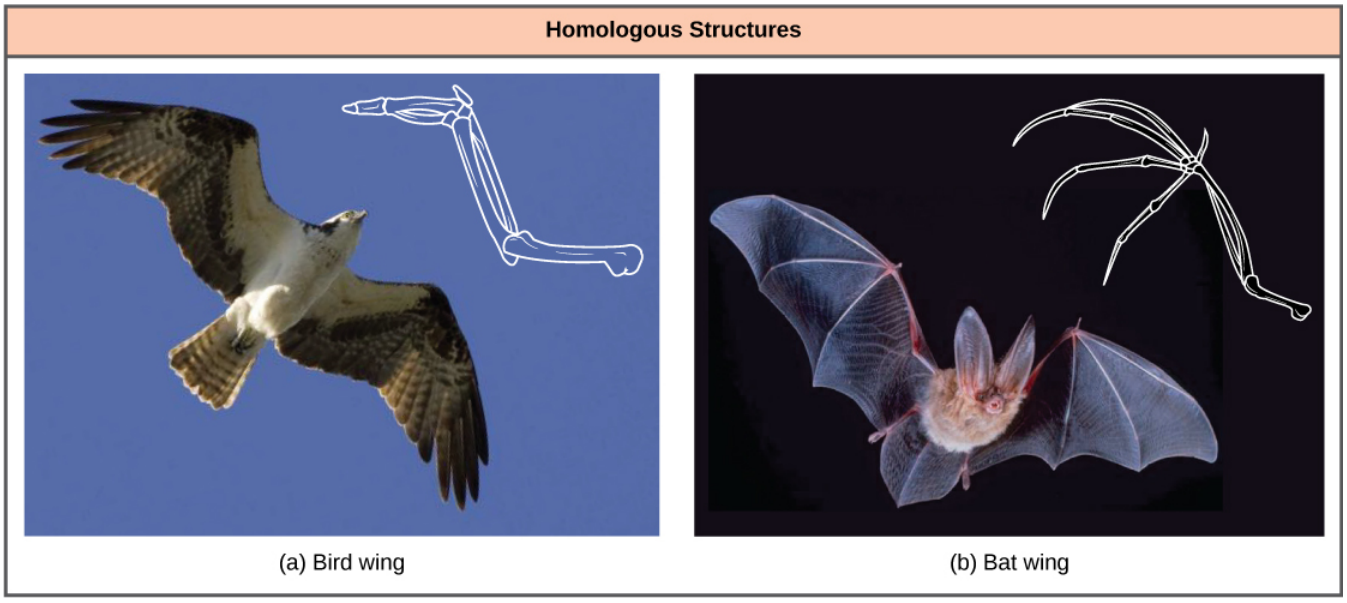



Figure 3.2.1.3.1: Bat and bird wings are homologous structures, indicating that bats and birds share a common evolutionary past. Both the bird wing and the bat wing share common bones, analogous to the bones in the arms and fingers of humans. However, in the bat wing, the finger bones are long and separate and form a scaffolding on which the wing's membrane is stretched. In the bird wing, the finger bones are short and fused together at the front of the wing. (credit a: modification of work by Steve Hillebrand, USFWS; credit b: modification of work by U.S. DOI BLM)

Notice it is not simply a single bone, but rather a grouping of several bones arranged in a similar way. The more complex the feature, the more likely any kind of overlap is due to a common evolutionary past. Imagine two people from different countries both inventing a car with all the same parts and in exactly the same arrangement without any previous or shared knowledge. That outcome would be highly improbable. However, if two people both invented a hammer, it would be reasonable to conclude that both could have the original idea without the help of the other. The same relationship between complexity and shared evolutionary history is true for homologous structures in organisms.

In plants, we see similar trends. An example of a homologous structure in plants is the leaf. Groups of vascular plants have evolved from a shared common ancestor that formed leaves. In particular, we could look at leaves formed by flowering plants (Angiosperms), the most recent major clade within kingdom Plantae. The developmental pathway and internal anatomy of these leaves have similarities due to shared ancestry, though they may appear outwardly different.

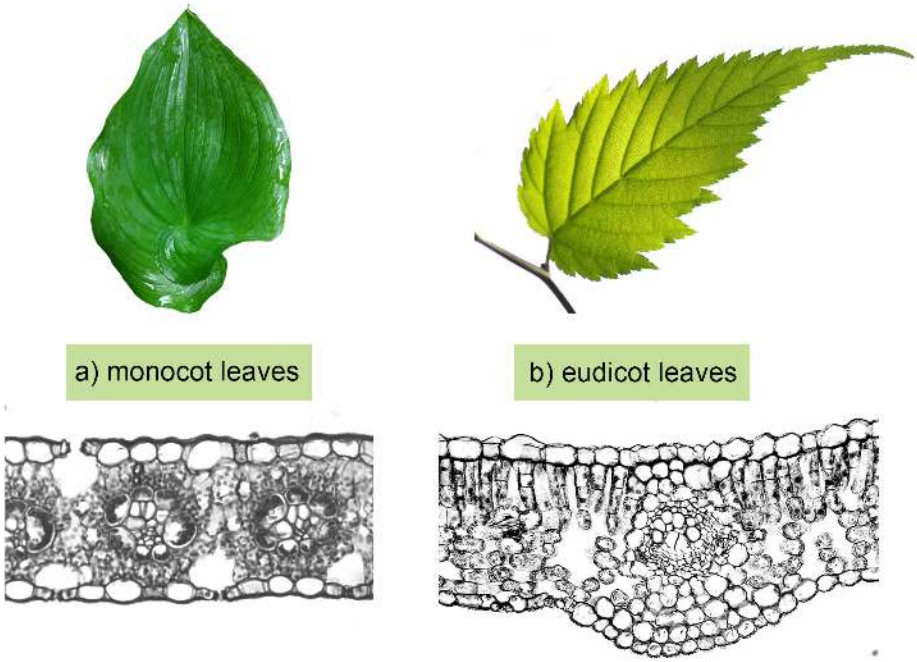



Figure 3.2.1.3.2: Monocots and eudicots are two major divisions within flowering plants. The leaves of these plants have differences in anatomy and morphology that allow us to distinguish between the two groups. However, the overall structure is very similar. This is because their leaves are homologous, derived from a shared common ancestor but diverging in appearance over evolutionary time. Figure created by Maria Morrow with modification of work by Simon A. Eugster (eudicot leaf), CC BY-SA 4.0, via Wikimedia Commons.

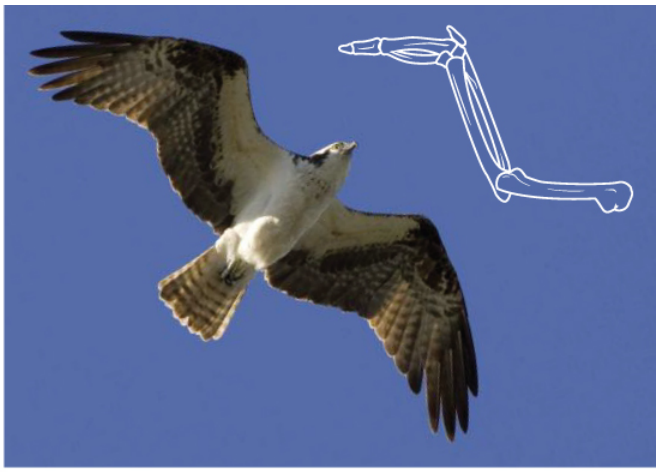
## Misleading Appearances

Some organisms may be very closely related, even though a minor genetic change caused a major morphological difference to make them look quite different. Similarly, unrelated organisms may be distantly related, but appear very much alike. This usually happens because both organisms were in common adaptations that evolved within similar environmental conditions. When similar characteristics occur because of environmental constraints and not due to a close evolutionary relationship, it is called an analogy or homoplasy. For example, insects use wings to fly like bats and birds, but the wing structure and embryonic origin is completely different. These are called **analogous structures** (Figure 3.2.1.3.3 and Figure 3.2.1.3.4).

Similar traits can be either homologous or analogous. Homologous traits are shared due to common ancestry; analogous traits have a similar function but are not similar due to common ancestory. For example, the bones in the front flipper of a whale are homologous to the bones in the human arm, though one is specialized for swimming and the other climbing. These structures are not analogous. The wings of a bee and the wings of a bird are analogous but not homologous, both specialized for flying but of completely different biological arrangement. Some structures are both analogous and homologous: the wings of a bird and the wings of a bat are both homologous and analogous, both used for flight and both with a similar biological arrangement. Scientists must determine which type of similarity a feature exhibits to decipher the phylogeny of the organisms being studied.



(a) Bat wing



(b) Bird wing



(c) Insect wing

Figure **3.2.1.3.3**: The (c) wing of a honeybee is similar in shape to a (b) bird wing and (a) bat wing, and it serves the same function. However, unlike the bat and bird wings, the honeybee wing is not composed of bones and has a distinctly different structure and embryonic origin. These wing types (insect versus bat and bird) illustrate an analogy—similar structures that do not share an evolutionary history. (credit a: modification of work by Steve Hillebrand, USFWS; credit b: modification of work by U.S. DOI BLM; credit c: modification of work by Jon Sullivan)

*Link to Learning: This website has several examples to show how appearances can be misleading in understanding the phylogenetic relationships of organisms.*

Analogous structures are often caused by **convergent evolution** of structures used for similar functions. For example, there are many different groups of unrelated organisms that photosynthesize. Plants are one lineage of photosynthetic organisms, whose ancestors are shared with the green and red algae. The brown algae have a completely different evolutionary history and do not share a common ancestor with plants (they are more closely related to water molds). However, many brown algae form flat, leaf-like structures similar to plants, as both groups use these structures for photosynthesis. Many brown algae, such as the kelps, also form stem- and root-like structures (see Figure **3.2.1.3.4**).



Figure **3.2.1.3.4**: Analogous structures. Brown algae, such as this sea palm (*Postelsia palmaeformis*) are not closely related to plants. However, because they have a similar nutritional strategy (photosynthesis), they have evolved similar looking features. Sea palms have an anchorage system called a holdfast that looks like roots emerging from the base. A stem-like stipe holds the leaf-like blades aloft. Photo by Peter Pearsall/U.S. Fish and Wildlife Service, USFWS - Pacific Region, Public domain, via Wikimedia Commons.

## Molecular Comparisons

With the advancement of DNA technology, the area of molecular systematics, which describes the use of information on the molecular level including DNA analysis, has blossomed. New computer programs not only confirm many earlier classified organisms, but also uncover previously made errors. As with physical characteristics, even the DNA sequence can be tricky to read in some cases. For some situations, two very closely related organisms can appear unrelated if a mutation occurred that caused a shift in the genetic code. An insertion or deletion mutation would move each nucleotide base over one place, causing two similar codes to appear unrelated.

Sometimes two segments of DNA code in distantly related organisms randomly share a high percentage of bases in the same locations, causing these organisms to appear closely related when they are not. For both of these situations, computer technologies have been developed to help identify the actual relationships, and, ultimately, the coupled use of both morphologic and molecular information is more effective in determining phylogeny.




Figure **3.2.1.3.5**: This image shows amino acid sequences for the same protein (VEGF) in humans and mice. Each line represents the sequence of a different individual. Each letter represents an amino acid. The sequences have been aligned to find similarities and differences. The bars across the sequences show amino acids that are unchanged across the organisms tested. These positions are considered shared ancestral characteristics. At all other locations, there may be differences in the amino acids between organisms. We can use these as synapomorphies to build a tree, assuming that organisms who share more similar sequences are more closely related. This information has revolutionized the way phylogenies are built. "Alignment of the VEGF Homology Domain of representative VEGFs (all mammalian VEGFs from human and mouse plus one VEGF-E (viral) and one VEGF-F (snake venom)" Mjeltsch, CC BY-SA 4.0, via Wikimedia Commons.

Why does phylogeny matter? Evolutionary biologists could list many reasons why understanding phylogeny is important to everyday life in human society. For botanists, phylogeny acts as a guide to discovering new plants that can be used to benefit people. Think of all the ways humans use plants—food, medicine, and clothing are a few examples. If a plant contains a compound that is effective in treating cancer, scientists might want to examine all of the relatives of that plant for other useful drugs.

A research team in China identified a segment of DNA thought to be common to some medicinal plants in the family Fabaceae (the legume family) and worked to identify which species had this segment (Figure **3.2.1.3.6**). After testing plant species in this family, the team found a DNA marker (a known location on a chromosome that enabled them to identify the species) present. Then, using the DNA to uncover phylogenetic relationships, the team could identify whether a newly discovered plant was in this family and assess its potential medicinal properties.




Figure **3.2.1.3.6**: Dalbergia sissoo (D. sissoo) is in the Fabaceae, or legume family. Scientists found that D. sissoo shares a DNA marker with species within the Fabaceae family that have antifungal properties. Subsequently, *D. sissoo* was shown to have fungicidal activity, supporting the idea that DNA markers can be used to screen for plants with potential medicinal properties.

## Building Phylogenetic Trees

How do scientists construct phylogenetic trees? After the homologous and analogous traits are sorted, scientists often organize the homologous traits using a system called cladistics. This system sorts organisms into **clades**: groups of organisms that descended from a single ancestor. For example, in Figure **3.2.1.3.7**, all of the organisms in the orange region evolved from a single ancestor that had amniotic eggs. Consequently, all of these organisms also have amniotic eggs and make a single clade, also called a **monophyletic** group. Clades must include all of the descendants from a branch point.

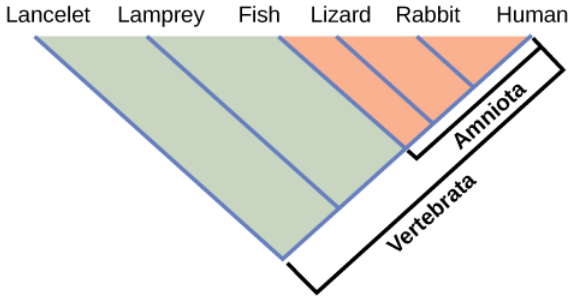



Figure **3.2.1.3.7**: A phylogeny of vertebrates. Lizards, rabbits, and humans all descend from a common ancestor that had an amniotic egg. Thus, lizards, rabbits, and humans all belong to the clade Amniota. Vertebrata is a larger clade that also includes fish and lamprey. Descriptive text: Lancelets are at the left tip of the V, and humans are at the right tip. Four more lines are drawn parallel to the lancelet line; each of these lines starts further up the right arm of the V than the next. At the end of each line, from left to right, are lampreys, fish, lizards, and rabbits. Lizards, rabbits, and humans are in the clade Amniota, which form a small V nested in the upper right-hand corner of the V-shaped Vertebrata clade.

Clades can vary in size depending on which branch point is being referenced. The important factor is that all of the organisms in the clade or monophyletic group stem from a single point on the tree. This can be remembered because monophyletic breaks down into “mono,” meaning one, and “phyletic,” meaning evolutionary relationship. Figure **3.2.1.3.8** shows various examples of clades. Notice how each clade comes from a single point, whereas the non-clade groups show branches that do not share a single point.

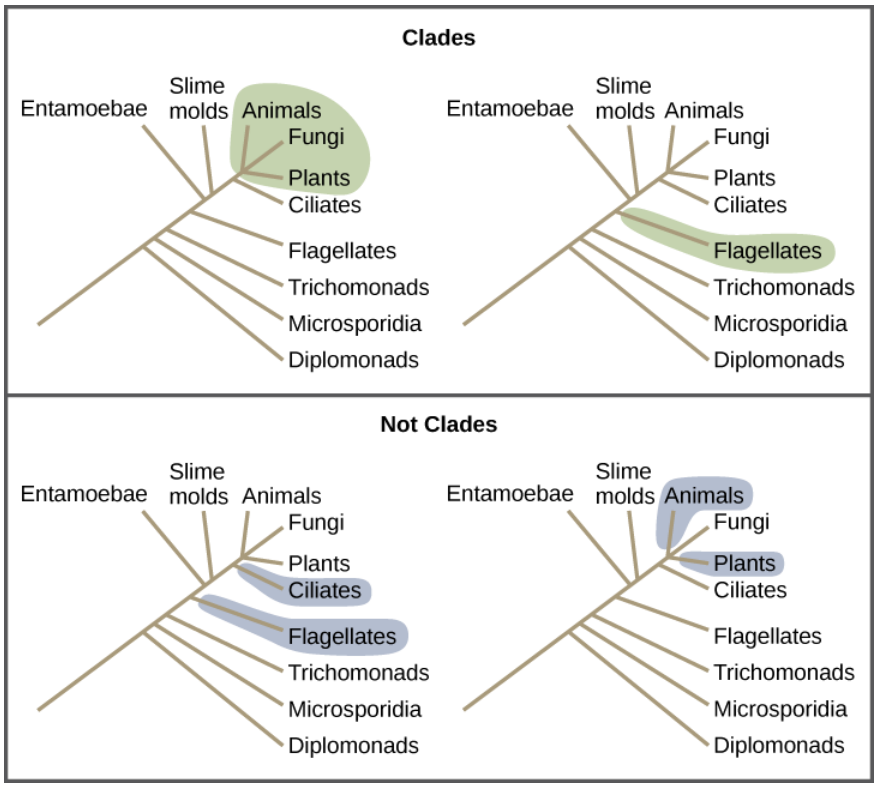



Figure **3.2.1.3.8**: All the organisms within a clade stem from a single point on the tree. A clade may contain multiple groups, as in the case of animals, fungi and plants, or a single group, as in the case of flagellates. Groups that diverge at a different branch point, or that do not include all groups in a single branch point, are not considered clades. Descriptive text: In order from the bottom, these are diplomonads, microsporidia, trichomonads, flagellates, entamoebae, slime molds, and ciliates. At the top of the tree, animals, fungi and plants all branch from the same point and are shaded to show that they belong in the same clade. Flagellates are on a branch by themselves, and they also form their own clade and are shaded to show this. In another image, Flagellates and ciliates are shaded to show that they branch from different points on the tree and are not considered clades. Likewise, a grouping of animals and plants but not fungi would not be considered a clade cannot exclude a branch originating at the same point as the others.

Phylogenetic trees can be constructed by scoring similarities and differences between the taxa of interest (check out this supplementary video to see how it is done). These traits can be morphological or developmental features (Figure **3.2.1.3.7**) or genetic traits called **single nucleotide polymorphisms** (SNPs, or snips, for short). Taxa with the most similarities are placed into the same clade.

## Shared Characteristics

Organisms evolve from common ancestors and then diversify. Scientists use the phrase “descent with modification” because even though related organisms have many of the same characteristics and genetic codes, changes occur. This pattern repeats over and over as one goes through the phylogenetic tree of life:

1. A change in the genetic makeup of an organism leads to a new trait which becomes prevalent in the group.
2. Many organisms descend from this point and have this trait.
3. New variations continue to arise: some are adaptive and persist, leading to new traits.
4. With new traits, a new branch point is determined (go back to step 1 and repeat).

If a characteristic is found in the ancestor of a group, it is considered a **shared ancestral character** because all of the organisms in the taxon or clade have that trait. The vertebrate in Figure **3.2.1.3.7** is a shared ancestral character. Now consider the amniotic egg

characteristic in the same figure. Only some of the organisms in Figure **3.2.1.3.7** have this trait, and to those that do, it is called a **shared derived character** because this trait derived at some point but does not include all of the ancestors in the tree.

The tricky aspect to shared ancestral and shared derived characters is the fact that these terms are relative. The same trait can be considered one or the other depending on the particular diagram being used. Returning to Figure **3.2.1.3.8**, note that the amniotic egg is a shared ancestral character for the Amniota clade, while having hair is a shared derived character for some organisms in this group. These terms help scientists distinguish between clades in the building of phylogenetic trees.

### Choosing the Right Relationships

Imagine being the person responsible for organizing all of the items in a department store properly—an overwhelming task. Organizing the evolutionary relationships of all life on Earth proves much more difficult: scientists must span enormous blocks of time and work with information from long-extinct organisms. Trying to decipher the proper connections, especially given the presence of homologies and analogies, makes the task of building an accurate tree of life extraordinarily difficult. Add to that the advancement of DNA technology, which now provides large quantities of genetic sequences to be used and analyzed. Taxonomy is a subjective discipline: many organisms have more than one connection to each other, so each taxonomist will decide the order of connections.

To aid in the tremendous task of describing phylogenies accurately, scientists often use a concept called **maximum parsimony.** Maximum parsimony is a principles that assumes the fewest evolutionary events occurred in a given phylogeny. This is also called **Ockham's razer** - that we should also select the simplest hypothesis that explains the data. **Maximum likelihood**, another principle used when constructing phylogenies, suggests that the most likely sequence of evolutionary events most likely occured.

For example, if you saw a friend who was wearing a blue shirt, then saw them again in the evening and they were still wearing that blue shirt, you'd probably assume that they had been wearing that same blue shirt all day. However, it is possible that they went home, changed, and changed back or changed into a shirt that looks very similar. It is just less likely, and so we often assume the former.

For scientists deciphering evolutionary pathways, the same idea is used: the pathway of evolution probably includes the fewest major events that coincide with the evidence at hand. Starting with all of the homologous traits in a group of organisms, scientists look for the most obvious and simple order of evolutionary events that led to the occurrence of those traits.

These tools and concepts are only a few of the strategies scientists use to tackle the task of revealing the evolutionary history of life on Earth. Recently, newer technologies have uncovered surprising discoveries with unexpected relationships, such as the fact that people seem to be more closely related to fungi than fungi are to plants. Sound unbelievable? As the information about DNA sequences grows, scientists will become closer to mapping the evolutionary history of all life on Earth.

## Summary

To build phylogenetic trees, scientists must collect accurate information that allows them to make evolutionary connections between organisms. Using morphologic and molecular data, scientists work to identify homologous characteristics and genes. Similarities between organisms can stem either from shared evolutionary history (homologies) or from separate evolutionary paths (analogies). Newer technologies can be used to help distinguish homologies from analogies. After homologous information is identified, scientists use cladistics to organize these events as a means to determine an evolutionary timeline. Scientists apply the principles of maximum parsimony and maximum likelihood, which state that the order of events probably occurred in the most obvious and simple way with the least amount of steps and that the the most likely sequence of evolutionary events probably occured. For evolutionary events, this would be the path with the least number of major divergences that correlate with the evidence.

## Contributors and Attributions

Curated and authored by Maria Morrow using the following sources:

- 20.2 Determining Evolutionary Relationships from *Biology* by OpenStax (licensed CC-BY). Access for free at openstax.org.

This page titled 3.2.1.3: Determining Evolutionary Relationships is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **2.1.3: Determining Evolutionary Relationships** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-SA 4.0.

# 3.2.1.4: Perspectives on the Phylogenetic Tree

**Learning Objectives**

- Describe horizontal gene transfer.
- Illustrate how prokaryotes and eukaryotes transfer genes horizontally.
- Describe the process of endosymbiosis and explain how this can produce membrane-bound organelles.
- Identify the web and ring models of phylogenetic relationships and describe how they differ from the original phylogenetic tree concept.

The concepts of phylogenetic modeling are constantly changing. It is one of the most dynamic fields of study in all of biology. Over the last several decades, new research has challenged scientists' ideas about how organisms are related. New models of these relationships have been proposed for consideration by the scientific community.

Many phylogenetic trees have been shown as models of the evolutionary relationship among species. Phylogenetic trees originated with Charles Darwin, who sketched the first phylogenetic tree in 1837 (Figure **3.2.1.4.1**a), which served as a pattern for subsequent studies for more than a century. The concept of a phylogenetic tree with a single trunk representing a common ancestor, with the branches representing the divergence of species from this ancestor, fits well with the structure of many common trees, such as the oak (**3.2.1.4.***a*b). However, evidence from modern DNA sequence analysis and newly developed computer algorithms has caused skepticism about the validity of the standard tree model in the scientific community.




(a) (b)

Figure **3.2.1.4.1**: The (a) concept of the "tree of life" goes back to an 1837 sketch by Charles Darwin. Like an (b) oak tree, the "tree of life" has a single trunk and many branches. (credit b: modification of work by "Amada44"/Wikimedia Commons)

## Limitations to the Classic Model

Classical thinking about prokaryotic evolution, included in the classic tree model, is that species evolve clonaly. That is, they produce offspring themselves with only random mutations causing the descent into the variety of modern-day and extinct species known to science. This view is somewhat complicated in eukaryotes that reproduce sexually, but the laws of Mendelian genetics explain the variation in offspring, again, to be a result of a mutation within the species. The concept of genes being transferred between unrelated species was not considered as a possibility until relatively recently. **Horizontal gene transfer** (HGT), also known as lateral gene transfer, is the transfer of genes between unrelated species. HGT has been shown to be an ever-present phenomenon, with many evolutionists postulating a major role for this process in evolution, thus complicating the simple tree

model. Genes have been shown to be passed between species which are only distantly related using standard phylogeny, thus adding a layer of complexity to the understanding of phylogenetic relationships.

The various ways that HGT occurs in prokaryotes is important to understanding phylogenies. Although at present HGT is not viewed as important to eukaryotic evolution, HGT does occur in this domain as well. Finally, as an example of the ultimate gene transfer, theories of genome fusion between symbiotic or endosymbiotic organisms have been proposed to explain an event of great importance—the evolution of the first eukaryotic cell, without which humans could not have come into existence.

## Horizontal Gene Transfer

Horizontal gene transfer (HGT) is the introduction of genetic material from one species to another species by mechanisms other than the vertical transmission from parent(s) to offspring. These transfers allow even distantly related species to share genes, influencing their phenotypes. It is thought that HGT is more prevalent in prokaryotes, but that only about 2% of the prokaryotic genome may be transferred by this process. Some researchers believe such estimates are premature: the actual importance of HGT to evolutionary processes must be viewed as a work in progress. As the phenomenon is investigated more thoroughly, it may be revealed to be more common. Many scientists believe that HGT and mutation appear to be (especially in prokaryotes) a significant source of genetic variation, which is the raw material for the process of natural selection. These transfers may occur between any two species that share an intimate relationship (Table **3.2.1.4.1**).

**Table 3.2.1.4.1:** Summary of Mechanisms of Prokaryotic and Eukaryotic HGT.

| | Mechanism | Mode of Transmission | Example |
|---|---|---|---|
| **Prokaryotes** | transformation | DNA uptake | many prokaryotes |
| | transduction | bacteriophage (virus) | bacteria |
| | conjugation | pilus | many prokaryotes |
| | gene transfer agents | phage-like particles | purple non-sulfur bacteria |
| **Eukaryotes** | from food organisms | unknown | aphid |
| | jumping genes | transposons | rice and millet plants |
| | epiphytes/parasites | unknown | yew tree fungi |
| | from viral infections | | |

### HGT in Prokaryotes

The mechanism of HGT has been shown to be quite common in the prokaryotic domains of Bacteria and Archaea, significantly changing the way their evolution is viewed. The majority of evolutionary models, such as in the **Endosymbiotic Theory**, propose that eukaryotes descended from multiple prokaryotes, which makes HGT all the more important to understanding the phylogenetic relationships of all extant and extinct species.

The fact that genes are transferred among common bacteria is well known to microbiology students. These gene transfers between species are the major mechanism whereby bacteria acquire resistance to antibiotics. Classically, this type of transfer has been thought to occur by three different mechanisms:

1. **Transformation**: naked DNA is taken up by a bacteria
2. **Transduction**: genes are transferred using a virus
3. **Conjugation**: the use a hollow tube called a pilus to transfer genes between organisms

More recently, a fourth mechanism of gene transfer between prokaryotes has been discovered. Small, virus-like particles called **gene transfer agents** (GTAs) transfer random genomic segments from one species of prokaryote to another. GTAs have been shown to be responsible for genetic changes, sometimes at a very high frequency compared to other evolutionary processes. The first GTA was characterized in 1974 using purple, non-sulfur bacteria. These GTAs, which are thought to be bacteriophages (viruses that infect bacteria) that lost the ability to reproduce on their own, carry random pieces of DNA from one organism to

another. The ability of GTAs to act with high frequency has been demonstrated in controlled studies using marine bacteria. Gene transfer events in marine prokaryotes, either by GTAs or by viruses, have been estimated to be as high as $10^{13}$ per year in the Mediterranean Sea alone. GTAs and viruses are thought to be efficient HGT vehicles with a major impact on prokaryotic evolution.

As a consequence of this modern DNA analysis, the idea that eukaryotes evolved directly from Archaea has fallen out of favor. While eukaryotes share many features that are absent in bacteria, such as the TATA box (found in the promoter region of many genes), the discovery that some eukaryotic genes were more homologous with bacterial DNA than Archaea DNA made this idea less tenable. Furthermore, the fusion of genomes from Archaea and Bacteria by endosymbiosis has been proposed as the ultimate event in eukaryotic evolution.

## HGT in Eukaryotes

Although it is easy to see how prokaryotes exchange genetic material by HGT, it was initially thought that this process was absent in eukaryotes. After all, prokaryotes are but single cells exposed directly to their environment, whereas the sex cells of multicellular organisms are usually sequestered in protected parts of the body. It follows from this idea that the gene transfers between multicellular eukaryotes should be more difficult. Indeed, it is thought that this process is rarer in eukaryotes and has a much smaller evolutionary impact than in prokaryotes. In spite of this fact, HGT between distantly related organisms has been demonstrated in several eukaryotic species, and it is possible that more examples will be discovered in the future.

In plants, gene transfer has been observed in species that cannot cross-pollinate by normal means. Transposons or “jumping genes” have been shown to transfer between rice and millet plant species. Furthermore, fungal species feeding on yew trees, from which the anti-cancer drug TAXOL® is derived from the bark, have acquired the ability to make taxol themselves, a clear example of gene transfer.

In animals, a particularly interesting example of HGT occurs within the aphid species (Figure **3.2.1.4.2**). Aphids are insects that vary in color based on carotenoid content. Carotenoids are pigments made by a variety of plants, fungi, and microbes, and they serve a variety of functions in animals, who obtain these chemicals from their food. Humans require carotenoids to synthesize vitamin A, and we obtain them by eating orange fruits and vegetables: carrots, apricots, mangoes, and sweet potatoes. On the other hand, aphids have acquired the ability to make the carotenoids on their own. According to DNA analysis, this ability is due to the transfer of fungal genes into the insect by HGT, presumably as the insect consumed fungi for food. A carotenoid enzyme called a desaturase is responsible for the red coloration seen in certain aphids, and it has been further shown that when this gene is inactivated by mutation, the aphids revert back to their more common green color (Figure **3.2.1.4.2**).



(a) (b)

Figure **3.2.1.4.2**: (a) Red aphids get their color from red carotenoid pigment. Genes necessary to make this pigment are present in certain fungi, and scientists speculate that aphids acquired these genes through HGT after consuming fungi for food. If genes for making carotenoids are inactivated by mutation, the aphids revert back to (b) their green color. Red coloration makes the aphids a lot more conspicuous to predators, but evidence suggests that red aphids are more resistant to insecticides than green ones. Thus, red aphids may be more fit to survive in some environments than green ones. (credit a: modification of work by Benny Mazur; credit b: modification of work by Mick Talbot)

## Endosymbiosis, Genome Fusion, and the Evolution of Eukaryotes

Scientists believe the ultimate in HGT occurs through genome fusion between different species of prokaryotes when two symbiotic organisms become **endosymbiotic**. This occurs when one species is taken inside the cytoplasm of another species (see Figure **3.2.1.4.3**), which ultimately results in a genome consisting of genes from both the endosymbiont and the host. This mechanism is an aspect of the Endosymbiont Theory, which is accepted by a majority of biologists as the mechanism whereby eukaryotic cells obtained their mitochondria and chloroplasts. However, the role of endosymbiosis in the development of the nucleus is more controversial. Nuclear and mitochondrial DNA are thought to be of different (separate) evolutionary origin, with the mitochondrial DNA being derived from the circular genomes of bacteria that were engulfed by ancient prokaryotic cells. Mitochondrial DNA can be regarded as the smallest chromosome. Mitochondrial DNA is usually inherited from the mother only. The mitochondrial DNA degrades in sperm when the sperm degrades in the fertilized egg or in other instances when the mitochondria located in the flagellum of the sperm fails to enter the egg. However, recent studies suggest fathers also occasionally contribute their mitochondrial DNA to their offspring as well (See this Nature Article).

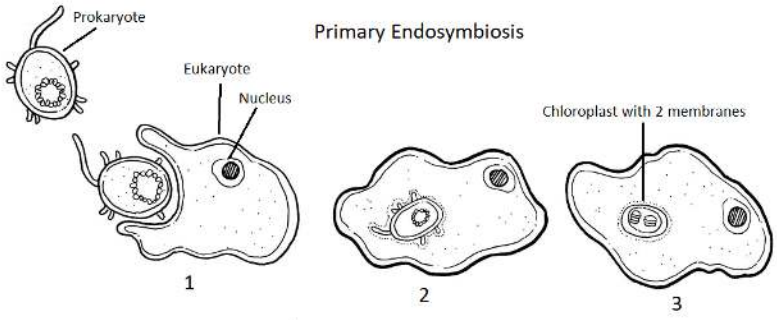



Figure **3.2.1.4.3**: This diagram shows a prokaryotic cell on the far left. In step one, this cell is engulfed by a eukaryotic cell. In step two, we see the prokaryotic cell trapped within the eukaryotic cell, though it still looks the same as before it was engulfed. It is surrounded by a membrane of the eukaryote (dotted line). In step three, assumedly after a long period of evolution and intermediate stages, we see a fully formed chloroplast with two membranes. Artwork by Nikki Harris CC BY-NC with added labels by Maria Morrow.

Within the past decade, the process of genome fusion by endosymbiosis has been proposed by James Lake of the UCLA/NASA Astrobiology Institute to be responsible for the evolution of the first eukaryotic cells (Figure **3.2.1.4.4**a). Using DNA analysis and a new mathematical algorithm called conditioned reconstruction (CR), his laboratory proposed that eukaryotic cells developed from an endosymbiotic gene fusion between two species, one an Archaea and the other a Bacteria. As mentioned, some eukaryotic genes resemble those of Archaea, whereas others resemble those from Bacteria. An endosymbiotic fusion event, such as Lake has proposed, would clearly explain this observation. On the other hand, this work is new and the CR algorithm is relatively unsubstantiated, which causes many scientists to resist this hypothesis.

More recent work by Lake (**3.2.1.4.4**b) proposes that gram-negative bacteria, which are unique within their domain in that they contain two lipid bilayer membranes, indeed resulted from an endosymbiotic fusion of archaeal and bacterial species. The double membrane would be a direct result of the endosymbiosis, with the endosymbiont picking up the second membrane from the host as it was internalized. This mechanism has also been used to explain the double membranes found in mitochondria and chloroplasts. Lake's work is not without skepticism, and the ideas are still debated within the biological science community. In addition to Lake's hypothesis, there are several other competing theories as to the origin of eukaryotes. How did the eukaryotic nucleus evolve? One theory is that the prokaryotic cells produced an additional membrane that surrounded the bacterial chromosome. Some bacteria have the DNA enclosed by two membranes; however, there is no evidence of a nucleolus or nuclear pores. Other proteobacteria also have membrane-bound chromosomes. If the eukaryotic nucleus evolved this way, we would expect one of the two types of prokaryotes to be more closely related to eukaryotes.

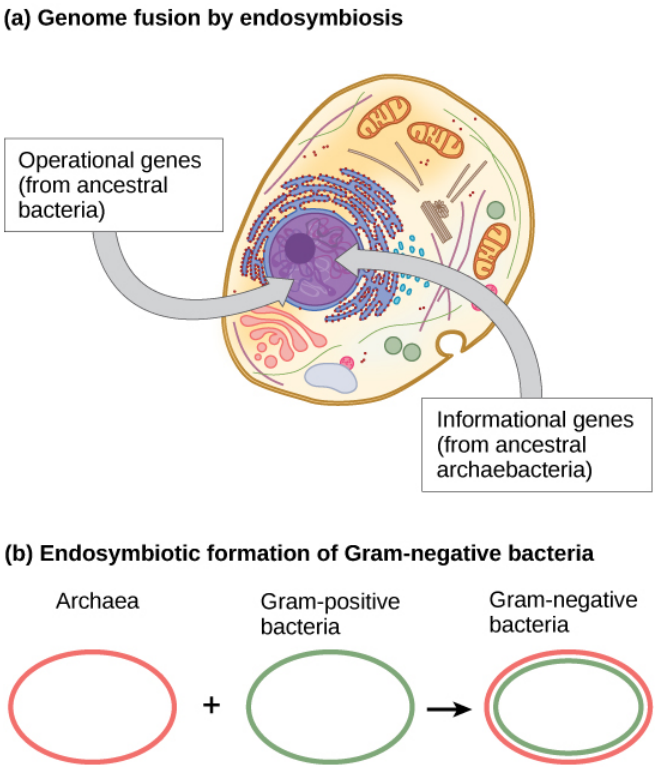



Figure **3.2.1.4.4**: The theory that mitochondria and chloroplasts are endosymbiotic in origin is now widely accepted. More controversial is the proposal that (a) the eukaryotic nucleus resulted from the fusion of archaeal and bacterial genomes, and that (b) Gram-negative bacteria, which have two membranes, resulted from the fusion of Archaea and Gram-positive bacteria, each of which has a single membrane. Descriptive text: The illustration indicates that, within the nucleus, operational genes were inherited from an ancestral Eubacteria, and informational genes were inherited from an ancestral Archaebacteria. Part B indicates that the outer membrane of Gram-negative bacteria is derived from Archaea, and the inner membrane is derived from Gram-positive bacteria.

The nucleus-first hypothesis proposes that the nucleus evolved in prokaryotes first (**3.2.1.4.5**a), followed by a later fusion of the new eukaryote with bacteria that became mitochondria. The mitochondria-first hypothesis proposes that mitochondria were first established in a prokaryotic host (**3.2.1.4.5**b), which subsequently acquired a nucleus, by fusion or other mechanisms, to become the first eukaryotic cell. Most interestingly, the eukaryote-first hypothesis proposes that prokaryotes actually evolved from eukaryotes by losing genes and complexity (**3.2.1.4.5**c). All of these hypotheses are testable. Only time and more experimentation will determine which hypothesis is best supported by data.

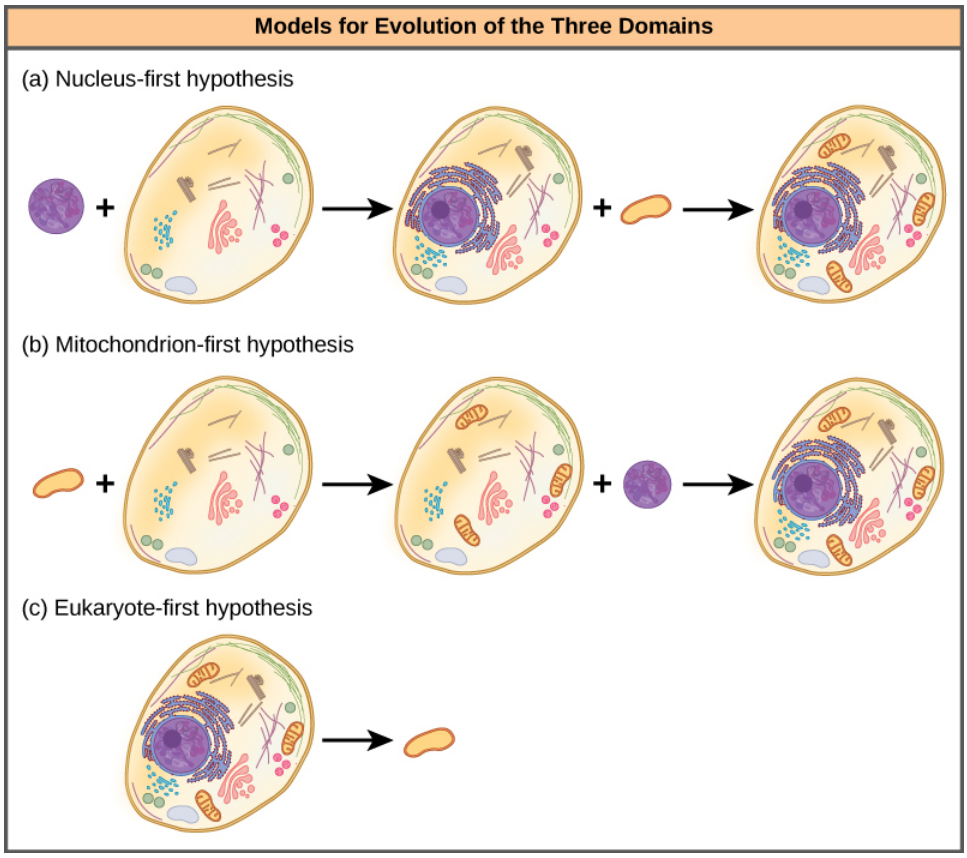
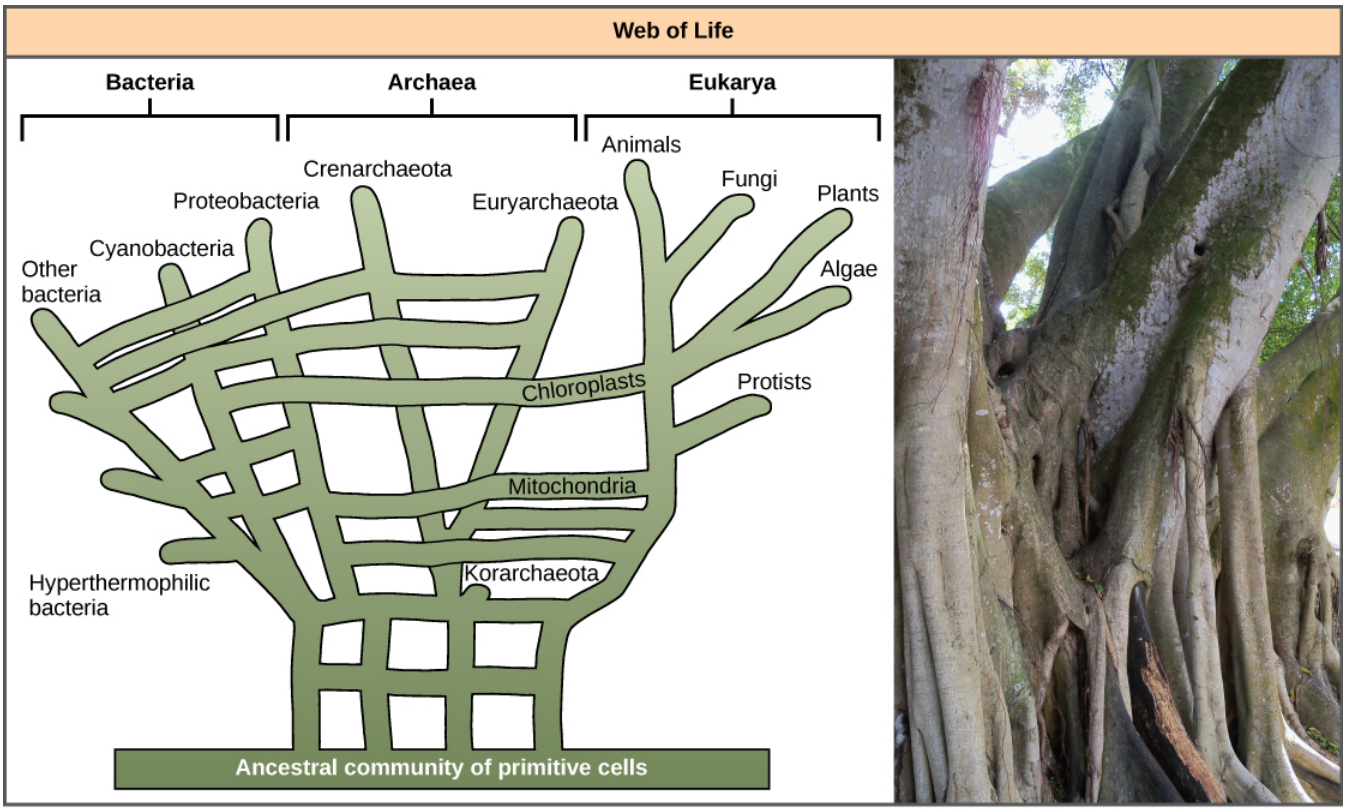



Figure **3.2.1.4.5**: Three alternate hypotheses of eukaryotic and prokaryotic evolution are (a) the nucleus-first hypothesis, (b) the mitochondrion-first hypothesis, and (c) the eukaryote-first hypothesis. In the nucleus-first hypothesis, a primary endosymbiotic event resulted in an ancestral eukaryotic cell acquiring a nucleus, and a secondary endosymbiotic event resulted in the acquisition of a mitochondrion. In the mitochondrion-first hypothesis, the mitochondrion was acquired before the nucleus, but both were acquired by endosymbiosis. In the eukaryote-first hypothesis, prokaryotes evolved from eukaryotic cells that lost their nuclei and organelles.

## Web and Network Models

The recognition of the importance of HGT, especially in the evolution of prokaryotes, has caused some to propose abandoning the classic "tree of life" model. In 1999, W. Ford Doolittle proposed a phylogenetic model that resembles a web or a network more than a tree. The hypothesis is that eukaryotes evolved not from a single prokaryotic ancestor, but from a pool of many species that were sharing genes by HGT mechanisms. As shown in Figure **3.2.1.4.6**a, some individual prokaryotes were responsible for transferring the bacteria that caused mitochondrial development to the new eukaryotes, whereas other species transferred the bacteria that gave rise to chloroplasts. This model is often called the "web of life." In an effort to save the tree analogy, some have proposed using the *Ficus* tree (Figure **3.2.1.4.6**b) with its multiple trunks as a phylogenetic to represent a diminished evolutionary role for HGT.




(a) (b)

Figure **3.2.1.4.6**): Web of life model showing the three domains of life. In (a), branches of the tree of life are connected laterally by genome transfer events (mitochondria and chloroplasts are labeled). Instead of appearing as a tree with distinct pathways to follow, the evolutionary "branches" form an interconnected web or net-like structure. At the base of the web, several paths emerge from a shared ancestral community of primitive cells. In (b), the complex aerial roots of a tropical tree cross and attach to each other, forming a similar structure to (a). (credit b: modification of work by "psyberartist"/Flickr) Illustration (a) shows the web of life.

## Ring of Life Models

Others have proposed abandoning any tree-like model of phylogeny in favor of a ring structure, the so-called “ring of life” (Figure **3.2.1.4.7**); a phylogenetic model where all three domains of life evolved from a pool of primitive prokaryotes. Lake, again using the conditioned reconstruction algorithm, proposes a ring-like model in which species of all three domains—Archaea, Bacteria, and Eukarya—evolved from a single pool of gene-swapping prokaryotes. His laboratory proposes that this structure is the best fit for data from extensive DNA analyses performed in his laboratory, and that the ring model is the only one that adequately takes HGT and genomic fusion into account. However, other phylogeneticists remain highly skeptical of this model.

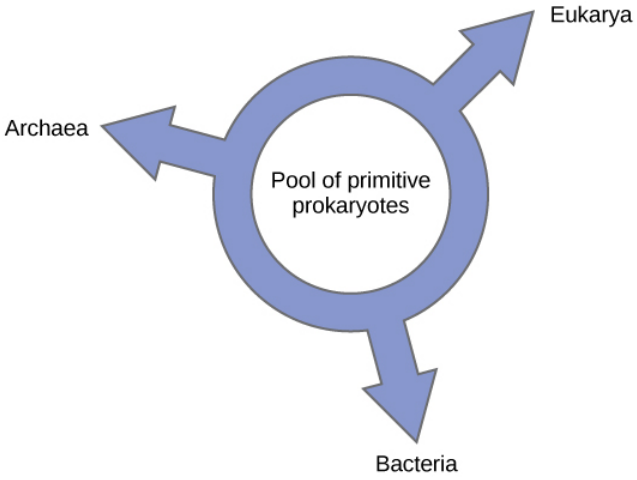



Figure **3.2.1.4.7**: According to the “ring of life” phylogenetic model, the three domains of life evolved from a pool of primitive prokaryotes. No distinct root is present in this model. a ring with the words “pool of primitive prokaryotes” in the middle.

In summary, the “tree of life” model proposed by Darwin must be modified to include HGT. Does this mean abandoning the tree model completely? Even Lake argues that all attempts should be made to discover some modification of the tree model to allow it to accurately fit his data, and only the inability to do so will sway people toward his ring proposal.

This doesn’t mean a tree, web, or a ring will correlate completely to an accurate description of phylogenetic relationships of life. A consequence of the new thinking about phylogenetic models is the idea that Darwin’s original conception of the phylogenetic tree is too simple, but made sense based on what was known at the time. However, the search for a more useful model moves on: each model serving as hypotheses to be tested with the possibility of developing new models. This is how science advances. These models are used as visualizations to help construct hypothetical evolutionary relationships and understand the massive amount of data being analyzed.

## Summary

The phylogenetic tree, first used by Darwin, is the classic “tree of life” model describing phylogenetic relationships among species, and the most common model used today. New ideas about HGT and genome fusion have caused some to suggest revising the model to resemble webs or rings.

## Contributors and Attributions

Curated and authored by Maria Morrow using the following sources:

- 20.3 Perspectives on the Phylogenetic Tree from *Biology* by OpenStax (licensed CC-BY). Access for free at openstax.org.

---

This page titled 3.2.1.4: Perspectives on the Phylogenetic Tree is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **2.1.4: Perspectives on the Phylogenetic Tree** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC 4.0.

## 3.2.1.5: Chapter Summary

All organisms on Earth are related at some point in evolutionary history. In western science, a taxonomic classification system is used to nest organisms into related groups of increasing specificity. Domain is the least specific (most inclusive) level of classification, followed by kingdom, phylum, class, order, family, genus, and finally, species. Organisms placed together in more specific levels of classification (such as family or genus) are thought to be more closely related, sharing a more recent common ancestor than they do with organisms outside those groups.

One way to depict evolutionary relationships between organisms is by using phylogenetic trees. Every phylogenetic tree is a hypothesis based on traits. Traits can be morphological, anatomical, or molecular. Visible characteristics such as morphology and anatomy were originally used to form many of these hypotheses. Included amongst these similar traits are homologous structures and analogous structures. Homologous structures are similar due to evolutionary relatedness, though sometimes they can look quite different due to divergent evolution from different selective pressures. Analogous structures look similar due to similar selective pressures, but have evolved convergently from different lineages.

Genetic information offers a relatively new wealth of molecular traits (single nucleotide polymorphisms) to consider and has upended and reorganized many of the previous hypotheses on evolutionary relationships. However, genetic information can be exchanged between groups of organisms through horizontal gene transfer and endosymbiotic events, rather than vertically through direct evolutionary decent. This complicates the traditional phylogenetic tree representation of evolutionary descent. Other models, such as the web of life and ring of life, have been proposed as alternatives that account for horizontal gene transfer.

Deciphering the relatedness of organisms is a complex task that requires considering a variety of information. The phylogenetic tree of life, like any hypothesis, is subject to change as new information emerges.

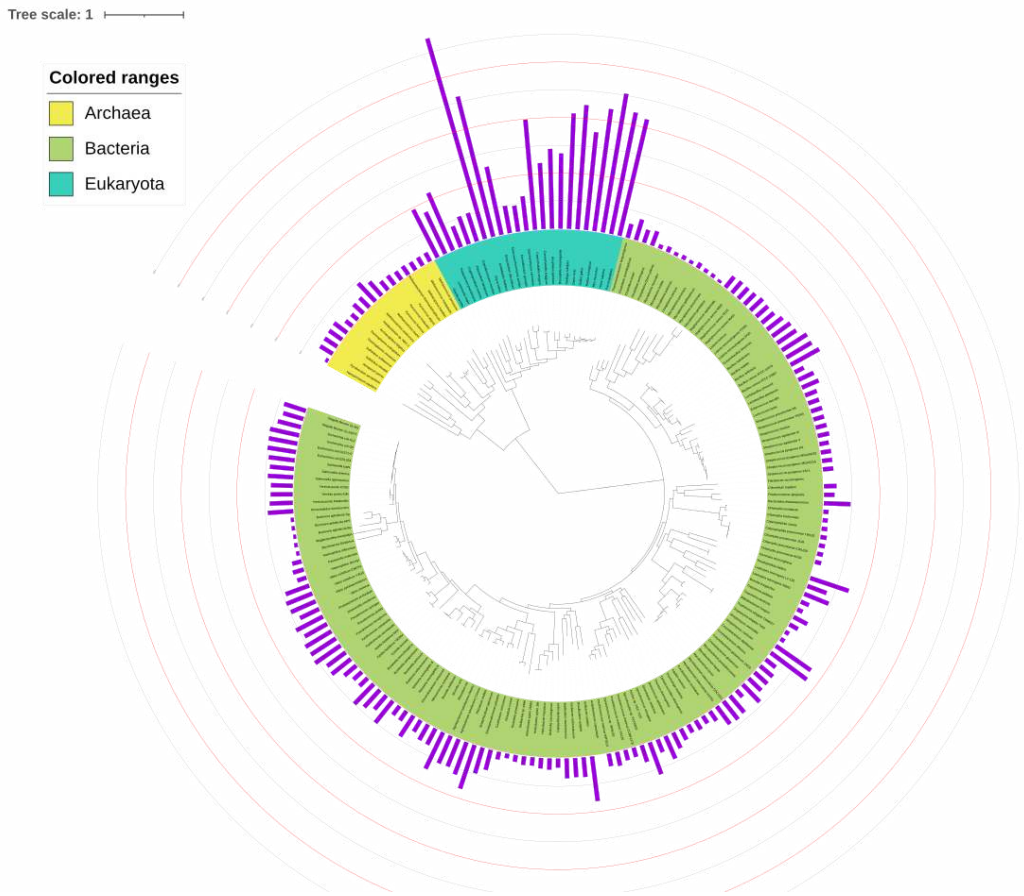



Figure **3.2.1.5.1**: An unrooted phylogeny for all organisms whose entire genome had been sequenced, as of 2006. As sequencing technology has advanced exponentially, many more organisms currently have fully sequenced genomes. The purple bars on the outiside represent the size of the genome for that organism. The eukaryotes have much larger genomes. What might this have to do with the number of prokaryotes vs. eukaryotes sequenced in these early days? This image was generated using iTOL: Interactive Tree Of Life, an online phylogenetic tree viewer and Tree Of Life resource.

## After completing this chapter, you should be able to...

- Discuss the components and purpose of a phylogenetic tree.
- Interpret relationships between organisms using a phylogenetic tree.
- Correctly order the different levels of taxonomic classification.
- Discuss the benefits of having a comprehensive classification system.
- Compare homologous and analogous traits.
- Discuss the purpose of cladistics.
- Describe the concept of maximum parsimony.
- Describe horizontal gene transfer.
- Illustrate how prokaryotes and eukaryotes transfer genes horizontally.
- Describe the process of endosymbiosis and explain how this can produce membrane-bound organelles.
- Identify the web and ring models of phylogenetic relationships and describe how they differ from the original phylogenetic tree concept.

## Attribution

- Content authored by Maria Morrow, CC-BY-NC

This page titled 3.2.1.5: Chapter Summary is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **2.1.5: Chapter Summary** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC 4.0.
- **2.1.3: Determining Evolutionary Relationships** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-SA 4.0.

# SECTION OVERVIEW

## 3.2.2: Early Land Plants

There are four major evolutionary groups of land plants: Bryophytes, Seedless Vascular Plants (SVPs), Gymnosperms, and Angiosperms. These groupings represent major changes in plant structure and life history characteristics over the course of time that coincide with major changes in the evolution of the Earth, as a whole. Early Earth would have looked quite different than the planet you know. When plants first ventured out of the water, there were no soils. The terrestrial landscape would have been rocky, potentially slick with microbial slime. The lack of surrounding water would mean tissues could dry out, as well as increased exposure to oxygen and damaging wavelengths of sunlight. They would also need more structural support, without water to float in, and changes in temperature would be far more extreme and rapid than their former aquatic habitat. However, they would have abundant $CO_2$ and increased access to sunlight for photosynthesis.


### 3.2.2.1: Introduction to Early Land Plants

### 3.2.2.2: Bryophytes

#### 3.2.2.2.1: Anthocerotophyta

#### 3.2.2.2.2: Marchantiophyta

#### 3.2.2.2.3: Bryophyta

### 3.2.2.3: Seedless Vascular Plants

#### 3.2.2.3.1: Lycopodiopsida

#### 3.2.2.3.2: Polypodiopsida

### 3.2.2.4: Chapter Summary


## Attribution

Maria Morrow (CC-BY-NC)


This page titled 3.2.2: Early Land Plants is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

# 3.2.2.1: Introduction to Early Land Plants

**Learning Objectives**

- List the shared derived characteristics of land plants.
- Relate these adaptations to the movement from aquatic to terrestrial habitats.
- List the ancestral characteristics that land plants share with green algae.
- Describe the basic life cycle shared by plants.

## Land Plants

Land plants are sometimes referred to as “embryophytes” due to the evolution of the **embryo**, a zygote that is retained and nourished by the female gametophyte as it grows. Embryophytes share many common features, most corresponding to the selective pressures from the initial movement onto land. The embryo is one of these, providing higher likelihood of success for offspring in a new, harsh environment. In addition to the embryo, all plants have the same basic life cycle: **alternation of generations** (Figure 3.2.2.1.1). Much like the marine algae, the first plants were living in an environment where they needed to increase their chances of reproductive events. Multicellular stages on both sides of the life cycle increases the number of reproductive propagules. All plants are also **multicellular,** with **tissues** and **multicellular gametangia**.

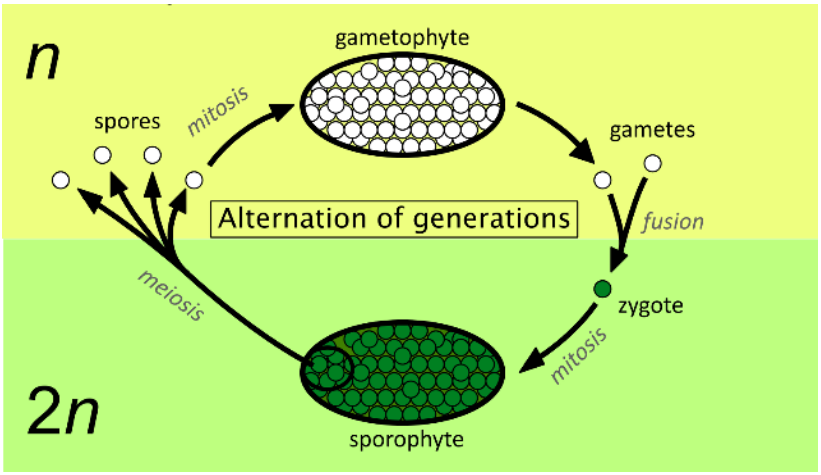



Figure 3.2.2.1.1: A generalized life cycle for plants. Alternation of generation involves two multicellular individuals. The top half is haploid and contains the spores, gametophyte, and gametes. The bottom half is diploid and contains the zygote and sporophyte. The multicellular haploid (n) individual is called the **gametophyte**. The gametophyte produces structures called **gametangia** where haploid **gametes** are produced by mitosis. Gametes do not grow, but instead must fuse together to form a diploid (2n) **zygote**. In plants, the zygote is retained on the megagametophyte as an **embryo**, where grows by mitosis into a multicellular diploid individual, the **sporophyte**. The sporophyte makes **sporangia** in which meiosis takes place, producing haploid **spores**. These spores are released and can grow by mitosis into haploid gametophytes. Diagram by Peter coxhead / derivative work: Peter coxhead, Public domain, via Wikimedia Commons.

Other adaptations to life on land include the desiccation-resistant compound **sporopollenin**. This is found in the cell walls of spores of early land plants and in pollen of seed plants, hence the name sporo - pollen - in. It is also found in the cell walls of a few green algae. On the exterior, plants are surrounded by a waxy **cuticle** that helps protect them from their outer environment.

Much like their green algal predecessors, plants store their carbohydrates as starch inside plastids, plastids with two membranes (the result of primary endosymbiosis), cell walls containing cellulose, and have the pigments chlorophyll a, chlorophyll b, and carotenoids. For this reason, along with genetic sequencing, land plants and green algae are grouped together in the Viridiplantae (Figure 3.2.2.1.2).

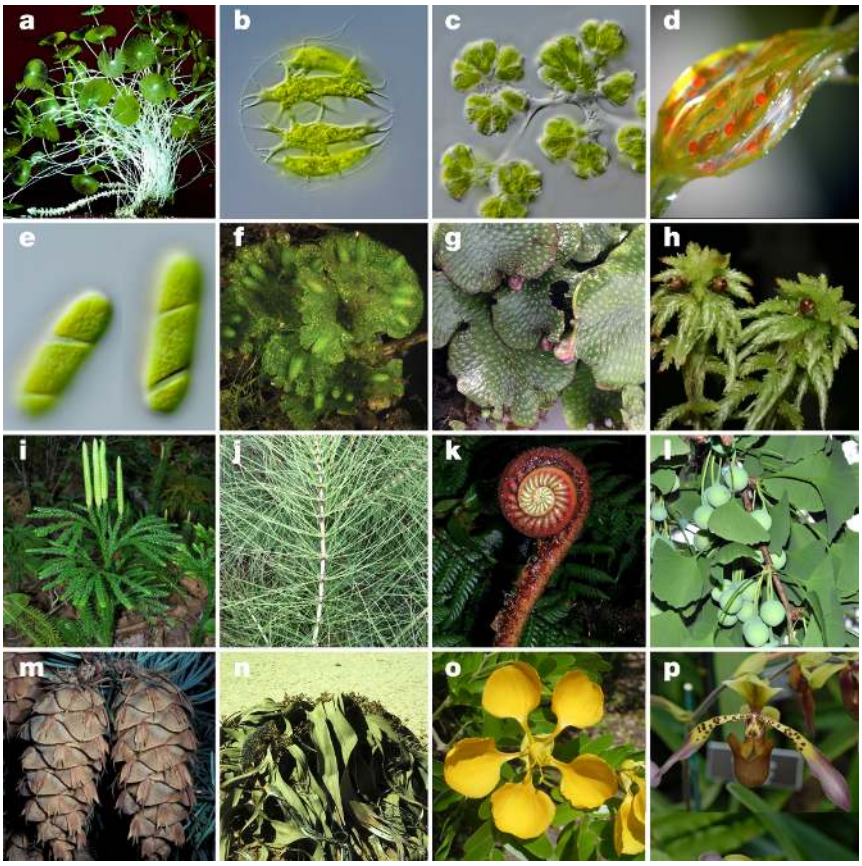



Figure **3.2.2.1.2**: This figure represents the lineages contained within the Viridiplantae. It was retrieved from an open-access paper analyzing over 1,000 transcriptomes to assess the relationships between these lineages. The original caption follows: "**a**–**e**, Green algae. **a**, *Acetabularia* sp. (Ulvophyceae). **b**, *Stephanosphaera pluvialis* (Chlorophyceae). **c**, *Botryococcus* sp. (Trebouxiophyceae). **d**, *Chara* sp. (Charophyceae). **e**, '*Spirotaenia*' sp. (taxonomy under review) (Zygnematophyceae). **f**–**p**, Land plants. **f**, *Notothylas orbicularis* (Anthocerotophyta (hornwort)). **g**, *Conocephalum conicum* (Marchantiophyta (thalloid liverwort)). **h**, *Sphagnum* sp. (Bryophyta (moss)). **i**, *Dendrolycopodium obscurum* (Lycopodiophyta (club moss)). **j**, *Equisetum telmateia* (Polypodiopsida, Equisetidae (horsetail)). **k**, *Parablechnum schiedeanum* (Polypodiopsida, Polypodiidae (leptosporangiate fern)). **l**, *Ginkgo biloba* (Ginkgophyta). **m**, *Pseudotsuga menziesii* (Pinophyta (conifer)). **n**, *Welwitschia mirabilis* (Gnetophyta). **o**, *Bulnesia arborea* (Angiospermae, eudicot, rosid). **p**, *Paphiopedilum lowii* (Angiospermae, monocot, orchid). **a**, Photograph reproduced with permission of Thieme Verlag, Stuttgart[66]. **b**–**e**, Photographs courtesy of M. Melkonian. **f**–**j**, **l**–**n**, **p**, Photographs courtesy of D.W.S. **k**, Photograph courtesy of R. Moran. **o**, Photograph courtesy of W. Judd." One Thousand Plant Transcriptomes Initiative., Leebens-Mack, J.H., Barker, M.S. *et al.* One thousand plant transcriptomes and the phylogenomics of green plants. *Nature* **574,** 679–685 (2019).

## The First Land Plants

Bryophytes and seedless vascular plants were the first groups to evolve on land. While the order of events during this period in plant evolution remains somewhat murky, evidence points to bryophytes evolving first, followed by the SVPs.

**Bryophytes** are the only group of land plants that lacks lignified vascular tissue, though some mosses do contain a form of conducting tissue. They tend to be small of stature and lack true stems, roots, or leaves. Bryophytes are also the only group of land plants to have a gametophyte dominant life cycle.

**Seedless vascular plants** transition to a sporophyte dominant life cycle with a branching sporophyte. They evolve lignified vascular tissue, developing true roots, stems, and leaves. This tough, lignified tissue allows some species within this group to form trees up to 100 feet tall.

## Attribution

Content by Maria Morrow, CC-BY-NC

This page titled 3.2.2.1: Introduction to Early Land Plants is shared under a not declared license and was authored, remixed, and/or curated by Tom Buckley.

- **2.5: Early Land Plants** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC 4.0.

# SECTION OVERVIEW

## 3.2.2.2: Bryophytes

**Learning Objectives**

- List the shared derived characteristics of bryophytes.
- Connect these characteristics to selection pressures these organisms would have faced.
- Name the three phyla included in the bryophytes.

### Introduction

Bryophytes arose in a period of Earth's history before soils had formed. The terrestrial surface was rocky and consisted primarily of crusts (microbial mats) composed of assemblages of prokaryotes. The exposure to sunlight would have been intense relative to the buffer provided by water. In addition, being surrounded by water would provide regulation of surrounding temperature and structural support. As green algae began to colonize the terrestrial surface, at least one of these lineages accumulated adaptations that were favorable to living on land--a waxy **cuticle** to prevent water loss, desiccation-resistant dispersal propagules called **spores**, and retention and feeding of the developing zygote. This lineage of green algae evolved into the ancestor of the bryophytes. These plants do not have true roots to absorb water, nor do they have vascular tissue to transport that water to other regions of the plant. Because of this, bryophytes tend to grow prostrate (close to the surface they are growing on) and stay quite small. They also tend to grow in moist areas where there is access to water and are reliant on water for the dispersal of gametes and fertilization.

#### Characteristics of Bryophytes

- **Morphology:** Generally small, prostrate plants. Complex tissues, including an exterior protective layer. Root-like structures called **rhizoids** provide anchorage for the gametophyte, which might be thalloid or leafy. Gametophytes possess simple pores (lacking guard cells) for gas exchange
- **Life cycle:** Alternation of generations; **gametophyte dominant**. Sporophytes grow from and are nourished by the female gametophyte. The gametophyte is nutritionally independent and is generally the larger and longer-lived of the two phases.
- **Ecology:** Terrestrial, gametes are dispersed in water.



Figure **3.2.2.2.1**: A thalloid liverwort gametophyte demonstrating the prostrate posture typical of bryophytes. It grows closely appressed to the surface of these rocks, sinking into the crevices to follow the path of the water. Photo retrieved from iNaturalist.org, posted by Alex Bairstow, CC-BY-NC.

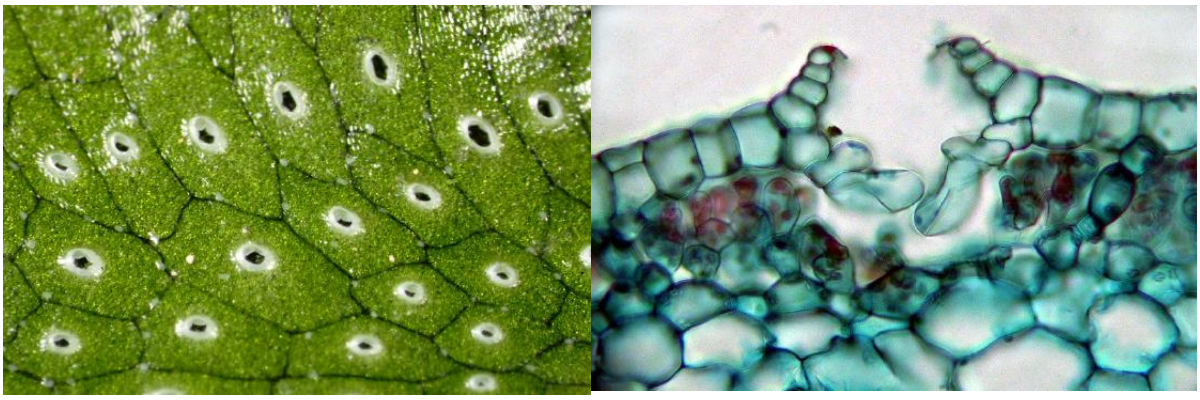


Figure 3.2.2.2.2: Simple pores on a thalloid liverwort. In the first photo, one simple pore can be seen in each section of the thallus, surrounded by a ring of lighter coloration. In the second photo, a cross section through a simple pore shows the smaller cells composing the epidermal layer surrounding the pore, as well as the lack of guard cells. Photos by George Shepherd, CC BY-NC-SA.

## Selection Pressures and Drivers

An important aspect of understanding the life history traits of the bryophytes is understanding the challenges of living in a terrestrial environment.

1. **Sun exposure**. Sunlight provides the power that drives our biosphere, but some wavelengths of sunlight can be damaging to cellular structure and even DNA. High frequency wavelengths, such as ultraviolet (UV), X-rays, and gamma rays can penetrate outer protective layers like skin, through cell membranes, and causing damage to DNA, proteins, and other biomolecules. Fortunately for organisms on Earth, almost all of these wavelengths are filtered by the atmosphere before they reach us, though some UV rays still make it through. These last UV rays are filtered out for aquatic organisms, but terrestrial organisms need adaptations to protect against UV radiation. Humans have skin with melanin pigments. Terrestrial plants have an **epidermis** and **carotenoid pigments**.
2. **Desiccation**. Transitioning from a completely aquatic environment to a terrestrial one leads to challenges of drying out, also known as desiccation. Temperatures are more extreme outside of the water and evaporation from tissues into the relatively dry air is constant. Terrestrial plants quickly adapted a waxy covering on the epidermis, called a **cuticle**. This water-tight covering required the evolution of **simple pores**, and eventually **stomata**, to allow gas exchange with the outer environment. Because these plants lack vascular tissue, water can only be transported around the organism via osmosis. Thus, these plants must keep all tissues close to water access.
3. **Lack of a soil environment**. The first organisms to move onto land would have found a relatively barren, rocky landscape. Soils did not yet exist. The rocky substrate experienced physical weathering from rain and wind that would help break it down. Chemical weathering through acidic rain or the interaction of water with compounds in the rock could also assist in breakdown. However, up to this point, contributions from organic matter would be minimal. Bryophytes lack true roots, instead producing structures called **rhizoids** whose function is anchorage (Figure **3.2.2.2.3**). There are genes present in bryophytes, as well as some fossil evidence, that indicate bryophytes likely had mycorrhizal relationships with fungi that helped them acquire nutrients in this new landscape.



Figure **3.2.2.2.3**: Root-like projections emerge from gametophytes. In the image, these are shown as transparent filaments extendending from the underside of a green, thalloid gametophyte. Photo by Yuval, CC-BY-NC.

## Bryophyte Lineages

This evolutionary group includes liverworts (phylum Marchantiophyta, Figure **3.2.2.2.4**), mosses (phylum Bryophyta, Figure **3.2.2.2.5**), and hornworts (phylum Anthocerophyta, Figure **3.2.2.2.6**). There are approximately 23,000 known extant species, most of these belonging to the mosses. As of 2019, much is unresolved on the early lineages of plants and who was first on land. Recent genetic analyses interpret bryophytes as being monophyletic, all deriving from a common ancestor that branched from the main line of plants. Read this open-access paper for further information.



Figure **3.2.2.2.4**: Liverworts, phylum Marchantiophyta, can be either leafy (first image) or thalloid (second image). Thalloid liverworts have no leaf-like structures, and look like a green, rubbery mat. Photo on the left by Maria Morrow, CC BY-NC. Photo on the right by Иван Матершев, CC-BY-NC-SA.



Figure **3.2.2.2.5**: Mosses, phylum Bryophyta, are always leafy. Photo by Maria Morrow CC BY-NC.



Figure **3.2.2.2.6**: Hornworts, phylum Anthoceratophyta, are always thalloid. Male gametophyte of *Phaeoceros laevis*. Photo by georgeg, CC-BY-NC.

**Topic hierarchy**

## 3.2.2.2.1: Anthocerotophyta

## 3.2.2.2.2: Marchantiophyta

## 3.2.2.2.3: Bryophyta

Content by Maria Morrow, CC-BY-NC

This page titled 3.2.2.2: Bryophytes is shared under a CC BY-NC-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

# 3.2.2.2.1: Anthocerotophyta

**Learning Objectives**

- Use morphological traits and cellular components to distinguish between hornworts and other bryophytes.
- Identify structures and phases in the hornwort life cycle; know their ploidy.
- Label a hornwort sporophyte and describe its development.

## Hornworts, Phylum Anthocerotophyta

The name Anthocerotophyta means 'horn flower plant'. These strange plants, called the hornworts, get their name from the horn-like sporophytes they produce. Hornworts have a flattened thalloid gametophyte, out of which grow their long photosynthetic sporophytes (Figure **3.2.2.2.1.1**), composed of a **sporangium** with a **columella** and **pseudoelaters**. The sporophyte grows from a basal meristem, with the oldest tissues at the apex. When spores have matured, the sporangium dries and dehisces, twisting open to release spores. The long, multicellular pseudoelaters (true elaters are a single cell) within the sporangium assist in dispersing the spores. Hornworts are somewhat rare and quite small, and they prefer shady and wet places. They are often found growing on the muddy sides of waterways, from small ditches to larger creeks.

The presence of **stomata** on sporophytes and the ability of some hornwort sporophytes to branch (and sometimes even live independently from the gametophyte!) lend support for the hypothesis that hornworts are sister to vascular plants (tracheophytes). However, hornworts are discussed first in this chapter due to their strictly thalloid gametophyte morphology.




Figure **3.2.2.2.1.1**: Hornworts growing in a cluster. The gametophytes are the leafy green material growing closer to the surface. The sporophytes are the emergent structures. The appearance of the sporophytes is what gives the hornworts their name. Photo by Maria Morrow, CC-BY-NC.

## Gametophyte Morphology

Hornwort gametophytes are exclusively thalloid, often with compartments of mutualistic cyanobacteria from the genus *Nostoc*. Cells within the gametophyte are **monoplastidic** (Figure **3.2.2.2.1.2**), containing one large chloroplast in each cell. Similar to the green algae, hornwort chloroplasts contain a **pyrenoid** where starch storage is concentrated. On the exterior of the thallus, **simple pores** allow for gas exchange. Unlike stomata, simple pores have no guard cells, meaning they are permanently open. Some hornwort species house colonies of *Nostoc* within the gametophyte thallus, providing access to nitrogen fixed by the cyanobacterial colony.

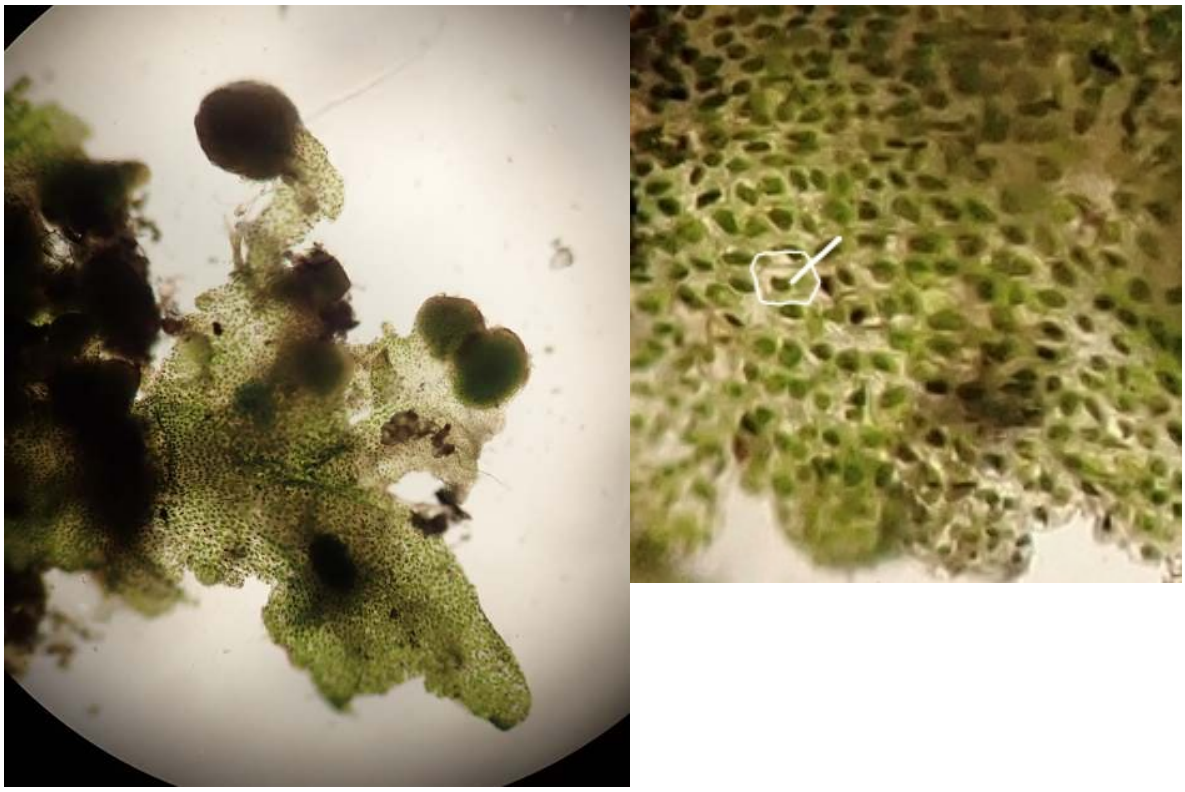


Figure 3.2.2.2.1.2: This image of part of a *Phaeoceros proskaueri* thallus shows the cells of the gametophyte each containing a single large plastid (monoplastidic). The second photo is a cropped view with a single cell encircled. A line indicates the single chloroplast within that cell. Photo by Amanda Heinrich, some rights reserved (CC-BY-NC).

## Sporophyte Morphology

Hornwort sporophytes are comprised of a linear sporangium that lacks a seta. It grows from a **basal meristem**, meaning the cells at the apex are the oldest. When you see the sporangia mature, this becomes more obvious, as the tip dries out first and dehisces (Figure 3.2.2.2.1.3) to release the spores. Unlike the gametophyte, the sporophyte possesses true stomata for gas exchange, though stomata have been lost in some lineages. Notably, hornwort sporophytes are photosynthetic and capable of transferring photosynthates to the gametophyte. In other bryophyte lineages, the sporophyte is almost entirely dependent on the gametophyte for nutrition.

Within the sporgangium, there is a central columella (Figure 3.2.2.2.1.4) and often pseudoelaters and/or sterile cells that aid in spore dispersal by twisting when dry.

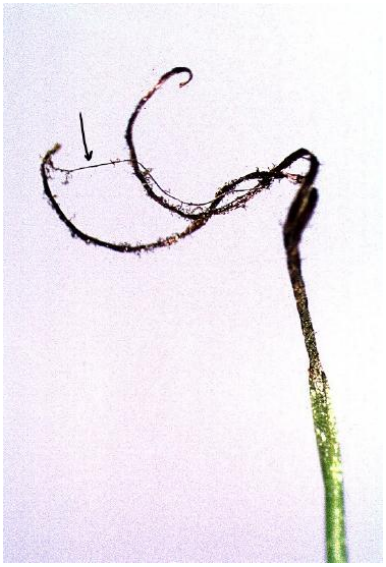


Figure **3.2.2.2.1.3**: The sporophyte of *Phaeoceros* opens by two "valves", liberating the spores. Between the valves a structure known as the columella is found (indicated by arrow). It consists of a column of sterile tissue in the center of the spore-forming tissue. In this image, the columella is visible as a very slender, black, wire-like structure between the valves. Photo and caption text by George Shepherd, CC BY-NC-SA with arrow added by Maria Morrow. Descriptive text: The tip of the sporophyte is blackened and has split in two. There is a thin black strand emerging from the center, indicated by an arrow. The base of the sporophyte is still green.

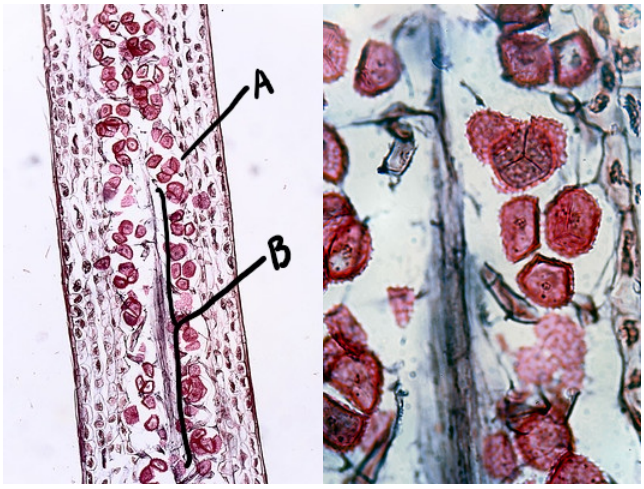



Figure **3.2.2.2.1.4**: A cross section through an *Anthoceros* sporophyte. Spore tetrads (A) fill the sporangium and surround the central columella (B). The second photo shows the spore tetrads at a higher magnification. Photos by George Shepherd, CC BY-NC-SA with labels added by Maria Morrow.

Stomata on the sporophyte may assist in spore dispersal by allowing the sporangium to dry, providing conditions necessary for dehiscence. Figure **3.2.2.2.1.5** walks through the stages of sporophyte maturation, showing the appearance of the stomata at each stage.

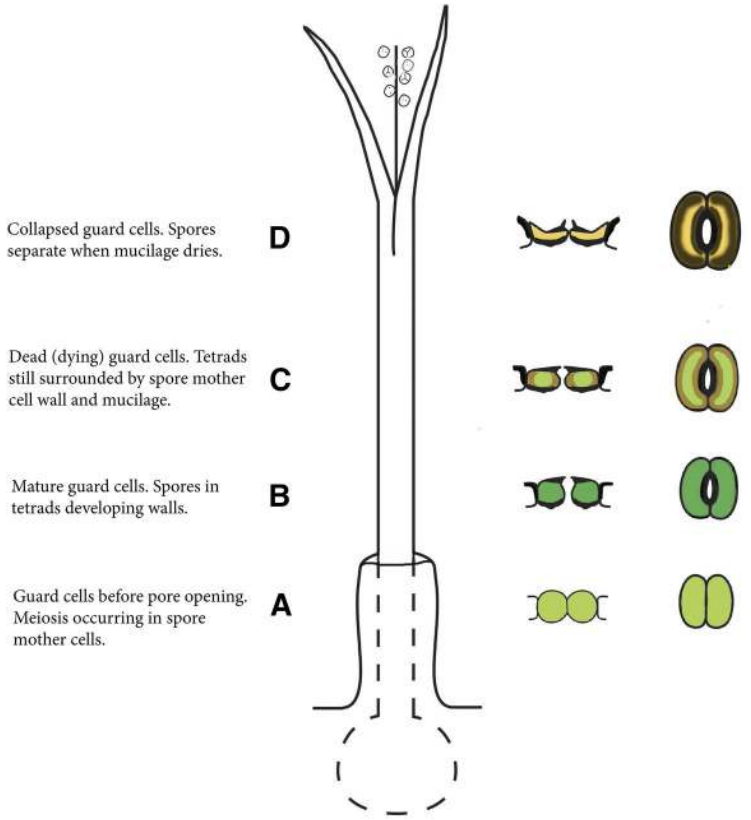



Figure **3.2.2.2.1.5**: Diagrammatic representation of a hornwort sporophyte with progressive development and color of stomata indicated from the base upward. Once open, stomata never close, but the outer aperture increases slightly in width after guard cell collapse. The stomata color does not necessarily coincide with the overall color of the sporophyte because stomata die and collapse while the sporophyte is actively photosynthesizing. A, Developing stoma. B, Mature, living, and open stoma. C, Dead (dying) guard cells at the onset of collapse of the outer walls. D, Dead, collapsed, and slightly larger stoma. Above D, the sporophyte dries, leading to dehiscence into two valves along two parallel suture lines, mucilage dries around the spore tetrads, the spore mother cell wall adheres to the spore surfaces, and the spores separate for dispersal. Image and caption text from the open-access paper Hornwort Stomata: Architecture and Fate Shared with 400-Million-Year-Old Fossil Plants without Leaves by Karen S. Renzaglia, Juan Carlos Villarreal, Bryan T. Piatkowski, Jessica R. Lucas, Amelia Merced. Plant Physiology Jun 2017, 174 (2) 788-797.

## Life Cycle

The hornwort life cycle, like all plants, is alternation of generations. The multicellular haploid stage, the gametophyte, is the longer-lived and larger phase of this life cycle. Most hornwort gametophytes are **monecious**, meaning both types of gametangia (antheridia and archegonia) are produced on the same gametophyte. The life cycle shown in Figure **3.2.2.2.1.6** features a monoecious gametophyte. If a hornwort is dioecious, the life cycle would have antheridia and archegonia produced on separate gametophytes and the sporophyte would grow from the gametophyte producing archegonia.

As will be the case with all plants, archegonia produce one or more eggs and antheridia produce many sperm. These haploid gametes are produced by mitosis. The sperm have two flagella and must swim through water to reach the egg at the base of the archegonium. Fertilization (fusion of the egg and sperm) results in a diploid zygote. This zygote grows within the archegonium, nourished by the gametophyte. All land plants retain and nourish the zygote, called an **embryo**, and so are sometimes referred to as the embryophytes. Meiosis occurs within the sporangium (also called a capsule), producing haploid spores that are dispersed aerially.

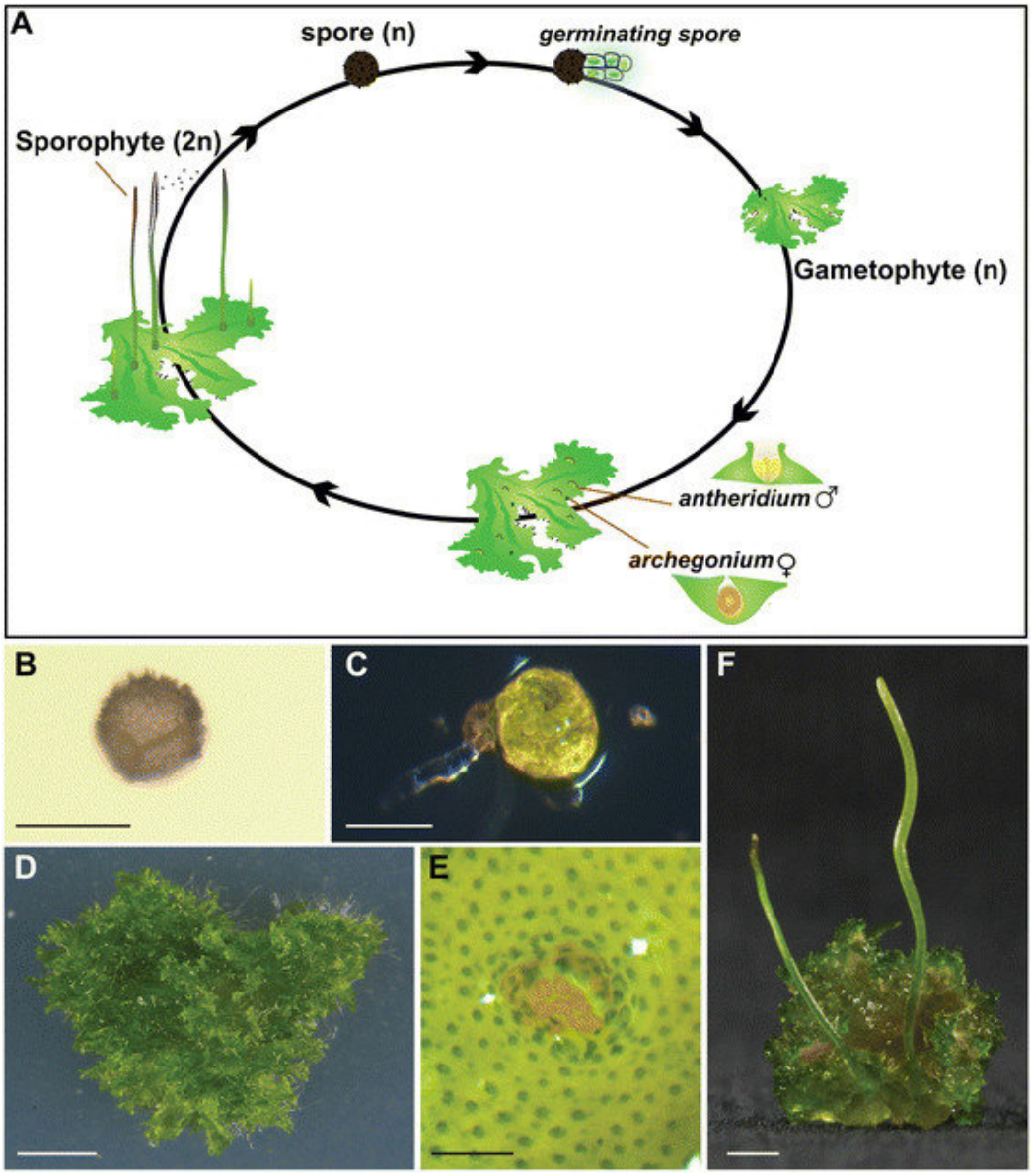



Figure 3.2.2.2.1.6: Life cycle of the hornwort *Anthoceros agrestis*. The life cycle of A. agrestis (A) starts with the spore (B) that germinates (C) and gives rise to the gametophyte (D). Gametophytes are monoecious and thus individual plants bear both male antheridia (E) and female archegonia. After fertilization of the egg by sperm from the antheridia, the zygote is retained within the archegonium. The resultant embryo develops into the sporophyte (F) in which spores are produced via meiosis. Scale bars = B: 40 µm; C: 100 µm; D: 2 mm; E: 200 µm; F: 2 mm. Caption text and image from Szövényi, Péter & Frangedakis, Eftychios & Ricca, Mariana & Quandt, Dietmar & Wicke, Susann & Langdale, Jane. (2015). Establishment of Anthoceros agrestis as a model species for studying the biology of hornworts. BMC Plant Biology. 15. DOI: 10.1186/s12870-015-0481-x. CC BY 4.0

## Attribution

Content by Maria Morrow, CC-BY-NC

This page titled 3.2.2.2.1: Anthocerotophyta is shared under a CC BY-NC-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **2.5.2.1: Anthocerotophyta** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC-SA 4.0.

# 3.2.2.2.2: Marchantiophyta

**Learning Objectives**

- Use morphological traits and cellular components to distinguish between liverworts and other bryophytes.
- Identify structures and phases in the *Marchantia* life cycle; know their ploidy.

## Liverworts, Phylum Marchantiophyta

The liverworts, formerly the Hepatophyta, got their name from their thalloid gametophytes being compared to the shape of a liver. However, many liverworts produce leafy gametophytes. This group is often presented as a basal lineage of bryophytes due to the lack of stomata present in either stage of the life cycle (among other traits). However, recent genetic evidence does not support this and instead places mosses and liverworts as sister taxa. Liverworts have a global distribution and can be found in many habitats, including a few desert and even arctic species. There are around 5,000 described species of liverworts, though estimates put this at about half of the actual number of species. The type genus for this group, *Marchantia*, is a common invader of greenhouses and potted plants.

### Gametophyte Morphology

There are two distinct type of liverwort gametophytes: leafy liverworts and thalloid liverworts. **Leafy liverworts** have leaves (though not true leaves, as they lack vascular tissue) without a central costa, which you will see in mosses. The leaves are arranged in a flat plane (Figure 3.2.2.2.2.1) with a set of smaller underleaves (Figure 3.2.2.2.2.2).



Figure 3.2.2.2.2.1: The leafy liverwort *Porella* has larger leaves running opposite each other down either side of the stem, making the liverwort look flat. The photo on the right shows a microscopic view of the leaves. Notice that there is no central rib on these leaves, which helps distinguish leafy liverworts from mosses. Photo on the left by Maria Morrow CC-BY-NC. Photo on the right by Rafael Medina, CC-BY-NC.

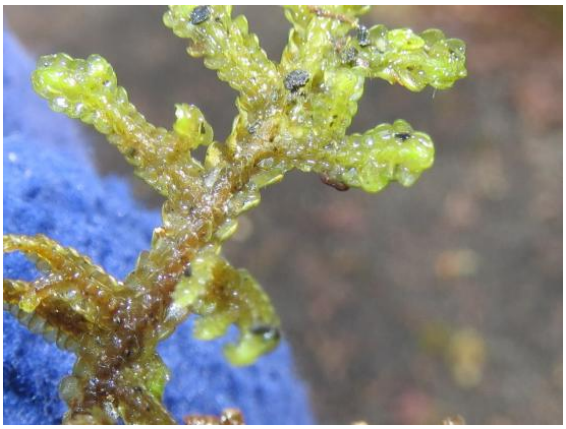


Figure **3.2.2.2.2.2**: Another distinguishing feature of leafy liverworts are their underleaves. These are smaller, scale-like leaves that run along the center of the thallus on the underside. This image shows the underside of a *Porella navicularis* thallus covered with underleaves. Photo by Howard Bruner, CC-BY-NC.

**Thalloid liverworts** have no leaves and their gametophytes look more similar to hornwort gametophytes. Another similarity to hornworts is the presence of simple pores for gas exchange (no guard cells, meaning pores are permanently open). Unlike hornworts, liverwort cells have multiple chloroplasts. Rhizoids in this group are unicellular. Asexual clones, called **gemmae** (sing. gemma), are sometimes produced in structures called **gemmae cups** (Figure **3.2.2.2.2.3**). These are haploid and genetically identical to the parent thallus.




Figure **3.2.2.2.2.3**: The thalloid liverwort *Lunularia* has crescent-shaped gemmae cups. Several of these are present in the image above. The small green pebble-looking structures within them are asexual clones of the thallus called gemmae. Liverwort gametophytes do not have stomata. Instead, the thallus is covered in raised bumps where simple pores are located. Photo by Maria Morrow, CC-BY-NC.

The thalloid liverwort *Marchantia* has complex reproductive structures. Palm tree-like structures called **archegoniophores** are formed from the haploid gametophyte tissue. Archegonia are produced on the underside of the extending arms. When fertilized, the sporophyte will grow within the archegonium and emerge on the underside of the archegoniophore (see the right side of Figure **3.2.2.2.2.4**). The antheridia are produced in a separate stalked structure with a flat top called an **antheridiophore** (see the left side of Figure **3.2.2.2.2.4**). Water droplets splash onto the flat top, dispersing flagellated spores from the embedded antheridia.



Figure 3.2.2.2.2.4: This image shows gametangia producing structures from both gametophytes. The antheridiophore is on the left, with a flat surface that water can splash onto. This carries sperm from the embedded antheridia to other sufaces (hopefully, to an awaiting egg). On the right, there is a fertilized archegoniophore. The palmtree-like branches have lifted upward. Beneath them, yellow sporangia emerge at the tips of transparent setae. Photo by Felix Riegel, CC-BY-NC.

## Sporophyte Morphology

Liverworts produce a single sporangium (also called a **capsule**) at the end of a **seta**, which is often fragile and transparent (Figure 3.2.2.2.2.5 – 6). The seta does not elongate until after the sporangium has formed. The sporangium dehisces, splitting into four valves (Figure 3.2.2.2.2.7). In thalloid liverworts, the sporophyte may emerge directly from the thallus or, as is the case with the genus *Marchantia*, from under archegoniophores. In leafy liverworts, the sporophyte often emerges laterally from the thallus. Within the sporangium, there are **elaters** (true unicellular elaters, Figure 3.2.2.2.2.8) that aid in spore dispersal. Unlike the hornworts, there is no columella. Unlike the mosses, the capsule lacks an operculum.




Figure 3.2.2.2.2.5: Liverwort sporophytes are comprised of a stalk called the seta and, at the top of the seta, a single capsule where spores are produced. In this liverwort (perhaps a *Fossombronia*), the sporophytes are short and stout with globose capsules. Photo by Maria Morrow, CC-BY-NC.

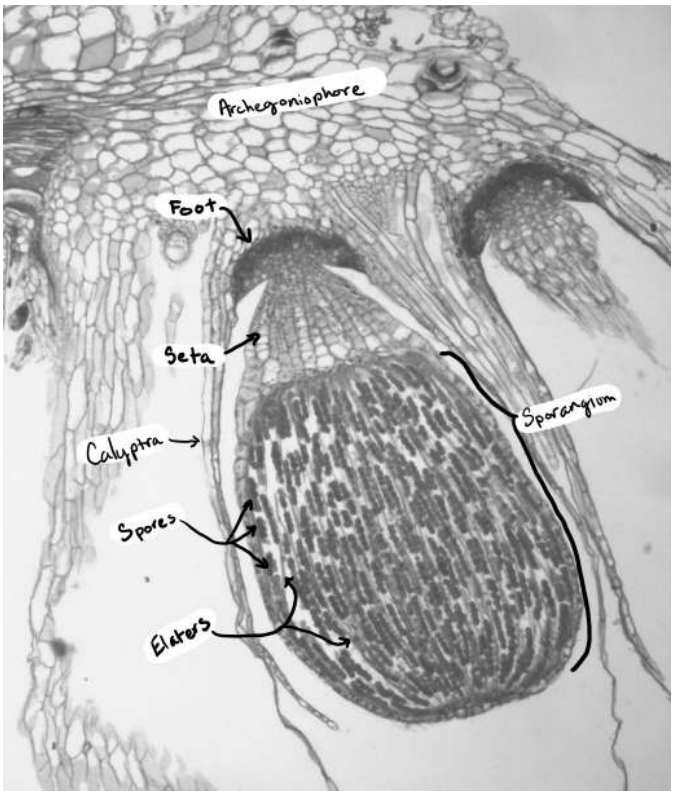



Figure **3.2.2.2.2.6**: A sporophyte produced on the underside of an archegoniophore. It emerges upside-down and will eventually become more horizontal as the branches of the archegoniophore raise upward. The sporophyte attaches to the gametophyte at a region called the foot. It grows within the archegonium, now labeled as the calyptra. From the foot a short seta emerges, topped by a large sporangium. The sporangium is filled with rows of haploid spores produce by meiosis. Between these rows of spores, long elaters await the dehiscence of the sporangium to aid in spore dispersal. Photo by Maria Morrow, CC-BY-NC.



Figure **3.2.2.2.2.7**: Noteroclada confluens capsule dehiscence. The capsule has split into four valves. Many elaters, as well as a few green spores, remain. Photo by George Shepherd, CC BY-NC-SA.



Figure **3.2.2.2.2.8**: Noteroclada confluens elaters and spores. The elaters in the capsule are specialized elongated cells with a spiral thickening in their walls. In this case they are hygroscopic and twist and actively move as they dry out, helping to liberate the spores gradually. Photos and caption text by George Shepherd, CC BY-NC-SA.

## Marchantia Life Cycle

*Marchantia polymorpha* is a thalloid liverwort with a complex life cycle (Figure **3.2.2.2.2.9**). Asexual reproduction is accomplished through the production of haploid gemmae from the gametophyte thallus. Sexual reproduction occurs from dioecious gametophytes: archegoniophores and antheridiophores are produced on separate gametophytes. Sperm splashed from the antheridial head swim through the water with their dual flagella to reach an egg at the base of an archegonium. These archegonia are situated on the underside of the archegonial head. The diploid zygote grows within the archegonium, surrounded by its remaining tissue (the **calyptra**). As the sporangium develops, meiosis occurs simultaneously to produce haploid spores. A short seta extends to push the developed sporangium outward, lifting the arms of the archegoniophore. The sporangium dehisces into four valves, exposing the elaters to the external environment where they rapidly twist, flinging the haploid spores into the air. These haploid spores can germinate and grow into male or female gametophytes.

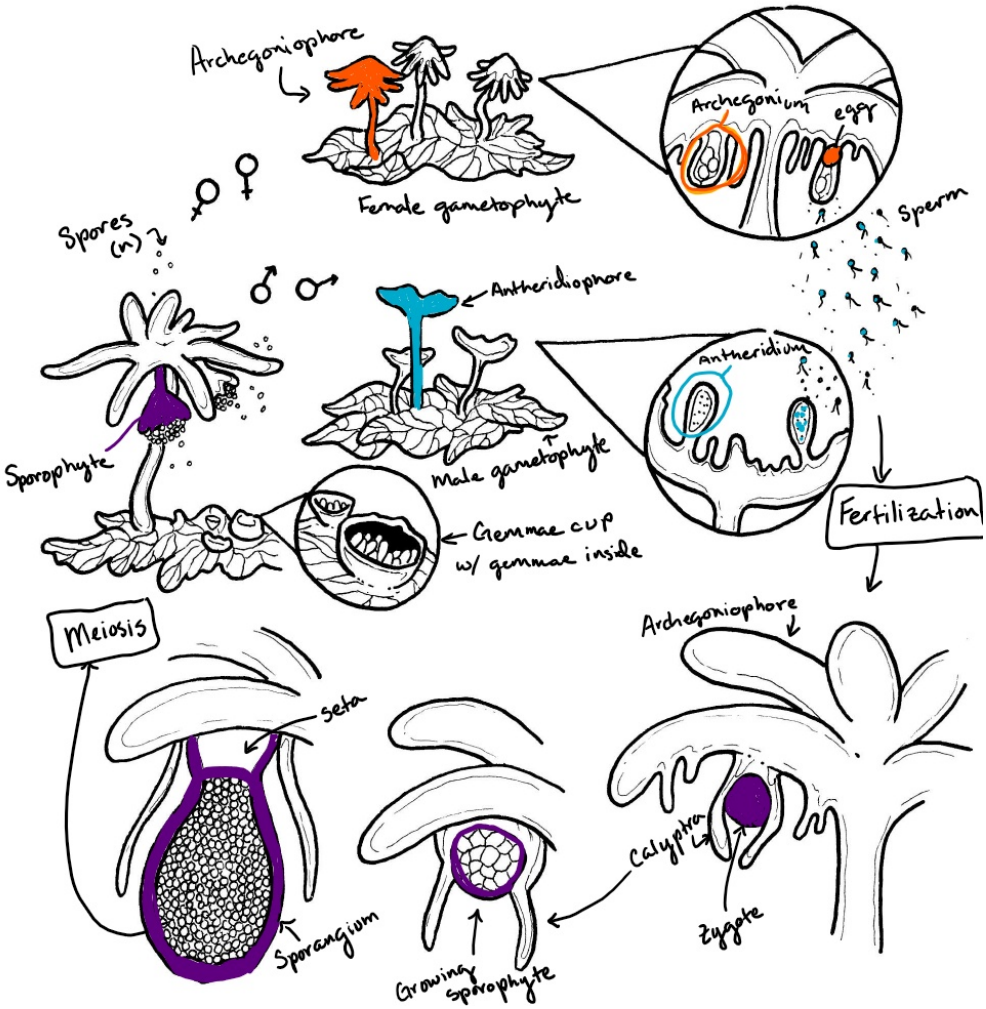



Figure **3.2.2.2.2.9**: The *Marchantia polymorpha* life cycle. Starting with meiosis (left, center): Meiosis produces haploid spores which will grow by mitosis into either male or female gametophytes. Either of these gametophytes can produce **gemmae cups**--structures that hold asexually produced clones of the gametophyte (**gemmae**). Male gametophytes produce tall structures with flat tops called **antheriodiophores**. Many **antheridia** are embedded in the flat top of the antheridiophore. Antheridia produce biflagellate **sperm** by mitosis. Female gametophytes produce palm tree-like structures called **archegoniophores**. These archegoniophores produce **archegonia** on the underside of the 'branches', each with a single **egg** that was produced by mitosis. When water hits the flat top of the antheridiophore, it can splash sperm onto a female gametophyte. If the sperm are able to swim through the water to an egg, fertilization occurs producing a diploid **zygote**. The zygote grows into a **sporophyte** from within the archegonium. The remaining archegonial tissue is called the **calyptra**. A mature sporophyte will have a sterile stalk called a **seta** and a **sporangium** containing cells that will undergo meiosis to make haploid spores. Within the sporangium (not pictured), long twisted structures called **elaters** help disperse the spores aerially. Drawing by Nikki Harris, CC-BY-NC, with colors and labels added by Maria Morrow.

Content by Maria Morrow, CC-BY-NC

---

This page titled 3.2.2.2.2: Marchantiophyta is shared under a CC BY-NC-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **2.5.2.2: Marchantiophyta** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC-SA 4.0.

# 3.2.2.2.3: Bryophyta

**Learning Objectives**

- Use morphological traits and cellular components to distinguish between mosses and other bryophytes.
- Identify structures and phases in the moss life cycle; know their ploidy.
- Label a moss sporophyte and describe its development.

## Mosses, Phylum Bryophyta

Most described bryophyte species diversity (around 13,000 species) belongs to the mosses. Unlike other bryophytes, mosses are exclusively leafy. Sporophytes in most species form complex capsules, involving multiple layers of structures. Members of the mosses have defied many of the typical bryophyte descriptors. For example, some mosses have evolved vascular tissue analogs called **leptoids** (analogous to phloem) and **hydroids** (analogous to xylem). Other mosses can grow quite tall: Dawsonia superba, the world's tallest moss, can grow up to be nearly 2 feet tall (50-60 cm).



Figure **3.2.2.2.3.1**: Gametophytes of *Dawsonia superba*, the world's tallest moss species, growing in New Zealand. Photo by Jacquinz, CC-BY-NC.

*Sphagnum* is an ancestral genus of mosses that grow in bogs and are commonly referred to as peat moss or peat, in its compressed form. They have large, empty cells (Figure **3.2.2.2.3.2**) capable of absorbing around 20 times their dry weight in water and can exude compounds to make their environment more acidic. Because of this, and the compounds in their cell walls, the bogs where they grow have slow decomposition, allowing plant matter to accumulate and compress over time. This makes peat, a common source of fuel in higher latitudes. It's use as fuel, flavoring (the smoke), and in horticulture for its water holding capacity have contributed to its commercial importance. Many peat bogs are frozen over for most of the year, halting metabolic activity and slowing the release of methane from anaerobic decomposition. As the climate in northern latitudes warms, so do the peat bogs, increasing the release of methane.



Figure 3.2.2.2.3.2: Sphagnum gametophytes and cells. The gametophytes in the first photo are growing submerged in water. In the second photo, the strange, empty cells of *Sphagnum* leaves have algae growing within them! These large, empty cells give *Sphagnum* their immense water holding capacity. First photo by Tarpinian, CC-BY-NC. Second photo by Казаков Александр Павлович, CC BY 4.0, via Wikimedia Commons.

## Gametophyte Generation

Moss gametophytes have spirally arranged leaves that emerge from all sides of the stem (Figure 3.2.2.2.3.3). In most mosses, the leaves have a central line of tissue called a **costa** that looks a bit like a midrib (though it is not, as bryophytes don't have lignified vascular tissue) and are only 1-2 cell layers thick. Rhizoids are produced at the base of the gametophytes. In the common haircap moss, *Polytrichum commune*, there are three kinds of gametophytes:

- **Female**, which develop **archegonia** at their tip. A single **egg** forms in each archegonium. (see Figure 3.2.2.2.3.6)
- **Male**, which develop **antheridia** at their tip. Multiple swimming **sperm** form in each antheridium. (see Figure 3.2.2.2.3.5)
- **Sterile**, which do not form sex organs.



Figure **3.2.2.2.3.3**: A closer look at spiral leaf arrangement, this time with *Polytrichum commune*, the haircap moss. Note that leaves emerge from all directions of each gametophyte. Photo by Mizuki Maeda, CC-BY-NC.



Figure **3.2.2.2.3.4**: These moss gametophytes show spiral leaf arrangement and a distinct, tan costa that emerges on each leaf. Can you spot them? Photo by Geoffrey Cox, CC-BY-NC.

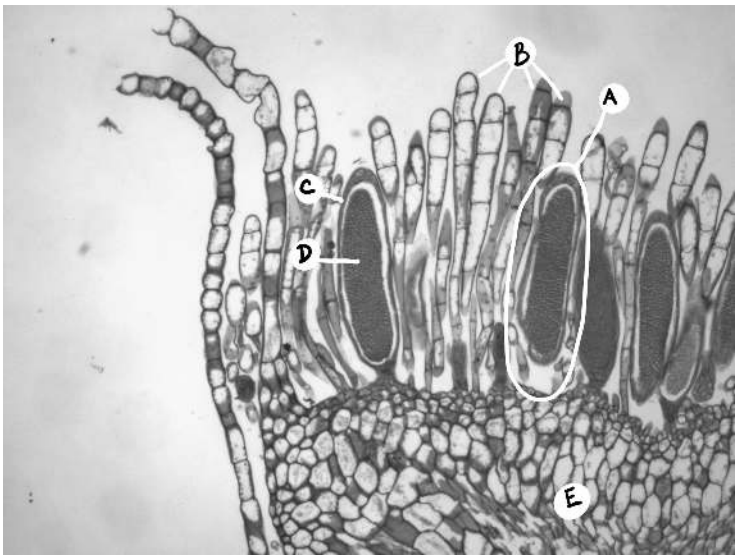





Figure **3.2.2.2.3.5**: On the left is a labeled cross section of the antheridial head of a *Mnium* male gametophyte. On the right is an actual image of the splash cup (antheridial head) from a bird's eye view. The cross section is labeled as follows: A) An antheridium, B) paraphyses, C) sterile jacket of the antheridium, D) sporogenous tissue, E) male gametophyte. First photo by Maria Morrow, CC-BY-NC. Second photo by Bosmon, CC-BY-NC.

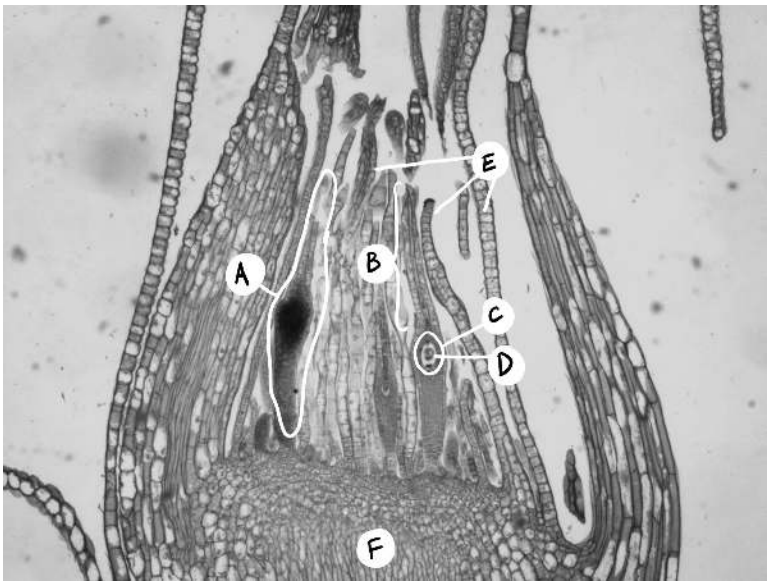





Figure **3.2.2.2.3.6**: On the left is a labeled cross section of the archegonial head of a *Mnium* female gametophyte. On the right is an actual image of a female gametophyte. The cross section is labeled as follows: A) An archegonium, B) neck of the archegonium, C) venter, D) egg, E) paraphyses, F) female gametophyte. First photo by Maria Morrow, CC-BY-NC. Second photo by Tisrel, CC-BY-NC.

## Sporophyte Generation

Moss sporophytes have a complex set of structures at the top of a seta. When the sporophyte emerges, it tears off a piece of the female gametophyte's archegonium, leaving a coating called the **calyptra**. Mosses have a **capsule**, where the sporangia are housed. This capsule has a lid-like structure called an **operculum**, which pops off when spores have matured. Depending on the moss, the sporophyte may have a **peristome** (teeth-like sheets of cells that aid in spore dispersal). True stomata are present for gas exchange.

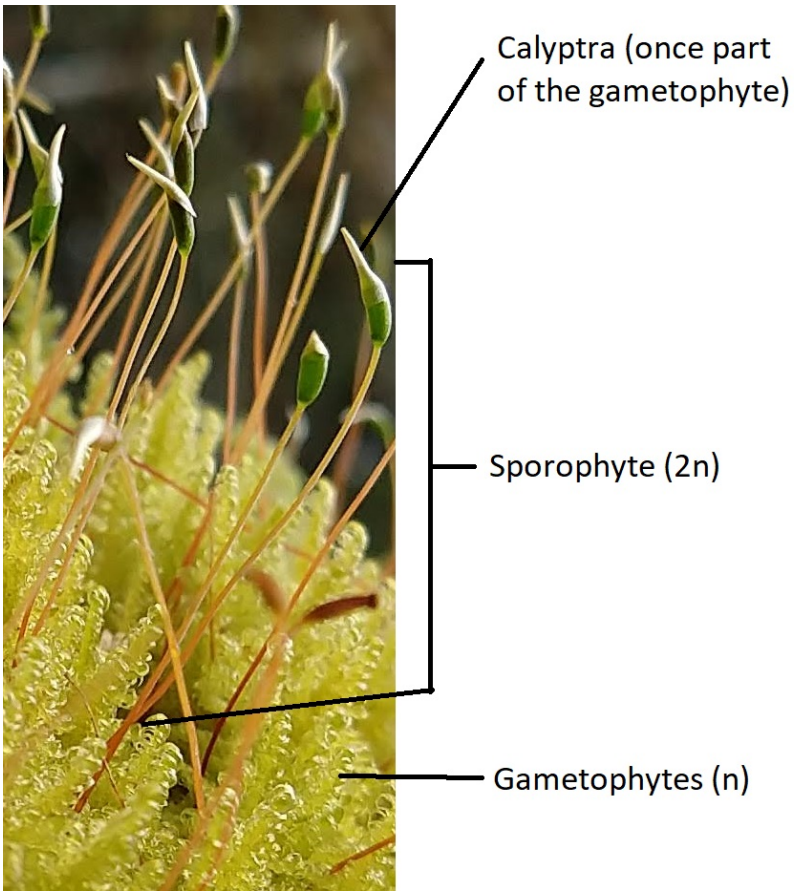



Figure **3.2.2.2.3.7**: Moss sporophytes are composed of a seta and capsule, much like liverworts. When the sporophyte emerges from the archegonium, it brings a piece of that archegonium with it. This gametophyte remnant sits on the capsule like a cap, which is why it is called a calyptra. Photo by Maria Morrow, CC-BY-NC.

When the calyptra falls off, another feature of the sporophyte is visible: the **operculum**. This is a lid-like structure on the capsule that pops off when the spores are mature. Most mosses have a structure under the operculum that lines the capsule opening, called the **peristome**. The peristome is a series of cellular flaps (peristome teeth) that line the edge of the capsule opening and aids in spore dispersal via hygroscopic movements.



Figure **3.2.2.2.3.8**: Moss sporophyte structures. In the first photo, the operculum of a *Polytrichum* sp. is visible. It is red and has a long, conical beak. In the second photo, the operculum of this moss has already popped off, revealing the peristome. There are two ranks of teeth in the peristome of this moss, the outer rank is bent and the tips are reaching inward. Green spores can bee seen clustered under the inner rank of teeth. Photos by George Shepherd, CC BY-NC-SA.

Tetraphis moss (*Tetraphis pellucida*) produces both asexual propagules (gemmae) and spores, which result from sexual reproduction (Figure **3.2.2.2.3.9**). In 1991, Robin Wall Kimmerer found that spores were dispersed an average of 20 times farther from the parent plant than gemmae were, but gemmae established more easily. Each reproductive strategy thus served a different purpose: gemmae helped the plant spread locally, and spores were important for colonization of an entirely new location.



Figure **3.2.2.2.3.9**: Sporophytes extend from the lush, green gametophyte in *Tetraphis pellucida*. The spores produced in the capsules of the sporophyte will function in long-distance dispersal. Photo by Nate Marineau, CC-BY-NC.

## Mnium Life Cycle

Male gametophytes form antheridia at the top of the gametophyte in a structure called the perigonium or antheridial head (Figure **3.2.2.2.3.10**). These are cup-shaped, and commonly referred to as splash cups. In early spring, raindrops splash sperm from male to female plants. These swim down the canal in the archegonium to the chamber containing the egg. The resulting zygote begins the sporophyte generation.

Mitosis of the zygote produces an embryo that grows into the mature sporophyte generation. It consists of:

- A **foot**, which absorbs water, minerals, and food from the parent gametophyte
- A stalk (**seta**), at the tip of which is formed a sporangium (the brownish objects in the photo).

The sporangium is

- filled with **spore mother cells**
- in most cases, ined by a **peristome** around the opening
- sealed by an **operculum**
- covered with a **calyptra**. The calyptra develops from the wall of the old archegonium and so is actually a part of the gametophyte generation. It is responsible for the common name ("haircap moss") of this species.

During the summer, each spore mother cell undergoes meiosis, producing four haploid spores - the start of the new gametophyte generation. Late in the summer, the calyptra and operculum become detached from the sporangium allowing the spores to be released. These tiny spores are dispersed so effectively by the wind that many mosses are worldwide in their distribution. If a spore reaches a suitable habitat, it germinates to form a filament of cells called a **protonema**. Soon buds appear and develop into the mature leafy shoots.

Thus the gametophyte generation is responsible for sexual reproduction. The sporophyte generation is responsible for dispersal.

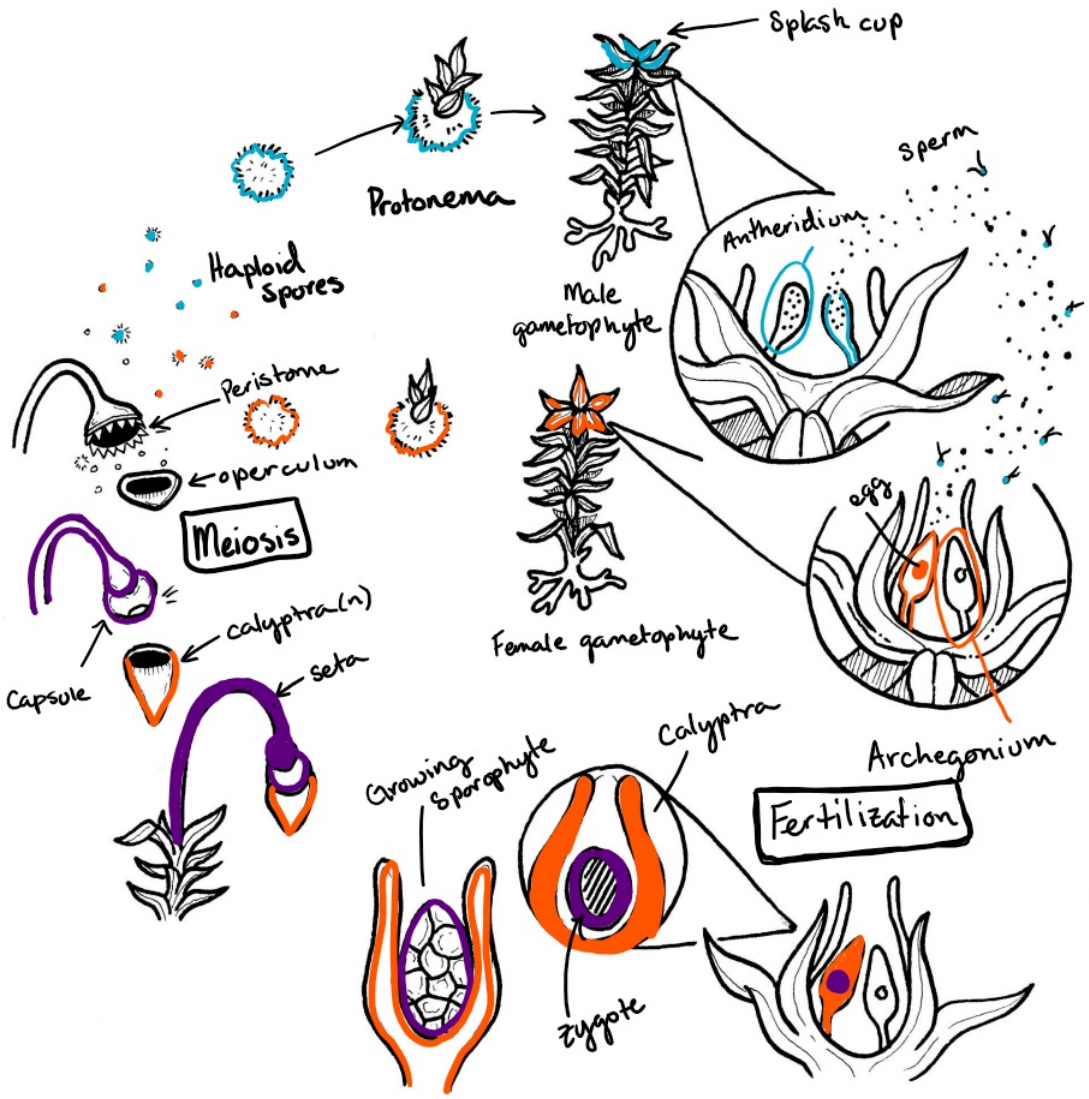



Figure 3.2.2.2.3.10: The *Mnium* life cycle. Starting with meiosis (left, center): Meiosis produces haploid spores which will grow by mitosis into either male or female gametophytes. Moss spores germinate and begin to grow into a chain of cells called a **protonema**. Male gametophytes are flat topped, called **splash cups**. Many **antheridia** are produced within the splash cup, surrounded by sterile cells called **paraphyses**. Antheridia produce biflagellate **sperm** by mitosis. Female gametophytes produce multiple **archegonia** at the top of the gametophyte. These are also surrounded by paraphyses. Each archegonium produces a single **egg** by mitosis. When water hits the splash cup, it can splash sperm onto a female gametophyte. If the sperm are able to swim through the water to an egg, fertilization occurs producing a diploid **zygote**. The zygote grows into a **sporophyte** from within the archegonium. The remaining archegonial tissue is called the **calyptra** and will remain on top of the sporophyte as a cap-like structure. A mature sporophyte will have a sterile stalk called a **seta.** Underneath the calyptra, there is a **capsule** containing cells that will undergo meiosis to make haploid spores. The capsule has a lid-like **operculum** that will pop off when the spores have matured. **Peristome** teeth along the opening of the capsule aid in spore dispersal. Drawing by Nikki Harris, CC-BY-NC, with colors and labels added by Maria Morrow.

## Attribution

Content by Maria Morrow, CC BY-NC, except the following:

- Life cycle text from 16.3B Moss Life Cycle from *Biology* by John. W. Kimball (licensed CC-BY)
- Paragraph that goes with Figure 3.2.2.2.3.9 by Melissa Ha (licensed CC BY-NC)

This page titled 3.2.2.2.3: Bryophyta is shared under a CC BY-NC-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **2.5.2.3: Bryophyta** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC-SA 4.0.

# SECTION OVERVIEW

## 3.2.2.3: Seedless Vascular Plants

**Learning Objectives**

- List the shared derived characteristics of seedless vascular plants.
- Connect these characteristics to selection pressures these organisms would have faced.
- Describe the importance of extinct seedless vascular plants in modern society.

### Introduction

As bryophytes began to colonize the terrestrial surface, they produced organic acids during metabolism that aided in the breakdown of the rocky substrate. When they died, their organic matter mixed with the weathered rock, forming the Earth's earliest soils. Formerly abundant to the first photosynthesizers to become terrestrial, access to sunlight became competitive as bryophytes expanded. This led to selection for individuals that could lift themselves higher and transport water throughout their tissues. Eventually, this selection resulted in the evolution of **vascular tissue** -- pipes that could bring water up from the ground so that parts of the plant could be raised upward, and those parts raised upward could transport their photosynthates down to the lower parts of the plant. The cells in the **xylem** (water-transporting vascular tissue) contained **lignin**, the tough, decay-resistant compound that wood is made out of. This rigid molecule in the vascular tissue allowed for structural support, allowing plants to grow taller -- some over 100 feet! The vascular system also allowed for the specialization of organs: **roots** for water absorption, **leaves** for photosynthesis, and **stems** for structural support.

Seedless vascular plants (SVPs) also began to rely more on the sporophyte stage. The sporophyte became the larger, nutritionally independent stage of the life cycle. **Branching sporophytes** offered more sites for meiosis to occur, resulting in increased opportunities for variation, which could be interpreted as more options in an increasingly competitive environment. There are approximately 20,000 known extant species, most of which are ferns.

SVPs are considered to be a paraphyletic group of organisms, forming two distinct lineages: Ferns and Lycophytes.

#### Characteristics

- **Morphology:** Sporophytes develop complex tissues, including **lignified vascular tissue**, true roots, stems, and leaves. Sporophytes are branched, producing many sporangia. Gametophytes are reduced and thalloid. In some groups, the gametophyte is subterranean and parasitizes mycorrhizal fungi for sugars.
- **Life cycle:** Alternation of generations; sporophyte dominant. Sporophytes still grow from the gametophyte, but are now photosynthetic and the larger, longer-lived phase of the life cycle.
- **Ecology:** Gametes are still dispersed in water, so moisture is still required for fertilization.

#### Selection Pressures and Drivers

1. **Competition for sunlight**. To get access to sunlight, SVPs needed to grow taller than bryophytes. However, this presents a problem of distributing water around the plant body to prevent drying out. Seedless vascular plants solved this problem with the adaptation of lignified vascular tissue. The lignin in the secondary walls of sclerenchyma cells allowed SVPs the structural support to grow taller.
2. **The initial forming of soils**. Before the bryophytes, terrestrial surfaces were primarily rocky. The first land plants would have contributed to the chemical weathering of these rocks by producing acids during metabolism. After death, these plants add their organic matter to these weathering rocks, beginning to form Earth's early soils. Fungi were likely involved in this process, as there are genes in the bryophytes for mycorrhizal relationships.

**Seedless Vascular Plants**

3.2.2.3.1: Lycopodiopsida

3.2.2.3.2: Polypodiopsida

## Attribution

Content by Maria Morrow, CC-BY-NC

This page titled 3.2.2.3: Seedless Vascular Plants is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

# 3.2.2.3.1: Lycopodiopsida

**Learning Objectives**

- Describe the characteristics of lycophytes.
- Differentiate between homosporous and heterosporous strobili.

**Lycopodiopsida**, or lycophytes, have at least four genera and more than 1,200 species. Extant lycophytes (those species still alive today) are represented by creeping forms, such as *Lycopodium* and *Selaginella*. Prominent members of this group are often called **club mosses**. They are not mosses at all, but **vascular plants** with **xylem** and **phloem** running through their roots, stems, and leaves. The leaves are quite simple and small with their vascular tissue in a single, unbranched vein. The "club" of their name comes from the appearance of their spore-forming structures called **strobili**. Some lycophytes (clubmosses *Huperzia* and *Lycopodium*) have equal spores and underground gametophytes, whereas *Selaginella* (spikemoss) and *Isoëtes* (quillwort) are both heterosporous with reduced aboveground gametophytes. Quillwort is a direct descendant of giant Carboniferous lycophyte trees, and despite being an underwater hydrophyte, it still retains the unusual secondary thickening of stem. Many spike mosses are poikilohydric (another similarity with mosses).

## Characteristics

- **Microphylls**. Leaves with a single, unbranched vein of vascular tissue. Microphylls may have evolved from **enations**, scale-like appendages that later gained vascular tissue. Another possibility is that microphylls evolved from sporangia. Note: The term microphyll, confusingly, is not an indication of the size of the leaf.
- **Rhizomes**. Asexual propogation of the sporophyte through underground stems.
- **Strobili**. Cone-like structures where sporangia are produced on leaves called sporophylls (Figure **3.2.2.3.1.1**).
- **Homosporous or heterosporous**. Haploid spores grow into bisexual gametophytes in *Lycopodium*. In Selaginella, **microspores** develop into **microgametophytes** that produce sperm and **megaspores** develop into **megagametophytes** that produce eggs.



Figure **3.2.2.3.1.1**: A club moss, genus *Lycopodium*. The upright, yellowish structures are developing strobili.

## Lycopodium

Members of this genus are homosporous, meaning they produce spores that develop into bisexual gametophytes, producing both antheridia and archegonia on the same thallus.

### Gametophyte Morphology

In seedless vascular plants, the sporophyte is the longer-lived, larger, leafy generation. This trend of sporophyte dominance throughout the evolutionary timeline of plants leads to continually smaller, less complex gametophytes. Gametophytes of this group are seldom seen. They are small and thalloid (Figure **3.2.2.3.1.2**). In *Lycopodium*, the gametophyte grows from a homospore and is bisexual, producing both antheridia and archegonia.



Figure 3.2.2.3.1.2: Image of a preserved *Lycopodium* gametophyte. The flat thallus extending out to the right is the gametophyte. The sporophyte emerges from its left side, the root system developing downward and shoot system developing upward. Photo by Curtis Clark, CC BY-SA 3.0, via Wikimedia Commons

## Sporophyte Morphology

Sporophytes branch dichotomously and have true roots, stems, and leaves due to the presence of lignified vascular tissue. This lignified vascular tissue provides rigid structural support, allowing sporophytes to grow tall. The leaves, called **microphylls**, have a single, unbranched vein of vascular tissue (Figure 3.2.2.3.1.3). Asexual propogation of sporophytes can occur via an underground stem that travels horizontally, called a **rhizome**.




Figure 3.2.2.3.1.3: A *Lycopodium* sporophyte growing vegetatively. The branches occur in Y-formations, showing dichotomous branching. There are many small, thin leaves (microphylls). Each one only has a single vein of vascular tissue, though this is not observable in this image. Photo by Maria Morrow, CC BY-SA 3.0.

To sexually reproduce, these plants produce cone-like structures at the end of their branches, called strobili. A **strobilus** is composed of leaves called **sporophylls** that bear sporangia (Figure **3.2.2.3.1.4**). Meiosis occurs within the sporangia to produce haploid homospores. Unlike the bryophytes, a single sporophyte can produce many sporangia (Figure **3.2.2.3.1.5**).

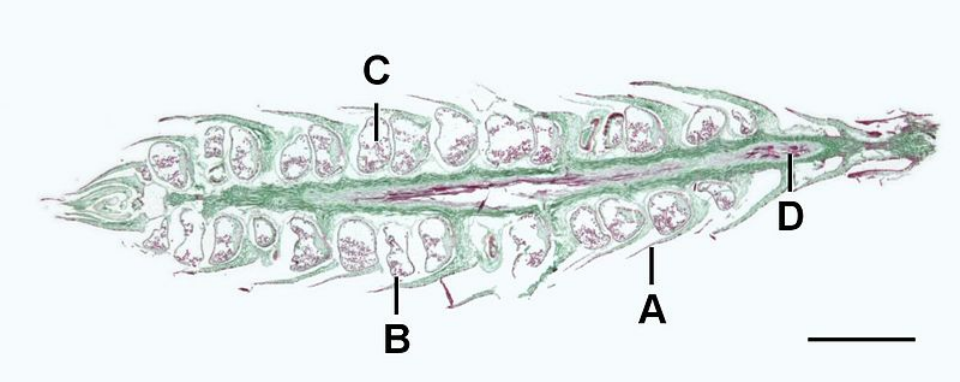



Figure **3.2.2.3.1.4**: A longitudinal section of a *Lycopodium* strobilus, shown horizontally, and labeled as follows: A) sporophyll, B) sporangium, C) spores, D) cone axis. Scale bar represents 1.5mm Photo by Jon Houseman, CC BY-SA 3.0, via Wikimedia Commons

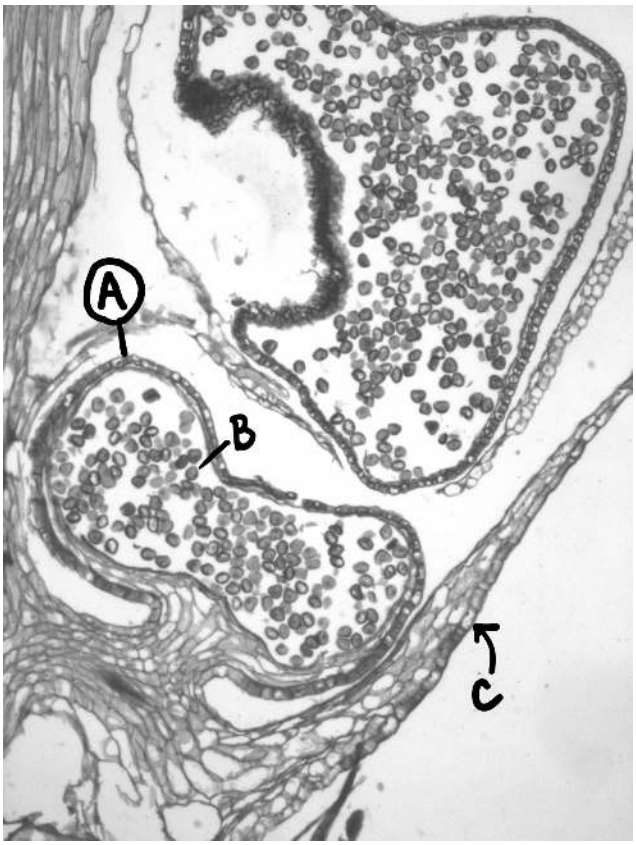



Figure **3.2.2.3.1.5**: Lycopodium is homosporous. All spores produced are approximately the same size. A sporangium (A) is enclosing homosporous spores (B). This sporangium is attached at a point to a leaf (sporophyll, labeled C) that cups around it. Photo by Maria Morrow, CC BY-SA 3.0.

## Selaginella

Members of the genus *Selaginella* are **heterosporous**, meaning they produce two different types of spores. Larger spores (megaspores) develop within **megasporangia** and are subtended by **megasporophylls**. Megaspores develop into gametophytes that produce archegonia. Smaller spores (microspores) develop within **microsporangia** and are subtended by **microsporophylls**. Microspores develop into gametophytes that produce antheridia. Megasporangia and microsporangia are found in the same strobilus (Figure **3.2.2.3.1.6**)




Figure **3.2.2.3.1.6**: In the first image there are liquid-preserved strobili of *Selaginella*, showing mega- and microsporangia through translucent sporophylls. The two types of sporangia appear different and several large, dark spores can be seen through the wall of each megasporangium. The second image is a cross section through a strobilus. Notice that the spores contained within the sporangia are quite different in size. Labels are as follows: A) cone axis, B) microsporangium, C) microspores, D) microsporophyll, E) megasporangium, F) megaspore, G) megasporophyll. Photo on the left is by Curtis Clark, licensed as noted, CC BY-SA 2.5, via Wikimedia Commons. Photo on the right is by Curtis Clark, CC BY-SA 3.0, via Wikimedia Commons with labels added by Maria Morrow.

### Extinct SVPs

Extinct lycophytes like *Lepidodendron* and *Sigillaria* grew into tall trees, branching dichotomously and producing a moss-like canopy of microphylls over 100 feet (30 m) in the air (Figures **3.2.2.3.1.7 – 8**). Some of these microphylls were several feet long! Lycophytes first appear in the fossil record over 400 million years ago. By the Carboniferous period (around 300 mya), the landscape was covered with lycophyte forests and shallow swamps. Much of the fossil fuels we use today are derived from these extinct arboreal lycophytes falling into swamps, slowing decomposition and creating layers of carbon-rich material that we now find as coal seams.



Figure 3.2.2.3.1.7: In the first image there is fossil from a *Lepidodendron* tree on display at the State Museum of Pennsylvania. This extinct lycophyte genus was perhaps one of the dominant features in the landscape during the carboniferous period. On the right is an artist's reconstruction of *Lepidodendron*, showing dichotomous branching of the roots and shoots. Microphylls and pendant strobili emerge in the canopy. Photo of the fossil by Jstuby at en.Wikipedia, Public domain, via Wikimedia Commons. Artist's reconstruction by Tim Bertelink, CC BY-SA 4.0, via Wikimedia Commons.



Figure 3.2.2.3.1.8: In the first image there is fossil from a *Sigillaria* (possibly a root fragment) that is on display at State Museum of Pennsylvania. On the right is an artist's interpretation of what these plants looked like during the Carboniferous period. Photo of the fossil by Jstuby at en.Wikipedia, Public domain, via Wikimedia Commons. Artist's reconstruction by Tim Bertelink, CC BY-SA 4.0, via Wikimedia Commons.

An ancestor of modern-day *Equisetum*, *Calamites*, is thought to look much like the *Equisetum* species we see today, excepting that it would have been 60 feet (20 m) tall (Figure **3.2.2.3.1.9**). Most ancient pteridophytes appeared in Silurian period, they were rhyniophytes. Rhyniophyles had well-developed aboveground gametophytes and relatively short, dichotomously branched leafless sporophytes. The next important steps were formation of leaves and further reduction of gametophytes.



Figure **3.2.2.3.1.9**: On the left are fossils of *Calamites*, an extinct relative of *Equisetum*, from the Sedgwick Museum's collection. On the right is an artist's interpretation of what these plants looked like. There is a large rhizome under the surface of the soil. The tree-like horsetail might have been 60 feet tall and has whorled branches with small leaves. Fossil photo by Verisimilus, CC BY 3.0, via Wikimedia Commons. Artist's reconstruction by Falconaumanni, CC BY-SA 3.0, via Wikimedia Commons.

## Attribution

- Curated and authored by Maria Morrow using 19.1.5 Diversity and Evolutionary Relationships of the Plants from *Biology* by John. W. Kimball (licensed CC-BY)
- Microphyll evolution added by Melissa Ha

---

This page titled 3.2.2.3.1: Lycopodiopsida is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **2.5.3.1: Lycopodiopsida** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-SA 4.0.
- **2.5.3: Seedless Vascular Plants** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-SA 4.0.

# 3.2.2.3.2: Polypodiopsida

**Learning Objectives**

- Differentiate between ferns, horsetails, and lycophytes.
- Identify features of vegetative and reproductive shoots of *Equisetum*.
- Identify features and phases of the fern life cycle; know their ploidy.
- Label a fern gametophyte and sporophyte.

The **Polypodiopsida** includes the horsetails and ferns. These plants produce leaves with branching veins of vascular tissue called megaphylls. Like the lycophytes, asexual reproduction of the sporophyte can be accomplished via rhizomes. Spores produced in this group develop into gametophytes that can produce both antheridia and archegonia.

## Characteristics

- **Megaphylls**. Leaves have branching veins of vascular tissue. Megaphylls are thought to have evolved from branching stems. Webbing filled in the spaces between the branches, forming the flat blade of the leaf. The arrangement of the leaf veins (vascular bundles) reflects the original branching pattern of the stems.
- **Rhizomes**. Asexual propogation of the sporophyte through underground stems.
- **Homosporous**. Haploid spores grow into bisexual gametophytes that produce both antheridia and archegonia, or are capable of producing one or the other, dependent upon conditions.

## Equisteum (subclass Equisetidae)

Horsetails are a small group with a single extant genus, *Equisetum*, which has about 30 different herbaceous species that typically live in moist habitats. The common name comes from the characteristic pattern of branching: whorls or rings of branches arising from an above-ground shoot. The leaves of these plants have been reduced to scales, and instead the segmented stems are photosynthetic. If you look closely at the nodes of a green vegetative shoot**,** you will see that branches and leaves have not only switched roles, they have also switched places, with the photosynthetic branches emerging below the papery, non-photosynthetic leaves.

Horsetails often grow in sandy places and incorporate silica in their stem epidermis, which gives it an abrasive surface. Because of this, American pioneers would use this plant to scour pots and pans. This is how it received the nickname “scouring rush.” The stem has multiple canals, an analogous characteristic to stems of grasses. The sporangia are associated with hexangular stalked **sporangiophores** produced on terminal strobili. Within the sporangia, there are **elaters** that are not separate cells but parts of the spore walls. Gametophytes are typically minute and dioecious, but the plants themselves are homosporous: smaller suppressed gametophytes develop only antheridia while larger gametophytes develop only archegonia.

### Gametophyte Morphology

Horsetail gametophytes are reduced and thalloid (figure **3.2.2.3.2.1**). Gametophytes grow from homospores and can produce both antheridia and archegonia.

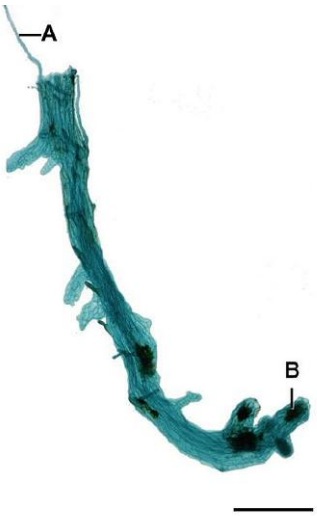



Figure 3.2.2.3.2.1: Whole mount of an *Equisetum* gametophyte. A indicates a long, thin rhizoid. B indicates one of several antheridia, each positioned on an extending lobe from the long, linear thallus. Scale=0.6mm. Jon Houseman, CC BY-SA 3.0, via Wikimedia Commons.

## Sporophyte Morphology

In some *Equisetum* species, there are two different types of shoots produced by the sporophyte: vegetative shoots that perform photosynthesis and reproductive shoots that form strobili and undergo meiosis. In other species, the strobilus is formed at the apex of a photosynthetic shoot.

## Vegetative Shoots

On the vegetative shoot, the leaves are dark, papery and non-photosynthetic. Branches are photosynthetic and produced in whorls. Branches and leaves emerge at **nodes**, separated by regions of the main stem called **internodes**. Unlike most plants, the branches emerge below the leaves in the node (Figure 3.2.2.3.2.2 – 3). The epidermis of the stems contain **silica**, which has an abrasive texture.




Figure 3.2.2.3.2.2: A vegetative shoot of *Equisetum*. There are rings of long, thin, green branches emerging from each node. Above each whorl of branches, a ring of pointy brown leaves are pressed up against the main stem. Photo by Maria Morrow, CC-BY 4.0.




Figure **3.2.2.3.2.3**: A close up of the vegetative shoot of *Equisetum*. In this image, you get a better view of the leaves. They start out as a united tube surrounding the main stem, then turn dry and brown, separating into individual, wispy points. The whorl of leaves looks a bit like a grassy crown encircling the stem. Photo by Maria Morrow, CC-BY 4.0.

## Reproductive Shoots

Sporangia are produced in a terminal strobilus on the **reproductive shoot** (figure **3.2.2.3.2.4 – 5**). In some species, this reproductive shoot lacks chlorophyll and is instead fed through the rhizome of connected vegetative shoots. Spores are photosynthetic and have four hygroscopic arms called **elaters.**




Figure **3.2.2.3.2.4**: Two reproductive shoots of *Equisetum*. These shoots are a very pale yellow, lacking chlorophyll and unable to do photosynthesis. The leaves on the reproductive shoots still occur in whorls and are larger than on the vegetative shoots shown above. At the top of each shoot, there is an elongated structure that comes to a point and looks like it is covered in polka dots. These are the strobili. Each polka dot is the top of a sporangiophore, each of which bear many sporangia, perhaps visible to you as little white frills surrounding the polka dots. Photo by Maria Morrow, CC-BY 4.0.

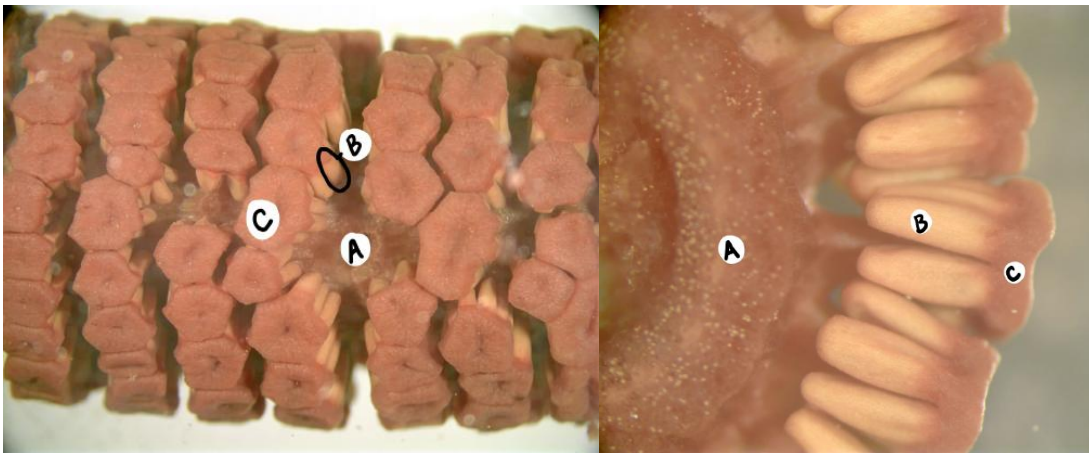



Figure 3.2.2.3.2.5: These images show a preserved strobilus. In the first image, e are looking straight at the tops of the sporangiophores (C), but some sporangia (B) are visible underneath them. There is a section where you can see the cone axis (A). In both images, the labels represent the same structures: A) cone axis, B) sporangium, C) sporangiophore. Copyright by Curtis Clark, licensed as noted, CC BY-SA 2.5, via Wikimedia Commons with labels added by Maria Morrow.



Video 3.2.2.3.2.1: This video shows how the elaters of *Equisetum* spores respond to changes in humidity. Retrieved from YouTube.

## Ferns (subclass Polypodiidae)

Some 15,000 species of ferns live on earth today. Many of these are found in the tropics where some — the "tree ferns" — may grow to heights of 40 ft (13 m) or more. The ferns of temperate regions are smaller. They are usually found in damp, shady locations. They produce perennial rhizomes that can overwinter. Their leaves, called **fronds** due to apical growth, emerge from the rhizome each spring as coiled **fiddleheads** (Figure 3.2.2.3.2.6). These fiddleheads open through a process called **circinate vernation**, where the growing tissues are protected at the center of the coil and emerge last.

True ferns are **megaphyllous**: their leaves originated from flattened branches and have branching veins of vascular tissue. True ferns have unique sporangia: **leptosporangia** (Figure 3.2.2.3.2.6). Leptosporangia originate from a single cell in a leaf, they have long, thin stalks, and the wall of one cell layer. They also open actively: when sporangium matures (dries), a row of cells with thickened walls on the outside of the sporangium (called an **annulus**) will shrink slower than surrounding cells and finally would break and release all spores at once. Leptosporangia are grouped in clusters called **sori** which are often covered with umbrella- or pocket-like **indusia**. Gametophytes are minute and grow aboveground. While most ferns are homosporous, some genera of true ferns (like the water fern *Azolla*, water shamrock *Marsilea* and several others) are heterosporous (Figure 3.2.2.3.2.7).

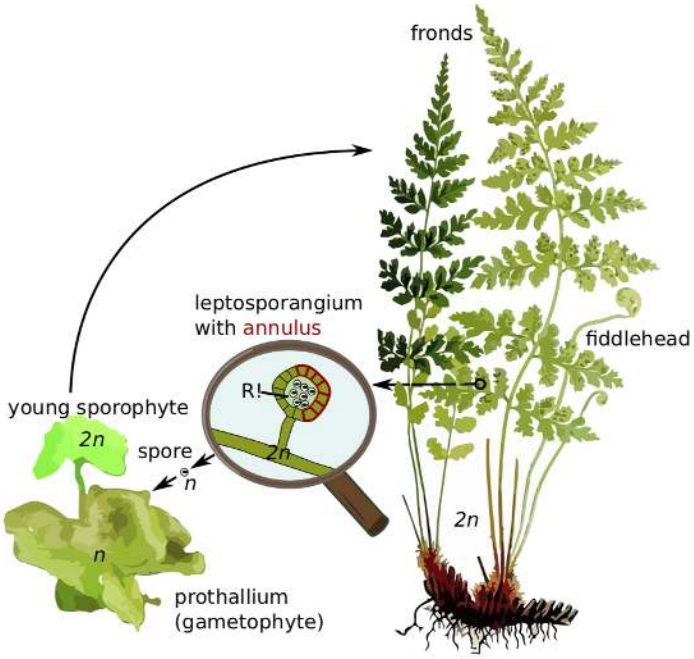



Figure 3.2.2.3.2.6: Selected stages of *Cystopteris* life cycle, representative of Pteridopsida. In this life cycle, a leptosporangium is featured in the middle. It has a thickened row of cells along the outside of the sporangium (the annulus) that will split the sporangium open as it dries. This produces a haploid (n) spore that develops into a prothallium (gametophyte, n). From the prothallium, a diploid (2n) sporophyte grows out. This then develops into several mature fronds and a developing fiddlehead.



Figure 3.2.2.3.2.7: *Salvinia natans* (left) is a heterosporous member of Polypodiidae. The hairs on the tops of the leaves repel water and help the leaves stay afloat. Kono Yasui (right), the first Japanese woman to earn her PhD, described the anatomy of this species in the *Annals of Botany*, making her the first Japanese woman to publish in a scientific journal centered outside of Japan. Over her career, she published 99 papers, including studies of plant cells (plant cytology), plant genetics, and even the formation of coal. Left image by Le.Loup.Gris, CC-BY-SA, and right image by 朝日新聞社 (public domain).

True ferns are highly competitive even to angiosperms. In spite of their “primitive” life cycle, they have multiple advantages: abilities to photosynthesize in deep shade (they are not obliged to grow fast), to survive high humidity, and to make billions of reproductive units (spores). Ferns do not need to spend their resources on flowers and fruits, and are also less vulnerable to vertebrate herbivores and insect pests, probably because they do not employ them as pollinators and, therefore, can poison tissues against all animals.

## Gametophyte Morphology

Fern gametophytes are reduced, thalloid, and heart-shaped (Figure 3.2.2.3.2.8). They are often referred to as a prothallus or **prothallium**. Rhizoids are produced from the underside of the thallus, just like in the bryophytes. Similar to the horsetails, whether

a gametophyte produces antheridia or archegonia can be regulated by environmental cues (Figure 3.2.2.3.2.9). Each antheridium produces many swimming sperm, but archegonia produce only a single egg (Figure 3.2.2.3.2.10).

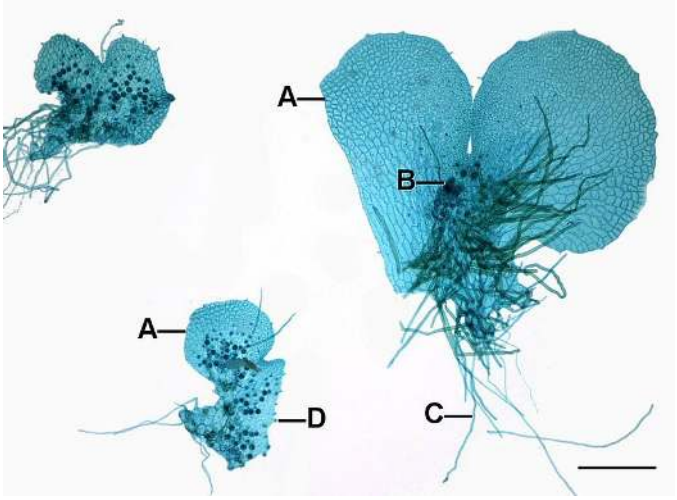



Figure 3.2.2.3.2.8: Three fern gametophytes that have been stained and so appear blue. The images are labeled as follows: A) Prothallus, B) Archegonium, C) Rhizoid, D) Antheridium. Scale=0.525mm. The rhizoids and archegonia emerge from the underside off the thallus. Descriptive text: A points to the flat, heart-shaped thallus, B points to structures with elongated necks close to the rhizoids, C points to long thin projections, D points to small dark structures spread across the thallus. Photo by Jon Houseman, CC BY-SA 4.0, via Wikimedia Commons.

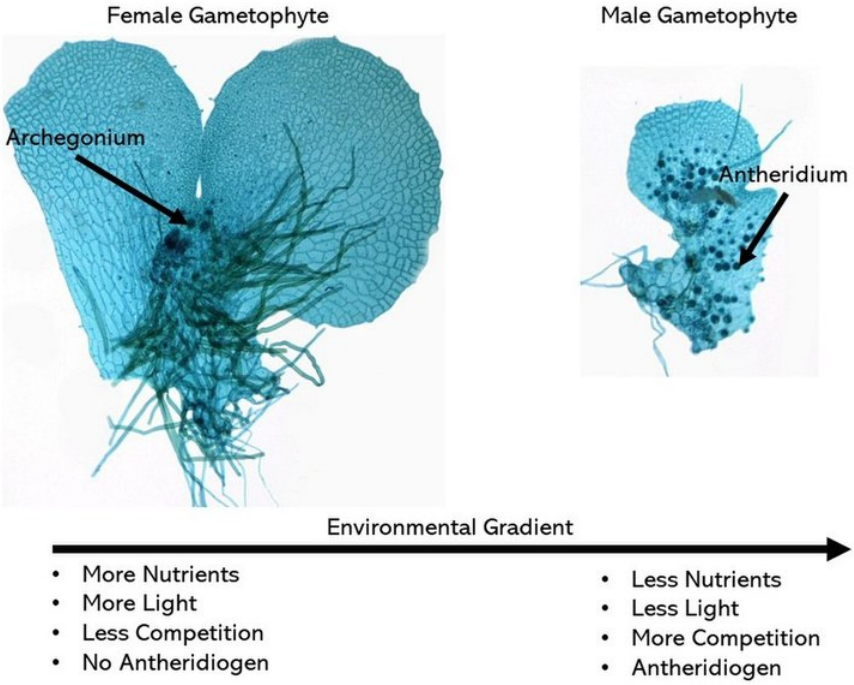



Figure 3.2.2.3.2.9: Fern gametophytes may develop either antheridia or archegonia based on environmental characteristics such as nutrients, competition, light, and antheridiogens. More nutrients, more light, less competition, and the absence of antheridiogen all select for the production of archegonia. Less nutrients, less light, more competition, and antheridiogen all select for the production of antheridia. Image by Jon Houseman, CC BY-SA 4.0, via Wikimedia Commons.

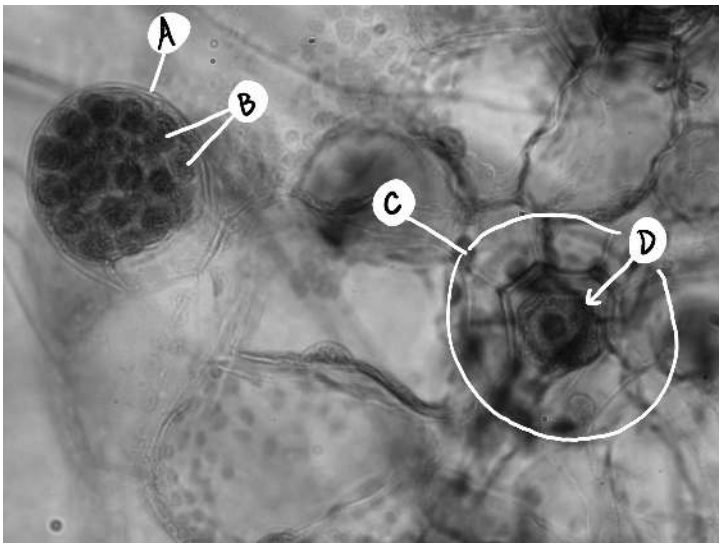



Figure 3.2.2.3.2.10: A magnified view of a fern gametophyte that has both antheridia and archegonia simultaneously. The antheridium (A) has many sperm inside (B) and does not appear three dimensional. The archegonium (C) is surrounded by enlarged cells--we are looking straight down the neck. At the center of the archegonium, there is only a single egg (D). Photo by Maria Morrow, CC-BY 4.0.

## Sporophyte Morphology

Fern sporophytes are composed of megaphylls, often pinnately compound **fronds** that emerging as coiled **fiddleheads** in the spring. Sporangia are produced in clusters called **sori** (sorus, singular) on the fronds (Figure 3.2.2.3.2.11).



Figure 3.2.2.3.2.11: The underside of *Polypodium* frond. Each fuzzy-look orange region is a developing sorus (a cluster of sporangia). These sori are not protected by an indusium. Photo by Maria Morrow, CC-BY 4.0.

**Circinate vernation** is a term used to describe the development of the fern fiddlehead (Figure 3.2.2.3.2.12) into a frond. Because plants grow apically, it is important to protect the apical meristems in growing organs (as we have seen in both axillary and terminal buds with the protective bud scales). The fiddlehead is essentially a structure that tucks away the growing tips of the fronds. As the frond develops, it gradually unfurls, releasing the tips last.



Figure 3.2.2.3.2.12: The two images above show fiddleheads of two different types of ferns, a deer fern in the first image and a sword fern in the second. Each has the same basic shape--a long stalk that transitions in a tightly coiled knot containing the developing leaf tissues. Photo by Maria Morrow, CC-BY 4.0.

A sorus (plural, sori) is a cluster of sporangia, often protected by an umbrella-like structure called the **indusium** as the spores mature (Figure 3.2.2.3.2.13). Some sori are protected by an extension of the leaf called a **false indusium** (Figure 3.2.2.3.2.14), while others lack any protective covering. Each **sporangium** is lined by an inflated strip of cells called an **annulus**. When the spores have matured, the cells in the annulus begin to dry out, causing the cells to collapse and pull the sporangium open, releasing the spores.

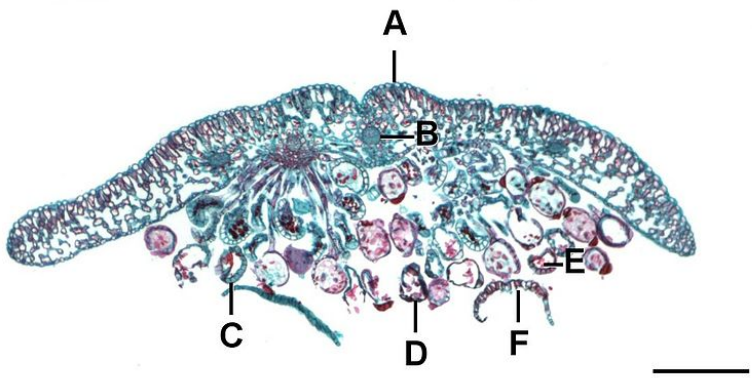



Figure 3.2.2.3.2.13: Cross section of a *Polystichum* sorus. The epidermis of the leaf (sporophyll) is labeled A. A large vascular bundle (B) is located in the center, as well as several others located along the length of the leaf. Under the leaf, a cluster of sporangia (D) are forming a sorus. Each sporangium is surrounded by a thickened layer of cells, the annulus (C). Within the sporangia, spores (E) are produced. The entire sorus was once covered by the residual structures labeled F, the indusium. Photo by Jon Houseman, CC BY-SA 3.0, via Wikimedia Commons.

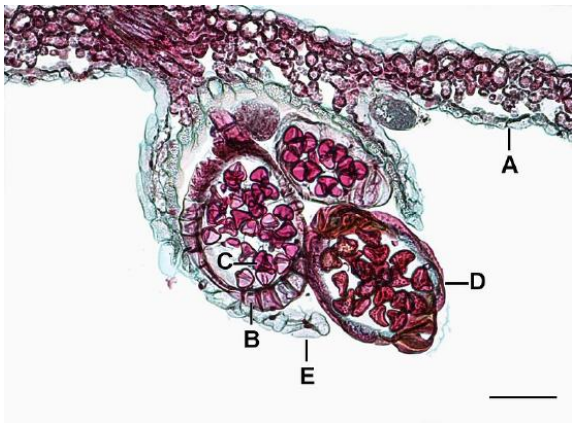



Figure 3.2.2.3.2.14: Cross section of a *Dicksonia* sorus. In this fern, the cluster of sporangia is enveloped by an extension of the leaf (E), a false indusium. A=Epidermis, B=Annulus, C=Spore, D=Sporangium, E=False indusium. Scale=0.1mm. Photo by Jon Houseman, CC BY-SA 3.0, via Wikimedia Commons.

## Full Life Cycle Diagram

Ferns rely on water for dispersal of the sperm, which must swim into an archegonium to fertilize an egg (Figure 3.2.2.3.2.15). If moisture is plentiful, the sperm swim to archegonia - usually on another prothallus because the two kinds of sex organs generally do not mature at the same time on a single prothallus.

Another method for promoting cross-fertilization: The first spores to germinate develop into prothallia with archegonia. These prothallia secrete a gibberellin into their surroundings. This is absorbed by younger prothallia and causes them to produce antheridia exclusively.

Fertilization restores the diploid number and begins a new sporophyte generation. The embryo sporophyte develops a foot that penetrates the tissue of the prothallus and enables the sporophyte to secure nourishment until it becomes self-sufficient. Although it is tiny, the haploid fern prothallus is a fully-independent, autotrophic plant. Soon, the sporophyte is nutritionally independent. It is the larger, longer-lived stage of the life cycle. To reproduce, many sori are formed on the undersides of the fronds. Within each sporangium of the sorus, the **spore mother cells** undergo meiosis producing four haploid spores each.

When the humidity drops, the thin-walled lip cells of each sporangium separate, the **annulus** slowly straightens out, then the annulus snaps forward expelling the spores. Each of these homospores can then grow into a gametophyte capable of producing antheridia and archegonia.

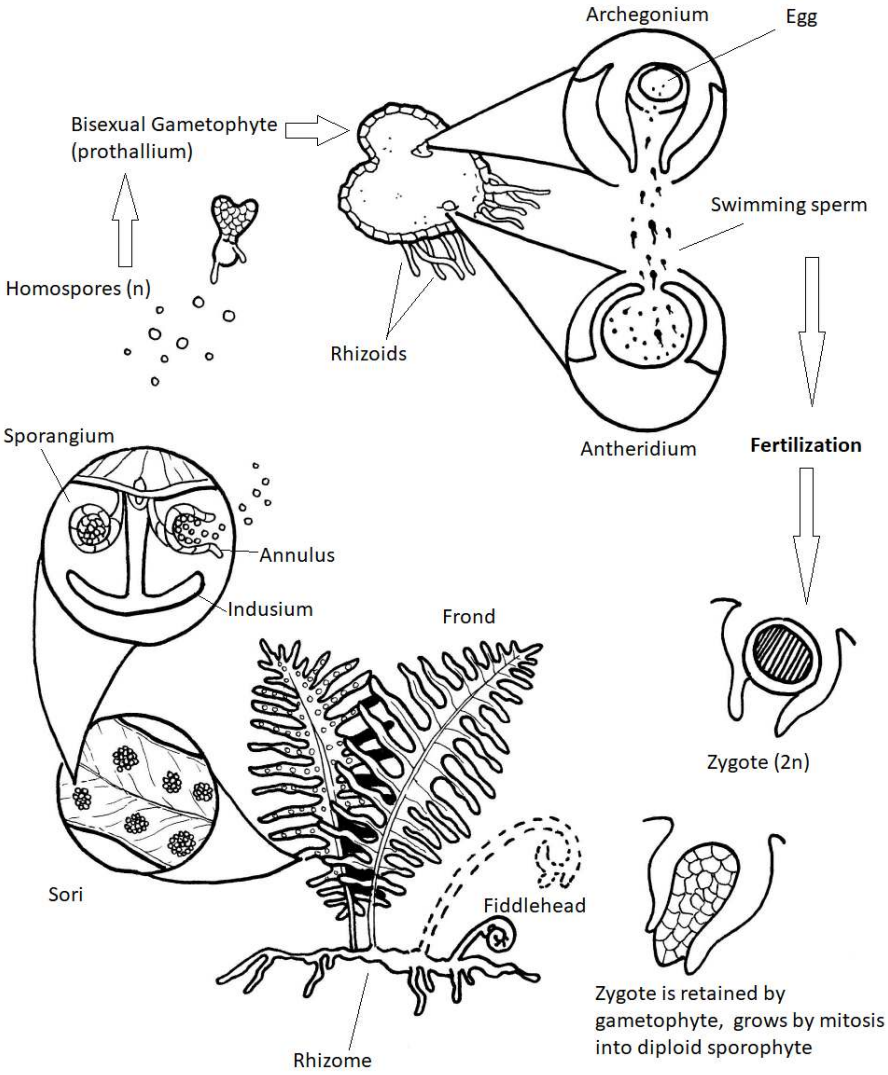



Figure 3.2.2.3.2.15: The diagram above shows the life cycle of a *Polypodium* fern. The gametophyte generation (n) is shown in the top half of the diagram and the sporophyte generation (2n) in the bottom half. Starting from the release of haploid homospores, these spores grow by mitosis into bisexual gametophytes. The gametophyte is heart-shaped, thalloid, and produces root-like structures called rhizoids. The antheridium produces many swimming sperm that are dispersed by water into an archegonium. A sperm swims down the neck/venter of an archegonium and fertilizes the single egg produced there. This produces a diploid zygote, which is retained on the gametophyte. The zygote grows by mitosis within the archegonium, producing a sporophyll (frond). When fully developed, the sporophyte will likely have multiple fronds and a rhizome. Fronds start as fiddleheads and uncoil by circinate vernation. The frond on the left is producing sori on the underside of the leaflets. Each sorus is a cluster of sporangia, which is protected by an indusium. Meiosis happens within the sporangia. Each sporangium has an inflated annulus to help release the spores when conditions are right. One of these has torn open to release its haploid homospores, which brings us back to the beginning. Diagram by Nikki Harris CC-BY 4.0 with labels added.

## Attributions

- Curated and authored by Maria Morrow using 16.3C Fern Life Cycle and 19.1.5 Diversity and Evolutionary Relationships of the Plants *Biology* by John. W. Kimball (licensed CC-BY)
- Megaphyll evolution and *Salvinia natans* information added by Melissa Ha

This page titled 3.2.2.3.2: Polypodiopsida is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **2.5.3.2: Polypodiopsida** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-SA 4.0.

## 3.2.2.4: Chapter Summary

The characteristics of early plants can be interpreted best as evolutionary adaptations to life outside of water (a waxy cuticle, stomata, decay- and desiccation-resistant sporopollenin) and a new harsh landscape (multicellular gametangia, matrotrophy, mutualistic symbioses with bacteria and fungi).

As these early plants evolved, so too did their environment. Early bryophytes, in association with their fungal partners and perhaps with the help of other lichens, caused chemical weathering of the rocky substrate due to their metabolic activity. Increased moisture retention would result in more physical weathering as water invaded new cracks in the rock, expanding and traveling deeper over cycles of freezing and thawing, respectively. In addition to the mineral substrate being formed, bryophytes would add organic matter as they lived, grew, reproduced, and died.

This activity formed Earth's first soils, paving the way for plants to evolve true roots that could excavate into the soil substrate for water and mineral nutrients, increasing both physical and chemical weathering. The non-vascular bryophytes remained relatively restricted to remain close to the substrate and water, but seedless vascular plants were less restricted. Water could be pulled from the soil through lignified xylem tissue and transported through stems and out leaves held over 100 feet in the air, exiting out pores regulated by guard cells. An abundance of photosynthates produced by newly branching sporophytes, able to make large leaves thanks to stomata and vascular tissue, can be transported around the plant through specialized phloem tissue and used to fuel faster growth and more complex structures. Relationships with mutualists continued to develop and forests are formed in tropical swamps, creating the world's first coal deposits.

Though they grew tall and adapted to aerial dispersal of spores, early plants continued to be dependent on water for fertilization.



Figure 3.2.2.4.1: Though not discussed in this chapter, you are likely to come across *Psilotum* in your botanical studies. These strange plants belong to the Polypodiopsida and are commonly referred to as whisk ferns. Oddly, they do not produce true leaves. Instead, photosynthesis is performed by the stems. These dichotomously branching stems extend underground, forming dichotomously branching rhizomes with projecting rhizoids. Their subterranean gametophytes parasitize mycorrhizal fungi, which later form a mutualism with the sporophyte generation. Fused sporangia are produced along the stems. Photo by Toshihiro Nagata, CC-BY-NC.

**After completing this chapter, you should be able to...**

- List the shared derived characteristics of land plants.

- Relate these adaptations to the movement from aquatic to terrestrial habitats.
- List the ancestral characteristics that land plants share with green algae.
- List the shared derived characteristics of bryophytes.
- Connect these characteristics to selection pressures these organisms would have faced.
- Name the three phyla included in the bryophytes.
- Use morphological traits and cellular components to distinguish between hornworts and other bryophytes.
- Identify structures and phases in the hornwort life cycle; know their ploidy.
- Label a hornwort sporophyte and describe its development.
- Use morphological traits and cellular components to distinguish between liverworts and other bryophytes.
- Identify structures and phases in the *Marchantia* life cycle; know their ploidy.
- Use morphological traits and cellular components to distinguish between mosses and other bryophytes.
- Identify structures and phases in the moss life cycle; know their ploidy.
- Label a moss sporophyte and describe its development.
- List the shared derived characteristics of seedless vascular plants.
- Connect these characteristics to selection pressures these organisms would have faced.
- Describe the importance of extinct seedless vascular plants in modern society.
- Describe the characteristics of lycophytes.
- Differentiate between homosporous and heterosporous strobili.
- Differentiate between ferns, horsetails, and lycophytes.
- Identify features of vegetative and reproductive shoots of *Equisetum*.
- Identify features and phases of the fern life cycle; know their ploidy.
- Label a fern gametophyte and sporophyte.

## Attribution

Content by Maria Morrow, CC-BY-NC

This page titled 3.2.2.4: Chapter Summary is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **2.5.4: Chapter Summary** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC 4.0.

# SECTION OVERVIEW

## 3.2.3: Seed Plants

Fossil from the Devonian period reveal fernlike plants that were **heterosporous**; that is, produced two kinds of spores: **microspores** and **megaspores**. The megaspores were not released from the parent sporophyte. Fertilization took place within the tissue of the parent sporophyte thus freed from dependence on surface water. However, the necessity for the microspores to be carried from one plant to another in order to reach the megagametophyte robbed them of their value as agents of dispersal. This function was taken over by **seeds** - dormant, protected, embryo sporophytes.


### 3.2.3.1: Introduction to Seed Plants

### 3.2.3.2: Gymnosperms

3.2.3.2.1: Cycads and Ginkos

3.2.3.2.2: Conifers and Gnetophytes

### 3.2.3.3: Angiosperms

3.2.3.3.1: Flowers

3.2.3.3.2: Angiosperm Life Cycle

### 3.2.3.4: Chapter Summary


### Attributions

Content by Maria Morrow, CC BY-NC


This page titled 3.2.3: Seed Plants is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

# 3.2.3.1: Introduction to Seed Plants

## Learning Objectives

- Explain how heterospory led to the evolution of seeds.
- Connect r- and k-strategies to propagules produced by plants (e.g. spores, gametes, pollen, and seeds).
- List a few ways gymnosperms and angiosperms differ in life history traits.

Fossil from the Devonian period reveal fernlike plants that were **heterosporous**; that is, produced two kinds of spores: **microspores** and **megaspores**. The megaspores were not released from the parent sporophyte. Fertilization took place within the tissue of the parent sporophyte thus freed from dependence on surface water. However, the necessity for the microspores to be carried from one plant to another in order to reach the megagametophyte robbed them of their value as agents of dispersal. This function was taken over by **seeds** - dormant, protected, embryo sporophytes.

## Heterospory: The Next Big Step for Life on Land

Vertebrate animals became fully terrestrial only when their fertilization became completely independent from water. Plants started to perform the similar "evolutionary efforts" even earlier, but while reptiles actively approach the sexual partner, plants evolved different solutions. Instead of the active sex, plants use "carpet bombing" with spores; this increased the chance that two spores land nearby and the distance between sperm and egg cell will be minimal.

However, increasing the number of spores also results in a waste of resources, so plants minimized spore size; this will also allow for the longer distance of dispersal and fewer resources invested in each spore. On the other hand, some spores must remain large because the embryo (if fertilization occurs) will need the support from the feeding gametophyte. Consequently, plants ended up with division of labor: numerous, minuscule microspores that grow into microgametophytes with antheridia only, and a few large megaspores that make megagametophytes producing only archegonia (Figure **3.2.3.1.1**). Megaspores are larger because they are rich in nutrients, ready to be fertilized and nourish a developing sporophyte.

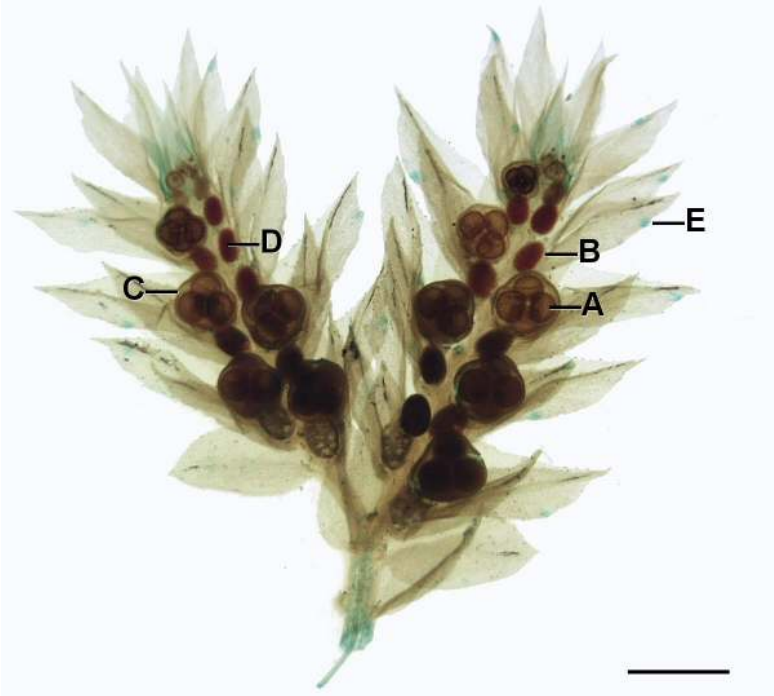



Figure **3.2.3.1.1**: Selaginella, one of the seedless vascular plants, is heterosporous. A few megaspores (A) are produced within the megasporangium (C), while many microspores (B, too small to distinguish individually) are produced within the microsporangium (D). The megaspores will grow into gametophytes that produce archegonia (megagametophytes), while the microspores will develop into gametophytes that produce antherida (microgametophytes). Scale bar represents 0.7 mm. Photo by Jon Houseman, CC BY-NC, via Wikimedia Commons.

This **heterosporic** cycle makes fertilization less dependent on water and more dependent on spore distribution and gametophyte features (Figure **3.2.3.1.2**). It also allows for increased variations for selection to act upon. Division of labor allows resources to be used more efficiently and also restricts self-fertilization. In plant evolution, there was a high need for heterospory because it independently arose in several groups of seedless vascular plants (e.g. *Selaginella* and *Azolla*) and even among mosses.

As the evolutionary trajectory of heterospory progresses, some megaspores do not leave the mother plant and instead germinate there, waiting for the fertilization from a nearby microgametophyte: a step towards the first seeds. Male gametophytes become so small that they can easily be transported as a whole. Entire male gametophytes, rather than just gametes, start to be a mobile stage —this is origin of *pollination*.

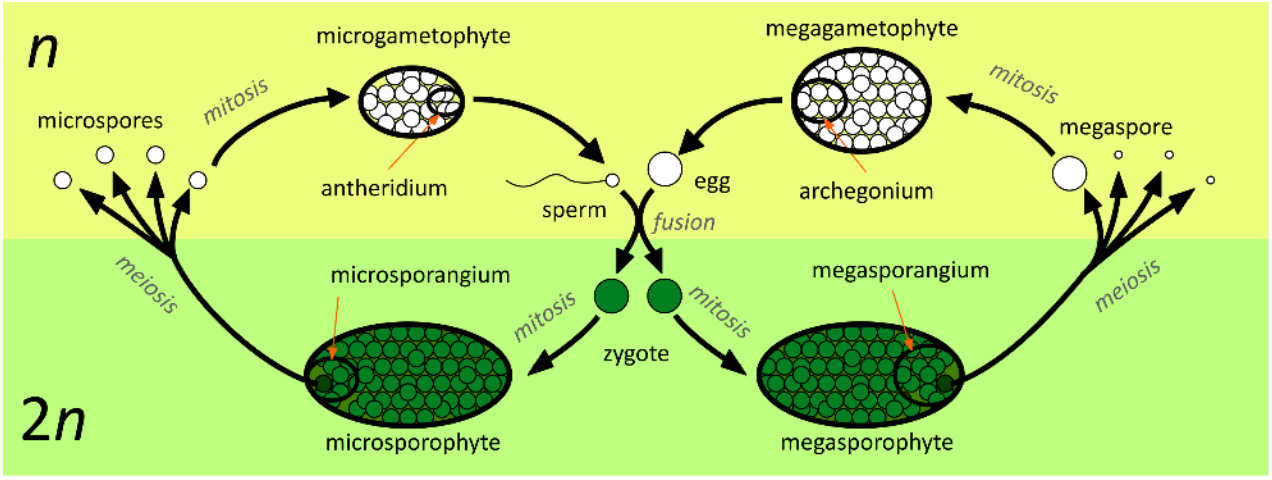



Figure **3.2.3.1.2**: A heterosporic life cycle with dioecious sporophytes. Plant life cycles can get quite complex! In **dioecious** plants, microsporangia are produced on the microsporophyte and megasporangia are produced on the megasporophyte. In **monoecious** plants, microsporangia and megasporangia are produced on the same sporophyte. If two different types of sporangia are produced (mega- and micro-), the life cycle is heterosporic. Descriptive text: In this diagram, a microsporophyte produces microspores that grow into microgametophytes that produce sperm. A megasporophyte produces megaspores that grow into megagametophytes that produce eggs. Fertilization occurs and produces either a mega- or micro- sporophyte. Diagram by Peter Coxhead, Public domain, via Wikimedia Commons.

## Getting Larger: Secondary Growth and the Transition From Seeds to Spores

When plants developed **secondary growth**, a type of growth that allowed for lateral expansion and accumulation of woody tissue, they were able to grow much larger. However, these giants faced a new problem. Big animals like elephants, lions, and whales tend to produce a small number of offspring but increase the child care to ensure survival. Another strategy, usually employed by smaller organisms, is to produce a large number of offspring with low investment in each (such as most fungal spores), though most of them will not survive (Figure **3.2.3.1.3**).

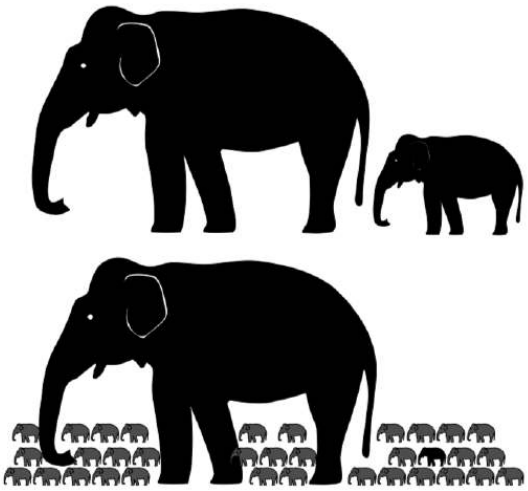


Figure **3.2.3.1.3**: This image shows an elephant reproducing using two different strategies. While we may be familiar with the first elephant, the second type of elephant does not exist. Why might this be?

Imagine these big, secondary thickening spore plants: they made billions of spores with little nutrients or protection for the developing offspring. Naturally, only few from these billions would survive to become fertilized. Spore reproduction is cheap and efficient but results are unpredictable. Even worse, these spore tree forests were not at all stable: in accidentally good conditions, many spores would survive and make sporophytes, which would all start to grow simultaneously and then suppress each other. But if the environmental conditions are poor, then none of the gametophytes will survive so there would be no new saplings to replace the old trees.

Plants evolved a solution to this conundrum: the **seed**. The idea of a seed is to hide most of the heterosporous life cycle inside the parent plant. In seed plants, everything happens directly on the parent sporophyte: development of gametophytes, syngamy, and growing of offspring sporophyte. Consequently, the megaspore never leaves the sporangium. It germinates inside, waits for fertilization and then the zygote grows into and embryo, still inside the same sporangium. What will finally leave the mother plant is the entire megasporangium with the megagametophyte and embryo inside. This is the seed's chimeric construction: sporophyte, megagametophyte, embryo, and (in angiosperms) endosperm genotypes encased within a single structure.

One problem is still left. How will sperm reach the retained megagametophyte and egg cell? The target is now perhaps high above the ground, on a branch of the giant tree. The only possible solution is pollination. **Pollination** is the distribution of the whole male gametophytes, also called **pollen**. Plants aren't able to physically go find a mate, so they always need a third party to transport their pollen, usually wind or insects.

Once the pollen gets to the intended destination, how would the sperm then swim to the egg cell? Some seed plants excrete a drop of liquid from the top of the ovule (a **pollen drop**) to create a fluid connection between the pollen grain to the ovule. Another sperm delivery tool, the **pollen tube** (Figure **3.2.3.1.4**), is made from one of the pollen grain cells in some plants. Fertilization with pollen tube is often called **siphonogamy**.

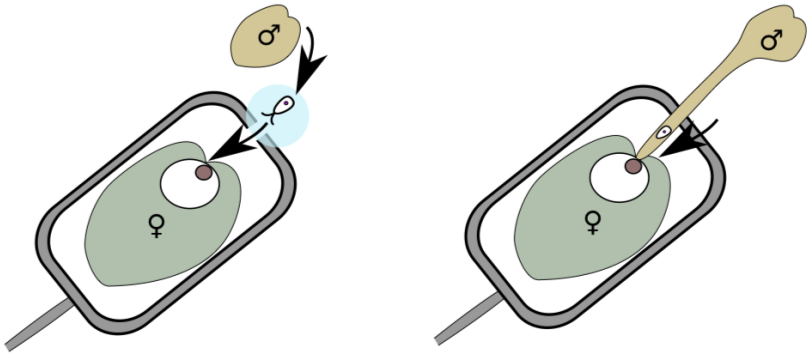



Figure **3.2.3.1.4**: Open fertilization in seed plants (left) with the help of liquid extracted by mother plant; and fertilization with pollen tube (right), or siphonogamy, with the help of pollen tube growing from male gametophyte. Among extant seed plants, only cycads and ginkgo have the open fertilization.

Consequently, seed plants with the pollen tube do not have flagella on male gametes; these cells are **spermatia**: non-motile male gametes. A pollen tube allows only two male gametes per gametophyte. Male gametes are usually competing for fertilization—this selects the best genotypes; whereas in higher seed plants, competition is between pollen tubes. The haploid pollen tube grows inside alien tissue of diploid sporophyte, so this growth is extremely slow in many seed plants. However, angiosperms made their pollen tubes grow fast.

With all these revolutionary adaptations, seed plants were first to colonize really dry places, and, in turn, allowed all other life to survive in arid climates. Read more about the evolution of seeds in this article from September, 2020.

## Gymnosperms and Angiosperms

Seed plants are composed of two major lineages: gymnosperms (meaning naked seed) and angiosperms (meaning covered seed). These two lineages represent major differences in life history traits connected to the evolutionary conditions during which each evolved.

Gymnosperm reproduction differs from that of angiosperms in several ways. In gymnosperms, the megagametophyte is contained within an ovule, present on exposed bracts of the megastrobilus, where seeds develop and are often passively released (though some are dispersed by animals). In angiosperms, the ovule is contained within an enclosed ovary. The ovary then develops into a **fruit**, specialized for seed protection and dispersal. **Double fertilization** is a key event in the life cycle of angiosperms, forming a second supply of nutrients for the developing embryo (the **endosperm**), but is absent in most gymnosperms. The gametophyte structures are produced in separate **strobili** in gymnosperms, whereas in angiosperms, they are often a part of the same **flower**. Wind plays an important role in pollination in gymnosperms because pollen is blown by the wind to land on the female cones. Although many angiosperms are also wind-pollinated, animal pollination is more common, resulting in specialized pollination syndromes present in flowers.

## Attributions

Curated and authored by Maria Morrow, CC BY-NC, using the following sources:

- 32.1 Reproductive Development and Structure from *Biology 2e* by OpenStax (licensed CC-BY). Access for free at openstax.org.
- 19.1.5 Diversity and Evolutionary Relationships of the Plants from *Biology* by John. W. Kimball (licensed CC-BY)
- 7.5 The Origin of Trees and Seeds from *Introduction to Botany* by Alexey Shipunov (public domain)

---

This page titled 3.2.3.1: Introduction to Seed Plants is shared under a not declared license and was authored, remixed, and/or curated by Tom Buckley.

- **2.6: Seed Plants** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC 4.0.

# SECTION OVERVIEW

## 3.2.3.2: Gymnosperms

**Learning Objectives**

- Describe the shared derived characteristics of gymnosperms.
- Connect these adaptations to the stressors this group of plants would have faced.

Toward the end of the Carboniferous period, major changes in the climate occurred. The current day European and North American continents slammed together, forming the Appalachian mountains (which were taller, at that time, than the present-day Himalayas). Fossil and geologic records show a tendency toward a drier climate, with evidence of glaciation and lowered sea levels. Inland seas were increasingly diverted into distinct river channels as woody debris channelled the movement of waterways. In short, the terrestrial surface began to dry out and there was much more of it. The ancestors of birds, reptiles and mammals were adapting eggs that could survive outside of the water -- plants were working toward a similar strategy. Dry conditions would have selected for plants with thicker cuticles, leaves with less surface area to evaporate from, propagules that could survive through dry periods to germinate when water was available, and those that could grow taller than the current canopy. Around this time, a group of animals likely took flight for the first time -- the insects! This would present both new challenges and new opportunities for plants.

The plants that would become the gymnosperms evolved **xerophytic leaves** to prevent desiccation in the dry air (Figure **3.2.3.2.1**).




Figure **3.2.3.2.1**: Xerophytic leaves tend to have a thick, waxy cuticle (note how shiny these giant Sequoia leaves are), a lower surface area to volume ratio with extra layers of densely packed cells, and sunken stomata. Photo by Maria Morrow, CC BY-NC.

These plants would have the ability to grow wider (and thus taller) via the production of a new layer of secondary xylem, AKA **wood**, each year. They could also produce exterior layers of dead cells, unlike the living epidermis, called **bark**. Together, the production of bark and wood are part of a process called **secondary growth** (Figure **3.2.3.2.2**). These traits allowed some gymnosperms to adapt to extreme environments like the frozen tundra, high alpine, and deserts, to resist herbivory, and live thousands of years.



Figure **3.2.3.2.2**: Secondary growth, viewed in a cross section through a woody stem. The outer layer is composed of bark, which surrounds the inner woody tissue. The wood is composed of lignified xylem cells. In gymnosperms, these cells would be tracheids. The bark forms a thick outer layer (red and fibrous) that surrounds the lighter, denser wood that composes the rest of the trunk. Photo by Maria Morrow, CC BY-NC, who is aware that this stump belongs to an angiosperm (in this case, an oak).

To increase the chances of fertilization in the absence of water, gametes began to be dispersed aerially via **pollen**. Perhaps most importantly, the zygote and female gametophyte were surrounded in a protective coating and dispersed as **seeds**. Both seeds and pollen develop within a structure called a **cone** (or strobilus, see Figure **3.2.3.2.3**).



Figure **3.2.3.2.3**: Megastrobilus and microstrobilus. The first photo shows a megastrobilus of *Araucaria*, where seeds are produced on each megasporophyll (distinguished by the curved bracts sticking out from under each one). The second photo shows a microstrobilus of *Pinus*. Each scale-like microsporophyll produces multiple microsporangia where the pollen grains develop. Photos by George Shepherd, CC BY-NC-SA.

The first fossil records of gymnosperms are from a period called the Permian, just after the Carboniferous. Gymnosperms used to have many more species, but it is likely that the event that wiped out most of the dinosaurs also represented the end for most of those lineages. Extant groups of gymnosperms include the conifers, cycads (similar in appearance to palms), gnetophytes, and

single species from the ginkgophytes, *Ginkgo biloba*. Of the approximately 1000 species of gymnosperms alive today, about 600 of these are conifers, 58 of which are found in California. In fact, some of the oldest (bristlecone pine), tallest (coast redwood), and most massive (giant sequoia) organisms on the planet are conifers and all are native to California.

Many lineages of gymnosperms are currently threatened with extinction. Check out this open-access paper (Gymnosperms on the EDGE) for more information about gymnosperm conservation.

## Selection Pressures and Drivers

1. **Competition for sunlight**. Seedless vascular plants were able to reach heights up to 100 feet tall. In the lineage leading to the gymnosperms and angiosperms, some plants developed the ability to grow wider as they grew taller. This secondary growth allowed for increased stability and, eventually, to reach heights over 300 feet.
2. **Drought**. Dry conditions would have selected for plants with thicker cuticles, leaves with less surface area to evaporate from, and propagules that could disperse without water and survive through dry periods to germinate when water was available.
3. **Herbivory**. In addition to leaves that could resist drought, the presence of insects would have driven selection for plants that could defend against herbivory. The thick cuticle and tough texture of xerophytic leaves made them difficult to eat, while resin canals in both leaves and stems provided another line of defense.

**Topic hierarchy**

### 3.2.3.2.1: Cycads and Ginkos

### 3.2.3.2.2: Conifers and Gnetophytes

## Attributions

Content by Maria Morrow, CC BY-NC

This page titled 3.2.3.2: Gymnosperms is shared under a CC BY-NC-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

# 3.2.3.2.1: Cycads and Ginkos

**Learning Objectives**

- Use morphological characteristics and life history traits to distinguish between ginkgos and flowering plants.
- Explain why *Ginkgo biloba* is called a living fossil.
- Use morphological characteristics and life history traits to distinguish between cycads and ferns.
- Define the term dioecious and provide an example.

## Ginkgophyta

As of 2019, the most recent genetic studies have placed ginkgos as the oldest of the extant gymnosperms. This does not mean that it was the first gymnosperm. From the fossil record, it seems that most early gymnosperms went extinct. The sole remaining species in this group, *Ginkgo biloba*, is a living fossil virtually unchanged from its fossilized ancestors (see Figure **3.2.3.2.1.1**). This plant is almost extinct in the wild--a few natural populations remain in China--but has a wide distribution as an ornamental tree. It is possible that this species was only kept alive due to cultivation efforts by Buddhist monks for its medicinal properties.



Figure **3.2.3.2.1.1**: Ginkgo leaves have a distinctive shape that has remained relatively unchanged from their fossil record: a fan-shaped leaf that is often deeply dissected in the center (the specific epithet *biloba* means two lobes). The fossil leaf on the right is around 60 million years old. First image: *Ginkgo biloba* leaves, photo by Onidiras, CC-BY-NC. Second image: Fossil Ginkgo leaf by Anders Sandberg from Oxford, UK, CC BY 2.0, via Wikimedia Commons.

*Ginkgo biloba* is dioecious (as an exception among plants, *Ginkgo* has sexual chromosomes like birds and mammals) and the pollen is transported by wind to ovulate trees. The microstrobili are reminiscent of the catkins produced on some flowering plants (Figure **3.2.3.2.1.2**). Pollen grains of ginkgos produce two multi-flagellate spermatozoa.



Figure **3.2.3.2.1.2**: Male *Ginkgo biloba* trees produce microstrobili that look a bit like inflorescences. Inside these structures, pollen is produced. Photo by Belvedere04, CC-BY-NC.

Ovulate have paired ovules at the tips of branches that look much like fruits (Figure **3.2.3.2.1.3**). The fleshy coating of the seed emits a foul odor as it decays, making staminate trees a more popular choice in ornamental settings.



Figure **3.2.3.2.1.3**: Female *Ginkgo biloba* trees produce fruit-like megastrobili as fleshy, paired ovules. Each globose structure contains a developing seed. Apparently, they can smell quite putrid. Photo by Kim, Hyun-tae, CC-BY

This species is also long-lived, a single tree can live for thousands of years (the oldest is 3,500 years old!), and they are resistant to most pests. This pest resistance, as well as the medicinal properties, can be attributed to a wide variety of secondary metabolites produced in the leaves, including terpenes and flavonoids. A ginkgo tree at the Zenpuku temple in Tokyo, Japan is approximately 750 years old (Figure **3.2.3.2.1.4**). Ginkgos were the first plants to regenerate after the Hiroshima bombing and were not found to contain any genetic abnormalities.



Figure **3.2.3.2.1.4**: Ginkgos can be quite long-lived. This ginkgo tree is approximately 750 years old. It bears burn scars from WWII and has a complex trunk structure. It is sometimes referred to as the inverted or upside down tree due to the numerous aerial roots growing steadily downward. *Ginkgo biloba* at Zenpuku-ji in Azabu. Photo by Belvedere04, CC-BY-NC.

# Cycadophyta

Although seed ferns are now extinct, some of their living descendants, the **cycads**, resemble them closely (Figure **3.2.3.2.1.5**). Cycads are one of the more ancient gymnosperm lineages, appearing in the fossil record around 300 million years ago. Similar to *Ginkgo biloba*, cycads have sperm with multiple flagella that swim toward the egg. For plants, this is considered an ancestral trait. Cycads and ginkgos emerge as sister taxa that are ancestral to the conifers.



Figure **3.2.3.2.1.5**: On the left is an image of what might be considered a "typical" cycad. The leaves are long, tough, and pinnately compound with long, thin leaflets arising from a central axis, like a feather. Unlike a fern, the leaves look tough. The plant in the photo on the right also shares these characteristics, yet it might not immediately stand out as a cycad. Left: *Dioon holmgrenii*, photo by Daniela Fernandez y Fernandez, CC-BY-NC. Right: *Bowenia spectabilis*, photo by kerrycoleman, CC-BY-NC.

Cycads produce leaves that are large and pinnately compound (have leaflets arising from a central axis, like a feather), making them appear frond-like. Unlike ferns, but like other gymnosperms, these leaves are xerophytic (Figure **3.2.3.2.1.6**): tough, waxy, and more resistant to desiccation.




Figure **3.2.3.2.1.6**: Each leaf blade shown here is a leaflet from the larger, pinnately compound leaf. There are many parallel veins of vascular tissue traversing each leaflet and the rachis of the leaf looks woody. *Zamia integrifolia*, photo by John C., CC-BY-NC.

Cycads are **dioecious.** The microstrobilus is produced on the "male" plant and consists of many microsporophylls bearing microsporangia. It is called a microstrobilus, not because *it* is small (these can be over a meter in height), but because the it produces smaller and more numerous spores than the megasporangium. Microstrobili are often larger than megastrobili in cycads (see Figure **3.2.3.2.1.7** and Figure **3.2.3.2.1.8**). In cycads, pollen is carried to the megastrobilus by insects. The megastrobilus is produced on the "female" plant, and is composed of overlapping megasporophylls. In some cycads, such as *Cycas* spp., the megasporophylls do not form into a strobilus structure. Ovules are produced on megasporophylls (Figure **3.2.3.2.1.9**); these ovules will develop into seeds after fertilization. Seeds are then dispersed by animals.



Figure **3.2.3.2.1.7**: The large microstrobilus, the pollen-producing cone. Photo by BillyH, CC BY 3.0, via Wikimedia Commons.



Figure **3.2.3.2.1.8**: A megastrobilus is composed of overlapping megasporophylls. Cycads are dioecious, meaning male and female strobili are produced on different individuals. These individuals are "female" and so produce a megastrobilus. Inside the megastrobilus, seeds are produced. These are visible in the photo on the right, the bright red structures that appear to be bubbling up from under the green megasporophylls. First: *Dioon merolae* Photo by Raul Ezequiel Gonzalez Trujillo, CC-BY-NC. Second: *Macrozamia macleayi*, photo by Blawson, CC-BY-NC.




Figure **3.2.3.2.1.9**: From the megastrobilus, seeds are produced. In the first photo, rounded ovules are embedded on the edges of feathery megasporophylls of *Cycas*. In the second photo, a longitudinal section of a *Cycas* ovule shows the female gametophyte (A) surrounded by the nucellus (B) and the integument (C). The remains of the micropyle (D, the tube that runs from the outside into the ovule and through which the pollen grains are sucked) are visible, and this opens into the pollen chamber, where the pollen germinates and forms a pollen tube. Photos and caption text (modified) by George Shepherd, CC BY-NC-SA with labels added by Maria Morrow.

Descriptive text for the second image: The megagametophyte is gelatinous looking and at the center, connected to the exterior by the micropyle. The megagametophyte is surrounded by a pithy-looking nucellus, which is encased by a rind-like integument.

## Attribution

Curated and authored by Maria Morrow, CC-BY-NC, using 7.6 Spermatophyta – Seed Plants from *Introduction to Botany* by Alexey Shipunov (public domain)

This page titled 3.2.3.2.1: Cycads and Ginkos is shared under a CC BY-NC-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **2.6.2.1: Cycads and Ginkos** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC-SA 4.0.

# 3.2.3.2.2: Conifers and Gnetophytes

**Learning Objectives**

- Use morphological features and life history traits to distinguish conifers from other plants.
- Connect the adaptations of conifers to dry and/or cold environments.
- Identify structures and phases in the *Pinus* life cycle; know their ploidy.
- Use morphological features and life history traits to distinguish gnetophytes from other plants.
- Describe the traits gnetophytes share with angiosperms.

Though the gnetophytes have been difficult to place, phylogenetically, recent genetic studies place them as sister to the Pinaceae (pine family, emerging from within the conifers. See this open-access paper for recent genetic work on the evolutionary relationships between gymnosperms.

## Conifers

Conifers are the most species-rich lineage of gymnosperms. From the fossil record, we think there were over 20,000 species of conifers. However, their diversity declined with the dinosaurs. Currently, there are around 600 extant species. These amazing plants represent some of the oldest, tallest, and most massive organisms on the planet. Though currently low in diversity, these amazing plants make up 30% of Earth's forests.

Conifers are the most widely known and economically important among gymnosperms. Conifers include the largest and the oldest of all living organisms. One redwood (*Sequoia sempervirens*) growing in California is almost 400 feet (122 meters) high. Bristlecone pines (*Pinus longaeva*, Figure **3.2.3.2.2.1**) growing in the mountains of eastern California some are more than 5,000 years old. Giant sequioas (*Sequiadendron giganteum*) Most of them are temperate evergreen trees, but some are deciduous, such as larch (*Larix*) and the dawn redwood (*Metasequoia*). The stem has a large amount of xylem, a small cork, and minute pith. Seeds are distributed by wind and animals.



Figure **3.2.3.2.2.1**: A bristlecone pine in the White Mountains of California. Gnarly, CC BY-SA 2.0, via Wikimedia Commons

Note: The Pinaceae is currently the largest family of conifers, so many of the examples for this group of gymnosperms will be from the type genus *Pinus* (pines).

## Xerophytic Leaves in Conifers

**Xerophytic leaves** are adapted to withstand drought conditions. In conifers, we see a wide range of xerophytic leaves with different morphologies that can be shaped by their local environment. Consider the leaves of the coast redwood and the giant sequoia (Figure **3.2.3.2.2.2 – 3**). Though these two trees belong to different genera--*Sequoia* and *Sequoiadendron*, respectively--they are sister taxa. However, the coast redwood has adapted to life on the coast, where the giant sequoia has evolved in inland, higher elevation forests with much more extreme climatic conditions. How can this be seen in the structure of their leaves?



Figure **3.2.3.2.2.2**: The image on the left shows the adaxial (upper) side and the image on the right shows the abaxial (under) side of coast redwood leaves. Note that, particularly in the photo on the left, the leaves look shiny. This is due to the presence of a thick cuticle. The stomata are also concentrated on the underside of the leaf, as indicated by the black arrow in the image on the right. They are clustered in two silvery rows on each leaf, called a stomatal bloom. However, for xerophytic leaves, these are relatively flat, with a fairly standard surface area to volume ratio. Photos by Maria Morrow, CC-BY 4.0.

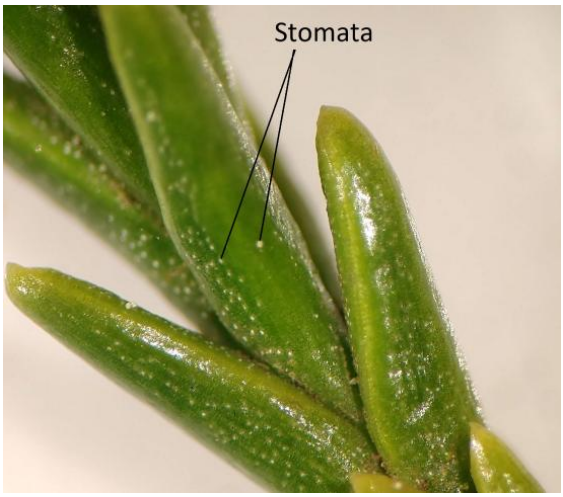



Figure \(\
PageIndex
{3}\):

These giant sequoia leaves were retrieved from a tree planted in a coastal environment, so the d ifferences here represent evolutionary history, alone. Much like the coast redwood, these shiny leaves have a thick cuticle. The big difference to note is the thickness of these leaves, maintaining a much lower surface area to volume ratio than the coast redwood. The second thing to note is the orientation of the leaves. They are held much more closely together, reducing exposure to the wider environment. Two stomata are indicated in the image, though there are many. They are present on both adaxial and abaxial leaf surfaces.

Photo by Maria Morrow,
CC-BY 4.0

.

Figure **3.2.3.2.2.4**), a thick cuticle surrounds the outside, coating the epidermis. Beneath the epidermis are several layers of tightly packed, small cells: the hypodermis. Stomata are sunken, located within the hypodermis. Under the hypodermis are the highly invaginated mesophyll cells. Further to the inside is a suberized ring of cells called the endodermis, just like in the root, which surrounds the vascular tissue. Transfusion tissue is located between the endodermis and the vascular tissue.

There are also resin canals that ring the needle, appearing as holes surrounded by small cells. These secrete **resin** to protect the plant. Resin is a sticky fluid rich in compounds that protect the plant. It flows through canals in the stems, roots, and leaves and can rush to fill a wound. The resin can gum up the mouth parts of herbivorous insects, offer chemical defense against pathogenic bacteria and fungi, and harden to close the wound (much like a scab).

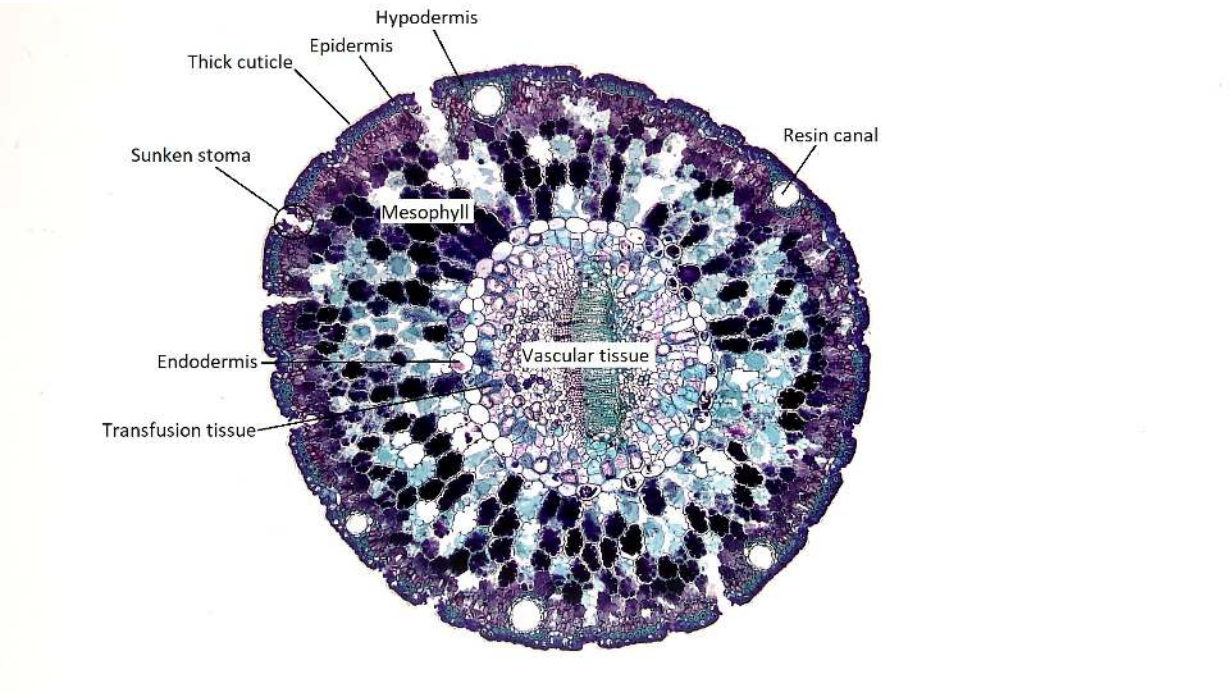



Figure **3.2.3.2.2.4**: Most pine needles you see in botany are flat on one side, however, they also come in round. The tissues of this xerophytic leaf are labeled in the diagram. The epidermis is a single layer on the outside, coated by a thick cuticle. Under the epidermis, there are several layers of similar small, tightly packed cells (hypodermis). Within the hypodermis region, there are sunken stomata. Resin canals look like large holes and are present periodically around the cross section near the hypodermis. The highly invaginated mesophyll cells are between the hypodermis and endodermis. The endodermis is a single ring of cells that surrounds the vascular tissue. Within the endodermis, there is a single vascular bundle surrounded by transfusion tissue. Image by Fayette A. Reynolds M.S., Public Domain with labels added by Maria Morrow.

## Reproduction in Conifers

Unlike other gymnosperms, conifers are **monoecious**, meaning megastrobili and microstrobili are produced on the same plant. In general, megastrobili tend to be larger and longer-lived, while microstrobili are smaller and ephemeral, disintegrating after pollen is dispersed (see Figure **3.2.3.2.2.5 – 6**). Some conifers, like junipers (*Juniperus*) and yews (*Taxus*), lack woody cones and have fleshy scales. In all, conifer life cycle takes up to two years. Conifers do not have flagellate spermatozoa; their non-motile male gametes (spermatia) move inside long, fast-growing pollen tube.




Figure **3.2.3.2.2.5**: The two images above show the strobili of the genus *Pinus*. On the first image, a seed cone from a Jeffrey pine does not have visible bracts but it does showcase a pointy umbo (B) at the tip of the ovuliferous scale (A). Dual markings where two seeds developed on each scale (C). Pines tend to form woody megastrobili (seed cones) that decay slowly, the one pictured is likely over a year old. In contrast, the second image shows a cluster of microstrobili. They are small with papery scales that will fall off after the pollen has dispersed. First photo by Maria Morrow, CC-BY 4.0. Second photo by Beentree, CC BY-SA 3.0.

The female cones are larger than the male cones and are positioned towards the top of the tree; the small, male cones are located in the lower region of the tree. Because the pollen is shed and blown by the wind, this arrangement makes it difficult for a gymnosperm to self-pollinate.

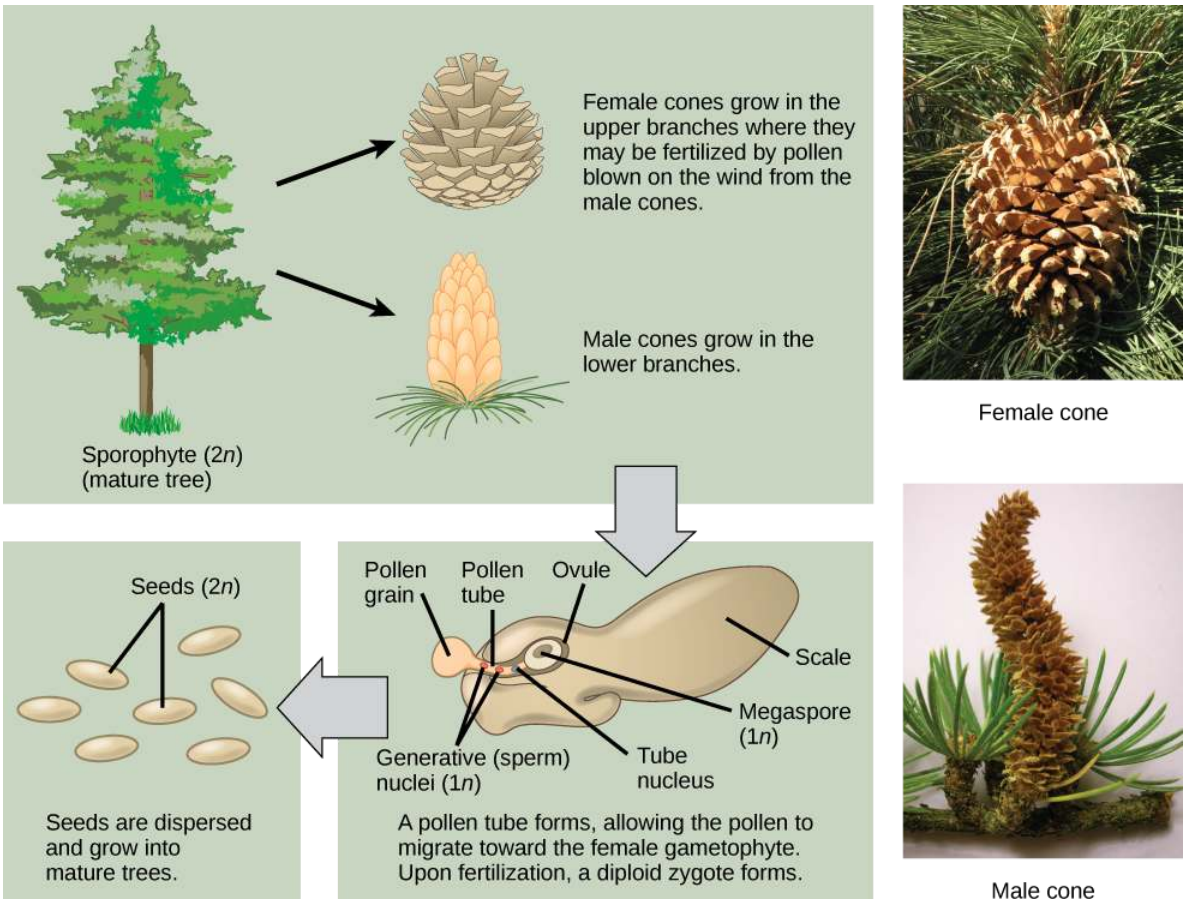



Figure **3.2.3.2.2.6**: This image shows the life cycle of a conifer. Pollen from male cones blows up into upper branches, where it fertilizes female cones. Examples are shown of female and male cones. Descriptive text: The conifer life cycle begins with a mature tree, which is called a sporophyte and is diploid (2n). The tree produces male cones in the lower branches, and female cones in the upper branches. The male cones produce pollen grains that contain two generative (sperm) nuclei and a tube nucleus. When the pollen lands on a female scale, a pollen tube grows toward the female gametophyte, which consists of an ovule containing the megaspore. Upon fertilization, a diploid zygote forms. The resulting seeds are dispersed, and grow into a mature tree, ending the cycle. Both the male and female cone are made up of rows of scales, but the male the female cone is round and wide, and the male cone is long and thin with thinner scales. (credit "female": modification of work by "Geographer"/Wikimedia Commons; credit "male": modification of work by Roger Griffith)

## Seed Cones

The megastrobilus, or seed cone, is composed of spirally arranged megasporophylls called ovuliferous scales (Figure **3.2.3.2.2.7**). Each scale produces two megasporangia, which contain a diploid megasporocyte (also called a megaspore mother cell). Each megasporocyte undergoes meiosis. Only one of the four cells produced will survive to develop into a haploid megagametophyte and the other three will die. The megagametophyte is part of the ovule and contains archegonia, each with an egg cell inside (Figure **3.2.3.2.2.8**). The megagametophyte is retained within the megasporangium, which becomes the nucellus. Surrounding the nucellus is the integument, which is initially continuous with the ovuliferous scale and has a small opening called a micropyle.

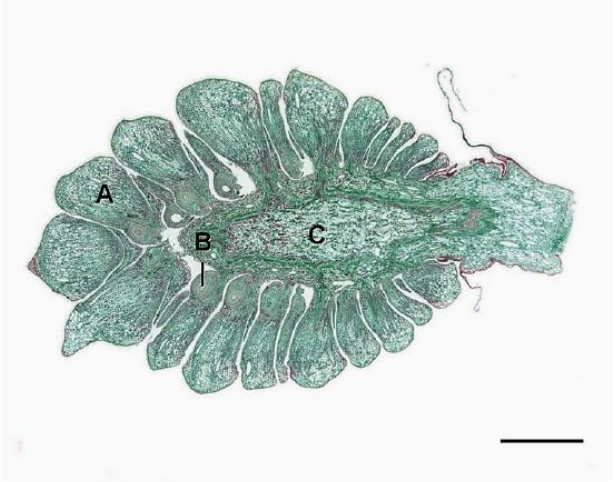



Figure **3.2.3.2.2.7**: A micrograph of a longitudinal section through a yearling *Pinus* megastrobilus, labeled as follows: A=Ovuliferous scale, B=Megasporangium, C=Cone axis. Many ovuliferous scales surround the cone axis. Each scale has a megasporangium at its base, where it connects to the axis. Scale=1.0mm. Image by Jon Houseman, CC BY-SA 4.0, via Wikimedia Commons.

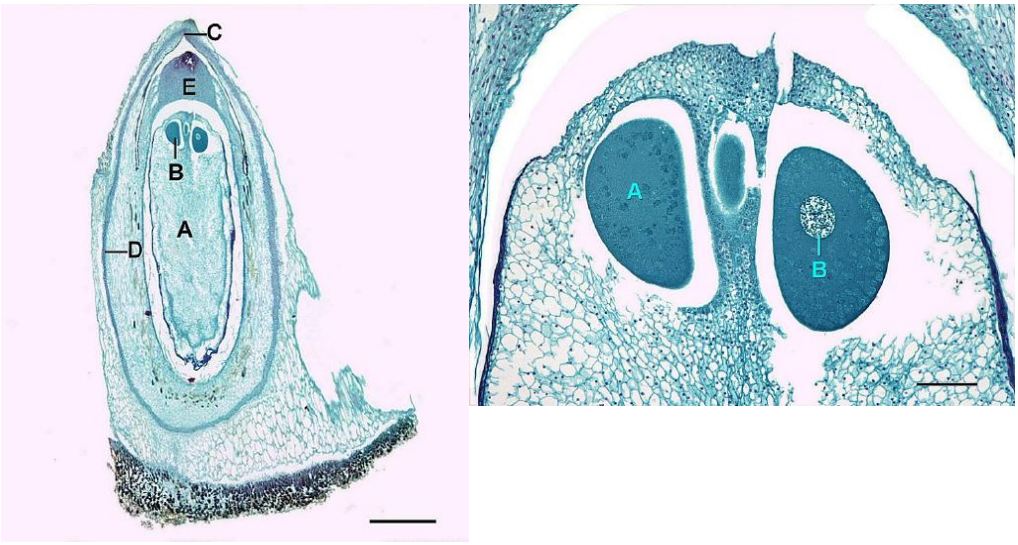



Figure **3.2.3.2.2.8**: The first image is a micrograph of a *Pinus* ovule, labeled as follows: A=Gametophyte, B=Egg cell, C=Micropyle, D=Integument, E=Megasporangium. The integument lines the outside with a small hole at the tip (micropyle). Inside the integument is the megasporangium. The megasporangium surrounds the gametophyte, which has two egg cells within it, on the end closest to the micropyle. Scale=0.8mm. The second image is a closer view, showing the eggs within the megagametophyte, labeled as follows: A=Egg cell, B=Egg nucleus. The eggs are large and one has a nucleus visible. Scale=0.31mm. Images by Jon Houseman, CC BY-SA 4.0, via Wikimedia Commons.

## Pollen Cones

Microstrobili (pollen cones) are formed from overlapping microsporophylls that bear multiple microsporangia. Within the microsporangium, there are microsporocytes (also called microspore mother cells), diploid cells that undergo meiosis to produce haploid microspores. Microspores grow by mitosis into microgametophytes, AKA pollen, within the microsporangium. The microgametophyte in gymnosperms is the four-celled, "winged" pollen grain.

Within the pollen grain (Figure **3.2.3.2.2.9**), there is a **generative cell**, a **tube cell**, and two **prothallial cells**. On either side of the pollen grain, two wing-like structures called **air sacs** may help orient the pollen grain toward the ovule.

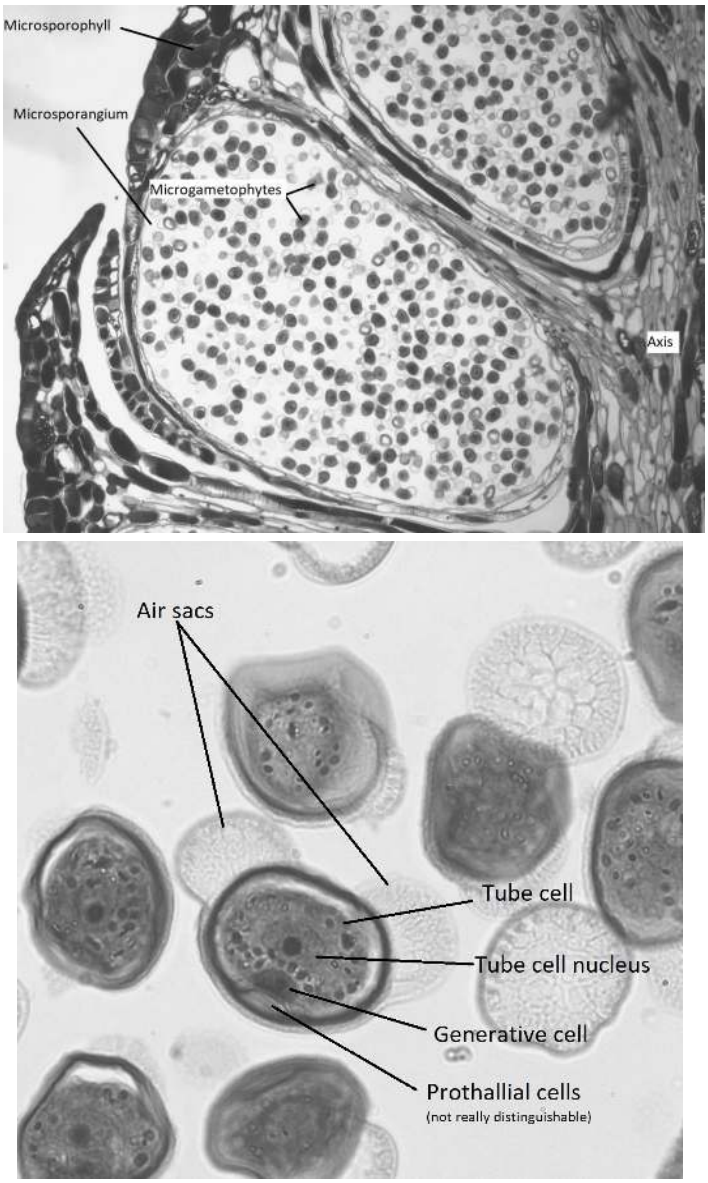



Figure **3.2.3.2.2.9**: The first image is a long section through a pine microstrobilus that shows inside a microsporangium. Each microsporangium is produced on a leaf-like structure called a microsporophyll that emerges from the cone axis. Within the microsporangium, many mature pollen grains are visible. You can tell the pollen grains are mature at this magnification by the presence of the air sacs. In the second image, we see a closer image of pollen grains. The two ear-like air sacs flank the four cells enclosed in the center: the tube cell, generative cell, and two prothallial cells. The tube cell takes up most of the internal space and its nucleus is about the same size, if not a little bigger, than the entire generative cell. The two prothallial cells are squished against the edge opposite the air sacs and are not really distinguishable in this image. Photos by Maria Morrow, CC-BY 4.0.

A grain of pollen will be transported on the wind and, if lucky, it will land on a seed cone. The seed cone has a drop of sugary liquid (a **pollen drop**) that it secretes, then retracts, pulling the pollen in toward the ovule. This stimulates the tube cell to germinate a **pollen tube**, while the generative cell divides by mitosis to produce two **spermatia** (no flagella). These spermatia travel with the pollen tube, through the micropyle, and into an archegonium where one will fertilize an egg (Figure **3.2.3.2.2.10 – 11**). It takes approximately one year for the pollen tube to grow and migrate towards the female gametophyte! When fertilization occurs, the micropyle closes and the integument becomes the **seed coat**.

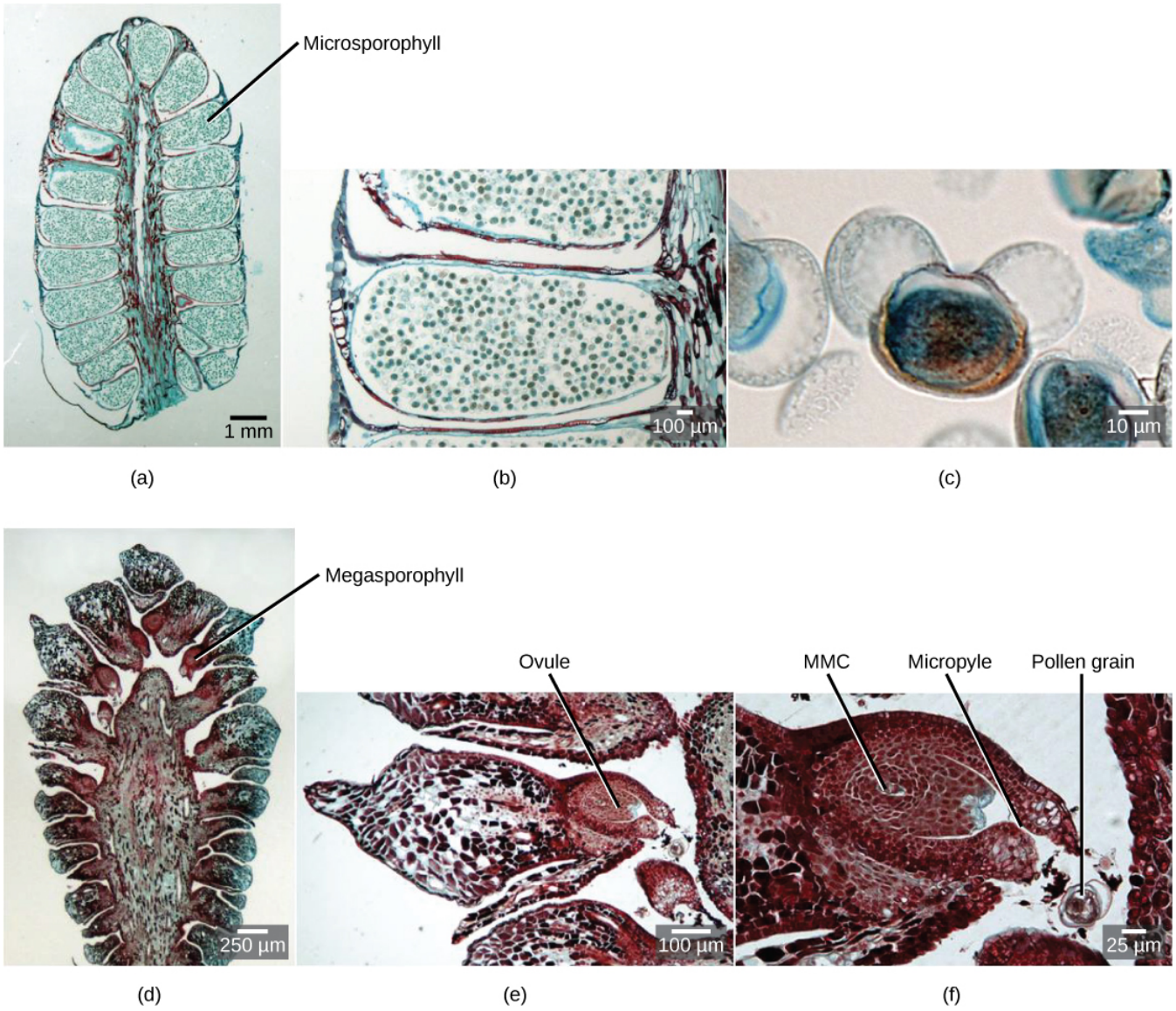



Figure **3.2.3.2.2.10**: These series of micrographs shows male and female gymnosperm gametophytes. (a) This male cone, shown in cross section, has approximately 20 microsporophylls, each of which produces hundreds of male gametophytes (pollen grains). (b) Pollen grains are visible in this single microsporophyll. (c) This micrograph shows an individual pollen grain. (d) This cross section of a female cone shows portions of about 15 megasporophylls. (e) The ovule can be seen in this single megasporophyll. (f) Within this single ovule are the megaspore mother cell (MMC), micropyle, and a pollen grain. Descriptive text: Part a shows a cross section of a male cone, which is oval with a flattened bottom. A stem-like structure runs up the middle, and oblong microsporophylls radiate from either side. Migrograph b shows a blowup of a microsphorphyll, which is filled with round pollen grains. Micrograph C shows a blowup of a pollen grain, which is oval with two lobes and resembles Mickey Mouse. Part D shows a cross section of a female cone, which is similar in shape to the male cone but with a wider central structure. Megasporophylls radiate from either side of this structure. At the base the megasprophylls are narrow, and the widen out into a roughly diamond shape. Part E shows a blowup of the megasprophyll, which has an oval ovule at its base. Part F shows a blowup of the ovule. The megaspore mother cell is at the center. An opening called a micropyle allows entry of the pollen tube from the base. (credit: modification of work by Robert R. Wise; scale-bar data from Matt Russell)

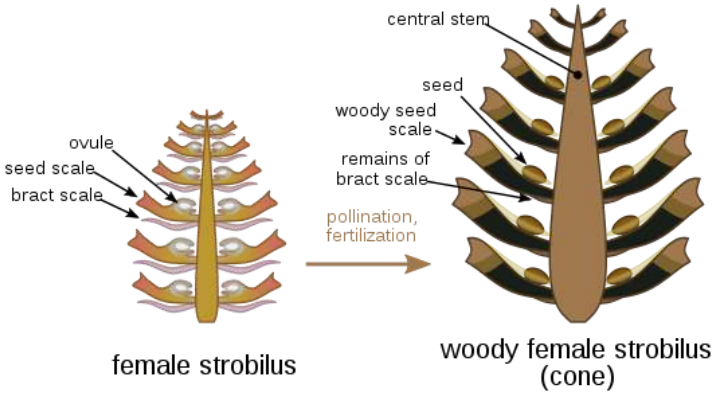



Figure **3.2.3.2.2.11**: The megastrobilus before (left) and after (right) fertilization. In the unfertilized cone on the left, there is an ovule on top of each ovuliferous scale. In the fertilized cone on the right, the ovule has become a seed, the cone has become woodier, and the sterile bract has been reduced. Image by Nefronus, CC BY-SA 4.0, via Wikimedia Commons.

The zygote will grow and develop as an embryo within the seed, nourished by the megagametophyte tissue, as well as the nucellus (Figure **3.2.3.2.2.12**). The scales of the cones are closed during development of the seed. Seed development takes another one to two years. Once the seed is ready to be dispersed, the bracts of the female cones open to allow the dispersal of seed; no fruit formation takes place because gymnosperm seeds have no covering. The seed will be dispersed by wind or animals and germinate to grow into a diploid pine tree once again.

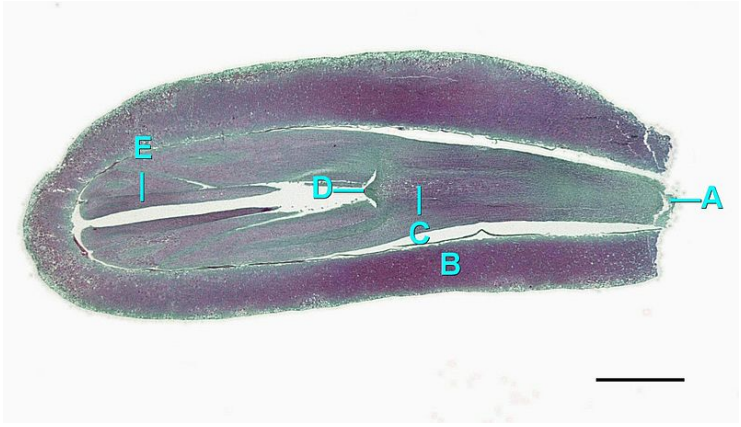


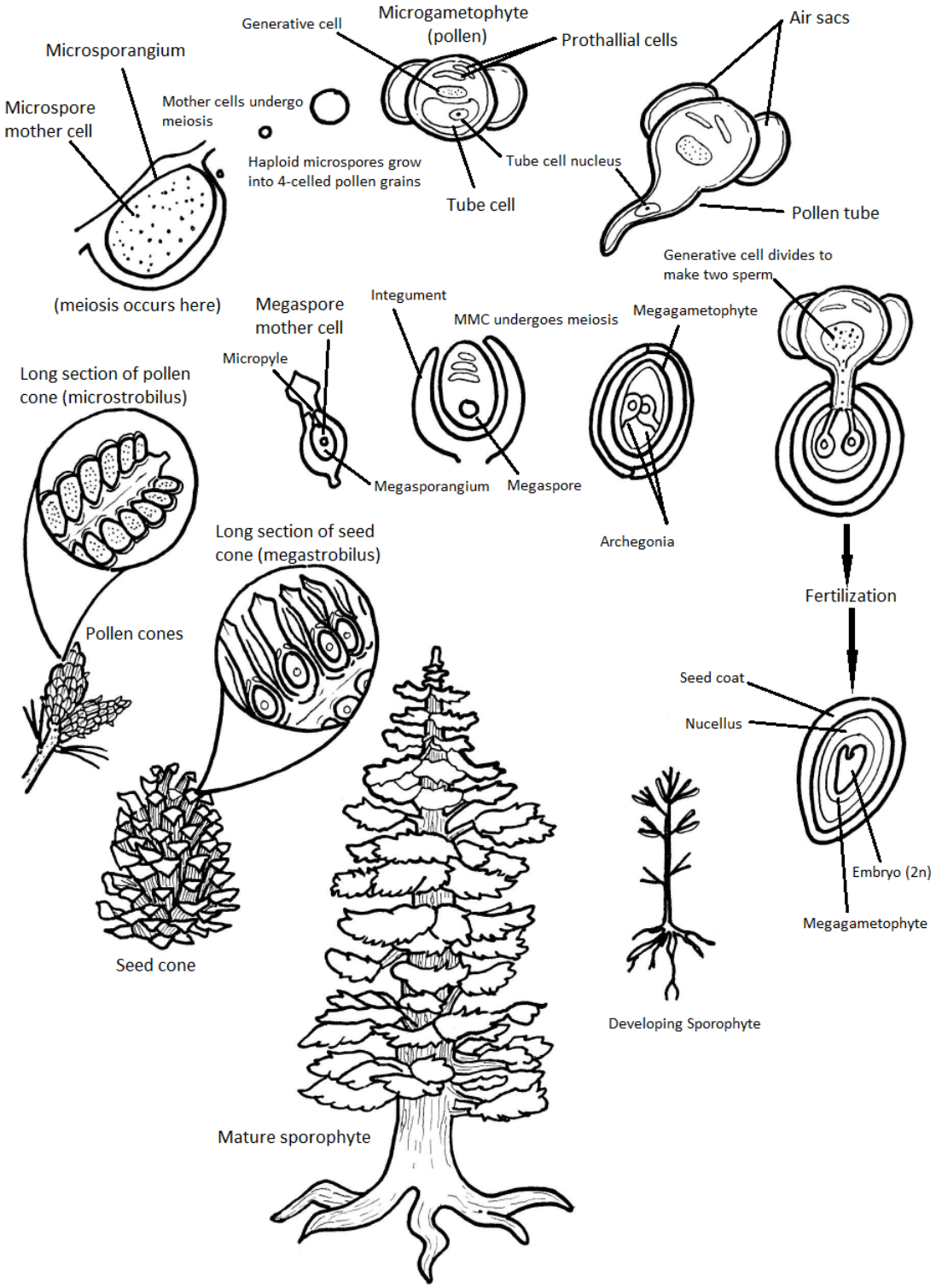

Figure **3.2.3.2.2.12**: A longitudinal section through a fertilized pine seed. The embryo is developing within the integument, labeled as follows: A=Root cap, B=Integument, C=Hypocotyl-root axis, D=Shoot apical meristem, E=Cotyledons. The integument forms the outer layer, surrounding the embryo. The embryo has a root cap at one end, connected to the shoot apical meristem by the hypocotyl-root axis. Two arm-like cotyledons flank the shoot apical meristem. Scale=1.3mm. Photo by Jon Houseman, CC BY-SA 4.0, via Wikimedia Commons.

## The Full Life Cycle

Video **3.2.3.2.2.1** is an extremely helpful narrated animation of the pine life cycle. You should watch this video or some other walkthrough of the pine life cycle before attempting to interpret the complex diagram (Figure **3.2.3.2.2.13**).



Video 3.2.3.2.2.1: A narrated video of the pine life cycle, sourced from Youtube.





https://bio.libretexts.org/@go/page/150478

Figure **3.2.3.2.2.13**: This is an illustrated diagram of the pine life cycle. Starting at the bottom of the image, there is a pine tree. This is the mature sporophyte (2n). It will produce both seed cones and pollen cones because it is monoecious. Seed cones will produce two megasporangia on each ovuliferous scale, each one surrounded by an integument. Within the megasporangium, a megaspore mother cell (2n) undergoes meiosis to produce four megaspores (n). Three die and one remains, developing by mitosis into the megagametophyte. The megagametophyte produces two archegonia, each with an egg. This trajectory occurs through the center of the diagram. Jumping back to the pollen cone, microsporangia are produced on each microsporophyll of the pollen cone. Initially, they are filled with microspore mother cells (2n) that then undergo meiosis to produce microspores (n). These microspores grow by mitosis (though only two rounds) into 4-celled microgametophytes: pollen. Each pollen grain is composed of two ear-like air sacs on the outside, a large tube cell, a small generative cell, and two tiny prothallial cells. The mature pollen grains are dispersed on the wind to seed cones where the tube cell will form a pollen tube into the megagametophyte by entering through a gap in the integument called the micropyle. The generative cell divides to produce to sperm cells, which travel down the pollen tube to fertilize an egg. Once fertilized, the integument closes, forming the seed coat. The embryo develops within the seed, consuming the megagametophyte and the megasporangium (now called the nucellus) as it grows. The seed is dispersed and, if in the right conditions, the embryo emerges from the seed coat and develops into a mature sporophyte. Diagram by Nikki Harris CC BY-NC with labels added.

## Gnetophytes

**Gnetophytes** are a small group with only three genera that, excepting from their opposite leaves, seem not at all similar: *Ephedra*, *Welwitschia*, and *Gnetum*. *Ephedra* are horsetail-like desert leafless shrubs, *Gnetum* are tropical trees, and *Welwitschia* are strange desert plants that form two large, continuously growing leaves (Figure **3.2.3.2.2.14**). Gnetophytes represent an anatomically and genetically difficult group to classify. They have several traits in common with angiosperms, such as vessel elements in the xylem, double fertilization, and a covering over their seeds. Even their leaves are angiosperm-like, with netted venation. However, these traits are convergently evolved, meaning that angiosperms and gnetophytes each evolved these traits separately. Genetically, recent studies have placed the gnetophytes as a sister group to the Pinaceae (pine family) within the conifers. This would mean that pines, firs, and spruces are more closely related to strange gnetophytes like *Ephedra* than they are to other conifers like redwoods, cedars, and Pacific yew. However, the true nature of this evolutionary relationship remains murky and contentious.



Figure **3.2.3.2.2.14**: These three genera of plants represent the gnetophytes: *Ephedra* (left), *Gnetum* (center two) and *Welwitschia* (right). *Ephedra* has thin stems with scale-like leaves. *Gnetum* has large, flat leaves on very angiosperm-like plants. *Welwitschia* has just two leaves emerging opposite each other, no stem is visible.

*Ephedra* has archegonia, but in *Gnetum* and *Welwitschia* they are reduced. On the other hand, *Ephedra* and *Gnetum* have **double fertilization**, a process that you will see in angiosperms where both male nuclei fuse with cells of the one female gametophyte. Double fertilization in gnetophytes results in two competing embryos, and only one of them will survive in the future seed.

Both *Gnetum* and *Welwitschia* have vessel elements (like angiosperms). *Gnetum* also has angiosperm-like opposite leaves with netted venation, like the coffee tree (however, this probably is a result of modification of dichotomous venation). Ovules are solitary and covered with an additional outer integument; the male gametes are spermatia moving with the pollen tube instead of swimming (no flagella).

*Welwitschia* is probably most outstanding among gnetophytes. There is only one species and it occurs only in the Namibian desert. The best way to describe this plant is an “overgrown seedling.” It has a small trunk with two wide leaves that have parallel venation. The secondary thickening is anomalous, the wood has vessels. This plant is insect-pollinated and its winged seeds are dispersed by the wind. Fertilization is not double, but, along with pollen tubes, involves some interesting structures: prothallial tubes which grow from female gametophyte and meet with pollen tubes.

### Characteristics of Gnetophytes

- Angiosperm-like features: vessel elements, double fertilization, fruit-like ovule coverings
- **Dioecious**. Female plants have covered ovules, while male plants have pollen cones.
- Leaves xerophytic with **opposite arrangement**
- Primarily insect pollinated; brightly colored seeds are dispersed by birds

### Welwitschia mirabilis

This strange plant grows in the desert of Namibia. It has two large leaves that grow from a **basal meristem**. As the plant gets older the leaves split and start to look like numerous long tentacles (Figure **3.2.3.2.2.15**). The tips of the leaves are ragged, as these are the oldest parts. The leaves are shiny and the setting is dry, indicating their xerophytic nature. In the center, where the two leaves meet, plants will produce either megastrobili or microstrobili (Figure **3.2.3.2.2.16**).



Figure **3.2.3.2.2.15**: A *Welwitschia* at the petrified forest, west of the town of Khorixas, Namibia. Photo by Nanosanchez, CC BY-SA 3.0, via Wikimedia Commons.



Figure **3.2.3.2.2.16**: Strobili of *Welwitschia mirabilis*. Megastrobili (first photo) are larger and rounder, composed of tightly overlapping megasporophylls. Microstrobili (second photo) are smaller and thinner than the megastrobili. First image by C T Johansson, CC BY-SA 3.0, via Wikimedia Commons. Second image by Krzysztof Ziarnek, Kenraiz, CC BY-SA 4.0, via Wikimedia Commons.

### *Ephedra*

*Ephedra* spp. have scale-like, opposite leaves produced on tough, photosynthetic stems. They produce swollen megastrobili that look like fruits (Figure **3.2.3.2.2.17**), and microstrobili have extruded microsporangia, making them look like catkins (a type of inflorescence produced by some angiosperms, (Figure **3.2.3.2.2.18**). Some *Ephedra* species produce alkaloids that have been extracted for stimulant use, including ephedrine and pseudoephedrine.



Figure **3.2.3.2.2.17**: A thin stem of *Ephedra* showing opposite leaf arrangement of two scale-like leaves. Megasporophylls are swollen and red, making the megastrobilus appear fruit-like. Seeds are produced within these structures. Descriptive text: Thin green stems end in swollen red structures that appear to be separated into a few different segments. Two tiny, scale-like leaves emerging from either side of a node. Photo by Germán Escorza, CC BY-SA 4.0, via Wikimedia Commons.



Figure **3.2.3.2.2.18**: Microstrobili of a male *Ephedra viridis*. These small structures look like inflorescenses with anthers emerging. From between the microsporophylls, branching structures emerge, topped with microsporangia releasing pollen. Photo by Stan Shebs, CC BY-SA 2.5, via Wikimedia Commons.

## Gnetum

*Gnetum* spp. could easily be mistaken for flowering plants. They produce leaves with netted venation and fruit-like megastrobili. These plants are restricted to tropical areas and generally take on a tree-like habit.



Figure **3.2.3.2.2.19**: *Gnetum* strobili. The leaves have a larger central vein with smaller, branching side veins (netted venation). In the first photo, a "female" plant has megastrobilus is covered with swollen structures that look like berries. These will eventually redden, increasing the berry similarity. In the second photo, a thin microstrobilus is shown on a "male" plant. These plants look very much like angiosperms and very little like gymnosperms. First photo by BotBln, CC BY-SA 3.0, via Wikimedia Commons. Second photo by Kembangraps, CC BY-SA 3.0, via Wikimedia Commons.

## Attribution

Curated and authored by Maria Morrow using the following sources:

- 19.1.5 Diversity and Evolutionary Relationships of the Plants from *Biology* by John. W. Kimball (licensed CC-BY)
- 26.2 Gymnosperms from *Biology 2e* by OpenStax (licensed CC-BY). Access for free at openstax.org.
- 7.6 Spermatophyta – Seed Plants from *Introduction to Botany* by Alexey Shipunov (public domain)

---

This page titled 3.2.3.2.2: Conifers and Gnetophytes is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **2.6.2.2: Conifers and Gnetophytes** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-SA 4.0.

# SECTION OVERVIEW

## 3.2.3.3: Angiosperms

**Learning Objectives**

- Describe the shared derived characteristics of angiosperms.
- Connect these characteristics to the stressors these plants would have faced.

At the end of the Permian period, there was the largest mass extinction this planet has ever experienced. It is estimated that 96% of species that lived at that time went extinct. This event signaled the downturn for some groups and opened up space for others to emerge. The exact timing of the emergence of angiosperms is unknown, so it is difficult to relate their evolution to specific climatic conditions. However, there is relatively new fossil evidence that may place flowering plants as early as the Jurassic period, 174 mya. This was the age of the dinosaurs and coincides with the emergence of the first feathered dinosaurs -- birds! Much like the insects, birds would present interesting opportunities for this new group of plants, working as both pollinators and seed dispersers.

Angiosperms can be distinguished from other plants by a set of specialized characteristics that allowed them to compete in an already full world. The (usually) easiest thing to identify about an angiosperm are its **flowers**. These collections of modified leaves allowed this group of plants to attract pollinators and increase the chances of successful fertilization. Once pollinated, the fertilized seeds are encased in a protective ovary whose structure can be specialized for different methods of dispersal, such as animal ingestion, animal attachment, flotation, or wind dispersal. This protective ovary and the encased seed(s) are more commonly called a **fruit**. Inside the developing seeds, angiosperms provide an additional food source to the developing zygote, the **endosperm**.

Competing with the gymnosperms for access to sunlight was perhaps hopeless, so the angiosperms adapted ways to work smarter, not harder. In the xylem, they evolved large diameter conducting cells for rapid water uptake called **vessel elements**, though this made them vulnerable to freezing conditions. In the phloem, sieve cells evolved into **sieve tube elements**, increasingly specialized for transportation of photosynthates.

As you might have guessed from the vast number of species, angiosperms occupy incredibly diverse habitats and span a range of morphologies, from tiny plants floating as a film on the surface of a pond (Figure **3.2.3.3.1**) to towering Eucalyptus trees dominating the forests of Tasmania, rivaling redwoods in height.




Figure **3.2.3.3.1**: The world's smallest flowering plants belong to the genus *Wolffia*. Flowers are produced in a cavity within the plant, the top of which is visible here as a small depression in the larger compartment. Photo by Stefan.lefnaer, CC BY-SA 4.0, via Wikimedia Commons.

## Selection Pressures and Drivers

1. **Competition for space**. Present day gymnosperms include the tallest, most massive, and some of the oldest organisms on the planet. With this in mind, you can imagine that they would be difficult to compete with. Angiosperms needed to evolve more efficient methods of transporting water and photosynthates, fertilization, and survival of offspring.
2. **Animals**. The primary response to animals that we see in gymnosperms is prevention of herbivory, though there is some insect pollination and animal seed dispersal. While herbivory is still a driver of selection for angiosperms, animals also served as a more efficient method of pollen delivery. Insects and birds could be lured in with sugary nectar or scents and colors that mimicked other resources, then dusted with pollen as they investigated. If the lures were specialized enough, they would continue seeking the same resource, leading them to another plant of the same species. These scents, colors, and nectar resources were produced by structures that also produced pollen and ovules -- the flower. Similarly, fruits allowed for the dual purpose of protecting seeds and co-opting animals as dispersal agents, whether by ingestion or attachment. Some fruits evolved production of sugary tissues and bright colors to attract animals, while others evolved hairs or spines to latch onto their bodies.

## 3.2.3.3.1: Flowers

## 3.2.3.3.2: Angiosperm Life Cycle

## Attribution

Content by Maria Morrow, CC-BY

This page titled 3.2.3.3: Angiosperms is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

# 3.2.3.3.1: Flowers

## Learning Objectives

- Identify the components of a flower and to which whorl each belongs.
- Write and interpret floral formulas.
- Differentiate between flowers and inflorescences.
- Explain the difference between raceme-based and cymose inflorescences.

Flowers are sets of highly modified leaves that function to attract a pollinator or, if no animal pollinator is used, to optimize spore dispersal in some way. Over the course of evolutionary history and coevolution, this has lead to an incredible diversity of shape, size, color, smell, and just about any other characteristic you can think of. Because most plants are angiosperms and because flowers are often so diverse, learning the terminology to describe flowers is a major step in learning to identify plants.

The modified leaves in flowers are called **sepals**, **petals**, **stamens**, and **carpels** (Figure 3.2.3.3.1.1). These components are arranged in whorls and attach to an area called the **receptacle**, which is at the end of the stem that leads to the flower. This stem is called the **peduncle**. In the case of an inflorescence, where multiple florets are produced in place of a single flower, the stems leading to the florets are called pedicels (Figure 3.2.3.3.1.2).

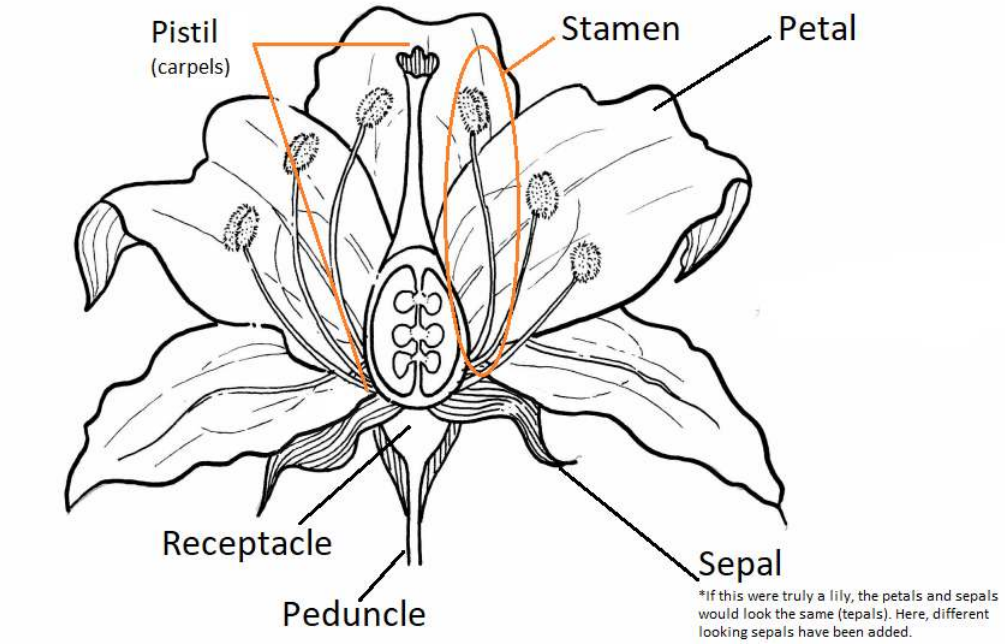



Figure 3.2.3.3.1.1: This diagram shows a long section through a flower. Starting from the bottom, there is a stem called the peduncle. The peduncle terminates in a region called the receptacle, where all of the parts of the flower are attached. Sepals are found on the outside of the flower, two are visible here, with petals located just within the ring of sepals. There are five petals visible. Inside the petals, six stamens encircle a central pistil (composed of fused carpels). Diagram by Nikki Harris CC BY-NC with labels added.

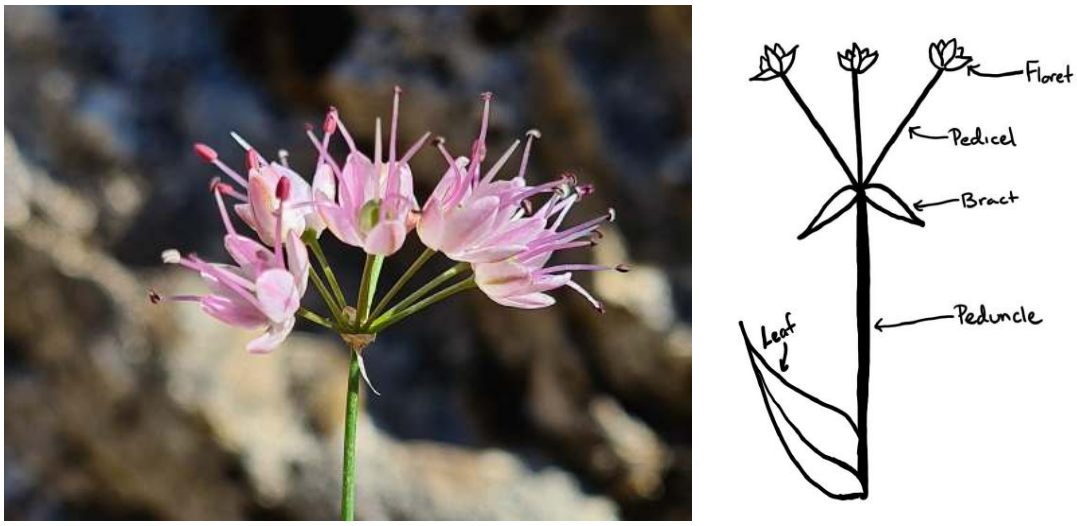



Figure **3.2.3.3.1.2**: An image of an *Allium* inflorescence. Many small florets on stalks (pedicels) emerge from a central point at the tip of the peduncle. At this junction, papery leaves (bracts) can be seen. These features are labeled in a sketch (second image). Photo by ramazan_murtazaliev, CC-BY-NC. Sketch by Maria Morrow, Public Domain.

The general characters that a flower has are whorl morphology, sex, merosity, symmetry, and the position of the gynoecium. **Merosity** is simply the number of parts in each whorl of a plant structure, whether it is the number of sepals, petals in a corolla, or the number of stamens. Each of these characters will be discussed below.

## Whorls

The outermost whorl of a flower is called the **calyx** and is composed of **sepals**. Inside the calyx is the **corolla**, which is composed of **petals**. The sepals are often smaller and less colorful than the petals, but this general rule can be misleading. For example, lilies and tulips have identical sepals and petals (called **tepals**, these can be seen in the florets in Figure **3.2.3.3.1.2**). The only way you can distinguish between them is by location: Which whorl is on the outside?

### The Perianth: Calyx and Corolla

Together, the calyx and corolla are called the **perianth** (peri- meaning around, anth- meaning flower; Figure **3.2.3.3.1.3**). The calyx is the outermost whorl of the flower. In most coses, the sepals are not showy--lacking bright colors and typically smaller--and instead serve a protective function in the developing flower. The corolla is the whorl just within the calyx. Petals tend to be the showy part of the flower, specialized for attracting animal pollinators.

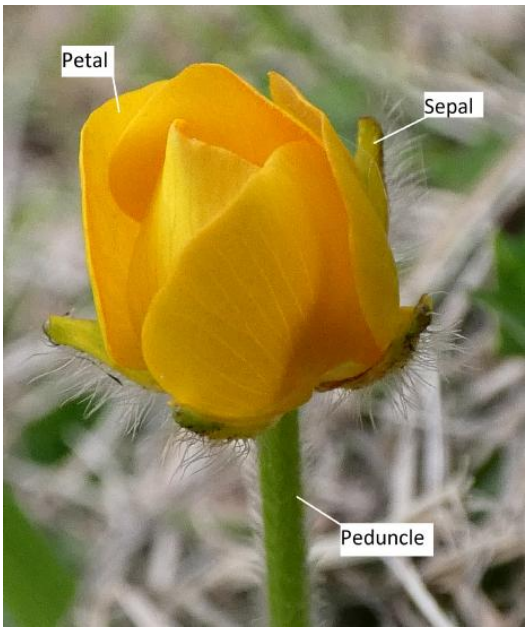



Figure **3.2.3.3.1.3**: A closed buttercup (*Ranunculus* sp.) flower shows the entire perianth. The sepals are smaller and covered in long trichomes. There are four sepals visible, though a fifth hides on the other side. Inside the sepal whorl (calyx), there are five overlapping, yellow petals. These petals form the corolla. Photo by Maria Morrow, CC BY-NC.

## Reproductive Whorls: Androecium and Gynoecium

Inside the perianth is the **androecium** (house of man), a whorl composed of **stamens**. Each stamen has a long **filament** holding up pollen sacs called **anthers** (Figure **3.2.3.3.1.4 – 5**). Each lobed anther contains microsporangia, within which meiosis of the diploid microspore mother cells in the anther produces four haploid microspores. Each of these develops into a pollen grain consisting of two cells: a larger vegetative cell (the tube cell), inside of which is a a smaller germ cell (also called the generative cell). At some point, depending on the species, the germ cell divides by mitosis to produce 2 spermatia.

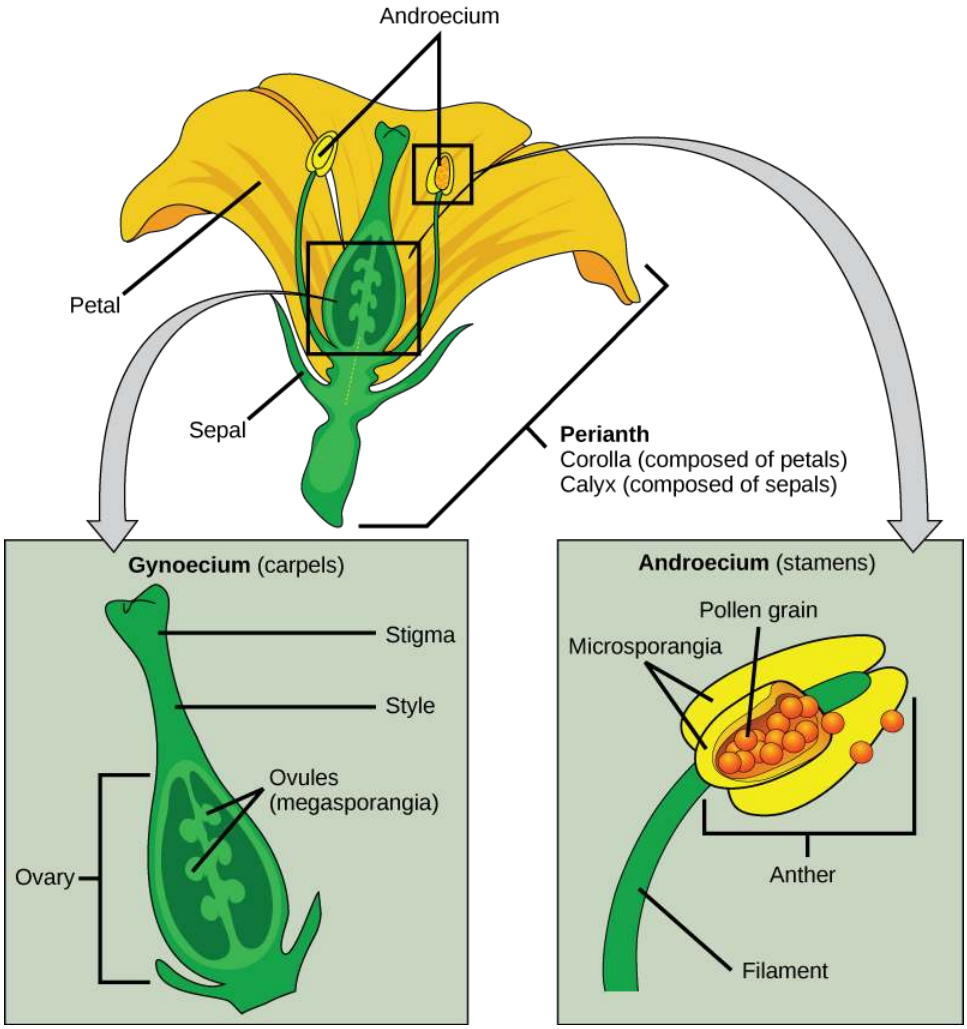



Figure **3.2.3.3.1.4**: The four main parts of the flower are the calyx, corolla, androecium, and gynoecium. The androecium is the sum of all the male reproductive organs, and the gynoecium is the sum of the female reproductive organs. Descriptive text: The calyx (outermost whorl) is composed of sepals and the corolla (inside the calyx) is composed of petals. These two whorls form the perianth. At the center of the perianth is a vase-like structure called the carpel. A flower may have one or more carpels, but the example shown has only one. The narrow neck of the carpel, called the style, widens into a flat stigma at the top. The ovary is the wide part of the carpel. Ovules, or megasporangia, are clusters of pods in the middle of the ovary. The androecium is composed of stamens which cluster around the carpel. The stamen consists a long, stalk-like filament with an anther at the end. The anther shown is tri-lobed. Each lobe, called a microsporangium, is filled with pollen. (credit: modification of work by Mariana Ruiz Villareal)

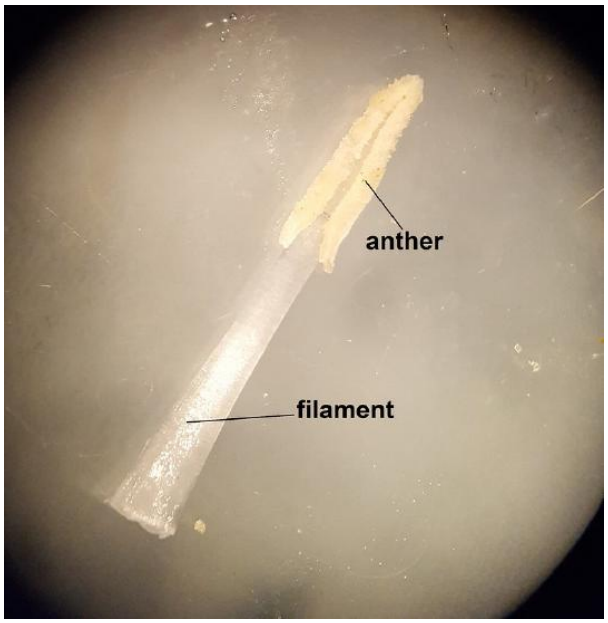



Figure **3.2.3.3.1.5**: A single stamen that has been removed from a flower. The filament is long and flattened. At the end of the filament, there is an anther that has split partially open, releasing pollen grains. Photo by Melissa Ha, CC BY-NC .

Inside the androecium is the **gynoecium** (house of woman), which is composed of **carpels**. Each carpel has an **ovary** at the base where **ovules** are housed. A **style** emerges from the ovary and is topped by the **stigma** (Figure **3.2.3.3.1.6**), where pollen is deposited. A carpel consists of a single ovary, style and stigma. Often several carpels are fused into a single structure, referred to as a **pistil**.

Within the ovule, a megasporangium produces a megaspore mother cell. Meiosis of the megaspore mother cell in each ovule produces 4 haploid cells, a large megaspore and 3 smaller cells that disintegrate. This megaspore develops into the megagametophyte, all within the ovule. Pollen grains land on the stigma and must grow a tube down the style to reach the ovule and complete fertilization.

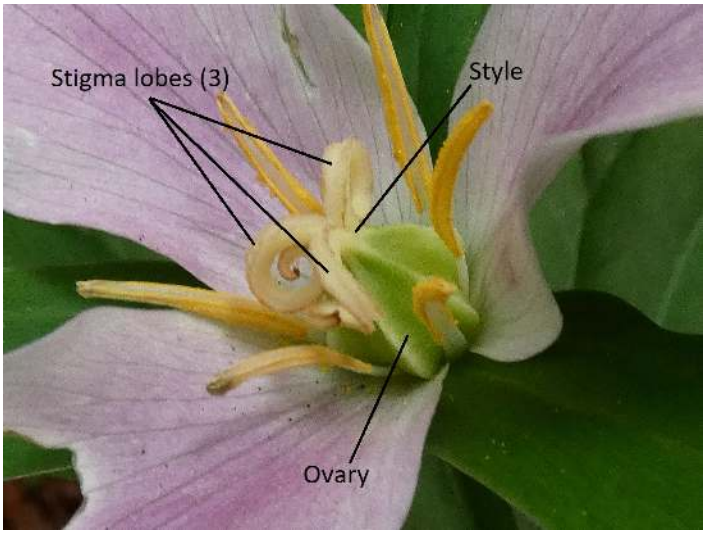



Figure **3.2.3.3.1.6**: All of the whorls of this Trillium flower are visible in this picture. The sepals are on the exterior and green. The three petals are a light pink. There are six stamens, each with much longer anthers than filaments. The stamens encircle the enlarged ovary of this fertilized flower, which is grooved and beaked into an odd shape. A short style connects the ovary to three long, curling stigma lobes. Is this flower a monocot or eudicot? Photo by Maria Morrow, CC BY-NC.

## Incomplete Flowers

Most flowers are composed of four whorls. If all whorls are present, a flower is said to be both **complete** and **perfect**. If any whorl is missing, the flower is **incomplete** (Figure **3.2.3.3.1.7**). If one of those missing whorls is either the androecium (pollen-producing)

or gynoecium (seed-producing), the flower is also **imperfect** (Figure **3.2.3.3.1.8**).



Figure **3.2.3.3.1.7**: This wild ginger flower (*Asarum caudatum*) has no corolla. It is incomplete, but it is still perfect. The hairy sepals are fused together at the base, then split into long, pointed tips that extend out like tendrils. These flowers are normally a deep wine red. Photo by mhays, CC-BY-NC.

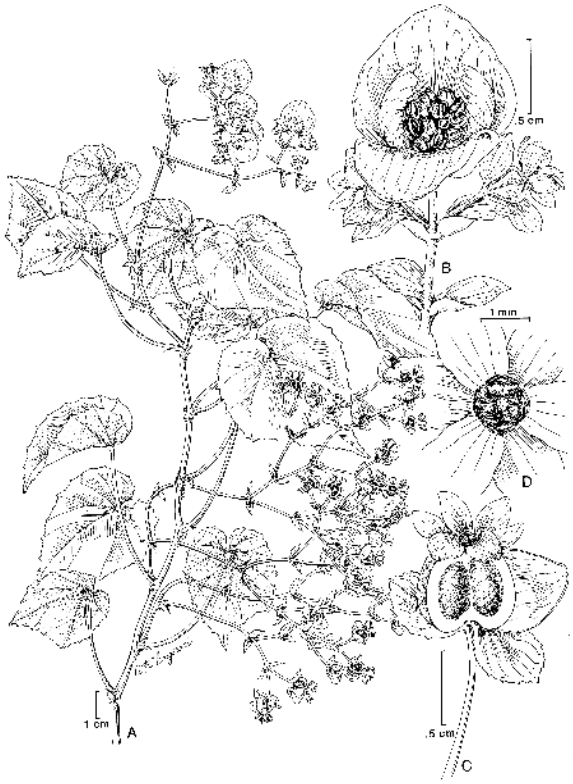



Figure **3.2.3.3.1.8**: Drawing of *Begonia ynesiae*, which has imperfect flowers. Flowers either have an androecium or gynoecium but not both. A shows the overall palnt struture, B shows staminate flower (which has an androecium but no gynoecium), C and D show pistillate flowers (which has a gynoecium but no androecium). This species is named after Ynés Mexía, the first female Mexican-American botanist. She collected over 145,000 specimens and discovered more than 500 new species. You can learn more about her life and work here. Image by Ynés E. J. Mexía (public domain).

Evolution seems to favor (and be favored by) genetic variability. Genetic variability is promoted by **outbreeding** - sexual reproduction between genetically dissimilar parents. Just why sexual reproduction is so popular throughout the world of living things is still a hotly-debated question, but the fact remains.

Plants, being anchored in position, have a special problem in this regard. Many employ the services of animals (e.g., insects, birds, bats) to transfer pollen from plant to plant. But if the flowers have both sex organs, what is to prevent the pollen from fertilizing its own eggs? Plants have evolved a variety of solutions. One of these is to produce imperfect flowers.

There are two types of imperfect flowers: staminate flowers contain only an androecium (Figure **3.2.3.3.1.9**), and carpellate (or pistillate) flowers have only a gynoecium. **Monoecious** plants have both types of imperfect flower on the same plant. **Dioecious** plants have imperfect flowers on separate plants; that is, some plants are male, some female. Examples include willows, poplars, and the date palm. Most dioecious plants use an X-Y system of of sex determination like that in mammals. However, a few species use an X-to-autosome ratio system like that of *Drosophila*, and a very few use a ZW system like that of birds and lepidopterans.



Figure **3.2.3.3.1.9**: This *Sirdavidia solannona* flower has no gynoecium, only tightly packed stamens at the center (a staminate flower). This flower is both imperfect and incomplete. Photo by Thomas L.P. Couvreur (Institut de Recherche pour le Développement , Montpellier, France), CC BY 4.0, via Wikimedia Commons.

But the vast majority of angiosperms have **perfect flowers**; that is containing both male and female sex organs. So how do they avoid self-fertilization? Many plants have self-incompatibility genes to prevent successful pollination between two of their own gametes. However, there is also a morphological solution: **heteromorphic flowers**. The flowers are perfect but come in two structural types; for example

- long stamens with a short style
- short stamens with a long style

A single plant has one type or the other. If the pollinator has a short tongue, pollination is favored from the first type to the second - but not the reverse. Heteromorphic flowers are not common, and even in the angiosperm families that favor them (e.g., primroses, flax), the same biochemical mechanisms of self-incompatibility that we will find in homomorphic flowers are usually present as well.

### Fusion Within and Between Whorls

Determining the merosity of flowers is complicated by floral fusion. In many flowers, parts of a single floral whorl will be partially or completely fused together. When the fusion is between parts of the same whorl, such as the petals fusing together to form a tubular structure (a sympetalous flower), it is called **connation**. When there is fusion of parts between whorls, such as the stamen fusing the the petals, it is called **adnation**.

A frequent form of connation occurs within the gynoecium. In an apocarpous gynoecium, the carpels are free. In a syncarpous gynoecium, some or all parts of the carpels are fused (see Figure **3.2.3.3.1.10**)

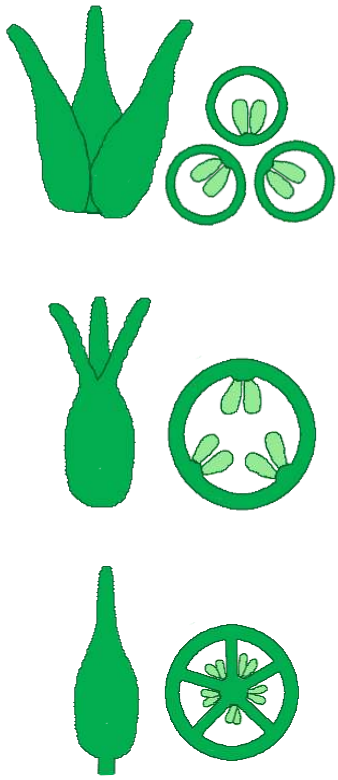


Figure 3.2.3.3.1.10: In an apocarpous gynoecium, the carpels are not fused together. The illustrated gynoecium on the left has three free carpels. A cross section of the ovaries shows the ovules inside. The gynoecium shown in the center is syncarpous, with fusion of the ovaries. A cross section of the ovary shows three sets of ovules. The gynoecium on the right is fully syncarpous with fusion of all parts (stigma, style, and ovary). The ovary cross section is divided into five distinct locules. Images by Michael G. Simpson. Redrawn and color: User:RoRo, Public domain, via Wikimedia Commons.

## Floral Symmetry

Flowers that have multiple lines of symmetry (like a starfish) are **radially symmetrical**, also called actinomorphic or regular. Flowers with only a single line of symmetry (like you) are **bilaterally symmetrical**, also called zygomorphic or irregular (Figure 3.2.3.3.1.11).

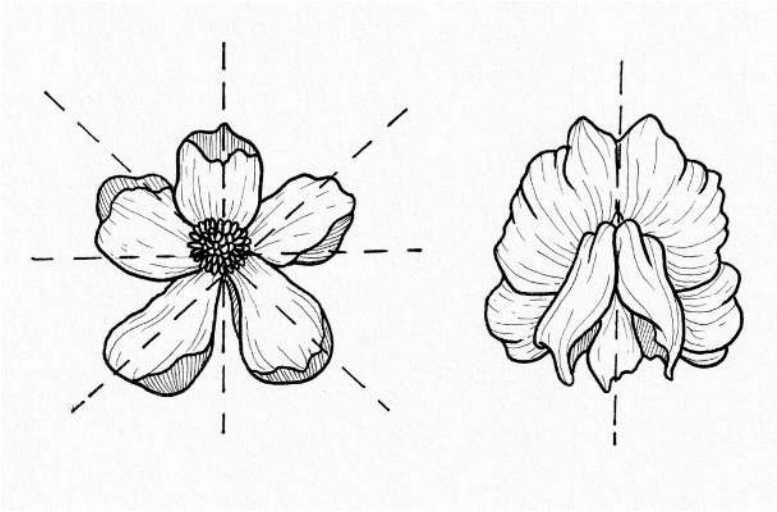


Figure **3.2.3.3.1.11**: On the left is a picture of a radially symmetrical flower. It has five petals that all radiate out from a central point, like a star. We can draw many lines of symmetry through this flower, where if we folded the flower along that line, the two sides would line up with each other. (Note: There may be a line out of place here. Can you find it?) On the right is a bilaterally symmetrical flower. Only one line of symmetry can be drawn through this flower. Much like for humans, this flower is mirrored from side to side, but not top to bottom or any other direction. Diagram by Nikki Harris, CC BY-NC.

## Ovary Position

We can use the location of the ovary to further distinguish between flowers (Figure **3.2.3.3.1.12**). If the other whorls of the flower meet below the ovary (the ovary or ovaries look a bit like an egg or eggs in a nest; Figure **3.2.3.3.1.13**), the ovary is **superior** (on top of the rest of the flower). This means that the rest of the flower parts are below the gynoecium, so we can also call this flower **hypogynous** (below the gynoecium). The two terms both describe the same situation, but superior refers only to the ovary while hypogynous refers to the flower, in general.

In the opposite situation, the other floral whorls join at a point above the ovary. In this case, the ovary is **inferior** and the flower is **epigynous** (on top of the gynoecium). As always, there are less clear situations. In some flowers, as in the rose family, the floral whorls join together and fuse at a point above the ovary, then travel down, around, and below the ovary as a fused unit. This fused unit is called a **hypanthium**. The ovary is termed **semi-inferior**, as it is located below the unfused parts of the floral whorls. Because the floral whorls travel around the ovary as the hypanthium, the flower is **perigynous** (peri- meaning around).

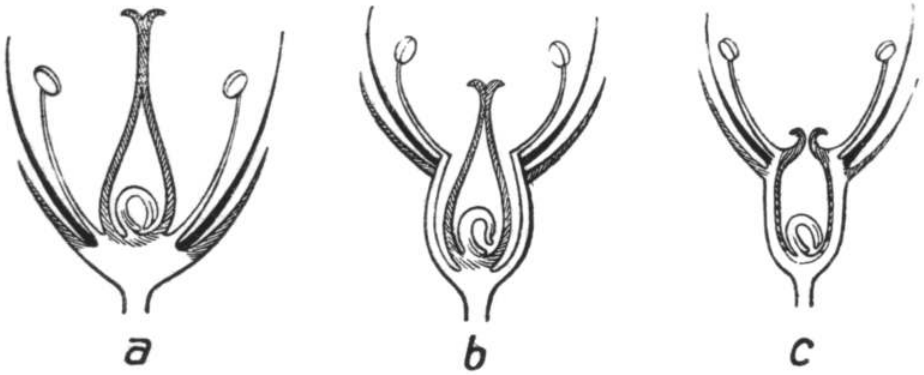



Figure **3.2.3.3.1.12**: The first flower (a) is a drawing of a hypogynous flower. The calyx, corolla, and androecium fuse to the receptacle below the gynoecium. The ovary sits on top of these other whorls, a superior ovary. The central flower (b) is a perigynous flower. The calyx, corolla, and androecium fuse together to form a layer of tissue (hypanthium) that surrounds and fuses with the ovary. The ovary appears to sit below the other whorls, but is surrounded by the hypanthium (fused or not), a semi-inferior ovary. The last flower (c) is an epiogynous flower. The calyx, corolla, and androecium fuse together above the gynoecium. The ovary sits below these other whorls, an inferior ovary. Images by Gustav Hegi (1876–1932), Gustav Dunzinger, Public domain, via Wikimedia Commons.

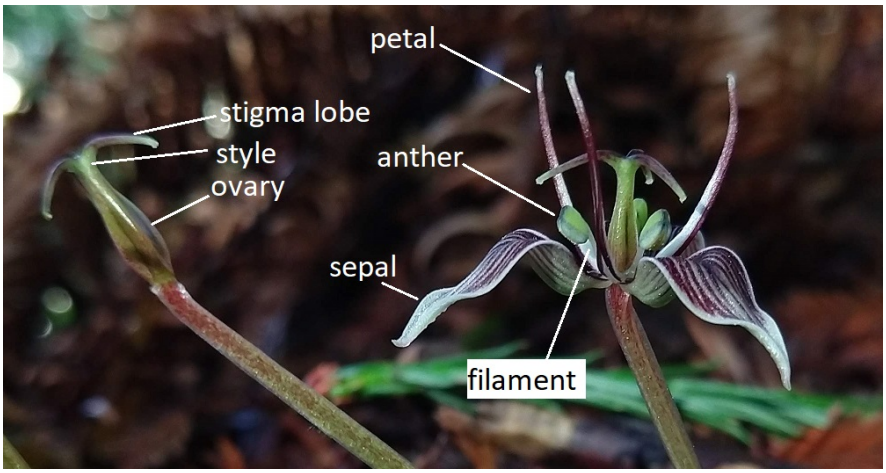



Figure **3.2.3.3.1.13**: This flower has a superior ovary and is considered hypogynous. In the image above, we see two flowers (actually two florets of an underground umbel!) of a fetid adderstongue, *Scoliopus bigelovii*. The one on the left has shed all whorls except the gynoecium. This allows you to see what the gynoecium looks like and where it is positioned in the one on the right. In the complete flower, the sepals, petals, and stamens all meet below the ovary, which sits in the middle like one giant egg in an alien nest. Photo by Maria Morrow, CC BY-NC.

## Inflorescences

An **inflorescence** is when, in the place of a single flower, multiple **florets** are formed. Florets can be sessile or attached by a stem called a **pedicel**. When leaf-like structures are found within the inflorescence, they are called **bracts**. There are a wide range of possibilities for the structure and development of inflorescences, though most can be split into four models: raceme-based, cymose, panicle, and intercalate (Figure **3.2.3.3.1.14**). Two models are most widespread.

Raceme-based inflorescences are mostly monopodial, having **indeterminate growth**. This means that the terminal bud continues producing lateral florets, never truly forming a terminal floret. The inflorescence can be simple or compound (Figure **3.2.3.3.1.15**).

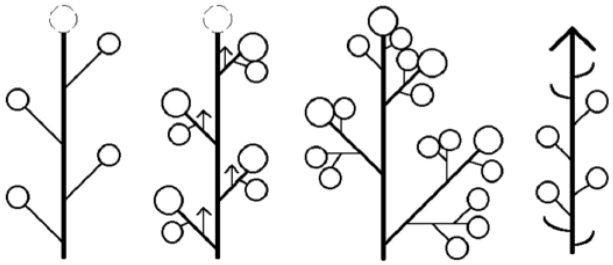


Figure **3.2.3.3.1.14**: Four kinds of inflorescences (left to right): Model I (raceme-based) has single florets emerging on pedicels from the main peduncle. Model II (thyrsoid or cymose) has racemes emerging alternately from the main pedicel; the terminal florets are the oldest. Model III (panicle) has branched racemes emerging from the main peduncle, but unlike model II, the peduncle terminates in a floret. and Model IV (intercalate) produces lateral florets along the peduncle, separated by bracts, and continues to grow.

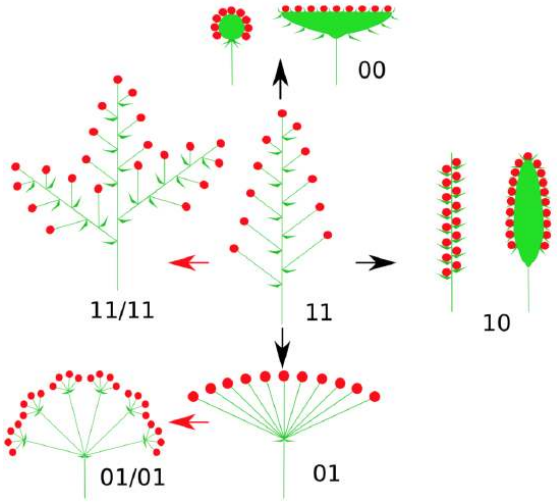



Figure **3.2.3.3.1.15**: Different Model I inflorescences and their evolutionary connections. Circles represent florets, larger circles are older. Digits represent the simple encoding system: first position is main axis, second position are secondary axes (flower pedicels), 1 means developed, 0 reduced. Compound inflorescences have four digit positions, for the first and second orders of branching. Some names for these inflorescences: 11 raceme, 11/11 compound raceme, 10 spike (left) and spadix (right), 01 umbel, 01/01 compound umbel, 00 head. All of these models are shown diverging from a central 11 raceme model.

Cymose inflorescences are sympodial, having **determinate growth**. This means there is a terminal floret that forms first, then other florets are produced laterally (Figure **3.2.3.3.1.16**). The order of lateral floret maturation can be a useful identification feature.

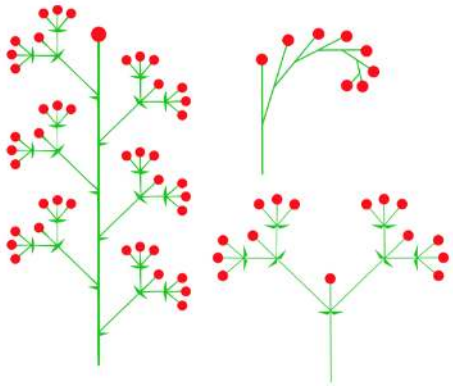


Figure **3.2.3.3.1.16**: Model II inflorescences. Circles represent florets, larger circles are older. Thyrse (left), cyme (top right), and dichasium (bottom right). The dichasium has a stunted central flower flanked by two long pedicels that each have a compound inflorescence with a stunted central floret flanked by two longer pedicels that end in a cluster of florets. It is fractal. The thyrse has a large terminal floret; each lateral floret has the same structure as the lateral florets in the dichasium. The cyme has a terminal flower that opens first, then a later floret that produces another later floret, which produces another lateral floret, and so on, forming a spiral.

## Attribution

Curated and authored by Maria Morrow, CC BY-NC, using the following sources:

- 16.3E Self incompatibility – How Plants Avoid Inbreeding, 16.3D Angiosperm Life Cycle, and 19.1.5 Diversity and Evolutionary Relationships of the Plants from *Biology* by John. W. Kimball (licensed CC-BY)
- 26.2 Gymnosperms and 32.1 Reproductive Development and Structure from *Biology 2e* by OpenStax (licensed CC-BY). Access for free at openstax.org.
- 8.2 The Flower and the Fruit from *Introduction to Botany* by Alexey Shipunov (public domain)

Figure **3.2.3.3.1.8** caption by Melissa Ha.

This page titled 3.2.3.3.1: Flowers is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **2.6.3.1: Flowers** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC 4.0.

# 3.2.3.3.2: Angiosperm Life Cycle

## Learning Objectives

- Identify structures and phases in the angiosperm life cycle; know their ploidy.
- Explain how fertilization occurs within a flower.
- Label a developing ovary cross section.

Angiosperms have a complex life cycle. The gametophytes have been further reduced: antheridia were lost in the gymnosperms and archegonia were lost in the angiosperms. Both gametophytes are now housed within the flower, a structure composed of highly modified leaves specialized for pollination. From flowers, fruits are produced, a protective structure that (usually) develops from the ovary wall and is specialized for seed dispersal.

### The Microgametophyte (AKA the Pollen Grain)

The microgametophyte develops and reaches maturity within the microsporangia (Figure **3.2.3.3.2.1**). The microsporangia, which are usually bi-lobed, are also called **pollen sacs**. These pollen sacs are found in the anther of the stamen, which is at the end of the filament.

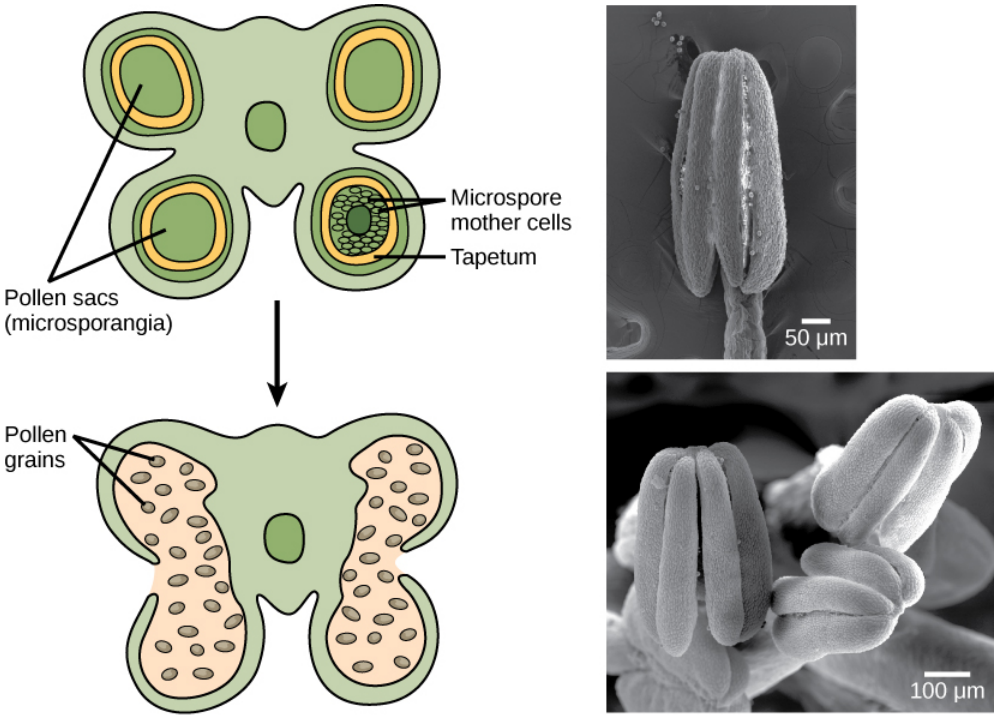



Figure **3.2.3.3.2.1**: Shown is (a) a cross section of an anther at two developmental stages. The immature anther (top) contains four microsporangia, or pollen sacs. Each microsporangium contains hundreds of microspore mother cells that will each give rise to four pollen grains. The tapetum supports the development and maturation of the pollen grains. Upon maturation of the pollen (bottom), the pollen sac walls split open and the pollen grains (male gametophytes) are released. (b) In these scanning electron micrographs, pollen sacs are ready to burst, releasing their grains. (credit b: modification of work by Robert R. Wise; scale-bar data from Matt Russell)

Within the microsporangium (pollen sac), many microspore mother cells divide by meiosis to each give rise to four haploid microspores, each of which will ultimately form a pollen grain (Figure **3.2.3.3.2.2**). An inner layer of cells in the microsporangium, known as the tapetum, provides nutrition to the developing microspores and contributes key components to the pollen wall. Upon maturity, the microsporangia burst, releasing the pollen grains from the anther.

Each pollen grain has two coverings: the exine (thicker, outer layer) and the intine (Figure **3.2.3.3.2.2**). The exine contains sporopollenin, a complex waterproofing substance supplied by the tapetal cells. Sporopollenin allows the pollen to survive under

unfavorable conditions and to be carried by wind, water, or biological agents without undergoing damage.

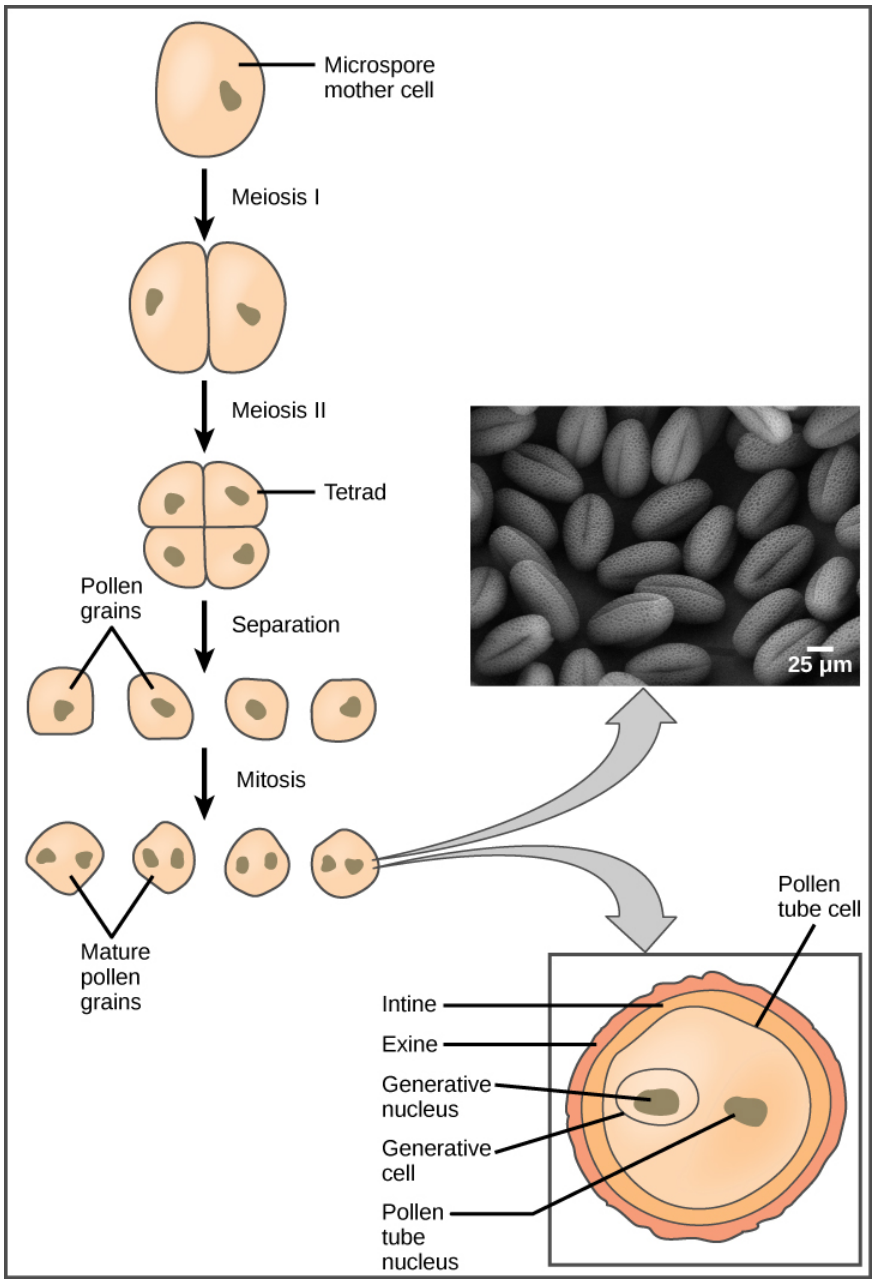



Figure **3.2.3.3.2.2**: Pollen develops from the microspore mother cells. The mature pollen grain is composed of two cells: the pollen tube cell and the generative cell, which is inside the tube cell. The pollen grain has two coverings: an inner layer (intine) and an outer layer (exine). The inset scanning electron micrograph shows Arabidopsis lyrata pollen grains. Descriptive text: The mother cell undergoes meiosis to form a tetrad of cells, which separate to form the pollen grains. The pollen grains undergo mitosis without cytokinesis, resulting in four mature pollen grains with two nuclei each. One is called the generative nucleus, and the other is called the pollen tube nucleus. Two projective layers form around the mature pollen grain, the inner intine and the outer exine. Micrograph shows a pollen grain, which looks like puffed wheat. (credit “pollen micrograph”: modification of work by Robert R. Wise; scale-bar data from Matt Russell)

Mature pollen grains contain two cells: a generative cell and a pollen tube cell. The generative cell is contained within the larger pollen tube cell. When a pollen grain reaches the stigma, it germinates into a **pollen tube**. The generative cell migrates with the pollen tube to enter the ovary. During its transit inside the pollen tube, the generative cell divides to form two gametes (spermatia). These, along with the tube nucleus (also known as the vegetative nucleus), migrate down the pollen tube as it grows through the style, the micropyle, and into the ovule chamber.

In *Arabidopsis*, the pollen tube follows a gradient of increasing concentration of a small defensin-like protein secreted by the synergids (see The Megagametophyte).

## The Megagametophyte

Within the ovary of the gynoecium, ovules are produced. Ovules consist of a double-layered integument with a small opening called the micropyle. The integument surrounds the megasporangium. Both the micropyle and megasporangium are diploid tissue of the sporophyte and are connected to the ovary wall by a region of tissue called the funiculus. The funiculus connects to a region of the ovary called the placenta, where nutritive support is provided the ovary wall and supplied to the developing ovule.

Within the megasporangium a single diploid megaspore mother cell divides by meiosis to produce four haploid megaspores. One of these will survive and three will disintegrate. The nucleus of the surviving megaspore undergoes 3 successive mitotic divisions. The 8 nuclei that result are distributed and partitioned off by cell walls to form the **embryo sac** (Figure **3.2.3.3.2.3**). The embryo sac is composed of 7 cells. The **egg cell**, located near the micropylar end, is flanked by 2 **synergid** cells. The large **central cell** contains 2 **polar nuclei** (a dikaryotic cell). The final three cells are the **antipodal** cells, located on the opposite side as the egg and synergids (Figure **3.2.3.3.2.4**).

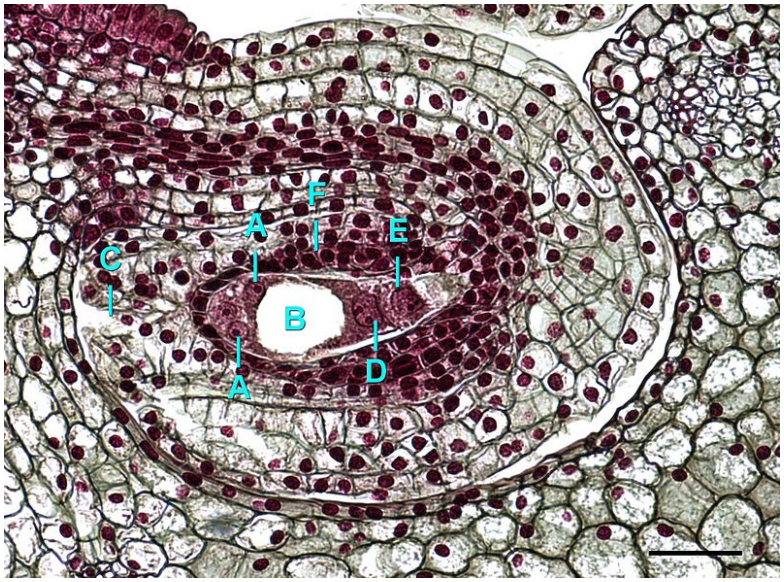



Figure **3.2.3.3.2.3**: Photomicrograph of a *Lilium* ovary at the eight nucleate stage. The integument surrounds the megasporangium, with a gap on one side (the micropyle). Inside the megasporangium, the megagametophyte is developing. It is composed of synergid cells (on the micropylar end) flanking an egg. There is a vacuole (space) in the center of the megagametophyte. The polar nuclei and antipodal cells are on the opposite side. A-Synergid cells, B-Vacuole, C-Micropyle, D-Polar nucleus, E-Antipodal cell, F-Integument. Scale=0.1mm. Jon Houseman, CC BY-NC, via Wikimedia Commons.

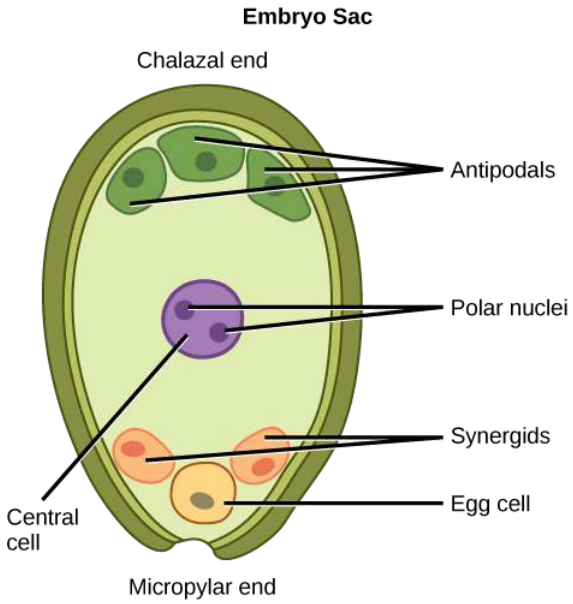



Figure **3.2.3.3.2.4**: As shown in this diagram of the embryo sac in angiosperms, the ovule is covered by integuments and has an opening called a micropyle. Inside the embryo sac are three antipodal cells, two synergids, a central cell, and the egg cell. Descriptive text: Illustration shows the embryo sac, which is egg-shaped. The narrow end, called the micropylar end, has an opening that allows pollen to enter. The other end is called the chalazal end. Three cells called antipodals are at the chalazal end. The egg cell and two other cells called synergids are at the micropylar end. Two polar nuclei are inside the central cell in the middle of the embryo sac.

The synergids help guide the pollen tube for successful fertilization, after which they disintegrate. One of the spermatia produced by the pollen's generative cell fuses with the egg to form a diploid zygote. This zygote will grow into the sporophyte. The second spermatium fuses with the polar nuclei to produce a triploid **endosperm** (Figure **3.2.3.3.2.5**). This event is called **double fertilization.** The endosperm will provide additional nutritive tissue for the growing embryo.

After fertilization, the integument will close the micropyle and develop into the **seed coat**, protecting the seed. The ovary wall will develop into the **pericarp** of the fruit.

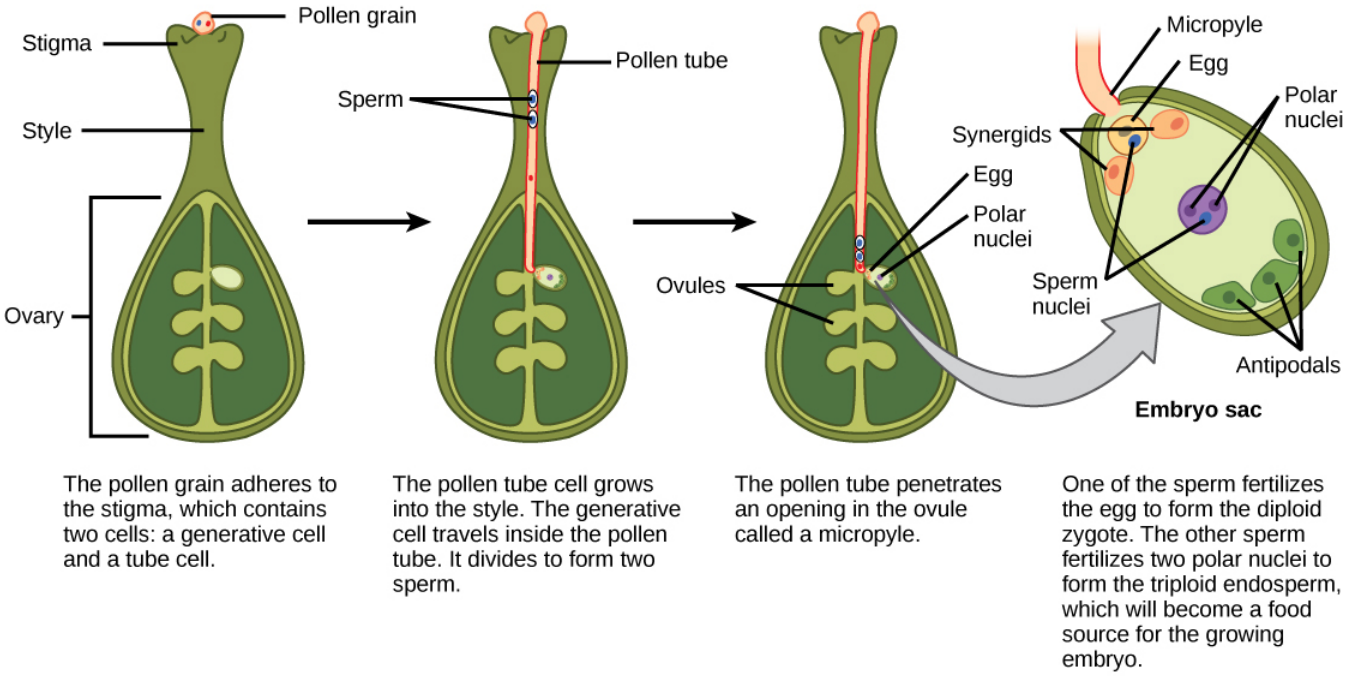



Figure **3.2.3.3.2.5**: In angiosperms, one sperm fertilizes the egg to form the 2n zygote, and the other sperm fertilizes the central cell to form the 3n endosperm. This is called a double fertilization. Descriptive text: Illustration shows a vase-like gynoecium composed of a swollen ovary at the base and a long style (forming the neck of the vase) ending in a stigma. A pollen grain adheres to the stigma. The pollen contains two cells: a generative cell and a tube cell. The pollen tube cell grows through the stigma and into the style. The generative cell travels inside the pollen tube. It divides to form two sperm. The pollen tube penetrates an opening in the ovule called a micropyle. One of the sperm fertilizes the egg (between the two synergids) to form the zygote. The other sperm fertilizes two polar nuclei to form a triploid endosperm, which becomes a food source for the growing embryo. Three antipodal cells remain on the other side of the embryo sac.

## Fruits

An unfertilized ovary, as shown in Figure **3.2.3.3.2.6**, contains one or more developing ovules produced in compartments called **locules**. Each ovule is attached to a nutritional region of the ovary called the **placenta** by a strand of tissue called the **funiculus**. The sporophyte supports the developing ovule through this tissue pathway. Prior to fertilization, there is a small gap in the integument called the **micropyle**.

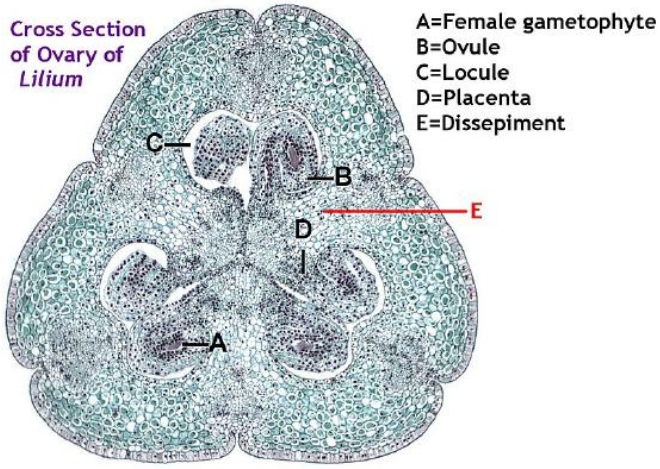



Figure **3.2.3.3.2.6**: Cross section of *Lilium* ovary, showing A=Female gametophyte, B=Ovule, C=Locule, D=Placenta, E=Dissepiment. The ovary has three locules, each with two developing ovules. Each ovule attached to the ovary by a region of tissue called the placenta. The label in red added to original contribution of File:Lilium ovary L.jpg provided by Jon Houseman and Matthew Ford. JonRichfield, CC BY-NC, via Wikimedia Commons.

After fertilization, the ovary wall develops into the fruit, surrounding the seeds. In fleshy fruits that use animals for dispersal, like the pears shown in Figure **3.2.3.3.2.7**, this might include a swelling of the cells, increased sugar production, and a change in pigmentation. These are the type of fruits we are familiar with. However, all flowers turn into fruits. The fruits might be dry, spiky, or in other ways completely unappetizing, and this is become many fruits do not use animal ingestion as their method of dispersal (more on this in Chapter 8.3 Fruits and Dispersal).



Figure **3.2.3.3.2.7**: These two images show clusters of pear blossoms from the same tree. The cluster on the left is in an earlier stage of development. The corolla is still attached and the stamens are radiating outward to disperse pollen. In the image on the right, the corolla has fallen off and the anthers have shriveled. The calyx is still visible and, just below it, the semi-inferior ovary and hypanthium are beginning to swell. Eventually, these will swell to many times their current size and form the fruits we know as pears. Photos by Maria Morrow, CC BY-NC.

## The Full Life Cycle

The angiosperm life cycle is shown in Figure **3.2.3.3.2.12** and Video **3.2.3.3.2.1**.

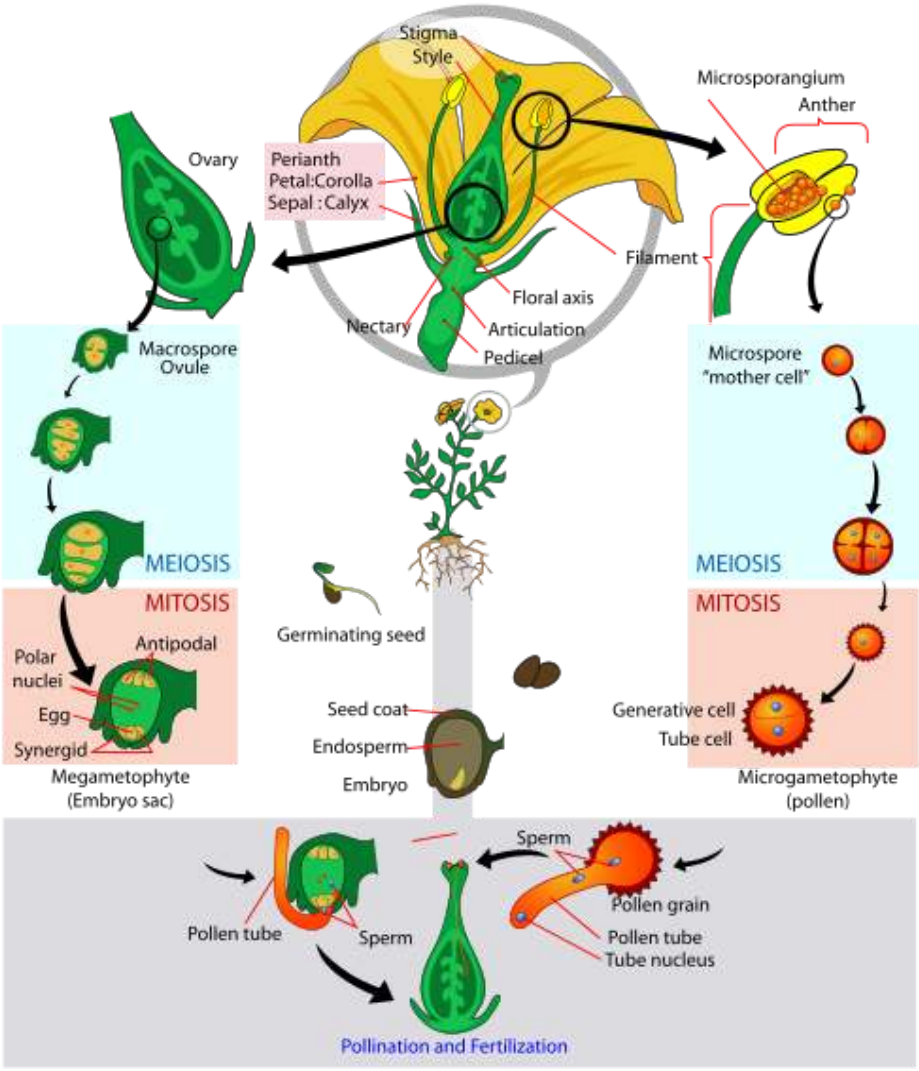



Figure 3.2.3.3.2.12: A diagram of the angiosperm life cycle. Pollination and fertilization take place within the ovary. The formation of the ovule takes place on the left hand side, moving from top to bottom. A macrospore ovule within the ovary undergoes meiosis, forming 4 nuclei, then mitosis, forming 8 nuclei but only 7 cells: 3 antipodals, two polar nuclei in the central cell, two synergids and an egg. This is the mature megagametophyte (embryo sac). The formation of the pollen grain takes place on the right hand side, again moving from top to bottom. Within one of the microsporangia, a microspore "mother cell" undergoes meiosis to form a pollen tetrad. Mitosis occurs within each pollen grain to produce a generative cell and a tube cell. This is the mature microgametophyte (pollen). At the center bottom of the image, pollination and double fertilization occurs, where the sperm cells fuse with the egg (forming a zygote) and polar nuclei (forming the triploid endosperm). The seed (composed of an external seed coat, small embryo, and large endosperm) develops through the center of the image, transitioning into a mature sporophyte at the top. Diagram by LadyofHats, Public domain, via Wikimedia Commons.

Watch Video 3.2.3.3.2.1 to help untangle this complex life cycle.



Video **3.2.3.3.2.1**: A digital, narrated rendition of the angiosperm life cycle. Sourced from YouTube.

## Attribution

Curated and authored by Maria Morrow, CC BY-NC, using the following sources:

- 32.1 Reproductive Development and Structure and 32.2 Pollination and Fertilization from *Biology 2e* by OpenStax (licensed CC-BY). Access for free at openstax.org.
- 8.1 Spermatophyta 2.0 from *Introduction to Botany* by Alexey Shipunov (public domain)

---

This page titled 3.2.3.3.2: Angiosperm Life Cycle is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **2.6.3.2: Angiosperm Life Cycle** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC 4.0.

## 3.2.3.4: Chapter Summary

Seeds represent one of the most important innovations in plant evolution: a protected, nutrient-supplied embryo with the ability to await appropriate conditions for germination. Seeds and pollen allowed plants to limit their reliance on water for completion of their life cycle. The first plants to evolve seeds were the gymnosperms. Angiosperms then improved upon seed dispersal and pollination strategies with the evolution of fruits and flowers.

In gymnosperms, protective seeds filled with nutritive tissue (including the megagametophtye) replace spores as the dispersal mechanism. Antheridia are lost in the microgametophyte, which is reduced to four cells and is dispersed as a whole (pollen). The evolution of secondary growth allows for the lateral deposition of woody tissues. This latter development, along with xerophytic leaves, allows gymnosperms to tolerate a wide variety of new environmental stressors.

Cycads and ginkgos are more ancestral lineages of gymnosperms. Ginkgos are represented by a single surviving species: *Ginkgo biloba*. Cycads are primarily tropical and usually have large pinnately compound leaves. Like the Ginkgos, seeds and pollen are produced in strobili produced on separate plants. Gnetophytes are a group of gymnosperms that have convergently evolved several characteristics with angiosperms: fruit-like cones, vessel elements, and double fertilization. However, it is likely that they are a highly-derived group within the conifers, sister to the pine family! Most extant gymnosperms are conifers; this group includes some of Earth's oldest, largest, and longest lived organisms.

The majority of plant species are angiosperms. This is the most recent lineage of plants and, though its origins are murky, its members appear to form a monophyletic clade. Within the angiosperms, there are two major groups: monocots and dicots (the latter of which can be further divided into some early diverging angiosperm lineages and the eudicots). Angiosperms have the most reduced gametophytes of all plant lineages: the mature microgametophyte is composed of just 2 cells, while the megagametophyte has 7 cells (with 8 nuclei!). These gametophytes are housed within flowers, structures composed of highly modified leaves specialized for pollination.

Flowers are composed of a series of concentric whorls. The outermost whorl is the calyx, composed of sepals. Inside the calyx is the corolla, which is composed of petals. Together, the calyx and corolla comprise the perianth, which is usually the showy part of the flower in animal-pollinated species. The internal whorls are the fertile whorls. The androecium is composed of stamens, formed from a filament and anther (microsporangia are produced within the anthers). The gynoecium is composed of carpels, formed from an ovary, style, and stigma. The stigma is where pollen is received. The pollen must grow a pollen tube from the stigma to the ovary, traveling down the style to get there. Within the ovary, ovules are housed (megasporangia are produced within the ovules).

During pollination, the generative cell of the pollen produces two spermatia. One spermatium fertilizes the zygote, as in most plants, but the second spermatium fertilizes a dikaryotic cell called the central cell, forming a triploid endosperm. This event is called double fertilization. After fertilization, the ovule becomes a seed and the ovary begins to develop into a fruit.

Other adaptations within this group include specialized vascular cells: vessel elements in the xylem and sieve tube elements with companion cells in the xylem.

### After completing this chapter, you should be able to...

- Explain how heterospory led to the evolution of seeds.
- Connect r- and k-strategies to propagules produced by plants (e.g. spores, gametes, pollen, and seeds).
- List a few ways gymnosperms and angiosperms differ in life history traits.
- Describe the shared derived characteristics of gymnosperms.
- Connect these adaptations to the stressors this group of plants would have faced.
- Use morphological characteristics and life history traits to distinguish between ginkgos and flowering plants.
- Explain why *Ginkgo biloba* is called a living fossil.
- Use morphological characteristics and life history traits to distinguish between cycads and ferns.
- Define the term dioecious and provide an example.
- Use morphological features and life history traits to distinguish conifers from other plants.
- Connect the adaptations of conifers to dry and/or cold environments.
- Identify structures and phases in the *Pinus* life cycle; know their ploidy.

- Use morphological features and life history traits to distinguish gnetophytes from other plants.
- Describe the traits gnetophytes share with angiosperms.
- Describe the shared derived characteristics of angiosperms.
- Connect these characteristics to the stressors these plants would have faced.
- Identify the components of a flower and to which whorl each belongs.
- Write and interpret floral formulas.
- Differentiate between flowers and inflorescences.
- Explain the difference between raceme-based and cymose inflorescences.
- Identify the components of a flower and to which whorl each belongs.
- Write and interpret floral formulas.
- Differentiate between flowers and inflorescences.
- Explain the difference between raceme-based and cymose inflorescences.

## Attribution

Content by Maria Morrow, CC BY-NC

This page titled 3.2.3.4: Chapter Summary is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **2.6.4: Chapter Summary** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC 4.0.

# SECTION OVERVIEW

## 3.2.4: Angiosperm Diversity

It is likely that most plants you see are angiosperms. Of the nearly 400,000 species of land plants described, almost 90% are angiosperms. With the production of flowers specialized for pollination and fruits specialized for dispersal, angiosperms formed complex, interconnected relationships with a wide variety of other organisms. These close coevolutionary relationships may have increased speciation within this group. Regardless, the radiation of angiosperms is unprecedented among plants.


### 3.2.4.1: Monocots and Eudicots

### 3.2.4.2: Pollination Syndromes

### 3.2.4.3: Fruits and Dispersal

### 3.2.4.4: Angiosperm Families

### 3.2.4.5: Chapter Summary


### Attribution

Content by Maria Morrow, CC BY-NC


This page titled 3.2.4: Angiosperm Diversity is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

# 3.2.4.1: Monocots and Eudicots

**Learning Objectives**

- Compare and contrast monocots and eudicots.
- Differentiate between monocot and eudicot flowers and leaves.

Of over 400 families of angiosperms, some 80 of them fall into a single clade, called **monocots** because their seeds have only a single cotyledon. The remainder have seeds that produce two cotyledons (Figure **3.2.4.1.1**). This group includes some early diverging angiosperms (ANA grade families and magnoliids), but the large majority of these occupy a single clade called the **eudicots**. In addition to developmental features, there are a few morphological and anatomical traits you can use to distinguish between these two major groups.



Figure **3.2.4.1.1**: Monocots like the grass shown on the left produce only one cotyledon (mono- for one, -cot for cotyledons). Eudicots (on right), also sometimes called dicots, get their name from having two cotyledons (eu- for true, di- for two). Cotyledons are the first, fleshy leaves that enveloped the embryo as it grew. Image from Pengo, CC BY-SA 2.5, via Wikimedia Commons.

## Monocots

Monocots have a single cotyledon in their seed, parallel venation in their leaves (Figure **3.2.4.1.2**), flower parts in multiples of three (3-merous, see Figure **3.2.4.1.3**), and vascular bundles dispersed throughout the stem in concentric circles. Monocots do not have true secondary growth, though some (such as bamboo) form tough, woody stems.



Figure **3.2.4.1.2**: These two monocot leaves both have parallel venation. It is more obvious in the second leaf. However, if you look closely at the first leaf, you'll see that those veins do not cross each other. Instead, they travel in the same direction without overlapping, just as in the leaf on the right. Photos by Maria Morrow, CC-BY 4.0.

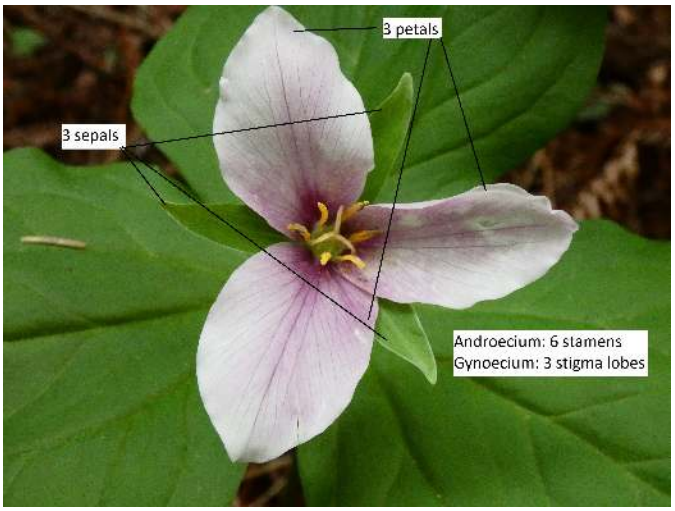



Figure **3.2.4.1.3**: This *Trillium* is a monocot, which you can tell because it is 3-merous. There are three sepals, three petals, six stamens, and three stigma lobes visible in the gynoecium. Monocots have floral parts in sets of three (3-merous). Photo by Maria Morrow, CC-BY 4.0.

Some major groups of monocots are:

- palms (Arecaceae)
- orchids (Orchidaceae)
- yams, sweet potatoes (Dioscoreaceae)
- lilies, onion, asparagus (Liliaceae)
- bananas (Musaceae)
- all the **grasses** (Poaceae), which include many of our most important plants such as
  - corn (maize)
  - wheat
  - rice
  - and all the other cereal grains upon which we depend so heavily for food as well as
  - sugar cane and bamboo

## Eudicots

Eudicots have two cotyledons in their seeds, netted venation in their leaves (Figure **3.2.4.1.4**), flower parts in multiples of 4 or 5 (4-merous or 5-merous, see Figure **3.2.4.1.5**), and vascular bundles in the stem arranged in a radial pattern like spokes of a wheel.



Figure 3.2.4.1.4: A skeletal holly leaf shows the network of vascular tissue. The lignified xylem and phloem fibers break down far more slowly than the parenchyma cells of the leaf. As the rest of the leaf tissues decompose, the lignified vascular tissue is left behind. This reveals the netted pattern of increasingly smaller side branches found in eudicot leaves. Photo by Maria Morrow, CC-BY 4.0.




Figure 3.2.4.1.5: Eudicot flowers tend to be 4-merous or 5-merous. The *Clarkia* flower (first image) is 4-merous. We cannot see the calyx, but there are four petals, 8 stamens, and 4 stigma lobes. The flax flower (second image) is 5-merous. There are five sepals poking out between the five petals and 5 stamens (with blue anthers!). The number of stigma lobes is not distinguishable in this image. Photos by Maria Morrow, CC-BY 4.0.

## Attribution

Content by Maria Morrow, CC-BY

This page titled 3.2.4.1: Monocots and Eudicots is shared under a not declared license and was authored, remixed, and/or curated by Tom Buckley.

- **2.7: Angiosperm Diversity** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-SA 4.0.

# 3.2.4.2: Pollination Syndromes

**Learning Objectives**

- Explain pollination strategies with regard to genetic diversity.
- Explain what is meant by the term pollination syndrome.
- Use floral characteristics to predict a plants pollinator(s).

In angiosperms, **pollination** is defined as the placement or transfer of pollen from the anther to the stigma of the same flower or another flower. In gymnosperms, pollination involves pollen transfer from the male cone to the female cone. Upon transfer, the pollen germinates to form the pollen tube and the sperm for fertilizing the egg.

Pollination has been well studied since the time of Gregor Mendel. Mendel successfully carried out self- as well as cross-pollination in garden peas while studying how characteristics were passed on from one generation to the next. Today's crops are a result of plant breeding, which employs **artificial selection** to produce the present-day **cultivars** (a term that refers to cultivated varieties). A case in point is today's corn, which is a result of years of breeding that started with its ancestor, a grass called teosinte (see Figure 3.2.4.2.1). The teosinte that the ancient Mayans originally began cultivating had small seeds—vastly different from today's relatively giant ears of corn and plump kernels. Interestingly, though these two plants appear to be entirely different, the genetic difference between them is miniscule.

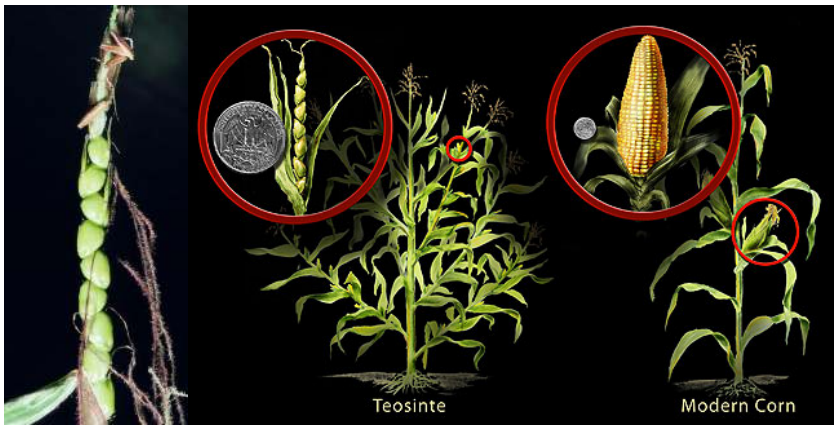



Figure 3.2.4.2.1: The first image shows the inflorescence and developing fruits produced by teosinte, while the second image shows a comparison between teosinte fruits (left) and the fruits produce by modern corn (right). In the second image, the fruits are compared to a quarter, as well as their approximate size on the plant. Note the difference in overall plant structure between the two. How might this relate to the size of the ears produced in modern corn? First image Matt Lavin from Bozeman, Montana, USA, CC BY-SA 2.0, via Wikimedia Commons. Second image by National Science Foundation, Public domain, via Wikimedia Commons. Descriptive text for second image: A diagram of a teosinte plant next to a modern corn plant. The teosinte plant has a central stem with many side branches; the fruits are produced on the side branches and the main stem; the fruits are shown next to a quarter and the line of fruits is about twice as high and much thinner. The modern corn plan has only a central stem with ears produced there; shown next to a quarter, the ear is perhaps 10 times as high and 3-4 times as wide.

## Pollination and Genetic Diversity

Pollination takes two forms: self-pollination and cross-pollination. **Self-pollination** occurs when the pollen from the anther is deposited on the stigma of the same flower, or another flower on the same plant. Self-pollination occurs in flowers where the stamen and carpel mature at the same time, and are positioned so that the pollen can land on the flower's stigma. This method of pollination does not require an investment from the plant to provide nectar and pollen as food for pollinators, but results in lower genetic diversity within the population. Self-pollination often exists like a "plan B", in case cross-pollination is, for some reason, impossible. Sometimes, self-pollinated flowers even do not open; these flowers are called **cleistogamous**.

**Cross-pollination** is the transfer of pollen from the anther of one flower to the stigma of another flower on a different individuals of the same species. This method relies on a pollen vector but results in higher genetic diversity.

Living species have adapted to ensure survival of their progeny; those that fail become extinct. Genetic diversity is therefore required so that in changing environmental or stress conditions, some of the progeny can survive. Self-pollination leads to the production of plants with less genetic diversity, since genetic material from the same plant is used to form gametes, and eventually, the zygote. In contrast, cross-pollination—or out-crossing—leads to greater genetic diversity because the microgametophyte and megagametophyte are derived from different plants.

Because cross-pollination allows for more genetic diversity, plants have developed many ways to avoid self-pollination. In some species, the pollen and the ovary mature at different times. These flowers make self-pollination nearly impossible. By the time pollen matures and has been shed, the stigma of this flower is mature and can only be pollinated by pollen from another flower. Some flowers have developed physical features that prevent self-pollination. The primrose is one such flower. Primroses have evolved two flower types with differences in anther and stigma length: the pin-eyed flower has anthers positioned at the pollen tube's halfway point, and the thrum-eyed flower's stigma is likewise located at the halfway point. Insects easily cross-pollinate while seeking the nectar at the bottom of the pollen tube. This phenomenon is also known as heterostyly. Many plants, such as cucumber, have male and female flowers located on different parts of the plant, thus making self-pollination difficult. In yet other species, the male and female flowers are borne on different plants (dioecious). All of these are barriers to self-pollination; therefore, the plants depend on pollinators to transfer pollen. The majority of pollinators are biotic agents such as insects (like bees, flies, and butterflies), bats, birds, and other animals. Other plant species are pollinated by abiotic agents, such as wind and water.

In summary, self-incompatibility is a mechanism that prevents self-fertilization in many flowering plant species to increase genetic diversity at the population level. The working of this self-incompatibility mechanism has important consequences for plant breeders because it inhibits the production of inbred and hybrid plants.

### Incompatibility Genes in Flowers

In recent decades, *incompatibility genes*—which prevent pollen from germinating or growing into the stigma of a flower—have been discovered in many angiosperm species. If plants do not have compatible genes, the pollen tube stops growing. Self-incompatibility is controlled by the S (sterility) locus. Pollen tubes have to grow through the tissue of the stigma and style before they can enter the ovule. The carpel is selective in the type of pollen it allows to grow inside. The interaction is primarily between the pollen and the stigma epidermal cells. In some plants, like cabbage, the pollen is rejected at the surface of the stigma, and the unwanted pollen does not germinate. In other plants, pollen tube germination is arrested after growing one-third the length of the style, leading to pollen tube death. Pollen tube death is due either to apoptosis (programmed cell death) or to degradation of pollen tube RNA. The degradation results from the activity of a ribonuclease encoded by the S locus. The ribonuclease is secreted from the cells of the style in the extracellular matrix, which lies alongside the growing pollen tube.

## Pollination Syndromes

Over time, angiosperms evolved different flower morphologies, smells, and colors that corresponded to their particular pollen vector. These sets of characteristics, called **pollination syndromes**, allow scientists to predict the pollinators for different plants. For example, cup-shaped flowers are usually pollinated with massive animals like beetles and even bats. Funnel-shaped flowers as well as labiate flowers (with lips), are adapted to flies and bees. Flowers with long spurs attract butterflies and birds (like hummingbirds or sugarbirds). Likewise, many of the organismal vectors evolved features or behaviors to specialize in pollination of particular plants. This tandem evolution toward increasing specificity is called **coevolution**. Interestingly, flower phenotypes can also correlate to other environmental factors (e.g. Peach et al. 2020). For more images of pollination syndromes, see Chapter 14.1 Pollination Syndromes in the Photographic Atlas.

### Pollination by Deception

Orchids are highly valued flowers, with many rare varieties (Figure **3.2.4.2.2**). They grow in a range of specific habitats, mainly in the tropics of Asia, South America, and Central America. At least 25,000 species of orchids have been identified.



Figure **3.2.4.2.2**: Certain orchids use food deception or sexual deception to attract pollinators. Shown here is a bee orchid (*Ophrys apifera*) that mimics the appearance of a *Eucera longicornis* female bee. Male *E. longicornis* bees try to mate with the petal, covering themselves in pollen from the overhanging anthers and depositing any pollen they may have from prior bee orchids onto the stigma. (credit: David Evans)

Flowers often attract pollinators with food rewards, in the form of nectar. However, some species of orchid are an exception to this standard: they have evolved different ways to attract the desired pollinators. They use a method known as food deception, in which bright colors and perfumes are offered, but no food. *Anacamptis morio*, commonly known as the green-winged orchid, bears bright purple flowers and emits a strong scent. The bumblebee, its main pollinator, is attracted to the flower because of the strong scent—which usually indicates food for a bee—and in the process, picks up the pollen to be transported to another flower.

Other orchids use sexual deception. *Chiloglottis trapeziformis* emits a compound that smells the same as the pheromone emitted by a female wasp to attract male wasps. The male wasp is attracted to the scent, lands on the orchid flower, and in the process, transfers pollen. Some orchids, like the Australian hammer orchid, use scent as well as visual trickery in yet another sexual deception strategy to attract wasps. The flower of this orchid mimics the appearance of a female wasp and emits a pheromone. The male wasp tries to mate with what appears to be a female wasp, and in the process, picks up pollen, which it then transfers to the next counterfeit mate.

## Bees

Bees are perhaps the most important pollinator of many garden plants and most commercial fruit trees (Figure **3.2.4.2.3**). Most bees that people notice are the social bees, bumblebees and honeybees, though there are thousands of species of solitary bees that have essential pollination roles. Bees have branched hairs covering their bodies, making them excellent pollinators as more pollen grains are likely to be caught upon their external surfaces and transferred onto other plants.

Bees collect energy-rich pollen and nectar for their survival and energy needs, so flowers that have coevolved with bees contain both nectar and pollen. Since bees cannot see the color red, bee-pollinated flowers usually have shades of blue, yellow, violet or other colors. They visit flowers that are open during the day, are brightly colored, have a strong aroma or scent, with a landing area of some kind, typically with the presence of a nectar guide. A **nectar guide** can include regions on the flower with pigments that are visible only to bees, and not to humans (such as UV); it helps to guide bees to the center of the flower, thus making the pollination process more efficient. The pollen sticks to the bees' fuzzy hair, and when the bee visits another flower, some of the pollen is transferred to the second flower.



Figure 3.2.4.2.3: Insects, such as bees, are important agents of pollination. The first image shows a bee covered in pollen. Bees are covered in branched hairs (unlike flies, which have unbranched hairs), specialized for pollen collection. The second image shows an *Iris*. This *Iris* flower has a bee pollination syndrome. The primary colors are purple and yellow. There are nectar guides (lines on the petals) leading the bee to the center of the flower. To get there, the bee must crawl under the stigma first, then under the anthers. This flower has a pleasant, sweet smell. First image: modification of work by Jon Sullivan. Second image: Photo by Maria Morrow, CC-BY 4.0.

Recently, populations of honeybees (an introduced European species) have been in decline due to a variety of factors, including pesticides (like neonicotinoids) and parasitic mites. Because solitary bees are not operated by commercial industry, impacts on these populations have been less well-documented. However, declines in bee populations will have extremely important impacts on our food security, as bees are used to pollinate many food crops.

Wasps are also important insect pollinators, and pollinate many species of figs.

### Flies

Many fly species are important pollinators. These flies often look and behave much like bees, performing important roles in pollination. However, since these flowers would generally be classified under a bee pollination syndrome, we will instead discuss a second category of fly for the fly pollination syndrome. These insects (flies and sometimes carrion beetles) are typically not looking for a flower, but for a corpse or some dung to feed on or lay eggs in. Some flowers have evolved to trick flies into pollination by emitting a decaying smell or an odor of rotting flesh. These flowers, which produce nectar, usually have dull colors, such as brown or purple. They often feature some kind of trap-like feature so when a fly visits, it has to bounce around inside the flower a bit before leaving (this increases the chance of pollen deposition, both on the flower and on the fly). Examples include the corpse flowers (*Amorphophallus* and *Rafflesia*) and dragon arum (*Dracunculus*).



Figure 3.2.4.2.4: Rafflesia arnoldii makes the world's largest known flowers. They can be over a meter across and are adapted to mimic rotting meat in smell and appearance. The rest of the plant lives parasitically inside the vines of *Tetrastigma*--it doesn't make any stems, roots, or leaves! Photo by User:Rendra Regen Rais, CC BY-SA 3.0, via Wikimedia Commons.

### Butterflies and Moths

Butterflies, such as the monarch, pollinate many garden flowers and wildflowers, which usually occur in clusters. These flowers are brightly colored, have a strong fragrance, are open during the day, and have nectar guides to make access to nectar easier. The pollen is picked up and carried on the butterfly's limbs.

Moths, on the other hand, pollinate flowers during the late afternoon and night. The flowers pollinated by moths are pale or white and are flat, enabling the moths to land. One well-studied example of a moth-pollinated plant is the yucca plant, which is pollinated by the yucca moth. The shape of the flower and moth have adapted in such a way as to allow successful pollination. The moth deposits pollen on the sticky stigma for fertilization to occur later. The female moth also deposits eggs into the ovary. As the eggs develop into larvae, they obtain food from the flower and developing seeds. Thus, both the insect and flower benefit from each other in this symbiotic relationship. The corn earworm moth and Gaura plant have a similar relationship (Figure 3.2.4.2.5).



Figure 3.2.4.2.5: A corn earworm moth sips nectar from a night-blooming *Gaura* plant. (credit: Juan Lopez, USDA ARS)

### Bats

In the tropics and deserts, bats are often the pollinators of nocturnal flowers such as agave, guava, and morning glory. The flowers are usually large and white or pale-colored; thus, they can be distinguished from the dark surroundings at night. The flowers have a strong, fruity, or musky fragrance and produce large amounts of nectar. They are naturally large and wide-mouthed to accommodate the head of the bat (Figure 3.2.4.2.6). As the bats seek the nectar, their faces and heads become covered with pollen, which is then transferred to the next flower.



Figure **3.2.4.2.6**: Bat pollinated flowers, like those shown here on *Cresentia alata*, are open at night and tend to be large, white, and have lots of pollen. They usually emit a strong fruity or musky smell. Photo by शैलजा देशपांडे, CC BY-SA 4.0, via Wikimedia Commons.

## Birds

Many species of small birds, such as the hummingbird (Figure **3.2.4.2.7**) and sun birds, are pollinators for plants such as orchids and other wildflowers. Flowers visited by birds are usually sturdy and are oriented in such a way as to allow the birds to stay near the flower without getting their wings entangled in the nearby flowers, such as dangling (pendant). The flower typically has a curved, tubular shape, which allows access for the bird's beak. Brightly colored, odorless flowers that are open during the day are pollinated by birds. As a bird seeks energy-rich nectar, pollen is deposited on the bird's head and neck and is then transferred to the next flower it visits. Botanists have been known to determine the range of extinct plants by collecting and identifying pollen from 200-year-old bird specimens from the same site.



Figure **3.2.4.2.7**: Hummingbirds have adaptations that allow them to reach the nectar of certain tubular flowers. These flowers have narrow tubes perfect for a hummingbird's long bill and tongue. There is not a great landing pad for insects, so the ability to hover makes it easier to gather the nectar. (Photo credit: Lori Branham)

## Wind

Most species of conifers, and many angiosperms, such as grasses, maples and oaks, are pollinated by wind. Pine cones are brown and unscented, while the flowers of wind-pollinated angiosperm species are usually green, small, may have small or no petals, and produce large amounts of pollen. Unlike the typical insect-pollinated flowers, flowers adapted to pollination by wind do not produce nectar or scent. In wind-pollinated angiosperm species, the anthers are often large and hang out of the flower, and, as the wind blows, the lightweight pollen is carried with it (Figure **3.2.4.2.8**). The flowers usually emerge early in the spring, before the leaves, so that the leaves do not block the movement of the wind. The pollen is deposited on the exposed feathery stigma of the flower (Figure **3.2.4.2.9**).



Figure 3.2.4.2.8: A person knocks pollen from a pine tree. The clusters of pollen cones release clouds of pollen grains. Mass production of pollen is part of the wind pollination strategy.




(a) (b)

Figure 3.2.4.2.9: These male (a) and female (b) catkins are from the goat willow tree (Salix caprea). Note how both structures are light and feathery to better disperse and catch the wind-blown pollen. Descriptive text: Photo A shows the long, thin flower male of the white willow, which has long, hair-like appendages jutting out all along its length. Photo B shows the female flower from the same plant. The shape is similar, but the hair-like appendages are missing.

### Water

Some plants, such as Australian sea grass and pond weeds, are pollinated by water. The pollen floats on water, and when it comes into contact with the flower, it is deposited inside the flower.

## Summary Table of Pollination Syndromes

Table 3.2.4.2.1 summarizes the pollination syndromes described in the categories above.

Table 3.2.4.2.1: Pollination Syndromes (adapted from the US Forest Service).

| Pollination Syndrome | Color | Structure | Scent | Nectar or Pollen |
|---|---|---|---|---|
| **Wind** | Dull, perianth often absent or reduced | Large feathery stigmas, large anthers | None | No nectar, large amounts of pollen |
| **Birds** | Reds and pinks | Often tubular or cupped | None | Lots of hidden nectar, moderate pollen |
| **Bees** | Purples, blues, yellows, white, UV | Flat and shallow or tubular, with landing area | Sweet, fresh, mild | Pollen often sticky and scented, nectar usually present |
| **Bats** | White, dull green, or purple | Often bowl-shaped or pendant, anthers protruding | Musty or fruity, strong, emitted at night | Lots of hidden nectar |
| **Moths** | White, pale pink or purple | Often tubular or cupped, no landing pad | Strong and sweet, emitted at night | Lots of hidden nectar, limited pollen |
| **Butterflies** | Bright colors | Tubular, with wide landing pad | Faint, fresh | Lots of hidden nectar, limited pollen |
| **Flies** | Dark red, purple, brown | Shallow, funnel, or trap-like | Putrid, rotting | No nectar, moderate pollen |

## Attributions

Curated and authored by Maria Morrow using the following sources:

- 32.2 Pollination and Fertilization from *Biology 2e* by OpenStax (licensed CC-BY). Access for free at openstax.org.
- 8.2 The Flower and the Fruit from *Introduction to Botany* by Alexey Shipunov (public domain)

---

This page titled 3.2.4.2: Pollination Syndromes is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **2.7.2: Pollination Syndromes** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-SA 4.0.
- **14.1: Pollination Syndromes** by Maria Morrow is licensed CC BY-NC 4.0.

# 3.2.4.3: Fruits and Dispersal

## Learning Objectives

- Describe the transition from ovary and ovule to fruit and seed.
- Use characteristics of fruits, including pericarp morphology, to identify fruit type.
- Use characteristics of fruits to predict the dispersal agent for a plant's seeds.

All flowers become fruits (Figure **3.2.4.3.1**). This may be surprising at first, as what we culturally refer to as a fruit is a bit different than the botanical definition. Many of the "vegetables" and other plant products (e.g. grains, legumes, and nuts) that you get from the store are actually fruits! The term angiosperm refers to the fruit: angio- means vessel and sperm refers to the seed; fruits are the vessel that houses the seed or seeds. Fruits are a development of the **ovary wall** and sometimes other flower parts. As seeds mature, they release the hormone auxin, which stimulates the wall of the ovary to develop into the fruit. In fact, commercial fruit growers may stimulate fruit development in unpollinated flowers by applying synthetic auxin to the flower. This chapter section will cover the anatomy of a fruit, including the ovary, different fruit types, and finally, how these fruits are specialized for different dispersal mechanisms.



Figure **3.2.4.3.1**: These two images show clusters of pear blossoms from the same tree. The cluster on the left is in an earlier stage of development. The corolla is still attached and the stamens are radiating outward to disperse pollen. In the image on the right, the corolla has fallen off and the anthers have shriveled. The calyx is still visible and, just below it, the semi-inferior ovary and hypanthium are beginning to swell. Eventually, these will swell to many times their current size and form the fruits we know as pears. Photos by Maria Morrow, CC-BY 4.0.

A fruit is defined as ripened ovary, flower, or whole inflorescence. Depending on how these parts interact to form the fruit, we can classify them into different fruit types. The **pericarp** (Figure **3.2.4.3.2**), which is comprised of the **exocarp**, **mesocarp**, and **endocarp**, is derived from the ovary wall.

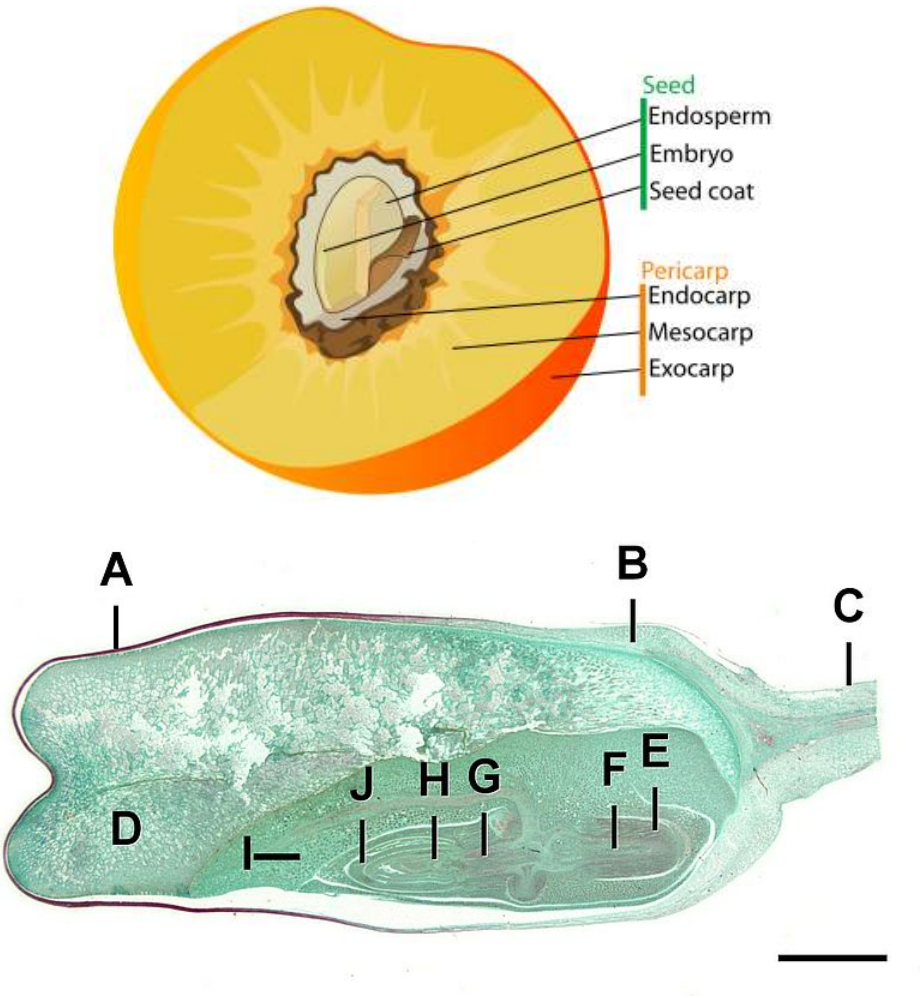



Figure 3.2.4.3.2: Two fruits with different pericarp morphology. The pericarp of a fruit can be separated into distinct layers, as in the first photo, or completely fused together, as in the second photo. The first photo shows a peach, which is a type of fruit called a drupe. It has a stony endocarp enclosing a single seed, a fleshy mesocarp, and a thin exocarp. The second photo shows a corn kernel, which is a type of fruit called a caryopsis. In this fruit type, the pericarp (A) is thin, layers are indistinguishable, and it is completely fused to the seed coat. First mage by LadyofHats, Public domain, via Wikimedia Commons. Second image by Jon Houseman, CC BY-SA 4.0, via Wikimedia Commons. Labels are as follows: A=Pericarp, B=Aleurone, C=Tip cap, D=Endosperm, E=Coleorhiza, F=Radicle, G=Hypocotyl, H=Plumule, I=Scutellum, J=Coleoptile. Scale=1.4mm.

## Ovary Anatomy

An unfertilized ovary, as shown in Figure 3.2.4.3.3, contains one or more developing **ovules** produced in compartments called **locules**. Within the ovule, the megasporangium is surrounded by tissue within the called the integument. Both of these are diploid tissues of the sporophyte. A diploid megaspore mother cell is produced within the megasporangium, which will divide by meiosis to produce the haploid megagametophyte (see Chapter 7.3.2: Angiosperm Life Cycle for a refresher). Each ovule is attached to a nutritional region of the ovary called the **placenta** by a strand of tissue called the **funiculus**. The sporophyte supports the developing ovule through this tissue pathway. Prior to fertilization, there is a small gap in the integument called the **micropyle**.

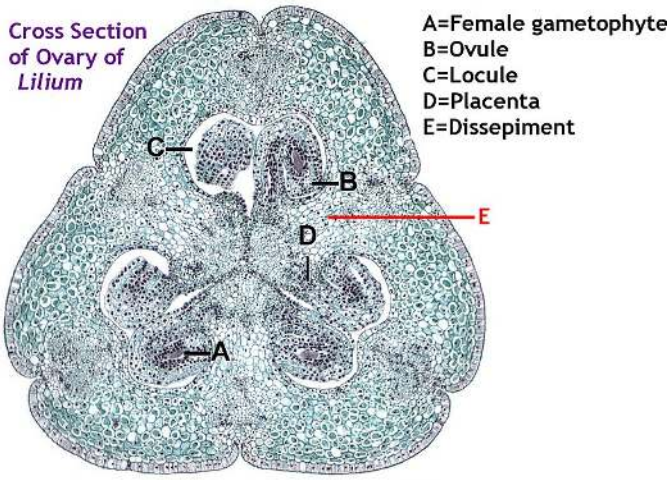



Figure **3.2.4.3.3**: Cross section of *Lilium* ovary, showing A=Female gametophyte, B=Ovule, C=Locule, D=Placenta, E=Dissepiment. The ovary has three locules, each with two developing ovules. Each ovule attached to the ovary by a region of tissue called the placenta. The ovary wall will develop into the fruit and the ovules will develop into seeds, if fertilized. The label in red added to original contribution of File:Lilium ovary L.jpg provided by Jon Houseman and Matthew Ford. JonRichfield, CC BY-SA 4.0, via Wikimedia Commons.

After fertilization, ovules become **seeds**. The micropyle closes and the integument becomes the **seed coat**. The megasporangium, called the **nucellus**, serves as nutritive tissue for the developing embryo. Angiosperms provide an additional food source to the developing zygote, the **endosperm**. The ovary wall develops into the pericarp.

## Fruit Types

Fruits may be classified as simple, aggregate, multiple, or accessory, depending on their origin (Figure **3.2.4.3.11**). If the fruit develops from a single carpel or fused carpels of a single ovary, it is known as a **simple fruit**, as seen in nuts and beans. An **aggregate fruit** is one that develops from more than one carpel, but all are in the same flower: the mature carpels fuse together to form the entire fruit, as seen in the raspberry. A **multiple fruit** develops from an inflorescence or a cluster of flowers. An example is the pineapple, where the flowers fuse together to form the fruit.

Fruits can be **dry** or **fleshy**. An example of dry fruit is a peanut (*Arachis*), the shell of the peanut is the pericarp, which is dry at maturity. Examples of fleshy fruits include apples (*Malus*) or oranges (*Citrus*), where the pericarp or some other part of the floral structure becomes swollen with liquid.

Dry fruits can be further classified into **dehiscent** fruits, which open at maturity, or **indehiscent** fruits, which do not open independently. **Schizocarp** fruits are in between: they do not open but break into several parts (usually the distinct locules), and each part contains one seed inside. For example, maple fruit consists of two “wings”, each of them contains part of the full fruit and one seed.

In addition, fruits can be monomerous (1-seeded) like a nut or an achene, or bear multiple seeds (like the follicle in a tulip, *Tulipa*).

### Accessory Fruits

**Accessory fruits** (sometimes called false fruits) are not derived from the ovary, but from another part of the flower, such as the receptacle (Figure **3.2.4.3.4**) or the hypanthium (Figure **3.2.4.3.5**).



Figure 3.2.4.3.4: Strawberries are accessory fruits formed from a swollen receptacle. The receptacle reddens and swells, pushing the developing fruits outward. The fruits are achenes that look like seeds, stuck to the outside of the receptacle. If you look closely, you can see the styles attached to the narrow end of each achene, each with a stigma at the end. Because strawberries are formed from multiple free carpels, they are also an aggregate fruit. In the second image, the green layer is the calyx. First strawberry photo by Troy Pemberton (found on Instagram as Infinitesimal Prints), used with permission. Sliced strawberry photo by Paolo Neo, Public domain, via Wikimedia Commons.

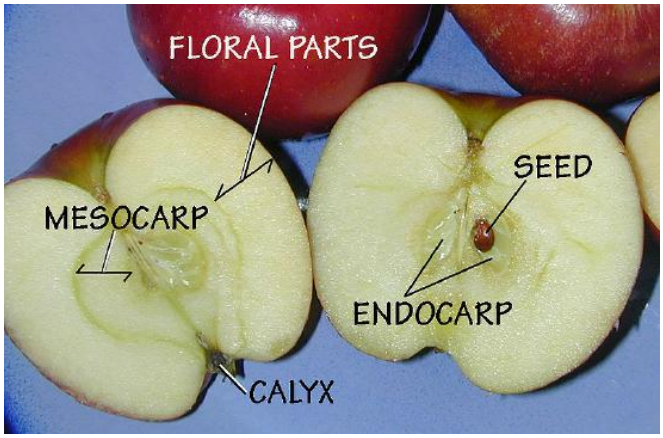



Figure 3.2.4.3.5: A pome is an accessory fruit made from a fleshy hypanthium. The papery core is the pericarp, which contains the seeds. Eric Guinther, CC BY-SA 3.0, via Wikimedia Commons.

## Dichotomous Key to Common Fruits

Use the following dichotomous key to identify fruit types! Note: If the fleshy part of the fruit is composed of something other than the ovary, it is an **accessory fruit**.

1. Fruit from one carpel of one flower .....[Simple Fruit].... 2

1. Fruit from more than one carpel or from an inflorescence .... 16

    2. Fleshy at maturity ..... 3

    2. Dry at maturity ..... 8

3. Thin exocarp, fleshy mesocarp, stony endocarp surrounding single, large seed ..... **Drupe**

3. Fruit not as described above..... 4

    4. Seeds in a linear order, separate from ovary wall, pericarp splits on two seams ...Legume (immature)

    4. Fruit not as described above..... 5

5. Papery endocarp forms a core. Derived from a perigynous flower.....**Pome**

5. Endocarp fleshy (not a papery core) ..... 6

    6. Thin exocarp, fleshy mesocarp, one to many seeds ..... **Berry**

6. Exocarp thickened and leathery (modified berries) ……..... 7

7. Exocarp and mesocarp form leathery rind, locules filled with juice-filled trichomes ……...**Hesperidium**

7. Exocarp forms tough skin/rind, thick mesocarp, not divided into separate locules ..... **Pepo**

8. Dehiscent (splits open at maturity), usually many seeds ..... 9

8. Indehiscent (does not split open), usually one seeded ..... 12

9. Derived from a carpel with one locule ..... 10

9. Derived from a carpel with more than one locule ..... 11

10. Dehiscent along one seam ..... **Follicle**

10. Dehiscent along two seams ..... **Legume**

11. From two locules with a central partition ..... Silique (elongate) or silicle (round)

11. From more than two locules..... **Capsule**

12. Ovary wall extends to form a wing ..... **Samara**

12. Fruit not winged ..... 13

13. Outer wall not especially thick or hard, seed small ... 14

13. Outer wall hardened, seed relatively large ..... 15

14. Seed not tightly attached to pericarp ..... **Achene**

14. Seed fused to pericarp, grains ..... **Caryopsis**

15. Stony pericarp surrounds one large seed ..... **Nut**

15. Relatively thin exocarp, fibrous mesocarp, single large seed ..... (dry) Drupe

16. Derived from one flower with many free carpels ..... **Aggregate Fruit**

16. Derived from an inflorescence (many florets) ..... **Multiple Fruit**

## Fruit and Seed Dispersal

The fruit has a single purpose: seed dispersal. Seeds contained within fruits need to be dispersed far from the mother plant, so they may find favorable and less competitive conditions in which to germinate and grow. Fruits promote the dispersal of their content of seeds in a variety of ways:

- **Ballistic.** Some fruits, as they dry, open explosively expelling their seeds. The pods of many legumes (e.g., wisteria) do this.
- **Wind.** Wind-dispersed fruit are lightweight and may have wing-like appendages that allow them to be carried by the wind. Some have a parachute-like structure to keep them afloat.
- **Water.** Many aquatic angiosperms and shore dwellers (e.g., the coconut palm) have floating fruits that are carried by water currents to new locations.
- **Animal attachment.** The cocklebur and sticktights achieve dispersal of their seeds by sticking to the coat (or clothing) of a passing animal.
- **Animal ingestion.** Nuts and berries entice animals to eat them. Buried and forgotten (nuts) or passing through their g.i. tract unharmed (berries), the seeds may end up some distance away from the parent plant.

All of the above mechanisms allow for seeds to be dispersed through space, much like an animal's offspring can move to a new location. Seed dormancy allows plants to disperse their progeny through time: something animals cannot do. Dormant seeds can wait months, years, or even decades for the proper conditions for germination and propagation of the species. These dormant seeds can accumulate in the soil, forming a **seed bank**. Areas prone to disturbances, like fire, often rely on the seed bank to regenerate plant communities post-disturbance.

## Ballistic

In ballistic dispersal, seeds are shot from the fruit. This can be accomplished via a build up of turgor pressure within the fruit (as in dwarf mistletoe and wild cucumber), a twisting action, or some other method. Watch Video **3.2.4.3.1** to see ballistic seed dispersal in action!



Video **3.2.4.3.1**: Watch this fun video of different plants utilizing ballistic seed dispersal. Sourced from YouTube.

## Wind

Fruits dispersed by wind, like samaras or the achenes of a dandelion, are generally winged (Figure **3.2.4.3.6**). In the case of a dandelion, each achene is attached to a modified calyx that forms an umbrella-like structure to catch on the wind.




Figure **3.2.4.3.6**: Samaras are winged achenes adapted to wind dispersal. The maple samaras on the left are also schizocarps, breaking apart at maturity into two separate fruits. Left image by Gmihail at Serbian Wikipedia, CC BY-SA 3.0 RS, via Wikimedia Commons. Right image by Marco Schmidt [1], CC BY-SA 3.0 via Wikimedia Commons.

## Water

Some fruits, such as those of some aquatic plants like lotus or plants adapted to island living, are specialized for water dispersal. This usually involves a buoyant pericarp, as in the fibrous husk of the water-dispersed coconut. Similarly, willow and silver birches produce lightweight fruit that can float on water. Watch Video **3.2.4.3.2** to see the journey of a water-dispersed sea bean.



Video **3.2.4.3.2**: Watch this clip to see the aquatic journey of the sea bean. Toward the end of the video, be on the lookout for mangrove pneumatophores. Sourced from YouTube.

## Animal Vectors

Many fruits have evolved to use animals for dispersal. Fruits with velcro-like projections or sticky pericarps latch onto mammal fur or bird feet and are transported to a new locale without needing to survive a journey through the digestive tract (Figure **3.2.4.3.7**). Other fruits have specialized for animal ingestion. Among these are the fruits we typically consider fruits, those that are typically sweet, fleshy, often brightly colored and intended for consumption. The seeds must either survive the digestive tract, deposited later in nutrient-rich substrate, or depend on animals who are sloppy eaters, dispersing some of the seeds as they eat others.

Some of these are highly specialized, with a single species or group of animals as the intended dispersal vector. For example, hot peppers like habañero chiles are hot because they contain a compound called capsaicin (see Figure **3.2.4.3.8**). They also tend to be red. This is because these peppers have specialized for bird dispersal vectors. Both birds and mammals are attracted to the color red. However, mammals often have a more thorough digestive tract, meaning seeds need more investment in protection to survive the journey. However, mammals like you and I interpret capsaicin as spicy, perhaps painful, and are often deterred by it (though many exceptions apply among humans), while birds are immune to these effects. Because of this interesting difference in physiology, some people add cayenne pepper to their suet bird feeders to keep the squirrels away.

Some animals, like squirrels, bury seed-containing fruits for later use; if the squirrel does not find its stash of fruit, and if conditions are favorable, the seeds germinate. Some birds are also known to cache nuts for later. Plants that produce nuts generally rely on this storage behavior in their animal dispersers.




Figure **3.2.4.3.7**: Animal attachment. Fruits of *Xanthium*, cockleburrs, have hooked spikes that allow them to attach to passing animals. Photo by Muséum de Toulouse, CC BY-SA 3.0 via Wikimedia Commons.



Figure **3.2.4.3.8**: Habañero chiles (and other spicy peppers) have specially adapted for bird dispersal. They contain a compound called capsaicin that is incredibly spicy to most mammals but does not bother birds. Photo from The original uploader was Fir0002 at English Wikipedia., CC BY 2.5 via Wikimedia Commons.

## Attributions

Curated and authored by Maria Morrow using the following sources:

- 16.3D Angiosperm Life Cycle from *Biology* by John. W. Kimball (licensed CC-BY)
- 32.2 Pollination and Fertilization from *Biology 2e* by OpenStax (licensed CC-BY). Access for free at openstax.org.
- 8.2 The Flower and the Fruit from *Introduction to Botany* by Alexey Shipunov (public domain)

---

This page titled 3.2.4.3: Fruits and Dispersal is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **2.7.3: Fruits and Dispersal** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-SA 4.0.

# 3.2.4.4: Angiosperm Families

**Learning Objectives**

- Interpret a floral formula.
- Describe the characteristics used to identify each of the four largest angiosperm families.

Knowing who is related to whom in the plant world can provide important information. Often, closely related organisms will have similar life history traits, such as defense compounds or other secondary metabolites. Identifying which family an unknown plant belongs to might provide insight into potential interactions with other organisms (see Orchidaceae below), its capability to resist particular environmental conditions or stressors, its edibility or toxicity, or whether it produces compounds that might be used medicinally.

For example, plants like poison oak (*Toxicodendron diversilobum*) and poison ivy (*Toxicodendron radicans*) are in the family Anacardiaceae and produce an oil called urushiol. This oil causes a (sometimes severe) allergic reaction in many people, resulting in an itchy, blistering rash. Mango (*Mangifera indica*) and cashew (*Anacardium occidentale*). also belong to this family, but these are not known for giving itchy rashes. However, as someone who is quite allergic to poison oak, I unknowingly ate a mango with the skin on and broke out in a rash all around my mouth and lower face, just like how I react to touching poison oak. Indeed, cashews are just the seed of the cashew fruit. The rest of the fruit and seed coat are removed due to the urushiol content.

Additionally, while there are over 350,000 species of flowering plants, there are only around 400 families. Being able to quickly narrow an unknown plant to family is an essential skill in plant identification. So how can we tell who belongs to the same family among plants? For flowering plants, we can use **floral formulas.**

## Floral Formulas

Since there are so many terms about flowers, and at the same time, flower structure and diversity always were of immense importance in botany, two specific ways were developed to make flower description more compact. First is a flower formula. This is an approach where every part of flower is designated with a specific letter, numbers of parts with digits, and some other features (whorls, fusion, position) with other signs.

- Symmetry: ***** means radial symmetry, while **X** means bilateral symmetry.
- Whorls: **K** is the calyx, **C** is the corolla, **A** is the androecium, and **G** is the gynoecium. The number that follows each letter represents the number of parts in that whorl. For the gynoecium, a line under the number indicates an inferior ovary, while a line above the number indicates a superior ovary.
- Fusion: In most representations, connation is indicated by circling the number, while adnation is indicated by drawing a line connecting the numbers of the fused whorls.

Here are a few examples of floral formulas, followed by their interpretation:

$*K_4C_4A_{2+4}\underline{G_{(2)}}$: flower actinomorphic, with four sepals, four petals and six stamens in two whorls, ovary superior, with two fused carpels

$\uparrow K_{(5)}[C_{(1,2,2)}A_{2,2}]\underline{G_{(2\times2)}}$: flower zygomorphic, with five fused sepals, five unequal fused petals, two-paired stamens attached to petals, superior ovary with two subdivided carpels

$*K_{(5)}C_{(5)}[A_5\underline{G_{(3)}}]$: actinomorphic flower with five fused sepals and five fused petals, five stamens attached to pistil, ovary inferior, with three fused carpels

The following signs are used to enrich formulas:

**PLUS** "+" is used to show different whorls; *minus* "–" shows variation; "v" = "*or*"

**BRACKETS** "[]" and "()" show fusion. In most representations, connation is indicated by circling the fused whorl, while adnation is indicated by drawing a line underneath the formula connecting those whorls.

**COMMA** "," shows inequality of flower parts in one whorl

**MULTIPLICATION** "×" shows splitting

**INFINITY** "∞" shows indefinite number of more than 12 parts

Flower diagram is a graphical way of flower description. This diagram is a kind of cross-section of the flower. Frequently, the structure of pistil is not shown on the diagram. Also, diagrams sometimes contain signs for the description of main stem (axis) and flower-related leaf (bract). The best way to show how to draw diagram is also graphical (Figure **3.2.4.4.1**); formula of the flower shown there is $*K_5C_5A_5G_{\underline{(5)}}$.

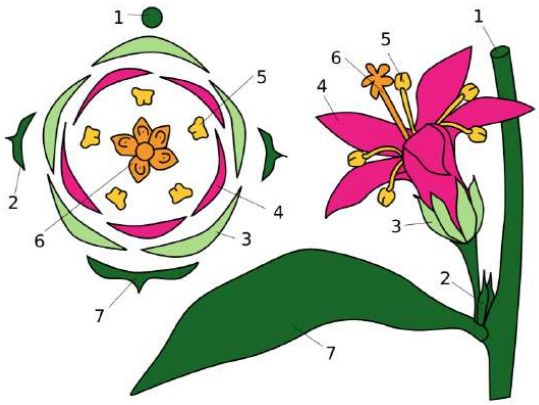



Figure **3.2.4.4.1**: How to draw a diagram (graphical explanation): compare numbers on plant and on diagram. On the left of the image, a simplified aerial view of the flower represents the floral diagram. In the center is a star-like 5-lobed stigma surrounded by 5 4-lobed anthers. There are 5 pink crescent shapes that form a circle around this (the petals) and 5 pale green crescents that form a circle around these (the calyx). Three darker green, bracket like shapes represent leaves and a single dark green circle represents the peduncle.

## Review of Terms and Formula Designations

**FLOWER PARTS** occur in whorls in the following order—sepals, petals, stamens, pistils.

(The only exceptions are flowers of *Eupomatia* with stamens then perianth, *Lacandonia* with pistils then stamens, and some monocots like *Triglochin*, where stamens in several whorls connect with tepals.)

**PEDICEL** flower stem

**RECEPTACLE** base of flower where other parts attach

**HYPANTHIUM** cup-shaped receptacle (Figure **3.2.4.4.2**)

**PERIANTH** = CALYX + COROLLA

**SEPALS** small and green, collectively called the CALYX, **formula**: K

**PETALS** often large and showy, collectively called the COROLLA, **formula**: C

**TEPALS** used when sepals and petals are not distinguishable, they form SIMPLE PERIANTH, **formula**: P

**ANDROECIUM** collective term for stamens: **formula**: A

**STAMEN** = FILAMENT + ANTHER

**ANTHER** structure containing pollen grains

**FILAMENT** structure connecting anther to receptacle

**GYNOECIUM** collective term for pistils/carpels, **formula**: G. Gynoecium can be composed of:

1. A single CARPEL = simple PISTIL, this is MONOMERY
2. Two or more fused CARPELS = compound PISTIL, this is SYNCARPY
3. Two or more unfused CARPELS = two or more simple PISTILS, this is APOCARPY

(Note that variant #4, several compound pistils, does not exist in nature.)

To determine the number of CARPELS in a compound PISTIL, count LOCULES, points of placentation, number of STYLES, STIGMA and OVARY lobes.**PISTIL** Collective term for carpel(s). The terms CARPEL and PISTIL are equivalent when there is no fusion, if fusion occurs then you have 2 or more CARPELS united into one PISTIL.

**CARPEL** structure enclosing ovules, may correspond with locules or placentas

**OVARY** basal position of pistil where OVULES are located. The ovary develops into the fruit; OVULES develop into seeds after fertilization.

**LOCULE** chamber containg OVULES

**PLACENTA** place of attachment of OVULE(S) within ovary

**STIGMA** receptive surface for pollen

**STYLE** structure connecting ovary and stigma

**FLOWER** Floral unit with sterile, male and female zones

**ACTINOMORPHIC FLOWER** A flower having multiple planes of symmetry, also called radially symmetrical, **formula**: ∗

**ZYGOMORPHIC FLOWER** A flower having only one plane of symmetry, also called bilaterally symmetrical, **formula**: ↑

**PERFECT FLOWER** A flower having both sexes

**MALE / FEMALE FLOWER** A flower having one sex, **formula**: ♂ / ♀

**MONOECIOUS PLANTS** A plant with unisexual flowers with both sexes on the same plant

**DIOECIOUS PLANTS** A plant with unisexual flowers with one sex on each plant, in effect, male and female plants

**SUPERIOR OVARY** most of the flower is attached below the ovary, **formula**: $\underline{G}_{...}$

**INFERIOR OVARY** most of the flower is attached on the top of ovary, **formula**: $\underline{\underline{G}}_{...}$

(Inferior ovary only corresponds with monomeric or syncarpous flowers.)

**WHORL** flower parts attached to one node

## Major Families

This section will cover some of the largest families of angiosperms, including their floral formula and general characteristics.

### Orchidaceae, the Orchid Family

Orchids are one of the most species-rich group of plants, containing over 28,000 species (Figure **3.2.4.4.1**). These plants tend to be tropical and epiphytic (growing on other plants). However, as can be assumed from their vast diversity, orchids can be found in many ecosystems and growing on a variety of substrates, including rocks! Their flowers are often highly modified, including long nectar spurs, hairy petals, and strange morphologies. Many orchids are fly pollinated. Follow this link to see observations of orchids from across the globe and in your region!

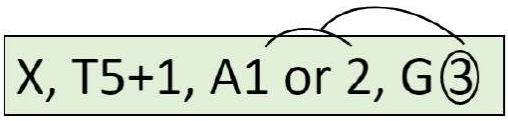



Figure **3.2.4.4.1**: Floral formula of the Orchidaceae. Flowers are bilaterally symmetrical. These flowers have tepals, so the K and C have been replaced by a T. There are 5 tepals that are similar in appearance and one that is different. The androecium contains one or two stamens that are fused to the gynoecium, which contains three fused carpels. Diagram by Melissa Ha, CC-BY-NC.

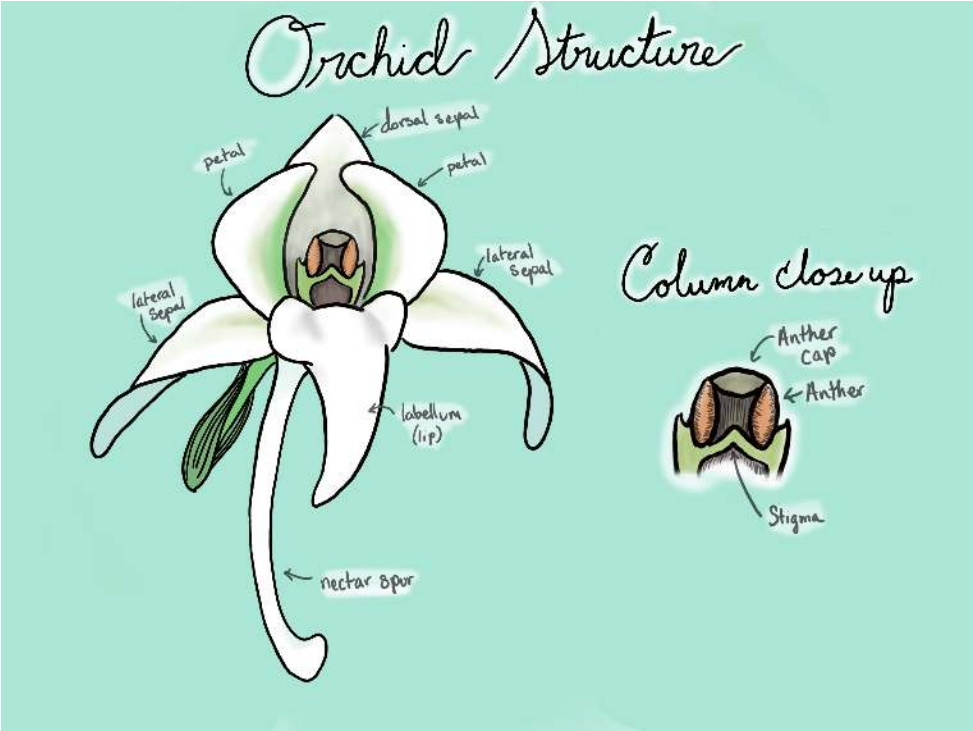



Figure 3.2.4.4.2: A diagram of general orchid flower structure, with a close up on the column. The column is a structure formed from the fusion of the androecium and gynoecium. This flower has two lateral sepals emerging from the sides and one vertically oriented dorsal sepal. There are two petals vertically oriented on either side of a the central column. In front of the column, a forward-extending petal is labeled as the labellum (or lip). A nectar spur (a tubular structure formed from the perianth) extends below the flower. Within the column, anthers flank a central stigma. Diagram by Maria Morrow, CC-BY-NC.



Figure 3.2.4.4.3: Orchids produce a spectacular diversity of floral morphologies. The first image is *Anoectochilus albolineatus*, an orchid whose labellum forms tendrils like spider legs. The second image is *Caleana major*, also called the large flying duck orchid for its uncanny similarity to a cartoon duck. First image by Safwanah Safwan, CC-BY-NC. Second image by Ambikab, CC-BY-NC.

Orchids make a large number of tiny seeds, i.e. the tiny black specks in vanilla bean ice cream are the seeds of the orchid *Vanilla plantifolia*. An interesting, r-selected strategy with a twist: the seeds parasitize mycorrhizal fungi. Orchid seeds will not germinate if they do not have a fungal partner. As the fungal hyphae penetrate into the orchid cells, they formed coiled structures. The orchid feeds on the fungal hyphae until it has produced its first leaves and can photosynthesize on its own. At this point, the relationship

can be shifted toward mutualism, with sugars transfered from plant to fungus. However, some orchids have lost the ability to make chlorophyll and instead, continue to feed from their fungal partner. These plants are referred to as **mycoheterotrophs**. The mycoheterotrophic orchid *Rhizanthella gardneri* undergoes its entire life cycle underground!

### Asteraceae, the Aster Family or Composite Family

There are more than 32,000 accepted species in Asteraceae—a recent and dramatic increase in described species has sent them soaring past the orchids (for the time being). They have a cosmopolitan distribution, but are better represented in temperate and subtropical regions. This family is primarily herbaceous but does contain some woody species. Members of this family produce head inflorescences with one or two different types of florets that all attach to a common receptacle (Figure **3.2.4.4.4**). Disc florets have radial symmetry, while ligulate florets have bilateral symmetry (Figure **3.2.4.4.5**). Some inflorescences contain only disc florets (e.g. thistle), some only ligulate florets (e.g. dandelions), and others contain a combination of the two (e.g. daisy). The inflorescence is subtended by layers of bracts called phyllaries, forming an involucre.

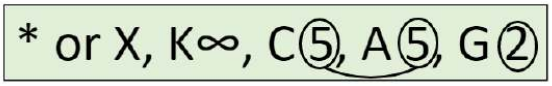



Figure **3.2.4.4.4**: Floral formula of the Asteraceae. Disc florets are radially symmetrical, while ray florets are bilaterally symmetrical. There are many unfused sepals. There are 5 fused petals. The androecium contains 5 fused stamens that are also fused to the petals. The gynoecium contains 2 fused carpels. Diagram by Melissa Ha, CC-BY-NC.



Figure **3.2.4.4.5**: A long section through a head inflorescence and and one ligulate (ray) floret. The cone (center) of the head inflorescence is composed of radially symmetrical disc florets that have fused yellow petals. These are encircled by a ring of ray florets with white, fused petals and bilateral symmetry. All florets are attached to an enlarged receptacle area. A single ray floret is shown on the right. This one has 5 fused yellow petals. The calyx is reduced to a ring of fuzz called a pappus. The stigma is two-lobed.

The calyx is reduced to hairs or bristles (**pappus**, see Figure **3.2.4.4.6 – 7**), petals are fused into a tube or ligula (with 5 or 3 teeth). The pollen is lifted up and distributed by the outer sides of the stigmas, called secondary pollen presentation (Figure **3.2.4.4.6**). Florets have inferior ovaries. The fruit is an achene and the mature seed has almost no endosperm.

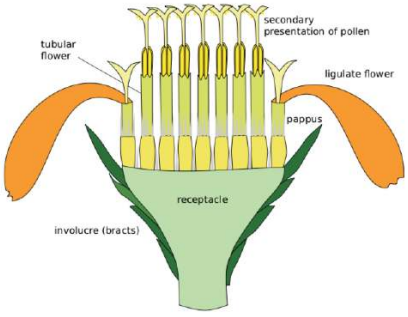



Figure **3.2.4.4.6**: Disc florets showing secondary pollen presentation by the stigmas, with anthers forming a tight ring around the styles. The modified calyx (pappus) is shown at the base of the florets. Ligulate florets are shown on each side; these lack anthers. All florets are attached to a common, swollen receptacle which is lined with bracts, forming an involucre.




Figure **3.2.4.4.7**: Pappus of *Cirsium vulgare* florets. These bull thistle florets have shed their corollas, revealing the modified, bristle-like calyx, the pappus. Photo by Tatyana Zarubo, CC-BY-NC.

Many plants withing the Asteraceae are used for oils, vegetables, ornamentals and medicinal plants are distributed in multiple subfamilies. The most commercially important of these are:

- Carduoideae: mostly tubular flowers

  -*Centaurea*—knapweed

  -*Cynara*—artichoke

  -*Carthamus*–safflower

- Cichorioideae: mostly 5-toothed ligulate (pseudo-ligulate) flowers + lacticifers with latex

  -*Taraxacum*—dandelion

  -*Lactuca*—lettuce

- Asteroideae: tubular + 3-toothed ligulate flowers

  -*Helianthus*—sunflower (BTW, “canola”, or Brassica napus from Cruciferae is the second main source of vegetable oil)

  -*Artemisia*—sagebrush

  -*Tagetes*—marigold and lots of other ornamentals

## Fabaceae, the Legume Family

With around 19,000 species, Fabaceae (Figure **3.2.4.4.8**) is the third largest angiosperm family after orchids and asters. This family is widely distributed throughout the world, but does particularly well in the tropics. These plants form root nodules with nitrogen-fixing bacteria. Leaves are alternate, pinnately compound (once or twice), with stipules. Plants in this family have legumes as fruits (one locule dehiscent along a single suture).




Figure **3.2.4.4.8**: Floral formula of the Fabaceae. Because of the differences between the three subfamilies, a single floral formula becomes complex. Most flowers are bilaterally symmetrical, though they are radially symmetrical in Mimosoideae. There are 5 sepals and 5 petals with varying degrees of fuision. In most cases, there are 10 stamens, but Mimosoideae has many. There is a single carpel with an inferior ovary. Diagram by Melissa Ha, CC-BY-NC.

There are three subfamilies (Caesalpinioideae, Mimosoideae, Papilionoideae) with distinct characteristics. In Papilionoideae the petals are mostly free, unequal and have special names: *banner*, *keel* and *wing* (Figure **3.2.4.4.9**). In Mimosoideae, they fuse and form a tube with radial symmetry. There are usually 10 stamens with 9 fused and one free; in Mimosoideae, stamens are numerous. There is a single carpel in the gynoecium, meaning the ovary will have a single locule.

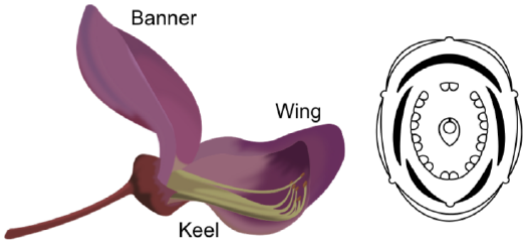



Figure **3.2.4.4.9**: Flowers of Papilionoideae subfamily. The large, upright petal in the back is the banner. Two wings extend out to the sides. A keel, composed of two fused petals, houses the reproductive whorls. The floral diagram shows that there are 9+1 stamens (one of the stamens is separate from the others.

Some representatives of Fabaceae include:

- Mimosoideae: stamens numerous, petals connected

  -*Acacia*—dominant tree of African and Australian savannas, often with phyllodes

  -*Mimosa*—sensitive plant

- Papilionoideae: stamens 9+1, petals mostly free; this subfamily contains many extremely important food plants with high protein value

  -*Glycine*—soybean

  -*Arachis*—peanut with self-buried fruits

  -*Phaseolus*—bean

  -*Pisum*—pea

## Poaceae, the Grass Family

Grasses are monocots. There are approximately 12,000 species of grasses widely distributed throughout the world, but most genera concentrate in the tropics. Grasses tend to be wind dispersed and prefer dry, sunny places. They often form turf (tussocks)—compact structures where old grass stems, rhizomes, roots, and soil parts are intermixed. Grasses form grasslands—specific ecological communities widely represented on Earth (for example, North American prairies are grasslands). Grasses are also important components of other ecosystems (e.g. wetlands). Stems of grasses are usually hollow and round. The leaves have sheathing bases.

Grass florets are reduced, wind-pollinated, usually bisexual (Figure **3.2.4.4.10**), and form complicated spikelets. Each spikelet bears two *glumes*; each flower has *lemma* and *palea* scales (Figure **3.2.4.4.11**). The perianth is reduced to lodicules. Stamens from 6 to 1 (most often 3), with large anthers. The fruit of grasses is a **caryopsis,** what we commonly refer to as a grain. Grasses are incredibly important commercially as food sources, construction, biofuels, and components of many products: rice, corn, wheat, sugarcane, barley, rye, sorghum, and bamboo are all grasses. The study of grasses is called agrostology--it can be both aggravating and glumey.

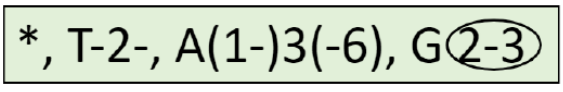



Figure **3.2.4.4.10**: Floral formula of the Poaceae. Grass florets are strange, indeed! They have a reduced perianth with two lodicules (T) due to their wind pollination syndrome. The androecium usually contains 3 stamens, but there may be 1 or 6. The gynoecium contains 2-3 fused carpels. Diagram by Melissa Ha, CC-BY-NC.

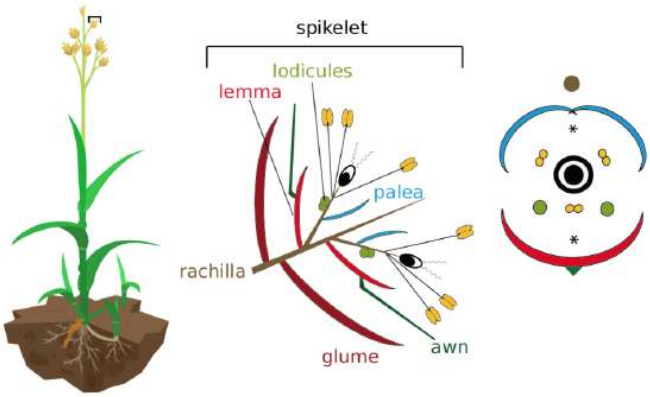



Figure **3.2.4.4.11**: Floral structures in the Poaceae. On the left is a grass plant with sheathing leaves around a single stem topped by an inflorescence composed of florets. In the center is a diagram of a spikelet. Each spikelet is composed of a central rachilla, two glumes on the outside that enclose a lemma and an awn, and two florets composed of lodicules, palea, stamens, and carpels. On the right is a flower diagram of a grass floret. The diagram shows a circle for the rachilla next to two palea. On the other side, the floret is enclosed by an awn or lemma. In the center, there are two lodicules, three anthers, and a single carpel with two feathery stigmas (each shown as asterix).

## Attribution

Curated and authored by Maria Morrow using the following sources:

- 19.1.5 Diversity and Evolutionary Relationships of the Plants from *Biology* by John. W. Kimball (licensed CC-BY)
- 8.3 Three plant families you wanted to know but were too afraid to ask from *Introduction to Botany* by Alexey Shipunov (public domain)
- Angiosperm Families presentation by Melissa Ha, (CC BY-NC)

---

This page titled 3.2.4.4: Angiosperm Families is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **2.7.4: Angiosperm Families** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC 4.0.
- **2.6.3.1: Flowers** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC 4.0.

# 3.2.4.5: Chapter Summary

Angiosperms are an incredibly diverse group of plants. They have many avenues in which to specialize and speciate. Lineages of flowering plants have evolved in tandem with their pollinators by forming increasingly specialized flowers. These sets of specialized floral characteristics--including morphology, color, smell, and the presence of nectar or pollen--are considered together as the plant's pollination syndrome. Wind pollinated flowers are reduced and lack strong odors or nectar, though they contain large amounts of pollen. Bird pollinated flowers contain lots of nectar that they hide in tubular structures, often pigmented red or pink (colors that birds see well, but bees can't distinguish from greens), and lacking strong scents. Bee pollinated flowers can be a variety of colors, but tend toward blues, purples, and yellows. They tend to have sweet, fresh scents and a place for the bee to land. Moth and bat pollinated flowers are white and open at night. Some flowers have even evolved to trick flies into accidental pollination by mimicking a corpse.

They have also evolved fruits specialized for their particular seed dispersal agent. Some fruits release seeds on their own through a variety of explosive mechanisms. Others rely on wind (using wing-like structures) or water (using floats) for dispersal. Still others have coevolved with animals. Some have evolved velcro-like spines or sticky substances to attach to passing animals. Others have evolved to be eaten, some only by specific animals, and hope to survive the digestive tract or have at least some seeds escape the process.

These opportunities for specialization, as well as perhaps the influence of self-incompatibility genes and other factors, has resulted in over 350,000 species of angiosperms classified into over 400 families. However, much of angiosperm diversity can be found in a few major families. Among these are the asters (32,000), orchids (28,000), legumes (19,000), and grasses (12,000).

**After completing this chapter, you should be able to...**

- Compare and contrast monocots and eudicots.
- Differentiate between monocot and eudicot flowers and leaves.
- Explain pollination strategies with regard to genetic diversity.
- Explain what is meant by the term pollination syndrome.
- Use floral characteristics to predict a plants pollinator(s).
- Describe the transition from ovary and ovule to fruit and seed.
- Use characteristics of fruits, including pericarp morphology, to identify fruit type.
- Use characteristics of fruits to predict the dispersal agent for a plant's seeds.
- Interpret a floral formula.
- Describe the characteristics used to identify each of the four largest angiosperm families.

## Attribution

Content by Maria Morrow, CC BY-NC

This page titled 3.2.4.5: Chapter Summary is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **2.7.5: Chapter Summary** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC 4.0.

# 3.3: Life Cycles

## Learning Objectives

- Describe the role of ploidy in the haplodiplontic (alternation of generations) life cycle of plants.
- Compare and contrast gametophyte and sporophyte generations.

Organisms or cells that contain two copies of each chromosome are considered **diploid, or 2n** (they contain homologous chromosomes in pairs that were acquired from their parents). Organisms or cells that contain one set of chromosomes are considered **haploid, or n**, meaning they only contain one of each chromosome, either material or paternal. Your body cells are diploid and contain pairs of chromosomes. Your gametes (egg and sperm cell) are haploid and contain unpaired chromosomes. For more on ploidy, see Biology 2e 11.1 Meiosis.

Plants have a **haplodiplontic (alternations of generations) life cycle**. In plants, there are two distinct generations that alternate: the gametophyte and the sporophyte generation. The gametophyte begins as a single-celled spore that germinate into a multicellular life stage. This mature gametophyte life stage is haploid and by **mitosis** (division of cells with identical genetic information) produces gametes. These gametes are either egg or sperm cells. Often cross fertilization occurs where the sperm cell of one plant individual fertilizes the egg cell of another plant individual. The results is a fertilized egg, or **zygote**, which is diploid. This begins the sporophyte generation in plants. The sporophyte then divides into a multicellular life stage (division occurs by mitosis). This mature sporophyte will now produce spores by meiosis, a type of cell division that reduces chromosome numbers to half. The sporophyte is diploid, but the spores are haploid. The spores disperse and germinate into new gametophytes, repeating the process (see Figure **3.3.1**).

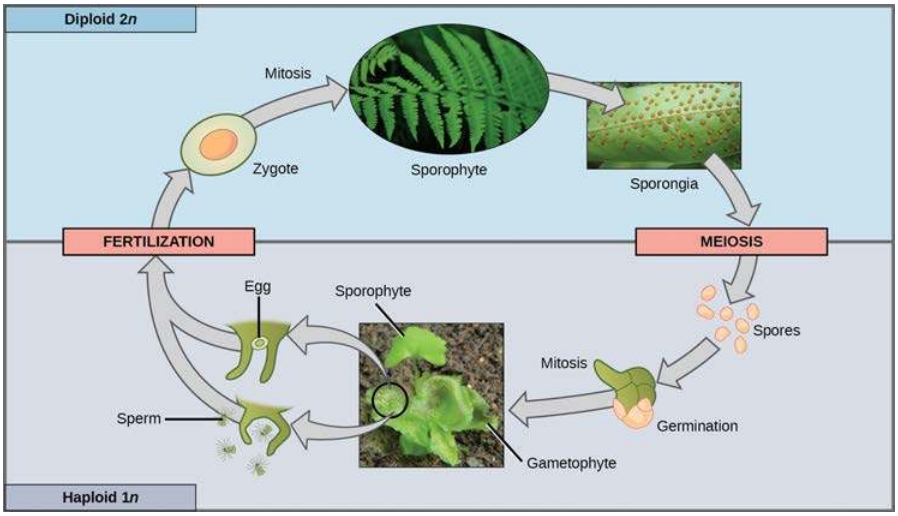



Figure **3.3.1**: The plant life cycle is haplodiplontic (alternations of generations). Fern is shown as an example. The haploid (n) multicellular life stage is called the gametophyte as it produces gametes (egg and sperm cells) that fuse during fertilization to form a diploid (2n) zygote. This zygote develops into a mature diploid sporophyte by mitosis, carrying both genetic information from the fused gametes. The mature sporophyte produces spores by meiosis, which are haploid. The spores germinate by mitosis to develop into a mature multicellular gametophytes, which is still haploid. The life cycle continues as gametes are produced (OpenStax licensed CC-BY).

Note that both the gametophyte and sporophyte are mature plants. However, they reproduce in different ways and have different chromosome counts. The gametophyte generation produces gametes by mitosis that are fertilized, undergoing sexual reproduction. The sporophyte generation produces spores by meiosis that are dispersed. Both gametophyte and sporophytes grow by mitosis.

## Contributors and Attributions

Curated and authored by Kammy Algiers using 11.2 Sexual Reproduction from *Biology 2e* by OpenStax (licensed CC-BY). Access for free at openstax.org.

This page titled 3.3: Life Cycles is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **1.1.4: Life Cycles** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC 4.0.

# 3.4: The Origins of Crop Plants

## Domestication of Plants and Animals

Tremendous natural variations exist among the individuals of any plant species. The traits that define color, shape, flavor, height, yield, and resistance to pests, pathogens, and environmental stresses are not fixed within a species. Individual plants and animals from the same species can be easily distinguished based on these characteristics.

Since the beginning of agriculture, humans have unconsciously been selecting plants and animals with desirable traits, such as large-sized grains, pods, fruits, and vegetables; sweeter and less-seeded fruits; less bitter and nonprickly vegetables; cereals with large panicles and tough rachis; non-seed-shattering plants; and so on. As a consequence of such artificial selections over many generations, unprecedented changes occurred in cultivated plants that set them apart from their ancestors and wild relatives. For example, the relentless efforts of humans led to the development of various crops, such as corn from a wild-grass teosinte; long-spiked, six-row barley from short-spiked, two-row wild barley; large tomatoes from a small berry; and a variety of less-seeded fruits and palatable vegetables from their bitter wild ancestors (see figures 2.1 and 2.2). These plants—enriched in traits that favor higher yields, productive harvest, and increased palatability—would not have come into being without the persistence of humans since the dawn of agriculture.

Artificial selection by humans counteracts the process of natural selection. In nature, small fruits are packed with seeds, thistles, thorns, and prickly leaves; have a bitter taste; ripen asynchronously; and have seeds that spontaneously shatter—all traits that favor the survival of the plants. Thus artificially selected and propagated species of cultivated plants, lacking necessary traits for survival, become more vulnerable to diseases, predators, and environmental stresses. These crops cannot survive in nature for a long time without human help.



Fig 2.1 Maize is a product of artificial selection by human. A comparison of maize's ancestor teosinte (Zea mays ssp. parviglumis) and maize (Zea mays). Photo of maize and teosinte by Hugh Iltis is open source.

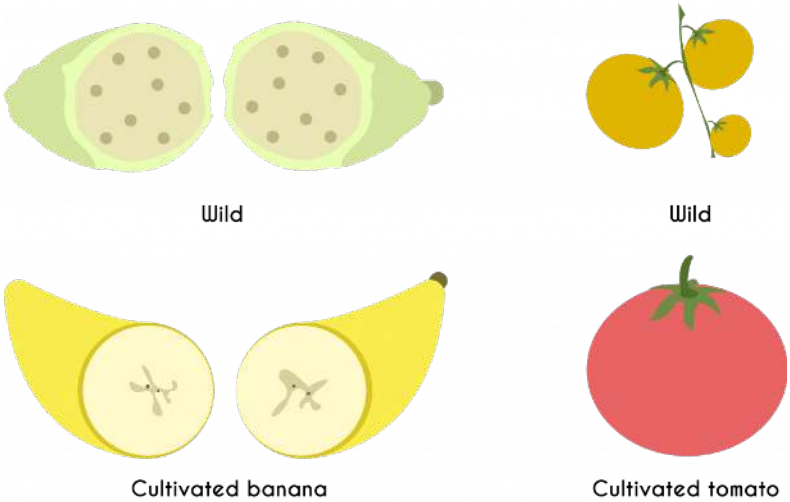



Fig 2.2 "Changes in crop plants as a result of artificial selection" by Sushma Naithani and OSU OERU is licensed under CC BY 4.0.

For several millennia, humans have put tremendous effort into providing protection and ensuring the continuous propagation of cultivated plants. We provide fertilizers, pesticides, and water and provide services such as weeding to promote the growth of crop plants. Thus domesticated plants need humans for their survival as much as human survival depends on them. These species cannot survive in nature for a long time by themselves, but with human help, they have spread globally. For some species, this dependency on humans has become total. For example, maize absolutely depends on humans for its survival. If you leave a mature cob in the field, some of its seeds may germinate on the cob, but they will soon die due to the lack of space for emerging seedlings to grow. Furthermore, maize seeds do not fall spontaneously and need human help to be detached from the cob and planted in the soil.

This mutual interdependence between crop plants and humans (and, similarly, between humans and artificially selected and bred animals) was achieved over several millennia, and this is the historical process we call “domestication.” Thus to a great extent, all crop plants and domesticated animals are man-made.

## Landraces of Crop Plants

n addition to artificial selection, cultivated plants were continuously subjected to the natural selection imposed by their immediate environment, geographical locality, and agricultural practices. Thus domesticated plants are products of artificial selection operating within environmentally enforced natural selection and the agricultural practices prevalent in a given region. The early domesticated plants flourished in their native environment, but when shifted to new locations, they performed poorly. Over time, the few offspring of the introduced plants acquired characteristics (i.e., via spontaneous mutations or hybridization with related species present in the new locality) that helped them stabilize in their new surroundings. This process has produced diversified varieties of crops known as *landraces*, each adapted to a specific geography, climate, or environment (seasonal variations in day length, temperature, water availability, soil quality, salinity, etc.) and its associated pests and pathogens.

The landraces differ from one another in taste, fragrance, flavor, nutrient composition, and tolerance to pathogens and environmental stresses. Before the industrialization of agriculture, traditional farmers had very small holdings but grew many varieties of the same crops for multiple uses. Typically, in a small village, one could find several cultivars of fruits and vegetables as well as many varieties of grains. Farmers have local names for each of these different varieties based on their special traits or origins. For example, more than 3,000 varieties of rice have been developed around the globe and grow in a range of climatic conditions and geographical locations, from temperate hillsides, to tropical planes, to flooded marshes in coastal regions. Each variety of rice has a name and specific usage in culinary dishes (e.g., sushi, pudding, pilaf, steamed rice, crackers, and baby food).

Similarly, more than fifty races of maize are found in Mexico—thirty races in the Oaxaca province alone. Each race includes hundreds to thousands of varieties adapted to the immediate environment and climatic conditions and each has a special use (see figure 2.3). For instance, the popcorn variety’s seeds possess a hard outer cover capable of holding steam for a sufficient amount of time when heated, allowing for the full transformation of starch required for making popcorn. Conversely, the seeds from other corn varieties containing a thin seed cover do not produce good popcorn because, upon heating, they break easily, causing steam leakage. Another example is the sweet corn variety, consumed primarily after boiling or roasting, which lacks an enzyme that efficiently converts sugar to starch and thus has higher sugar content. Dent corn, the most popular corn variety grown today, has soft starch and is lightly sweeter; thus it is used for making chips and tortillas. Before 1920, flint corn was the most widespread variety because it is naturally resistant to many pests and pathogens prevalent in the tropics and is highly productive.

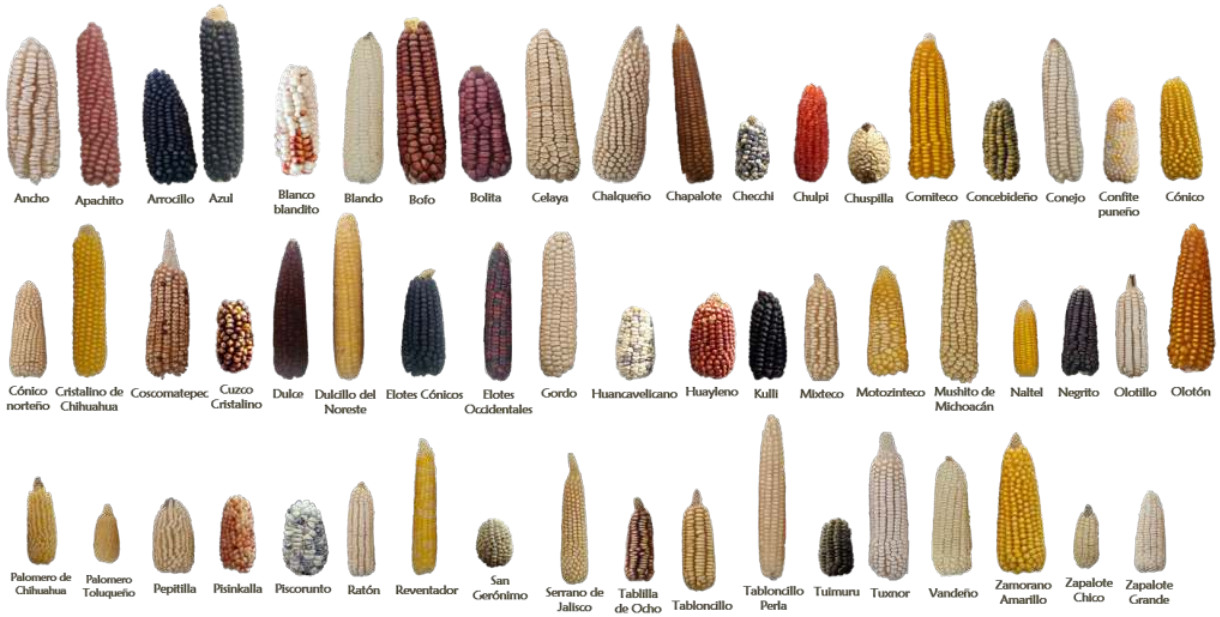



Fig 2.3 Examples of some of the 59 native Mexican maize landraces. Photo of maize by CIMMYT Maize Germplasm Bank is licensed under CC BY 2.0.

For centuries, farmers have been stocking seeds of different varieties separately to ensure their purity and have been careful about not mixing the seeds from multiple varieties. To avoid cross-contamination, farmers usually save seeds for the next year's sowing from the plants growing in the middle of their fields. This way, the individual varieties are maintained, but their independent evolution and development are also continued. The landraces of the various crops that have survived today are not 100 percent identical to their ancestors that existed 200 or 1,000 years ago. They are constantly changing, keeping in tune with their growing environment and adapting to the changes in it.

## Centers of Crop Domestication

Nikolai Vavilov, a Russian agricultural scientist, was one of the first scientists in the world to infer that the process of domestication—the enrichment of desirable traits by human/artificial selection—also led to the loss of many useful traits (see figure 2.4). He noted that in comparison to their wild relatives, most crops easily succumb to parasites, pests, and pathogens and are less resilient under unfavorable environmental conditions. Vavilov proposed that these lost traits can be traced back to the wild progenitors and related species of crop plants, which are likely to still be present in the regions where crops were first domesticated. He further proposed that useful traits can be reintroduced in crops by employing the kind of systematic plant breeding rooted in the principles of Mendelian genetics (we describe the work of Mendel and the basic principle of genetics in chapter 5).

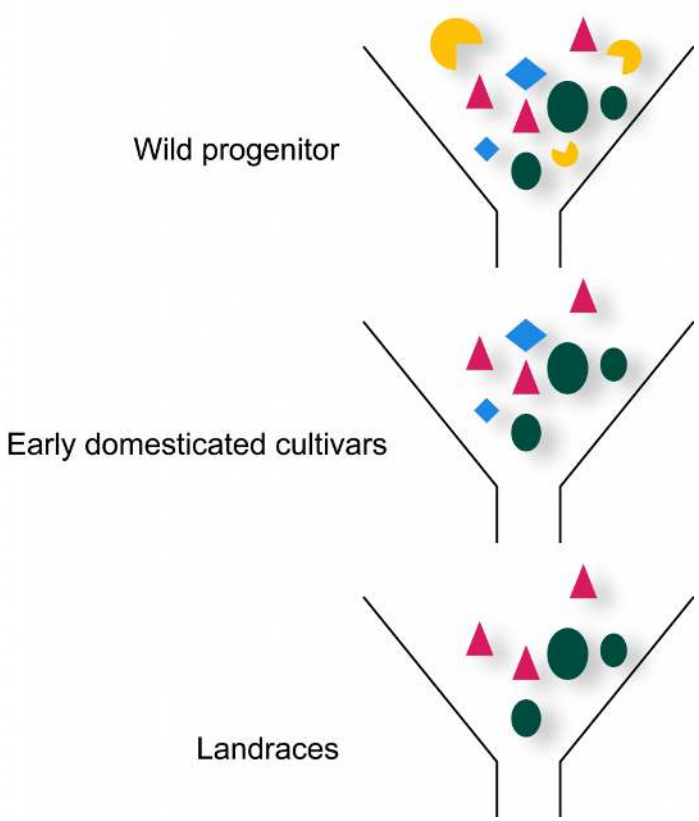



Fig 2.4 Loss of gene pool during crop domestication due to artificial selection. “Loss of gene pool” by Sushma Naithani and OSU OERU is licensed under CC BY 4.0.

In the 1920s, knowledge about the domestication centers of crop plants was lacking. So Vavilov took this herculean task upon himself and set forth on a mission to collect the germplasm (seeds, tubers, roots) of all domesticated crops and their wild relatives. He led nearly a hundred expeditions to sixty-four countries on five continents over the course of twenty years and built the world’s biggest plant germplasm collection, which included 350,000 accessions of seeds, roots, and tubers representing about 2,500 plants. Based on the study of this comprehensive collection and observations about human cultures and linguistics, Vavilov proposed eight geographic centers as the birthplaces or “centers of origin” of crops—the places where the ancestors, wild relatives, and other related species of crops still live and where mankind first began their cultivation. These eight centers include China, India and the Indo-Malayan region, Central Asia (including Pakistan, Afghanistan, Turkestan, and the northwest Indian provinces of Punjab and Kashmir), the Near East, the Mediterranean, Ethiopia, southern Mexico and Central America, and South America (Ecuador, Peru, Bolivia, Chile, and Brazil-Paraguay; see figure 2.5). Overall, Vavilov associated about 640 crops with their biodiversity centers. Five-sixths of these came from the Old World (Asia, Africa, Europe) and one-sixth from the New World (Australia, North and South America).

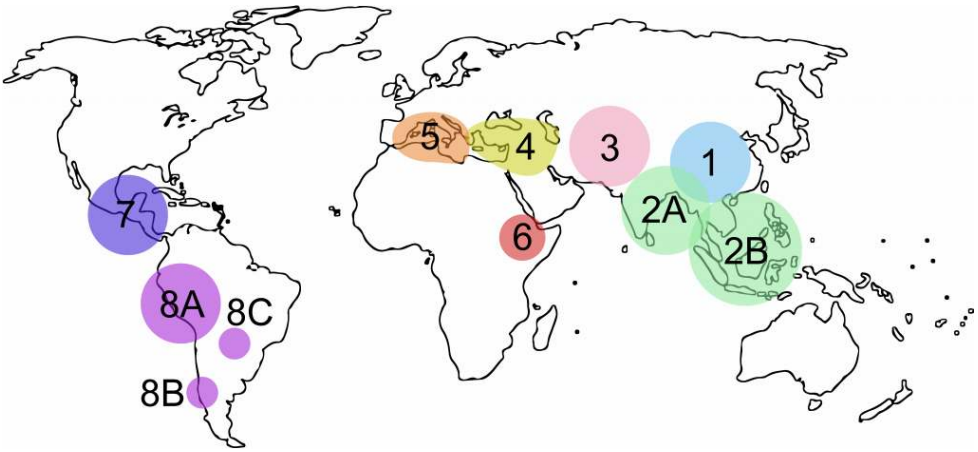



Fig 2.5 The centers of origin of cultivated plants identified by Nikolai Vavilov: 1. China; 2. India; 2a. the Indo-Malayan region; 3. Central Asia (including Pakistan, Punjab, Kashmir, Afghanistan and Turkestan); 4. the Near East (Fertile Crescent); 5. the Mediterranean; 6. Ethiopia; 7. Southern Mexico and Central America; 8. South America (small regions of Ecuador, Peru, Bolivia, Chile, and Brazil-Paraguay). "Centers of origin of cultivated plants" by OSU OERU is licensed under CC BY 4.0.

Contrary to popular belief, Vavilov's research revealed that crops did not originate in the large river valleys associated with the rise of human civilization. Rather, most crops were born in the kinds of geographically isolated regions (hills, desert-ridden areas, or cold or extremely hot regions) that comprise only 2–3 percent of the world's area. In these challenging localities, the pressure of natural selection on vegetation is robust and variable compared to other areas, and so we find high biodiversity in these areas. The list below identifies the eight centers of origin of crops and associated plant species that Vavilov identified (along with a ninth, discovered after his death).[1]

It is eye-opening to see how the various kinds of produce, grains, fruits, vegetables, and spices available in supermarkets today have originated in such distant places. Since human societies have been continuously in motion, crops have moved with them, away from their centers of origin, and have been subjected to additional artificial and natural selection in their new environments. They continued to evolve and diversify as a result of spontaneous mutations, hybridization, and agricultural practices. Thus most crops also acquired genotypic and phenotypic diversity postdomestication. As a result, for many crops, their primary center of origin and the center of diversification (where many varieties of crops evolved) differ.[2] For example, the center of origin and center of diversification of maize differ significantly. However, compared to the primary centers of origin, the secondary centers occupy a large area and possess less biodiversity of plant species. The secondary centers are relatively rich in domesticated crop varieties (landraces) but lack the immediate wild progenitor and other related wild species.

After Vavilov, many archeological digs ascertained the centers of origin of additional crop species, and a new center of crop origin was identified as well (New Guinea). The fundamental research work conducted by Vavilov and his colleagues still stands; however, now scientists recommend the use of *center of diversity* instead of *center of origin* because only a crop's center of biodiversity can be identified based on data—at best, we can only guess at the center of origin. Currently, those identified by Vavilov are known as "Vavilov's Centers of Biodiversity."

Since, typically, the "centers of origin" of crops are rich in their biodiversity,[3] their exploration helps scientists comprehend the full spectrum of the gene pool available for a given crop, which can then be utilized for breeding experiments. It is important to note that the plant breeders only transfer useful traits from one variety to another by crossing and then selecting the progeny that have desirable combinations of traits. The breeders do not *create* traits. If a trait is absent in cultivated varieties of a crop species and its ancestors, progenitors, and related species, it cannot be introduced by classical breeding. Biodiversity serves as the resource bank from which scientists can borrow useful traits. It also defines the limits of classical breeding. Therefore, biodiversity centers are the insurance policies for the continuation of today's crops. Scattered across these centers are the genes/traits that provide resistance to pests and pathogens or the ability to tolerate environmental stresses—the raw materials for breeding advanced varieties of crops.

Table 2.1: Centers of origins (biodiversity) of crops

| Center | Remarks |
|---|---|
| 1. China | 136 crops were domesticated in this region including rice, sorghum, soybeans, barley, radish, cabbage, mustard, onion, cucumber, pear, apple, apricot, peach, cherry, walnut, litchi, sugarcane, and poppy. Rice was one of the first crop (~ 8,000 years ago) cultivated in the Yangtze River Valley. Pigs, roosters, and dogs were also domesticated here. |
| 2a. Indo-Malay | This region includes parts of India, parts of China and the Malay Archipelago. Here, clove, nutmeg, black pepper, coconut, hemp, banana, grapefruit, reed and velvet beans were domesticated. |
| 2b. Indo Burma | This center includes North-East region of India and present day Myanmar (Burma). Here, ~117 crops including jute, sandalwood, indigo, bamboo, neem, rice, gram, pigeon pea, mung, cowpea, eggplant, cucumber, radish, carrot, mango, orange, lemon, tamarind, coconut, banana, hemp, pepper, cloves, nutmeg, reed, sesame, and cotton were domesticated. |
| 3. Central Asia | This center includes North-Western India (Punjab, Haryana, and Kashmir provinces), Pakistan, Afghanistan, Tajikistan, and Uzbekistan. ~ 43 crops developed in this area, including three varieties of wheat, peas, lentils, horse lentil, gram, mung bean, mustard, linseed, sesame, cotton, hemp, onions, garlic, spinach, carrots, pistachio, almond grapes, pears and apples. |
| 4. Near East<br>(Fertile Crescent) | This center includes present day Turkey, Israel, Syria, Jordan, Lebanon, Iran, Iraq, Turkmenistan and the interiors of Asia Minor. ~ 150 crops including rye, barley, oats, Einkorn wheat, Durum wheat, Persian wheat, Pollard wheat, common Bread Wheat, Oriental wheat, lentils, lupine, peas, gram, pomegranate, mulberry, apple, grapes, pears, cherries, walnut, almonds, pistachios, dates, fennel, cumin, carrots, onions, and garlic were domesticated in this region. ~ 10,000 year old fossils of rye have been found at many archeological sites in this area. Evidence of earliest rye cultivation ~13,000 years ago has been found in Syria and the remains of ~ 9000 year old domesticated sheep, goats and pigs have been found in Turkey. |
| 5. Mediterranean | This center includes regions around the Mediterranean Sea. Here, 84 crops including durum wheat, Emmer wheat, Polish wheat, oats, peas, lupine, clover, black mustard, olives, beets, cabbage, turnip, lettuce, asparagus, rhubarb, mint, hop, sage, celery, etc. were domesticated. |
| 6. Ethiopian Center | This center includes Abyssinia, Eretria, Somaliland, and Ethiopia. 38 important crop plants including Abyssinian and emmer varieties of wheat, millet, sorghum, cowpea, flaxseed, tef, sesame, coffee, okra, indigo, castor, and gum Arabica were domesticated in this region. |
| 7. Southern Mexico and Central America | This center includes Southern Mexico, Guatemala, Honduras and Costa Rica. Here, maize, potato, tomato, pumpkin, capsicum, chili, papaya, guava, cashew, chocolate, cotton, passion flower, tobacco, various beans, sisal, sweet potato, arrowroot etc. were domesticated. in this region, ~7000-year-old remains of maize and |

| Center | Remarks |
|---|---|
| | 10,000-8,000 years old seeds of squash have been found in the archaeological excavation. |
| 8a. Peru, Ecuador, Bolivia Sub center (South America) | In this region, 62 species of crop plants including potatoes, maize, lima beans, tomatoes, pumpkin, capsicum, cotton, guava, passion flower, tobacco etc. were domesticated. |
| 8b. Chile (South America) | Several varieties of potato and strawberry were domesticated in this center. |
| 8c. Brazilian-Paraguay (South America) | Peanuts, pineapples, cashew nuts, Brazil nuts, rubber, etc. developed here. |
| 9. New guinea*<br>(Far East) | Recent research proves that ~ 7000 years ago, agriculture started independently in the mountainous region of New Guinea. In this area, bananas, knives, reeds etc. developed.<br>*This center was identified after Vavilov death. |

## Life and Work of Nikolai Vavilov

Nikolai Vavilov (1887–1943), a Russian scientist of the early twentieth century, was a pioneer in the field of plant biogeography and germplasm conservation. He was among the first few scientists of the early twentieth century who championed Mendelian genetics for crop improvement.

Nikolai Vavilov (see Figure 2.6) was born on November 25, 1887, in Moscow, before the Russian Revolution. He studied agriculture, and after graduating in 1911, he worked with Dmitry Pryanishnikov, a world-renowned soil scientist, for a year while also teaching at Petrovskaya Agricultural Academy. Soon, Vavilov joined a PhD program under the supervision of the Russian professor Robert Eduardovich Regel (of the Bureau of Applied Botany in Leningrad) and famous English biologist William Bateson (the director of the John Innes Horticultural Institution in Norwich, England). In the early years of the twentieth century, Bateson was the champion of Mendelian genetics; he in fact coined the term genetics to describe the study of Mendelian inheritance and the science of variation. Vavilov spent two years in Bateson's laboratory at John Innes, where he acquired necessary knowledge about Mendelian genetics.

In 1914, Vavilov returned to Russia and was appointed as a professor at Moscow University. In 1917, he became the director of the Lenin Academy of Agricultural Sciences in Saratov. He was the first scientist to start work on genetics in the Soviet Union. In this position, he set the primary agenda of the institute: to collect germplasm from all over the world in order to develop advanced crop varieties by employing the principles of Mendelian genetics. For the first decade, the newly formed Soviet government provided Vavilov with plenty of resources and grants for several germplasm collection expeditions.

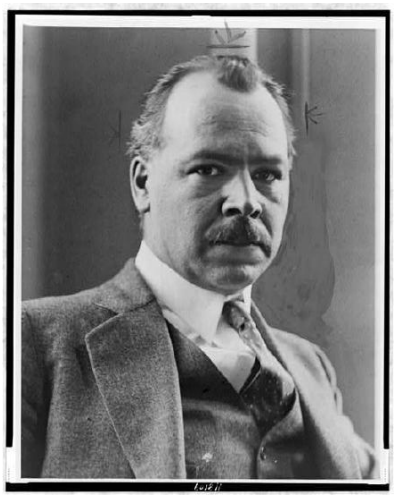


Fig 2.6 Nikolai Vavilov in 1933. "Nikolai Vavilov" by Library of Congress is licensed under no known restrictions on publication.

Vavilov, along with his team, traveled to sixty-four countries on five continents to collect seeds, tubers, and germplasm. In Kazakhstan, they found wild apples, and thus the world came to know the birthplace of this fruit. In Peru, they found countless varieties of potatoes, and in Iran, Syria, and Afghanistan, they found relatively quick-ripening varieties of wheat that possessed natural resistance to pests and parasites. Overall, Vavilov led a hundred explorations, which resulted in the collection of over 300,000 samples, accompanied by detailed descriptions. He had remarkable success in managing his extensive field trips in such diverse nations as Ethiopia, Italy, Kazakhstan, Mexico, Brazil, and the United States. In the early 1900s, traveling was rather difficult and required hopping between various modes of transportation, including extensive journeys on foot and horseback. An equally daunting task was the recruitment of local crews of porters, guides, and collaborators. However, many of Vavilov's personal qualities and his demeanor helped make these missions successful. He was physically fit, mentally sharp, and a polyglot who could converse in eight languages. He was capable of quickly developing friendships and collaborations with strangers, common folk and international scientists alike. On a personal level, Vavilov took care of everyone on his team and the people he interacted with around the world. Among his various field trips, the most historic missions included three visits to North America, Mexico, and South America in 1921, 1930, and 1932; the Mediterranean Sea and Ethiopia expedition in 1926–27; and the trip to Afghanistan in 1924, for which he received a gold medal from the Russian Geographic Society. Later, he also served as the president of that society, from 1931 to 1940. In the first decade of his career, he became the leader of Soviet agricultural policies and headed 111 institutions.

In addition to germplasm collection, Vavilov directed projects at Saratov and other research centers aimed at breeding crop varieties that could tolerate the extremely cold climate of the Soviet Union. These projects were deemed of national importance because a large area of the country suffered agricultural losses due to frost, and the damages to the wheat crop were especially devastating. However, the success of these projects required sustained work on classical breeding and the evaluation of the crossings.

Unfortunately, year after year, in the Soviet Union, grain remained in short supply and hunger was prevalent. To improve agriculture, in 1929, Stalin announced his Great Break from the Past policy, which led to the establishment of collective farms through the merging of individual family farms. The big government-run farms employed monocropping, which led to more loss of harvest. Before government-run collective farming, individual farmers sowed many varieties of seeds. If the crop was ruined in some areas due to the weather, then it would have been saved in other places, and so a good yield could be obtained elsewhere. With monocropping, the impacts of disease and frost were instead widespread. The failure of collective farms, along with rapid industrialization, caused famine. Millions of people died of hunger in the Soviet Union.

Stalin wanted to make the Soviet Union self-sufficient in terms of food production, and the responsibility for improving agricultural yields rested on Vavilov's team. Stalin gave Vavilov three years to develop advanced varieties of grains that could perform in the extremely cold and unpredictable climate of the USSR. At that time, even the best breeder could succeed only after ten to twelve years. Nikolai Vavilov knew that advanced crops could be developed by following the principles of genetics in a very methodical and systematic manner for a decade, but not in a shorter time frame. Thus he could not promise a miracle to Stalin. But he kept working hard and kept up the morale of his colleagues.

Meanwhile, scientist Trofim Lysenko claimed that soaking seeds in cold water for a day or two prior to sowing would result in higher germination rates and could possibly enhance the resilience of a crop in colder climates. Unlike Vavilov, Lysenko was from a poor proletariat background and thus more trustworthy to Soviet policy makers and Stalin, who actively sought to replace bourgeois scientists with party cadres hailing from impoverished families. They deemed Trofim Lysenko a proletarian genius who could provide an alternative to bourgeois science and thought Lysenko's experiments to be consistent with Darwin's theory of evolution.

In his desperation to bring revolutionary changes to agriculture, in 1938, Stalin appointed Lysenko as the president of Lenin Academy, the highest post for an agricultural scientist in the Soviet Union. Vavilov, as an expert geneticist, knew that Lysenko's methods would not work. He firmly opposed Lysenko's claims and, to the best of his ability, provided scientific explanations to Stalin and his cabinet, but they did not trust Vavilov. Vavilov challenged Lysenko to a scientific debate on the merit of his claims, but Lysenko campaigned against Vavilov and the science of genetics with the help of the Communist Party cadres.

Stalin and his cabinet took a highly negative stand toward genetics based on their political ideology in response to the inhumane experiments of eugenics in Germany and the US at the time. Since Vavilov was a world-renowned scientist in genetics, he was declared the leader of this unacceptable science. Thus the end of genetics in the Soviet Union meant the end of Vavilov and his

colleagues. His funding was ceased, and in 1937, Vavilov's foreign travels were banned forever. More than a hundred of Vavilov's fellow scientists were sentenced to death on charges of treason. Stalin also ordered the execution of two of his (Stalin's) closest associates, Nikolai Bukharin and Nikolai Gorbunov, for supporting the science of genetics. Vavilov's position was downgraded to the head of the Institute of Applied Botany and New Crops in Leningrad, where he was to work under Lysenko. Even while working in difficult circumstances and without resources, Vavilov stood firmly by his principles. He continued to write letters to the government for the release of his associates, though his correspondence with foreign scientists was blocked. He wrote his last letter to Professor Harry Harlan in 1937. Harry's son Jack Harlan was interested in doing his PhD under Vavilov's supervision, and he had sent his application to Vavilov. In reply, Vavilov addressed Harry Harlan (not Jack) and described a variety of wheat found in China. Vavilov normally addressed Harry Harlan as "Dear Doctor Harlan." This was the first letter in which Vavilov addressed him as "My Dear Doctor Harlan" and derailed from addressing a question. The senior Harlan asked his son to abandon the idea of research with Vavilov.

On August 6, 1940, Nikolai Vavilov was arrested while on a field trip in Ukraine, though the information of his arrest was not made public for three years. However, since Vavilov was a scientist of international repute and used to correspond with scientists from all over the world, the scientific fraternity became concerned about Vavilov's well-being after his correspondence ceased. So in 1942, the Royal Society of London elected him as a member, sending a letter along with the associated certificates to Vladimir Komarov, president of the Soviet Academy. In order to accept this honor, a signature from Nikolai Vavilov was required (which would have confirmed him being alive). In reply, Komarov had the certificate signed merely "Vavilov"—by Sergei Vavilov, the younger brother of Nikolai and the physicist who headed the Soviet nuclear program. The British embassy wrote back to Komarov stating that the signature of *Nikolai* Vavilov was expected, not that of his brother. However, the Soviet government went silent, and so after this, a rumor was spread in the scientific community that Nikolai Vavilov had been murdered by Stalin.

Actually, Nikolai had been accused of misuse of government grants and treason and was sentenced to death in 1942. But from prison, Vavilov appealed to Marshal Leverentia Beria to reconsider his sentence. Beria was one of Stalin's trusted allies and the head of the Supreme Department of Legal Affairs (NKVD). In addition, Vavilov's old professor Dmitry Pryanishnikov tried his best to reduce Nikolai's punishment. He too had friendly relations with the Beria family: Beria's wife was also a student of Pryanishnikov. Despite the hopelessness, the British Royal Society also continued to press for Vavilov's safety. Whatever the reason, Beria converted Vavilov's death sentence to twenty years of rigorous imprisonment. But on January 26, 1943, Vavilov died of starvation in Saratov prison.

After Stalin's death in 1953, Russian scientists pressured Nikita Khrushchev to reinvestigate Vavilov's case. This time, all the charges against Vavilov were dismissed, and he was awarded a place in the history of the Soviet Union with posthumous honors.

Although many of Vavilov's unpublished research papers and research data were destroyed between 1940 and 1953, some material was saved by his wife, Yelena Berulina. Fatikh Bakhtev, a close associate of Vavilov who was involved in many of his field trips collecting germplasm, also survived the Stalin era. In 1957, Yelena Berulina and Fatikh Bakhtev published Vavilov's remaining material and data. This fundamental research work conducted by Vavilov's team of scientists provided insight and the direction to future research on crop domestication.

The building of the Bureau of Applied Botany is now known as the Nikolai Vavilov Institute of Plant Genetic Resources, and Vavilov is counted among the greatest scientists of the twentieth century. Vavilov's collection, his research papers, and information about his life are available on the Nikolai Vavilov Research Institute website (http://www.vir.nw.ru).

## World's First Seed Bank

In the 1920s, Nikolai Vavilov established the world's first seed bank in the building of the Bureau of Applied Botany in Leningrad, housing major collections of seeds and germplasm there that included 300,000 varieties of seeds and germplasm of 2,500 plant species. His team of scientists was also involved in conducting the detailed characterization of major crop varieties and systematic crossing experiments in experimental centers across the Soviet Union.

Hitler had a keen interest in genetics. During World War II, Germany formed a special commando squad to capture Vavilov's seed bank. On June 22, 1941, Germany invaded the Soviet Union. As the Germans advanced, they captured small seed banks in the western region, but the main seed bank in Leningrad was still out of their reach.

After the incarceration of Vavilov and many of his senior colleagues in 1942, the remaining scientists of the institute voluntarily shared the responsibility of protecting the germplasm collection during World War II. Apart from Hitler, this seed bank was also threatened by the starving people of Leningrad. In those years of war, 700,000 people died of hunger in Leningrad—including many of Vavilov's colleagues who stood protecting the seed bank. One by one, they starved to death while safeguarding the vast storehouse of seeds and tubers. Stalin was not interested in saving the seed bank, and thus the government did not provide any support. As Vavilov wasted away in prison, his associates successfully protected the germplasm collection for 900 days during the siege of Leningrad. This is a unique story of the sacrifice made by scientists to protect a seed collection for future generations.

The Leningrad seed bank also survived by pure chance. Hitler had planned to host a celebration of his victory at the Astoria Hotel on St. Isaac's Square; thus Germans did not bomb that area. The seed bank was right in front of the hotel. Similarly, when the war ended in 1944, the Germans were defeated before reaching Leningrad.

In the years since World War II, more seed banks have been established around the world, many of which also contain large amounts of seeds from Vavilov's collection. Today, this seed bank exists as part of the N. I. Vavilov Scientific Research Institute of Plant Industry in St. Petersburg (see figure 2.7). For the past century—and still today—the seeds and germplasm of various crops from this collection have been used by plant breeders worldwide to produce improved varieties of cereals, vegetables, and fruits. Much of the raw material for making advanced varieties of various crops, fruits, vegetables, and so on remains in Vavilov's seed collection for free.



Fig 2.7 Card catalogue at Vavilov Institute of Plant Industry. Photo of card catalogue by Petr Kosina is licensed under CC BY-NC 2.0.

Even though the world population has increased more than three times over the last century, the world is now producing more food than people need. Vavilov and his fellows—many of whom themselves died of hunger—made tremendous contributions toward achieving global food security by creating a tremendous genetic resource for future crop improvement. Now that many species of plants are extinct in their centers of origin, Vavilov's seed and germplasm collection has become invaluable.

The work of Vavilov and his colleagues helped further our understanding of the importance of biodiversity and the conservation of germplasm in ensuring food security for mankind. Thanks to them, today, there are more than a hundred large and many thousands of small seed and germplasm banks in the world.

## Further Readings


Darwin, C. (1859). *On the origin of species by means of natural selection, or the preservation of favored races in the struggle for life.* John Murray, London.

Harlan, J. R. (1973). On the quality of evidence for origin and dispersal of cultivated plants. *Current Anthropology*, 14(1–2), 51–62.

Harlan, J. R. (1975). Agriculture origins: Centers and noncenters. *Science, 174*, 465–74.

Nabhan, G. P. (2009). *Where our food comes from: Retracing Nickolay Vavilov's quest to end famine. Island Press.*

Pringle, P. (2009). *The murder of Nikolai Vavilov: The story of Stalin's persecution of one of the great scientists of the twentieth century.* JR Books.

Vavilov, N. I. (1931). The problem of the origin of the world's agriculture in the light of the latest investigation. https://www.marxists.org/subject/science/essays/vavilov.htm.

Vavilov, N. I. (1987). *Proiskhozhdenie i geografi i a kul'turnykh rastenii* [The origin and geography of cultivated plants]. Nauka.

1. A clickable world map showing the center of origin of various crops is available at https://www.biodiversidad.gob.mx/v_ingles/genes/centers_origin/centers_plants1.html↵
2. This is also sometimes due to reasons other than human migration. One classical example is pine, which has its center of origin in northwestern China but its center of diversification in Central America (Mexico, Guatemala, and Honduras). At present, 49 out of a total of 111 species of pine are found in Mexico. The difference in the center of origin and center of diversification of pine resulted from a geological event (continental drift) long before the beginning of agriculture, which led to the isolation of various flora and fauna and thus their diversification in a new environment. ↵
3. In simple terms, *biodiversity* refers to all cultivated varieties of crops along with their wild progenitor(s) and evolutionarily related species. ↵

This page titled 3.4: The Origins of Crop Plants is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley via source content that was edited to the style and standards of the LibreTexts platform.

- **1.2: The Origins of Crop Plants** is licensed CC BY-NC 4.0. Original source: https://open.oregonstate.education/cultivatedplants/.

# 4: Asexual reproduction

**Skills to Develop**

- Compare the mechanisms and methods of natural and artificial asexual reproduction
- Describe the advantages and disadvantages of natural and artificial asexual reproduction
- Discuss plant life spans

Many plants are able to propagate themselves using asexual reproduction. This method does not require the investment required to produce a flower, attract pollinators, or find a means of seed dispersal. Asexual reproduction produces plants that are genetically identical to the parent plant because no mixing of male and female gametes takes place. Traditionally, these plants survive well under stable environmental conditions when compared with plants produced from sexual reproduction because they carry genes identical to those of their parents.

Many different types of roots exhibit asexual reproduction Figure **4.1**. The corm is used by gladiolus and garlic. Bulbs, such as a scaly bulb in lilies and a tunicate bulb in daffodils, are other common examples. A potato is a stem tuber, while parsnip propagates from a taproot. Ginger and iris produce rhizomes, while ivy uses an adventitious root (a root arising from a plant part other than the main or primary root), and the strawberry plant has a stolon, which is also called a runner.

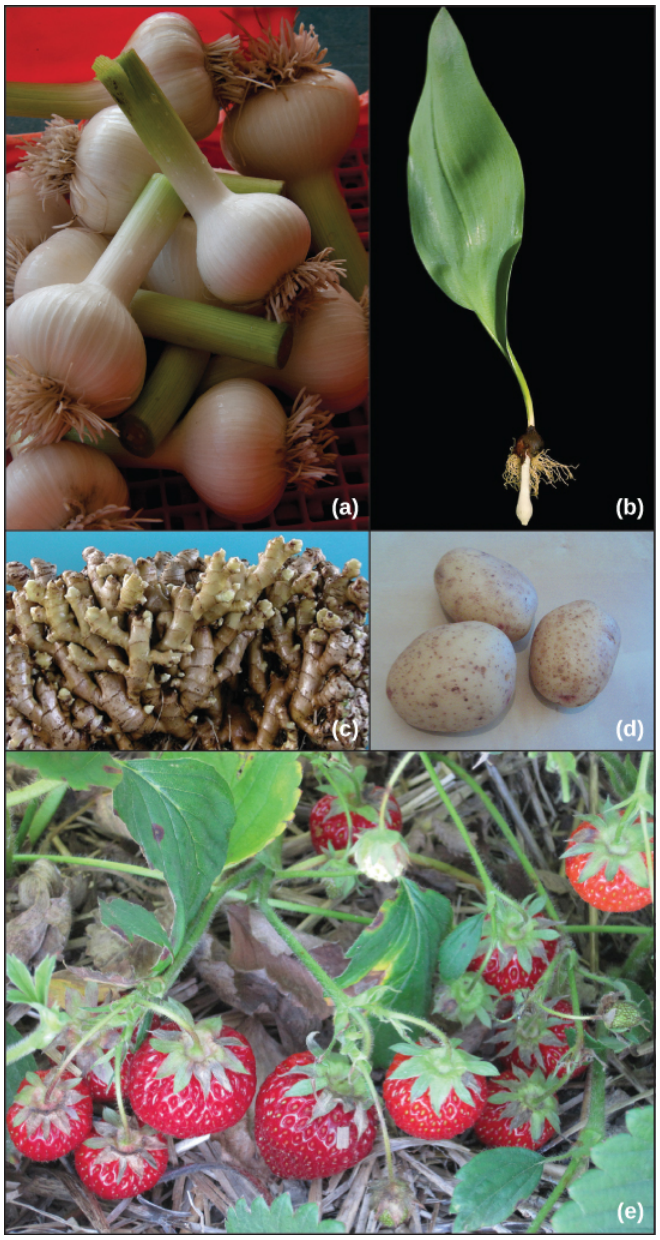



Figure **4.1**: Different types of stems allow for asexual reproduction. (a) The corm of a garlic plant looks similar to (b) a tulip bulb, but the corm is solid tissue, while the bulb consists of layers of modified leaves that surround an underground stem. Both corms and bulbs can self-propagate, giving rise to new plants. (c) Ginger forms masses of stems called rhizomes that can give rise to multiple plants. (d) Potato plants form fleshy stem tubers. Each eye in the stem tuber can give rise to a new plant. (e) Strawberry plants form stolons: stems that grow at the soil surface or just below ground and can give rise to new plants. (credit a: modification of work by Dwight Sipler; credit c: modification of work by Albert Cahalan, USDA ARS; credit d: modification of work by Richard North; credit e: modification of work by Julie Magro)

Some plants can produce seeds without fertilization. Either the ovule or part of the ovary, which is diploid in nature, gives rise to a new seed. This method of reproduction is known as apomixis.

An advantage of asexual reproduction is that the resulting plant will reach maturity faster. Since the new plant is arising from an adult plant or plant parts, it will also be sturdier than a seedling. Asexual reproduction can take place by natural or artificial (assisted by humans) means.

## Natural Methods of Asexual Reproduction

Natural methods of asexual reproduction include strategies that plants have developed to self-propagate. Many plants—like ginger, onion, gladioli, and dahlia—continue to grow from buds that are present on the surface of the stem. In some plants, such as the

sweet potato, adventitious roots or runners can give rise to new plants Figure 4.2. In *Bryophyllum* and kalanchoe, the leaves have small buds on their margins. When these are detached from the plant, they grow into independent plants; or, they may start growing into independent plants if the leaf touches the soil. Some plants can be propagated through cuttings alone.

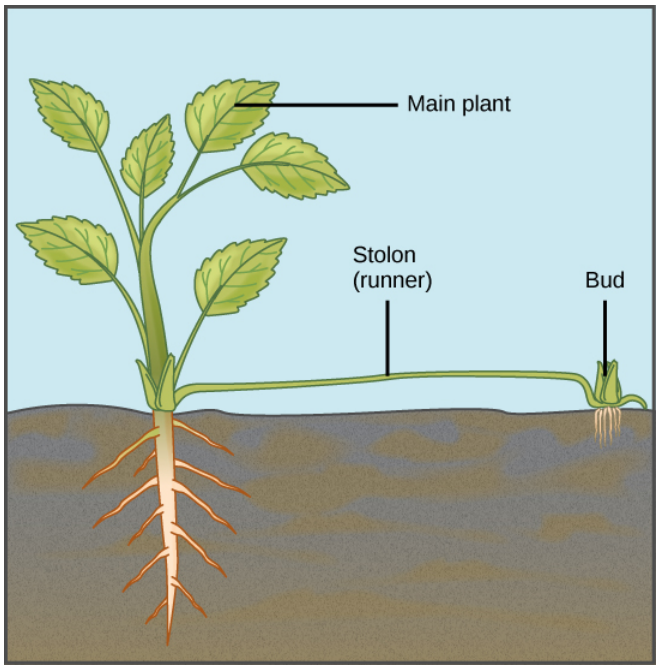



Figure 4.2: A stolon, or runner, is a stem that runs along the ground. At the nodes, it forms adventitious roots and buds that grow into a new plant.

## Artificial Methods of Asexual Reproduction

These methods are frequently employed to give rise to new, and sometimes novel, plants. They include grafting, cutting, layering, and micropropagation.

### Grafting

Grafting has long been used to produce novel varieties of roses, citrus species, and other plants. In grafting, two plant species are used; part of the stem of the desirable plant is grafted onto a rooted plant called the stock. The part that is grafted or attached is called the scion. Both are cut at an oblique angle (any angle other than a right angle), placed in close contact with each other, and are then held together Figure 4.3. Matching up these two surfaces as closely as possible is extremely important because these will be holding the plant together. The vascular systems of the two plants grow and fuse, forming a graft. After a period of time, the scion starts producing shoots, and eventually starts bearing flowers and fruits. Grafting is widely used in viticulture (grape growing) and the citrus industry. Scions capable of producing a particular fruit variety are grated onto root stock with specific resistance to disease.

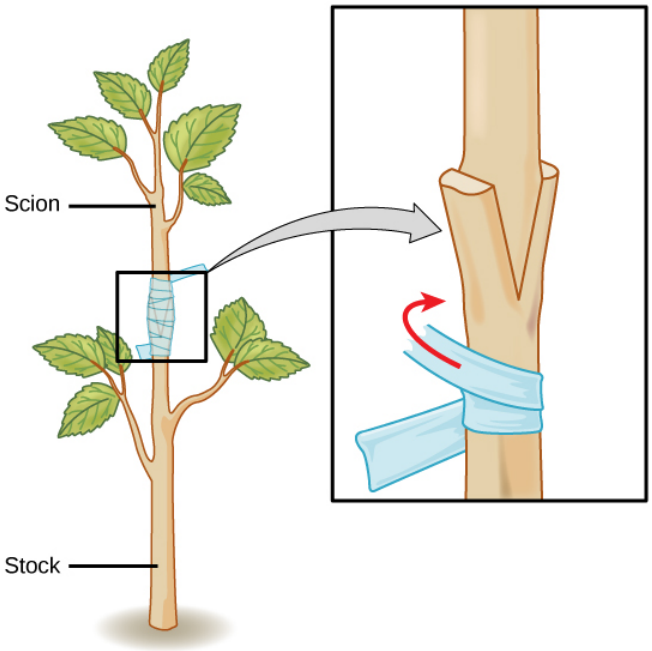



Figure **4.3**: Grafting is an artificial method of asexual reproduction used to produce plants combining favorable stem characteristics with favorable root characteristics. The stem of the plant to be grafted is known as the scion, and the root is called the stock.

### Cutting

Plants such as coleus and money plant are propagated through stem cuttings, where a portion of the stem containing nodes and internodes is placed in moist soil and allowed to root. In some species, stems can start producing a root even when placed only in water. For example, leaves of the African violet will root if kept in water undisturbed for several weeks.

### Layering

Layering is a method in which a stem attached to the plant is bent and covered with soil. Young stems that can be bent easily without any injury are preferred. Jasmine and bougainvillea (paper flower) can be propagated this way Figure **4.4**. In some plants, a modified form of layering known as air layering is employed. A portion of the bark or outermost covering of the stem is removed and covered with moss, which is then taped. Some gardeners also apply rooting hormone. After some time, roots will appear, and this portion of the plant can be removed and transplanted into a separate pot.

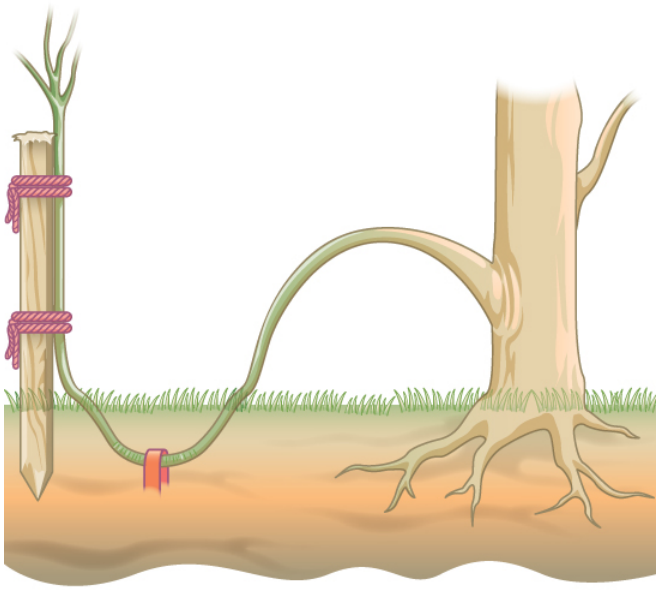


Figure 4.4: In layering, a part of the stem is buried so that it forms a new plant. (credit: modification of work by Pearson Scott Foresman, donated to the Wikimedia Foundation)

## Micropropagation

Micropropagation (also called plant tissue culture) is a method of propagating a large number of plants from a single plant in a short time under laboratory conditions Figure 4.5. This method allows propagation of rare, endangered species that may be difficult to grow under natural conditions, are economically important, or are in demand as disease-free plants.



Figure 4.5: Micropropagation is used to propagate plants in sterile conditions. (credit: Nikhilesh Sanyal)

To start plant tissue culture, a part of the plant such as a stem, leaf, embryo, anther, or seed can be used. The plant material is thoroughly sterilized using a combination of chemical treatments standardized for that species. Under sterile conditions, the plant material is placed on a plant tissue culture medium that contains all the minerals, vitamins, and hormones required by the plant. The plant part often gives rise to an undifferentiated mass known as callus, from which individual plantlets begin to grow after a period of time. These can be separated and are first grown under greenhouse conditions before they are moved to field conditions.

## Plant Life Spans

The length of time from the beginning of development to the death of a plant is called its life span. The life cycle, on the other hand, is the sequence of stages a plant goes through from seed germination to seed production of the mature plant. Some plants, such as annuals, only need a few weeks to grow, produce seeds and die. Other plants, such as the bristlecone pine, live for thousands of years. Some bristlecone pines have a documented age of 4,500 years Figure **4.6**. Even as some parts of a plant, such as regions containing meristematic tissue—the area of active plant growth consisting of undifferentiated cells capable of cell division—continue to grow, some parts undergo programmed cell death (apoptosis). The cork found on stems, and the water-conducting tissue of the xylem, for example, are composed of dead cells.



Figure **4.6**: The bristlecone pine, shown here in the Ancient Bristlecone Pine Forest in the White Mountains of eastern California, has been known to live for 4,500 years. (credit: Rick Goldwaser)

Plant species that complete their lifecycle in one season are known as annuals, an example of which is *Arabidopsis*, or mouse-ear cress. Biennials such as carrots complete their lifecycle in two seasons. In a biennial's first season, the plant has a vegetative phase, whereas in the next season, it completes its reproductive phase. Commercial growers harvest the carrot roots after the first year of growth, and do not allow the plants to flower. Perennials, such as the magnolia, complete their lifecycle in two years or more.

In another classification based on flowering frequency, monocarpic plants flower only once in their lifetime; examples include bamboo and yucca. During the vegetative period of their life cycle (which may be as long as 120 years in some bamboo species), these plants may reproduce asexually and accumulate a great deal of food material that will be required during their once-in-a-lifetime flowering and setting of seed after fertilization. Soon after flowering, these plants die. Polycarpic plants form flowers many times during their lifetime. Fruit trees, such as apple and orange trees, are polycarpic; they flower every year. Other polycarpic species, such as perennials, flower several times during their life span, but not each year. By this means, the plant does not require all its nutrients to be channelled towards flowering each year.

As is the case with all living organisms, genetics and environmental conditions have a role to play in determining how long a plant will live. Susceptibility to disease, changing environmental conditions, drought, cold, and competition for nutrients are some of the factors that determine the survival of a plant. Plants continue to grow, despite the presence of dead tissue such as cork. Individual parts of plants, such as flowers and leaves, have different rates of survival. In many trees, the older leaves turn yellow and eventually fall from the tree. Leaf fall is triggered by factors such as a decrease in photosynthetic efficiency, due to shading by upper leaves, or oxidative damage incurred as a result of photosynthetic reactions. The components of the part to be shed are recycled by the plant for use in other processes, such as development of seed and storage. This process is known as nutrient recycling.

The aging of a plant and all the associated processes is known as senescence, which is marked by several complex biochemical changes. One of the characteristics of senescence is the breakdown of chloroplasts, which is characterized by the yellowing of leaves. The chloroplasts contain components of photosynthetic machinery such as membranes and proteins. Chloroplasts also contain DNA. The proteins, lipids, and nucleic acids are broken down by specific enzymes into smaller molecules and salvaged by the plant to support the growth of other plant tissues.

The complex pathways of nutrient recycling within a plant are not well understood. Hormones are known to play a role in senescence. Applications of cytokinins and ethylene delay or prevent senescence; in contrast, abscissic acid causes premature onset of senescence.

## Summary

Many plants reproduce asexually as well as sexually. In asexual reproduction, part of the parent plant is used to generate a new plant. Grafting, layering, and micropropagation are some methods used for artificial asexual reproduction. The new plant is genetically identical to the parent plant from which the stock has been taken. Asexually reproducing plants thrive well in stable environments.

Plants have different life spans, dependent on species, genotype, and environmental conditions. Parts of the plant, such as regions containing meristematic tissue, continue to grow, while other parts experience programmed cell death. Leaves that are no longer photosynthetically active are shed from the plant as part of senescence, and the nutrients from these leaves are recycled by the plant. Other factors, including the presence of hormones, are known to play a role in delaying senescence.

## Glossary

**apomixis**
: process by which seeds are produced without fertilization of sperm and egg

**cutting**
: method of asexual reproduction where a portion of the stem contains notes and internodes is placed in moist soil and allowed to root

**grafting**
: method of asexual reproduction where the stem from one plant species is spliced to a different plant

**layering**
: method of propagating plants by bending a stem under the soil

**micropropagation**
: propagation of desirable plants from a plant part; carried out in a laboratory

**monocarpic**
: plants that flower once in their lifetime

**polycarpic**
: plants that flower several times in their lifetime

**scion**
: the part of a plant that is grafted onto the root stock of another plant

**senescence**
: process that describes aging in plant tissues

This page titled 4: Asexual reproduction is shared under a CC BY 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **32.3: Asexual Reproduction** by OpenStax is licensed CC BY 4.0.

# 4.1: ASEXUAL REPRODUCTION

## LEARNING OBJECTIVES

By the end of this section, you will be able to do the following:

- Compare the mechanisms and methods of natural and artificial asexual reproduction
- Describe the advantages and disadvantages of natural and artificial asexual reproduction
- Discuss plant life spans

Many plants are able to propagate themselves using asexual reproduction. This method does not require the investment required to produce a flower, attract pollinators, or find a means of seed dispersal. Asexual reproduction produces plants that are genetically identical to the parent plant because no mixing of male and female gametes takes place. Traditionally, these plants survive well under stable environmental conditions when compared with plants produced from sexual reproduction because they carry genes identical to those of their parents.

Many different types of roots exhibit asexual reproduction (Figure 32.24). The corm is used by gladiolus and garlic. Bulbs, such as a scaly bulb in lilies and a tunicate bulb in daffodils, are other common examples. A potato is a stem tuber, while parsnip propagates from a taproot. Ginger and iris produce rhizomes, while ivy uses an adventitious root (a root arising from a plant part other than the main or primary root), and the strawberry plant has a stolon, which is also called a runner.

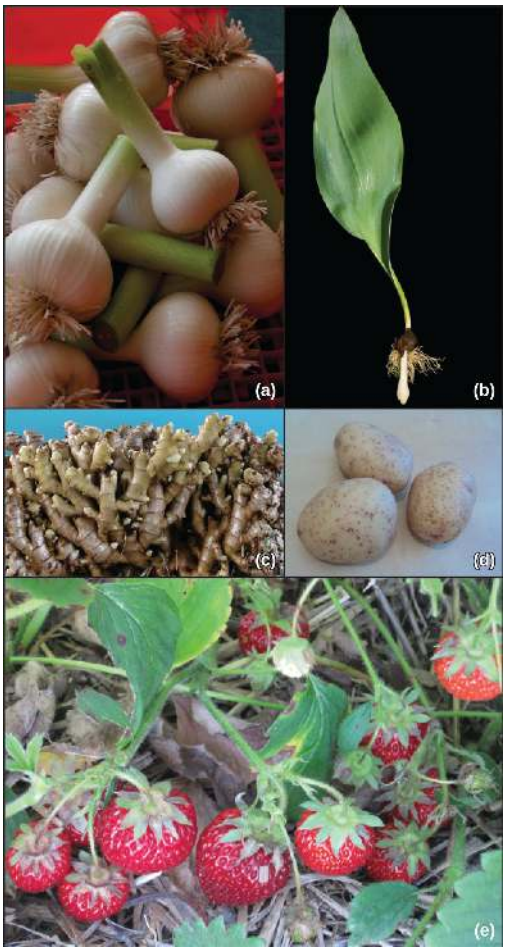



Figure 32.24 Different types of stems allow for asexual reproduction. (a) The corm of a garlic plant looks similar to (b) a tulip bulb, but the corm is solid tissue, while the bulb consists of layers of modified leaves that surround an underground stem. Both corms and bulbs can self-propagate, giving rise to new plants. (c) Ginger forms masses of stems called rhizomes that can give rise to multiple plants. (d) Potato plants form fleshy stem tubers. Each eye in the stem tuber can give rise to a new plant. (e) Strawberry plants form stolons: stems that grow at the soil surface or just below ground and can give rise to new plants. (credit a: modification of work by Dwight Sipler; credit c: modification of work by Albert Cahalan, USDA ARS; credit d: modification of work by Richard North; credit e: modification of work by Julie Magro)

Some plants can produce seeds without fertilization. Either the ovule or part of the ovary, which is diploid in nature, gives rise to a new seed. This method of reproduction is known as apomixis.

An advantage of asexual reproduction is that the resulting plant will reach maturity faster. Since the new plant is arising from an adult plant or plant parts, it will also be sturdier than a seedling. Asexual reproduction can take place by natural or artificial (assisted by humans) means.

## NATURAL METHODS OF ASEXUAL REPRODUCTION

Natural methods of asexual reproduction include strategies that plants have developed to self-propagate. Many plants—like ginger, onion, gladioli, and dahlia—continue to grow from buds that are present on the surface of the stem. In some plants, such as the sweet potato, adventitious roots or runners can give rise to new plants (Figure 32.25). In *Bryophyllum* and kalanchoe, the leaves have small buds on their margins. When these are detached from the plant, they grow into independent plants; or, they may start growing into independent plants if the leaf touches the soil. Some plants can be propagated through cuttings alone.

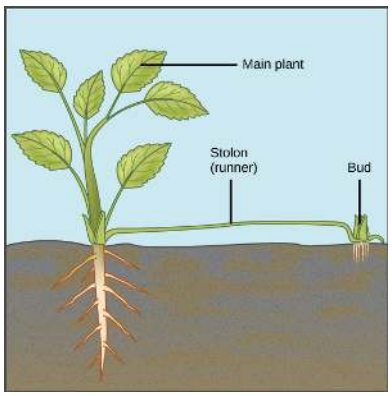



Figure 32.25 A stolon, or runner, is a stem that runs along the ground. At the nodes, it forms adventitious roots and buds that grow into a new plant.

## ARTIFICIAL METHODS OF ASEXUAL REPRODUCTION

These methods are frequently employed to give rise to new, and sometimes novel, plants. They include grafting, cutting, layering, and micropropagation.

### *GRAFTING*

Grafting has long been used to produce novel varieties of roses, citrus species, and other plants. In grafting, two plant species are used; part of the stem of the desirable plant is grafted onto a rooted plant called the stock. The part that is grafted or attached is called the scion. Both are cut at an oblique angle (any angle other than a right angle), placed in close contact with each other, and are then held together (Figure 32.26). Matching up these two surfaces as closely as possible is extremely important because these will be holding the plant together. The vascular systems of the two plants grow and fuse, forming a graft. After a period of time, the scion starts producing shoots, and eventually starts bearing flowers and fruits. Grafting is widely used in viticulture (grape growing) and the citrus industry. Scions capable of producing a particular fruit variety are grafted onto root stock with specific resistance to disease.

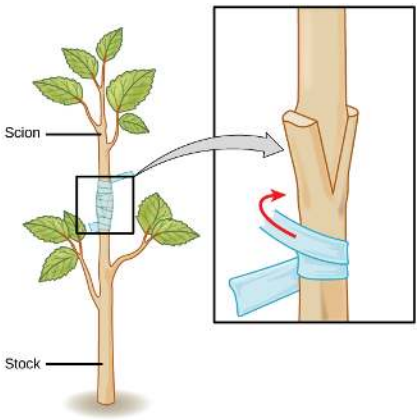



Figure 32.26 Grafting is an artificial method of asexual reproduction used to produce plants combining favorable stem characteristics with favorable root characteristics. The stem of the plant to be grafted is known as the scion, and the root is called the stock.

### CUTTING

Plants such as coleus and money plant are propagated through stem cuttings, where a portion of the stem containing nodes and internodes is placed in moist soil and allowed to root. In some species, stems can start producing a root even when placed only in water. For example, leaves of the African violet will root if kept in water undisturbed for several weeks.

### LAYERING

Layering is a method in which a stem attached to the plant is bent and covered with soil. Young stems that can be bent easily without any injury are preferred. Jasmine and bougainvillea (paper flower) can be propagated this way (Figure 32.27). In some plants, a modified form of layering known as air layering is employed. A portion of the bark or outermost covering of the stem is removed and covered with moss, which is then taped. Some gardeners also apply rooting hormone. After some time, roots will appear, and this portion of the plant can be removed and transplanted into a separate pot.

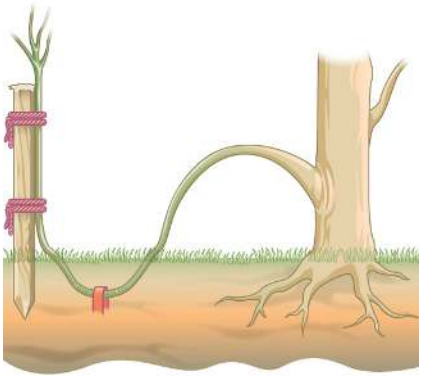


Figure 32.27 In layering, a part of the stem is buried so that it forms a new plant. (credit: modification of work by Pearson Scott Foresman, donated to the Wikimedia Foundation)

### MICROPROPAGATION

Micropropagation (also called plant tissue culture) is a method of propagating a large number of plants from a single plant in a short time under laboratory conditions (Figure 32.28). This method allows propagation of rare, endangered species that may be difficult to grow under natural conditions, are economically important, or are in demand as disease-free plants.



Figure 32.28 Micropropagation is used to propagate plants in sterile conditions. (credit: Nikhilesh Sanyal)

To start plant tissue culture, a part of the plant such as a stem, leaf, embryo, anther, or seed can be used. The plant material is thoroughly sterilized using a combination of chemical treatments standardized for that species. Under sterile conditions, the plant material is placed on a plant tissue culture medium that contains all the minerals, vitamins, and hormones required by the plant. The plant part often gives rise to an undifferentiated mass known as callus, from which individual plantlets begin to grow after a period of time. These can be separated and are first grown under greenhouse conditions before they are moved to field conditions.

## PLANT LIFE SPANS

The length of time from the beginning of development to the death of a plant is called its life span. The life cycle, on the other hand, is the sequence of stages a plant goes through from seed germination to seed production of the mature plant. Some plants, such as annuals, only

need a few weeks to grow, produce seeds and die. Other plants, such as the bristlecone pine, live for thousands of years. Some bristlecone pines have a documented age of 4,500 years (Figure 32.29). Even as some parts of a plant, such as regions containing meristematic tissue—the area of active plant growth consisting of undifferentiated cells capable of cell division—continue to grow, some parts undergo programmed cell death (apoptosis). The cork found on stems, and the water-conducting tissue of the xylem, for example, are composed of dead cells.



Figure 32.29 The bristlecone pine, shown here in the Ancient Bristlecone Pine Forest in the White Mountains of eastern California, has been known to live for 4,500 years. (credit: Rick Goldwaser)

Plant species that complete their lifecycle in one season are known as annuals, an example of which is *Arabidopsis*, or mouse-ear cress. Biennials such as carrots complete their lifecycle in two seasons. In a biennial's first season, the plant has a vegetative phase, whereas in the next season, it completes its reproductive phase. Commercial growers harvest the carrot roots after the first year of growth, and do not allow the plants to flower. Perennials, such as the magnolia, complete their lifecycle in two years or more.

In another classification based on flowering frequency, monocarpic plants flower only once in their lifetime; examples include bamboo and yucca. During the vegetative period of their life cycle (which may be as long as 120 years in some bamboo species), these plants may reproduce asexually and accumulate a great deal of food material that will be required during their once-in-a-lifetime flowering and setting of seed after fertilization. Soon after flowering, these plants die. Polycarpic plants form flowers many times during their lifetime. Fruit trees, such as apple and orange trees, are polycarpic; they flower every year. Other polycarpic species, such as perennials, flower several times during their life span, but not each year. By this means, the plant does not require all its nutrients to be channelled towards flowering each year.

As is the case with all living organisms, genetics and environmental conditions have a role to play in determining how long a plant will live. Susceptibility to disease, changing environmental conditions, drought, cold, and competition for nutrients are some of the factors that determine the survival of a plant. Plants continue to grow, despite the presence of dead tissue such as cork. Individual parts of plants, such as flowers and leaves, have different rates of survival. In many trees, the older leaves turn yellow and eventually fall from the tree. Leaf fall is triggered by factors such as a decrease in photosynthetic efficiency, due to shading by upper leaves, or oxidative damage incurred as a result of photosynthetic reactions. The components of the part to be shed are recycled by the plant for use in other processes, such as development of seed and storage. This process is known as nutrient recycling.

The aging of a plant and all the associated processes is known as senescence, which is marked by several complex biochemical changes. One of the characteristics of senescence is the breakdown of chloroplasts, which is characterized by the yellowing of leaves. The chloroplasts contain components of photosynthetic machinery such as membranes and proteins. Chloroplasts also contain DNA. The proteins, lipids, and nucleic acids are broken down by specific enzymes into smaller molecules and salvaged by the plant to support the growth of other plant tissues.

The complex pathways of nutrient recycling within a plant are not well understood. Hormones are known to play a role in senescence. Applications of cytokinins and ethylene delay or prevent senescence; in contrast, abscissic acid causes premature onset of senescence.

---

This page titled 4.1: Asexual Reproduction is shared under a CC BY 4.0 license and was authored, remixed, and/or curated by Tom Buckley via source content that was edited to the style and standards of the LibreTexts platform.

# SECTION OVERVIEW

## 4.2: Grafting

**Learning objectives**

- Understand why plants are grafted or budded and the techniques used for specific outcomes.
- Describe how a graft union heals.
- Compare and contrast how a plant responds to wounding versus healing a graft union.
- Characterize the differences between bulbs and other storage organs.
- Describe techniques for propagating plants with different clonal strategies from storage organs.

Some plants do not produce sufficient seed or lack competency to form adventitious roots by making cuttings, and we are left with grafting as a method of choice for asexual propagation. Grafting is the cloning of a scion or bud onto a rootstock, but adds the possibility of manipulating shoot properties through the choice of rootstock. Other plants clone themselves naturally and may use special storage organs to help with perenniation. These can develop offsets, pups, and other clonal storage organs. The plant propagator can also induce these tissues to form more propagules. Excellent examples include bulbs, corms, and rhizomes.

### 4.2.1: Grafts and Wounds

### 4.2.2: Unique Storage Organs

### 4.2.3: Terms

This page titled 4.2: Grafting is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley via source content that was edited to the style and standards of the LibreTexts platform.

# 4.2.1: Grafts and Wounds

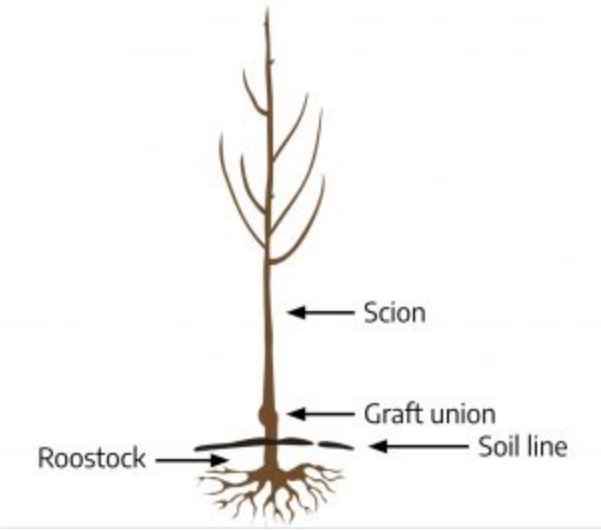
**Learning objectives**

By the end of this lesson you will be able to:

- Explain why plants are grafted or budded and the techniques employed for specific uses.
- Describe how a graft union heals.
- Compare and contrast how a plant responds to wounding versus healing a graft union.

## Grafting

Grafting is the art and science of connecting two pieces of living plant tissue together in such a manner that they will unite and subsequently grow and develop into one composite plant. The union of these two different plant materials via grafting creates a chimera, — two different plant genotypes growing together in the same plant. The roots of an apple tree in a commercial orchard, for instance, likely came from a plant with a genotype that induces dwarfing of the tree. The picture below shows the swelling of the graft union a few inches above the soil surface.




Grafted apple tree. Emily Tepe

Grafting is means of asexual reproduction, which is vegetative propagation. The scions are exact genetic copies, and are sometimes called clones or clonal propagation. Although the graft can combine two different plant types, species, or even genera between the scion and rootstock, the scion material being propagated is an exact genetic copy of the parent plant that donates the vegetative parts used in the graft. Usually the scion or bud and rootstock are the same species, because this favors compatibility and successful grafting. The rootstock can thus be from mixed types, but the scion is from the same plant type for clonal propagation.

The shoot of a grafted apple tree, for example, comes from a plant with great-tasting apples, while the rootstock may not produce great apples. The root and shoot were grafted together and the tree grows as one plant, but with two genotypes: the roots have one genotype — one set of genes — and the shoot another, yet they are all growing as one plant. That's a chimera.

When a horticulturist makes a graft, as in the apple trees above, one genotype of the tree species is typically used for the above-ground part of the plant, called the scion, and another for the below-ground portion, called the rootstock. A grafted plant has a scion growing on a rootstock, and the scion and rootstocks have different genotypes. In many grafting situations the scion and rootstock are of similar diameter, uniting the two genotypes where the graft union is made.

Grafting is a very old horticultural technique; there are historic records of horticulturists grafting olives 2,000 years ago. They may not have known how the cells divided and healed, but they knew how and why to graft.

## Reasons to graft

While grafting is a valuable vegetative propagation technique, not all plants are easily grafted. For those that do respond well to grafting, there are different reasons for employing the technique.

### Create unique, commercially desirable ornamentals



Grafted cactus. hmerinomx. CC BY-NC-SA 2.0

For photosynthesis to take place, a cacti growing as yellow or orange cannot live without the rootstock. Cactus propagation is commonly done by grafting; the cambiums are aligned, and the two are held together, often by rubber bands. This is often referred to as a modified method of cleft grafting.

## Perpetuate genotypes that do not root from cuttings



Japanese maple tree. Brian Holsclaw. CC BY-ND 2.0

Japanese maples, above, have highly desirable leaf and plant forms. Genotypes don't root successfully from cuttings, but can be grafted onto a rootstock grown from seeds of less desirable types. The seedlings provide great rootstocks, and the shoot that has been grafted onto this rootstock expresses the highly desirable plant type. In this process horticulturists usually use T-budding, addressed later in the course.



Colorado blue spruce. Ali Eminov. CC BY-NC 2.0

Conifers: Colorado blue spruce cuttings don't root easily either, but blue spruce scions can be grafted onto Norway spruce rootstocks grown from seed to form a strong plant with the highly desirable blue spruce color and form.

## Change cultivars

Most fruit trees, including apple trees, can survive for many years. In commercial apple orchards, some trees might be of cultivars that are no longer popular. Instead of pulling out these trees and planting young trees of a new cultivar, which difficult and expensive, new scions can be grafted from popular cultivars onto older trees after cutting those trees back to stumps. This is called **cleft grafting** or, more commonly, “topworking.” By putting the new scion on an established rootstock, an orchard will come back into production much sooner than if new, young trees were planted.

## Produce trees with specialized forms



Weeping flowering tree. Janine and Jim Eden. CC BY 2.0

In the case of some flowering trees, like cherry and dogwood, propagators graft a weeping-type scion (one that looks like an umbrella rather than growing upright) onto a 3′ to 5′ standard rootstock. The “weeping” form has branches that arch downward rather than upright. The graft union is far above the ground rather than down by the soil, as is typically the case with grafted maple, spruce, and fruit trees. These weeping-habit trees are more prone to poor wound healing and regrowth of the rootstock at the point of the graft union.

## Repair damaged plants

The idea here is to create a graft that re-unites the cambium in the tree trunk after being severed by a chewing rodent or mechanical damage such as might be dished out by an indiscriminately piloted weed whipper. The graft is inserted into a point below the damage and runs to a point above the damage. This grafting operation is particularly important when the tree is girdled or nearly girdled (the cambium is damaged all the way around the trunk) because otherwise the tree will die. This technique is called bridge grafting and can be quite successful in saving a tree. The picture is from Maple Valley Orchards where they bridged grafted several trees to save them from dying. You can see how the cambium and phloem have both been disrupted.



Bridge graft. John Kring. Used with permission.

### Take advantage of rootstock characteristics

All fruit trees grown in Minnesota are grafted, primarily in order to make the trees shorter. In apples, there are numerous rootstocks to choose from. If you are interested in growing Honeycrisp apples, for instance, you can grow a tree that will be anywhere from 6 feet tall at maturity to 25 feet tall at maturity, depending on which rootstock you choose. Same cultivar, “Honeycrisp,” but a different root system.

In a home landscape, many of us can think of a place for a tree that might grow to 12 feet high, but not many of us have places to grow trees that will get to 25 feet. In commercial orchards, almost all the trees that have been planted in the last 30 years are on dwarfing rootstocks. These trees are far easier to harvest, prune, and maintain.

Some rootstocks offer improvements in disease and insect resistance, or environmental stress such as cold or drought tolerance.

Watch this video to see an example of grafted oak trees and a graft union (1:11)

Watch this video of grafted cherry trees, and learn what to do if you find shoots growing from the rootstock (2:15)

## Grafting challenges

There must be a good reason to graft, and no easier or cheaper way to produce the desired plant. For most plant material that is grafted commercially, such as apple or peach trees, there is no other way to preserve the desired scion cultivar.

Grafting is an art. People who have grafted a lot of plant material understand aspects of their plants that will increase success, such as choosing compatible genotypes and matching stem diameters. Experienced grafters also know the timing of growth stages to increase grafting success. For example, whip and tongue grafts are done when both the rootstock and scion are dormant. In contrast, t-budding is done in August when the bark is “slipping” and the buds themselves are newly formed.

So why don’t grafts heal and produce new plants? Some of the reasons include:

- The type of plant is not conducive to grafting. Dicots and gymnosperms both have cambium encircling the stems, so aligning is possible. Monocot stems have cambium scattered around the stem, so aligning cambia between two plants is basically impossible.
- While the same species are often compatible and a successful graft results, as the relatedness decreases between the scion and rootstock, for example with different genera, grafting success is significantly reduced.
- Time of year and growing season both make a difference in graft success. Grafting success is more likely when the cambium is actively growing, but leaf growth is minimal, because water loss is at a minimum.
- The environment under which the grafts are healing, including temperature and humidity, is important. Light is less important.

- Technique is VERY important. If there is poor cambial contact, the callus bridge does not form, no vascular tissue is produced, and the grafted plant does not grow.

While most reasons to graft relate to desirable characteristics of the scion, there are situations in which the rootstock genotype or characteristics are also important. For example, apple and grape rootstocks are critical for correct plant form and disease resistance. Outside of those and perhaps a few other exceptions, the point of grafting is to propagate the scion.

Again, because of the expertise, time, and expense required for grafting, grafting is used only if it's not possible to propagate a plant by other easier and cheaper methods, like planting seeds or taking cuttings. If a plant roots easily, and doesn't require special rootstock characteristics like dwarfing or resistance to diseases and insects, there is no need for a graft.

## Types of grafting and budding

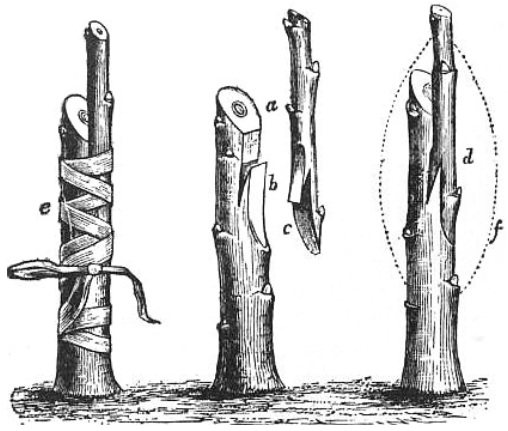
Techniques for grafting have different names and are based on the type of plant material available and its stage of growth. Here are a few of the grafting or budding methods and when they are used.

### Bridge grafting

Bridge grafting is used to repair damage to tree trunks. Smaller-size woody branches are used to reconnect the vascular tissues in the trunk so that water can flow up the trunk and sugars can flow down. These branches are the conduits.

### Whip and tongue grafting

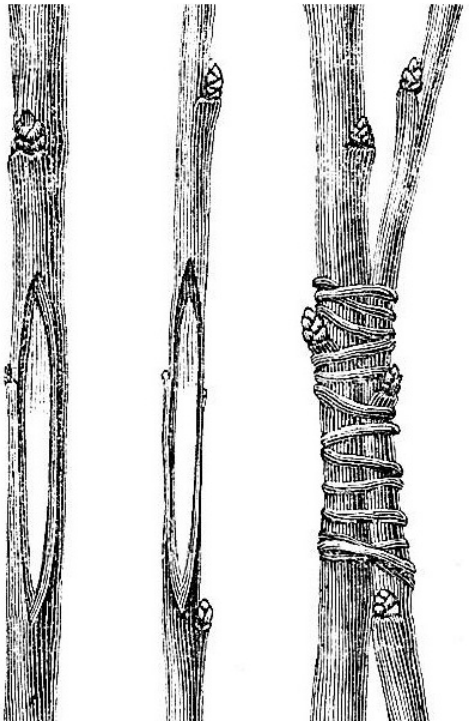
Watch this short video for a demonstration of whip and tongue grafting (3:57)




Whip-and-tongue grafting. Anonymous. Public domain.

The whip and tongue graft is used when the rootstock and scion are the same size. If you have two pieces of woody plant material that are the same size in diameter, it is fairly easy to line up the cambium of each piece and slip the two pieces together. The video linked above shows the steps of this type of grafting, including the cuts that need to be made, how to tie the two pieces together, and the finishing step of reducing water loss at the graft union by applying a wax. For additional pictures and an explanation of the entire method, Texas A&M has an excellent short article with more information.

## Approach graft



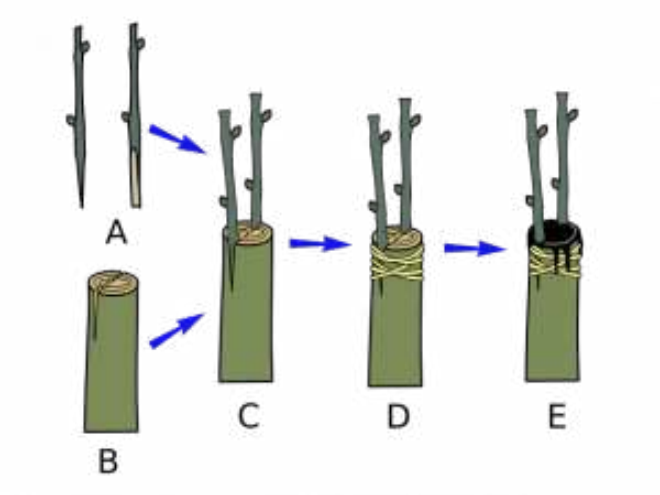
Approach graft. Gmihail. CC BY-SA 3.0 RS

In approach grafting, the scion is often smaller than the rootstock. As the name indicates, the two plant materials are brought close together, the cambiums of both are aligned, and they are allowed to grow together. Often, in plant propagation, we have done approach grafting by using potato as the rootstock and tomato as the scion (remember that these two plants are closely related). Using the same methodology described above, the tomato and potato plants are potted into the same pot, a thin slice is taken off each stem to reveal the cambium, and the stems are tied together. When the graft heals, the plant on the top will produce tomatoes, and the one on the bottom will produce potato tubers that can be harvested at the end of the season. For a bit more reading, and a few more pictures, see the Texas A&M article.

## Cleft grafting

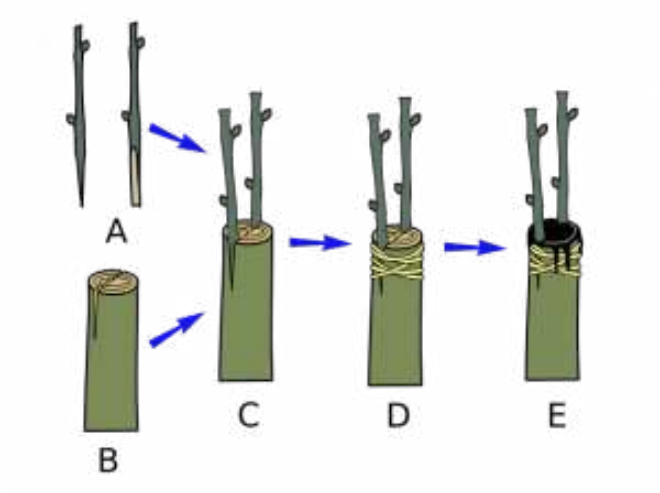


Cleft graft photo. London Permaculture. CC BY-NC-SA 2.0




Cleft graft diagram. Giancarlodessi. CC BY-SA 3.0

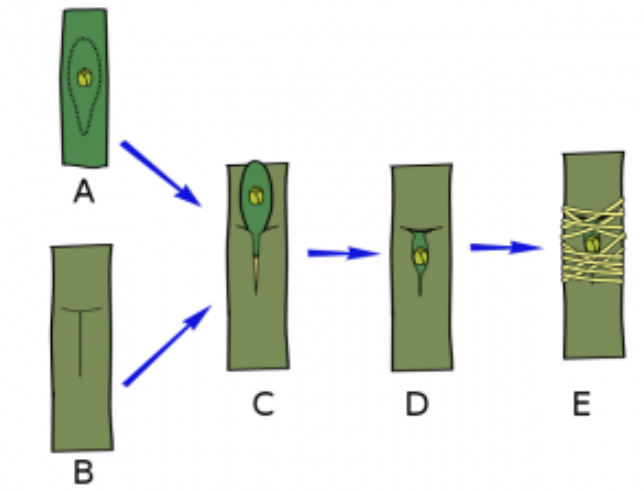
Cleft grafting is a technique which allows the union of a rootstock that is much larger in size than the scion. It is conducted in late winter, when both the rootstock and the scion are dormant. Common applications for cleft grafting include changing the variety of an existing orchard (also called topworking), adding a branch of an untested scion cultivar to an existing tree for observation, or repairing a tree that may have had a branch broken off by storm damage or fruit overloading. The technique can also be used for producing one tree with multiple cultivars on it. Have you ever read about an apple tree with 10 different types of apples on it? This is one method that can be used to make that happen.




Cleft graft diagram. Giancarlodessi. CC BY-SA 3.0

## T-budding

Watch this video to see how t-budding is done (3:57)




T-budding. Giancarlodessi. CC BY-SA 3.0

T-budding is done when bark is “slipping,” meaning the plant is actively growing. The technique is used frequently because it does not require as much plant material of the scion. This is particularly true with new plants, such as a new apple genotype, from which you want to propagate as many trees as possible. T-budding requires only one bud to make one tree, while whip and tongue grafting uses more buds per tree.



Flowering tree with multiple species. Mojo0306. CC BY-SA 4.0

The grafting site at University of Missouri Extension is a great place to visit for more information.

Another interesting video highlights the work of a Syracuse art professor and his development of a single tree with 40 different types of plums, peaches, and apricots on it. What type of grafting did he practice?

## ? Review questions

1. How does grafting result in a chimera?
2. What is the difference between grafting and budding? Why would you use one over the other?
3. What types of plant habit can be produced through grafting onto special rootstock? Why are these habits desirable?
4. Provide three good reasons to use grafting and three reasons not to use it.
5. Provide two reasons why grafts are not successful.

6. What type of grafting is recommended to repair trunk damage?

## Wound healing

Watch this video to see how pruning wounds heal on trees (1:19)

### What happens when you graft?

First, recall what happens when you do a stem cutting:

- The cells along the cut surface are sliced open, die, and become necrotic (dead) tissue.
- The surviving cells one layer in from the cut (parenchyma cells in the cortex) respond to the wound. There are two responses:
  - The cells rapidly exude compounds like suberin (gummy substance) to protect the plant from excess water loss and invasion by diseases and insects.
  - The cells are stimulated to divide and produce a mass of new cells to cover and protect the wound. The mass of new cells is called callus. This response takes quite a bit more time (like years) compared to the time required to exude suberin (hours).

From the plant's point of view, the slicing that happens when making a graft is similar to the slicing that happens when you make an incision in the stem for a cutting. You are still slicing open cells, but because the rootstock and scion are in close contact, the environment around the cut ends is quite different from a cutting in which the wound is exposed to the environment. With a graft you have two stems that are held in close proximity and therefore are more protected than the open wound of a cutting.

- Within a few days, cell division starts and a callus of undifferentiated cells forms. The callus cells will continue to differentiate by developing cells with specialized form and function maturation of new cambium, xylem and phloem.
  - The callus originates from parenchyma cells in the cortex, pith, or vascular bundles. The origin depends on the species.
  - The callus grows from both the scion and rootstock.
- Callus from the rootstock and scion grow together to form a callus bridge.
- The parenchyma cells in the callus bridge that lie between the cambium of the rootstock and the scion differentiate into cambium cells.
  - Additional parenchyma cells on either side of the cambium may differentiate into xylem and phloem until a connection among xylem, cambium, and phloem has been formed across the callus bridge.
- Once these links are formed, the cambium begins to initiate new xylem and phloem.
- Differentiation of the xylem and phloem is faster where cambium layers are closely aligned.

Again, it is important when grafting to get good cambium-to-cambium alignment between scion and rootstock. This will promote development of cambium cells that will differentiate into the callus bridge. The callus bridge is what joins the scion and rootstock. If your technique has poor cambial alignment, or gaps between scion and rootstock at the graft junction, the cell-to-cell linkage will not happen, or it will only happen weakly, and the graft will fail because there is no new xylem and phloem production, and therefore no water or sugar transport pathways. In addition to this being a linkage of plumbing so that water and sugars flow, it is also a structural linkage that gives the plant strength and rigidity across the graft union.



T-budding. Chrizz. CC BY-SA 3.0

## Five requirements for making a successful graft

1. The rootstock and scion must be compatible. Even if they are from the same species, some scions won't graft on to some rootstocks.
2. The cambial layers of the rootstock and scion must be closely aligned and in contact.
3. The graft must be done at the appropriate time of year. The buds, whether grafting whole stems or just the buds themselves, must be dormant. In temperate latitudes, grafting is typically done in winter when rootstock is also dormant, but budding is done late in the growing season when buds are formed, but dormant, and the bark is "slipping" so that a T-shaped cut in the bark can be opened into a pocket for the bud (image on the right).
4. Grafts must be protected from drying.
5. The grafted plant must receive proper post-graft care such as removing sprouts and suckers that emerge from the rootstock and might be mistaken for scion, and pruning or training the scion so that it develops the appropriate plant form.

### ? Review questions

1. Shortly after a plant is wounded, what is the first response of the surviving plant cells adjacent to the wound?
2. When a wound heals, what cells are stimulated to divide?
3. What types of tissues must be formed from the parenchyma callus if the graft is to be successful?
4. How does the stage of plant growth differ for budding compared to whip-and-tongue grafting?

This page titled 4.2.1: Grafts and Wounds is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley via source content that was edited to the style and standards of the LibreTexts platform.

- **10.1: Grafts and Wounds** by Tom Michaels, Matt Clark, Emily Hoover, Laura Irish, Alan Smith, and Emily Tepe is licensed CC BY-NC 4.0. Original source: https://open.lib.umn.edu/horticulture.

# 4.2.2: Unique Storage Organs

**Learning objectives**

By the end of this lesson you will be able to:

- Characterize the differences between bulbs and other storage organs.
- Describe techniques for propagating plants with different clonal strategies from storage organs.
- Demonstrate other ways in which plants colonize through natural clonal propagation.

## Geophytes

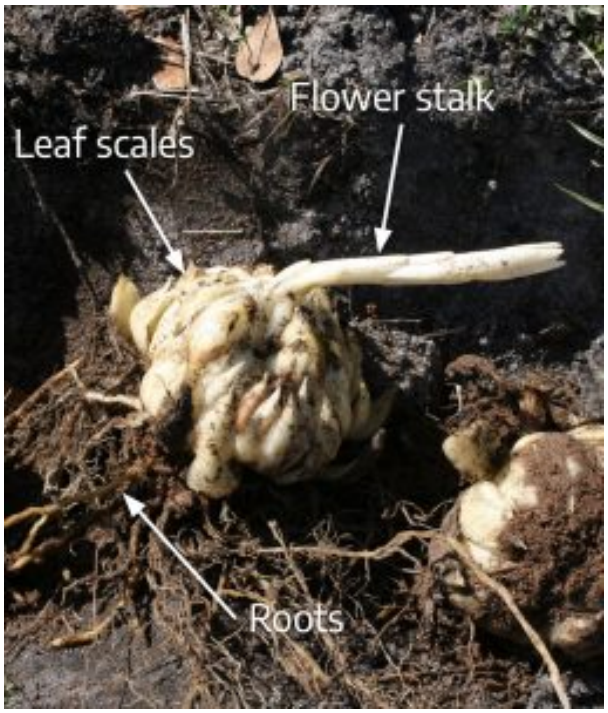
Plants called geophytes have evolved to store carbohydrates and nutrients underground in special structures which allow them to regenerate during the growing season.

Unlike trees and shrubs that keep their dormant buds above ground during the winter, some plants keep their dormant nodes underground. Other plants may grow and store their nodes under water in a pond or stream. Many orchid species live in trees and are called **epiphytes**. The specialized storage organs have several roles which allow them to perenniate and colonize. This short video will introduce some of the special organs that you are likely already familiar with (3:27).

These organs store carbohydrates that can be used for rapid growth when favorable conditions return. They protect the nodes from injury from herbivory and injury (frost and freeze), and are a natural form of cloning by producing new daughter plants away from the mother plant. The plant propagator uses techniques that take advantage of these natural processes and can therefore rapidly increase the number of plants.

### Bulbs

The onion and lily family (Liliaceae; monocots) are typical examples of bulb-producing herbaceous perennials. The bulbs are subterranean, which prevents them from predation and weather conditions. Bulbs consist of a highly condensed stem (with nodes and internodes) and adventitious roots that form along the basal plate. Two main types of bulbs include imbricate and tunicate. Imbricate bulbs, typical of some lily species, consist of scales, as shown in the photo below. Scales are specialized leaves that form radially around the meristem. During the growing season, leaves and a stem emerge from the soil from the center of the plant, where the apical meristem is located. These above-ground leaves are able to photosynthesize. The central meristem converts to a floral meristem where flowers are produced. New lateral bulblets form from the meristem in axils underground, allowing the plant to colonize and perenniate. In some cases, the main bulb may not continue to grow as the meristem has converted to flowering. The new bulbelts can be removed to produce new daughter plants. The plant propagator can remove scales from the bulb and create a new daughter plant from each. This scaling technique is highly effective, though it may take several years for the new plantlet to flower again.



The common Easter lily (Lilium longiflorum) has an imbricate bulb structure. Gardening Solutions. CC BY-NC 2.0

Tunicate bulbs (below), or those with paper coverings, are exemplified by onions, tulips, and garlic. Specialized leaves make up the mass of the storage organ for the plant and form concentric rings around the meristem. Typically, when we cut an onion from the tip through the root end, we can see the layers of leaves (the parts that we eat) and then stem at the bottom. We know it is a stem because there are nodes and internodes. When cooking, we typically discard the stem, basal plate, and adventitious roots. To view the different structures of a bulb during the growing season, look in particular at green onions, scallions, and leeks. Newer leaves form in the interior of the bulb (the apical meristem is in the middle) and the papery skin is the oldest layer formed. From the middle of the bulb, leaves emerge to photosynthesize when the conditions are right, and the floral meristem emerges from the middle. Lateral tunicate bulblets may form inside the main bulb, or along the exterior at the basal plate, especially if there is an injury. Scooping the basal plate is one way to induce bulblet formation. The basal plate can also be scored to have a similar effect.


Lateral tunicate bulblets on Albuca bracteata. CloveMill. CC BY-SA 4.0



Garlic is an example of a tunicate bulb. Scouse Smurf. CC BY-ND 2.0

To propagate a tunicate bulb, it can be sectioned in many pieces by cutting from top to bottom through the basal plate. The sections are allowed to dry for a few days, treated with a fungicide, and then planted in a cold frame or other suitable system to induce bulb formation and plant regeneration. It may take several seasons for the bulbs to develop a suitable size for flowering. When doing any sectioning, scaling, scoring, or scooping the tools should be cleaned between cuts, or at the very least between bulbs, to prevent the spread of disease. Alcohol is suitable for killing microbes and for cleaning the cutting surface and fingers.



Bulbils on Allium vineale v. vineale. Dr Mary Gillham Archive Project. CC BY 2.0

Liliaceae is unique in that bulb-like organs may also form above ground. In this family, bulbils, shown in the photo above, are formed in the leaf axils above ground or in some flowers. Bulbils are clonal (asexual) propagation and not formed through pollination. When the lily's flower stalk dies, it falls to the ground and the bulbils are scattered away from the mother plant. This colonization strategy is highly effective and can be very weedy for the gardener. Mature or "ripe" bulbils can be removed from the plant and potted as soon as they easily detach. Alternatively they can "self sow" and be moved the following spring.

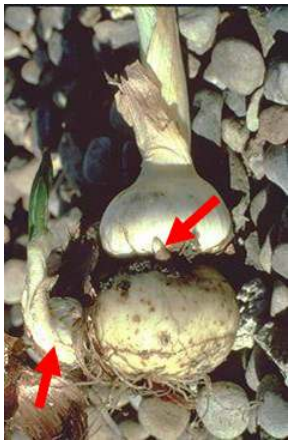
Some bulbs develop contractile roots that pull the bulbs into the soil. As bulbs grow each year, they would logically move closer to the surface, putting them at risk. The contractile roots are able to get the bulb to the proper depth after a growing season.

## Corms



Giant elephant ear corm. Matthew Clark

Like bulbs, corms are underground storage structures that have evolved in some plants. Corms are a storage unit made of compressed stems, unlike the leaves that provide the storage function in bulbs. Because they are stems, corms have nodes, internodes, and meristems just like above-ground stems. The roots of corms are adventitious and develop from a basal plate and nodes. Corms may be short-lived in herbaceous perennials like Gladiolus, where a new corm is replacing itself regularly; in tropical climates, taro (Alocasia) may grow for several years with the same corm structure. The giant elephant ear plant above shows a corm structure. Corms reproduce asexually through cormels, akin to the bulblets produced by bulbs. Watch this short video (0:47) to see a closeup of this corm.



Corm with 2 cormels formed. Matthew Clark

Corms can be induced to produce cormels by removing the apical bud, which removes dominance and stimulates new growth at the nodes. This is generally not necessary, as many corm-producing plants naturally increase with new corms annually. In the photo above, the corm on the left shows the aggressive nature of colonization. The oldest corm at the bottom is being replaced by the actively growing corm attached above it. We can also see two cormels that have formed (red arrows). Eventually the lower, older corm will dessicate and decompose. This is a great example of why some geophytes have contractile roots, for in one growing season the newest cormel could grow above the soil surface.

## Rhizomes

Rhizomes are also underground stems. The Canna lily (below) produces large rhizomes each year. Notice how it looks a lot like ginger “root;” the two plants are in the same family. As stems, they have nodes that produce shoots and they have adventitious roots. Rhizomes typically grow horizontally at or near the soil surface. Some grasses use rhizomes to help with rapid colonization from the crown. Rhizomes can be divided into many pieces as a way to produce multiple clonal propagules.



Canna lily rhizome. Matthew Clark

## Tubers

Potato (*Solanum tuberosum* L.) is the typical example of a common plant that uses a tuber for storage and propagation. Tubers are another example of an underground stem, with nodes and internodes. The nodes may not be obvious when the potato is fresh from the grocery store, but in storage the potato may grow “eyes” which are new shoots that are growing from the once dormant nodes. Most people have seen this in their pantry or on the kitchen counter. To plant potatoes, the farmer cuts up pieces of the last year’s potatoes so there are enough carbohydrates and nodes for a new plant to emerge from the soil.

## Roots

We’ve already learned that roots play an important role in storing nutrients for plants. Biennial plants like carrots, parsnip, and beets have fleshy roots which help them overwinter. These are not easy to propagate into new plants and typically are grown from seed. Horseradish and some poppy plants, however, can easily be propagated from root cuttings. A common example of a tuberous root is the sweet potato (looks like a tuber, functions like a root). The common garden radish (Raphanus sativus) may seem like a root, but close investigation reveals that it is mostly the swollen hypocotyl (image below).



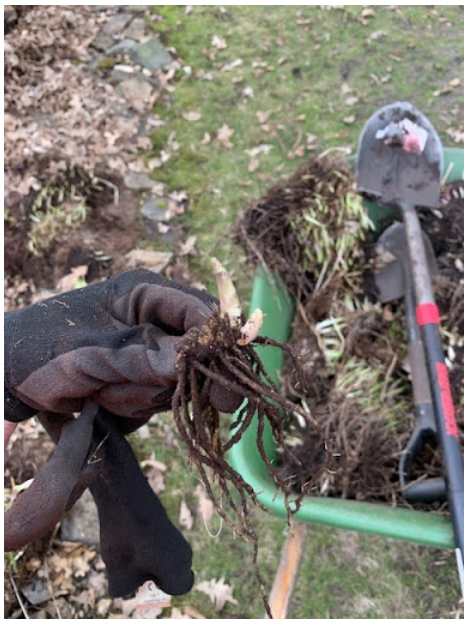
Radish hypocotyls in 4 stages of growth. Matthew Clark

## Other methods of colonization

### Crowns

Hosta plants are common examples of herbaceous perennials that are excellent at colonizing through an underground crown. The underground stem grows radially each year. New shoots can be removed, as shown below. Notice the adventitious roots. Many perennial grasses, asparagus, and other herbaceous perennial plants can be divided into multiple new plants, taking advantage of this colonization strategy. Offshoots (sometimes called pups) can be removed from the mother plant and replanted elsewhere.

Agave plants – which are used to produce tequila – are clonally reproduced this way, as seed production results in new genetic recombinations that are different from the mother plants. Clonal propagation ensures reproducibility for uniform forms and consistent tequila production. Gardeners have been using this method to propagate plants for millenia.



Hosta crowns. Matthew Clark

### Stolons

Perennial grasses and strawberry (Fragaria spp., photo below) are excellent examples of plants that produce runners or stolons that extend the reach of the mother plant for colonization. These above-ground stems (there are underground examples as well) are not for storage, as in the previous examples, but are adaptations to reduce local competition with the mother plant while also spreading her genetic material. A strawberry stolon may root adventitiously at a node and produce a new plant from the bud (remember, buds

are located at nodes and form into new shoots). The stolon likely will continue to grow and do the same at each node thereafter. A gardener can peg the stolon into the soil to help the plant root, then remove it later and replant it.



This ‘Pink Panda’ ornamental strawberry has produced many stolons. Frank Vincentz. CC BY-SA 3.0

## Stem layering

Plants with stems that creep along the soil or whose shoot tips bend and touch the soil take advantage of being able to form adventitious roots for colonization. Some raspberry species (Rubus occidentalis), for example, grow long canes after fruiting, which extend beyond the mother plant and push their shoot tips into the soil. In the photo below, the plant grows roots and reorganizes the developing shoot (see how the leaves face upward). Now anchored into place, a new crown can form, often several feet from the mother plant. Vining and climbing plants often can root at each node, which makes them able to grow along the forest floor until they find a structure to climb. This adaptation can allow clones of the same plant to “move” over time to conditions that are more favorable. This may be more evident in tropical regions, where plants grow faster and local conditions can change suddenly. Vining plants, like grape (Vitis), are often easy to root from hardwood cuttings because they have evolved to root quickly at a node.



Raspberry stem with roots from tip-layering. Matthew Clark

This page titled 4.2.2: Unique Storage Organs is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley via source content that was edited to the style and standards of the LibreTexts platform.

- **10.2: Unique Storage Organs** by Tom Michaels, Matt Clark, Emily Hoover, Laura Irish, Alan Smith, and Emily Tepe is licensed CC BY-NC 4.0. Original source: https://open.lib.umn.edu/horticulture.

# 4.2.3: Terms

| | |
|---|---|
| Approach graft | A type of grafting where two independent plants are grafted together and severed only once the graft has “taken.” |
| Bridge graft | A type of repair graft used when a plant has been girdled; scion pieces are inserted above and below the girdled site and act to repair the disruption of the cambium. |
| Budding | A form of grafting where a single scion is used rather than an entire stem. |
| Callus | Growing mass of unorganized parenchyma cells produced in response to wounding. |
| Callus bridge | Parenchyma cells that lie between the cambium of the rootstock and the scion and differentiate into cambium cells. |
| Chimera | When two different genotypes are growing on a single plant. |
| Cleft grafting | A form of grafting where the rootstock is much larger than the scion; both are dormant. |
| Corm | A condensed stem and storage organ; typically growing underground and covered in scale leaves. |
| Differentiation | Process by which cells or tissues undergo a change toward a more specialized form or function. |
| Genotype | Genetic composition of an organism. |
| Geophyte | New growth begins underground and the function of the underground growth is storage of food, nutrients, and water during adverse environmental conditions. |
| Graft union | Location where the rootstock and scion meet. |
| Grafting | Art and science of connecting two pieces of living plant tissue together in such a manner that they will unite and subsequently grow and develop into one composite plant. |
| Imbricate bulb | Underground storage organ formed primarily of modified leaves (scales) without a papery covering. Individual scales do not encircle the entire bulb. |
| Pruning | Cutting away dead, overgrown, or unwanted branches or stems to improve safety, aesthetics, or productivity. |
| Rhizome | Stem that grows horizontally underground and is a swollen storage organ for the plant. |
| Rootstock | Portion of a graft that contains the root system. |
| Scion | Portion of a graft that contains the shoot system and all above-ground parts. |
| Stolon | Creeping horizontal stem, sometimes called a runner, that roots and forms plantlets at nodes that extend away from the mother plant. |
| Suberin | Impermeable (to water and gases), waxy substance present in the cell walls of corky tissues. |
| T-budding | A type of budding performed using dormant scion buds on actively growing rootstocks; typically done outdoors in late summer. |

| | |
|---|---|
| Topworking | A type of grafting performed on established orchard trees. |
| Tuber | A thickened underground stem used as a storage organ for many plants to allow for perennation. |
| Tunicate bulb | An underground storage organ formed primarily of modified leaves formed in concentric circles around the active meristem. The bulb is covered with a papery covering. |
| Whip and tongue graft | A type of graft where both scion and rootstock are dormant and the same diameter; much more secure than other types of bench grafts. |

This page titled 4.2.3: Terms is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley via source content that was edited to the style and standards of the LibreTexts platform.

- **10.3: Terms** by Tom Michaels, Matt Clark, Emily Hoover, Laura Irish, Alan Smith, and Emily Tepe is licensed CC BY-NC 4.0. Original source: https://open.lib.umn.edu/horticulture.

# CHAPTER OVERVIEW

## 5: Sexual reproduction

5.1: Reproductive Development and Structure
5.2: Pollination and Fertilization

This page titled 5: Sexual reproduction is shared under a not declared license and was authored, remixed, and/or curated by Tom Buckley.

# 5.1: Reproductive Development and Structure

**Skills to Develop**

- Describe the two stages of a plant's lifecycle
- Compare and contrast male and female gametophytes and explain how they form in angiosperms
- Describe the reproductive structures of a plant
- Describe the components of a complete flower
- Describe the development of microsporangium and megasporangium in gymnosperms

Sexual reproduction takes place with slight variations in different groups of plants. Plants have two distinct stages in their lifecycle: the gametophyte stage and the sporophyte stage. The haploid gametophyte produces the male and female gametes by mitosis in distinct multicellular structures. Fusion of the male and females gametes forms the diploid zygote, which develops into the sporophyte. After reaching maturity, the diploid sporophyte produces spores by meiosis, which in turn divide by mitosis to produce the haploid gametophyte. The new gametophyte produces gametes, and the cycle continues. This is the alternation of generations, and is typical of plant reproduction (Figure **5.1.1**).

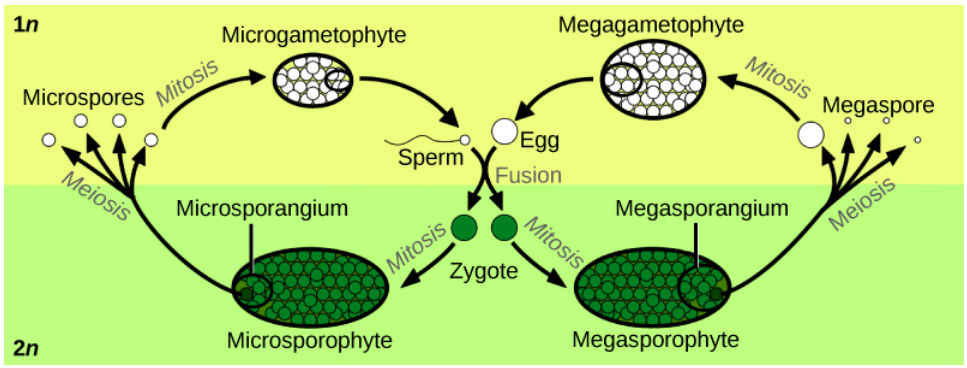



Figure **5.1.1**: The alternation of generations in angiosperms is depicted in this diagram. (credit: modification of work by Peter Coxhead)

The life cycle of higher plants is dominated by the sporophyte stage, with the gametophyte borne on the sporophyte. In ferns, the gametophyte is free-living and very distinct in structure from the diploid sporophyte. In bryophytes, such as mosses, the haploid gametophyte is more developed than the sporophyte.

During the vegetative phase of growth, plants increase in size and produce a shoot system and a root system. As they enter the reproductive phase, some of the branches start to bear flowers. Many flowers are borne singly, whereas some are borne in clusters. The flower is borne on a stalk known as a receptacle. Flower shape, color, and size are unique to each species, and are often used by taxonomists to classify plants.

## Sexual Reproduction in Angiosperms

The lifecycle of angiosperms follows the alternation of generations explained previously. The haploid gametophyte alternates with the diploid sporophyte during the sexual reproduction process of angiosperms. Flowers contain the plant's reproductive structures.

### Flower Structure

A typical flower has four main parts—or whorls—known as the calyx, corolla, androecium, and gynoecium (Figure **5.1.2**). The outermost whorl of the flower has green, leafy structures known as sepals. The sepals, collectively called the calyx, help to protect the unopened bud. The second whorl is comprised of petals—usually, brightly colored—collectively called the corolla. The number of sepals and petals varies depending on whether the plant is a monocot or dicot. In monocots, petals usually number three or multiples of three; in dicots, the number of petals is four or five, or multiples of four and five. Together, the calyx and corolla are known as the perianth. The third whorl contains the male reproductive structures and is known as the androecium. The androecium has stamens with anthers that contain the microsporangia. The innermost group of structures in the flower is the gynoecium, or the

female reproductive component(s). The carpel is the individual unit of the gynoecium and has a stigma, style, and ovary. A flower may have one or multiple carpels.

Art Connection

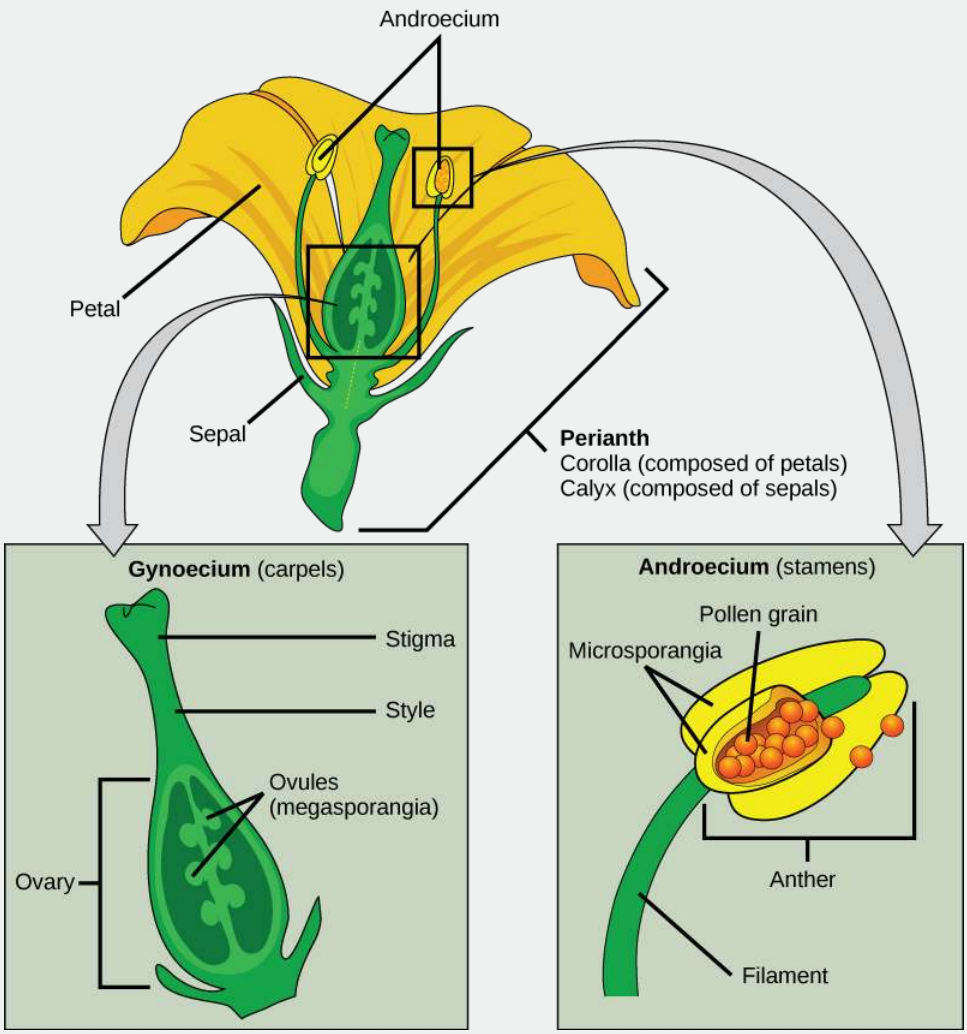



Figure 5.1.2: The four main parts of the flower are the calyx, corolla, androecium, and gynoecium. The androecium is the sum of all the male reproductive organs, and the gynoecium is the sum of the female reproductive organs. (credit: modification of work by Mariana Ruiz Villareal)

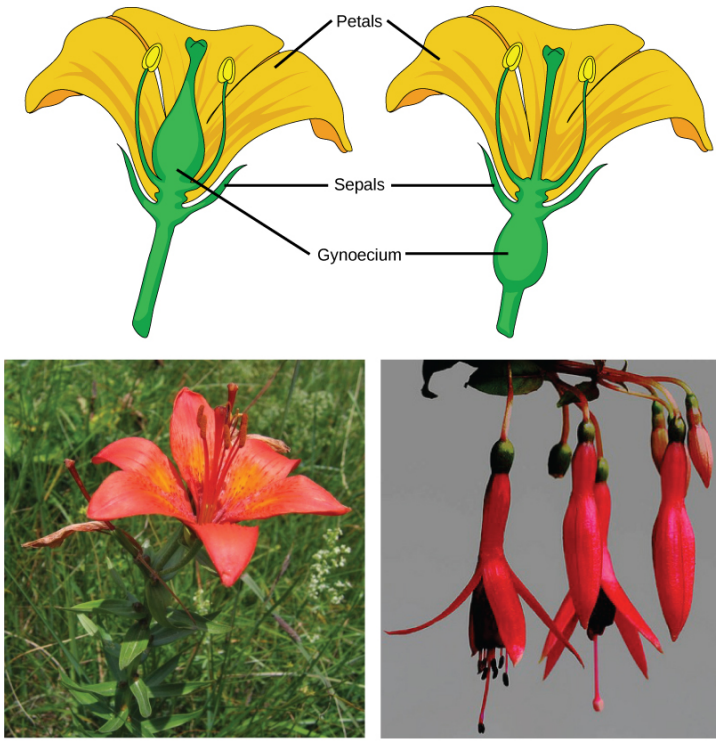
If the anther is missing, what type of reproductive structure will the flower be unable to produce? What term is used to describe an incomplete flower lacking the androecium? What term describes an incomplete flower lacking a gynoecium?

If all four whorls (the calyx, corolla, androecium, and gynoecium) are present, the flower is described as complete. If any of the four parts is missing, the flower is known as incomplete. Flowers that contain both an androecium and a gynoecium are called perfect, androgynous or hermaphrodites. There are two types of incomplete flowers: staminate flowers contain only an androecium, and carpellate flowers have only a gynoecium (Figure 5.1.3).




Figure 5.1.3: The corn plant has both staminate (male) and carpellate (female) flowers. Staminate flowers, which are clustered in the tassel at the tip of the stem, produce pollen grains. Carpellate flower are clustered in the immature ears. Each strand of silk is a stigma. The corn kernels are seeds that develop on the ear after fertilization. Also shown is the lower stem and root.

If both male and female flowers are borne on the same plant, the species is called monoecious (meaning “one home”): examples are corn and pea. Species with male and female flowers borne on separate plants are termed dioecious, or “two homes,” examples of which are *C. papaya* and *Cannabis*. The ovary, which may contain one or multiple ovules, may be placed above other flower parts, which is referred to as superior; or, it may be placed below the other flower parts, referred to as inferior (Figure 5.1.4).




(a) Superior flower (b) Inferior flower

Figure 5.1.4: The (a) lily is a superior flower, which has the ovary above the other flower parts. (b) Fuchsia is an inferior flower, which has the ovary beneath other flower parts. (credit a photo: modification of work by Benjamin Zwittnig; credit b photo: modification of work by "Koshy Koshy"/Flickr)

## Male Gametophyte (The Pollen Grain)

The male gametophyte develops and reaches maturity in an immature anther. In a plant's male reproductive organs, development of pollen takes place in a structure known as the microsporangium (Figure 5.1.5). The microsporangia, which are usually bi-lobed, are pollen sacs in which the microspores develop into pollen grains. These are found in the anther, which is at the end of the stamen—the long filament that supports the anther.

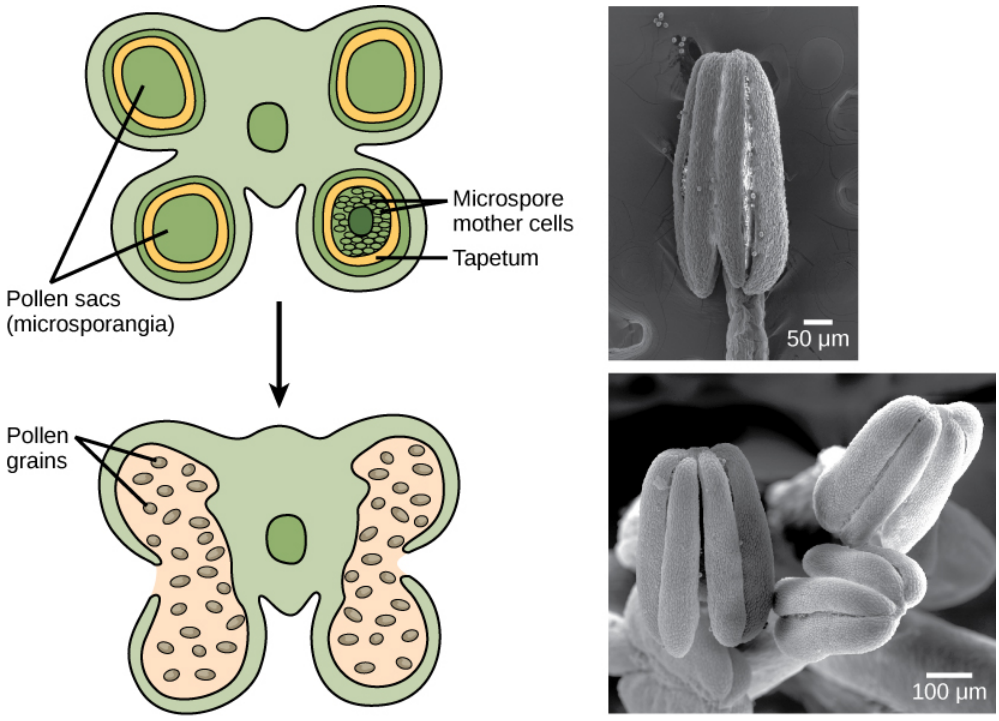



Figure 5.1.5: Shown is (a) a cross section of an anther at two developmental stages. The immature anther (top) contains four microsporangia, or pollen sacs. Each microsporangium contains hundreds of microspore mother cells that will each give rise to four pollen grains. The tapetum supports the development and maturation of the pollen grains. Upon maturation of the pollen (bottom), the pollen sac walls split open and the pollen grains (male gametophytes) are released. (b) In these scanning electron micrographs, pollen sacs are ready to burst, releasing their grains. (credit b: modification of work by Robert R. Wise; scale-bar data from Matt Russell)

Within the microsporangium, the microspore mother cell divides by meiosis to give rise to four microspores, each of which will ultimately form a pollen grain (Figure 5.1.6). An inner layer of cells, known as the tapetum, provides nutrition to the developing microspores and contributes key components to the pollen wall. Mature pollen grains contain two cells: a generative cell and a pollen tube cell. The generative cell is contained within the larger pollen tube cell. Upon germination, the tube cell forms the pollen tube through which the generative cell migrates to enter the ovary. During its transit inside the pollen tube, the generative cell divides to form two male gametes (sperm cells). Upon maturity, the microsporangia burst, releasing the pollen grains from the anther.

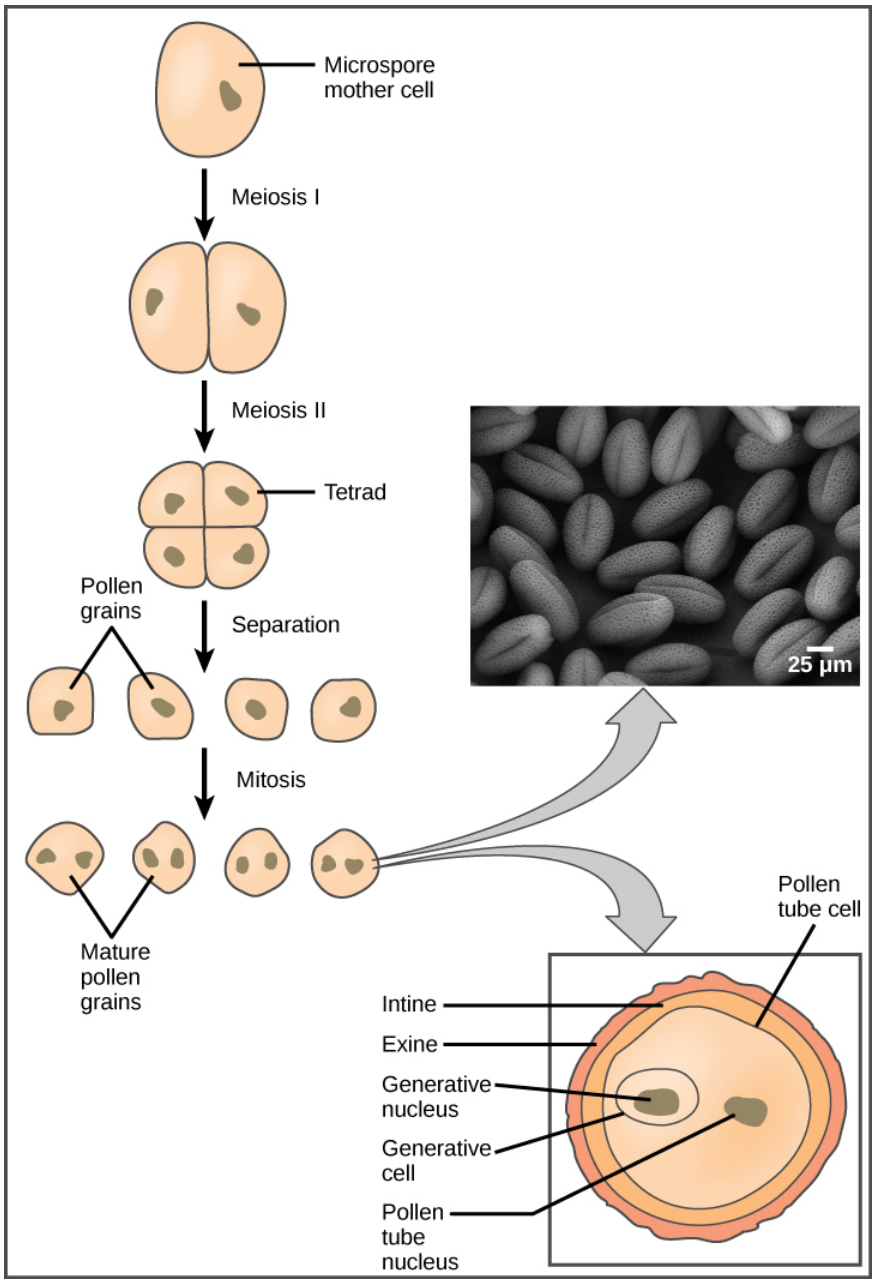



Figure 5.1.6: Pollen develops from the microspore mother cells. The mature pollen grain is composed of two cells: the pollen tube cell and the generative cell, which is inside the tube cell. The pollen grain has two coverings: an inner layer (intine) and an outer layer (exine). The inset scanning electron micrograph shows *Arabidopsis lyrata* pollen grains. (credit "pollen micrograph": modification of work by Robert R. Wise; scale-bar data from Matt Russell)

Each pollen grain has two coverings: the exine (thicker, outer layer) and the intine (Figure 5.1.6). The exine contains sporopollenin, a complex waterproofing substance supplied by the tapetal cells. Sporopollenin allows the pollen to survive under unfavorable conditions and to be carried by wind, water, or biological agents without undergoing damage.

## Female Gametophyte (The Embryo Sac)

While the details may vary between species, the overall development of the female gametophyte has two distinct phases. First, in the process of megasporogenesis, a single cell in the diploid megasporangium—an area of tissue in the ovules—undergoes meiosis to produce four megaspores, only one of which survives. During the second phase, megagametogenesis, the surviving haploid megaspore undergoes mitosis to produce an eight-nucleate, seven-cell female gametophyte, also known as the megagametophyte or embryo sac. Two of the nuclei—the polar nuclei—move to the equator and fuse, forming a single, diploid central cell. This central cell later fuses with a sperm to form the triploid endosperm. Three nuclei position themselves on the end of the embryo sac

opposite the micropyle and develop into the antipodal cells, which later degenerate. The nucleus closest to the micropyle becomes the female gamete, or egg cell, and the two adjacent nuclei develop into synergid cells (Figure 5.1.7). The synergids help guide the pollen tube for successful fertilization, after which they disintegrate. Once fertilization is complete, the resulting diploid zygote develops into the embryo, and the fertilized ovule forms the other tissues of the seed.

A double-layered integument protects the megasporangium and, later, the embryo sac. The integument will develop into the seed coat after fertilization and protect the entire seed. The ovule wall will become part of the fruit. The integuments, while protecting the megasporangium, do not enclose it completely, but leave an opening called the micropyle. The micropyle allows the pollen tube to enter the female gametophyte for fertilization.

Art Connection

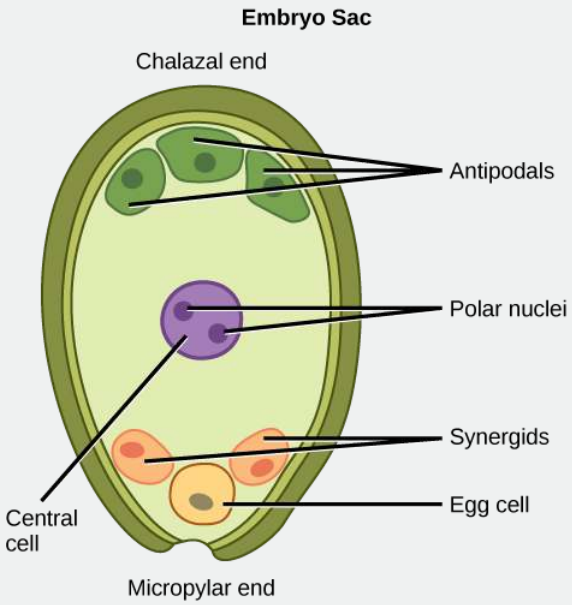



Figure 5.1.7: As shown in this diagram of the embryo sac in angiosperms, the ovule is covered by integuments and has an opening called a micropyle. Inside the embryo sac are three antipodal cells, two synergids, a central cell, and the egg cell.

An embryo sac is missing the synergids. What specific impact would you expect this to have on fertilization?

A. The pollen tube will be unable to form.
B. The pollen tube will form but will not be guided toward the egg.
C. Fertilization will not occur because the synergid is the egg.
D. Fertilization will occur but the embryo will not be able to grow.

## Sexual Reproduction in Gymnosperms

As with angiosperms, the lifecycle of a gymnosperm is also characterized by alternation of generations. In conifers such as pines, the green leafy part of the plant is the sporophyte, and the cones contain the male and female gametophytes (Figure 5.1.8). The female cones are larger than the male cones and are positioned towards the top of the tree; the small, male cones are located in the lower region of the tree. Because the pollen is shed and blown by the wind, this arrangement makes it difficult for a gymnosperm to self-pollinate.

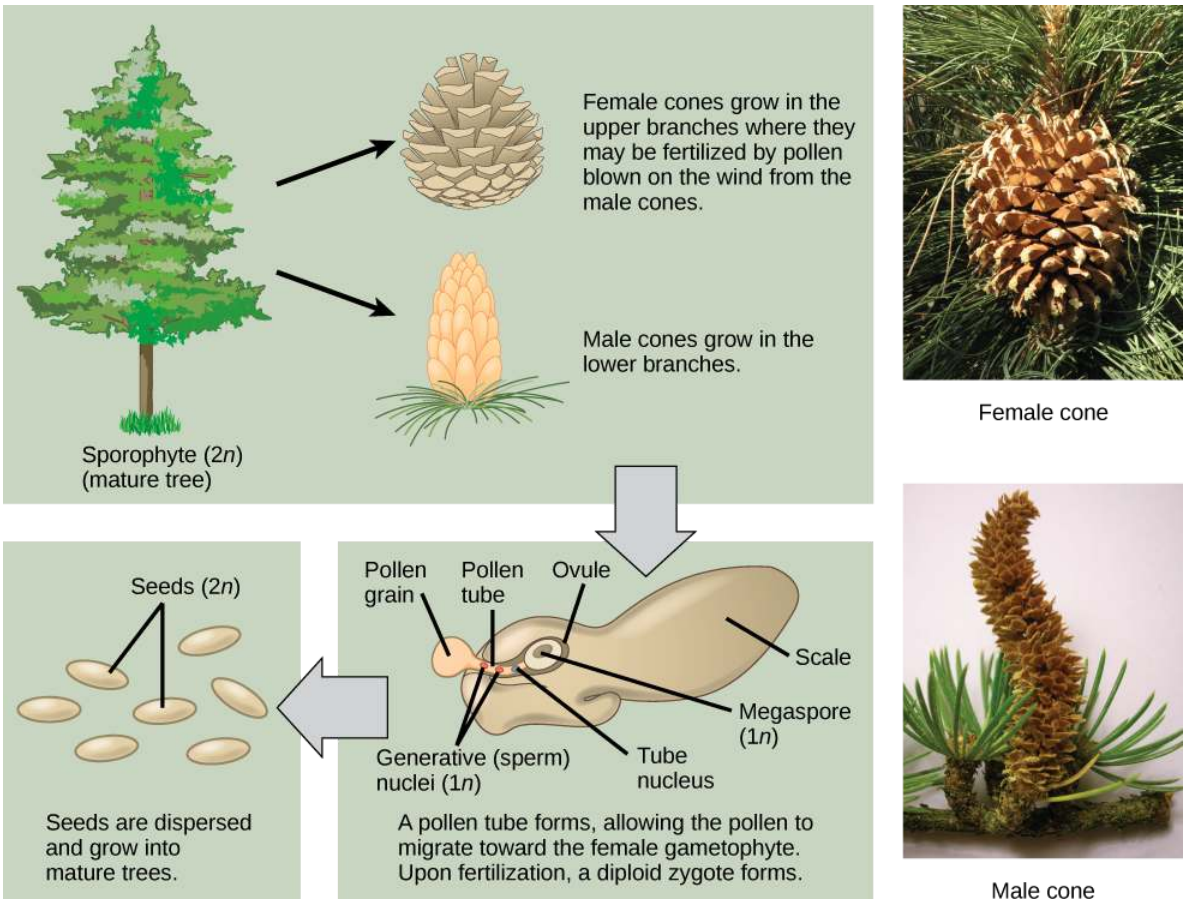



Figure 5.1.8: This image shows the life cycle of a conifer. Pollen from male cones blows up into upper branches, where it fertilizes female cones. Examples are shown of female and male cones. (credit "female": modification of work by "Geographer"/Wikimedia Commons; credit "male": modification of work by Roger Griffith)

## Male Gametophyte

A male cone has a central axis on which bracts, a type of modified leaf, are attached. The bracts are known as microsporophylls (Figure 5.1.9) and are the sites where microspores will develop. The microspores develop inside the microsporangium. Within the microsporangium, cells known as microsporocytes divide by meiosis to produce four haploid microspores. Further mitosis of the microspore produces two nuclei: the generative nucleus, and the tube nucleus. Upon maturity, the male gametophyte (pollen) is released from the male cones and is carried by the wind to land on the female cone.

Link to Learning



Watch this video to see a cedar releasing its pollen in the wind.

## Female Gametophyte

The female cone also has a central axis on which bracts known as megasporophylls (Figure **5.1.9**) are present. In the female cone, megaspore mother cells are present in the megasporangium. The megaspore mother cell divides by meiosis to produce four haploid megaspores. One of the megaspores divides to form the multicellular female gametophyte, while the others divide to form the rest of the structure. The female gametophyte is contained within a structure called the archegonium.

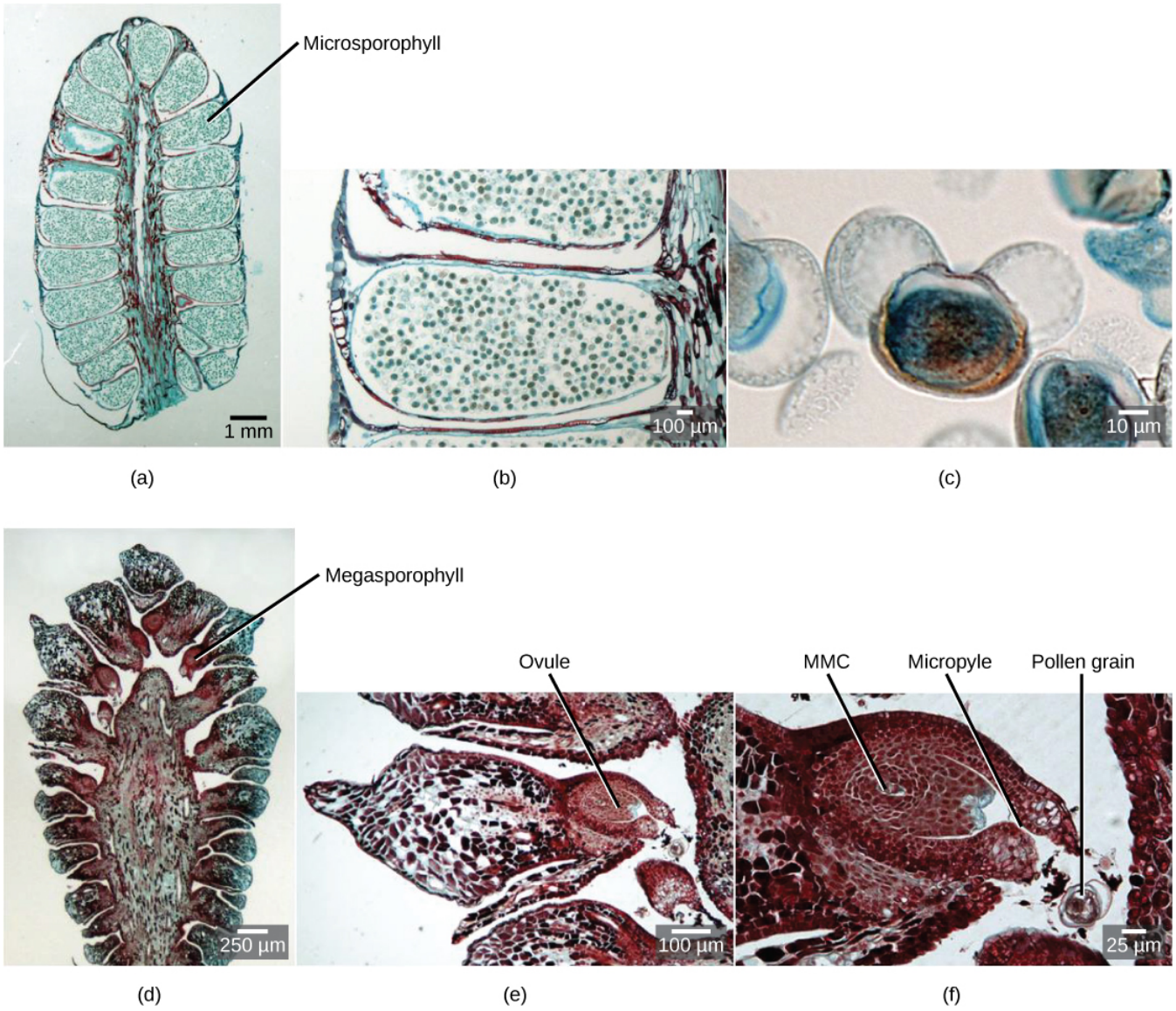



Figure **5.1.9**: These series of micrographs shows male and female gymnosperm gametophytes. (a) This male cone, shown in cross section, has approximately 20 microsporophylls, each of which produces hundreds of male gametophytes (pollen grains). (b) Pollen grains are visible in this single microsporophyll. (c) This micrograph shows an individual pollen grain. (d) This cross section of a female cone shows portions of about 15 megasporophylls. (e) The ovule can be seen in this single megasporophyll. (f) Within this single ovule are the megaspore mother cell (MMC), micropyle, and a pollen grain. (credit: modification of work by Robert R. Wise; scale-bar data from Matt Russell)

## Reproductive Process

Upon landing on the female cone, the tube cell of the pollen forms the pollen tube, through which the generative cell migrates towards the female gametophyte through the micropyle. It takes approximately one year for the pollen tube to grow and migrate towards the female gametophyte. The male gametophyte containing the generative cell splits into two sperm nuclei, one of which

fuses with the egg, while the other degenerates. After fertilization of the egg, the diploid zygote is formed, which divides by mitosis to form the embryo. The scales of the cones are closed during development of the seed. The seed is covered by a seed coat, which is derived from the female sporophyte. Seed development takes another one to two years. Once the seed is ready to be dispersed, the bracts of the female cones open to allow the dispersal of seed; no fruit formation takes place because gymnosperm seeds have no covering.

## Angiosperms versus Gymnosperms

Gymnosperm reproduction differs from that of angiosperms in several ways (Figure **5.1.10**). In angiosperms, the female gametophyte exists in an enclosed structure—the ovule—which is within the ovary; in gymnosperms, the female gametophyte is present on exposed bracts of the female cone. Double fertilization is a key event in the lifecycle of angiosperms, but is completely absent in gymnosperms. The male and female gametophyte structures are present on separate male and female cones in gymnosperms, whereas in angiosperms, they are a part of the flower. Lastly, wind plays an important role in pollination in gymnosperms because pollen is blown by the wind to land on the female cones. Although many angiosperms are also wind-pollinated, animal pollination is more common.



(a) (b)

Figure **5.1.10**: (a) Angiosperms are flowering plants, and include grasses, herbs, shrubs and most deciduous trees, while (b) gymnosperms are conifers. Both produce seeds but have different reproductive strategies. (credit a: modification of work by Wendy Cutler; credit b: modification of work by Lews Castle UHI)

Link to Learning



Visit this website to view an animation of the double fertilization process of angiosperms.

## Summary

The flower contains the reproductive structures of a plant. All complete flowers contain four whorls: the calyx, corolla, androecium, and gynoecium. The stamens are made up of anthers, in which pollen grains are produced, and a supportive strand called the filament. The pollen contains two cells— a generative cell and a tube cell—and is covered by two layers called the intine and the exine. The carpels, which are the female reproductive structures, consist of the stigma, style, and ovary. The female gametophyte is formed from mitotic divisions of the megaspore, forming an eight-nuclei ovule sac. This is covered by a layer known as the integument. The integument contains an opening called the micropyle, through which the pollen tube enters the embryo sac.

The diploid sporophyte of angiosperms and gymnosperms is the conspicuous and long-lived stage of the life cycle. The sporophytes differentiate specialized reproductive structures called sporangia, which are dedicated to the production of spores. The microsporangium contains microspore mother cells, which divide by meiosis to produce haploid microspores. The microspores develop into male gametophytes that are released as pollen. The megasporangium contains megaspore mother cells, which divide by meiosis to produce haploid megaspores. A megaspore develops into a female gametophyte containing a haploid egg. A new diploid sporophyte is formed when a male gamete from a pollen grain enters the ovule sac and fertilizes this egg.

## Art Connections

Figure **5.1.2**: If the anther is missing, what type of reproductive structure will the flower be unable to produce? What term is used to describe a flower that is normally lacking the androecium? What term describes a flower lacking a gynoecium?

**Answer**

Pollen (or sperm); carpellate; staminate.

Figure **5.1.7**: An embryo sac is missing the synergids. What specific impact would you expect this to have on fertilization?

A. The pollen tube will be unable to form.
B. The pollen tube will form but will not be guided toward the egg.
C. Fertilization will not occur because the synergid is the egg.
D. Fertilization will occur but the embryo will not be able to grow.

**Answer**

B: The pollen tube will form but will not be guided toward the egg.

## Glossary

**androecium**
sum of all the stamens in a flower

**antipodals**
the three cells away from the micropyle

**exine**
outermost covering of pollen

**gametophyte**
multicellular stage of the plant that gives rise to haploid gametes or spores

**gynoecium**
the sum of all the carpels in a flower

**intine**
inner lining of the pollen

**megagametogenesis**
second phase of female gametophyte development, during which the surviving haploid megaspore undergoes mitosis to produce an eight-nucleate, seven-cell female gametophyte, also known as the megagametophyte or embryo sac.

**megasporangium**
tissue found in the ovary that gives rise to the female gamete or egg

**megasporogenesis**
first phase of female gametophyte development, during which a single cell in the diploid megasporangium undergoes meiosis to produce four megaspores, only one of which survives

**megasporophyll**
bract (a type of modified leaf) on the central axis of a female gametophyte

**micropyle**
opening on the ovule sac through which the pollen tube can gain entry

**microsporangium**
tissue that gives rise to the microspores or the pollen grain

**microsporophyll**
central axis of a male cone on which bracts (a type of modified leaf) are attached

**perianth**
(also, petal or sepal) part of the flower consisting of the calyx and/or corolla; forms the outer envelope of the flower

**polar nuclei**
found in the ovule sac; fusion with one sperm cell forms the endosperm

**sporophyte**
multicellular diploid stage in plants that is formed after the fusion of male and female gametes

**synergid**
type of cell found in the ovule sac that secretes chemicals to guide the pollen tube towards the egg

This page titled 5.1: Reproductive Development and Structure is shared under a CC BY 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **32.1: Reproductive Development and Structure** by OpenStax is licensed CC BY 4.0.

# 5.2: Pollination and Fertilization

**Skills to Develop**

- Describe what must occur for plant fertilization
- Explain cross-pollination and the ways in which it takes place
- Describe the process that leads to the development of a seed
- Define double fertilization

In angiosperms, pollination is defined as the placement or transfer of pollen from the anther to the stigma of the same flower or another flower. In gymnosperms, pollination involves pollen transfer from the male cone to the female cone. Upon transfer, the pollen germinates to form the pollen tube and the sperm for fertilizing the egg. Pollination has been well studied since the time of Gregor Mendel. Mendel successfully carried out self- as well as cross-pollination in garden peas while studying how characteristics were passed on from one generation to the next. Today's crops are a result of plant breeding, which employs artificial selection to produce the present-day cultivars. A case in point is today's corn, which is a result of years of breeding that started with its ancestor, teosinte. The teosinte that the ancient Mayans originally began cultivating had tiny seeds—vastly different from today's relatively giant ears of corn. Interestingly, though these two plants appear to be entirely different, the genetic difference between them is miniscule.

Pollination takes two forms: self-pollination and cross-pollination. Self-pollination occurs when the pollen from the anther is deposited on the stigma of the same flower, or another flower on the same plant. Cross-pollination is the transfer of pollen from the anther of one flower to the stigma of another flower on a different individual of the same species. Self-pollination occurs in flowers where the stamen and carpel mature at the same time, and are positioned so that the pollen can land on the flower's stigma. This method of pollination does not require an investment from the plant to provide nectar and pollen as food for pollinators.

**Link to Learning**

Explore this interactive website to review self-pollination and cross-pollination: http://passel.unl.edu/pages/animatio...erbreeding.swf

Living species are designed to ensure survival of their progeny; those that fail become extinct. Genetic diversity is therefore required so that in changing environmental or stress conditions, some of the progeny can survive. Self-pollination leads to the production of plants with less genetic diversity, since genetic material from the same plant is used to form gametes, and eventually, the zygote. In contrast, cross-pollination—or out-crossing—leads to greater genetic diversity because the microgametophyte and megagametophyte are derived from different plants.

Because cross-pollination allows for more genetic diversity, plants have developed many ways to avoid self-pollination. In some species, the pollen and the ovary mature at different times. These flowers make self-pollination nearly impossible. By the time pollen matures and has been shed, the stigma of this flower is mature and can only be pollinated by pollen from another flower. Some flowers have developed physical features that prevent self-pollination. The primrose is one such flower. Primroses have evolved two flower types with differences in anther and stigma length: the pin-eyed flower has anthers positioned at the pollen tube's halfway point, and the thrum-eyed flower's stigma is likewise located at the halfway point. Insects easily cross-pollinate while seeking the nectar at the bottom of the pollen tube. This phenomenon is also known as heterostyly. Many plants, such as cucumber, have male and female flowers located on different parts of the plant, thus making self-pollination difficult. In yet other species, the male and female flowers are borne on different plants (dioecious). All of these are barriers to self-pollination; therefore, the plants depend on pollinators to transfer pollen. The majority of pollinators are biotic agents such as insects (like bees, flies, and butterflies), bats, birds, and other animals. Other plant species are pollinated by abiotic agents, such as wind and water.

**Everyday Connection: Incompatibility Genes in Flowers**

In recent decades, *incompatibility genes*—which prevent pollen from germinating or growing into the stigma of a flower—have been discovered in many angiosperm species. If plants do not have compatible genes, the pollen tube stops growing. Self-incompatibility is controlled by the S (sterility) locus. Pollen tubes have to grow through the tissue of the stigma and style

before they can enter the ovule. The carpel is selective in the type of pollen it allows to grow inside. The interaction is primarily between the pollen and the stigma epidermal cells. In some plants, like cabbage, the pollen is rejected at the surface of the stigma, and the unwanted pollen does not germinate. In other plants, pollen tube germination is arrested after growing one-third the length of the style, leading to pollen tube death. Pollen tube death is due either to apoptosis (programmed cell death) or to degradation of pollen tube RNA. The degradation results from the activity of a ribonuclease encoded by the S locus. The ribonuclease is secreted from the cells of the style in the extracellular matrix, which lies alongside the growing pollen tube.

In summary, self-incompatibility is a mechanism that prevents self-fertilization in many flowering plant species. The working of this self-incompatibility mechanism has important consequences for plant breeders because it inhibits the production of inbred and hybrid plants.

## Pollination by Insects

Bees are perhaps the most important pollinator of many garden plants and most commercial fruit trees (Figure **5.2.1**). The most common species of bees are bumblebees and honeybees. Since bees cannot see the color red, bee-pollinated flowers usually have shades of blue, yellow, or other colors. Bees collect energy-rich pollen or nectar for their survival and energy needs. They visit flowers that are open during the day, are brightly colored, have a strong aroma or scent, and have a tubular shape, typically with the presence of a nectar guide. A nectar guide includes regions on the flower petals that are visible only to bees, and not to humans; it helps to guide bees to the center of the flower, thus making the pollination process more efficient. The pollen sticks to the bees' fuzzy hair, and when the bee visits another flower, some of the pollen is transferred to the second flower. Recently, there have been many reports about the declining population of honeybees. Many flowers will remain unpollinated and not bear seed if honeybees disappear. The impact on commercial fruit growers could be devastating.



Figure **5.2.1**: Insects, such as bees, are important agents of pollination. (credit: modification of work by Jon Sullivan)

Many flies are attracted to flowers that have a decaying smell or an odor of rotting flesh. These flowers, which produce nectar, usually have dull colors, such as brown or purple. They are found on the corpse flower or voodoo lily (*Amorphophallus*), dragon arum (*Dracunculus*), and carrion flower (*Stapleia*, *Rafflesia*). The nectar provides energy, whereas the pollen provides protein. Wasps are also important insect pollinators, and pollinate many species of figs.

Butterflies, such as the monarch, pollinate many garden flowers and wildflowers, which usually occur in clusters. These flowers are brightly colored, have a strong fragrance, are open during the day, and have nectar guides to make access to nectar easier. The pollen is picked up and carried on the butterfly's limbs. Moths, on the other hand, pollinate flowers during the late afternoon and night. The flowers pollinated by moths are pale or white and are flat, enabling the moths to land. One well-studied example of a moth-pollinated plant is the yucca plant, which is pollinated by the yucca moth. The shape of the flower and moth have adapted in such a way as to allow successful pollination. The moth deposits pollen on the sticky stigma for fertilization to occur later. The female moth also deposits eggs into the ovary. As the eggs develop into larvae, they obtain food from the flower and developing

seeds. Thus, both the insect and flower benefit from each other in this symbiotic relationship. The corn earworm moth and Gaura plant have a similar relationship (Figure **5.2.2**).



Figure **5.2.2**: A corn earworm sips nectar from a night-blooming Gaura plant. (credit: Juan Lopez, USDA ARS)

## Pollination by Bats

In the tropics and deserts, bats are often the pollinators of nocturnal flowers such as agave, guava, and morning glory. The flowers are usually large and white or pale-colored; thus, they can be distinguished from the dark surroundings at night. The flowers have a strong, fruity, or musky fragrance and produce large amounts of nectar. They are naturally large and wide-mouthed to accommodate the head of the bat. As the bats seek the nectar, their faces and heads become covered with pollen, which is then transferred to the next flower.

## Pollination by Birds

Many species of small birds, such as the hummingbird (Figure **5.2.3**) and sun birds, are pollinators for plants such as orchids and other wildflowers. Flowers visited by birds are usually sturdy and are oriented in such a way as to allow the birds to stay near the flower without getting their wings entangled in the nearby flowers. The flower typically has a curved, tubular shape, which allows access for the bird's beak. Brightly colored, odorless flowers that are open during the day are pollinated by birds. As a bird seeks energy-rich nectar, pollen is deposited on the bird's head and neck and is then transferred to the next flower it visits. Botanists have been known to determine the range of extinct plants by collecting and identifying pollen from 200-year-old bird specimens from the same site.



Figure **5.2.3**: Hummingbirds have adaptations that allow them to reach the nectar of certain tubular flowers. (credit: Lori Branham)

## Pollination by Wind

Most species of conifers, and many angiosperms, such as grasses, maples and oaks, are pollinated by wind. Pine cones are brown and unscented, while the flowers of wind-pollinated angiosperm species are usually green, small, may have small or no petals, and produce large amounts of pollen. Unlike the typical insect-pollinated flowers, flowers adapted to pollination by wind do not produce nectar or scent. In wind-pollinated species, the microsporangia hang out of the flower, and, as the wind blows, the lightweight pollen is carried with it (Figure **5.2.4**). The flowers usually emerge early in the spring, before the leaves, so that the leaves do not block the movement of the wind. The pollen is deposited on the exposed feathery stigma of the flower (Figure **5.2.5**).



Figure **5.2.4**: A person knocks pollen from a pine tree.




Figure **5.2.5**: These male (a) and female (b) catkins are from the goat willow tree (*Salix caprea*). Note how both structures are light and feathery to better disperse and catch the wind-blown pollen.

## Pollination by Water

Some weeds, such as Australian sea grass and pond weeds, are pollinated by water. The pollen floats on water, and when it comes into contact with the flower, it is deposited inside the flower.

### Evolution Connection: Pollination by Deception

Orchids are highly valued flowers, with many rare varieties (Figure **5.2.6**). They grow in a range of specific habitats, mainly in the tropics of Asia, South America, and Central America. At least 25,000 species of orchids have been identified.



Figure **5.2.6**: Certain orchids use food deception or sexual deception to attract pollinators. Shown here is a bee orchid (*Ophrys apifera*). (credit: David Evans)

Flowers often attract pollinators with food rewards, in the form of nectar. However, some species of orchid are an exception to this standard: they have evolved different ways to attract the desired pollinators. They use a method known as food deception, in which bright colors and perfumes are offered, but no food. *Anacamptis morio*, commonly known as the green-winged orchid, bears bright purple flowers and emits a strong scent. The bumblebee, its main pollinator, is attracted to the flower because of the strong scent—which usually indicates food for a bee—and in the process, picks up the pollen to be transported to another flower.

Other orchids use sexual deception. *Chiloglottis trapeziformis* emits a compound that smells the same as the pheromone emitted by a female wasp to attract male wasps. The male wasp is attracted to the scent, lands on the orchid flower, and in the process, transfers pollen. Some orchids, like the Australian hammer orchid, use scent as well as visual trickery in yet another sexual deception strategy to attract wasps. The flower of this orchid mimics the appearance of a female wasp and emits a pheromone. The male wasp tries to mate with what appears to be a female wasp, and in the process, picks up pollen, which it then transfers to the next counterfeit mate.

## Double Fertilization

After pollen is deposited on the stigma, it must germinate and grow through the style to reach the ovule. The microspores, or the pollen, contain two cells: the pollen tube cell and the generative cell. The pollen tube cell grows into a pollen tube through which the generative cell travels. The germination of the pollen tube requires water, oxygen, and certain chemical signals. As it travels through the style to reach the embryo sac, the pollen tube's growth is supported by the tissues of the style. In the meantime, if the generative cell has not already split into two cells, it now divides to form two sperm cells. The pollen tube is guided by the chemicals secreted by the synergids present in the embryo sac, and it enters the ovule sac through the micropyle. Of the two sperm cells, one sperm fertilizes the egg cell, forming a diploid zygote; the other sperm fuses with the two polar nuclei, forming a triploid cell that develops into the endosperm. Together, these two fertilization events in angiosperms are known as double fertilization

(Figure 5.2.7). After fertilization is complete, no other sperm can enter. The fertilized ovule forms the seed, whereas the tissues of the ovary become the fruit, usually enveloping the seed.

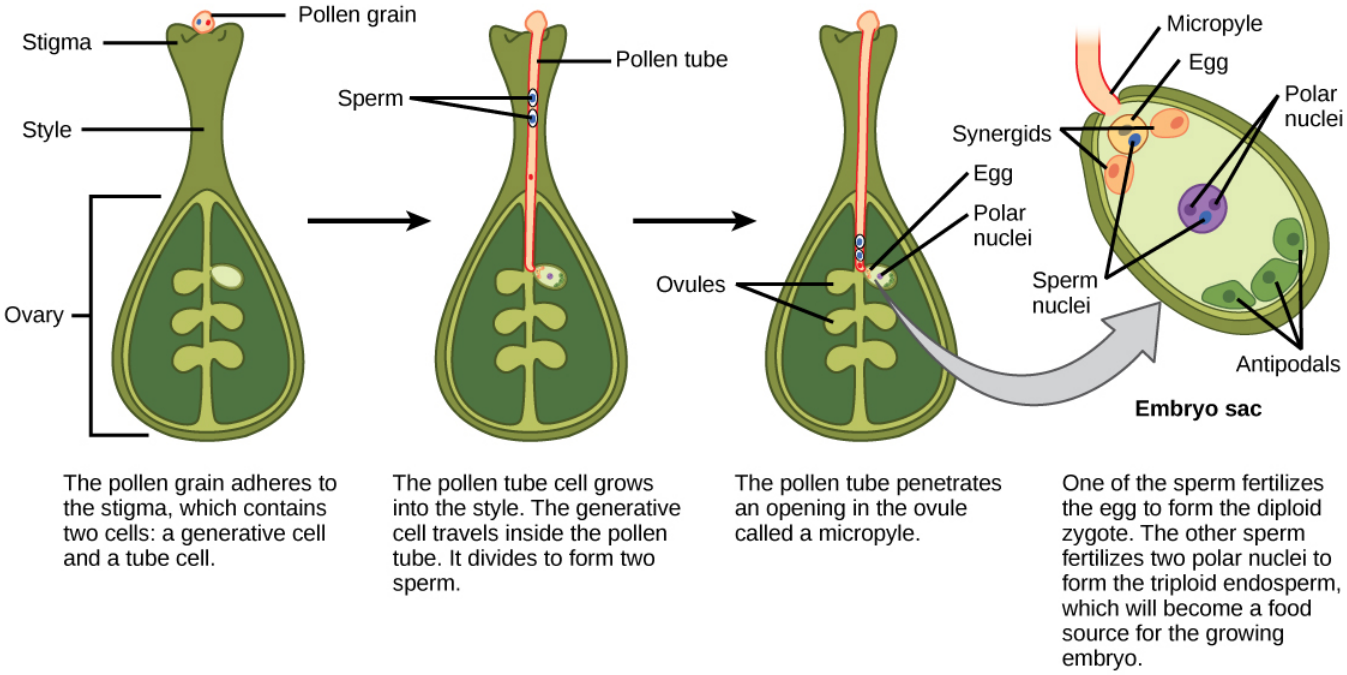



Figure 5.2.7: In angiosperms, one sperm fertilizes the egg to form the 2*n* zygote, and the other sperm fertilizes the central cell to form the 3*n* endosperm. This is called a double fertilization.

After fertilization, the zygote divides to form two cells: the upper cell, or terminal cell, and the lower, or basal, cell. The division of the basal cell gives rise to the suspensor, which eventually makes connection with the maternal tissue. The suspensor provides a route for nutrition to be transported from the mother plant to the growing embryo. The terminal cell also divides, giving rise to a globular-shaped proembryo (Figure 5.2.8a). In dicots (eudicots), the developing embryo has a heart shape, due to the presence of the two rudimentary cotyledons (Figure 5.2.8b). In non-endospermic dicots, such as *Capsella bursa*, the endosperm develops initially, but is then digested, and the food reserves are moved into the two cotyledons. As the embryo and cotyledons enlarge, they run out of room inside the developing seed, and are forced to bend (Figure 5.2.8c). Ultimately, the embryo and cotyledons fill the seed (Figure 5.2.8d), and the seed is ready for dispersal. Embryonic development is suspended after some time, and growth is resumed only when the seed germinates. The developing seedling will rely on the food reserves stored in the cotyledons until the first set of leaves begin photosynthesis.

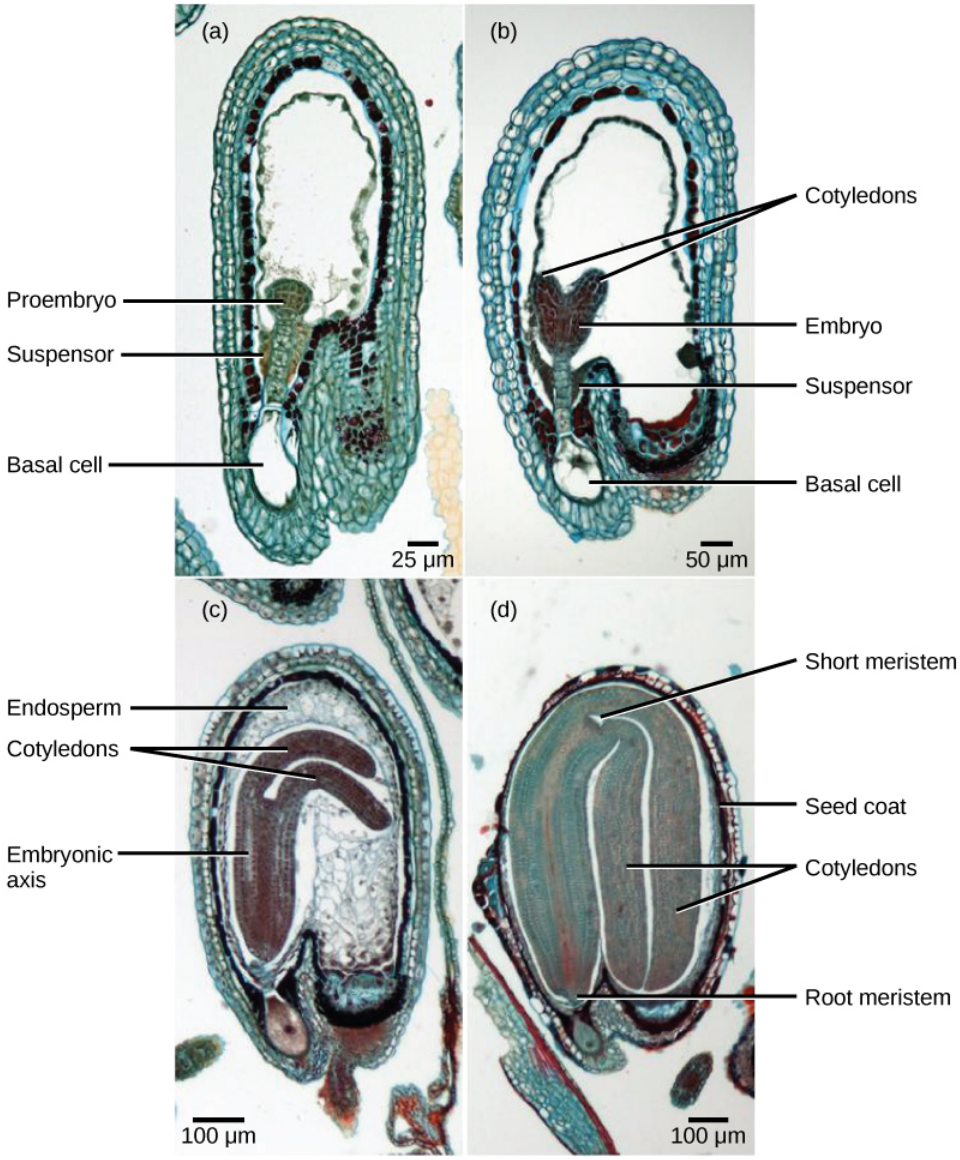



Figure 5.2.8: Shown are the stages of embryo development in the ovule of a shepherd's purse (*Capsella bursa*). After fertilization, the zygote divides to form an upper terminal cell and a lower basal cell. (a) In the first stage of development, the terminal cell divides, forming a globular pro-embryo. The basal cell also divides, giving rise to the suspensor. (b) In the second stage, the developing embryo has a heart shape due to the presence of cotyledons. (c) In the third stage, the growing embryo runs out of room and starts to bend. (d) Eventually, it completely fills the seed. (credit: modification of work by Robert R. Wise; scale-bar data from Matt Russell)

## Development of the Seed

The mature ovule develops into the seed. A typical seed contains a seed coat, cotyledons, endosperm, and a single embryo (Figure 5.2.9).

Art Connection

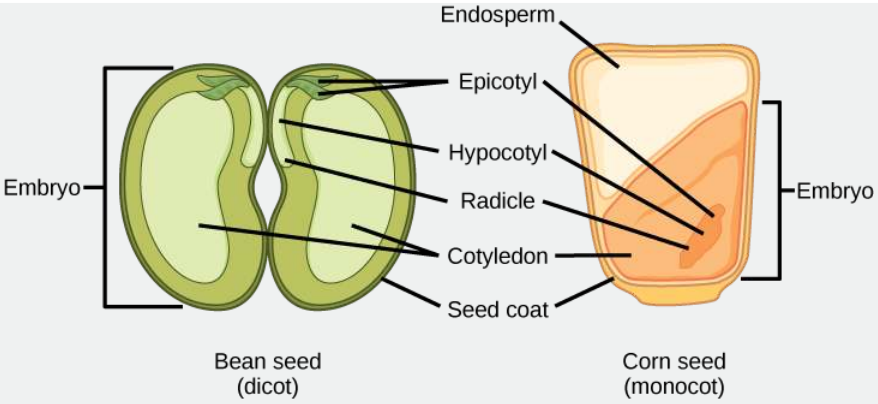



Figure 5.2.9: The structures of dicot and monocot seeds are shown. Dicots (left) have two cotyledons. Monocots, such as corn (right), have one cotyledon, called the scutellum; it channels nutrition to the growing embryo. Both monocot and dicot embryos have a plumule that forms the leaves, a hypocotyl that forms the stem, and a radicle that forms the root. The embryonic axis comprises everything between the plumule and the radicle, not including the cotyledon(s).

Which of the following statements is true?

A. Both monocots and dicots have an endosperm.
B. The radicle develops into the root.
C. The plumule is part of the epicotyl.
D. The endosperm is part of the embryo.

The storage of food reserves in angiosperm seeds differs between monocots and dicots. In monocots, such as corn and wheat, the single cotyledon is called a scutellum; the scutellum is connected directly to the embryo via vascular tissue (xylem and phloem). Food reserves are stored in the large endosperm. Upon germination, enzymes are secreted by the aleurone, a single layer of cells just inside the seed coat that surrounds the endosperm and embryo. The enzymes degrade the stored carbohydrates, proteins and lipids, the products of which are absorbed by the scutellum and transported via a vasculature strand to the developing embryo. Therefore, the scutellum can be seen to be an absorptive organ, not a storage organ.

The two cotyledons in the dicot seed also have vascular connections to the embryo. In endospermic dicots, the food reserves are stored in the endosperm. During germination, the two cotyledons therefore act as absorptive organs to take up the enzymatically released food reserves, much like in monocots (monocots, by definition, also have endospermic seeds). Tobacco (*Nicotiana tabaccum*), tomato (*Solanum lycopersicum*), and pepper (*Capsicum annuum*) are examples of endospermic dicots. In non-endospermic dicots, the triploid endosperm develops normally following double fertilization, but the endosperm food reserves are quickly remobilized and moved into the developing cotyledon for storage. The two halves of a peanut seed (*Arachis hypogaea*) and the split peas (*Pisum sativum*) of split pea soup are individual cotyledons loaded with food reserves.

The seed, along with the ovule, is protected by a seed coat that is formed from the integuments of the ovule sac. In dicots, the seed coat is further divided into an outer coat known as the testa and inner coat known as the tegmen.

The embryonic axis consists of three parts: the plumule, the radicle, and the hypocotyl. The portion of the embryo between the cotyledon attachment point and the radicle is known as the hypocotyl (hypocotyl means “below the cotyledons”). The embryonic axis terminates in a radicle (the embryonic root), which is the region from which the root will develop. In dicots, the hypocotyls extend above ground, giving rise to the stem of the plant. In monocots, the hypocotyl does not show above ground because monocots do not exhibit stem elongation. The part of the embryonic axis that projects above the cotyledons is known as the epicotyl. The plumule is composed of the epicotyl, young leaves, and the shoot apical meristem.

Upon germination in dicot seeds, the epicotyl is shaped like a hook with the plumule pointing downwards. This shape is called the plumule hook, and it persists as long as germination proceeds in the dark. Therefore, as the epicotyl pushes through the tough and abrasive soil, the plumule is protected from damage. Upon exposure to light, the hypocotyl hook straightens out, the young foliage leaves face the sun and expand, and the epicotyl continues to elongate. During this time, the radicle is also growing and producing the primary root. As it grows downward to form the tap root, lateral roots branch off to all sides, producing the typical dicot tap root system.

In monocot seeds (Figure 5.2.10), the testa and tegmen of the seed coat are fused. As the seed germinates, the primary root emerges, protected by the root-tip covering: the coleorhiza. Next, the primary shoot emerges, protected by the coleoptile: the covering of the shoot tip. Upon exposure to light (i.e. when the plumule has exited the soil and the protective coleoptile is no longer needed), elongation of the coleoptile ceases and the leaves expand and unfold. At the other end of the embryonic axis, the primary root soon dies, while other, adventitious roots (roots that do not arise from the usual place – i.e. the root) emerge from the base of the stem. This gives the monocot a fibrous root system.

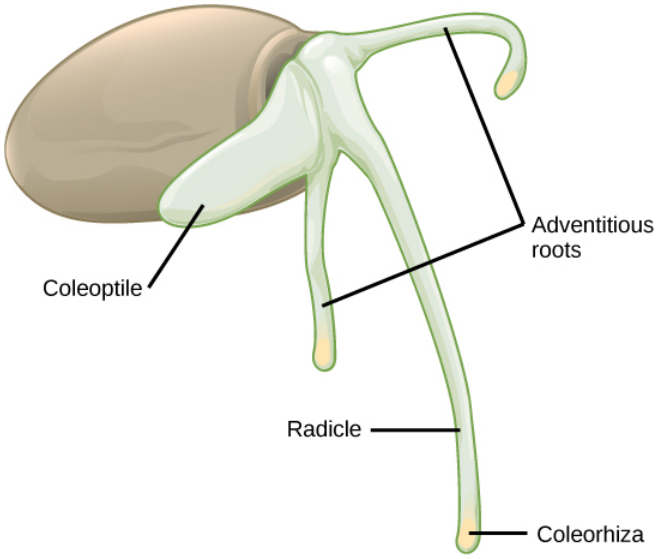



Figure 5.2.10: As this monocot grass seed germinates, the primary root, or radicle, emerges first, followed by the primary shoot, or coleoptile, and the adventitious roots.

## Seed Germination

Many mature seeds enter a period of inactivity, or extremely low metabolic activity: a process known as dormancy, which may last for months, years or even centuries. Dormancy helps keep seeds viable during unfavorable conditions. Upon a return to favorable conditions, seed germination takes place. Favorable conditions could be as diverse as moisture, light, cold, fire, or chemical treatments. After heavy rains, many new seedlings emerge. Forest fires also lead to the emergence of new seedlings. Some seeds require vernalization (cold treatment) before they can germinate. This guarantees that seeds produced by plants in temperate climates will not germinate until the spring. Plants growing in hot climates may have seeds that need a heat treatment in order to germinate, to avoid germination in the hot, dry summers. In many seeds, the presence of a thick seed coat retards the ability to germinate. Scarification, which includes mechanical or chemical processes to soften the seed coat, is often employed before germination. Presoaking in hot water, or passing through an acid environment, such as an animal's digestive tract, may also be employed.

Depending on seed size, the time taken for a seedling to emerge may vary. Species with large seeds have enough food reserves to germinate deep below ground, and still extend their epicotyl all the way to the soil surface. Seeds of small-seeded species usually require light as a germination cue. This ensures the seeds only germinate at or near the soil surface (where the light is greatest). If they were to germinate too far underneath the surface, the developing seedling would not have enough food reserves to reach the sunlight.

## Development of Fruit and Fruit Types

After fertilization, the ovary of the flower usually develops into the fruit. Fruits are usually associated with having a sweet taste; however, not all fruits are sweet. Botanically, the term "fruit" is used for a ripened ovary. In most cases, flowers in which fertilization has taken place will develop into fruits, and flowers in which fertilization has not taken place will not. Some fruits develop from the ovary and are known as true fruits, whereas others develop from other parts of the female gametophyte and are known as accessory fruits. The fruit encloses the seeds and the developing embryo, thereby providing it with protection. Fruits are of many types, depending on their origin and texture. The sweet tissue of the blackberry, the red flesh of the tomato, the shell of the

peanut, and the hull of corn (the tough, thin part that gets stuck in your teeth when you eat popcorn) are all fruits. As the fruit matures, the seeds also mature.

Fruits may be classified as simple, aggregate, multiple, or accessory, depending on their origin (Figure 5.2.11). If the fruit develops from a single carpel or fused carpels of a single ovary, it is known as a simple fruit, as seen in nuts and beans. An aggregate fruit is one that develops from more than one carpel, but all are in the same flower: the mature carpels fuse together to form the entire fruit, as seen in the raspberry. Multiple fruit develops from an inflorescence or a cluster of flowers. An example is the pineapple, where the flowers fuse together to form the fruit. Accessory fruits (sometimes called false fruits) are not derived from the ovary, but from another part of the flower, such as the receptacle (strawberry) or the hypanthium (apples and pears).

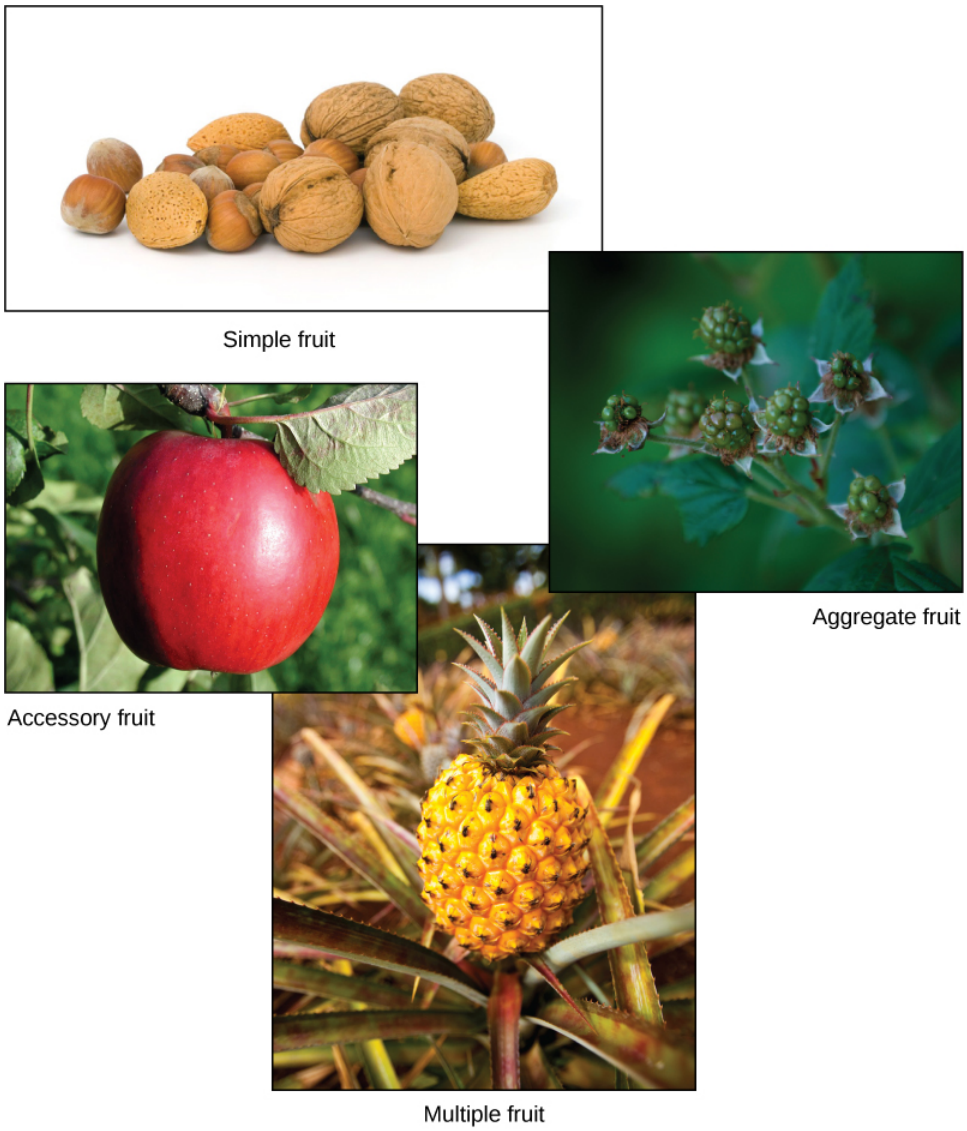



Figure 5.2.11: There are four main types of fruits. Simple fruits, such as these nuts, are derived from a single ovary. Aggregate fruits, like raspberries, form from many carpels that fuse together. Multiple fruits, such as pineapple, form from a cluster of flowers called an inflorescence. Accessory fruit, like the apple, are formed from a part of the plant other than the ovary. (credit "nuts": modification of work by Petr Kratochvil; credit "raspberries": modification of work by Cory Zanker; credit "pineapple": modification of work by Howie Le; credit "apple": modification of work by Paolo Neo)

Fruits generally have three parts: the exocarp (the outermost skin or covering), the mesocarp (middle part of the fruit), and the endocarp (the inner part of the fruit). Together, all three are known as the pericarp. The mesocarp is usually the fleshy, edible part of the fruit; however, in some fruits, such as the almond, the endocarp is the edible part. In many fruits, two or all three of the layers are fused, and are indistinguishable at maturity. Fruits can be dry or fleshy. Furthermore, fruits can be divided into dehiscent

or indehiscent types. Dehiscent fruits, such as peas, readily release their seeds, while indehiscent fruits, like peaches, rely on decay to release their seeds.

## Fruit and Seed Dispersal

The fruit has a single purpose: seed dispersal. Seeds contained within fruits need to be dispersed far from the mother plant, so they may find favorable and less competitive conditions in which to germinate and grow.

Some fruit have built-in mechanisms so they can disperse by themselves, whereas others require the help of agents like wind, water, and animals (Figure 5.2.12). Modifications in seed structure, composition, and size help in dispersal. Wind-dispersed fruit are lightweight and may have wing-like appendages that allow them to be carried by the wind. Some have a parachute-like structure to keep them afloat. Some fruits—for example, the dandelion—have hairy, weightless structures that are suited to dispersal by wind.

Seeds dispersed by water are contained in light and buoyant fruit, giving them the ability to float. Coconuts are well known for their ability to float on water to reach land where they can germinate. Similarly, willow and silver birches produce lightweight fruit that can float on water.

Animals and birds eat fruits, and the seeds that are not digested are excreted in their droppings some distance away. Some animals, like squirrels, bury seed-containing fruits for later use; if the squirrel does not find its stash of fruit, and if conditions are favorable, the seeds germinate. Some fruits, like the cocklebur, have hooks or sticky structures that stick to an animal's coat and are then transported to another place. Humans also play a big role in dispersing seeds when they carry fruits to new places and throw away the inedible part that contains the seeds.

All of the above mechanisms allow for seeds to be dispersed through space, much like an animal’s offspring can move to a new location. Seed dormancy, which was described earlier, allows plants to disperse their progeny through time: something animals cannot do. Dormant seeds can wait months, years, or even decades for the proper conditions for germination and propagation of the species.



a b



c

**Figure 5.2.12:** Fruits and seeds are dispersed by various means. (a) Dandelion seeds are dispersed by wind, the (b) coconut seed is dispersed by water, and the (c) acorn is dispersed by animals that cache and then forget it. (credit a: modification of work by "Rosendahl"/Flickr; credit b: modification of work by Shine Oa; credit c: modification of work by Paolo Neo)

## Summary

For fertilization to occur in angiosperms, pollen has to be transferred to the stigma of a flower: a process known as pollination. Gymnosperm pollination involves the transfer of pollen from a male cone to a female cone. When the pollen of the flower is transferred to the stigma of the same flower, it is called self-pollination. Cross-pollination occurs when pollen is transferred from one flower to another flower on the same plant, or another plant. Cross-pollination requires pollinating agents such as water, wind, or animals, and increases genetic diversity. After the pollen lands on the stigma, the tube cell gives rise to the pollen tube, through which the generative nucleus migrates. The pollen tube gains entry through the micropyle on the ovule sac. The generative cell divides to form two sperm cells: one fuses with the egg to form the diploid zygote, and the other fuses with the polar nuclei to form the endosperm, which is triploid in nature. This is known as double fertilization. After fertilization, the zygote divides to form the embryo and the fertilized ovule forms the seed. The walls of the ovary form the fruit in which the seeds develop. The seed, when mature, will germinate under favorable conditions and give rise to the diploid sporophyte.

## Art Connections

Figure **5.2.9**: What is the function of the cotyledon?

A. It develops into the root.
B. It provides nutrition for the embryo.
C. It forms the embryo.
D. It protects the embryo.

**Answer**

B

## Glossary

**accessory fruit**
fruit derived from tissues other than the ovary

**aggregate fruit**
fruit that develops from multiple carpels in the same flower

**aleurone**
single layer of cells just inside the seed coat that secretes enzymes upon germination

**coleoptile**
covering of the shoot tip, found in germinating monocot seeds

**coleorhiza**
covering of the root tip, found in germinating monocot seeds

**cotyledon**
fleshy part of seed that provides nutrition to the seed

**cross-pollination**
transfer of pollen from the anther of one flower to the stigma of a different flower

**dormancy**
period of no growth and very slow metabolic processes

**double fertilization**
two fertilization events in angiosperms; one sperm fuses with the egg, forming the zygote, whereas the other sperm fuses with the polar nuclei, forming endosperm

**endocarp**
innermost part of fruit

**endosperm**
triploid structure resulting from fusion of a sperm with polar nuclei, which serves as a nutritive tissue for embryo

**endospermic dicot**
dicot that stores food reserves in the endosperm

**exocarp**
outermost covering of a fruit

**epicotyl**
embryonic shoot above the cotyledons

**gravitropism**
response of a plant growth in the same direction as gravity

**hypocotyl**
embryonic axis above the cotyledons

**mesocarp**
middle part of a fruit

**multiple fruit**
fruit that develops from multiple flowers on an inflorescence

**nectar guide**
pigment pattern on a flower that guides an insect to the nectaries

**non-endospermic dicot**
dicot that stores food reserves in the developing cotyledon

**pericarp**
collective term describing the exocarp, mesocarp, and endocarp; the structure that encloses the seed and is a part of the fruit

**plumule**
shoot that develops from the germinating seed

**pollination**
transfer of pollen to the stigma

**radicle**
original root that develops from the germinating seed

**scarification**
mechanical or chemical processes to soften the seed coat

**scutellum**
type of cotyledon found in monocots, as in grass seeds

**self-pollination**
transfer of pollen from the anther to the stigma of same flower

**simple fruit**
fruit that develops from a single carpel or fused carpels

**suspensor**
part of the growing embryo that makes connection with the maternal tissues

**tegmen**
inner layer of the seed coat

**testa**
outer layer of the seed coat

**vernalization**
exposure to cold required by some seeds before they can germinate

---

This page titled 5.2: Pollination and Fertilization is shared under a CC BY 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **32.2: Pollination and Fertilization** by OpenStax is licensed CC BY 4.0.

# CHAPTER OVERVIEW

## 6: Plant genetics and breeding


6.1: The Early History of Genetics

6.2: Cataloging, Classification, and Deliberate Hybridizations

6.3: Plant Breeding

6.4: Genetic Improvement in Cereal Crops and the Green Revolution


---

This page titled 6: Plant genetics and breeding is shared under a not declared license and was authored, remixed, and/or curated by Tom Buckley.

# 6.1: The Early History of Genetics

> No-one can say why the same peculiarity in different individuals…is sometimes inherited and sometimes not so: why the child often reverts in certain characters to its grandfather, or other much more remote ancestor; why a peculiarity is often transmitted from one sex to both sexes, or to one sex alone, more commonly but not exclusively to the like sex.
>
> —Charles Darwin, *On the Origin of Species*

Our ancestors started agriculture with a certain sense that traits are inherited from parents to progeny. Centuries of breeding domestic animals and plants showed that useful traits could be accentuated by controlled mating, and as we have discussed in chapter 2, domestication and artificial selection gave rise to most modern crops. However, there was no rational way to predict the outcome of a cross between two parents or understanding how and why certain traits show up while others remain hidden (see figure 5.1). Until the nineteenth century, the prevailing theory was the *blending inheritance*, which was similar to the mixing of two different color paints: progeny were expected to have traits that were a blend of those of its two parents.



Fig 5.1 "Un Nouveau Nez," ("A New Nose"), a caricature by Honore Daumier, 1833. "Un nouveau nez" by Honore Daumier is in the public domain.

Darwin was puzzled about the mechanism of heredity and how the substance that carries parental traits into offspring could possess two seemingly contradictory qualities: its flexibility to give rise to variations and the stability required to maintain the species. He proposed the pangenesis theory to explain the mechanism of heredity. This theory suggests that an organism continually produces a specific type of small organic particle called a gemmule that accumulates in the gonads and then is transmitted to the gametes. When gametes form embryos after fertilization, their gemmules from the parents mix like the paint of two colors. Interestingly, pangenesis was in direct contradiction with Darwin's theory of (bio)evolution. If the principles of pangenesis were correct, then the natural variations that spontaneously arise within any species would have been an exception among most individuals. Therefore, as a result of mating between an exceptional variant with "normal" individuals (and mating of its progenies with normal members for generation after generation), the variations would gradually disappear. However, Darwin's extensive research suggested that variations in different birds of the Galápagos Islands were maintained over generations. Eventually, Darwin realized that pangenesis does not explain evolution, and these two hypotheses—(bio)evolution and pangenesis—were contradictory. But he could not solve the riddle.

The greatest challenge to pangenesis came from the German zoologist August Weismann (1834–1914). Weismann experimented with mice to see if cutting off their tails generation after generation would cause any change in their offspring. However, the progeny of those mice had normal tails. He proposed the germplasm theory, which suggests that multicellular organisms consist of two types of cells: (1) germ cells, which are present in the gonads (ovaries and testes) and contain and transmit heritable information from parents to progeny, and (2) somatic cells, which carry out ordinary bodily functions. Thus the gametes (egg cells and sperm cells) produced by the germ cells serve as carriers of heredity information, and other cells of the body do not function as agents of heredity. This hypothesis discredited the ideas of inheritance of acquired characteristics as proposed by Lamarckism and pangenesis. In this way, the distinction between the hardwired inherited traits contained within the germ cells and the soft-wired traits acquired by the somatic cells was established.

However, it remained to be known how much biological contribution the mother and father make to their offspring and what rules govern heredity.

## Gregor Johann Mendel: The Mathematics of Heredity

During Darwin's lifetime, a clergyman in a monastery in Moravia, Gregor Johann Mendel (1822–84), studied the laws of genetics by crossing pea plants. Moravia, where Mendel (figure 5.2) was born and educated, was the center of plant crossing since the eighteenth century. As discussed in the previous chapter, various pastors took on crossing and hybridization experiments for improving crops and domestic animals. They included crossing and breeding experiments in natural science curricula in the classes they taught at schools. Thus Mendel's curiosity and his experiments aimed at understanding the laws of heredity come as no surprise.



Fig 5.2 Gregor Johann Mendel (1822-1884) was the first person to analyze patterns of inheritance. "Gregor Mendel" is in the public domain.

From 1856 to 1863, Mendel grew pea plants in the five-acre garden of the monastery and conducted about 29,000 crossing experiments. The pea proved to be the ideal plant for investigating heredity. The pea is a selfing plant, but it is also easy to perform artificial pollination on it. It has a short life cycle of two and a half months and can be grown in large numbers with very few resources. Thus it is possible to study several generations of this plant within a short period. Mendel selected seven contrasting characteristics of the pea plant (see figure 5.3) in his experiment: stem length (tall or dwarf), flower color (purple or white), pod shape (inflated or constricted), pod color (green or yellow), seed shape (round or wrinkled), seed color (yellow or green), and flower position (axil or terminal). For many years, Mendel developed purebreds by self-pollination. All the offspring produced by the selfing of purebreds are the same. For example, tall plants give rise to 100 percent tall progeny, and dwarf plants produce 100 percent dwarf progeny.

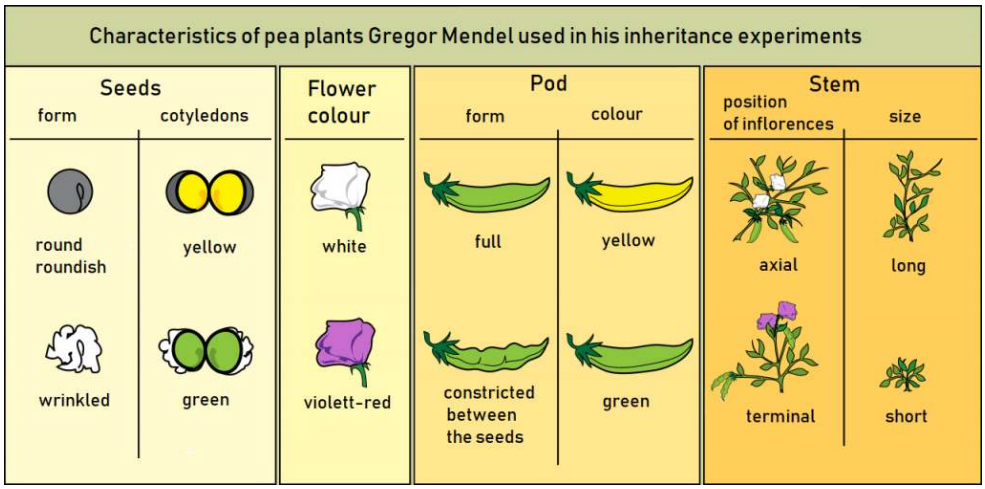



Fig 5.3 The seven characteristics of pea plants selected by Gregor Mendel. "Gregor Mendel – characteristics of pea plants" by Mariana Ruiz Villarreal and Sciencia58 is licensed under CC0 1.0.

Subsequently, he used purebreds of peas for generating hybrids and for studying the pattern of inheritance of various characteristics. He observed that the crossing of the purebred purple-flowered plant with the white-flowered plant produced only purple flowers in the hybrid (first hybrid generation, or F1). He repeated these experiments on the seven pairs of pea plants that exhibited contrasting traits and found every time that all the hybrids of the F1 generation showed traits from one parent, while the contrasting trait from the other parent remained hidden. He did not observe the mixing of two contrasting traits. Based on these observations, Mendel proposed the first principle of heredity, known as the law of dominance, postulating that within any (multicellular) organism, at least two factors determine a given trait, of which only the dominant factor appears in the hybrid, and the recessive factor remains hidden or masked by the dominant trait.

In the second step, Mendel crossed F1 hybrids and analyzed their progeny (second hybrid generation, or F2) and found that 75 percent of F2 plants contained purple flowers and 25 percent of F2 plants contained white flowers (see figure 5.4). Thus after skipping the F1 generation, the white flower color reappeared in the F2 generation, but the distribution of dominant (purple) versus recessive (white) traits in their flowers was 3:1 (refer back to figure 5.1). Mendel repeated these experiments on all seven traits and always got a ratio of 3:1 between dominant and recessive traits in F2 progeny.

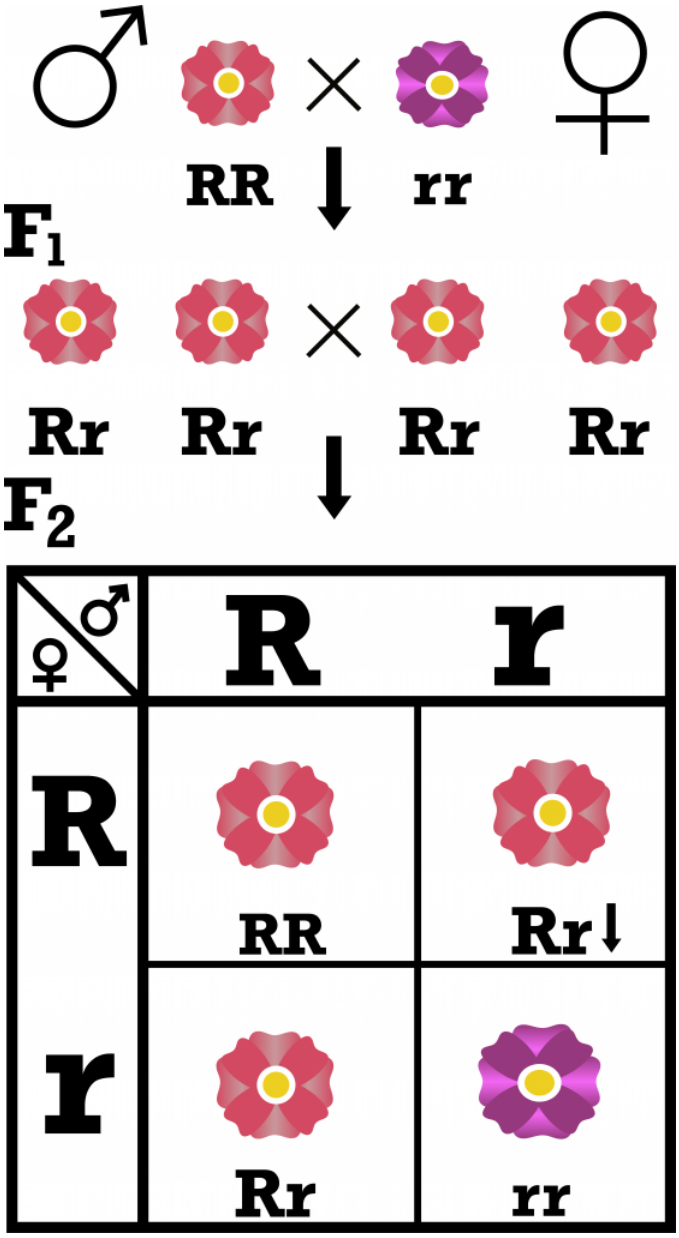



Fig 5.4 The results of monohybrid cross between purple and red flowers. "Results of monohybrid cross" by Sushma Naithani and OSU OERU is licensed under CC BY 4.0.

For the first time in history, it became known that the contrasting parental traits do not mix like paints of two colors; instead, they are maintained and transmitted as independent entities. During the gamete formation, the two factors separate and are distributed equally in the gametes. The fertilization between egg and sperm cells that both contain the recessive factor gives rise to the progeny containing both recessive factors, and thus the corresponding trait reappears. Mendel suggested the second law of heredity as the following:

1. The individual has two copies of each factor. Each parent contributes one factor of each trait shown in the offspring.
2. Some traits can mask others, but the traits don't blend. The two members of each pair of factors segregate from each other during gamete formation.

Today, these factors are known as the *alleles* of a gene, which behave like alternatives to each other. Most recessive alleles cause/indicate a functional deficiency. If one allele of the pair works properly, then it hides the other's deficiency. If both alleles of a gene are effective/functional or if at least one allele of the pair is functional, then in both cases, we see a dominant trait.

Subsequently, Mendel studied the inheritance of two different traits simultaneously. For example, he crossed homozygous plants producing yellow, smooth peas with plants producing homozygous green, wrinkled peas. As expected, the F1 generation peas were yellow and smooth; only dominant traits showed up. Mendel made crosses between the F1 individuals and found that of the sixteen plants in the F2 generation, nine produced yellow, smooth peas (resembling the dominant ancestor); one produced green, wrinkled peas (resembling the recessive ancestor); three produced smooth, green peas; and three produced yellow, wrinkled peas (see figure 5.5). In the F2 generation, he found a new combination of smooth, green and yellow, wrinkled peas in equal ratio. The overall result suggested that two different traits (such as the color and shape of a pea) are transmitted independently of each other to future generations. Mendel postulated the third law of heredity (a.k.a. the law of independent assortment), suggesting that different traits —like seed shape and seed color—are inherited independently of each other.

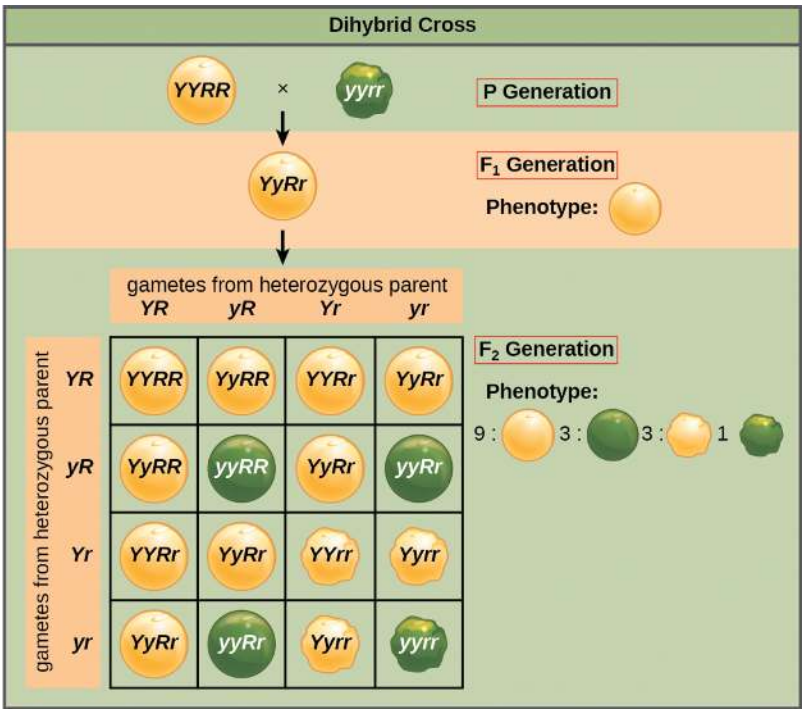



Fig 5.5 The di-hybrid cross of pea plants for seed color and seed shape. "Image of dihybrid cross" by OpenStax CNX is licensed under CC BY 4.0.

Thus Mendel's experiment revealed the role of sexual reproduction in generating variations within the same species. Today, Mendel's three laws are known as the fundamental principles of genetics. Mendel was not aware of the physical and chemical properties of the genetic material, but his discoveries led to the first concrete understanding of how the genetic material behaves.

Understanding the behavior of heredity required a mathematical approach rooted in deduction, the fragmentation of big questions into small workable hypotheses, and a good model system for studying heredity. Mendel, a trained meteorologist, had the ability to look at the data and apply math to it. In contrast, Darwin and most biologists of his time implemented the cataloging and description of the morphology of plants and animals. Today, Mendel is the father of genetics, but during his lifetime, his contributions were not valued by his peers. In later years, Mendel did the monastery's administrative work, and his three principles of genetics were forgotten for thirty-five years.

Mendel's work was no less important than Darwin's. In fact, his work explained Darwin's theory of evolution in concrete terms. Many people now wonder why Mendel's discoveries were ignored, while Darwin became one of the most popular scientists during his lifetime. Perhaps, to some extent, Darwin benefited from his family background. Both his father and grandfather were well-known doctors, and he graduated from the University of Cambridge. He developed his academic network at an early age while working with John Henslow and then got an opportunity to join the HMS *Beagle as a naturalist* (a volunteer who was not paid a salary). In contrast, Mendel was born into a peasant family. After his initial education in the village, he became a monk and pursued further education in the monastery. During his youth, he struggled to become a high school teacher and carried out experiments with pea plants in the garden. He did not get much opportunity to discuss theories with other scientists, as he was not a part of academia; none took cognizance of his work. Also, most of his contemporary scientists were naturalists involved in cataloging and

describing plant and animal diversity; they lacked mathematical understanding. Therefore, most academics and scientists ignored Mendel's published papers. We have no way of knowing if Darwin ever knew about Mendel's research work.

## Rediscovery of Mendel's Laws and the Birth of Genetics

In 1900, Hugo de Vries, Carl Correns, and Erich von Tschermak independently rediscovered Mendel's work. Thus Mendel's three laws of heredity resurfaced after being buried after thirty-five years, but even then, these principles were not easily accepted. The first few who recognized the importance of Mendel's laws include Cambridge University biologist William Bateson. Bateson zealously lectured on the laws of heredity in European and American institutions to popularize Mendel's work and became known as "Mendel's bulldog." Bateson established the first genetics laboratory in Cambridge. Bateson proposed the term *genetics* for a new branch of biology rooted in the Mendelian approach and the study of inheritance and the structure function of genetic material. During this period, Vavilov had joined Bateson's laboratory and thus became the first geneticist in the USSR. Botanist Wilhelm Johannsen proposed the word *gene* for the Mendelian units of heredity (factor) and called two different versions of a gene-defining trait *alleles*, since hybrid plants show only dominant traits and appear similar to purebreds even though their genetic configuration is different. Hence in 1909, Johannsen proposed the terms *genotype* for the genetic configuration and *phenotype* for the manifested trait—that is, its outward appearance. Hugo de Vries proposed the term *mutant* for organisms with rare traits (whose numbers are less than 1 percent in a population or have a defect). In this way, gradually, terminology and vocabulary for genetics increased, and slowly it was established as a subdiscipline of biology.

## Exceptions and Extension of Mendelian Genetics

In the early twentieth century, many scientists repeated Mendel's experiments and began analyzing their crossing experiments using a framework provided by Mendelian genetics. Often, the laws of heredity successfully explained their results, but less frequently, exceptions were encountered, which added new dimensions to and knowledge of heredity. Here we discuss several of such examples and how they contributed to furthering knowledge in the field.

### Partial or Incomplete Dominance and Codominance

One exception to Mendel's first law is partial dominance. When scientists crossed the white- and red-flower varieties of the "four o'clock," they found pink flowers in the F1 hybrids. Thus in this case, the presence of a dominant allele did not completely mask the recessive allele, and the phenotype of the heterozygous F1 hybrid differs from its homozygous dominant parent. Furthermore, the selfed progeny of heterozygous F1 hybrid segregated in a ratio of 1 red: 1 white: 2 pink. However, the pink flower in the hybrid is not a result of the mixing of red and white but is due to the diminished quantity of red pigment. In fact, both allele coding for red and white are transmitted from one generation to another as discrete factors, but the red flowers are produced by plants where both factors are functional. When only one of the two works, only half the pigment is formed, and the pink color is seen.

Another exception is codominance, where both alleles (factors) determining a trait are functional. For example, in people with AB blood group, both A and B alleles are equally active and produce A and B antigens. A third allele, i, is also found in some people that do not produce any antigen due to mutations. Therefore, people with AA or Ai have blood group A; those with BB or Bi have blood group B, and others with ii have blood group O (no antigen).

Mendel proposed the basic rules of genetics based on the assumption that there are two alleles (dimorphic) of any gene. While it stands true for an individual, multiple alleles for the same trait exist within any population of a plant or animal. Many genes have several common alleles (they are polymorphic), which may show a complicated pattern of dominance and can be placed in a hierarchy. The interactions of these various alleles cannot be understood without concerted efforts of crossing and establishing a dominance series. For example, if we look carefully at the whole lentil grain, there are many patterns of small or big dots on the light-colored surface. If a lentil with a clear surface is crossed with one with a dotted surface, then the F1 hybrid shows a dotted trait. However, a crossing of the dotted lentil with spotted lentil plants produces an F1 hybrid showing a spotted pattern (here the dotted trait behaves recessively). Based on the results from such crossings, the dominance hierarchy of different alleles can be prepared, and then the results can be explained using Mendel's laws. But without understanding this hierarchy, the results cannot be explained. It is noteworthy to mention that in such cases, the dominance relations affect only the correspondence between genotype and phenotype; however, the alleles still segregate and unite randomly and follow the Mendelian pattern. The difference lies in the complex relationship between genotype and phenotype.

## Lethal Mutations

There are many essential genes found in a living organism, known as the *housekeeping genes*, that are required for that organism's survival. Some of these genes are active in all cells of an organism, whereas others act specifically in a particular type of cell, tissue, or organ. Mutations in housekeeping genes can be lethal. Sometimes heterozygotes exhibit a phenotype or a disease, which leads to recessive homozygotes dying (and thus a progeny class is eliminated). In these cases, we do not find the segregation of F2 progeny according to Mendel's laws.

In contrast, the gametes (egg or sperm cells) contain only one allele, and thus the gametes carrying a nonfunctional allele of housekeeping genes are destroyed. As a result, only the gametes carrying the functional alleles are transmitted to the next generation. In such cases, the results of the crossing do not fit into the Mendelian hypothesis, and only the functioning allele is seen in the progeny. However, close observation can reveal decreased pollination and lower seed formation. In other instances, after successful pollination and fertilization, the embryo does not develop because both alleles of a housekeeping gene required for embryonic development are mutants. Similarly, some plants die after seed germination due to a lack of functional alleles (e.g., albino mutants that lack photosynthesis capacity). There are also instances where both alleles are necessary for the normal development of an organism. For instance, in healthy individuals, both alleles of the fibroblast growth receptor gene function, but people with a mutant allele suffer from the most common form of dwarfism (known as achondroplasia, with a normal-length body but shortened limbs).

## Pleiotropy

Sometimes a single gene affects several unrelated phenotypic traits in the same organism, and this phenomenon is known as pleiotropy. For example, specific mutations in the hemoglobin B gene cause changes in the shape of red blood cells (from round to sickle shaped) that causes sickle cell anemia (termed this to differentiate it from dietary deficiency and other causes of anemia). Due to their shape, these cells obstruct the smooth flow of blood and have a short life compared to normal cells. As a result, people carrying the mutant gene become anemic. In addition to anemia, an enlarged spleen, muscle and heart pains, a weak immune system, resistance to malaria, and early death are associated with the mutations in the hemoglobin B gene.

## Penetrance or Expressivity in Phenotype

Researchers also noticed that certain traits are expressed fully only under a certain environment. Thus two new terms were added:

1. *Penetrance* is whether a trait is expressed or not.
2. *Expressivity* is the degree to which a trait is expressed (fully or partially).

We see many such examples in our day-to-day lives. For instance, genetically identical hydrangeas growing in soils of different acidity (different environments) produce flowers of a different color. Many houseplants change color if their exposure to light changes or the temperature changes. We also find different pigmentation in cats, dogs, and other animals, where the colder body parts are darker while the warm body parts are lighter.

## Epistasis

In many instances, a single phenotype is controlled by the interaction of two or more genes. This phenomenon is known as epistasis. The epistatic genes may code for proteins involved in different steps of a biosynthetic pathway or may have an additive function. In such cases, we see alterations in F2 segregation ratios. Examples of such interactions can explain the various sizes and shapes of squashes, the different skin colors of onions, or the diversity in flower colors of many plants.

Unlike animals, plants contain many duplicate genes, and some of these have redundant and/or additive functions. Thus when both alleles of a gene are mutated and are nonfunctional, we see no phenotype due to the presence of a duplicated gene that functions properly. In such cases, a phenotype is only visible if both genes (all four alleles) become nonfunctional. In contrast, the opposite is also true: sometimes, a phenotype is only visible when two or more duplicate genes are simultaneously functional in the organism. For example, for zucchini, two genes (four alleles in total) determine the fruit size. If both genes work or at least one allele of both works, then a very small disk-shaped fruit is produced. If only one gene (or one of its alleles) is functional, then a big, rounded fruit is produced. If both genes (all four alleles) become nonfunctional, then a long fruit is produced. Here crossing between the long and flat breeds of zucchini will give rise to an F1 hybrid bearing round fruits. And the selfing of F1 progeny will result in the segregation of this trait in F2 progeny as 9 disk shaped (A_B_):6 round (A_bb or aaB_):and 1 long (aabb).

## Genetic Linkage and Chromosome Theory

Mendel was extremely fortunate with the plant model he selected for deciphering the basic laws of heredity. He chose seven traits of pea plants that gave a consistent pattern of dominance and recessiveness between two contrasting alleles. Many of Mendel's contemporaries could not find such a great experimental model or traits, and due to many deviations, their efforts were derailed. Even Bateson, the biggest supporter of Mendelian genetics, could not find an easy path and got entangled with unexpected results not explainable by Mendel's laws. In 1905, Bateson and Reginald C. Punnett made a dihybrid cross between purebreds of sweet pea plants, where the dominant parent produced purple flowers and long pollen grains (PP LL), and the recessive parent produced red flowers and round pollens (pp ll). Bateson and Punnett observed that the F1 hybrid had purple flowers and long pollen grains (Pp Ll), as expected.

However, the F2 population generated by the selfing of F1 hybrids showed a skewed ratio that did not match what was expected based on Mendel's second law of independent assortment of two independent traits. The data clearly showed that the characteristics of pollen size and flower color did not transmit independent of each other from parents to offspring. The expected ratio of the dihybrid cross was 9:3:3:1, but the results did not fit this pattern. As shown in table 5.1, the gene coding for flower color and pollen shape appears to be linked to some extent: the two phenotypic classes (purple flower + long pollen and red flower + round pollen) are larger than expected, and the number of recombinants is less than expected (1). Bateson was puzzled and could not explain these results in terms of epistasis either. However, Bateson and Punnett proposed that the F1 hybrid produced more P L and p l gametes due to some sort of physical coupling between the dominant alleles P and L and between the recessive alleles p and l (1).

Table 5.1: The results of the di-hybrid cross in sweet peas observed by Bateson and Punnett)

| Phenotypes | Observed (12.3:1:1:3.4) | Expected (9:3:3:1) |
|---|---|---|
| Purple flower and long pollen (dominant traits; PP LL+Pp Ll) | 4831 | 3911 |
| Purple flower and, round pollens (recombinant; PP ll+pP ll) | 390 (17.8%) | 1303 |
| Red flower and long pollen (recombinant; pp LL+pp Ll) | 393 (17.7%) | 1303 |
| Red flower and round pollen (recessive traits; pp ll) | 1338 | 435 |
| Total plants | 6952 | 6952 |

American scientist Thomas Hunt Morgan chose the fruit fly (Drosophila melanogaster) to study genetics. The fruit fly has several advantages for this study, including a short life cycle (forty to fifty days), easy propagation within milk bottles, and being amenable to the crossing. Also, with the help of a microscope, changes in the structure of the fruit fly can be easily identified. Thus it was a cheap and accessible model for the study of genetics and since then has served as an important model organism to study eukaryotic genetics. When Morgan crossed a female fly containing a purple eye (pr) and a normal wing (vg; both dominant traits: pr/pr.vg/vg) with a male fly containing a red eye (pr+) and the vestigial wing (vg+; both recessive traits: pr+/pr+.vg+/vg+), he got an F1 hybrid with the purple eye and the normal wing (pr/pr+.vg/vg+), as expected. Then he made a backcross between the F1 hybrid female (pr/pr+.vg/vg+) and the recessive male parent (pr+/pr+.vg+/vg+) (2). In these experiments, the recessive male can only produce one type of gamete, one that carries recessive red eye and vestigial wing traits. Thus the alleles contributed by the F1 female specify the F2 progeny. If both traits are sorted independently of each other, the expected ratio of these traits in the F2 progeny would be 1:1:1:1, representing both parental genotypes and two new recombinant classes.

As shown in table 5.2, he found unexpected results: a much larger number of offspring with purple eyes and normal wings or red eyes and vestigial wings was obtained in the F2 progeny. Like Bateson, he also observed a linkage between two independent traits: the linkage was not absolute, and the two types of recombinant class of progeny were in a similar proportion.

Table 5.2: The results of fruit fly backcross observed by Morgon

| Genotypes and Phenotypes | Observed |
|---|---|
| pr+/pr. vg/vg+<br>(pruple eye+ normal wing) | 1195 |
| pr+/pr+. vg+/vr+ :<br>(red eye+ vestigial wing) | 1339 |
| pr+/pr+. vg/vg+<br>(reg eye +normal wing) | 151 |
| pr+/pr. vg+/vg+<br>(purple eye + vestigial wing) | 154 |
| Total | 2839 |

The progress in the field of cytology[1] helped us understand the phenomenon of linkage between genes that were observed by Bateson and Morgan independently. From the seventeenth century onward, scientists studied the structure of different organisms through microscopes and understood that organisms are made of one or more cells. The simplest forms of life, such as bacteria, are made of only one cell (unicellular), and various animals and plants are made of many cells (multicellular). Therefore, the unit of the structure and the function of life are the cell. In the late nineteenth century, high-resolution microscopes became available, which allowed the identification of various subcellular structures. It was natural that scientists started probing the location of genetic material within the cell. In 1879, Walter Fleming noticed a fine, threadlike structure in the center of salamander cells that shrunk and assumed a clear shape during cell division that was named chromosomes. It was clear from a series of studies that the number of chromosomes is constant for a species, and chromosome numbers vary between species. Typically, multicellular organisms have two copies of each chromosome (two sets of chromosomes) within the somatic cells, and the mother and father each contribute one set of chromosomes to their offspring. For example, human somatic cells have 46 chromosomes (23 pairs; diploid). In contrast, one set of chromosomes (23 chromosomes) is present in the gametes (eggs and sperm cells).

At the time of cell division, chromosomes first double in number and then divide equally into two daughter cells. In this way, two cells are made from one mother cell, and both daughter cells have the same number of chromosomes as their mother cell. In contrast, the cell division of a mother germ cell gives rise to gametes that only contain one set of chromosomes (haploid) and thus only one copy of each chromosome. During sexual reproduction, the fusion of male and female gametes produces a diploid embryo, and the two sets of chromosomes are restored in progeny. The behavior of chromosomes during the cell division of the germ cell grossly reminds us of Mendel's laws.

By the beginning of the twentieth century, it was recognized that chromosomes play a role in transmitting genetic traits from parents to offspring. Incidentally, the seven traits chosen by Mendel for his crossing experiments are encoded by seven genes that reside in seven different chromosomes, and thus he did not observe linkage. Therefore, Mendel did not see any contradiction in his experiments. However, besides gene linkage, Bateson and Morgan made another important observation that the linkage between two genes was not absolute and that a few recombinants are present in the F2 population. Morgan hypothesized that during germ cell division (meiosis), homozygous chromosomes interchange small regions before being divided into daughter cells, and thus the linkage between two genes located on the same chromosome occurs, resulting in the formation of recombinants (2). Thus based on the findings of cell biology and results from his laboratory, Morgan provided an explanation of the linkage between genes (2). He proposed the following:

- Genes occur in a linear order on chromosomes, and their location on chromosomes is fixed.
- Genes on the same chromosome are linked together and do not exhibit an independent assortment.
- Genes can be exchanged between chromosomes during meiosis.
- The closer genes are located on a chromosome, the less likely they will separate and recombine in meiosis.
- Chromosomes undergo segregation and independent assortment. Therefore, genes on different chromosomes follow the law of independent assortment.

## Chromosome Mapping

Several experiments in Morgan's laboratory revealed that the closer the two genes are, the stronger their association. As the distance between the two genes increases, the probability of crossing over increases, and the number of newly combined progeny (recombinant) increases in the same proportion. Thus the distance between two genes can be estimated by the number of recombinants present among the total progeny. By this method, the distance between genes can be measured in centimorgan (cM). Thus a distance of 1 cM between the two genes meant that in such cases, 1 percent of F2 progeny (of dihybrid cross) would be recombinant. Morgan's laboratory generated a vast amount of fruit fly crossing data. Eventually, one of his students, Alfred Henry Sturtevant, analyzed this data and constructed the first genetic map of fruit flies' chromosomes one by one. Subsequently, this method was applied to many other animals and plants to generate their chromosome maps.

Morgan did not directly observe the reciprocal exchange of segments between homologous chromosomes, but the assumptions he made about crossing over during meiosis proved to be correct. The crossing over (see figure 5.6) was experimentally confirmed almost two decades later by Barbara McClintock. But by then, scientists had constructed genetic maps of many organisms by following Morgan's lead. Genetic maps proved to be very useful for breeders. Genes whose phenotypes are visible served as a marker for selecting other nearby/adjacent genes that had no visible phenotype but contributed to important agronomic traits. Similarly, if one desired gene is linked to another undesirable gene, with the help of a genetic map, it became possible to estimate how many crossings will be required to break this linkage.

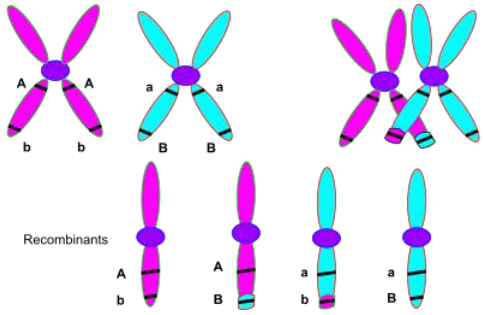



Fig 5.6 Crossing over between genes A and B results in recombinant chromosomes with new allele combinations a, b and A, B, in addition to the original parental combinations A, b and a, B. "Chromosomal Crossover" by Abbyprovenzano is licensed under CC BY-SA 3.0.

## Polyploidy

The study of the cells of various animals and plants revealed that the number of chromosomes within a species is fixed. Moreover, most animals are unable to tolerate a slight change in chromosome numbers. Usually, embryos that have lost or gained one or more chromosomes are unable to survive. Unlike animals, plants have a tremendous capacity to harbor multiple sets of chromosomes; this phenomenon is known as polyploidy. Many plant species have two (diploid), three (triploid), four (tetraploid), six (hexaploid), or eight (octoploid) copies of the entire set of chromosomes. Many polyploid crops have come into existence by spontaneous hybridization events between two closely related species naturally. For example, there are 28 chromosomes within emmer wheat (*Triticum dicoccoides*), 14 of which are from diploid einkorn wheat (*Triticum Urartu*; AA genome donor) and 14 from a diploid goat grass related to *Aegilops speltoides* (the BB-genome donor). Therefore, emmer wheat is a tetraploid (AABB) species. Another natural hybridization event between *T. dicoccoides* and *Aegilops tauschii* (the DD-genome donor) gave rise to hexaploid modern bread wheat (*Triticum aestivum*; AABBDD). Thus hexaploid common bread wheat has 42 chromosomes, of which 28 are from the emmer (AABB) and 14 are from *A. tauschii*.

Often the increased ploidy has a direct effect on the structure of the plant in the form of an increase in the size of the leaf, fruit, or grain—thus it adds to the agronomic value of a crop. Multiplication of chromosomes in emmer and common bread wheat had resulted in an increase in grain size and greater tolerance for adverse environmental conditions. Similarly, as discussed in an earlier chapter, the octoploid ananassa strawberry (8 sets of chromosomes) is much larger than diploid wild strawberry varieties. Sometimes, breeders also create sterile hybrids by crossing two closely related species of different ploidy levels that disrupt the formation of seeds in hybrids. The seedless watermelon (a triploid) is one such example that was made by crossing a tetraploid with a diploid variety.

## Summary

In later decades of the nineteenth century, a tremendous amount of geological and biological data suggested that both the earth and the living species inhabiting it have changed over time; in the process of adapting to new environments, new species emerge from the previously existing species, and some existing species also disappear. Mendel extended the knowledge by postulating three fundamental laws of heredity—which provided a correct theoretical explanation for Darwin's theory of evolution—to describe the origin of species in the natural world. Many new discoveries in cell biology led to the birth of genetics, a subdiscipline of biology that studies heredity and the physical and structural properties of genetic material. By 1900, cells and chromosomes were sufficiently understood to give Mendel's abstract ideas physical context. It was discovered that chromosomes contain the genes that code the various traits of an organism and that during germ cell division, the reciprocal exchange of chromosomal segments further adds to genetic diversity within a species. The observation of recombination frequencies was exploited to construct chromosomal maps and decipher the location of genes on various chromosomes and their physical relationship with one another. Chromosomal maps provided breeders with the tools for designing a rational experiment for creating improved varieties of plants and animals.

## References

Bateson, W., & Saunders, E. R. (1902). Experimental studies in the physiology of heredity. In *Reports to the Evolution Committee of the Royal Society.* Harrison & Sons. (↵ Return 1) (↵ Return 2)

Morgan, T. H. (1909). What are "factors" in Mendelian explanations? *American Breeders Association Reports*, 5, 365–68. http://www.esp.org/foundations/genetics/classical/thm-09.pdf (↵ Return 1) (↵ Return 2) (↵ Return 3)

## Further Readings

Landmarks in the History of Genetics. http://www.dorak.info/genetics/notes01.html

Mendel, J. G. (1865). *Versuche über Pflanzenhybriden Verhandlungen des naturforschenden Vereines in Brünn, Bd. IV für das Jahr.* Abhandlungen. 3–47 [for English translation, see http://www.mendelweb.org/Mendel.plain.html].

Mitosis and Meiosis Simulation (video for cell division of two types). https://www.youtube.com/watch?v=zGVBAHAsjJM

Winther, R. (2001). August Weismann on germ-plasm variation. *Journal of the History of Biology*, 34(3), 517–55. https://doi.org/10.1023/A:1012950826540

---

1. The following are major discoveries in cell biology that played important role in the progress of genetics: 1839: M. J. Schleiden and T Schwann develop the cell theory. 1866: E. H. Haeckel (Häckel) hypothesizes that the nucleus of a cell transmits its hereditary information. 1869: Friedrich Miescher isolates DNA for the first time. 1879: Walter Flemming observes mitosis. 1902: W. S. Sutton and T. Boveri independently propose the chromosome theory of heredity: a full set of chromosomes are needed for normal development; individual chromosomes carry different hereditary determinants; and independent assortments of gene pairs occur during meiosis. ↵

---

This page titled 6.1: The Early History of Genetics is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley via source content that was edited to the style and standards of the LibreTexts platform.

- **1.5: The Early History of Genetics** is licensed CC BY-NC 4.0. Original source: https://open.oregonstate.education/cultivatedplants/.

## 6.2: Cataloging, Classification, and Deliberate Hybridizations

After the sixteenth century, when Europeans reached Asia, Africa, and the Americas, they saw many numerous new species of domesticated and wild plants and animals. Soon, surveying and systematic cataloging of the natural and biological resources ensued under the supervision of various experts. First, three or four experts went in small ships to survey the coastal areas of South America, Africa, and Asia. Typically, a geologist/naturalist would collect samples of rocks, soil, mineral, fossils, and plants and attach a note with each sample describing its features; an engineer's job was to draw or update the navigational maps and gather information about ports and structures of strategic importance; an artist painted landscapes and helped experts prepare sketches of valuable items. From time to time, the collections from survey ships were sent to Europe via other ships. As a result of the various surveys and expeditions, the royal gardens of Europe were overwhelmed with the vast collections from around the world, and several experts were recruited for the analysis, classification, and systematic cataloging of fauna, flora, fossils, and other types of samples.

Besides experts, both elites and common folks, especially the elites and middle-class Europeans, were taken aback by seeing thousands of varieties of fruits, vegetables, and ornamental plants from around the world. Also, many small institutions got interested in acquiring exotic plants and gardening different plant varieties. Around 1650, when the educated elites got involved in growing ferns, tulips, fruits, and so on, the publication of gardening books and nursery catalogs began, and the first nurseries and seed and landscaping companies were founded. Amateur horticulturists in Europe and around the world started the conscious selection of a variety of fruits, vegetables, flowers, and cereals. Today, many of what we consider "natural" fruits, vegetables, and flowers are the result of this conscious selection in the last 300 years. For example, in the seventeenth century, orange carrots were developed in the Netherlands for the first time by the artificial selection of yellow carrots. In the natural form, wild carrots are white and thin. Around the tenth century, the people of Afghanistan had domesticated light yellow carrots, which the Arabs had taken to Europe. In the same way, larger tomatoes, berries, and corn were developed via conscious selection. The variety selection was upheld by several organizations, and annual exhibitions of fruit and flower products began in many cities. Even today, annual agricultural fairs and exhibitions continue throughout the world, and gardeners and farmers still consciously select varieties. For example, in South Asia, farmers have developed thousands of rice varieties to thrive in different climatic and geographical conditions.

### Discovery of Sex in Plants: Self- versus Cross-Pollinated Crops

The detailed investigation of plant morphology and anatomy and how these features change in relation to the plant's habitat and/or in response to its environment led to tremendous advances in knowledge about the natural world and unveiled many mysteries. In this series, German botanist Camerarius (1665–1721) discovered sex in plants,[1] identified various parts of the flower (see figure 4.1), and classified plants into seven categories based on sex (flower structure).

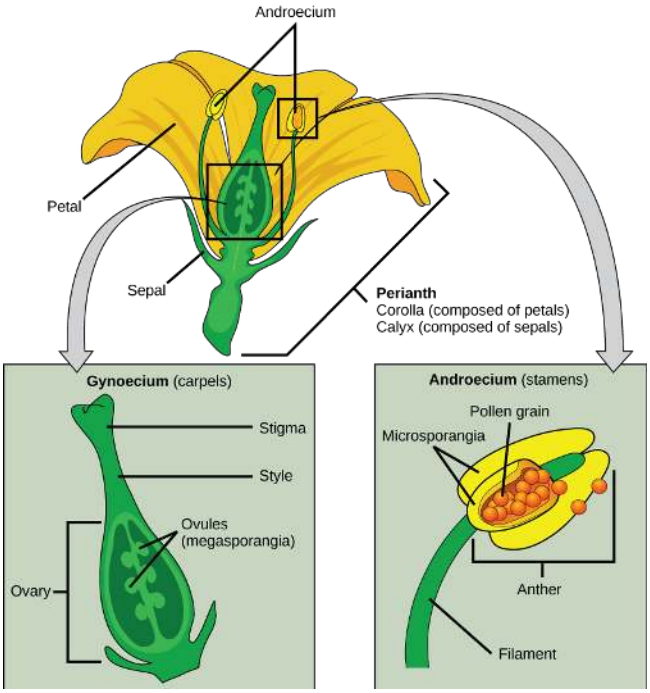



Fig 4.1 A flower is the reproductive organ of the angiosperms (flowering plants). A typical flower has four main parts—or whorls—known as the calyx, corolla, androecium, and gynoecium. The function of a flower is to produce gametes (egg cells and sperm cells), mediate the union of male and female gametes (pollination) thus forming zygotes (fertilization) with new genetic combinations and site of seed set. "Image of flower" by OpenStax CNX is licensed under CC BY 4.0.

In the seventeenth century, it became common knowledge in Europe that seeds are the product of sexual union and flowers contain sexual organs.[2] If we look around carefully, we can easily spot the difference in the structure of flowers and identify the following seven types of sexes in flowering plants:

1. *Perfect/Hermaphrodite*. These flowers contain all four floral organs (sepals, petals, stamens, and carpels). Examples are various flowers of the Brassicaceae family (i.e., mustard, radish, broccoli, etc.).
2. *Monoecious*. These plants bear both male and female reproductive organs. *Monoecious* means "one home." In cucumber, pumpkin, and gourd, separate male and female flowers are distributed randomly, whereas, in maize, the male flowers (tassel) hang on the top, and the female flowers are on the branch, which can be identified by their silk.
3. *Dioecious*. In some species, separate male and female plants are present (e.g., dates, papaya, and *Cannabis*).
    a. *Androecious*. These plants contain only male flowers.
    b. *Gynoecious*. These plants contain only female flowers.
4. *Andromonoecious*. These plants have male and perfect flowers (e.g., saffron).
5. *Gynomonoecious*. These plants have female and perfect flowers.
6. *Trimonoecious*. These plants have male, female, and perfect flowers (e.g., Datura).

Camerarius stated that pollen is required to reach the stigma to form fruit and seeds; this process is called pollination. Self-pollination (selfing) refers to the process when the pollen from the anther is transferred on the stigma of the same flower or another flower on the same plant. Cross-pollination (outcrossing) occurs when pollen from one plant is deposited on the flower (stigma) of a different plant of the same species. The structure of flowers determines the mode of pollination. Often, one can tell just by looking at a flower whether it self-pollinates or cross-pollinates. The self-pollinating flowers are small and monocolored; are unscented; have anthers close to stigma; and lack nectar guides. In these types of flowers, pollination and fertilization often occur in an unopened flower bud (wheat, barley, peanut), and resulting offspring are uniform. Typically, manual crossing is needed to produce hybrids.

In the wild, most flowers promote outcrossing, which supports the continuous mixing of gametes and new combinations of traits. Many species of animals (e.g., bees, butterflies, birds, and mammals) serve as pollinators; however, wind and water can also carry pollen from one plant to another. The outbreeders have many large, scented, bright-colored flowers that have nectaries present and

stigmatic areas well defined and away from the anthers. We find extraordinary structural adaptations in flowers to attract a specific pollinator, and the shape and form of pollen are adapted to their mode of pollination (e.g., wind, water, insects, and mammals). For example, insect-pollinated species have sticky, barbed pollen grains, and wind-pollinated species have light, small, and smooth-surfaced pollens. The cross-pollination increases genetic variability and results in strong evolutionary potential for a species, allowing for adaptations to changing environmental and climatic conditions. However, it can be disadvantageous in certain circumstances; for example, cross-pollination can destroy well-adapted genotypes and relies on vectors for effective pollination and seed set.

Table 4.1. Examples of self- and cross-pollinated crops.

| Self-pollinated crops | Cross-pollinated crops | Cross/self-pollinated crops |
|---|---|---|
| Rice | Alfalfa | Cotton |
| Wheat | Cassava | Oilseed Rape |
| Barley | Corn | Tomato |
| Millet | Pearl Millet | Brassicas |
| Oats | Rye | Potato |
| Flax | Safflower | |
| Legumes (cowpea, beans, chickpea, lentil, mung bean, etc.) | Sugar Beet | |
| Tobacco | Sugar Cane | |
| Potato | Sunflower | |
| Tomato | Carrot | |
| Sesame | Cucumber family (cucumber, melons, pumpkin, squash, etc.) | |
| Jute | | |

## Classification of Plants

From the 1750s to the 1760s, the Swedish government sponsored a number of expeditions under the supervision of Carolus von Linné (Linnaeus), a professor of medicine and botany at Uppsala University (see figure 4.2). His team collected thousands of fauna and flora samples, and after a comprehensive study, Linnaeus proposed the binomial system of naming plants and animals (see figure 4.3).

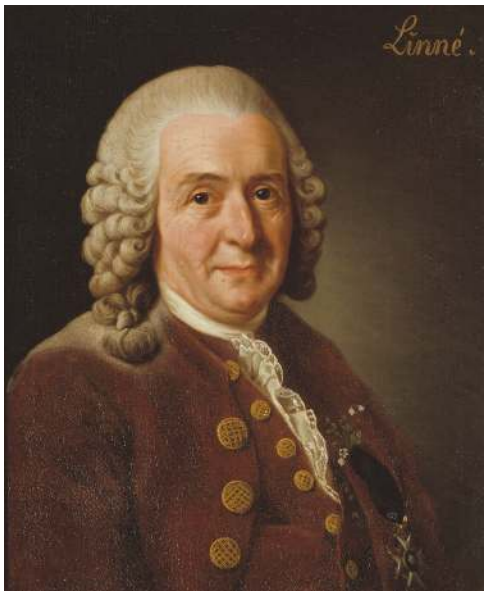



Fig 4.2 Portrait of Linnaeus (1707-1778). "Carl von Linné" by Alexander Roslin is in the public domain.

The smallest unit in the Linnaeus system[3] of classification of organisms is species. He proposed that the males and females of one species can give birth to a healthy progeny, but in a different species, they may not. He then organized the species that are closest in their structure under one genus and many genera having similar characteristics into a family. Then based on further similarities, many families were grouped into an *order*, several orders were grouped into a class, and several classes were grouped into a *phylum*. Finally, all the plant phyla were grouped into the plant kingdom, and all the animal phyla were grouped into the animal kingdom (see figure 4.3). Linnaeus proposed two Latin names for the scientific nomenclature of organisms, of which the first name indicates genus and the second indicates the species. Thus the scientific name of a human is *Homo sapiens*, and the rice plant is *Oryza sativa*. In this system, the genus part of the name comes first and is always capitalized; it is followed by the species name, which is not capitalized. Both names are italicized. Later, Linnaeus's binomial method was also used for naming and classifying bacteria, fungi, and other microscopic organisms.

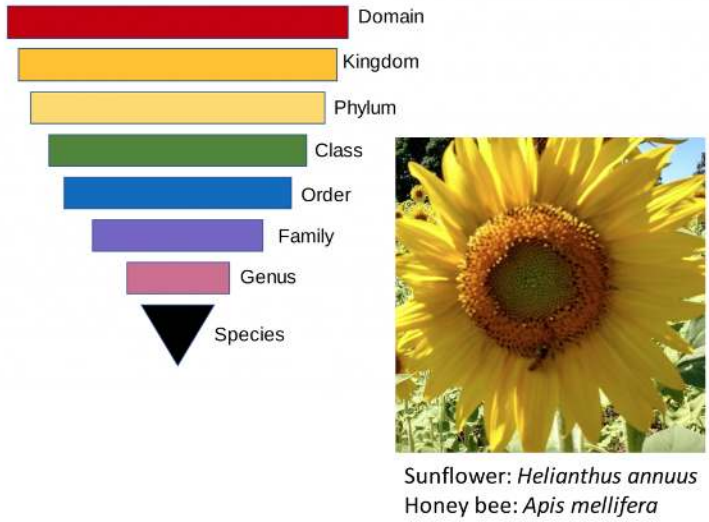



Fig 4.3 Binomial nomenclature proposed by Carl Linnaeus. "Binomial nomenclature" by Sushma Naithani is licensed under CC BY 4.0.

Linnaeus laid the foundation of taxonomy, which aims to study biological diversity and provides guidelines for classification, description, identification, and naming of living organisms. Classification is the grouping of organisms based on their shared characteristics (anatomy, structure, morphology, reproductive behavior, etc.).[4] In general, organisms that share similar features are

closely related and are placed in a group. Thus the binomial system also provides an insight into the evolutionary history (phylogeny) of organisms. Just as Mendeleev's periodic table of elements helps in understanding the atomic structure of various elements, the basic understanding of the structure and relationship of organisms is derived from the classification schema proposed by Linnaeus. Historically, the binomial method of Linnaeus was the first major theoretical understanding in the field of biology. Linnaeus became Europe's greatest scientist in his lifetime.

## Deliberate Hybridizations

Understanding the flower structure and the pollination process made artificial pollination possible and paved the path for crop improvement by deliberate hybridization. It became possible to develop new and improved varieties by crossing two varieties with desirable traits. However, in the absence of a theoretical understanding of laws that govern heredity, the selection of desirable hybrids was almost impossible and a work of trial and error. Thomas Fairchild (1667–1729), a nursery owner in England, was likely the first breeder who succeeded in creating a hybrid pink by crossing carnation and sweet William in 1717. His hybrid is also known as Fairchild's mule. Fairchild gave a lecture on the crossing in the meeting of the Royal Society that was subsequently published in its journal, *Philosophical Transactions* as "Some New Experiments Relating to the Different and Sometimes Contrary Motion of the Sap in Plants and Trees." He is also credited for writing the first book on gardening.

After forty years of Fairchild's research, Linnaeus carried out extensive crossing experiments. He described flowers as "marriage beds" of plants and considered the flower structure as one of the important criteria for developing classification schema for plants. In 1757, Linnaeus crossed two species of *Tragopogon* and identified many plants that were products of spontaneous hybridization. Because of Linnaeus, European scientists, naturalists, teachers, and amateur gardeners got interested in crossing experiments, and the information about flower structure became public knowledge. In the following sections, we describe a brief review of some of the historic crossing experiments and the success of early plant breeders.

### Story of the Annanasa Strawberry

In 1711, Louis XIV sent Captain Amédée-François Frézier (1682–1773) on an espionage mission to Chile and Peru, as France didn't deem it appropriate to show overt interest in Spain's colonies. Captain Frézier, an engineer by profession, traveled to South America and gathered information on fortresses, armies, supply routes, governors, and Indians (indigenous people). In Chile, he noticed a very large strawberry (see figure 4.4), almost quadruple the size compared to the alpine or woodland strawberry (*Fragaria vesca*) found in Europe or the Virginia strawberry (*Fragaria virginiana*) in North America that was brought to France by Jack Cartier (known for discovering the St. Lawrence River in the US) in the seventeenth century. Both *F. vesca* and *F. virginiana* were wild varieties and have not been domesticated. People often used to collect their fruits from the forest during the season. However, from the fourteenth century onward, wild strawberry plants were introduced as ornamental plants in European churches and in royal gardens.

Interestingly, the Chilean strawberry (*Fragaria chiloensis*) spotted by Frézier was the only species of strawberry that humans had domesticated. The indigenous people of Chile were cultivating strawberries for more than 1,000 years. In 1550–51, when Spanish general Pizarro took over Chile, his army included strawberries in the list of plunders. Later, the Spanish expanded the cultivation of strawberries in Chile, and the royalty and elites of Spain enjoyed this delicacy. However, other Europeans remained ignorant of the existence of *F. chiloensis* (see figure 4.4) for almost 150 years. In 1714, Frézier brought five stolen plants of *F. chiloensis* (also known as the beach strawberry) into France. On his return voyage, Frézier faced many challenges (the inspection and search by Spanish customs officers, a pirate attack, and a shortage of drinking water) but was successful in keeping the strawberry plants alive. In the history of the modern strawberry, this journey of the Chilean strawberry was the most important event. Surprisingly, for the next fifty years, these strawberry plants never produced a single fruit in the French royal garden despite plenty of flowering. Bernard de Jussieu, head of the king's garden, preserved and maintained several specimens of *F. chiloensis* and gifted its plantlets to other gardeners and his acquaintances. Finally, in 1766, Antoine Nicholas Duchesne explained that Frézier had selected fruit-bearing female plants in Chile, and all five plants that reached France were female. These female plants needed pollen to form fruits.

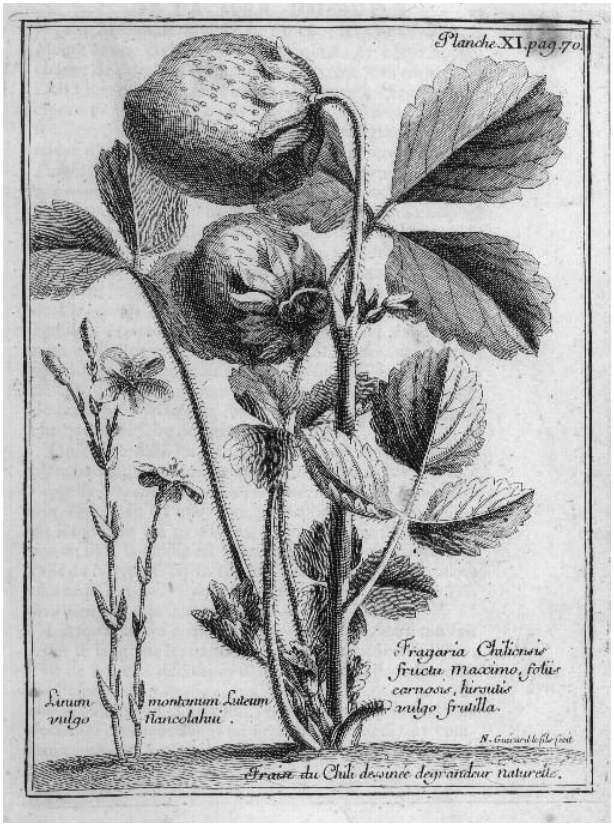



Fig 4.4 An illustration of Fragaria chiloensis (beach strawberry) by Amédée François Frézier (published in 'A voyage to the South-sea, and along the coasts of Chili and Peru, in the years 1712, 1713, and 1714'). "Planche XI" by Jean-Baptiste Scotin is in the public domain.

Duchesne was appointed the gardener of the royal gardens of France in 1760, and he worked under the supervision of Antoine de Jussieu. In the garden at Versailles, Duchesne noticed that the Chilean strawberry planted in between *F. virginiana* and the musky strawberry (*Fragaria moschata*) had produced a large fruit due to accidental cross-pollination. He then pollinated the female flowers of Chilean strawberries with pollens of the musky strawberry, which produced a huge and succulent strawberry fruit with a pineapple aroma. On July 6, 1764, Duchesne presented a bowl full of this large fruit to King Louis XVI. Madeleine Françoise Basseporte, the famous artist, painted strawberries for the royal botanic library, and Duchesne was given a grant to pursue his research on strawberries.

Bernard de Jussieu, the mentor of Nicholas Duchesne, was familiar with Linnaeus's work and had instructed Duchesne about binomial nomenclature and the role of sexes in plants. Duchesne carefully observed the various strawberry plants present in the French royal garden and learned to differentiate between their male and female flowers. After this, he started experimenting with artificial pollination. First, he pollinated Chilean strawberries with the pollen from European woodland strawberry plants, but this did not result in fruit formation, but the pollination of the Chilean strawberry with pollens from *F. moschata* or *F. virginiana* did. Today we know that these compatibilities were related to the ploidy level of different strawberry species. *F. vesca* is diploid (two sets of chromosomes), and both *F. virginiana* and *F. chiloensis* are octoploids (eight sets of chromosomes).xiii *F. virginiana* produces small, highly aromatic fruits in abundance, and *F. chiloensis* bears big fruits (the size of walnuts). Duchesne crossed *F. virginiana* with *F. chiloensis* to make the hybrid *Fragaria x ananassa* (ananassa strawberry; x indicates that the strawberry is of hybrid origin), which produces large and flavorful fruits with pineapple (ananassa) aroma (see figure 4.5). The widespread cultivation of strawberries began with *F. x ananassa*. Therefore, the evolution of the strawberry from a wild to a cultivated plant is relatively recent, and it is a by-product of transatlantic exploration that involved three continents.

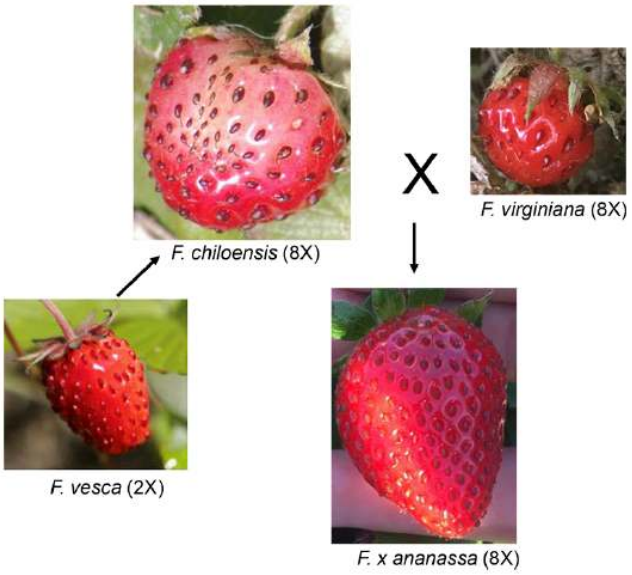



Fig 4.5 Garden strawberry, Fragaria x ananassa is an octoploid hybrid. "Garden Strawberry, Fragaria x ananassa" is a derivative of "Wild Strawberry – Fragaria vesca" by Björn S…, used under CC BY-SA 2.0, "Beach Strawberry Fragaria chiloensis" by Marisa Rafter, used under CC BY-NC 4.0, "Virginia Strawberry Fragaria virginiana" by spacecowboy, used under CC BY 4.0, and "Garden Strawberry Fragaria x ananassa" by rishnessjn, used under CC BY-NC 4.0. "Garden Strawberry, Fragaria x ananassa" is licensed under CC BY-SA 4.0 by Sushma Naithani.

Duchesne also collected strawberry plants from all over Europe, recorded the relevant information, and wrote a report on the natural history of the strawberry. He also interviewed Captain Frézier fifty years later. There are species of strawberry native to regions all around the world, and after Duchesne, many other scientists collected thousands of varieties of strawberries. These varieties of strawberries have different ploidy, fragrance, flavor, and other physical attributes and are adapted to a wide variety of climates. Today, the largest germplasm collection of strawberries is in Corvallis, Oregon.

## Monks of the Austro-Hungarian Empire

Interestingly, the province of Moravia of the Austro-Hungarian Empire became one of the early centers of plant breeding in Europe.[5] The educated elites of Moravia held liberal beliefs in comparison to the remaining Catholic Europe and were invested in improving both education and local agriculture. Many clergymen got inspired by Linnaeus and quickly grasped the utility of deliberate hybridization in improving the local economy. Christian Andre (1763–1831), a social reformer, was one of the pioneers who advocated for plant and animal breeding in Moravia. He founded the Moravian Sheep Breeders Association and the Pomological and Oenological Society of Brno. He collaborated with many of his contemporary horticulturists and breeders, including Jan Sedlacek and G. C. L. Hempel. Abbot F. C. Knapp (1792–1867) of the monastery of Brno was another early influence in Moravia's breeders and took a keen interest in improving fruit trees and grapevine. He had planted over a hundred varieties of grapes in the monastery's nursery and encouraged local farmers to plant fruit trees. In 1840, Knapp organized a large gathering of local farmers and forest officials and explained to them how to make hybrids.

The breeding efforts in Kuninn were also noteworthy. In 1796, Father J. Schreiber began teaching crossing as a part of the natural science curriculum in Kuninn. This school was founded by the countess Maria Walpurga Truchsess-Zeil and provided education to village children for free.

It is said that the greatest concern of the bishop of Brno around 1854 was that his subordinate clergy were paying more attention to natural science, crossing, and nursery than to religious work. It is believed that Brno's monastery narrowly escaped being closed. Some decades later, one of those priests, Gregor Johann Mendel, discovered the fundamental principles of genetics.

However, breeding in those early stages was more of an art than a standardized scientific technique. The common understanding of heredity was similar to the mixing of two colors: the mother's and father's traits mix and reach their offspring. It was with this understanding that the breeders chose the desired characteristics from the cross between two varieties. The task was as difficult as finding a needle in a haystack, and using trial and error, the breeders sometimes found the plants and animals they wanted. Only

fewer than a dozen successful hybrids were made during that era, and fewer still had any significant traits. The ananassa strawberry has special significance in hybrid plants made in this era, and equally impressive is its story.

## Professors and Other Professional Breeders

Apart from monks and gardeners, many professors, teachers, and other professionals pursued crossings and plant breeding experiments out of their intellectual curiosity. Particularly in Germany, Joseph Gottlieb Kölreuter, Christian Konrad Sprengel, and Karl Friedrich von Gartner have contributed significantly to the current knowledge of pollination, hybridization, and heredity. Kölreuter (1733–1806), a professor of natural history at the University of Karlsruhe, Germany, carried out more than 500 artificial hybridization experiments involving 138 species. He made important observations about the role of insects as pollinators and examined the shape, color, and size of pollen grains from ~1,000 different plant species. He noted that successful hybridization occurs only between closely related species, and in offspring, some parental traits show up more often than others. Although he did not dwell deep enough in quantifying the ratio of various inherited traits, his experimental results foreshadowed Gregor Johann Mendel's work.

Sprengel (1750–1816) followed Kölreuter's work on hybridization and made the additional observation that normal sexual reproduction in plants leads to the mixing of traits from both male and female parents and thus creates new combinations in the offspring. This was a big conceptual leap toward understanding the source of diversity among the individual of the same species and an acknowledgment that living species are constantly changing rather than being fixed.

Gartner (1772–1850) was another contemporary of Sprengel, who pursued hybridization experiments as an amateur breeder. He was the physician son of famous botanist Joseph Gartner, who was familiar with the work of both Kölreuter and Sprengel. Over twenty-five years, he carried out ~10,000 individual crossings on ~700 plants (belonging to over 80 genera) and created 350 different hybrids. He also noticed that many hybrids bore larger flowers and fruits than their parents and appeared to be from a different species from their parents. Over the years, this phenomenon was noticed by many and was later named *Hybrid vigor*.

In England, botanist Thomas Andrew Knights (1759–1838) bred fruit trees and successfully made several hybrids, including those of pears and apples. He successfully crossed apple and Siberian crab apple and produced a hybrid that is known for making good quality cider. Like Sprengel, he observed the differences between plants of the same species and the mutability of various characteristics that constantly emerge and then disappear. In addition, Knights published over a hundred research papers on various aspects of plant physiology and founded the Royal Horticulture Society. He was also a member of the Royal Society and, in 1806, received the prestigious Copley Medal. Thomas Knight also conducted extensive crossing experiments in peas and found many of the same results as Mendel. However, he lacked the mathematical framework to analyze his results and could not decipher laws governing heredity.

Overall, by the early decades of the nineteenth century, numerous experiments of crossing drew the attention of experts and amateur gardeners on the variations among members of the same species and the potential of deliberate hybridization in improving crops and animal stock.

## Darwin's Insights from Crossing Experiments

Charles Darwin (1809–82) conducted extensive crossings in plants to understand the implications of self-pollination and outcrossing in plants and made two important observations: (1) In nature, the floral structure of most plants favor cross-pollination, and several structural and genetic barriers prevent selfing. (2) As a result of cross-pollination, new combinations of traits continue to emerge by mixing parental characteristics, which provides the raw material for natural selection. Since plants lack mobility, the traits promoting outcrossing were enriched as a result of natural selection to ensure the continued survival of the species. Darwin also reviewed the work of his predecessors and contemporary botanists, including Kölreuter, Sprengel, Gartner, and Knights. He highlighted the differences between crops and wild plants and identified the various domestication traits in both crop plants and domesticated animals. He made it clear that the direction of artificial selection moved in the opposite direction of natural selection, which led to the development of man-made crops and domestic animals.

Darwin's most famous treatise, On the Origin of Species (published in 1859), began with a chapter entitled "*Variation under Domestication*," which encapsulated his decade-long comparative study of domesticated plants and animals with their wild ancestors, their origins, and artificial selection by humans—all of which provides a basis for his theory of the bioevolution of living organisms using natural selection. In 1868, Darwin independently published *The Variation of Animals and Plants under*

*Domestication* to cover a detailed description of the improvement in crop plants and livestock through artificial selection, the beneficial effects of outcrossing, and the harmful effects of inbreeding.

## Star Breeders of the Early Twentieth Century

### Luther Burbank: A Plant Wizard

Overall, the concept of deliberate hybridization and selection for a desired combination of traits in offspring gained popularity during the nineteenth century and continued until the first two decades of the twentieth century. The most successful and well-known breeder of this tradition was American gardener Luther Burbank (1849–1926). Luther Burbank (see figure 4.6) was born in 1849 in the city of Lancaster, Massachusetts. He received only an elementary education before starting work on a market garden. When he was twenty-one, his father died, and with his share of the inheritance, he purchased a seventeen-acre farm in Lunenburg. On this farm, he identified a natural genetic variant of potato that was large with russet-colored skin, famously known as the russet Burbank potato. This potato variety soon became popular and is used for making french fries. Burbank sold the rights to the russet potato for $150 and bought a four-acre farm in Santa Rosa, California. A few years later, he purchased an eighteen-acre farm in the nearby town. In both these farms, he laid the necessary infrastructure for greenhouses, nursery beds, and so on so that he can carry out crossings and selection work.

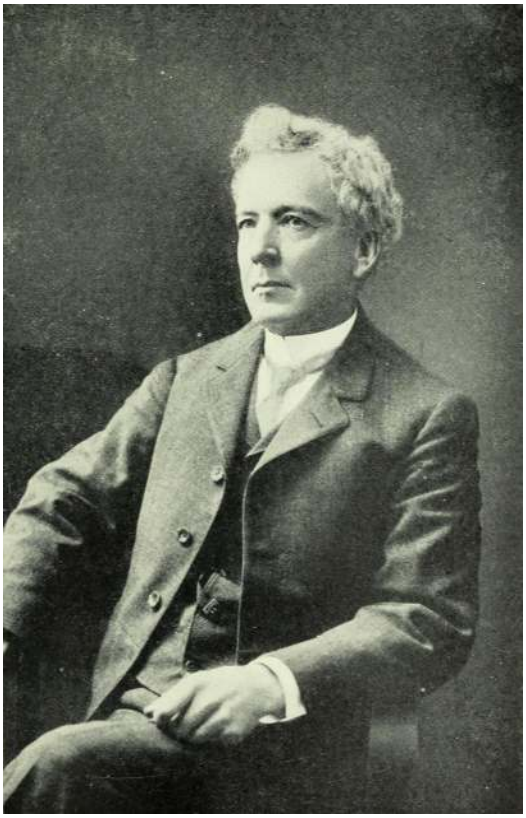


Fig 4.6 “Luther Burbank in 1915” by Gabriel Moulin is in the public domain.

Although Burbank’s formal education was only up to primary school, he had learned about horticulture and farming from experience and an interest in the field. His breeding experiments were driven more by an artist’s instinct rather than the scientific understanding of the laws of heredity. He read Charles Darwin’s article about the changes in plants and animals as a result of artificial selection during the process of domestication. This was the article that sparked his interest in plant breeding. He understood that crossings could bring together unconnected gene pools and that finding the desired combinations of traits in the progeny is a rare event and thus requires extensive selection. From his crossing experiments, he selected the best, discarded the rest, and did not keep systematic records of crossing results and the parental strains involved. It is said that Luther simultaneously conducted more than 3,000 crossings at a given time, and millions of plants grew on his farms. Burbank perfected grafting, crossings, and hybrid selection. In his fifty-five-year career, he developed more than 800 new varieties of plants derived from 121

genera: 250 new varieties of fruit, including 113 plums and prunes, 10 strawberries, 10 apples, the russet potato; 34 spineless cacti; about 50 varieties of lilies; and the Shasta daisy. He inevitably sold his new varieties to other growers or nurseries for further commercial production. Andrew Carnegie showed a keen interest in Burbank's work. And the Dale Carnegie Institute provided financial support to Burbank from 1905 to 1911. In 1893, Burbank published a catalog of his best plant varietals, *New Creation in Fruits and Flowers*, and also wrote other books on breeding experiments. It was the result of Burbank's efforts that, in 1930, America began to patent advanced varieties of plants.

Because Burbank worked from his own experience and did not keep accurate records, it was not possible for other scientists to review and repeat his work. Famous plant breeders and geneticists, such as George Harrison Shull, Hugo de Vries, Liberty Hyde Bailey, and Nikolai Ivanovich Vavilov, visited him to learn his methods. Shull and de Vries invested time to understand and evaluate Burbank's work and ultimately became frustrated with his random approach and lack of proper record keeping. However, Burbank became a celebrity in his lifetime and was referred to as the "high priest of horticulture" and the "plant wizard."

Burbank died on April 11, 1926, in Santa Rosa from a heart attack. Nikolai Vavilov wrote a lengthy tribute in remembrance of Burbank. In 1940, a US postage stamp was released in his honor, and in 1991, he was elected to the American Society for Horticultural Science Hall of Fame. The Luther Burbank Home and Gardens, in downtown Santa Rosa, was designated a National Historic Landmark in 2003.

## "Crank Gardener" Ivan Vladimirovich Michurin

Ivan Vladimirovich Michurin (1855–1935), a breeder in the Soviet Union, was a contemporary of Luther Burbank, but while Burbank became a celebrity breeder in his youth, Michurin remained hidden from the world until he reached old age. Michurin (see figure 4.7) lived on a rental farm in a small town named Kozlov near Saratov. Michurin was discovered by chance by Nikolai Vavilov. In 1920, Vavilov attended a conference in Saratov. After lunch, a junior scientist from the conference took the delegates for a walk in Michurin's garden. The first meeting between young Vavilov and the sixty-five-year-old Michurin lasted several hours. Vavilov was deeply impressed by Michurin's work but was stunned by the financial condition of this breeder, who was reclusive, paid all his attention to plants, and was considered "crazy" by people in the community.

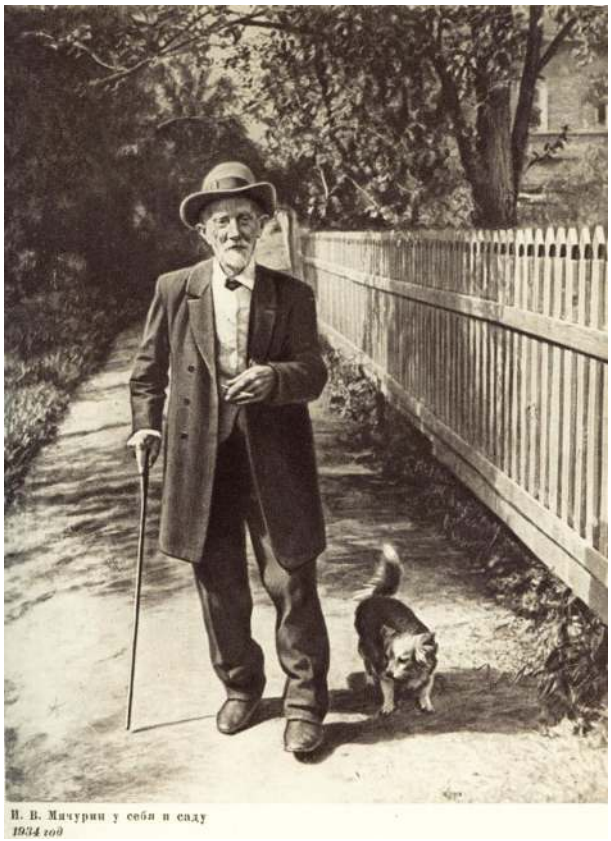



Fig 4.7 Ivan Vladimirovich Michurin, circa 1934. "Michurin in garden 1934" by Ivan Vladimirovich Michurin is in the public domain.

Like Burbank, Michurin had little formal education. His mother had died when he was a child, and his father had gone mad as Michurin reached his teens. At the age of twenty, he rented a small piece of land and started planting fruit trees in it. For fifteen years, he earned a living by working as a clerk, a watchmaker, and a telegraph operator, and when he was not working, he would continue to expand his garden. In 1899, he rented thirteen hectares (thirty-two acres) of land in Kozlov with his savings and brought along his plants. Then he spent thirty years grooming the farm. He had the passion of an artist with a keen eye of a clever gardener. He did not socialize with people and seems to be driven constantly by some sense of urgency for his nursery (that was not profitable). His economic condition did not improve, but he became famous as a "crank gardener" among the people. Throughout his life, Michurin's focus was on developing new varieties of fruit trees. He learned crossing, grafting, and plant training through trial and error. He acquired many varieties of apples, pears, peaches, apricots, and grapes from distant provinces of Russia and used grafting techniques to make them flourish in Kozlov. Typical fruit trees could not quickly grow in this wintry area, but Michurin had worked for forty-five years and developed about 350 new breeds of fruit trees that could thrive in extremely cold climates.

Vavilov sent a proposal to the Ministry of Agriculture to have experts review Michurin's breeding efforts, which was accepted. On top of that, the Soviet government rewarded him with 500 rubles, granted him the lease of the rental farm where he had set up those marvelous collections, and made that farm tax-free for his lifetime.

Vavilov's meetings with Michurin revealed new information and important details such as how to create the best hybrid variety, how to select hybrids, and so on. Vavilov succeeded in extracting and distilling the life experiences of a clever gardener and provided scientific explanations for why a particular technique worked or not. Subsequently, the Soviet government awarded Michurin the Order of Lenin and the Order of the Red Banner of Labor for his contribution to the field of agriculture. In 1928, Michurin's farm came to be known as the Genetic Station of Fruit and Berries, and in 1932, his town was renamed Michurinsk in his honor. In 1934, his farm was used for the I. V. Michurin Central Genetic Laboratory. In the last years of life, Michurin became a celebrity breeder in the Soviet Union.

## Summary

Overall, in the nineteenth century, it became public knowledge that living organisms change and are not constant. One source of change in living organisms is sexual reproduction, which allows the mixing of parental traits in the offspring. It also became clear that deliberate hybridization and selection can be used for crop improvement and that many species of plants found in nature were the results of the hybridization of related plant species. Linnaeus himself saw this phenomenon and identified many naturally occurring hybrid plants. Later, many success stories of hybrids emerged, and the hit-and-miss approach of hybrid selection reached its prime in the first decades of the twentieth century with Luther Burbank and Ivan Vladimirovich Michurin. However, simultaneously efforts to understand the laws of heredity began, and a new field of genetics came into existence.

### Further Readings


Chisholm, H. (Ed.). (1911). Camerarius, Rudolf Jakob. In *Encyclopædia Britannica* (11th ed., Vol. 5). Cambridge University Press.

Crow, J. F. (2001). Plant breeding giants: Burbank, the artist; Vavilov, the scientist. Genetics, 158, 1391–95. https://journals.ashs.org/hortsci/view/journals/hortsci/50/2/article-p153.xml

Darrow, G. M. (1966). *The strawberry: History, breeding, and physiology* (1st ed.). Holt, Rinehart and Winston. specialcollections.nal.usda.gov/speccoll/collectionsguide/darrow/Darrow_TheStrawberry.pdf

Darwin, C. (1868). *The variation of animals and plants under domestication*. John Murray.

Darwin, C. (1876). *On the origin of species by means of natural selection, or the preservation of favored races in the struggle for life*. John Murray. https://www.darwinproject.ac.uk

Janick, J. (2015). Luther Burbank: Plant breeding artist, horticulturist, and legend. *HortScience*, 50, 153–56. https://doi.org/10.21273/HORTSCI.50.2.153

Mayr, E. (1986). Joseph Gottlieb Kolreuter's contributions to biology. *Osiris*, *2*, 135–76. https://doi.org/10.1086/368655. JSTOR:301833.

Strawberry: A Brief History can be found at https://ipm.missouri.edu/meg/2012/5/Strawberry-A-Brief-History/

1. Artificial pollination was in use since ancient times: Stone carvings from ancient Assyria (2400–612 BCE) clearly depict the artificial pollination of date palms (*Phoenix dactylifera*) and suggest that the knowledge of different sexes of date palms and the need for sexual reproduction did exist. However, this knowledge was not extended to other plants for deliberate hybridization and crop improvement. This phenomenon was also unknown to Europeans. Camareus made the first intellectual attempt to understand the structure of flowers and extended this knowledge to all plants ↵
2. Many plants reproduce only asexually and do not produce seeds and flowers (e.g., money plant and duckweed). In addition, some flowering plants can reproduce asexually—including onion, potato, and gladiolus—as well as many trees that are propagated by using cuttings. The plants generated from asexual reproduction are genetically identical to their siblings and parent plant. ↵
3. The original publications of Carolus von Linné (Linnaeus) are available at the Biodiversity Heritage Library website: https://www.biodiversitylibrary.org/browse/collection/37. ↵
4. The schema proposed by Linnaeus served as a primer for the classification of plants and animals as well as provided a framework for comparative studies for the past 300 years. However, with the advancement of gene and genome sequencing, this schema is now being modified/updated. You can find the latest information on the Tree of Life web project at http://tolweb.org/tree. ↵
5. Until World War I, Austria, the Czech Republic, Slovakia, Croatia, and Hungry were part of the Austro-Hungarian Empire ruled by the House of Habsburg. Moravia is now in the Czech Republic. ↵

---

This page titled 6.2: Cataloging, Classification, and Deliberate Hybridizations is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley via source content that was edited to the style and standards of the LibreTexts platform.

- **1.4: Cataloging, Classification, and Deliberate Hybridizations** is licensed CC BY-NC 4.0. Original source: https://open.oregonstate.education/cultivatedplants/.

# 6.3: Plant Breeding

**Learning objectives**

By the end of this lesson you will:

- Understand how to get started breeding two common ornamental and food species.
- Know the purpose of emasculation when making hybridizations (crosses) between parents.
- Recognize the difference that propagation method makes in a plant breeding program.

## Overview

This lesson presents examples of plant breeding of two common garden plants, rose and tomato. The strategies for the two plants differ because of how the final plant will be propagated. Roses are propagated asexually, while tomatoes are propagated by seed. For both, breeding starts with a cross between two different plants (called a bi-parental cross).

## General information about rose

Watch this video for an introduction to breeding roses and identifying rose hips (1:49)

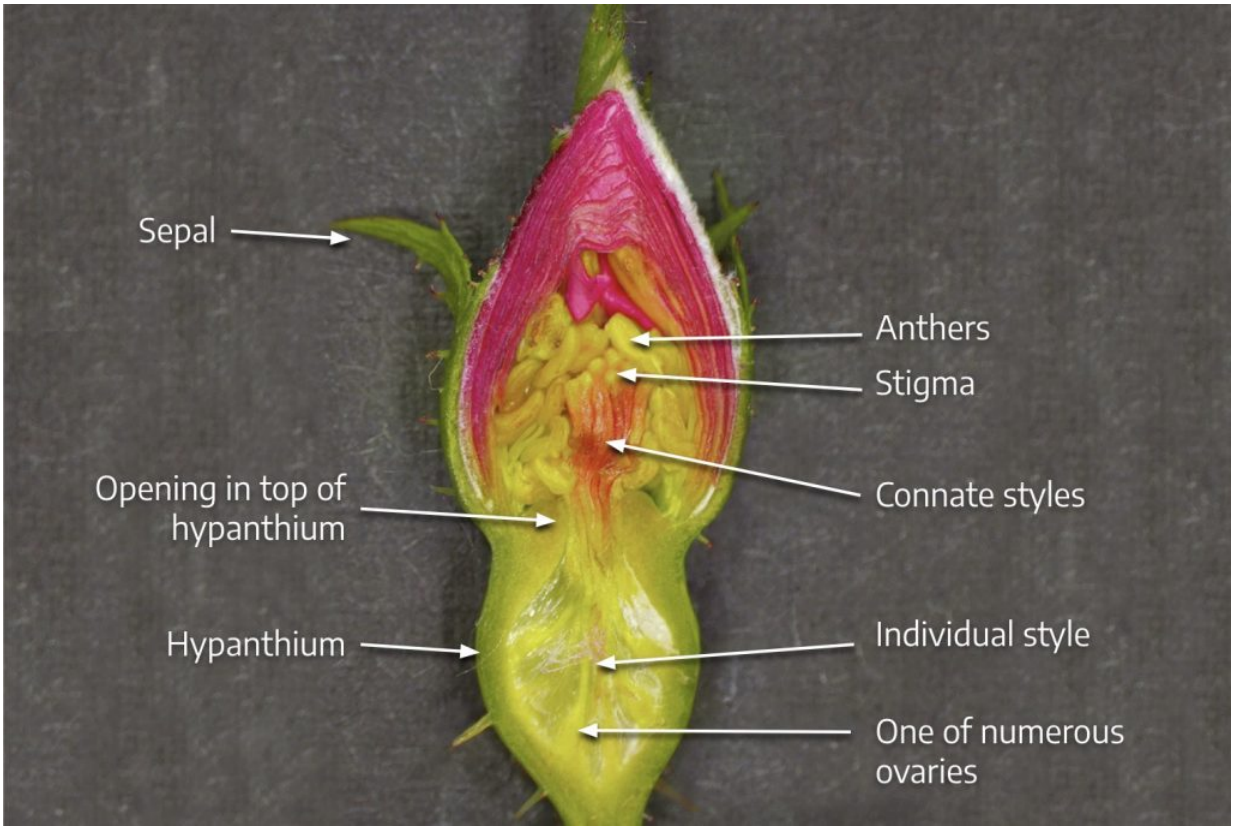



Photo by Eastfield College Microscopy Lab, Mesquite, TX, CC BY-NC.

Rose (genus *Rosa* with many species) is a perennial, mostly deciduous (they annually lose their leaves), mostly temperate-climate shrub in the Rosaceae family. The rose flower is perfect. The calyx, corolla, and androecium whorls are fused at their bases to form a small cup-shaped structure called a **hypanthium** that surrounds the ovary. (Refer to Chapter 8 if these are not familiar terms.) The base of the hypanthium is attached to the receptacle. The hypanthium is the structure that ripens into a bright red or red-orange fruit called a "hip," recall that this is also the tissue that forms the fleshy part of the apple. Within the hypanthium are hard achenes containing the rose seeds. In summary, the rose hip is an accessory fruit (parts other than ovary wall constitute the fleshy ripe portion) and an aggregate fruit (one flower, many carpels forming separate fruits) where the subsidiary fruits are achenes (optional).



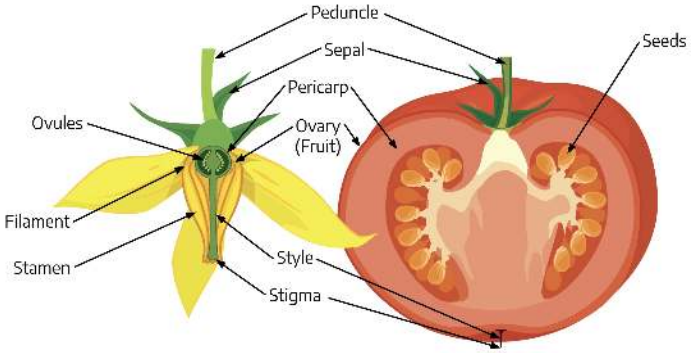
Nevada rose. T. Kiya. CC BY-SA 2.0

The species of rose differ in their chromosome number, or ploidy. Roses have seven different types of chromosomes, so the total number of chromosomes in a rose is normally a multiple of seven. Some species, particularly wild species, are diploids with two sets of chromosomes, and so have a total of 14 (2 x 7 = 14) chromosomes. The large-flowered hybrid tea roses have four sets of chromosomes, so they are tetraploids with 28 (4 x 7 = 28) chromosomes. There are even triploid roses with 21 chromosomes. This optional journal article by Cédric Grossi & Maurice Jay on Chromosomes studies of rose cultivars provides more information on chromosome numbers. Some roses are sterile because of triploidy or an imbalance in chromosome numbers, and never form rose hips. Sterile roses cannot be used to breed new roses. From a practical standpoint, if the rose is fertile you can use it in backyard breeding without much concern about whether it is diploid or tetraploid.

Roses can self-pollinate or cross-pollinate. A breeding project should be started with a cross. Because the flowers are perfect, you need to emasculate (remove the anthers from) the flowers you intend to use as the female. Emasculation happens at the bud stage before the pollen has been released and before the stigma is receptive. If you wait too long, the pollen will be shed and the stigma may have received pollen from its own anthers. The commercial roses that you grow in your garden are normally the result of cross-pollination and are genetically highly heterozygous (the opposite of inbred), which in this case refers to most of the loci of plant being in a heterozygous condition or having two different alleles. High heterozygosity results in a more vigorous plant because the genome has increased diversity. Roses are asexually propagated by rooting or grafting cuttings of desirable plants so that superior genotypes are maintained and not broken up by meiotic cell division, as would happen through seed propagation.

## General information about tomato

Tomato, *Solanum lycopersicon*, is a member of the Solenaceae family, the same family that contains potato, pepper, tobacco, and nightshade. The crop has a fascinating history, starting with its likely origin in Peru, importation to Europe with returning explorers, gradual introduction into European cuisine (some cultures associated tomato with nightshade and considered it poisonous), and introduction to North America. This optional tomato history page describes one version of this history.




Tomato flower and fruit. © Shutterstock. Adapted and labeled by Emily Tepe.

The tomato flower is perfect (in the botanical sense). The anthers form a cone that completely surrounds the gynoecium. In wild tomatoes, the stigma and style protrude up above the cone of anthers, so these wild types tend to cross-pollinate. The stigma of domesticated tomatoes is either just slightly above the cone, or buried within the cone. Domesticated tomatoes self-pollinate, so we will also need to emasculate the female plants in our crosses. The pistil is made up of several fused carpels, and the mature fruit is a berry.

In contrast to rose, all tomatoes, whether wild or domesticated, are diploids where $2n = 24$. They will all cross with each other. Domesticated tomatoes that you grow in your garden are either highly homozygous (inbred) or are $F_1$ hybrids and highly heterozygous. Heirloom and older style tomatoes are typically inbreds (sometimes called pure lines or [incorrectly] open pollinated in seed catalogs), while modern and commercial tomatoes are $F_1$ hybrids. You can use either heirloom or commercial hybrid types in your breeding experiments. Tomatoes are propagated by seeds.

**? Review questions**

1. Compare and contrast rose and tomato for their ploidy and method of propagation.
2. How does the variation in ploidy affect rose breeding? Does it have the same impact on tomato breeding?
3. What is emasculation and why is it done? Which parent do you emasculate, or do you emasculate both parents?

## Rose breeding

The overall strategy:

- Identify your objective.
- Choose your parents.
- Make controlled crosses among parents.
- Plant the $F_1$ seeds.
- Evaluate the offspring over a few years.
- Keep seeds from the best plants and compost the rest.
- Asexually propagate the very best one or two by stem cuttings.
- Sell the rights to your award-winning rose to a nursery who distributes it worldwide.

You should start a breeding project with an objective in mind. At first, your objective will probably be just to see if the process works. Later, you will have specific characteristics in mind that you would like to emphasize in the progeny from the cross. Step two is to choose your parents; at least one of the parents should have the trait you are interested in — like flower color, disease resistance, or cold hardiness for surviving Minnesota winters. The other parent should have complementary traits, like size, branching, floral scent, or long vase life.

In a rose, you might choose as the female a nice shrub rose with an attractive red flower and that has made it through several winters without special care. If it has nice full rose hips at the end of the year, you know it's fertile. Perhaps you'd like the new rose to have the same flower type and color, but in a dwarf plant. And perhaps your neighbor has a dwarf rose that sets hips and must be fertile, and you can use some pollen from that rose even though you don't like the color of its flower. Hopefully, you'll get some

offspring that show the same red as your female, but in the dwarf growth habit. (You'll probably get some sprawling, gangly rose plants with ugly flowers as well, but you can toss them in the compost.)

Try the cross in the opposite direction as well (switch which plant is male and which is female). This is called a **reciprocal cross**. Sometimes the cross is easier to make in one "direction" (A x B vs B x A) than the other. When writing a pedigree for the cross, which shows the names of the two parents, remember to write the female first — cross A x B, for instance, means plant A was the female. Breeders sometimes write the pedigree with a slash ("/") rather than an "X:" A/B.

By making several crosses that meet your objectives, you increase your chance of obtaining the specific combination of alleles for the specific traits. If a plant meets your objectives it can be asexually propagated, not by seed, so that you keep the genotype intact in your propagules.

### Rose hybridization

The main steps in crossing are:

- Choose buds at the right stage.
- Emasculate the female.
- Collect pollen from the male.
- Transfer pollen from anther of male to stigma of female.
- Identify the cross with a tag.
- Protect the carpel until the ovary begins to swell.

Rose hybridization is a sufficiently popular hobby among gardeners that there are websites with reasonably easy-to-follow instructions. This is a good example from a rose breeding project (12:18 min).

The Santa Clarita Rose Society in California has an informative hybridization page, with photos and descriptions of the rose flower before and after emasculation, pollen transfer with an artist's brush, and the resulting hips and achenes.

While you may get your first bloom when your new hybrid is just a seedling, you won't know whether you have a really good rose until you have grown it outdoors for two or three years. Once you think you have something you want to propagate, use stem cuttings to propagate the selected plant.

Roses are a good example of a common garden plant you can hybridize. You germinate the resulting seeds, evaluate the progeny, and then asexually propagate the plants you like. It will take at least three years or more to identify plants that maintain the traits you desire to continue through multiple years and environments.

**? Review questions**

1. When making a cross, why is staging the flower development important for emasculation and pollination?
2. In the cross MN5125 / ND163 which of the two parents do you emasculate?
3. What is a reciprocal cross?

## Tomato breeding

The overall strategy:

- Identify your objective.
- Choose your parents.
- Make controlled crosses among parents.
- Plant the $F_1$ seeds.
- Evaluate the offspring for the characteristics you are most interested in.
- Keep the seed from the best plants and begin inbreeding.
- Grow the seed from the best plants next spring or in a greenhouse.
- Select the best plants, allow their flowers to self, and keep the seed.
- Repeat the last two steps for about 5–7 generations. Notice that the progeny are now very similar to each other.

- Somewhere around year 5 or 6, identify the best plant that will be the founder of your new, pure line (true breeding) tomato cultivar.
- Sell the rights to your award-winning tomato to a seed company who distributes it worldwide.

Notice that the rose and tomato strategy lists are not identical. With roses, we planted out the seeds from the hybridization, took a few years identifying the best plants, and propagated them asexually. With tomatoes, we want to develop pure lines by inbreeding. Inbreeding is producing seed by selfing over 5–7 generations to develop plants that are highly homozygous at most loci in their genomes. Homozygosity results in identical plants propagated by seed. This is done so the resulting progeny look more and more alike until, after 4–6 years, plants grown from seeds harvested off the same plant are indistinguishable from each other. At that point you have an inbred pure line that will be true breeding if self-pollinated, and you can be pretty sure that you know what you're going to get when you plant seed from year to year. The seed from inbred pure lines are the same because all loci are homozygous, so all gametes are the same and fertilization produces clonal seeds.

Again, identify your objectives and then choose the parents. You might like the cherry tomato that you've been growing on the patio because the fruits are perfect for salads. But being a loyal Gopher, you'd like a gold fruit rather than one that's Badger red. So you reciprocally cross the red patio tomato with the gold beefsteak type tomato and begin assessing progeny.

## Tomato hybridization

- Choose buds at the right stage.
- Emasculate the female.
- Collect pollen from the male.
- Transfer pollen from anther of male to stigma of female.
- Identify the cross with a tag.
- Collect seed at maturity.

This is a practical video on crossing tomatoes (2:18 min).

Review the information on this site on tomato hybridization.

Tomato is a diploid. This series of web pages (optional) walks you through the outcomes of meiosis in a diploid (click on the links at the bottom of the page to get the whole story), and has graphics illustrating how self-pollination leads to inbred pure lines. There is also a page that runs you through calculations to estimate the number of plants you will need to have a reasonable probability of finding the combination of characteristics you seek. Don't sweat the probabilities of success. Despite the statistics, some of breeding is a chance event at combining the correct set of alleles. Choose your parents wisely, make the cross, evaluate your progeny, and plant out seed from crossing the best progeny the next year. Keep it simple.

Be sure to keep accurate notes, and to tag and identify your crosses, seeds, and plants. Recall the rose breeding website, and how the breeder clipped the sepals of the female flower he was pollinating so he could tell which rosehip contained hybridized seeds. That's an efficient way of avoiding self-pollinated seed.

## Dehybridizing

Most new commercial tomatoes, including new garden tomatoes, are $F_1$ hybrids. The seeds you plant in the field are the result of crossing two parents, as described above. By planting the $F_1$ hybrid, the grower capitalizes on the extra vigor associated with a highly heterozygous hybrid genotype. This website (optional) discusses hybrid tomatoes vs. saving the seed from the hybrid to plant. It's an interesting discussion, but remember that science is a systematic study and requires replications, something you don't get from planting seeds from a hybrid in a single year. If you collect seed from a hybrid tomato fruit, whether from a hybrid plant in your garden or a fruit from the grocery store, those seeds are $F_2$ seeds. By planting those seeds out, selecting the most vigorous seedlings, and later in the year keeping seeds from the plants with the best fruits, you are following the same steps laid out in the tomato breeding section, except that you fast-forwarded past the crossing and $F_1$ grow-out stage and went directly to the $F_2$. If you continue to grow out the seed and select the best plants for a few more years, you will end up with a stable variety of your own. This process is called **dehybridizing** because you are starting with a hybrid, but after several generations of production, selection, and seed saving you are creating new pure lines from that hybrid.

This approach will work well with hybrid tomatoes and hybrid peppers because they are naturally self-pollinating. Garden catalogs will tell you whether the seed you are buying is hybrid. If you are getting your fruits from the store, you can count on them being hybrids unless they are marked as heirloom. The upside of dehybridizing is that it's the easiest way to breed your own crop because you don't have to emasculate and cross. The downside is that you are breeding "blind." You didn't choose the parents for the $F_1$ cross to achieve your objective, and you don't know the parents' characteristics, so the phenotypes that you get from dehybridizing are anyone's guess.

**? Review questions**

1. Why do you have to allow tomato to self-pollinate for several generations after you make the hybridization?
2. Why dehybridize? What type of crop (naturally inbreeding or naturally outcrossing) would you be most likely to dehybridize? What is the downside of dehybridizing?

---

This page titled 6.3: Plant Breeding is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley via source content that was edited to the style and standards of the LibreTexts platform.

- **14.4: Plant Breeding** by Tom Michaels, Matt Clark, Emily Hoover, Laura Irish, Alan Smith, and Emily Tepe is licensed CC BY-NC 4.0. Original source: https://open.lib.umn.edu/horticulture.

# 6.4: Genetic Improvement in Cereal Crops and the Green Revolution

As the field of genetics matured, it became possible for breeders to develop improved crop varieties using Mendelian genetics, genetic maps, and markers. A breeder usually combines the desired genes from two varieties via crossing and then selects progeny containing desired traits. If four different useful genes are found in four different wheat varieties, using a step-by-step approach, a breeder could bring all four genes in the one preferred variety. However, a breeder does not create new genes; he or she only combines preexisting genes present within the genetic pool. Therefore, the biodiversity of any species determines the limits of classical breeding. This chapter summarizes the genetic improvements made in three main cereal crops—maize, wheat, and rice—using the classical breeding approach and their role in making the green revolution successful in the latter part of the twentieth century. In the process, various international agricultural research centers evolved under the Consultative Group for International Agriculture (CGIAR) umbrella, which is playing a critical role in achieving global food security.

## Story of Maize

Maize—more popularly known as corn—is the main staple crop of the Americas. Maize (*Zea mays L.*) is a member of the grass family Poaceae (Gramineae). Mexico is the center of the domestication and diversification of maize (1). Maize's ancestor is a wild grass, *Teosinte parviglumis*(2).[1] Until 1492, people outside of South, Central, and North America were unaware of maize's existence. Native Americans have been cultivating maize for ~7,000 years.

Maize is unique among the cereal crops because it is monoecious (it bears separate male and female inflorescences on the same plant). The main stem terminates in a tassel (male inflorescence), and the silk containing female flowers is on the stem. The natural structure of the maize plant favors cross-pollination. The pollen from the male flowers reaches the female flowers (of the mother plant or other nearby maize plants) via wind. Thus in maize, an equal possibility of self-pollination and cross-pollination exists. The pollen of different plants can reach a female flower, leading to the fertilization of the egg cell independent of one another. After successful pollination, the seeds on a cob are not uniform because each seed results from an independent pollination event. In nature, genes are exchanged continuously between maize plants, which results in new combinations.

### Discovery of Hybrid Vigor and F1 Hybrids of Maize

In 1876, William Beal, a scientist at the Michigan Agricultural College, conducted crossings between maize varieties. To control pollination, Beal cut off the male flowers of the female parent (this process is known as detasseling) to ensure 100 percent cross-pollination from the chosen male parent and 100 percent hybrid progeny. Beal observed that the yields obtained from hybrids were higher than either of their parental varieties. In 1877, Charles Darwin also experimented with crossing maize varieties. He observed that the offspring resulting from outcrossing produced 25 percent larger cobs than from selfing and that the hybrids had a greater ability to tolerate chilling stress.

In 1908, George H. Shull and Edward East independently experimented and developed purebreds of maize. They noticed that after successive cycles of selfing, the maize plants' size and their yields decreased. This phenomenon was named *inbreeding depression* (see figure 6.1). Like Beal and Darwin, Shull also noticed that F1 hybrids are taller and healthier than their parents and produce higher yields; he named this phenomenon *hybrid vigor* or *heterosis* (see figure 6.1). Shull further made a very useful observation that after three generations of inbreeding, maize behaves almost like a purebred that can be used for producing the F1 hybrid. Such an approach could ensure 100 percent human control over pollination and good yields year after year. However, Shull did not have enough resources to continue his work on F1 hybrids of maize. In 1913, Shull migrated to Germany and became the editor of the scientific journal *Genetics*. East, a Harvard University professor, was also not able to pursue his research on maize, but he encouraged a new generation of scientists. One of his students, Donald F. Jones, crossed the two purebreds of maize to create an F1 hybrid, and afterward, by crossing two different F1 hybrids, he successfully created double-cross hybrids (see figure 6.1). Jones observed that the yield of the double hybrids was higher than single hybrids. Therefore, the most successful corn crop was the double-cross hybrid, and it laid the foundation for the widespread use of double-cross hybrids in the US. The hybrid vigor of maize was only maintained if new seeds were purchased every year, which made the seed industry commercially viable.

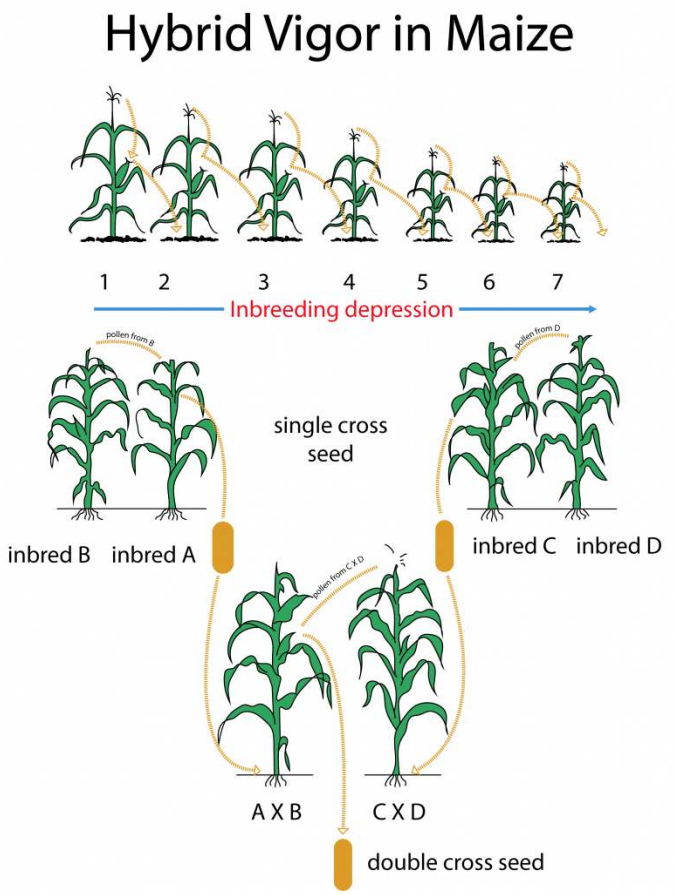



Fig 6.1 Inbreeding depression and Hybrid vigor in maize. “Hybrid vigor in maize” by Sushma Naithani and OSU OERU is licensed under CC BY 4.0.

In the 1930s, the US Department of Agriculture helped farmers adopt F1 double-cross hybrid varieties of maize, leading to progressively higher yields. The first two hybrid varieties were grown side-by-side, and later to ensure 100 percent double hybrids, one row of pollen donor (male) was planted between every four rows of detasseled female plants. Gradually, most American farmers adopted this practice of maize cultivation. In 1933, less than 1 percent of total maize grown in the US was a double hybrid, but by 1944, it increased up to 56 percent. From 1930 to 1990, American scientists released about thirty-six improved hybrid varieties of maize, and farmers gladly adopted better varieties one after the other.

## US–Mexico Collaboration on Agriculture Research

In 1941, the vice president of the United States, Henry A. Wallace (1888–1965), traveled to Mexico to attend the inauguration ceremony of the newly elected president of Mexico, Manuel Ávila Camacho. Roosevelt and Wallace had also won elections in the US that same year. After attending Camacho’s ceremony, Wallace spent the first two days in the Bajio region with outgoing president Lázaro Cárdenas and newly elected agriculture secretary Marte Gómez. Wallace noticed that due to maize’s continuous cultivation, the Mexican soil had lost its fertility, and farming had become very unproductive. While the Iowa farmer spent ten hours to produce ten bushels of corn, it took a Mexican farmer 200 hours for the same. Wallace and his hosts discussed how the United States could help increase the productivity of Mexican farms. Wallace promised to help.

Upon his return to the US, Wallace contacted Raymond Fosdick, then the president of the Rockefeller Foundation, about providing US aid to Mexico and developing the appropriate project. Fosdick set up a three-member committee that consisted of maize geneticist Paul Mangelsdorf (Harvard University), agronomist Richard Bradfield (Cornell University), and plant pathologist Elvin Stakman (University of Minnesota) to evaluate a plan on agricultural cooperation between the US and Mexico. In 1942, these three experts recommended a pilot research program that led to the establishment of the Oficina de Estudios Especiales (OEE) program in 1943 with support from the Rockefeller Foundation and the Mexican government. The OEE’s mission was to train Mexican scientists across all disciplines to support the agricultural production of four major crops: maize, beans, wheat, and potatoes. The

objective of establishing the Colegio de Postgraduados at Chapingo University in Texcoco, near Mexico City, was added in later years. Mangelsdorf supervised the maize research program, and Stakman was given the responsibility of directing the wheat breeding program.

### Maize Germplasm Collection and Breeding from the 1950s to the 1960s

In 1943, a research project on maize was started under the supervision of Professor Paul Menzaldorf with the support of the Rockefeller Foundation. Menzaldorf's team promoted F1 and double-cross hybrid varieties of maize developed by American scientists in Mexico. They also developed hybrids of local Mexican maize varieties. By 1947, ten new high-yielding double hybrids were released in Mexico under this program. In 1948, Mexico broke old records in maize production and became self-sufficient. By 1960, one-third of Mexico's farms were cultivating high-yielding hybrids, and corn production had tripled. Menzaldorf's team also began the collection of maize germplasm from Mexico and Central America. Since then, 28,000 maize varieties have been collected. This collection, representing almost all local maize varieties from eighty-eight countries, is stored at the Corn Germplasm Bank at the International Maize and Wheat Advancement Center (CIMMYT; https://www.cimmyt.org) located in Mexico City.

## Story of Wheat

Wheat is the second widely grown cereal in the world after maize. However, unlike maize, most of the wheat is consumed as food. Wheat (*genus Triticum*) has many diploid and polyploid species (see figure 6.2). The einkorn (*T. monococcum L.*), the oldest among domesticated wheat varieties, is a diploid species that contains the AA genome. A natural hybridization event between einkorn and a diploid weed goat grass with the BB genome gave rise to the emmer/durum wheat (*T. turgidum*). Therefore, emmer is tetraploid (AABB). Archaeological evidence suggests that the domestication of einkorn and emmer varieties occurred almost simultaneously (10,000–12,000 years ago) in the Fertile Crescent. Wild emmer (*T. turgidum* ssp. dicoccoides) is the progenitor of today's tetraploid durum wheat (3).

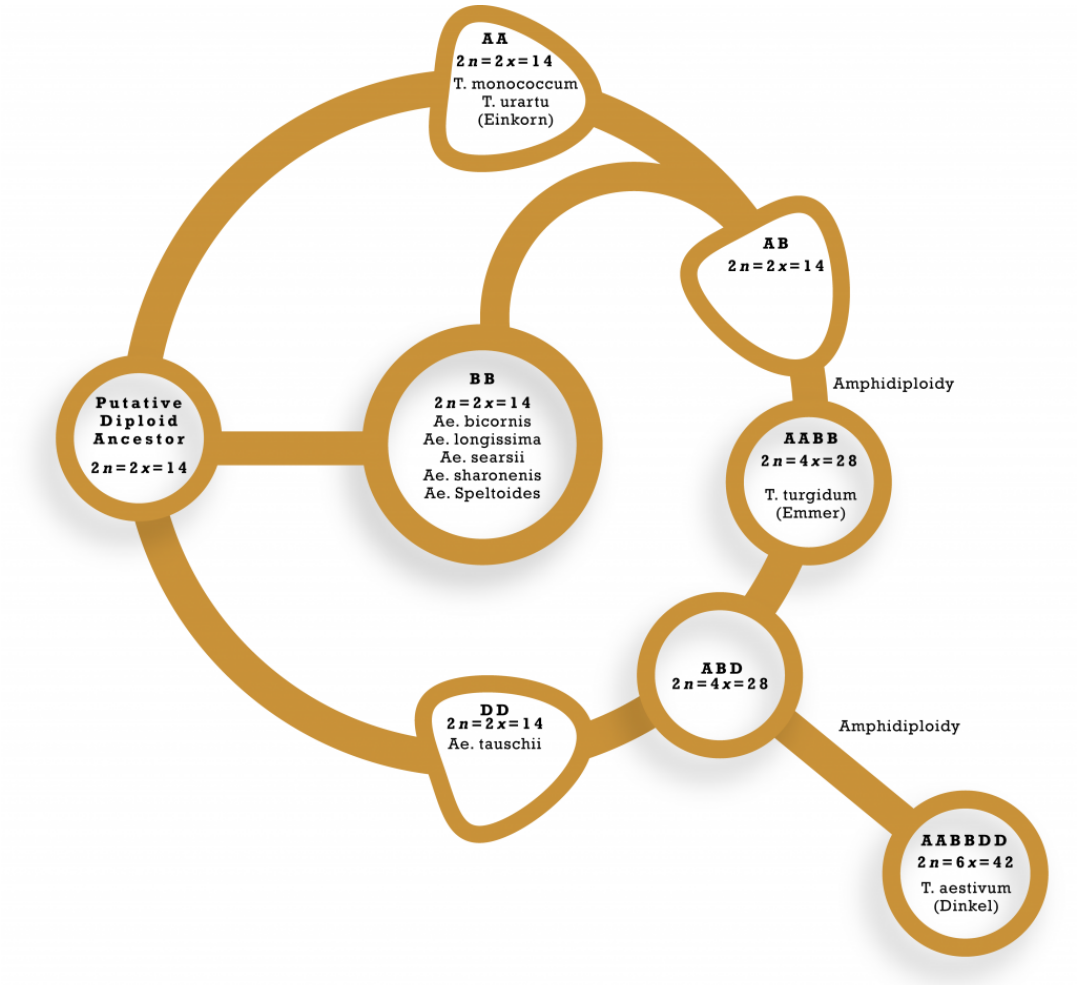



Fig 6.2 “Origins of the polyploid wheat” by Sushma Naithani and OSU OERU is licensed under CC BY 4.0.

A subsequent spontaneous natural hybridization event between emmer (AABB) and another species of wild grass, *Aegilops tauschii* (DD), gave rise to the hexaploid (AABBDD) spelt/dinkle or common bread wheat (*T. aestivum*) (3). Archaeological evidence suggests that spelt’s birthplace is the southeastern mountainous region of present-day Turkey. The polyploid durum and bread wheat produce larger seeds than the diploid species and their wild ancestors and also have a greater capacity to tolerate adverse conditions. Scientists estimate that around 7,000 years ago, the emmer wheat had spread outside its center of domestication and reached India, Central Asia, Egypt, and Europe. Emmer was the main cereal crop in Egypt at the time of the Pharaohs, while spelt was one of the major cereals of the Alemannians in southern Germany, Austria, and Switzerland between the twelfth and nineteenth centuries. Over time, many local varieties of wheat emerged in different regions due to the continued artificial selection of einkorn, emmer, and spelt in a variety of climates. Although these varieties show adaptations to local climates and may differ in morphological traits, most are subspecies of *T. turgidum* and *T. aestivum*. The wild einkorn and wild emmer have brittle rachis, while their domesticated descendants have nonbrittle rachis (see figure 6.3). This domestication trait caused the loss of shattering of mature seeds, and it became possible for the farmer to harvest the crop all at the same time.

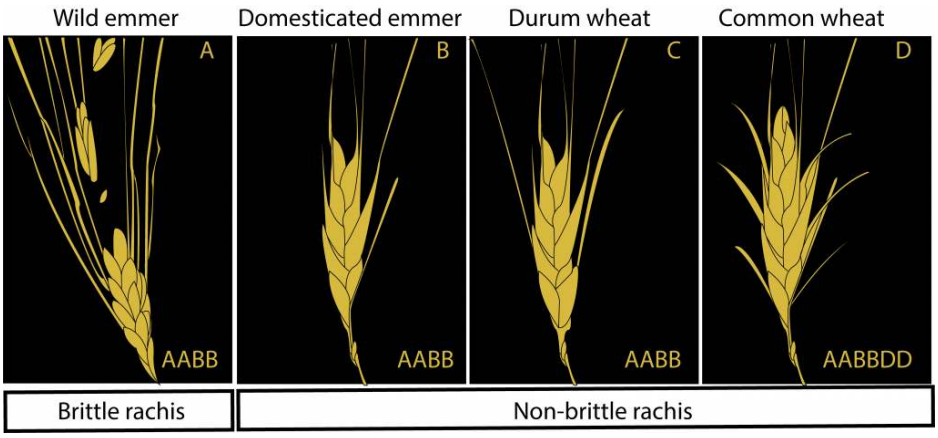



Fig 6.3 Mature seeds of the domesticated wheat species do not shatter. "Seeds of domesticated wheat" by OSU OERU is licensed under CC BY 4.0.

Spelt, emmer, and einkorn are hulled wheat species; their kernels cannot easily be extracted by threshing, and thus at harvest, the chaff remains at the kernels, and a special dehulling of the kernels is required in the mill to separate the chaff from the grain. A mutation in two genes, tenacious glume (*Tg1*) and *q* resulted in free-threshing wheat. Thus mutations in the Br1 loci on chromosomes 3A and 3B, *Tg1* on 2D, and *q* on 5A had the most profound impacts on wheat's domestication. In the last centuries, einkorn, emmer, and spelt were replaced by free-threshing durum and bread wheat. Durum (*T. durum*) is mainly used in the making of pasta and semolina. The common wheat (*T. aestivum*) is most suitable for bread, cookies, cakes, crackers, pastries, and noodles (it forms a spongier dough due to its higher gluten content and low gliadins/glutenins ratio). Ninety-five percent of wheat grown worldwide is common bread wheat, and the remaining is mostly durum. Recently, interest in ancient wheat species has been renewed for producing high-value baking goods due to their high nutrition content, and a market for catering to food-conscious elites is slowly growing.

## Beginning of Wheat Breeding Program in Mexico

In 1943, Stakman directed the OEE's Cooperative Wheat Research and Production Program in Mexico. At that time, agricultural research in Mexico was almost at a standstill. There was no single agriculture scientist with a PhD and no active research program on agriculture in Mexico and South America. He recommended that Norman Ernest Borlaug (1914–2009), his former student, be brought to Mexico for a leading wheat breeding program. Borlaug had finished his PhD under the supervision of Stakman a year earlier, and he was working for DuPont as a scientist. In Mexico, George Harrar, a plant pathologist, oversaw the local unit. The three other scientists in his team (besides Norman Borlaug) were Edward Wellhausen, John Niederhauser, and William Colwell, all from the US.

Borlaug arrived in Mexico in 1944 to lead the International Wheat Improvement Program at El Batátan, Texcoco, outside of Mexico City. This was his first time traveling outside the US, and he didn't know Spanish. He camped at a research center in the Yaqui Valley in Sonora, Mexico. In the 1930s, the governor of Sonora, Rodolfo Elias Calles, had set up that research station to help farmers. The station owned land for experimental research and some animals. The first director of this station, Edmundo Teboada, worked on some varieties of Mexican wheat and built a small wheat germplasm collection. But the research station did not have any modern farm equipment or any trained scientist.

There was no maintenance for this research station. So when Borlaug reached there, it was a mess. There was no electricity, and the windows and doors were broken. But Borlaug was not discouraged and managed to set up humble arrangements for his living quarters, and in the early morning, he started working like a farmer. Borlaug established connections with farmers in the Yaqui Valley, who were relatively prosperous and had a good irrigation system compared to other wheat-growing regions of Mexico. Borlaug borrowed tractors and other machinery for research from these farmers as needed. Between 1939 and 1941, the problem farmers faced in this area was primarily rust, a plant disease that would infect their wheat. So Borlaug initiated work on the development of a wheat that can fight rust. First, he selected the wheat varieties from Teboada's collection, which showed some ability to resist rust. He then began a series of crossing and backcrossing experiments with wheat varieties to develop high-yielding, rust-resistant wheat (see figure 6.4).



Fig 6.4 "Norman Borlaug – LIFE" by Lou Gold is licensed under CC BY-NC 2.0.

## Shuttle Breeding: Stem Rust-Resistant Wheat Varieties

Generally, it takes ten to twelve generations to combine useful desirable traits from two varieties of a crop by implementing classical breeding and selection methods. Thus at least ten years were needed for making a new breed of rust-resistant wheat. Borlaug thought that if two wheat crops could be grown per year, then a new variety of wheat could be made in five years. Fortunately for Borlaug, this opportunity was available in Mexico. In Sonora, wheat is sown in October and harvested in April. In the mountainous region of Toluca Valley in central Mexico, wheat is sown in April and May and harvested in October. Thus taking advantage of this, Borlaug began shuttle breeding. As soon as the wheat crop was harvested in Sonora (in April), Borlaug sent these seeds for sowing in Toluca. Similarly, after the crop harvest in Toluca (in October), new seeds were sent to Sonora. Borlaug's shuttle breeding program was not well received by his seniors at the Rockefeller Foundation. Until that point, there was a general agreement that the wheat seeds need a resting period after harvest (or before sowing the following year). Stakman advised Borlaug not to waste time and resources. When Borlaug submitted his resignation in response, no one stopped him from using shuttle breeding.

Interestingly, the two locations (Yaqui and Toluca) used for shuttle breeding not only were 1,000 kilometers apart but also differed in latitude (by 10°) and elevation (by 2,000 meters; see figure 6.5). The Yaqui Valley is located at latitude 22° north and the Toluca Valley is located at latitude 12° north. Apart from this, the days of wheat cultivation in Yaqui Valley are shorter than in Toluca. As a result, the new wheat varieties developed by shuttle breeding became neutral to day length and regional climates. Those varieties could be grown on long and short days, on highland and valley, and at any elevation. These characteristics proved to be very helpful in spreading the improved varieties of wheat worldwide. The shuttle breeding experiment also reduced the time by half required for producing a variety using traditional breeding.




Fig 6.5 Locations of Norman Borlaug's research stations in Mexico. "Borlaug Mexico locations" by CIA is in the public domain.

There was no agricultural extension program in Mexico to help Borlaug; he worked directly with the farmers. As he developed new breeds, he gave them directly to the local farmers for preliminary testing. If farmers had positive results, then the seeds of those varieties were sent to experts worldwide for detailed testing. In this way, he built collaborations with local farmers and scientists from all over the world. Between 1948 and 1950, Borlaug released eight new wheat varieties in Mexico, each of which seemed to be more resistant to rust. In addition to developing advanced varieties of wheat, Borlaug advised farmers on the right quantity of fertilizer to use and how to improve irrigation facilities. The best wheat yield in the Bajio region in Mexico without the use of

fertilizers and irrigation yielded 1 ton/hectare. But after using sufficient fertilizers, irrigation, and weed management, these same wheat varieties yielded 7.5–8 tons/hectare.

In 1951–54, a rust epidemic devastated the wheat crop in North America due to the explosion of a highly pathogenic strain, 15b. By 1955, rust disease became a major challenge for American farmers. Under the pressure of this epidemic, many wheat nurseries were built around the world with the help of scientists from seventeen countries, and research on almost every kind of rust strain began. Also, the collection of wheat germplasm was undertaken afresh.

Since Borlaug already had several wheat varieties with rust resistance, he was assigned the responsibility of developing new varieties of American wheat and training other scientists. He built nurseries in Yaqui to test the wheat varieties' ability to fight rust. He selected those varieties that had larger, more seeded panicles; were rust resistant; and could produce higher yields when a sufficient amount of fertilizer and irrigation was supplied. In this way, rust-resistant, high-yielding varieties were developed.

### High-Yielding Dwarf Wheat

By 1950, the prevalent wheat varieties were six to eight feet long, and their thin stalk was weak, which often collapsed under the weight of their own grain—a trait called lodging. Moreover, the high-yielding varieties were more damaged by thunderstorms, as they grew even taller in response to synthetic fertilizer. Therefore, the breeders wanted to create a rust-resistant dwarf variety of wheat with a strong stem that can bear more weight. Borlaug had developed the rust-resistant, high-yielding wheat varieties, but he did not have any dwarf wheat in his collection. Thus the search for dwarf wheat was ongoing. Finally, S. Sisil Samon of the US Agricultural Research Service spotted a dwarf wheat variety, Norin-10, in Japan. He sent Norin-10 seeds to Professor Orville Fogle, who sent it to Borlaug.

In 1959, Borlaug crossed Norin-10 with some of his best North American varieties to create dwarf wheat varieties with a thicker, stronger stalk (e.g., Penjamo 620, Pittic 62, Gaines, Lerma Rojo 64, Siete Cerros, Sonora 64, and Super X). These high-yielding, rust-resistant dwarf varieties can stand the high winds, are amenable to machine harvests, and respond well to the application of fertilizers and irrigation. By 1963, 95 percent of Mexico's wheat acreage was sown with these dwarf varieties. Thus a complete package was developed to increase wheat production, including improved seeds, synthetic fertilizer, pesticides and weedicides, irrigation, and machines. The implementation of this package in Mexico led to unexpected success in wheat production. In 1958, Mexico became self-sufficient, and in 1960, it started exporting wheat to other countries. The US also shared this success; from 1960 on, it became the leading exporter of wheat. These advancements in US agriculture laid the foundation for the green revolution, and millions of people worldwide were saved from starvation.

## Green Revolution

The Cold War began with the end of World War II. The world was divided into American and Soviet (USSR) camps. Apart from these two poles, there were many Asian, African, and Latin American countries that adopted a policy of remaining neutral to both camps. The nations were part of the Non-aligned Movement (NAM) in 1955, which was under the leadership of Jawaharlal Nehru (prime minister of India), Gamal Abdel Nasser (president of Egypt), and Josip Broz Tito (president of Yugoslavia). Most of the NAM countries had recently emerged from enslavement by former European empires, were economically weak, and were unable to produce enough grain for their populations. Due to continuous starvation and famine, there was a possibility of a "Red revolution" in these countries (like China and regions like Eastern Europe), which could have aligned with the USSR and alienated the US in the global politics; thus the US proposed a "green revolution" to neutralize the threat. The green revolution aimed at making developing countries self-sufficient in grain production. The hope was that if poor people could get enough food, then the need for a Red revolution would automatically disappear, and the US would not be isolated in the world.

At the heart of the green revolution were improved maize and wheat varieties developed by American scientists between 1930 and 1960 that yielded eight- to tenfold more grains when sufficient fertilizer, water, pesticides, and weedicides were applied. These modern packages of farming had been successfully implemented in Mexico and the US. The green revolution intended to repeat this experiment in Asia, Africa, and Latin America. The Rockefeller Foundation, Ford Foundation, and several other government and semigovernment organizations were given the responsibility to make the green revolution a success.

In 1960, Borlaug represented the Rockefeller Foundation in a Food and Agriculture Organization (FAO) committee. This committee reviewed the wheat-producing capacity of fifteen countries and concluded that except for India, Pakistan, Morocco, Bangladesh, Turkey, and Iran, most of the third world countries did not have agricultural scientists, and even the countries that had

agriculture research programs were not capable of achieving food self-sufficiency. Thus the committee recommended training young breeders from developing countries in Mexico under Borlaug's direction. The OEE project first proposed by Wallace eventually evolved into the International Maize and Wheat Improvement Center, a training center for breeders from all around the globe with the support of the Rockefeller and Ford Foundations and the Mexican government. Borlaug was appointed its director, where he served for the next thirty years.

In addition, Menzaldorf was given the responsibility of a maize breeding program for Latin America and Africa. Under the green revolution campaign, advanced varieties of maize developed by American scientists were introduced in Latin American countries. By 1980, high-yielding maize varieties were grown in 50 percent of South America's arable land. However, the program was not as successful in introducing maize to Africa. Notably, the genetic improvement of rice was included in the green revolution's agenda, as it was the major cereal crop of Asia.

Apart from improved seeds, institutional and infrastructural changes were needed for the green revolution to succeed. Farmers of developing countries used to save the seeds for the next sowing. They did not have the money to buy seeds, synthetic fertilizer, pesticides, and farming equipment. Thus the US entered into policy agreements with developing countries, including India, Pakistan, Bangladesh, Thailand, Indonesia, Egypt, and so on. The US provided seeds, fertilizer, technology, and training. Also, the US promised continued food aid to partner countries until they achieved self-sufficiency in food production. The host governments of developing countries had to build the necessary infrastructure and banking system to provide loans to farmers.

## Success of the Wheat Breeding Program in Asia

In the early 1960s, under Borlaug's supervision, wheat breeding experiments began in India, Pakistan, and other Asian countries. In 1968, India harvested 16.6 million tons of wheat, for which an extra storage system was needed. Indira Gandhi, the then prime minister of India, used government schools as temporary godowns for grains during the summer months. Despite the drought in 1969 and 1970, 20 million tons of wheat were produced in India. Earlier, the average wheat production from 1963 to 1967 was 9–11 million tons. Pakistan also got about a 60 percent increase in wheat production. Between 1965 and 1970, Pakistan's wheat yield increased from 4.6 million tons to 8.4 million tons and became self-sufficient in wheat production by 1968. Thus the green revolution had tremendous success in India and Pakistan and was met with similar success in Jordan, Lebanon, Turkey, and Indonesia. In many countries, the average life expectancy and living standards improved, and mortality rates declined significantly.

## Story of Rice

Unlike wheat and maize, very little research and breeding experiments were done on rice when it was included in the green revolution agenda. Thus in 1960, the Ford and Rockefeller Foundations, in collaboration with many international agencies, established the International Rice Research Institute[2] (IRRI; http://irri.org) in Los Baños in the Philippines. Robert Chandler (1907–91) was appointed as the first director of this institute and was responsible for establishing a rice germplasm collection and supervising the rice breeding program. Most of the research about rice's origin and domestication, its genetic diversity, and its genetic improvement began after the 1960s.

However, before the improved rice varieties were made available, the farmers were encouraged to use synthetic fertilizer in rice fields, and an infrastructure for irrigation was developed. From 1950 to 1970, a 25 percent increase in rice production was achieved due to the availability of synthetic fertilization and irrigation. In the 1970s, rice production increased by five to six times due to improved rice germplasm; this helped the green revolution reach a peak because more than one-third of the world's population is fed with rice. Even though there is more maize and wheat production in the world, maize only fulfills the need of 5 percent of the world's population, and wheat fulfills 20 percent. In this sense, rice was the most important and representative crop of the green revolution. Here we summarize rice's origin and genetics and the achievements of rice breeding in Asia and Africa.

### Origins of Rice

In nature, there are twenty-four species of grasses that are closely related to rice and are classified within the genus *Oryza*. These species are distributed in tropical and temperate regions in Asia, Africa, Australia, and South America. Some of these are diploid (2n = 24 chromosomes), and others are tetraploids (48 chromosomes). However, only two diploid species, *Oryza sativa* and *Oryza glaberrima*, were domesticated by humans. Interestingly, rice was independently domesticated in three different continents. *O. sativa* was domesticated in Asia and Australia. Archaeological and genetic evidence suggests that 9,000 to 11,000 years ago, the *O. sativa* subspecies japonica was first domesticated in the Yangtze River valley of China from the wild grass *O. rufipogon*. Another

subspecies of rice, *O. sativa indica*, was independently domesticated 5,000 years ago in the Indo-Gangetic Plain of northern India from the wild grass *O. nivara*. In Australia, another subspecies of *O. sativa* was developed 2,000 years ago from *O. rufipogon*(4). The *O. glaberrima* was domesticated in Africa 3,500 years ago. *O. glaberrima* has evolved from the wild grass *O. barthii* in West Africa (in Mali), and then it was brought to North Africa and the Zanzibar islands (5). This rice arrived in the Americas with African slaves in the seventeenth century and has been grown in North Carolina (5). Among the two cultivated rice species, the *O. sativa* (Asian rice) is most widely grown globally and is the main staple for one-third of the human population.

## Diversity of Asian Rice

*O. sativa* is the most widely cultivated rice species in the world. Its japonica subspecies are grown in Southeast Asia, including China, Japan, Korea, Indonesia, Bali, Java, Sumatra, Vietnam, Cambodia, and so on. The japonica subspecies includes several thousand cultivars; some are adapted for the cold climate, while others flourish in the tropics. The varieties of japonica subspecies are broadly known as sticky/sushi rice and have a slightly sweet taste. The indica subspecies of *O. sativa* is mainly grown in the Indian subcontinent and South Asia. It also has tremendous diversity as well, including varieties adapted to rain-fed highlands and coastal regions. The cooked indica rice grains do not stick to one another and are known as basmati-type. Interestingly, the “sticky” feature is not found in the wild ancestors of rice and related wild species of the grass family. This trait, selected during domestication of the japonica subspecies, is caused by a mutation in the gene *Waxi* that blocks amylose production within the rice grain. Usually, two types of starch—amylose and amylopectin—are found in the rice grain, but only amylopectin is present in sticky rice. The glucose molecules in amylose form a simple linear structure, while in amylopectin, glucose molecules form branch chains that make amylopectin dissolve faster in hot water than amylose. Thus in sticky rice, the presence of amylopectin makes it sticky. In basmati rice, a high amount of amylose keeps the rice grain separated after cooking. In general, the ratio of amylose and amylopectin varies across cultivars, and accordingly, the different levels of stickiness and the variation in cooking time are observed (for this reason, two varieties of rice are not mixed for cooking).

Another interesting fact about rice is that rice grains are naturally red. The white color (or straw color; white is because of polishing) results from a mutation in a gene involved in the anthocyanin pigment’s[3] biosynthesis. For many years, it was a mystery to scientists why humans selected white over red for grain color. This feature was selected independently in both japonica and indica subspecies. It had been speculated that it was for its aesthetics or for some cultural belief. But in both China and India (the two birthplaces of Asian rice), red is considered auspicious, and there is no indication of any cultural preference for white. Genetic studies have recently revealed that the anthocyanin biosynthesis genes are linked to seed-shattering genes, and the loss of shattering also leads to the loss of the red pigment in rice. All the wild ancestors of rice have red seeds that spontaneously shatter upon maturation. This trait is useful for the survival of the wild grasses, but humans can’t harvest the crop at once. Thus a mutation that disrupted both seed shattering and anthocyanin biosynthesis gave rise to the rice plant whose straw-colored seeds did not fall upon maturation. Perhaps early humans picked a straw-colored mutant or collected seeds from more of such plants that favored its selection and propagation. Humans probably carried these plants forward in the process of domestication. Because color and seed-shattering genes are linked, red-colored seeds became less prevalent in the cultivated rice species.

The Asian rice *O. sativa* contains more than one gene for seed shattering and the biosynthesis of anthocyanin pigments. In domestication, two mutant (shattering) genes were selected in japonica that eliminated seed shattering and the red color. In indica, only one (shattering) gene was selected, and thus many cultivars have partial seed-shattering and red-colored seeds. Therefore, farmers in India harvest the paddy before it turns yellow and then dry it in the sun. It is believed that some of the traits of japonica were later introgressed in indica cultivars, and therefore, the modern varieties of indica rice are white.

Some varieties of both indica and japonica are found to contain long-grain rice. The comparison of 174 species of *O. sativa* found in different regions and forty species of its wild ancestor *O. rufipogon* has shown that the trait of grain length has been fixed in the process of domestication in tropical japonica, indica, and basmati. Basmati rice is the longest among them. The grains of other fragrant rice are also long. In contrast, japonica and Australian rice grown in temperate regions have relatively round and small rice grains (figure 6.6). Like all cereals, humans selected rice for large seeds and panicles and for its adaptation to various climates. This is how thousands of landraces of rice came into existence.

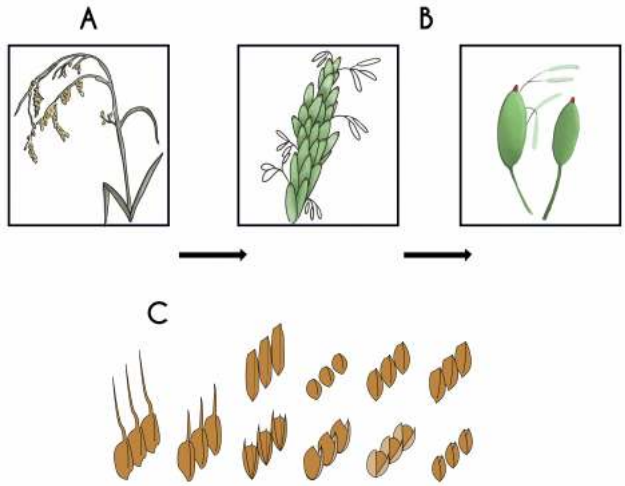



Fig 6.6 The structure of Asian rice (O. sativa) plant (A), inflorescence and flower (B), and a sample of grain diversity among various cultivars. “Rice, inflorescence, and grain diversity” by OSU OERU is licensed under CC BY 4.0.

## Genetic Improvement of Rice at IRRI

After World War II, the shortage of grain and an increase in population caused widespread hunger in Asia. In 1949, the FAO established the International Rice Commission with the goal of increasing the yield of rice. The main obstacle in increasing the yield of the indica subspecies was the structure of this plant. Most indica cultivars were tall, had weak stems, and often collapsed on the ground when hit by storms or rains. Thus a strong dwarf stem was required for increasing rice productivity that can bear a heavy grain load.

In the 1950s, with FAO’s help, Indian scientists at Rice Research Center, Cuttack, developed rice ADT-27 and Mahsuri rice varieties by crossing Indian rice cultivars with a dwarf Taiwanese Taichung Native 1. In the 1960s, these hybrid rice varieties were grown on a large scale in India but received only a modest increase in yields. After the IRRI opened in the Philippines in the 1960s, Robert Chandler created a team of scientists to develop high-yielding rice varieties. Two members of this team, Peter Jenning and Akiro Tanaka, formulated the strategy for creating improved rice varieties. First, they carefully studied various indica and japonica cultivars. They concluded that if indica plants can be kept standing until maturity (they used bamboo sticks to support these plants), their yields are similar to those of dwarf japonica cultivars. Second, they observed that indica cultivars respond well to the application of synthetic fertilizer. Thus the main problem in the indica subspecies was the tall and weak stem. Jenning crossed dwarf Dee-geo-woo-gen (DGWG) rice variety (Taichung Native 1’s dwarf ancestor) with some indica and tropical japonica cultivars. By 1962, Jenning conducted thirty-nine crossings. He observed that first generation (F1) hybrid progeny was always tall and the F2 population segregated in the ratio of 3 tall:1 dwarf, suggesting that only one gene is responsible for stem’s tallness in Asian rice. Thus dwarfism could be easily introgressed into other rice varieties. Jenning also noticed that some of the dwarf plants matured one month earlier than the traditional rice varieties. The early maturation trait was of great importance because it could save thirty days of land use, fertilizer, and water, and in some regions, three rice crops could be grown a year instead of two. Afterward, Jenning tested seeds of early maturing dwarf plants in the nursery for resistance to blast disease and observed a partial resistance in one plant labeled as IR8-288-3 (IR8). The parents of IR8 were the dwarf DGWG and the Peta rice variety of Indonesia; IR8 was 120 centimeters tall; had a strong, thick stem capable of bearing a huge panicle full of seeds; and was not affected by the change in day length and altitude (thus it could be grown anywhere). Another scientist, S. K. D. Dutta, observed that IR8 yields are 9–10 tons/hectare when synthetic fertilizer, water, and weedicide are applied in adequate amounts.

In contrast, the average yield of traditional varieties was 1.2 tons/hectare. In that scenario, the IR8 emerged as a great alternative. It is said that when the news of IR8 reached Ferdinand Marcos (then the president of the Philippines), he immediately went to IRRI and ordered a large-scale multiplication of IR8 seeds. Marcos wanted to showcase this achievement in the next election. The US was also eager to hear some good news in Asia while engaged in the Vietnam War. So amid these pressures, IR8 was released in 1966 without further testing. It is said that 3,000 farmers from the Philippines’ remote islands came to IRRI to procure IR8 seeds.

As expected, farmers got an increase of 5-10 times in yields by sowing IR8. With the help of IR8, starvation was temporarily avoided, and the foundation for making high-yielding rice varieties was laid.

The yield of IR8 was phenomenal, but it tasted chalky and was hard to chew. IR8 was also susceptible to various diseases, including bacterial blight and viral disease, and had only partial resistance to blast disease. Thus it required a heavy application of chemicals to keep the pests and pathogens away. In 1977, IRRI released IR36, which has a resistance to the blight and tungro viruses, and later IR64, which has an increased resistance to various diseases. Afterward, many rice varieties were developed by IRRI that showed increased resistance against many pathogens. These improved rice varieties were distributed across many rice-growing developing countries using governmental extension centers. Although the arms race between rice and its various pathogens continues, there has been no major famine due to rice shortage. The scientists at IRRI and in several other laboratories around the world are still breeding new rice varieties that can be more tolerant to abiotic stress and can withstand changing climates.

## Yuan Longping's Hybrid Rice Varieties

In wild ancestors of cultivated rice (*O. rufipogon* or *O. barthii*), self- and cross-pollination occur. In contrast, domesticated rice species *O. sativa* and *O. glaberrima* favor selfing over cross-pollination. Thus unlike in corn, the phenomenon of hybrid vigor is not easily observed in rice. In 1964, a Chinese scientist, Yuan Longping, decided to change the selfing nature of cultivated rice to make high-yielding hybrids rice varieties. When Longping began his research, the predominant thinking in the field was that hybrid vigor could not be applied to naturally self-fertilizing species such as rice, but he was convinced otherwise. After nine years of hard work, he developed three varieties of rice: the first breed was a male-sterile line incapable of making pollen; the second was a maintainer line that served as a source of pollen, and the third was a restorer line that can rescue a male-sterile line from sterility. Thus a cross between male-sterile and restorer lines produces completely fertile progeny. He demonstrated that hybrid progeny obtained by crossing the male-sterile line with the maintainer line shows hybrid vigor resulting in a significant increase in the grain yield. Generally, under favorable conditions, the yield of the most popular rice varieties is 5–6 metric tons/hectare. However, under similar growing conditions, hybrid rice released by Longping in 1974 gave an average yield of 7.2 metric tons/hectare (a 20 percent increase). Since 1976, this hybrid rice has been grown in China and provides food for an additional 70 million people. Since 1994, hybrid rice varieties have been sown in India, the Philippines, Bangladesh, and Indonesia. However, Longping continued his research on increasing grain yields. In 1997, yields of hybrid rice progeny were 10 metric tons/hectare, and by 2004, it reached 12 metric tons/hectare.

Professor Yuan Longping, the father of the hybrid rice, was awarded the UNESCO Science Prize in 1987; the World Food Prize,[4] with Monty Jones (who developed NERICA rice varieties for Africa and is discussed in the following section), in 2004; and the Wolf Prize in 2004 for his contribution to agriculture. In 2007, he was elected a foreign member of the US National Science Academy.

## NERICA: The New Rice for Africa

African rice (*O. glaberrima*) was developed 3,500 years ago in West Africa from the wild *O. barthii* in the delta region of the Niger River (present-day Mali). African rice plants are more elongated and have weaker stems than Asian rice. These plants are relatively more susceptible to lodging and cannot bear the load of a heavy panicle. Also, seed shattering in African rice results in a significant loss in yields, as this trait was not selected against during domestication of African rice. However, this rice has the ability to survive in the harsh and challenging environment of Africa; it has a natural resistance against the various pests, parasites, and pathogens prevalent in its environment. Like Asian rice, African rice consists of many cultivars that represent a rich biodiversity, and many useful genes are hidden within these varieties. For example, the *O. glaberrima* CG-14 variety has a natural ability to tolerate drought, grows faster than weeds, and thrives on marginal land (e.g., deficient in phosphorus or acidic soil). Although the input costs for growing this crop are less, it has less productivity, and thus it is not widely grown.

For a long time, the Asian rice *O. sativa* has been grown in Africa on a large scale, as it is highly productive. Asian rice was introduced about 450 years ago in many countries of Africa. But Asian rice does not possess the ability to cope with Africa's environment. Its yield decreases in drought conditions, and it cannot protect itself from parasites, pests, pathogens, and insects. The input cost for growing Asian rice is very high, as farmers use large amounts of synthetic fertilizer, pesticides, weedicides, and so on. Thus the sustainable cultivation of Asian rice in Africa poses a challenge. Unfortunately, the useful traits of African and Asian rice cannot be combined using classical breeding methods, as crossings between *O. sativa* and *O. glaberrima* yield sterile hybrids.

Thus the green revolution failed in improving the productivity of African rice or the resilience of Asian rice for the African environment using classical breeding methods.

However, in the 1970s, African scientist Monty Jones, working at the West Africa Rice Advancement Institute (WARDA), collected 1,500 varieties of *O. glaberrima* and developed genetically improved varieties of African rice that show high resilience in the African environment. In the 1990s, when the technology of tissue culture became easier to apply on rice, Jones's team created hybrid rice cells by fusing Asian and African rice cells to create hybrid plants from them. These plants were not sterile and can be grown from seeds. This new hybrid variety, called NERICA (New Rice for Africa), has a yield that is five times that of African rice cultivars, is resistant to various biotic and abiotic stress conditions prevalent in Africa, and has fewer input costs. NERICA also matures within three months, while its ancestral African varieties take six months. Thus Jones and his team could combine the useful characteristics of two rice species using advanced in vitro technology of plant tissue culture and surpassed the limits of traditional plant breeding. Farmers who grow NERICA also save three months of land use and labor cost and grow extra short-duration crops such as vegetables.

NERICA was Africa's first successful genetically improved crop. For this work, the United Nations awarded the 2004 World Food Prize to Jones. In the wake of this success, *Time* magazine included Jones in the list of the most influential people in the world in 2007 (6). Jones's method was subsequently applied to generate 3,000 new varieties of NERICA, which are being grown in African countries like Benin, Ivory Coast, Gambia, Nigeria, Mali, Guyana, Togo, and so on, and many of these countries have become rice exporters.

## Green Revolution's Achievements

The green revolution was successful in increasing grain production in Asia, Latin America, and Africa. It saved the lives of millions from hunger and starvation. It can be said that the green revolution played an important role in maintaining peace in the world.

It also laid the foundation of mutual cooperation among various international institutes and scientists that lasted beyond the duration and need of the green revolution. Due to the political understanding, various international institutions and government machinery, private foundations, and banks worked together to foster scientific progress and ensure the food security of the world.

The green revolution was most successful in Asia because Asian countries already had the infrastructure and roads and had already developed a capitalist market system. During this period, many Asian countries—including India, Pakistan, Turkey, China, Sri Lanka, Indonesia, Malaysia, Vietnam, and Cambodia—became not only self-sufficient in food production but exporters of grains. For example, Pakistan achieved self-sufficiency in grain production in 1969; India followed this success in 1974, which was not expected by the world at that time. Similarly, when the IR8 rice variety was first released in the Philippines, it changed the country from an importer of rice to an exporter within just three years.

Overall, due to the increase in the yield of rice and wheat, food grains became cheaper, and the conditions of starvation and famine in developing countries could be avoided. The increase in grain yield per hectare prevented the expansion of cultivated land and helped protect the forests. According to one estimate, in the absence of the green revolution, by the year 2000, the world grain production would have been reduced by 20 percent, an additional 2–2.5 million hectare of agricultural land would have been needed to satisfy the food requirement of the current world population, and the cost of grain would be 30 percent higher.

Research in international centers also benefited the US, and the country's domestic agriculture also increased. Between 1960 and 2000, in developed countries, the yield of wheat increased by 208 percent, rice by 109 percent, maize by 157 percent, potato by 78 percent, and cassava by 36 percent. Overall, the standard of living in developed countries was also improved due to the availability of cheaper food grains. Furthermore, the green revolution brought prosperity to the lives of many farmers and helped agriculture-related businesses flourish. US companies made tremendous profits by selling fertilizers, pesticides, weedicides, and agricultural equipment in the international market, and the green revolution helped recover the US from the post–World War II recession.

The green revolution failed in Africa due to various reasons, including the late inclusion of Africa on the agenda and the promotion of maize[5] instead of African crops. Furthermore, African countries lacked the agricultural infrastructure and trained professionals for disseminating adequate training to farmers about the use of fertilizers, pesticides, machines, and so on. Consequently, maize varieties that were successful in the US and Mexico were not successful in Africa. By 1998, while 82 percent of agricultural land in Asian countries, including China, India, and Pakistan, was growing genetically improved varieties of cereal crops, in Africa, only 27 percent of the area had these crops. However, many useful lessons were learned from the first phase of the green revolution

(1965–85). The biggest gift of this period has been to lay the foundation for cooperation between agricultural scientists around the world. Later, scientists and policymakers succeeded in solving Africa's problems in the second phase of the green revolution (1985–2000). During this period, fourteen other CGIAR research centers were opened, each focusing on the prime regional crop (eleven major crops, including potatoes, pulses, cassava, peanuts, beans, millets, and sorghums). The goal of each of these centers, which are spread around the world, is to conserve and improve the germplasm of local crops. From time to time, these international centers release advanced varieties of one or more crops to farmers. Studies show that worldwide production of wheat, rice, and maize has increased by 1 percent, 0.8 percent, and 0.7 percent, respectively, due to germplasm improvement during the second phase of the green revolution. Similarly, yields of minor grains like sorghum and millet have increased about 0.5 percent annually since 2000. International cooperation among scientists and various governmental and private agencies was also beneficial to many African countries, and after 1980, efforts to improve the local African crops, including rice, yam, cassava, and so on, began. Even after the end of the green revolution, these efforts are continuing.

Despite a nearly threefold increase in the world's population in the last fifty years, no major famine occurred. Even today, the world's population is producing more food than is needed. The green revolution played an important role in achieving global food security.

## Limits of the Green Revolution

The green revolution stood on the maximum exploitation of resources. Therefore, after about fifty to seventy years of intensive grain cultivation, soil fertility has decreased, groundwater levels have fallen significantly, and the overflow of agrochemicals led to the pollution of various water bodies. But by 1980, wheat production showed a slow decline by about 1.5 percent annually, and so far, it has fallen more than 20 percent than the 1970s and '80s. On average, there has been a one-third decline in wheat production per hectare since the green revolution despite the continuous use of synthetic fertilizer, irrigation, and other mandated agrochemicals required to keep a check on pathogens and weeds. The high-yielding varieties of wheat, rice, and maize absorb large quantities of nutrients from the soil. The synthetic fertilizers replenish three major elements—nitrogen, phosphorus, and potassium (a.k.a. NPK)—but do not replace micronutrients and soil organic matter. Thus in many places, the soil has lost its normal texture, and it has turned almost sand-like. Recuperating the health of the soil is necessary, which cannot be done by continuing the green revolution's model. The industrial method of farming needs to be reviewed and improved.

The goal of the green revolution was to achieve an increase in global food production, and during its implementation, the health of the ecosystem was not taken into consideration. The excessive use of pesticides, fertilizers, and weedicides polluted the groundwater, water bodies, and the air. Today, the entire food chain has become contaminated, and cancer and other diseases have increased in farmers and consumers. In some countries, positive efforts have been made in this direction. Today, breeders around the world are trying to develop varieties of crops that require less synthetic fertilizer, less irrigation, and fewer pesticides to grow. Recently, a super green rice variety has been released in the Philippines, which can maintain its productivity with less fertilizer and water use.

Before the green revolution, the staple diet of most Asian countries consisted of a wide variety of coarse cereals such as sorghums, millets, pulses, starchy tubers, and roots, which provided essential nutrients such as iron, calcium, vitamins, and micronutrients. There was no help for farmers growing other crops in the green revolution scheme, so these crops' production decreased. The majority of the population's diet has become homogenous, mainly consisting of rice, wheat, and maize. Therefore, malnutrition and devastating lifestyle diseases like diabetes increased despite getting plenty of calories.

The varieties of crops that are being grown today are few, and thousands of local varieties of crops have disappeared. Farmers no longer grow them, and thus our food sources are very limited and the diversity of crops has decreased significantly. The outbreak of several diseases has also revealed the importance of biodiversity and the limits of monocropping, which was encouraged by the green revolution. Thus despite achieving a high productivity of cereal crops, the green revolution package was not sustainable.

## Life of Norman Borlaug

Norman Borlaug, the father of the green revolution, was born on a farm near Cresco, Iowa, to Henry and Clara Borlaug.[6] He worked on the 106-acre family farm raising corn, oats, cattle, pigs, and chickens from age seven to nineteen. After completing his primary and secondary education in Cresco, Borlaug enrolled in the University of Minnesota and received a bachelor's degree in 1937, a master's degree in 1939, and a PhD in 1942. From 1942 to 1944, he was a microbiologist for DuPont, where he worked on

industrial and agricultural bactericides, fungicides, and preservatives. In 1944, he accepted a position as a geneticist and plant pathologist assigned the task of wheat research and production program in Mexico, supported by the Rockefeller Foundation and the Mexican government. As described earlier, in that position, Borlaug successfully developed high-yielding, dwarf, disease-resistant wheat varieties.

He built collaborations with local farmers and scientists from all over the world. Borlaug had a deep connection with the farmers, and farming was no stranger to him. Childhood experiences had been with Barlog throughout his life. He was always trying to end hunger in the world. Equally important to his training with Stakman were his life experiences, which helped him sustain hardships for nearly two decades in Mexico's difficult conditions. When the Rockefeller and Ford Foundations cooperated with the Mexican government to establish CIMMYT, Borlaug was its first director.

He is credited with saving more than a billion people around the world from starvation. In 1970, Borlaug received the Nobel Peace Prize. For the first time, a scientist received this award. Shortly after receiving the Nobel Prize, Borlaug established the World Food Prize to honor other scientists and breeders who made outstanding contributions.

Borlaug was also awarded the US Congressional Gold Medal, US Presidential Medal of Freedom, Pakistan's Sitara-e-Imtiaz (1968), and India's second-highest civilian honor, Padma Vibhushan (2006). Overall, Borlaug was a member of the Agricultural Sciences Academies of eleven countries and received more than sixty honorary doctoral degrees and around fifty other awards. Borlaug also received extensive recognition from universities and organizations in six countries: Canada, India, Mexico, Norway, Pakistan, and the United States.

## References


Hastorf, C. A. (2009). Rio Balsas most likely region for maize domestication. *Proc. Natl. Acad. Sci. USA*, *106*, 4957–58. (↵ Return)

Beadle, G. W. (1939). Teosinte and the origin of maize. *Journal of Heredity, 30*, 245–47. (↵ Return)

Faris, J. D. (2014). Wheat domestication: Key to agricultural revolutions past and future. In R. Tuberosa, A. Graner, & E. Frison (Eds.), *Genomics of plant genetic resources: Vol. 1, Managing, sequencing, and mining genetic resources* (pp. 439–64). Springer. (↵ Return 1) (↵ Return 2)

Kovach, M. J., Sweeney, M. T., & McCouch, S. R. (2007). New insights into the history of rice domestication. *Trends in Genetics*, 23, 578–87. https://doi.org/10.1016/j.tig.2007.08.012 (↵ Return)

Carney, J. A. (2002). *Black rice: The African origins of rice cultivation in the Americas* (1st ed.). Harvard University Press. (↵ Return 1) (↵ Return 2)

Sachs, J. (2007, May 3). Monty Jones. *Time*. http://content.time.com/time/specials/2007/time100/article/0,28804,1595326_1595329_1616316,00.html (↵ Return)


## Further Readings


Borlaug, N. E. (2007). Sixty-two years of fighting hunger: Personal recollections. *Euphytica*, *157*, 287–97. https://doi.org/10.1007/s10681-007-9480-9

Brown, L. R. (1970). *Seeds of change: The green revolution and development in the 1970s*. Praeger.

Coffman, R. (2010). *Mentored by greatness. Indo-US science & technology forum*. World Food Prize. https://www.worldfoodprize.org/index.cfm/88533/18129/mentored_by_greatness

Myrdal, G. (1970). Agriculture. In *The challenge of world poverty: A world anti-poverty program in outline* (chap. 4, pp. 78–138). Pantheon.


---

1. For the story of maize's domestication and origin, see the video "Popped secret: The mysterious origin of corn—HHMI BioInteractive Video" on YouTube: https://www.youtube.com/watch?v=mBuYUb_mFXA&t=51s. ↵
2. Borlaug and Chandler discuss the origins of the International Rice Research Institute in a discussion filmed in 1994, now available as a multipart series on YouTube: Part 1: https://www.youtube.com/watch?v=17ySNZo3AMs Part 2: https://www.youtube.com/watch?v=TW8hpPi0rqI Part 3: https://www.youtube.com/watch?v=mEjQbo-2nZQ Part 4:

https://www.youtube.com/watch?v=rQon8EfQblY Part 5: https://www.youtube.com/watch?v=jhqQwfc0-No Part 6: https://www.youtube.com/watch?v=jtuB2cTEfTU↵

3. Anthocyanin pigments are also found in many flowers, fruits, and vegetables and are beneficial for health. ↵
4. “A world-brand name: Yuan Longping, the father of hybrid rice,” World Food Prize, 2007, https://www.worldfoodprize.org/index.cfm/87428/40007/a_worldbrand_name_yuan_longping_the_father_of_hybrid_rice. ↵
5. Maize cultivation requires a lot of fertilizer and irrigation, but most areas of Africa lack water, and large dams could not be built for irrigation. ↵
6. For Norman Borlaug’s biography, see https://achievement.org/achiever/norman-e-borlaug and http://nobelprize.org/nobel_prizes/peace/laureates/1970/borlaug-bio.html. ↵

---

This page titled 6.4: Genetic Improvement in Cereal Crops and the Green Revolution is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley via source content that was edited to the style and standards of the LibreTexts platform.

- **1.6: Genetic Improvement in Cereal Crops and the Green Revolution** is licensed CC BY-NC 4.0. Original source: https://open.oregonstate.education/cultivatedplants/.

# CHAPTER OVERVIEW

## 7: Biotechnology


7.1: Genetically Engineered Crops

7.2: Genetic Modification

7.2.1: Introduction

7.2.2: GMO Food (Activity)

7.3: GMOs


---

This page titled 7: Biotechnology is shared under a not declared license and was authored, remixed, and/or curated by Tom Buckley.

# 7.1: Genetically Engineered Crops

The knowledge of naturally occurring intra- and interspecies gene transfer events, the advances in recombinant DNA technology, and plant tissue culture helped scientists transcend traditional breeding limits and introduce desired genes from any organism into crops. The crops containing one or more genes from other species (trans/foreign gene) are known as genetically engineered/modified (GE/GM) crops.[1] For example, many insect-resistant GE crops contain the delta-endotoxin gene from a bacterium, *Bacillus thurigiensis* (Bt).

The purpose of making transgenic crops could be to increase the crop yield, prevent damage from pests and pathogens, and increase the nutritional quality. In 1994, the Food and Drug Administration (FDA) approved the first GE crop, *Flavr Savr* tomato, for human consumption. This tomato variety has a longer shelf life due to delayed fruit ripening. Since then, the FDA has approved more than fifty GE crops.[2]

This chapter summarizes the advances made in genetics and other related technology that led to the development of genetically engineered crops and provides examples of a few success stories.

## Genetic Material

In the early 1950s, it was proven that DNA is genetic material. In 1954, Francis Crick and James Watson proposed the double-helix model of DNA based on evidence from Morris Wilkins's and Rosalind Franklin's experiments. They suggested that DNA is a double-stranded, helical structure made of four nucleotide bases: adenine (A), thiamine (T), cytosine (C), and guanine (G). The two strands of DNA are antiparallel and are connected by covalent bonds: adenine from one strand binds to thiamine in another strand, whereas cytosine of one strand binds to guanine of the second strand (see figure 7.1). Thus the nucleotide sequence of one strand is complementary to another strand. If the sequence of one strand is known, it is easy to deduce the second strand sequence. Watson and Crick explained that one strand could serve as a template for making the other strand due to their complementary nature. Thus DNA contains information for self-replication—a necessary qualifier for being genetic material. In 1962, Crick, Watson, and Wilkins received the Nobel Prize for the elucidation of DNA structure.

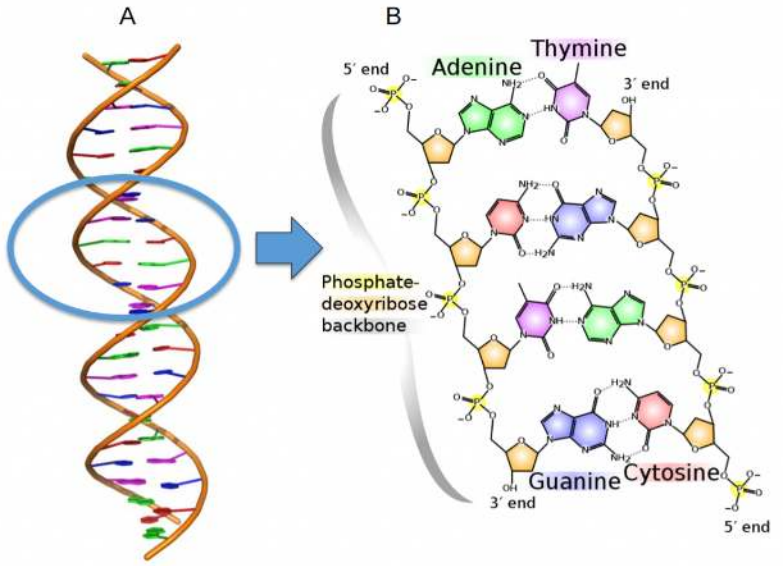



Fig 7.1 (A) Simplified representation of a double stranded DNA helix with alternating adenine residues in green, thymidine in red, cytosine in dark blue, and guanine residues in cyan. The phosphate backbone is displayed as an orange ribbon. (B) Chemical structure of DNA with colored labels identifying the four bases as well as the phosphate and deoxyribose components of the backbone. "DNA double helix" is a derivative of "DNA chemical structure" by Madeleine Price Ball, used under CC0 1.0, and "Double stranded DNA with coloured bases" by Vcpmartin, used under CC BY-SA 4.0. "DNA double helix" is licensed under CC BY-SA 4.0 by Sushma Naithani.

In 1958, Arthur Kornberg extracted a DNA polymerase enzyme from *E. coli* cells that was capable of copying DNA. He demonstrated the replication of a small DNA fragment in vitro using DNA polymerase and proved that either strand of DNA could serve as a template during DNA replication. DNA replication is a semiconservative process: four strands of DNA are made from

two parental strands, and eventually, two double helixes form; each helix contains one old and one new strand. Other scientists' research showed that DNA replication is not completely foolproof, and a proofreading and repair process ensures the removal of mismatched bases and repairs DNA. Thus DNA sequences are preserved for millions of years and ensure the continuity of a biological species. However, a permanent change in the DNA sequence (mutation) can occur due to the extremely low level of proofreading errors during the DNA replication. Most single nucleotide mutations are harmless and don't affect a phenotype. However, after many generations, the accumulation of mutations could result in phenotypic changes. Thus DNA also acts as raw material for evolution.

The complete set of genetic material present in an organism is called its genome.[3] The genome of prokaryotes is made of a single circular chromosome, whereas the genome of eukaryotes consists of more than one chromosome. Individuals of the same species have the same genome size (same number of chromosomes), and chromosomes between different species vary. The structural and functional unit of the genome is a gene. The order of the four nucleotide bases determines the composition of individual genes. Several thousand genes are present within the organisms. Typically, the information from the DNA (gene) is transcribed into RNA, and a subset of RNA (messenger [m] RNA) is then translated into proteins. The proteins carry out most of the structural and functional activities within the cells. This unidirectional flow of genetic information from DNA to protein is called *central dogma* and serves as the fundamental principle for the basis of life. In addition to protein-coding mRNAs, organisms' genomes contain genes that encode various other types of structural and regulatory RNA molecules (e.g., rRNA, tRNA, and microRNA).

## Recombinant DNA Technology

After the 1970s, a new branch of biology, molecular biology, came into existence. Its focus is to understand the structure and functions of genes and gene products. It was expected that the sum of the knowledge about all genes could help in understanding the whole organism. The basic principles of molecular biology were discovered by experiments conducted on unicellular bacteria and fungi, and later studies on higher eukaryotes, including plants, began.

First, scientists succeeded in extracting DNA from various organisms. The next challenge was to identify the thousands of genes and then determine their function within the cell. The discovery of restriction enzymes and ligase enzymes made the identification and cloning of the individual genes possible. The restriction enzymes recognize a specific sequence of four/six/eight nucleotides within DNA and make a cut in the strand. The sites of restriction enzymes are randomly scattered within the genome, and hence they cut double-stranded DNA into small pieces. So far, more than 3,000 restriction enzymes have been discovered, of which 600 are available in the market. These enzymes were named after the bacteria where they were first identified. For example, the *EcoR1* enzyme is found in the *Escherichia coli* strain RY13, and *HindIII* was discovered in *Hemophilus influenzae*.

Bacteria make restriction enzymes to protect themselves against virus infection. When viral DNA enters the bacterial cells, these restriction enzymes slice the virus DNA and block the virus's growth. However, bacterial DNA remains protected from their own restriction enzymes by methylation of the corresponding restriction sites. In 1978, Werner Arbor, Hamilton Smith, and Daniel Nathans were jointly awarded the Nobel Prize for the discovery of restriction enzymes. In 1967, a special enzyme, ligase, capable of joining two DNA fragments, was discovered in Gellert, Lehmann, Richardson, and Hurwitz's laboratories. For scientists, the restriction enzymes served as molecular scissors, and ligase served as a molecular glue for cutting and joining DNA fragments.

The next question was how to amplify small DNA strands for their detailed analysis. Here, the knowledge about a bacteriophage lambda that infects *E. coli* bacteria explicitly came in handy. Esther Lederberg discovered the bacteriophage lambda in 1951. Esther Lederberg observed that after infecting *E. coli*, lambda could undergo either an active lytic or a latent lysogenic cycle. When the bacterial cell grows in the rich medium (rapidly dividing), then the lambda enters the lytic cycle, makes 1,000 of its copies by using resources and machinery of bacterial cells, and then destroys the host. These 1,000 lambda offspring then infect 1,000 new cells and produce 1,000,000 new progenies in the next cycle. In this way, the virus grows at the speed of a rocket. However, if bacterial cells are deprived of nutrients and are in the stationary phase (not dividing), lambda enters the lysogenic cycle resulting in the insertion of the lambda DNA into the bacterial genome without causing any trouble. However, if the situation worsens for bacteria (or it experiences heat stress), lambda enters the lytic cycle to makes use of whatever resources are available for making its copies before host cells die. For lambda, going to a lytic or lysogenic state is controlled by the repressor protein encoded in lambda DNA. When lambda DNA enters the bacterial cell, first, the repressor protein is made, which blocks the rest of lambda's genes. The rapidly dividing bacterial cells contain high levels of proteases, which can break down the repressor and allows the lambda to enter into the lytic cycle. Under nutritional deprivation, bacterial cells come to a stationary stage where the protease levels remain low,

and the lambda goes into the dormant lysogenic cycle. When the host cells face stress (e.g., high temperatures), protease protein increases to mitigate the situation and recycle the nutrients. Thus in such a situation, the repressor protein is destroyed, and lambda enters the lytic cycle. Based on this knowledge of the lambda life cycle, scientists created versions of lambda in which researchers could easily turn the lytic and lysogenic cycle on or off. Furthermore, scientists found that only 75 percent of the lambda genome is indispensable; 25 percent of the lambda genome can be replaced with any DNA fragment. Thus if a gene is inserted within the lambda genome, millions of clones can be made quickly in *E. coli*. Then this DNA could be isolated, stored, and used for further experimentation. The lambda served as the first vector for cloning genes.

In the 1950s, Esther and Joshua Lederberg also observed that bacteria have many (10–1,000) small, circular DNA structures called fertility (F) plasmids in addition to a large genome. Before cell division, plasmids undergo autonomous replication and are inherited by the daughter cells. Soon, from a pathogenic bacteria, Shigella, another type of plasmid was discovered that contained antibiotic resistance genes (known as resistance [R] plasmids). It was easy to isolate plasmid DNA from bacterial cells, and also, bacterial cells have a natural capability of uptaking these small plasmids. The introduction of these plasmids into bacterial cells is called transformation. Scientists optimized protocols for increasing the efficiency of transformation and created chimeric plasmids by joining parts of F and R plasmids that contained one or two antibiotic-resistance genes, sites of restriction enzymes, and the autonomous origin of replication for *E. coli*. Thus these plasmids served as excellent vectors for cloning small DNA fragments. If a mixture of plasmid DNA and bacterial cells are plated in a medium containing a specific antibiotic, then the normal bacterial cells will die, and only transformed cells containing the desired plasmid (clone) will grow.

After the 1970s, the cloning of small DNA fragments (less than 20 kilobase pair [Kb]) in plasmid vectors and lambda-based phasmids became routine. Soon methods for DNA sequencing were invented, which made it possible to read the coded information (the order of four nucleotide bases, A, T, G, C) present within the genes. Computer analysis was used for analyzing sequencing data, and the field of bioinformatics was born. By comparing the genes present within living beings, it was found that the genetic code and genetic mechanisms are conserved among bacteria, plants, and animals. Computer algorithms are also used for assessing the similarity between the homologous genes from different organisms. The homologous genes between closely related species are more similar than distantly related species. In the late 1990s, due to advances in sequencing technology, it became possible to sequence whole genomes of bacteria, fungi, plants, and animals. Comparing the entire genome of different organisms allowed quantifying the similarities among the various organisms and deciphering the evolutionary distance between the species (see figure 7.2). In the light of modern genetics, molecular biology, and phylogenomics, we can now understand the process of biological evolution in reverse order.[4]

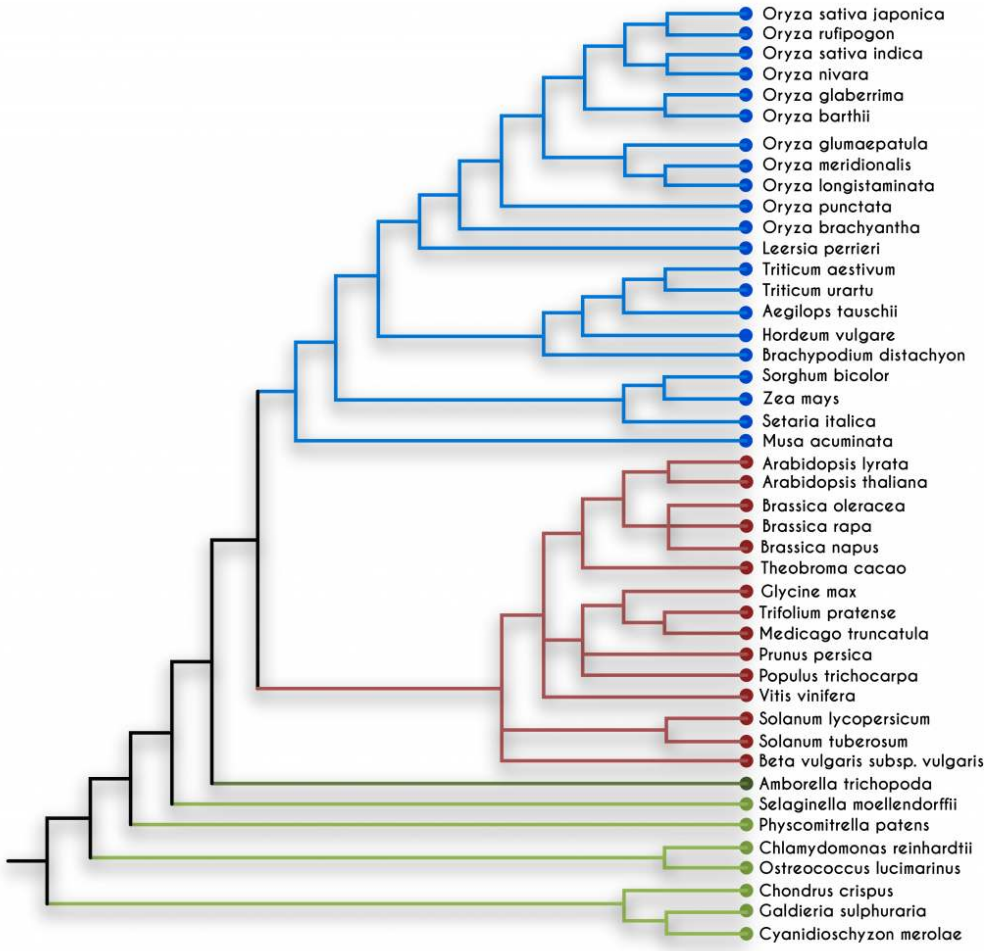



Fig 7.2 Genome sequence comparisons could reveal evolutionary histories and phylogenetic relationships between plant species. Genome sequence comparisons and phylogenetic tree were generated by Sushma Naithani using Gramene database. "Genome sequence comparisons" by Sushma Naithani and OSU OERU is licensed under CC BY 4.0.

## Gene Transfer in Plants

We often see swollen, round, tumor-like knots on the roots, twigs, and branches of many plants around us (see figure 7.3). These knots, called crown galls, are caused by a soil bacterium, *Agrobacterium tumefaciens*. These galls do not cause the death of the host plant but stunt their growth. The virulence of *Agrobacterium* strains is determined by a Ti plasmid present within the bacterium. Marc Van Montagu and his colleagues studied eleven pathogenic and eight nonpathogenic strains of *Agrobacterium* and found that all pathogenic strains had Ti plasmids and all nonpathogenic strains lacked Ti plasmids. They also noticed that the introduction of Ti plasmids into nonpathogenic strains transforms those into pathogenic strains. Thus it was concluded that *Agrobacterium* needs Ti plasmids for infecting the plants. The sequencing of the Ti plasmid revealed that it contains virulence (vir) genes and genes for the biosynthesis of auxin, cytokinins (plant growth hormones), and opines. The vir genes help bacterium infect host plants. The plant hormones promote the rapid growth of the cells at the site of infection (formation of crown galls), and opines serve as sources of energy, carbon, and nitrogen for *Agrobacterium*. Research in the 1970s and 1980s showed that *Agrobacterium*'s persistent presence within galls is not required for tumors to grow. In fact, after infecting a plant cell, *Agrobacteria* leave the Ti plasmid in the host cell, and then a large fragment of Ti plasmid, called T-DNA, gets inserted into the plant genome. The T-DNA in the plant genome continues to provide instructions for promoting the growth of the crown gall tumor and the biosynthesis of opines.

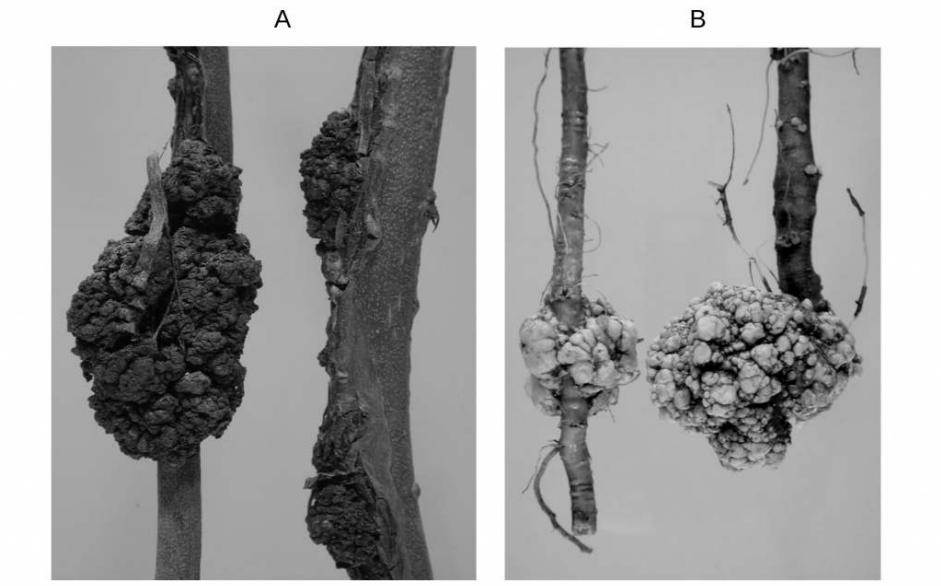



Fig 7.3 Crown galls in blueberry stem (A), and apple root (B) infected with Agrobacterium. Photos of blueberry stem and apple root by Melodie Putnam (Plant Clinic, Botany and Plant Pathology, Oregon State University) are licensed under CC BY 4.0.

If a gene is inserted within the T-DNA of the Ti plasmid using recombinant DNA technology, it can be easily transferred within a plant genome using *Agrobacterium*. Scientists modified Ti plasmid by replacing genes responsible for tumor growth with restriction enzyme sites, antibiotic resistance genes, and the E. coli plasmid replicons. Thus chimeric Ti plasmids allowed cloning of foreign genes in them and were able to replicate within both *E. coli* and *Agrobacterium*. Scientists had the flexibility of efficiently cloning genes in *E. coli* and then use *Agrobacterium* for transferring the desired gene into the plant genome (plant transformation). Since *Agrobacterium* strains have a limited host range, they cannot transform all species of plants. The gene gun was used for transforming plant species, for which agroinfection was not an option. In this alternative method, very fine particles of gold or tungsten coated with desired DNA are bombarded on plant tissue by the gene gun. The advances in plant tissue culture made it possible to regenerate whole plants from small plant parts. Thus the combination of recombinant DNA technology and plant tissue culture allowed the bioengineering / genetic engineering of plants for important quality traits (that were not available in a given plant species' diversity pool). It became possible to introduce useful genes from bacteria, animals, and other plant species into the crop species.

Both methods of plant transformation use small plant parts to start with, and after agroinfection or gene bombardment, the selection of transgenic cells is carried out in the synthetic tissue culture media (see figure 7.4). One or more antibiotic selection makers accompany the transgene; thus only transgenic cells grow in this media while normal cells die. After several rounds of selection and multiplication of transgenic cells in the tissue culture, tests for the desired transgene are carried out. Once the insertion of the transgene is confirmed, the expression analysis and other assays are conducted, and whole plants are regenerated.

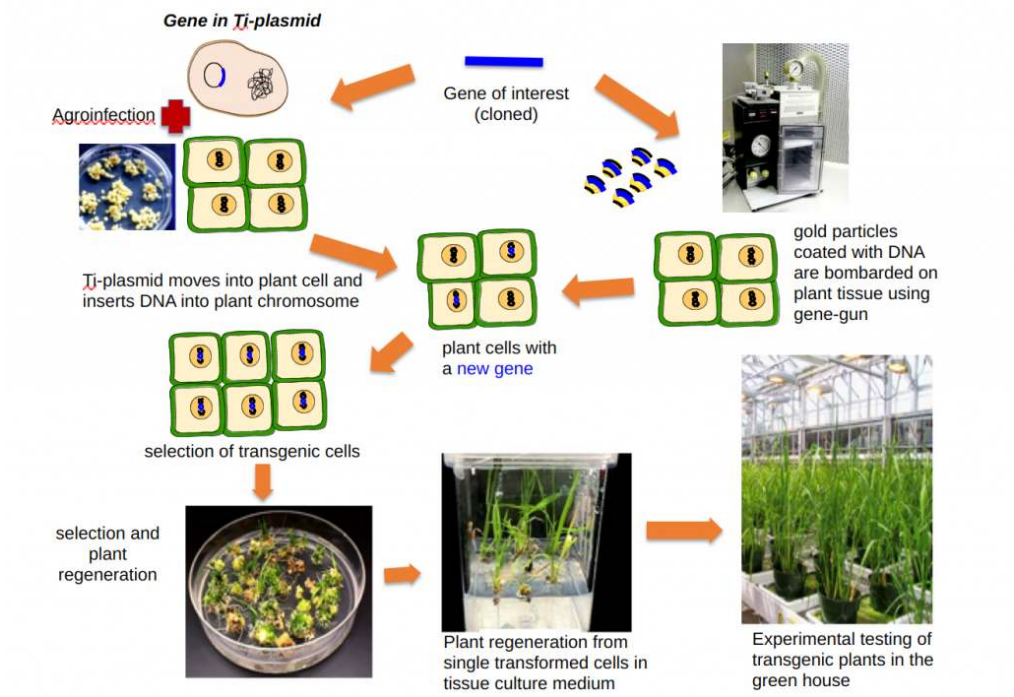



Fig 7.4 An overview of plant (rice) transformation. Sushma Naithani created the figure using photos provided by Dr. Ajay Garg (Cornell University). "An overview of plant (rice) transformation" by Sushma Naithani and Ajay Garg is licensed under CC BY-SA 4.0.

In general, both plant transformation methods have a low efficiency, and then among the transformed plant cells, only a few show the desired level of transgene expression. Once the transgenic plants are fully developed, the second round of testing begins, and one to five of the best-performing plants are selected.

## Crops

The GE crops made so far can be divided into three classes: (i) pest or pathogen resistant, (ii) herbicide tolerant, and (iii) biofortified with improved nutritional value (see table 7.1). At present, ~15 GE crops are being grown in 12 percent (179.7 million hectares) of the total agricultural land worldwide. In the US alone, ten GE crops are being grown on 70 million hectares. Maize, soybean, and cotton are among the most grown GE crops. Other GE crops include apple, mustard, sugar beet, papaya, potato, pumpkin, eggplant, alfalfa, poplar, rose, golden rice, golden cassava, and so on.[5]

### Story of Virus-Resistant Rainbow Papaya

The delicious papaya fruit is a rich source of vitamins A and C, calcium, and potassium. Papaya (*Carica papaya*) is the native plant of Central and South America. When Christopher Columbus tasted it for the first time, he was overwhelmed and named it the "fruit of the angels." After the fifteenth century, papaya spread throughout the world under the umbrella of European colonialism. Today it is grown in India, Brazil, the Philippines, Indonesia, Malaysia, Thailand, Hawaii, and the Caribbean islands. Usually, within six months after sowing the seed, the papaya grows as high as the average tree and starts bearing fruit within a year. Within three years, the papaya tree matures and produces a full yield. The cost of setting up papaya plantations is less than that of other plantations, and the farmers make decent profits from it.

The commercial cultivation of papaya first began in the Hawaiian Islands. Around 1940, papaya plantations were first established on the island of Oahu, which provided a livelihood to many local farmers. In the 1950s, an outbreak of the papaya ringspot virus (PRSV) occurred in Oahu's papaya plantations. This virus causes the stunting of trees, the deformation of leaves, the decline in their yields, and rounded spots in the infected fruit (see figure 7.5). Within a short period, the infected plant dies. Within a few years, the papaya plantations of Oahu were destroyed by the PRSV, so the industry moved to the big island of Hawaii, where the papaya industry flourished and expanded without any problems for the next four decades. In 1984, Hawaii's papaya production reached its highest point (80.5 million pounds). However, around 1990, the PRSV appeared in Hawaii. As expected, the papaya

plantations of Hawaii were devastated. By 1997, the papaya production declined up to 40 percent, Hawaii's economy staggered, and many farmers' livelihoods were destroyed.

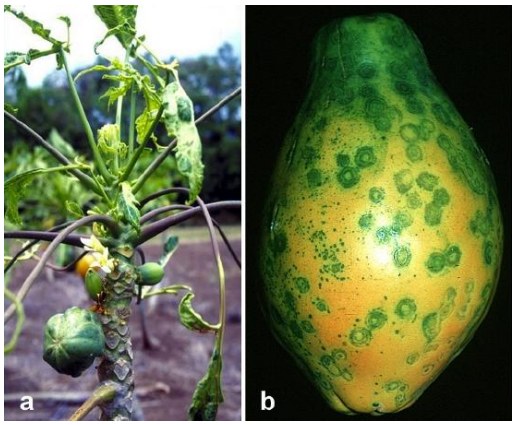



Fig 7.5 Image of Papaya Ringspot Virus symptoms on trees and fruit. "Papaya Ringspot Virus Symptoms" by APS is in the public domain.

Most of Hawaii's papaya farmers were first-generation, less-educated immigrant Filipinos. Fortunately, Dennis Gonsalves, a Cornell University professor, grew up in Hawaii and knew the importance of papaya for the local economy. He noticed the PRSV when its outbreak began in Hawaii and started a research project to save the papaya plantations from PRSV. First, he tried to find a PRSV-resistant papaya variety so that trait could be transferred to the high-yielding productive papaya varieties using traditional plant breeding methods. But he didn't succeed in finding such a variety. After this, Gonsalves identified less harmful strains of PRSV and experimented with them. He observed that if a papaya plant is first infected with a less aggressive strain, then the more harmful PRSV strain does not attack it. Until 1983, Gonsalves kept doing these experiments, but no permanent solution emerged for the disease's practical management.

Around 1983, Roger Beachy made a kind of transgenic tobacco that was resistant to the tobacco mosaic virus (TMV). After entering a living cell, TMV (like most other viruses) makes replicas of its genome using the host cells' resources, and then genome replication stops, and the synthesis of coat protein begins. The coat protein forms the virus's outer shell; thus the viral genome gets packed one by one, and the progeny of TMV busts out by destroying the host cells. Beachy cloned the coat protein gene of TMV and then transferred it into tobacco plants. Beachy's transgenic tobacco expressed high quantities of coat protein, so when TMV infected them, the coat protein present in the transgenic plant prevented replication of the viral genome, and infection was contained. Professor Gonsalves, inspired by Roger Beachy's success, decided to introduce the PRSV's coat protein gene in the papaya. In 1986, he successfully cloned this gene and transferred it within papaya plants with the help of a gene gun. As expected, the transgenic papaya showed resistance to the devastating PRSV. Field trials of these GE varieties, known as Rainbow and SunUp, began in 1992, and in late 1996, the US government approved transgenic papaya for commercial planting.

In 1998, Hawaiian farmers received Rainbow papaya seeds and the necessary advice free of cost, and Hawaii's papaya plantations got a new life. Currently, a cooperative society sells seeds of PRSV-resistant papaya varieties in Hawaii to farmers at very low prices. For the past twenty-two years, the papaya of Hawaii has been selling globally and contributes $50 million annually to Hawaii's economy. Gonsalves did not receive any grant from any government or private institution to make the GE papaya varieties. The only help he received was a small grant of $20,000 from Hawaii's senator Daniel Inouye. He created the world's first successful GE crop at a very low cost and made it available to farmers free of charge. In 2002, Gonsalves's research team was awarded the Humboldt Research Award for their contribution to agriculture.

Later, others made virus-resistant GE squash, zucchini, potatoes, and plums (see table 7.1).

## Roundup Ready Soybeans

Weed control has always been a challenge for farmers. Weeds are wild plants (sometimes closely related to crops), are well adapted to various environments, and are more resilient than crops. Weeds compete for nutrients, sunshine, and water with crops and negatively affect crop yields (20–40 percent). In traditional societies, farmers used to burn the weeds before sowing and then afterward spent time weeding. However, this is not an option for very large agricultural fields. After 1950, chemicals were

discovered that can destroy the foliage. Initially, they were sprayed in the area before sowing to eradicate weeds. But these chemicals are hazardous for human health and have chronic and acute toxicity. Furthermore, many herbicides are carcinogens, and their use poses a risk of polluting water, air, and the food chain.

In 1970, John Franz, a scientist at the Monsanto Company, discovered herbicidal activity in glyphosate.[6] Furthermore, it was found that some soil bacteria can convert glyphosate into harmless substances within a few days. Hence it posed relatively less risk of environmental pollution compared to previously used chemicals. In 1974, it was marketed as an herbicide with the trademark Roundup. In the 1970s, Monsanto also invested in plant biotechnology and began developing herbicide-resistant transgenic crops. They already had information that soil microorganisms can metabolize glyphosate into harmless products. Soon scientists discovered a gene within a bacterium that coded for an enzyme capable of degrading glyphosate. Subsequently, this gene was introduced in soybean and corn to create Roundup Ready GE varieties that survive herbicide (glyphosate) sprays while all the weeds die. In 1996, a Roundup Ready soybean was approved by the FDA for its cultivation in the US. In this way, weed management became simpler, cheaper, and more manageable. Also, farmers can plant soybeans in a closer, tighter row and get higher yields. However, the second-generation soybeans are sterile, so farmers must buy new seeds every year from the seed company. This strategy was also used for creating herbicide-tolerant corn, rice, and many other crops. More than 50 percent of GE crops currently grown in the US and worldwide are herbicide resistant (see table 7.1).

Today, more than 90 percent of soybeans, corn, cotton, and mustard growing in the US are Roundup Ready varieties. Farmers around the world are increasingly relying on herbicides for weed management. Since 1996, when genetically engineered glyphosate-tolerant Roundup Ready crops were first released, glyphosate use has risen fifteenfold globally; these quantities are beyond the natural capacity of soil bacteria to metabolize glyphosate. Therefore, glyphosate and other herbicides have generated concern among the public and policymakers due to their harmful effects on human health and the environment.

## Insect-Resistant Bt Crops

Most of us do not like to eat any fruit or vegetable that is infested by insects. We see the clean fruit and vegetables in the market because farmers have used plenty of pesticides. If pesticides are not sprayed, one-third of the yields of most crops would be lost due to pest infestation. However, pesticides have harmful effects on human health and pollute the environment.

Scientists have been looking for an alternative to pesticides for a long time. In 1901, a Japanese scientist, Shigetane Ishiwata, was investigating the cause of silkworms' sudden deaths and found the bacterium *Bacillus* in dead larvae. He concluded that Bacillus is responsible for their deaths. In 1911, Ernst Berliner also noticed that the Mediterranean floor moths' larvae were dying due to *Bacillus*'s presence. He named the bacterium *Bacillus thuringiensis* after the German city of Thuringia.

*B. thuringiensis* (or Bt) is a gram-positive soil bacterium that contains crystals of a delta-endotoxin protein that kills a broad category of insects. Upon ingestion, the crystal protein is cleaved into small fragments by proteases present in the alkaline environment of an insect's gut. One of the fragments generated from the crystal protein acts as a toxin. This toxin kills insects by forming pores into the cell membranes of the insect midgut. From 1920 onward, European farmers began spraying the Bt bacteria to protect their crops from pests. In 1938, commercial spore-based formulations known as Sporine made it to the market in France. Even today, organic farmers spray a similar formulation of Bt bacteria on their crops.

In the 1980s, the Monsanto Company succeeded in cloning the "cry" gene from *B. thuringiensis* that codes for the crystal protein. Subsequently, this gene was optimized for high expression in plant cells to develop insect-resistant crops (e.g., cotton, maize, eggplant, and rice). When insects feed on Bt plants, the delta endotoxin reaches their intestine, and they die. Therefore, Bt crops can protect themselves from insects. In 1995, the US government approved Bt cotton (*Bollgard cotton*) and Bt corn for cultivation. Since then, these crops are being grown in the US and many other countries. These seeds of Bt varieties sold in the market are of the heterozygous F1 hybrid. Thus, farmers cannot save seeds of Bt crops for the following year's sowing, because in the F2 generation, resistance and susceptibility traits segregate, and the insect-resistant traits get diluted in every subsequent generation. The farmers are required to buy these seeds every year, and their input costs increase.

The Bt crops do not eradicate insects completely, but their use could reduce the quantities of chemical pesticides manifold. The farm management is crucial for integrating these bioengineered crops and the chemical spray and keeping a sufficient refuge of non-GE crops to reduce the pests' selection pressure. In the US, Brazil, Argentina, and so on, practicing integrated pest management (IPM) is easy because thousands of acres of the farm are run by a single person or company. But in other developing

countries, farmers have smaller agricultural land holdings and do not have enough space for “refuge.” The farms are also surrounded by many neighboring farms.

Since living organisms constantly evolve, the protection offered by the Bt gene is not going to last for a long time, and eventually, it will be ineffective against insects. That is why scientists continue to make new versions of the Bt gene and search for other genes with similar properties. Thus it is expected that from time to time, scientists will release new GE varieties as the arms race between hosts and pests continues.

## Golden Rice

The diet of poor people living in Asia, Africa, and Latin America mainly consists of rice and lacks fruits, vegetables, dairy, and meat. Consequently, millions of people have a huge deficiency of vitamin A in their bodies. According to a survey by the World Health Organization, more than 400 million people in twenty-six countries living on rice are deficient in vitamin A, due to which 500,000 children suffer from night blindness/blindness and 1 million children die annually.[7]

Vitamin A is essential for the proper development of humans and animals. It supports the healthy development of eyes, bones, and muscles and maintains adequate calcium levels and immunity. Humans cannot biosynthesize vitamin A of their own, but they get it from dairy, meat, and colorful vegetables and fruits. Red, orange, and yellow vegetables and fruits (e.g., sweet potatoes, carrots, oranges, and mangoes) contain provitamin A (β-carotene), which gets converted into vitamin A inside the human body.

For a long time, plant breeders have been searching for a rice variety in which β-carotene is found. In 1991, Ingo Potrykus, at the Institute of Plant Sciences of the Swiss Federal Institute of Technology, Zurich, started a project to bioengineer the β-carotene biosynthesis pathway in rice. In plants, the biosynthesis pathway consists of eight reactions, which are catalyzed by four enzymes. Rice contains most of the precursors for making β-carotene, but three out of four enzymes are nonfunctional. In 2000, Potrykus and his colleague Peter Beyer cloned two genes, phytoene synthase and lycopene cyclase, from the daffodil and the *phytoene*/carotene desaturase (crt1) gene from bacteria and then successfully introduced all three genes in rice plants to create the provitamin-rich variety by reconstructing the β-carotene biosynthesis pathway (see figure 7.6). One kilogram of this rice contains about eight milligrams of β-carotene, which gives them a golden hue, and thus this variety was named golden rice.[8] Once this basic strategy was successful, Potrykus signed a contract with the company Syngenta for enhancing the content of β-carotene and for large-scale experimental testing and handling. Syngenta produced an SGR2 variety of golden rice (~27mg β-carotene/kg) by replacing the phytoene desaturase in a daffodil with maize homolog. The Golden Rice Humanitarian Board has made golden rice free for farmers in developing countries with an annual income below $10,000. Later, with the help of research institutes of various countries, β-carotene biosynthesis pathways have also been enabled in many rice varieties (IR 64, Boro, PSB, RC82, etc.). After extensive testing, these GE rice varieties were found to be safe for human consumption. Unlike other GE crops, farmers who grow golden rice can save the seeds of the next year’s sowing. It took almost two decades before the golden rice was approved for farmers’ use. In 2018, the FDA, Health Canada, and Food Standards Australia New Zealand recognized the IRRI’s evaluation and approved the release of golden rice’s GR2E variety. Bangladesh and China have begun the cultivation of golden rice.

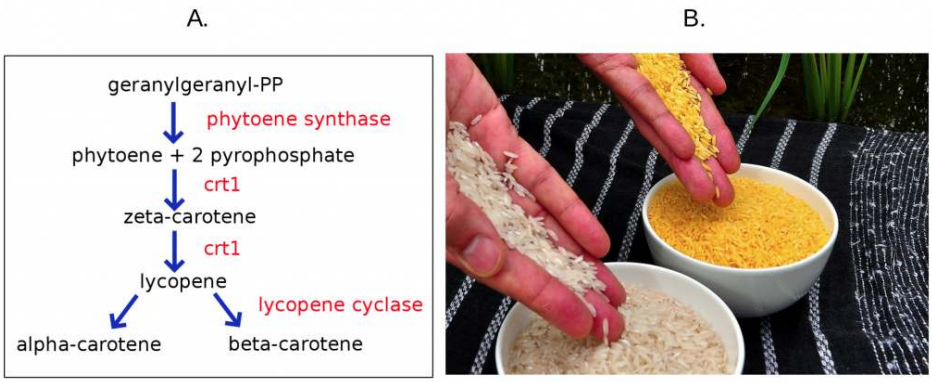



Fig 7.6 (A) Reconstruction of β-carotene biosynthesis pathway. (B) Comparison of Golden Rice with white rice. “Golden Rice, a rich source of vitamin A” is a derivative of “Golden Rice” by International Rice Research Institute (IRRI), used under CC BY 2.0. “Golden Rice, a rich source of vitamin A” is licensed under CC BY 4.0 by Sushma Naithani.

After rice, scientists started to work on biofortifying other crops using a similar strategy. For example, Maria Andrade, Robert Mwanga, and Jan Low created the golden sweet potato[9] with the support of global nonprofit agricultural research program HarvestPlus (https://www.harvestplus.org/), USAID, the Bill and Melinda Gates Foundation. Similarly, the golden cassava variety has also been developed, which has special importance for Africa.

Table 7.1 Herbicide-tolerant GE crops

| Crop | Herbicide | Year | Inventor |
|---|---|---|---|
| Canola | *Glufosinate* | 1995 | Bayer |
| Canola | glyphosate | 1999 | *Monsanto* |
| Cotton | *Bromoxynil* | 1994 | Calgene |
| Cotton | glyphosate | 1996 | *Monsanto* |
| Cotton | Sulphonylurea | 1996 | *DuPont* |
| Cotton | *Glufosinate* | 2003 | Bayer |
| Cotton | Dicamba | 2015 | *Monsanto* |
| Cotton | 2,4-Dichlorophenoxyacetic acid (2,4-D) | 2015 | Dow |
| Maize (corn) | Glufosinate | 1995 | AgrEvo GmbH |
| Maize | glyphosate | 1996 | *Monsanto* |
| Maize | 2,4-D | 2014 | Dow |
| Sweet corn | glyphosate | 2011 | *Monsanto* |
| Rice | *Glufosinate* | 1999 | *AgrEvo GmbH* |
| Soybean | glyphosate | 1994 | *Monsanto* |
| Soybean | *Glufosinate* | 1996 | Bayer |
| Soybean | Sulphonylurea | 2007 | *DuPont* |
| Soybean | Isoxaflutole | 2013 | Sygenta |
| Soybean | Mesotrione | 2014 | Sygenta |
| Soybean | Imidazolinone | 2014 | BASF |
| Soybean | 2,4-D | 2015 | Dow |
| Soybean | Dicamba | 2015 | *Monsanto* |
| Sugar beets | glyphosate | 2005 | *Monsanto* |
| Sugar beets | *Glufosinate* | 1998 | *AgrEvo GmbH* |

Table 7.2 Insect (pest)-resistant crops

| Crop | Transgene | Year | Inventor |
|---|---|---|---|
| Cotton | Bt | 1995 | *Monsanto* |
| Field corn | Bt | 1995 | *Monsanto* |
| Sweet corn | Bt | 1998 | *Monsanto* |
| Potato | Bt | 1995 | *Monsanto* |
| Soybean | Bt | 2016 | *Monsanto* |

Table 7.3 Virus-resistant crops

| Crop | Coat protein gene | Year | Inventor |
|---|---|---|---|
| Papaya (Rainbow and SunUp) | Ring Spot Virus | 1996 | Dannis Gonsalves (Cornell University, and ARS-USDA) |
| Plum | Plum pox virus | 2007 | USDA |
| Potato | *Potato Virus Y* | 1999 | *Monsanto* |
| Potato | *potato leaf roll virus* | 2000 | *Monsanto* |
| Squash (not widely grown) | zucchini yellow mosaic virus | 1994 | Asgrow |
| Squash (not widely grown) | watermelon mottle virus 2 | 1994 | Asgrow |

Table 7.4 Nutritional value improved crops

| Crop | Trait | Year | Inventor |
|---|---|---|---|
| Canola | *High Iysine* | 1994 | Calgene |
| Maize | *High-Iysine* | 2006 | *Monsanto* |
| Golden Rice | Rich in β-carotene (pro-vitamin A) | 2005 | Sygenta |
| Plenish Soybean | High oleic acid content (no trans fat) | 2010 | *DuPont* |
| Potato | Less *acrylamide, when cooked/fried at a high temperature.* | 2014 | J R Simplot Company |
| Arctic Apple | The GE Apples resist browning after being cut. | 2015 | Okanagan Specialty Fruits Inc. |

## Impact of GE Crops

Humans have been selecting plants and animals for desired traits that suited their needs since the beginnings of agriculture 10,000 years ago. GE crops are the latest advancements made in this direction, with goals of achieving agricultural productivity and improving the available genetic stocks' quality. After 1930, these objectives were achieved using traditional breeding. In the early twenty-first century, scientists genetically engineered crops by introducing useful genes from any living forms and/or by rationally designed genes. A GE crop may contain one or more transgenes from bacteria, viruses, animals, or plants. However, more than 99 percent of it is similar to its mother plant (see figure 7.7). In general, crop plant species contain 30,000–50,000 genes, and less than five genes are introduced in any given GE crop. In this sense, GE crops are closer to the domesticated varieties.

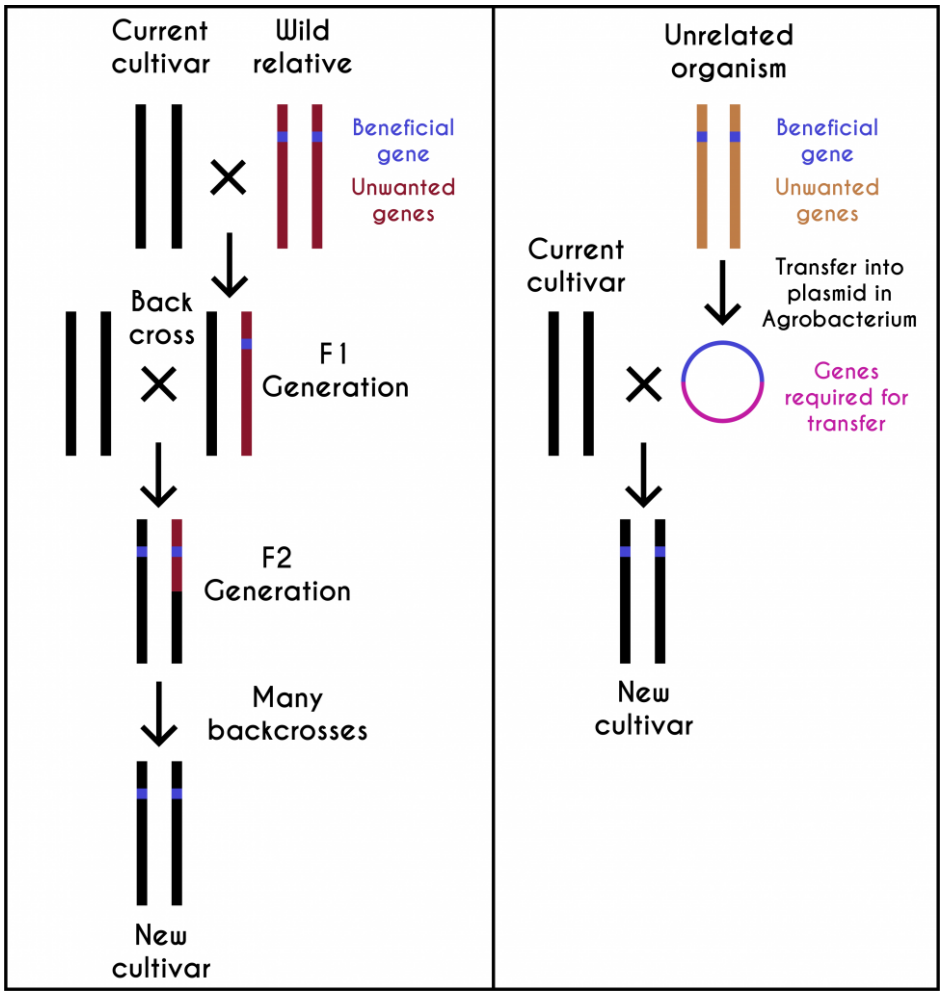



Fig 7.7 A comparison between conventional plant breeding and genetic engineering. "Breeding transgenesis cisgenesis" by Smartse is licensed under CC BY-SA 3.0 / image cropped.

Interestingly, people have adopted more than 1,000 high-yielding varieties (generated by traditional breeding), but GE crops have aroused significant anxiety around the world and have faced consistent opposition globally. There has been a constant debate about the technology and impacts of GE crops. The first and foremost concern is if GMO food is safe. GE crops undergo extensive safety trials before they are released for cultivation and are approved by the FDA. The data from various GE crops' safety trials in the last twenty-five years show that GMO food is safe. In 2016, the US National Academy of Sciences published a review of GE crops prepared by an independent committee of eighteen experts. This 600-page report (1) concluded that there is no evidence that anyone has had a problem digesting GMO foods so far. However, people have raised issues related to allergies and the presence of toxins in GMO food. Overall, GMO food is deemed safe by the experts. Today most experts, scientific institutions, and governments agree that GMO food does harm human health. According to an estimate, millions of people in twenty-eight countries have been consuming GMO food products daily for the past twenty-five years, and so far, none died due to eating such foods (1).

Contrary to what the experts have revealed, there is increasing anxiety among consumers about GMO products. This issue has not been settled for the people yet. Many nongovernmental organizations, consumer groups, and ordinary people worldwide are worried about the safety of consuming GMO food. No one has currently investigated GMO products' long-term effects on humans; therefore, both opponents and supporters of GMOs can't say anything definitively on the matter. For a long time, consumer groups had been advocating to clearly label products that are GMO, since in the US, this had not been required by law. Under consumers' pressure, the labeling of GMO (and more of non-GMO) products appeared increasingly, and in 2016, US Congress passed a law requiring the labeling of GE food (the bioengineered). Hence, the data on the long-term effects of GMO food on human and animal health may become available in the future.

Another issue is how much more productive GE crops are than the high-yielding breeds developed during the green revolution. In the last twenty-five years, the claims made about GE crops' increased productivity have not been fully met. The 2016 National Science Academy report (1) stated that the productivity of GE crops grown from 1990 to 2015 is not significantly higher than the high-yielding varieties of the green revolution era. Overall, the GE crops made the farmers less prosperous than the green revolution because agriculture's input cost (for buying seeds, fertilizer, irrigation, pesticides, fungicides, herbicides, etc.) is very high and leaves a small margin for profit. Compared to the green revolution era, today's farmers have smaller and less fertile farms in developing countries, and government assistance and subsidies have declined.

Did GMO technology improve the quality of food? Without a doubt, this technology has created many nutrient-rich crops—like golden rice, cassava, and sweet potato; high oleic acid–containing canola; Plenish soybeans; and so on—and offers an opportunity for further improvements. There is tremendous scope for solving malnutrition by using GMO technology. In addition, the genetic engineering of model and crop plants has provided a conceptual understanding of gene functions and many fundamental biological processes. Besides genetics and genomics, immense progress has been made in vitro tissue culture technology. Together, the new knowledge and advancement in tools served as a foundation for next-generation CRISPR/Cas9 gene-editing technology that has a high potential for developing new biofortified and stress-tolerant varieties of crops.

At the beginning of the twenty-first century, GE crops were presented as a promising alternative to a non–environmentally friendly industrial farming system. But looking at the last twenty-five years, it is clear that GE crops have become an integral part of it. The folks who oppose GMOs argue that most GE crops ensure profit to corporations by encouraging increased use of pesticides, weedicides, fungicides, and fertilizers. To date, more than 50 percent of GE crops are herbicide resistant. The use of glyphosate and other herbicides has exceeded the safety threshold and poses threats to human health and the environment. The continuous spray of herbicides has led to the rise of superweeds that are increasingly adapting to various herbicides and require more potent mixtures (including two or more chemicals) or higher doses for effective control. Thus GM crop-based weed management is not sustainable. Additionally, the reliance on both high-yielding and GM crops on heavy inputs of energy and fertilizers also needs careful reevaluation.

## Toward a Sustainable Future

The FAO projects the global population to grow to 9.7 billion by 2050. The biggest challenge of the twenty-first century is to keep the productivity of crops sustainable without causing further destruction to the environment and depletion of natural resources. Despite its overall efficiency, the current industrial agricultural system relies heavily on natural resources and energy. For example, half of the world's habitable land and more than 70 percent of global freshwater withdrawals are used for agriculture. Also, agriculture is a significant source of global pollution: 26 percent of global greenhouse gas emissions[10] and 78 percent of the global ocean and freshwater eutrophication is caused by agriculture.[11] Agriculture is the prime source of greenhouse gases, including carbon dioxide (CO2) and nitrous oxide (N2O), which cause the depletion of the stratospheric ozone layer and global warming. Therefore, the agricultural production systems have a big impact on global climate change, natural resources, and all living beings' health.

It is important to note that a continuous increase in agriculture productivity alone cannot solve hunger in the world. Natural resources are finite, and their overexploitation will have disastrous consequences. Therefore, we must explore other avenues for bringing efficiency to ensure food security. Today, enough grain is being produced worldwide to meet the need of 10 million people. Theoretically, if food is distributed equally among all the people of the world, then 75 percent of it is enough to feed the entire population of the world, and one-fourth can be saved, although achieving such equity at the global level is difficult to achieve due to various sociopolitical reasons. Nonetheless, it suggests that there are additional avenues where progress can be made beyond agriculture production.

It is noteworthy that more than 40 percent of all food produced worldwide is wasted in processing, transportation, supermarkets, and kitchens. Many fruits and vegetables are discarded because of their lack of aesthetic appeal or uniformity. Moreover, readymade, cheap, and readily available food requires extra production to compensate for its regular trashing as it expires on the supermarkets' shelves. When food is wasted, all the resources to grow, process, package, and transport are wasted along with it. Besides, the waste is a source of significant greenhouse gases. Overall, the current agricultural production systems and consumers' lifestyles put a burden on natural resources, the environment, and energy. If consumers do not change their habits, then the

agricultural production system will remain in its current form. Both farmers and consumers will have to strive together to build a new sustainable agricultural production system.

In past decades, the gradual progress in plant genetics, genomics and breeding, precision agriculture, organic agriculture methods, and growing consumer awareness has been paving the way for the agricultural production system's future. Better management of agriculture, natural resources, the environment, and human resources is required in the agriculture sector. The formula for successful and sustainable agriculture will have elements from industrial farming, GM technology, precision agriculture, and organic farming. Equally important is to foster a culture of conscious consumption and change in consumers' behavior to create new, sustainable, just, diverse, and healthy agricultural production systems. The issue of agriculture has never been limited to production. It has given rise to human civilization and its polytheistic cultures. Change in agriculture is intricately associated with a change in human society. Only a better society can build a better agricultural system.

## References


National Academies of Sciences, Engineering, and Medicine. (2016). *Genetically engineered crops: Experiences and prospects*. National Academies Press. https://doi.org/10.17226/23395 (↵ Return 1) (↵ Return 2) (↵ Return 3)


## Further Readings


Benbrook, C. M. (2016). Trends in glyphosate herbicide use in the United States and globally. *Environ. Sci. Eur., 28*, 3.

Beyer, et al. (2000). Engineering the provitamin A (-carotene) biosynthetic pathway into (carotenoid-free) rice endosperm. *Science, 287*(5451), 303–5. doi.org/10.1126/science.287.5451.303

Gillam, C. (2018, May 8). Weedkiller products more toxic than their active ingredient, tests show. *The Guardian*. https://www.theguardian.com/us-news/2018/may/08/weedkiller-tests-monsanto-health-dangers-active-ingredient

Gonsalves, D. (1998). Control of papaya ringspot virus in papaya: A case study. *Annu. Rev. Phytopathol, 36*, 415–37.

Jenkins, M. (2018). *Food fight: GMOs and the future of the American diet*. Avery.

Oerke, E. C. (2006). Crop losses to pests. *J. Agric. Sci., 144*, 31–43. https://doi.org/10.1017/S0021859605005708

Pingali, P. L. (2012). Green revolution: Impacts, limits, and the path ahead. *PNAS, 109*, 12302–8. doi.org/10.1073/pnas.0912953109

Pollan, M. (2006). *The omnivore's dilemma: A natural history of four meals*. Penguin.

Poore, J., & Nemecek, T. (2018). Reducing food's environmental impacts through producers and consumers. *Science, 360*(6392), 987–92.

Searchinger, T., et al. (2018). *Creating a sustainable food future—a menu of solutions to feed nearly 10 billion people by 2050*. World Resources Institute. https://www.wri.org

Tian, H., et al. (2020). Comprehensive quantification of global nitrous oxide sources and sinks. *Nature, 586*(7828), 248–56. https://doi.org/10.1038/s41586-020-2780-0

Watson, J. D. (1968). *The double helix: A personal account of the discovery of the structure of DNA*. Atheneum.


1. An organism containing a transgene is known as a genetically modified organism (GMO). ↵
2. Not all GE crops are in cultivation today. Only a few are grown in the US. To see the updated information on GE crops, visit the FDA's website: https://www.fda.gov/food/consumers/agricultural-biotechnology. ↵
3. The animals have additional DNA inside mitochondria; plants have DNA inside chloroplast and mitochondria. These are identified separately as organellar genomes. ↵
4. Have a look at the Tree of Life at http://tolweb.org/tree, and see the Tree of Life segment of BBC One's "Charles Darwin and the Tree of Life," narrated by David Attenborough, at https://youtu.be/H6IrUUDboZo. ↵
5. See https://www.fda.gov/food/consumers/agricultural-biotechnology. ↵
6. Glyphosate (N-[phosphonomethyl] glycine) was discovered by Henri Martin in 1950. ↵
7. For current data, visit https://ourworldindata.org/micronutrient-deficiency. ↵

8. The story of golden rice, as told by Ingo Potrykus, is available at http://www.agbioworld.org/biotech-info/topics/goldenrice/tale.html. ↵
9. Learn more about the golden sweet potato at www.worldfoodprize.org/en/laureates/20102019_laureates/andrade_mwanga_low_and_bouisold_template/?nodeID=88375&AudienceID=1&preview=1. ↵
10. Agriculture is the prime source of greenhouse gases, including carbon dioxide (CO2), nitrous oxide (N2O), and methane, which cause the depletion of the stratospheric ozone layer and global warming. N2O has 300 times the warming potential of CO2. Usually, N2O is destroyed in the upper atmosphere by solar radiation. But current human activities (e.g., agriculture and livestock) have significantly increased N2O emissions and caused the perturbation in its natural cycle, resulting in its accumulation in the atmosphere. A comprehensive study by the Global Carbon Project and the International Nitrogen Initiative suggests that agriculture has contributed to a 70 percent rise in the global N2O levels. See the Global Carbon Project website for more details: https://www.globalcarbonproject.org/nitrousoxidebudget. ↵
11. See https://ourworldindata.org/environmental-impacts-of-food. ↵

---

This page titled 7.1: Genetically Engineered Crops is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley via source content that was edited to the style and standards of the LibreTexts platform.

- **1.7: Genetically Engineered Crops** is licensed CC BY-NC 4.0. Original source: https://open.oregonstate.education/cultivatedplants/.

# SECTION OVERVIEW

## 7.2: Genetic Modification

### 7.2.1: Introduction

### 7.2.2: GMO Food (Activity)

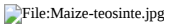
---

This page titled 7.2: Genetic Modification is shared under a CC BY-NC-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

# 7.2.1: Introduction

## Genetic Manipulation (Selection)

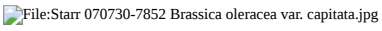
Genetic modification of organisms has been occurring through human manipulation since the beginning of agriculture. Humans selectively bred crops and livestock to propagate desirable traits in a process termed **artificial selection**. The original grass that gave rise to domesticated corn called teosinte hardly resembles what we think of when imagining modern maize.




*Teosinte, the progenitor of maize. Corn came about due to selective breeding. Credit: John Doebley (CC-BY)*

### Variation: Crop Domestication

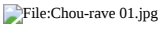
Selective breeding can yield a variety of features even within the same species. Below is a selection of vegetables of the species *Brassica oleracea* that have been developed into different varieties over the course of agricultural history.



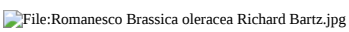

*Cabbage: Brassica oleracea var. capitata Credit: Forest & Kim Starr* ***(CC-BY 3.0)***



*Broccoli: Brassica oleracea var. italica Credit: Coyau (CC-BY-SA 3.0)*

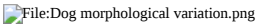



*Kohlrabi: Brassica oleracea var. gongylodes Coyau (CC-BY-SA 3.0)*

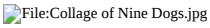



*Romanesco: Brassica oleracea var. botrytis Credit: Richard Bartz (CC-BY-SA 2.5)*

### Variation: Animal Domestication




*Credit: Mary Bloom, American Kennel Club (CC-BY-SA 4.0)*



Companion animals like dogs underwent thousands of years of domestication and selection for traits that were desirable for different circumstances. A high degree of morphological diversity exists between dog breeds and their ancestral grey wolf progenitor.

## Genetic Manipulation (Engineered)

Artificial selection takes multiple generations over a long period of time. With the advent of recombinant DNA and biotechnology, scientists can now genetically modify organisms through the introduction of foreign genes to provide desirable characteristics within one generation. This process does not require traits to naturally arise in a species.



File:Zebrafisch.jpg

*GloFish are transgenic zebrafish (Danio rerio) expressing variants of GFP. Bottom features a wild-type fish. Credit: Azul (CC-BY)*

GloFish® are novelty pets that have the insertion of various cnidarian fluorescent protein genes into the genome. These fish were released in the United States in 2003 and have subsequently been developed in red, orange, and blue varieties. Black tetras and tiger barbs are also now available.



*Black tetra (Gymnocorymbus ternetzi) GloFish Credit: https://www.flickr.com/photos/fergy08/ (CC-BY 2.0)*

File:BlackTetraCloseUp.JPG

*Wild-type Black Tetra Credit: Fernandograu (CC-BY-SA 3.0)*

## Genetic Engineering in Plants

With the advent of agribusiness, agriculture has become a profit-driven venture independent of food production. In this case, high production is paramount. Whereas traditional agriculture or artificial selection was slow and methodical, genetic modification in the context of agribusiness is instantaneous through **genetic engineering**. The ***objective*** of genetic engineering is to transfer the DNA encoding a useful or favorable gene from an organism that carries that gene to one that does not. Simply inserting DNA into an organism does not result in expression. An appropriate promoter for the transgenic organism must be upstream of the gene of interest in order to drive transcription. In mammals, a strong promoter that will result in expression in every cell is the CMV promoter that is derived from cytomegalovirus. Likewise in plants, a strong promoter that works in every cell is derived from viral promoters like the **CaMV promoter** from cauliflower mosaic virus from the **35S gene** (a ribosomal RNA). (CaMV 35S sequence on NCBI)

Examples of useful traits include:

- Degrade herbicides
- Kill agricultural pests
- Synthesize critical nutrients
- To improve color and taste
- Resist damage during transit or prolonged storage.
- Increase in size
- Reduce time to market (more rapid growth or maturation)

Genetically Modified foods have become a hot topic of contention in recent times. These crops are generated through the infection of plant cells by a bacterium called ***Agrobacterium tumefaciens***. *Agrobacterium* is a gram-negative alphaproteobacterium of the family Rhizobiaceae which includes symbiotic nitrogen fixers found in legumes. Unlike those symbionts, *Agrobacterium* is a pathogenic soil bacterium known as a causative agent of crown galls (tumors).

File:Crown-gall detail.jpg

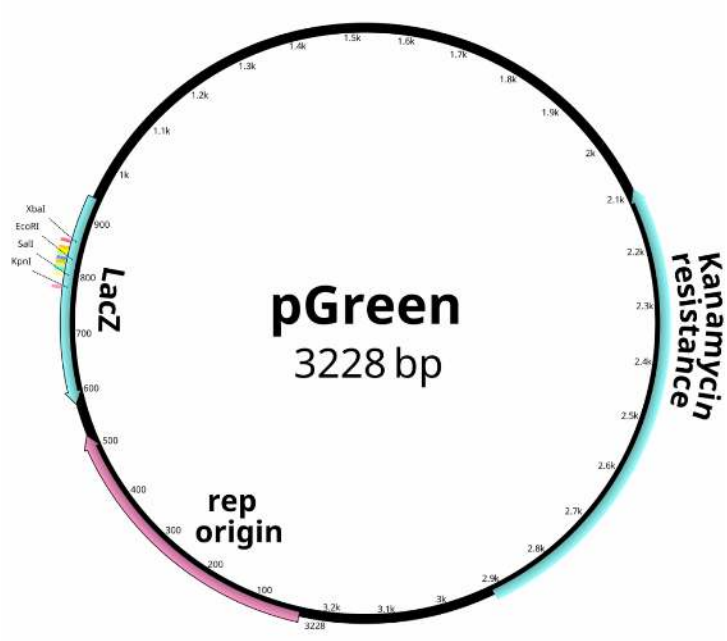
*Crown gall on a Kalanchoë infected with Agrobacterium tumefaciens Credit: Bhai (CC-BY-SA 3.0)*

The tumors are caused by the infection of plant cells by the bacterium and the subsequent insertion of the **T-DNA** ("Transfer DNA") that has a tumor inducing capability (**Ti**). Through the engineering of the T-DNA in a plasmid, selected genes can be delivered to plant cells through infection of transformed bacteria.

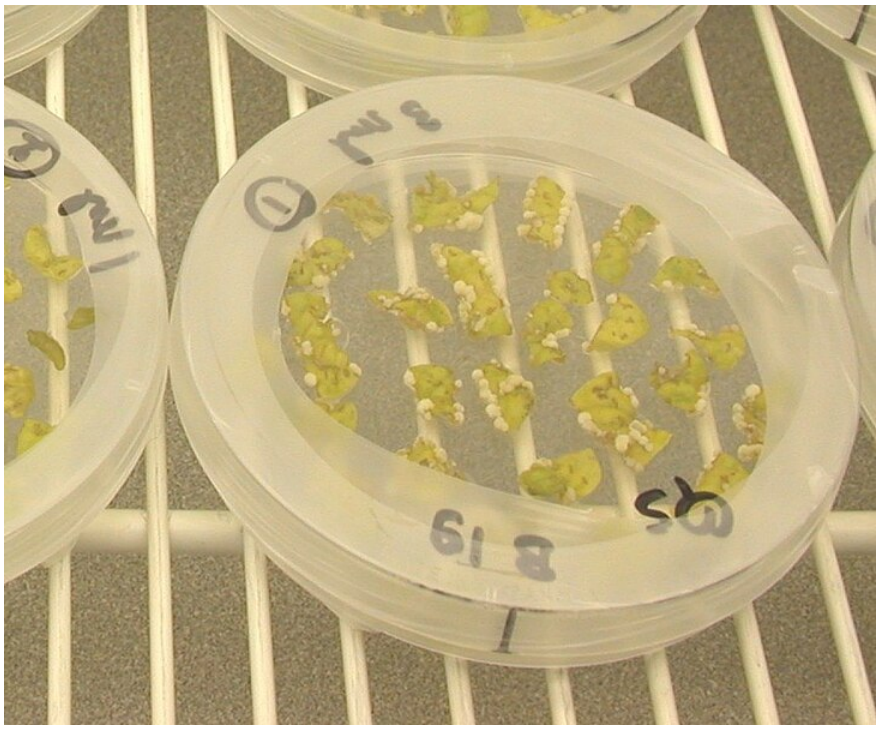
File:Ti plasmid.svg

*Ti plasmid has the T-DNA region replaced by the transgene. Ti is transformed into Agrobacterium which transduces the DNA into plant cells.*

A modified Ti plasmid called **pGreen** was engineered to provide an MCS and selection marker for insertion of foreign genes of interest. In order for these genes to be expressed, they are driven by strong plant promoters like those from the CaMV 35S gene.

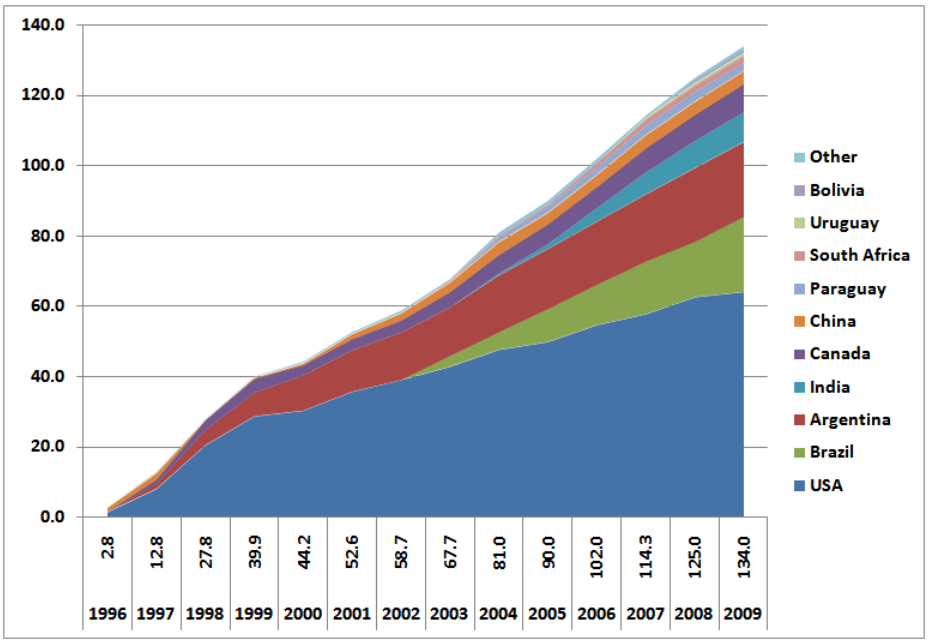



The plant to be engineered is cultured and infected with the transformed *Agrobacteria* that will then induce cysts that eventually root. The strong promoter of the CaMV 35S will constitutively express the gene in all cells of the plant.



*Transformation of wild potato in culture using agrobacterium Credit: Seb951 (CC-BY-SA 3.0)*

## Growth of GMO Crops

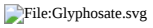



*Land area used in millions of hectares.*

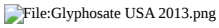
### Damage Resistance

The first genetically modified crop FDA approved for sale was known as the Flavr Savr tomato. Tomatoes are prone to damage during shipping and are therefore picked before ripening. However, vine-ripened tomatoes have a richer flavor. Calgene developed the Flavr Savr and sold it to market between 1994-1997 in the United States. Flavr Savr was modified by inserting antisense into the genome that knocked-down the expression of polygalacturonase. Polygalacturonase degrades pectin in the cell walls of the fruit that results in softening, proclivity to damage, and eventual rotting.

## Herbicide Resistance




**Roundup** is the trade-name of the herbicide **glyphosate** used in agriculture to control weed populations developed and patented by Monsanto. Glyphosate is absorbed through the foliage of plants and interferes with the enzymes that aid in the production of tyrosine, phenylalanine, and tryptophan. Plants and lower organisms generate aromatic amino acids through an enzyme 5-enolpyruvylshikimate-3-phosphate (EPSP) synthase which is the target of this compound. A series of Roundup Ready crops were designed by the insertion of the *Agrobacterium* EPSP gene driven by the CaMV 35S promoter. This version of the gene is inherently resistant to glyphosate poisoning.




## The Emergence of Superweeds



*Palmer amaranth (Amaranthus palmeri), commonly referred to as pigweed, is a pest species in cotton and soy fields that have become glyphosate-resistant.*

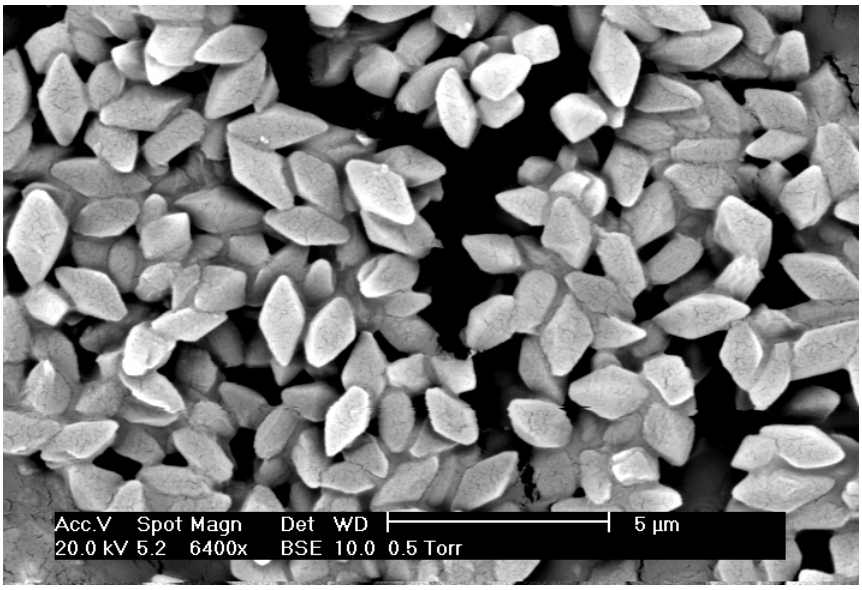
*Credit: Pompilid (CC-BY-SA 3.0)*

## Pest Resistance



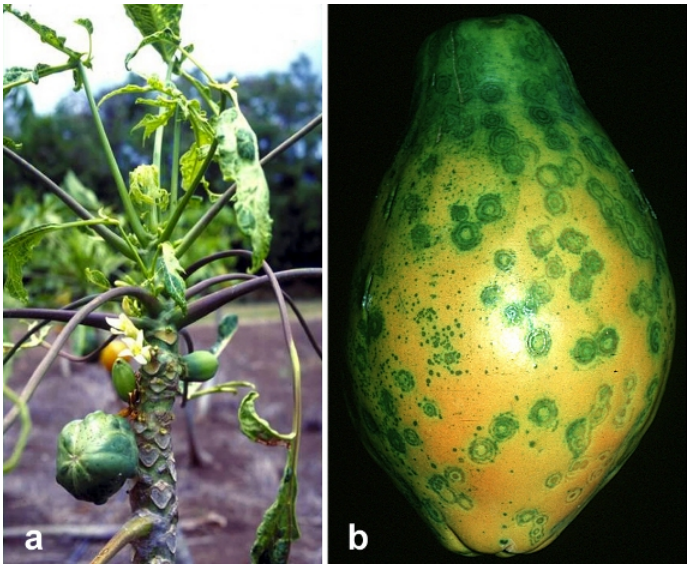

*Credit: Cyndy Sims Parr (CC-BY-SA)*

Crystals from the *Bacillus thuringiensis* (**Bt**), called ***Cry*** protein, are toxic to various insects: moths & butterflies, beetles, ants, wasps, flies & mosquitoes, bees, nematodes. The insertion of this gene into plants like corn (Bt-Corn) was designed to be resistant to pests.




## Disease Resistance

Papayas in the United States primarily come from Hawaii. A virus known as Papaya Ringspot Disease threatened the papaya crop in Hawaii. To combat this, papayas were genetically engineered to block viral entry into the papaya cells. Papayas purchased in Latin markets are most likely unmodified and usually come from Mexico where the ringspot disease is not yet a problem.




Plum Pox Virus is a threat to the genus *Prunus*. A genetically modified plum plant has been developed called C5. The cells in these plants silence the expression of plum pox coat protein if infected to block propagation of the virus.

File:Plum pox in apricot.jpg

*An apricot infected with plum pox.*

File:C5 plum pox resistant plum.jpg

*C5 resistant plums*

## Nutritional Engineering

File:Carotenoidsynthesis.svg

*Credit: en:user: Petaholmes, (CC-BY-SA 3.0)*

**Golden rice** is a genetically engineered rice that is meant to address Vitamin A deficiency. It introduces enzyme genes from other species involved in the biosynthetic pathways for β-carotene production, a vitamin A precursor. It is estimated that millions of deaths and irreversible blindness occur in the third world each year due to Vitamin A deficiency and creating this rice was meant to address the problem.

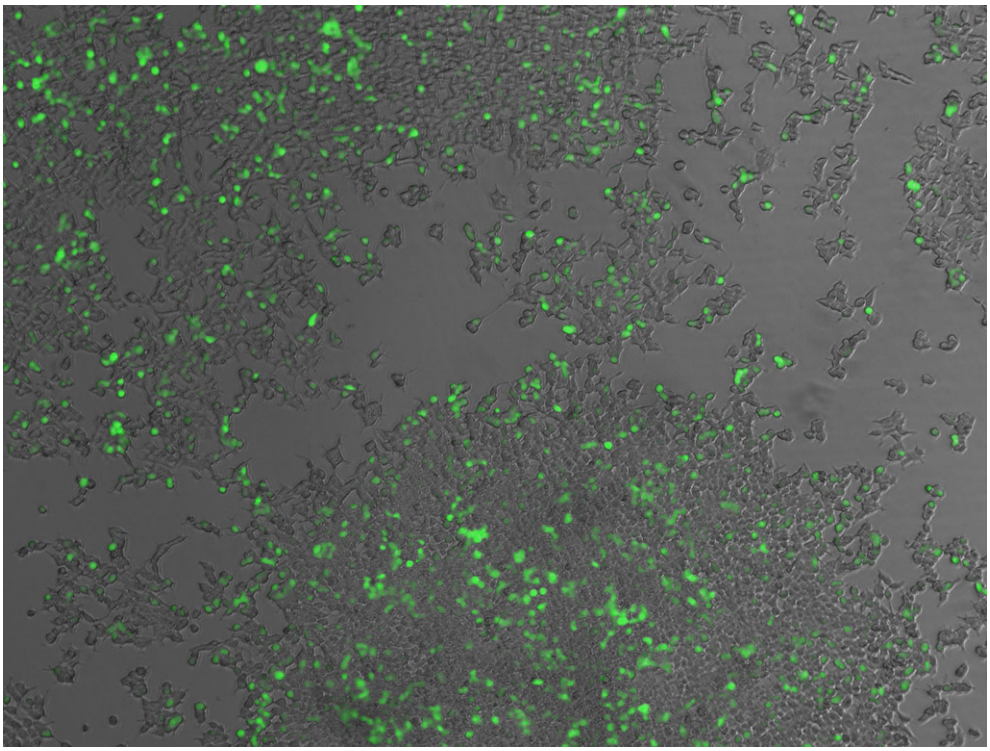
Rice is a staple in many cultures, therefore it is a good delivery system. Many controversies exist surrounding Golden Rice due to anti-GMO sentiment (from patenting systems), cultural sensitivities (white rice revered in certain cultures), and Vitamin A content/conversion doubts.

File:Golden Rice.jpg

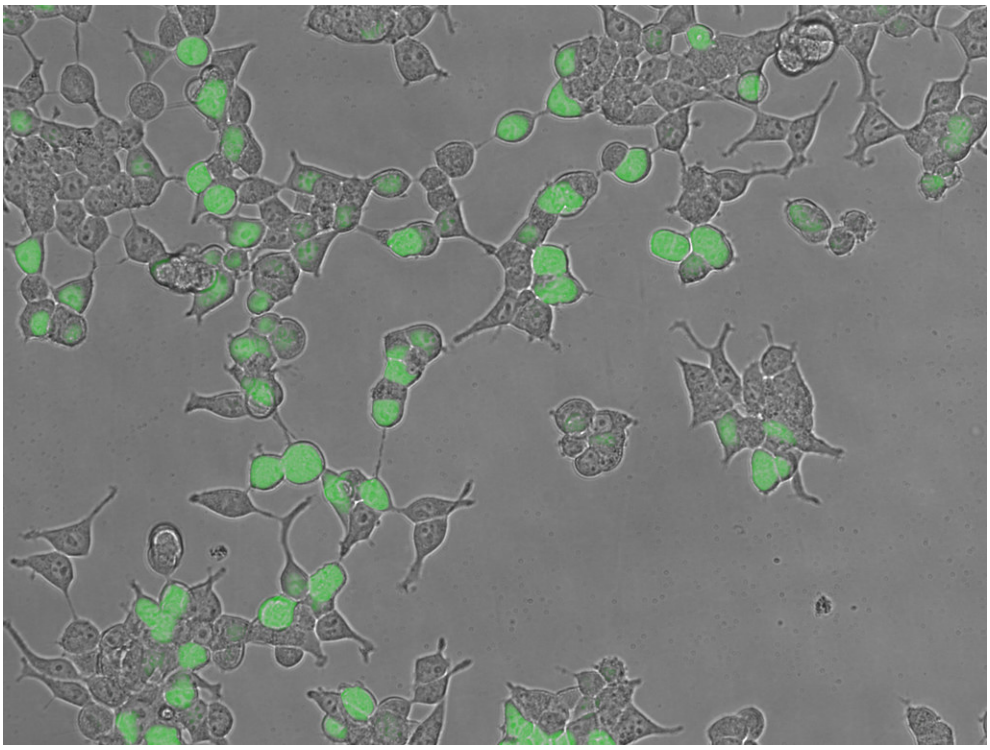
## Explore the Debate

- Case studies reveal the complex truths behind GM crop myths.
- Case studies: A hard look at GM crops. Gilbert N. Nature. 2013 May 2;497(7447):24-6. doi: 10.1038/497024a

## Heterologous Expression in Tissue Culture

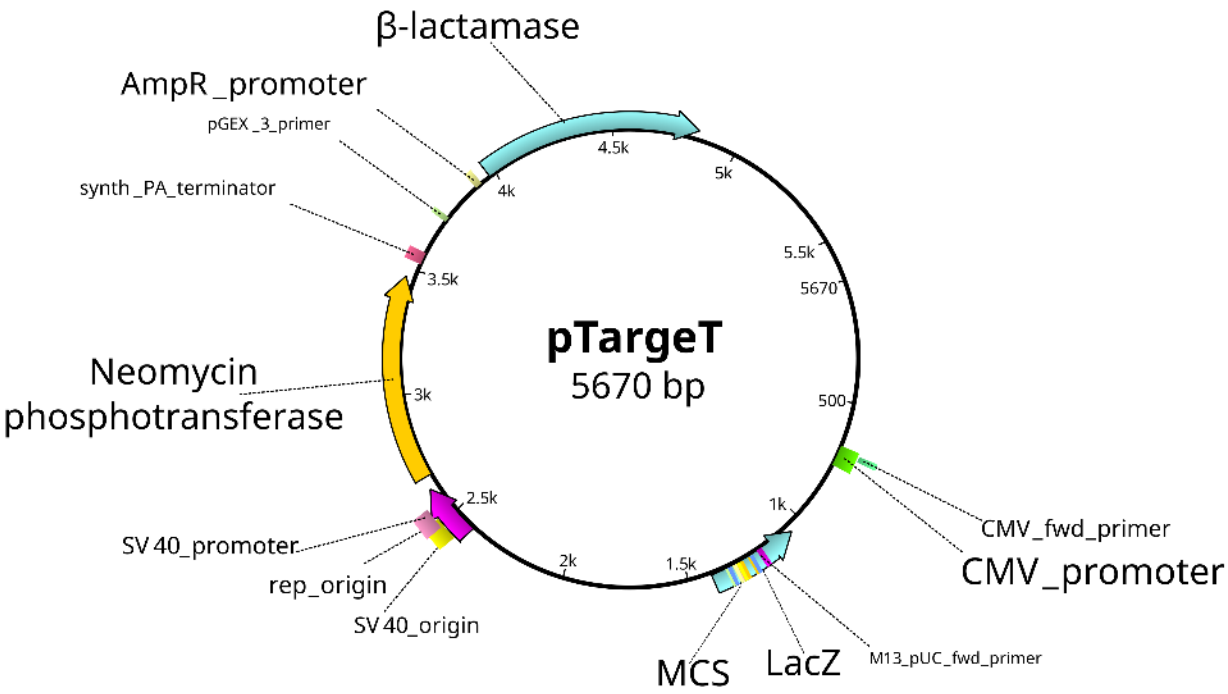


*Human Embryonic Kidney cells (HEK293T) expressing the green fluorescent protein.*



*Higher magnification of HEK293T expressing the green fluorescent protein.*

## Plasmid Structure




*pTarget mammalian expression vector. The MCS is inside the LacZ gene which permits for blue/white screening of the bacteria after cloning. The LacZ runs in the opposite orientation as the CMV promoter which will drive the gene transcription when inside a mammalian cell. SV40 origin servers as a plasmid replication origin if the cell line also expresses SV40 large T antigen, such as HEK293T cells.*

Mammalian expression vectors contain the same hallmark features as bacterial plasmids: bacterial replication of origin and bacterial antibiotic resistance gene (β-lactamase or **$Amp_R$**). General bacterial plasmid features allow for the carrying and the propagation of the plasmid in a bacterial cell. Mammalian expression vectors additionally include a strong mammalian promoter (like **CMV** from the cytomegalovirus immediate early promoter) upstream of a multiple cloning site (**MCS**). Plasmids transfected into cells are transient in nature unless the DNA is selected for. The inclusion of a mammalian antibiotic resistance gene, like neomycin phosphotransferase (**$Neo_R$**), allows for the integration of the plasmid into the genome of the cell by using high concentrations of Neomycin or the analog G418.

### Lipofection

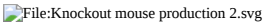
Cationic lipids can encapsulate plasmid DNA in liposomes. The cationic portions interact with the negatively charged plasma membrane to deliver the DNA into cells.

### Calcium Phosphate Transfection

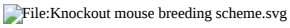
Calcium chloride solution can be used to incubate with plasmid DNA. When this solution is mixed with a HEPES-buffered saline solution (HeBS) containing phosphate ions, the solution precipitates onto the surface of mammalian cells where they are taken up with the DNA.

## Knock-Out & Transgenesis

In the laboratory, model organisms are modified in order to understand the basic mechanisms of genes. The transformation of recombinant DNA into bacteria is an example of a genetic modification. Other model organisms, like mice, are used to study genes. Through recombinant DNA scientists can selectively ablate a gene, or create a **knock-out** (KO).
Embryonic stem (**ES**) cells are pluripotent cells with the capacity to differentiate into other cell types. Cultured ES cells can be transfected with plasmid DNA in order to genetically alter them. Linearized vectors containing a disrupted gene can homologously recombine with the native gene to replace it. Selection of cells with the disrupted gene by an antibiotic (like G418) enables the isolation and propagation of engineered ES cells.

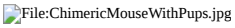


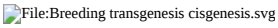

*Credit: Kjaergaard (CC-BY- 3.0)*




*Credit: Kjaergaard (CC-BY- 3.0)*

ES cells can be injected into mouse blastocysts and partially contribute to the subsequent mouse upon implantation into a mouse. These first mice are referred to as **chimeras** because they arise from mixtures of cells from 2 genetic sources. Germ-line transmission of the modified cells is desired and breeding of the chimera reveals heterozygous offspring of the engineered background. Full knock-out mice can be generated in the subsequent generation of breeding.




*Credit: Smartse (CC-BY-SA 3.0)*

Scientists can also overexpress or heterologously express foreign genes in what is termed **transgenic** organisms. As the name sounds, transgene refers to a gene from one place brought across into another.

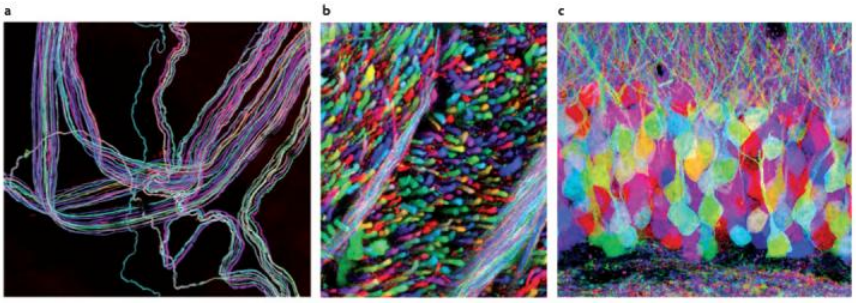
Transgenic and KO models permit scientists to study the roles of genes inside the organism and understand basic functioning.

Through mutagenesis, derivatives of the green fluorescent protein (GFP) have been produced to provide a palette of colors. Additionally, the subsequent discovery of similar genes from other cnidarian species have aided biotechnology by providing tracer molecules within developing organisms or within cells.

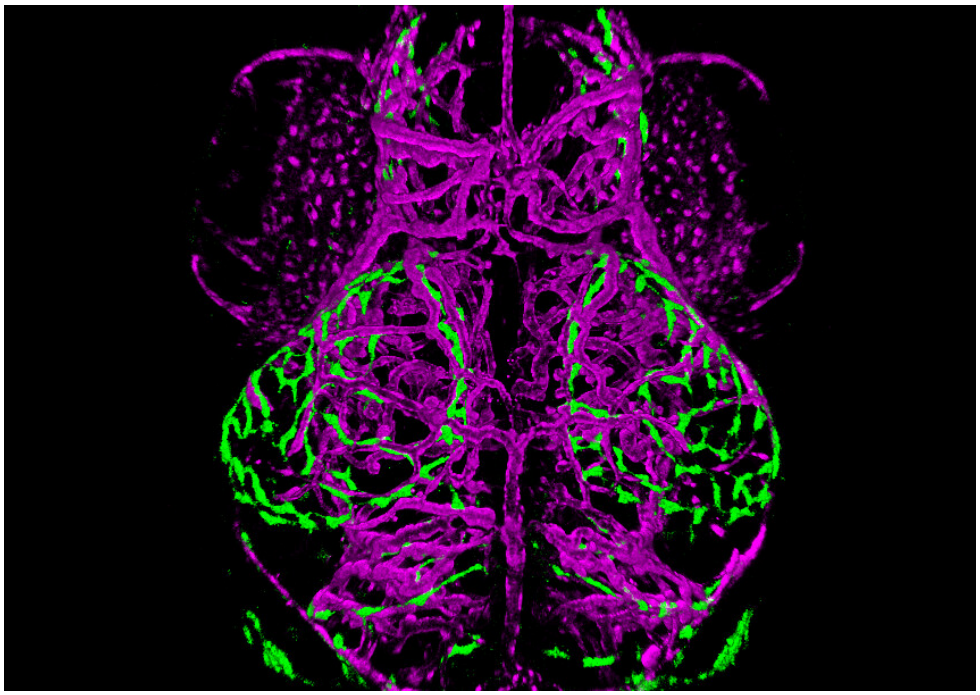



*Bacteria expressing various GFP derivatives on agar from the lab of Nobel Laureate Roger Tsien.*

While commercial organisms like GloFish are a novelty, directed insertion of GFP and the variants into the genome under different promoter systems allow scientists to understand the cell-specific functioning or contribution to the organism. An example of this can be found in developmental neurobiology where individual axons can be traced.




*A "brainbow" is a system where a cassette of GFP variant genes are placed downstream of a neuronal promoter to permit the tracing of individual neurons and their axons in mice. Credit: Jeff W. Lichtman and Joshua R. Sanes (CC-BY 3.0)*



*Brain of a 10-day old double-transgenic zebrafish. Blood vessels are shown in magenta (Kdrl:mcherry) and a novel population of perivascular endothelial cells are shown in green (MRC1a:eGFP).*

## Further Reading

- CRISP-Cas9 https://www.neb.com/tools-and-resources/feature-articles/crispr-cas9-and-targeted-genome-editing-a-new-era-in-molecular-biology

---

This page titled 7.2.1: Introduction is shared under a CC BY-NC-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **14.1: Introduction** by Bio-OER is licensed CC BY-NC-SA 4.0.

# 7.2.2: GMO Food (Activity)

## PCR Detection of GM Food

Briefly, genomic DNA will be isolated from food items derived from vegetation. Genetic modification will then be identified by PCR of the plant promoter used in genetic engineering, **CaMV 35S**. As a **positive control** for the appropriate extraction of DNA, PCR for **plant-specific tubulin** will be used.

1. Add 100 µL of lysis buffer to each tube containing the plant or food material.
2. Twist a clean plastic pestle against the inner surface of the 1.5-mL tube to forcefully grind the plant tissue or food product for 1 minute.
3. Add 900 µL of lysis buffer to each tube containing
4. Boil the samples for 5 minutes in a water bath
5. Spin for 2 minutes to pellet cell and food debris.
6. Transfer 350 µL of each supernatant to a fresh tube
7. Add 400 µL of isopropanol to each tube
8. Mix and leave at room temperature for 3 minutes.
9. Spin for 5 minutes.
10. Carefully pour off and discard the supernatant from each tube. Air-dry pellet.
11. Add 100 µL of TE buffer to each tube. 5 min at room temperature then keeps on ice.

### PCR for 35S Promoter

1. Label one tube “35S FP” for food product.
2. Label one tube “35S WT” for wild-type soy: Negative control.
3. Label “35S RR” for Roundup Ready® soy plant: Positive control.
4. Different groups will only do one control.
5. Add **22.5 µL** of the 35S primer/loading dye mix to each tube containing PCR bead.
    - 5′-CCGACAGTGGTCCCAAAGATGGAC-3′ (Forward Primer)
    - 5′-ATATAGAGGAAGGGTCTTGCGAAGG-3′ (Reverse Primer)
6. Add **2.5 µL** of food product DNA to the reaction tube marked “35S FP.”
7. Add **2.5 µL** of wild-type or Roundup Ready® soybean DNA to the appropriate reaction tube marked “35S WT” or “35S RR.”

### PCR for Tubulin: (Positive Control for DNA Quality and PCR Conditions)

1. Label one tube “T FP” for food product.
2. Label one tube “T WT” for wild-type soy.
3. Label “T RR” for Roundup Ready® soy plant.
4. Different groups will only do one control.
5. Add **22.5 µL** of the Tubulin primer/loading dye mix to each tube containing PCR bead.
    - 5′-GGGATCCACTTCATGCTTTCGTCC-3′ (Forward Primer)
    - 5′-GGGAACCACATCACCACGGTACAT-3′ (Reverse Primer)
6. Add **2.5 µL** of food product DNA to the reaction tube marked “T FP.”
7. Add **2.5 µL** of wild-type or Roundup Ready® soybean DNA to the appropriate reaction tube marked “T WT” or “T RR.”

This page titled 7.2.2: GMO Food (Activity) is shared under a CC BY-NC-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **14.2: GMO Food (Activity)** by Bio-OER is licensed CC BY-NC-SA 4.0.

# 7.3: GMOs

**Learning objectives**

By the end of this lesson you will:

- Understand why and how GMO technology is applied to plant improvement.
- List examples of GMO crops and explain why they were adopted.
- Explain why GMO technology is controversial.

## Overview

A GMO is a genetically modified organism — a plant carrying one or more transgenes as part of its genome. GMOs are produced through genetic engineering, where a transgene from any organism is manipulated to produce a trait in a plant after it has been introduced. Transgenes are DNA that are manipulated to function in a plant to produce a specific trait. They can originate from any other organism, and the new DNA need not be introduced through sexual reproduction as in making crosses for plant breeding. (In non-GMO crops, all genes originate from sexual reproduction.) As discussed in the chapter on DNA, the genetic code is the sequence of bases along a strand of DNA, and is universal among all living organisms, enabling the transfer of a gene from a bacteria, virus, or any organism to a plant. )A transfer of DNA across kingdoms would never occur by sexual reproduction, because interkingdom crosses cannot be made.) GMO technology offers, for example, the possibility of engineering resistance to the corn rootworm by introducing a bacterial transgene into corn or the ability to test a gene from any source in a plant.

This lesson offers insight into how GMOs offer a novel mechanism for plant improvement that can add significant traits to forestry, agronomy, and horticulture crops. Their contributions include herbicide tolerance for improved weed control, resistance to insect and viral pests, and improved health benefits for crops.

Unlike rose and apple breeding, in which hobbyists can breed new crops in their gardens, GMO technology integrates knowledge from genetics, molecular biology, and tissue culture to produce a new GMO crop. These skills would be difficult to combine in the garden, but the plants that are produced are propagated identically to their conventional counterparts. It would be difficult to distinguish the GMO “Innate” potato from a non-GMO potato, unless they were tested for browning, acrylamide production, or disease resistance. GMO potatoes look and behave like other potatoes. Adoption of GMO technology by a farmer requires no new equipment or cultivation techniques.

## What is a GMO?



Papaya tree infected with Papaya ringspot virus (PRSV).. Scot Nelson. Public domain.

GMOs begin where plant breeding ends. An excellent example of GMO technology occurred after the introduction of Papaya Ringspot Virus (PRSV) to Hawaii. PRSV devastated papaya production to the where point growers could not produce a crop. Attempts to use plant breeding to produce a virus-resistant plant were unsuccessful. No sexually compatible plant with resistance to PRSV could be located, so no amount of traditional plant breeding by crossing would produce resistance. This viral disease prevented papaya production in Hawaii until Dennis Gonsalves, of the US Department of Agriculture, adopted a GMO strategy that had previously been used to produce potatoes resistant to several viruses, and made papayas resistant to PRSV. Today, any papaya produced in Hawaii is likely to be either “SunUp” or “Rainbow,” the GMO cultivars. Although the virus-resistant papaya seems like a win for growers and consumers, it is very controversial. In the 1980s, the early development of GMO technology was tied to large agricultural companies that patented and used the technology in corn, soybeans, and cotton. Others see the “unnatural” movement of a gene from a bacteria to a plant as a process that we should not use.

The GMO papaya is a good example for presenting the process involved in producing a GMO. A first step in developing GMO papaya was to understand the virus, its genome, and its replication. Virologists, those devoting their lives to the study of virus biology, knew that the virus’ genome had a gene encoding a coat protein that surrounded the virus’ genetic material and that was essential to its infection of plant cells. The GMO strategy added a copy of the viral coat protein gene into the plant’s chromosomes. The coat protein protects the virus as it is transmitted from plant to plant, and is essential for replication. The viral gene is

engineered to be in the opposite orientation from its orientation in the virus. This opposite orientation of the viral gene, now acting as plant gene, effectively shuts down viral replication before it can cause disease, making the plant resistant.



John Sanford. FMSResearcher. CC BY-SA 4.0.



Gene gun. Z33 House for Contemporary Art, Design & Architecture. CC BY-NC-ND 2.0.

To introduce the engineered viral gene into the plant's chromosome without crossing, horticulturist John Sanford invented a means of introducing genes into plant cells by literally shooting the gene into the nucleus of a cell. (John graduated in 1976 from the University of Minnesota with a BS in horticulture, and continued in horticulture to become a professor and researcher at Cornell University.) In this process, DNA of the gene of interest is coated onto particles much smaller than the plant cell's nucleus. The gun works off of compressed air, similar to a BB gun. The particle coated with the DNA (gene of interest), now in the nucleus, diffuses away from the particle and integrates into the plant's chromosome. The gene is then expressed and is hertible in the same qualitative manner as other single gene traits. The process of introducing a transgene into a plant is called transformation. The plant cell or the whole plant carrying the engineered gene is said to be transformed or transgenic (synonyms for GMO).



Alan pointing to gall on a redwood in Muir Woods that may have been produced from *A. tumefaciens*.

Could this process ever happen in nature? *Agrobacterium tumefaciens* is a bacterial plant pathogen that produces crown gall disease. This bacterium transfers a small amount of its DNA (several genes) to the plant as part of its pathogen attack. The photo to the left shows a large gall on a redwood that may have been caused by *Agrobacterium*. The pathogen's genes have been engineered through evolution to take over the plant cell's normal regulation and produce a gall — a callus of rapidly dividing undifferentiated cells similar to a callus. The introduced bacterial genes, now functioning in the gall or callus, produce compounds that feed the *Agrobacterium*, which produces more pathogenic cells to infect other plants. This is crown gall disease of plants. Biologists studying *Agrobacterium's* life cycle realized they could use the natural DNA transfer process to introduce genes into plants by piggy-backing a gene of interest from any organism onto the *Agrobacterium's* transfer process. This has been very successful, and is the most used method of gene introduction into many crops. Although the genes to produce a GMO virus-resistant papaya were introduced with the gene gun, most of those in GMO crops were introduced using *Agrobacterium*.

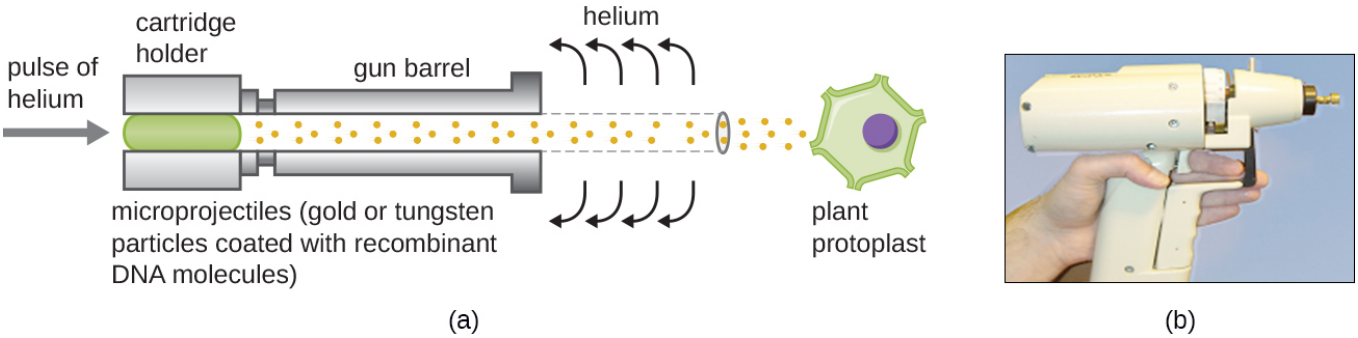



Diagram of gene gun process. OpenStax. CC BY 4.0.

The gene gun (above) and *Agrobacterium*-mediated gene introductions are inefficient processes that introduce the gene into only a very small number of plant cells. Since only a single cell receives the gene, plant tissue culture is used to regenerate an entire plant from that single cell. Plant tissue culture uses synthetic growth media to provide the environment for mitotic cell divisions and organization of those cells into shoot and root meristems. When the meristems are formed, the tiny plants can be removed from tissue culture and transferred to soil. This is possible because plant cells are totipotent — they can regenerate a whole plant from a single cell. (Think about about adventitious rooting, where parenchyma cells can divide and differentiate into a root meristem when buried in potting mix.) This capability has been identified in only a few plant species using very specific components in the tissue culture medium to coax the cells to divide and regenerate a whole plant.

As in plant breeding, GMO plants must be assessed and selected for the traits of interest. Introducing a single gene into a plant can produce a large phenotypic change — as in the naturally occuring Shrunken-2 allele that transforms field corn to sweet corn, or the introduction of the Papaya Ringspot Virus coat protein gene to provide virus resistance. Introducing a new gene using GMO technology does not, however, change other genes or traits of the plant's genome. Being able to maintain all of a cultivar's characteristics and add a gene for resistance from any organism is a major advantage of GMO technology.

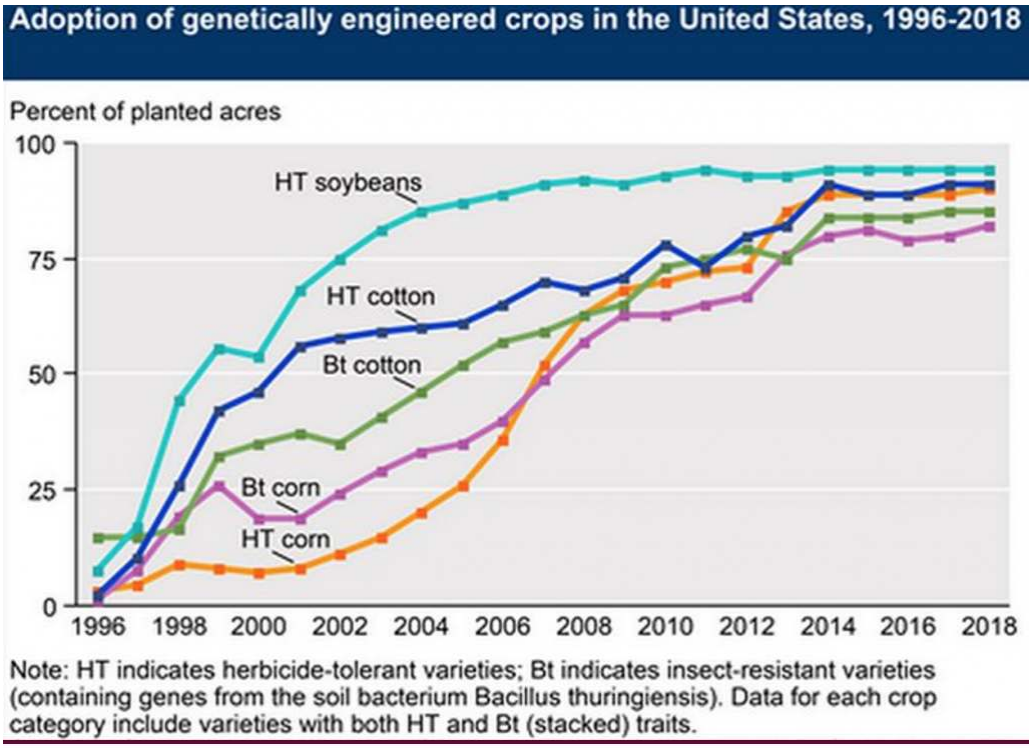
The art of GMO technology is discovering how non-plant organisms (virus, bacteria, fungi, insects, and so on) might contribute a gene to improve a plant, be it through weed control, increased nutrition in foods, or resistance to pests or viruses. GMO crops are produced by interdisciplinary teams with members expert in gene identification, gene engineering, plant breeding, gene introduction, and tissue culture. These skills mimic the steps required for GMO technology: identifying a gene or genes and their source to solve a problem, engineering the gene for plant expression, using the gene gun or *A. tumefaciens* to introduce into the crop of interest, and assessing the new plant. It is possible that the predicted gene action may not occur and that other genes or gene modifications are necessary. All genes used in crop production today have been through several iterations that improved the outcome after introduction. When a plant has the introduced gene integrated into its chromosomes, it can be crossed with other plants to move the new gene and its traits into other varieties.

**? Review questions**

1. What is a GMO?
2. What are the two significant advantages of GMO technologies over traditional plant breeding?
3. What are the differences between the two processes used to introduce a novel gene into a plant?
4. Can a GMO seed, seedling, or mature plant be distinguished from a non-GMO one just by looking at it? What distinguishes the two, either visibly or genetically?
5. Where do transgenes come from and how are they introduced into a GMO crop?

## Why do farmers pay extra for GMO seeds?

GMO technology has been rapidly adopted by farmers in the US and worldwide (the graph below shows adoption rates for the US in 1996–2018). In the US, corn, soybean, and sugar beet crops are GMO for herbicide tolerance (which allows for improved weed control), insect-resistant GMO cotton is extensively adopted to prevent boll weevil damage. For a more comprehensive list of crops and GMO traits, see the GM Approval Database from the ISAAA.




From:https://www.canr.msu.edu/news/why-many-growers-are-quick-to-adopt-genetic-modification-technology

As it implies, the “approval” in the name of this database indicates that GMO crops must go through extensive testing and a review process before being allowed into production and into our food stream. The rapid adoption of GMO technology triggered questions of risks that resulted in a review process for all GMO crops by the US Department of Agriculture, the Food and Drug Administration, and the Environmental Protection Agency. The overwhelming scientific evidence indicates GMO crops are safe for the environment and for humans. To read more (optional) on the safety of GMO technology, see the Academics Review’s site on Genetic Roulette for science-based information and critical review of GMO technology risks.

GMO crops have economic, environmental, and convenience advantages for farmers. Several economic analyses have shown that increased yields from GMO crops are a major impetus for adoption by farmers, even though GMO seeds cost more than conventional seeds. A good example is the rapid adoption of GMO sugar beets that were modified for resistance to the non-selective herbicide Roundup. This allowed the beets to be sprayed with Roundup, killing weeds in the field and leaving the beets unharmed. A 2008 survey of GMO sugar beet growers showed the highest weed control ratings in the history of the survey and the near elimination of mechanical and manual weeding. Weed control had previously been inefficient, requiring herbicide and mechanical controls. Making beets herbicide tolerant increased yield and made weed control convenient. Adoption was greater than 90% one year after the GMO herbicide tolerant seed was made available.

The most significant environmental benefits of GMO technology come from GMO insect resistance. Most insecticides are non-specific, killing beneficial insects as well as the pest, and are toxic to humans, birds, fish, and other organisms. The basis of GMO resistance is the introduction of the *Bacillus thuringiensis* gene, Bt, into the plant, so the plant produces Bt. You may have heard of Bt as an insect control used in organic food production or mosquito control. Bt has a very low environmental impact because it is highly specific for the target insect, unlike conventional insecticides that can have wide ranging collateral damage when applied. Bt is also very labile, breaking down rapidly in the soil. The Bt gene from *B. thuringiensis* has been introduced into several crops. Currently, Bt crops include corn (field and sweet), cotton, potato, eggplant, tobacco, and soybean for control of several insect pests. Each crop has a specific Bt that targets the insect pest in that crop. Where the GMO crop is grown in place of conventional crops, insecticide applications have been greatly reduced. The battle continues, however, as insects develop resistance to Bt, leaving the crop susceptible to insect damage.

Although using GMO technology requires a significant investment to develop a crop, propagation and use by a farmer is identical to that of conventional counterparts. The simplicity and effectiveness of GMO crops has accelerated their adoption by farmers.

GMO herbicide tolerance, for example, allows for a single post-germination application that provides improved weed control, eliminating the need to apply several different herbicides at different times and to use mechanical weed removal. This single application reduces fuel cost for farmers, reduces carbon emission, and provides excellent weed control. It is called **herbicide tolerance** because genes are introduced into the crop to make it tolerant (resistant) to a specific herbicide that kills weeds. The convenience to the farmer comes from using a single herbicide with flexible timing of application to the crop.

**? Review questions**

1. What advantages does a GMO crop present to a farmer?
2. Do any of the advantages of a GMO crop for a farmer translate to advantages to the consumer?
3. Why were GMO crops adopted so rapidly by farmers?
4. What are two examples of GMO crops that were rapidly adopted?
5. What does a farmer need to do to adopt a GMO crop with insect resistance?

## GMO crops benefiting human health

Early in the technology's development, most GMO work focused on the farmer and/or on production problems. Herbicide tolerance, insecticide resistance, and virus resistance each protected the crop or made farming easier. There are now, however, several GMO crops developed primarily for the consumer. The iconic, increased-nutrition GMO crop is Golden Rice. It contains introduced genes that synthesize carotene in the endosperm. You can easily distinguish Golden Rice from conventional rice by its yellow color from the accumulated carotene, the same pigment found in carrots (see photo below). When humans consume the carotene in Golden Rice, it is converted to vitamin A, an essential vitamin for human health. Conventional milled-rice contains no vitamin A, which results in vitamin A deficiencies in millions of adults and children who consume most of their calories by eating rice. The Golden Rice Project estimates the number of child deaths caused by vitamin A deficiency at 1.15 million/year. Vitamin A deficiency also causes loss of sight, increased susceptibility to a number of diseases, and reduced intellectual development. While Golden Rice would greatly mitigate the problem and has been crossed into many regional cultivars, adoption has been slowed or blocked by anti-GMO organizations. Research continues with the development of golden bananas and cassava.



Golden Rice grain compared to white rice grain in screenhouse of Golden Rice plants. International Rice Research Institute. CC BY 2.0.

A recently approved GMO crop for production, the "Innate" potato has introduced genes that reduce the production of the neurotoxin acrylamide. Acrylamide forms in many cooked foods from the reaction of amino acids, sugars, and heat. The risk of consuming acrylamide is somewhat controversial, but the fact that it is a neurotoxin makes this an important improvement to the potato. The "Innate" potato has two other introduced genes that make it resistant to the potato blight fungus and prevents browning of the tuber after being cut or bruised. It remains to be seen whether this potato is accepted by consumers and the fast food industry, where many potatoes are consumed. One of the first GMO crops marketed was the "New Leaf" potato, which had both insect and virus resistance. Consumers and the fast food industry, led by anti-GMO organizations, mounted a campaign of GMO fear that effectively ended cultivation of this potato. The "Innate" potato reopens the discussion of GMO foods.

**? Review questions**

1. What are the differences in traits that benefit the farmer vs. benefiting consumers?
2. What human health issues can be addressed using GMO technology?

## Why are GMOs controversial?




March Against Monsanto in Lethbridge Alberta. John Novotny. CC BY 2.0.

The overwhelming evidence from peer-reviewed science is that GMO crops are safe for growers, consumers, and the environment. There are several anti-GMO organizations that have been effective in sensationalizing concerns and controversy concerning GMO technology. The first concern about GMOs is that the technology is not natural. A gene from a bacteria would have slim chances of integrating into a plant's chromosome without technology intervening — or would it? Concerns have been raised about genetic pollution, where genes from GMO crops would escape to conventional crops or weedy relatives, producing superweeds. The second leading cause of controversy is that several large chemical and agricultural companies invested heavily in GMO technology, and then produced the first GMO crops. GMO technology was patented by these large companies, increasing concerns due to the environmental records of these companies. The lack of a federal requirement to label foods as GMO also fanned fears of potential risks.

Other concerns have originated in the technical nature and rapid development of GMOs, which many argue prevented a full assessment of risk. Arguments centered around a new technology's potential to have unintended or unknown consequences. Some speculated on the possibility that the introduced genes could lead to the production of toxins, allergens, or carcinogens, despite thorough testing for these compounds in the review process. Adding to these concerns was the US Department of Agriculture's decision to not require labeling of food from or containing GMO plants. Additionally, growers' concerns led to the rejection of GMO crops in certified organic production. Each of these issues has been amplified by anti-GMO organizations such as the Non-GMO Project, the Center for Food Safety, and Greenpeace. The message from these organizations was and continues to be that GMO foods are unsafe for people and the environment, despite the overwhelming scientific evidence to the contrary. This is the partial story of the development and adoption and controversy of GMO crops. You can look forward to hearing more about the GMOs, especially the "Pinkglow" that Jimmy Kimmel says "tastes exactly like a pineapple."

**? Review questions**

1. What issues contribute to the GMO technology being controversial?
2. What are the most significant advantages of using GMO technology vs. conventional plant breeding?
3. Why are crops produced from GMO technology reviewed by federal agencies, and what risks might they pose?

This page titled 7.3: GMOs is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley via source content that was edited to the style and standards of the LibreTexts platform.

- **15.2: GMOs** by Tom Michaels, Matt Clark, Emily Hoover, Laura Irish, Alan Smith, and Emily Tepe is licensed CC BY-NC 4.0. Original source: https://open.lib.umn.edu/horticulture.

# CHAPTER OVERVIEW

## 8: Basic chemistry and biochemistry


8.1: The Chemical Foundation of Life

8.1.1: Prelude to The Chemical Foundation of Life

8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks

8.1.3: Water

8.1.4: Carbon

8.1.E: The Chemical Foundation of Life (Exercises)

8.2: Biological Macromolecules

8.2.1: Prelude to Biological Macromolecules

8.2.2: Synthesis of Biological Macromolecules

8.2.3: Carbohydrates

8.2.4: Lipids

8.2.5: Proteins

8.2.6: Nucleic Acids

8.2.E: Biological Macromolecules (Exercises)

8.3: Unit I- The Chemistry of Life


---


This page titled 8: Basic chemistry and biochemistry is shared under a not declared license and was authored, remixed, and/or curated by Tom Buckley.

# SECTION OVERVIEW

## 8.1: The Chemical Foundation of Life

Elements in various combinations comprise all matter, including living things. Some of the most abundant elements in living organisms include carbon, hydrogen, nitrogen, oxygen, sulfur, and phosphorus. These form the nucleic acids, proteins, carbohydrates, and lipids that are the fundamental components of living matter. Biologists must understand these important building blocks and the unique structures of the atoms that make up molecules, allowing for the formation of cells, tissues, organ systems, and entire organisms.


### 8.1.1: Prelude to The Chemical Foundation of Life

### 8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks

### 8.1.3: Water

### 8.1.4: Carbon

### 8.1.E: The Chemical Foundation of Life (Exercises)



This page titled 8.1: The Chemical Foundation of Life is shared under a CC BY 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

# 8.1.1: Prelude to The Chemical Foundation of Life

Elements in various combinations comprise all matter, including living things. Some of the most abundant elements in living organisms include carbon, hydrogen, nitrogen, oxygen, sulfur, and phosphorus. These form the nucleic acids, proteins, carbohydrates, and lipids that are the fundamental components of living matter. Biologists must understand these important building blocks and the unique structures of the atoms that make up molecules, allowing for the formation of cells, tissues, organ systems, and entire organisms.

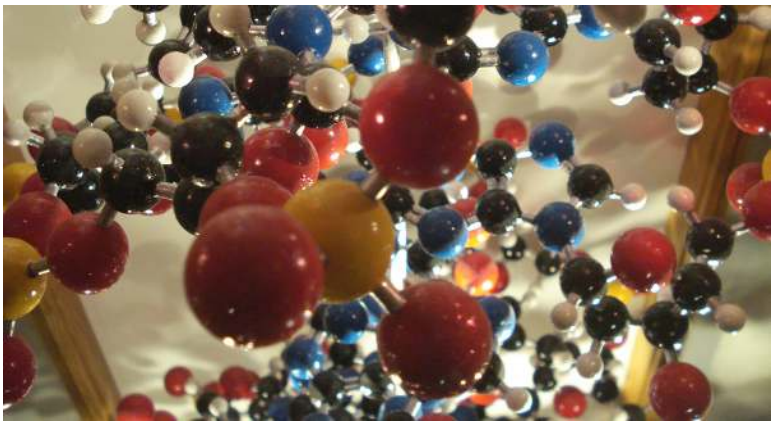


Figure **8.1.1.1**: Atoms are the building blocks of molecules found in the universe—air, soil, water, rocks ... and also the cells of all living organisms. In this model of an organic molecule, the atoms of carbon (black), hydrogen (white), nitrogen (blue), oxygen (red), and sulfur (yellow) are shown in proportional atomic size. The silver rods indicate chemical bonds. (credit: modification of work by Christian Guthier)

All biological processes follow the laws of physics and chemistry, so in order to understand how biological systems work, it is important to understand the underlying physics and chemistry. For example, the flow of blood within the circulatory system follows the laws of physics that regulate the modes of fluid flow. The breakdown of the large, complex molecules of food into smaller molecules—and the conversion of these to release energy to be stored in adenosine triphosphate (ATP)—is a series of chemical reactions that follow chemical laws. The properties of water and the formation of hydrogen bonds are key to understanding living processes. Recognizing the properties of acids and bases is important, for example, to our understanding of the digestive process. Therefore, the fundamentals of physics and chemistry are important for gaining insight into biological processes.

---

This page titled 8.1.1: Prelude to The Chemical Foundation of Life is shared under a CC BY 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **2.0: Prelude to The Chemical Foundation of Life** by OpenStax is licensed CC BY 4.0.

# 8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks

**Skills to Develop**

- Define matter and elements
- Describe the interrelationship between protons, neutrons, and electrons
- Compare the ways in which electrons can be donated or shared between atoms
- Explain the ways in which naturally occurring elements combine to create molecules, cells, tissues, organ systems, and organisms

At its most fundamental level, life is made up of matter. Matter is any substance that occupies space and has mass. Elements are unique forms of matter with specific chemical and physical properties that cannot be broken down into smaller substances by ordinary chemical reactions. There are 118 elements, but only 92 occur naturally. The remaining elements are synthesized in laboratories and are unstable.

Each element is designated by its chemical symbol, which is a single capital letter or, when the first letter is already "taken" by another element, a combination of two letters. Some elements follow the English term for the element, such as C for carbon and Ca for calcium. Other elements' chemical symbols derive from their Latin names; for example, the symbol for sodium is Na, referring to *natrium*, the Latin word for sodium.

The four elements common to all living organisms are oxygen (O), carbon (C), hydrogen (H), and nitrogen (N). In the non-living world, elements are found in different proportions, and some elements common to living organisms are relatively rare on the earth as a whole, as shown in Table 8.1.2.1. For example, the atmosphere is rich in nitrogen and oxygen but contains little carbon and hydrogen, while the earth's crust, although it contains oxygen and a small amount of hydrogen, has little nitrogen and carbon. In spite of their differences in abundance, all elements and the chemical reactions between them obey the same chemical and physical laws regardless of whether they are a part of the living or non-living world.

Table 8.1.2.1: Approximate Percentage of Elements in Living Organisms (Humans) Compared to the Non-living World

| Element | Life (Humans) | Atmosphere | Earth's Crust |
|---|---|---|---|
| Oxygen (O) | 65% | 21% | 46% |
| Carbon (C) | 18% | trace | trace |
| Hydrogen (H) | 10% | trace | 0.1% |
| Nitrogen (N) | 3% | 78% | trace |

## The Structure of the Atom

To understand how elements come together, we must first discuss the smallest component or building block of an element, the atom. An atom is the smallest unit of matter that retains all of the chemical properties of an element. For example, one gold atom has all of the properties of gold in that it is a solid metal at room temperature. A gold coin is simply a very large number of gold atoms molded into the shape of a coin and containing small amounts of other elements known as impurities. Gold atoms cannot be broken down into anything smaller while still retaining the properties of gold.

An atom is composed of two regions: the nucleus, which is in the center of the atom and contains protons and neutrons, and the outermost region of the atom which holds its electrons in orbit around the nucleus, as illustrated in Figure 8.1.2.1. Atoms contain protons, electrons, and neutrons, among other subatomic particles. The only exception is hydrogen (H), which is made of one proton and one electron with no neutrons.

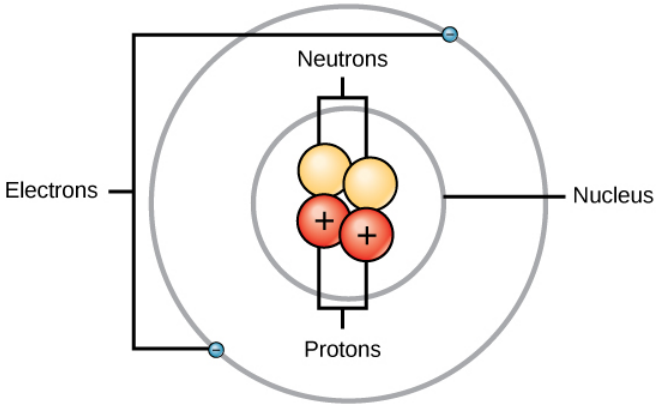



Figure 8.1.2.1: Elements, such as helium, depicted here, are made up of atoms. Atoms are made up of protons and neutrons located within the nucleus, with electrons in orbitals surrounding the nucleus.

Protons and neutrons have approximately the same mass, about $1.67 \times 10^{-24}$ grams. Scientists arbitrarily define this amount of mass as one atomic mass unit (amu) or one Dalton, as shown in Table 8.1.2.2. Although similar in mass, protons and neutrons differ in their electric charge. A proton is positively charged whereas a neutron is uncharged. Therefore, the number of neutrons in an atom contributes significantly to its mass, but not to its charge. Electrons are much smaller in mass than protons, weighing only $9.11 \times 10^{-28}$ grams, or about 1/1800 of an atomic mass unit. Hence, they do not contribute much to an element's overall atomic mass. Therefore, when considering atomic mass, it is customary to ignore the mass of any electrons and calculate the atom's mass based on the number of protons and neutrons alone. Although not significant contributors to mass, electrons do contribute greatly to the atom's charge, as each electron has a negative charge equal to the positive charge of a proton. In uncharged, neutral atoms, the number of electrons orbiting the nucleus is equal to the number of protons inside the nucleus. In these atoms, the positive and negative charges cancel each other out, leading to an atom with no net charge.

Accounting for the sizes of protons, neutrons, and electrons, most of the volume of an atom—greater than 99 percent—is, in fact, empty space. With all this empty space, one might ask why so-called solid objects do not just pass through one another. The reason they do not is that the electrons that surround all atoms are negatively charged and negative charges repel each other.

Table 8.1.2.2: Protons, Neutrons, and Electrons

| | Charge | Mass (amu) | Location |
|---|---|---|---|
| Proton | +1 | 1 | nucleus |
| Neutron | 0 | 1 | nucleus |
| Electron | –1 | 0 | orbitals |

## Atomic Number and Mass

Atoms of each element contain a characteristic number of protons and electrons. The number of protons determines an element's atomic number and is used to distinguish one element from another. The number of neutrons is variable, resulting in isotopes, which are different forms of the same atom that vary only in the number of neutrons they possess. Together, the number of protons and the number of neutrons determine an element's mass number, as illustrated in Figure 8.1.2.2. Note that the small contribution of mass from electrons is disregarded in calculating the mass number. This approximation of mass can be used to easily calculate how many neutrons an element has by simply subtracting the number of protons from the mass number. Since an element's isotopes will have slightly different mass numbers, scientists also determine the atomic mass, which is the calculated mean of the mass number for its naturally occurring isotopes. Often, the resulting number contains a fraction. For example, the atomic mass of chlorine (Cl) is 35.45 because chlorine is composed of several isotopes, some (the majority) with atomic mass 35 (17 protons and 18 neutrons) and some with atomic mass 37 (17 protons and 20 neutrons).

## Art Connection

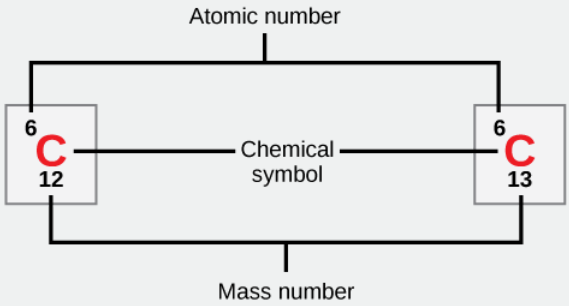



Figure **8.1.2.2**: Carbon has an atomic number of six, and two stable isotopes with mass numbers of twelve and thirteen, respectively. Its atomic mass is 12.11.

How many neutrons do carbon-12 and carbon-13 have, respectively?

### Isotopes

Isotopes are different forms of an element that have the same number of protons but a different number of neutrons. Some elements—such as carbon, potassium, and uranium—have naturally occurring isotopes. Carbon-12 contains six protons, six neutrons, and six electrons; therefore, it has a mass number of 12 (six protons and six neutrons). Carbon-14 contains six protons, eight neutrons, and six electrons; its atomic mass is 14 (six protons and eight neutrons). These two alternate forms of carbon are isotopes. Some isotopes may emit neutrons, protons, and electrons, and attain a more stable atomic configuration (lower level of potential energy); these are radioactive isotopes, or radioisotopes. Radioactive decay (carbon-14 losing neutrons to eventually become carbon-12) describes the energy loss that occurs when an unstable atom's nucleus releases radiation.

## Evolution Connection: Carbon Dating

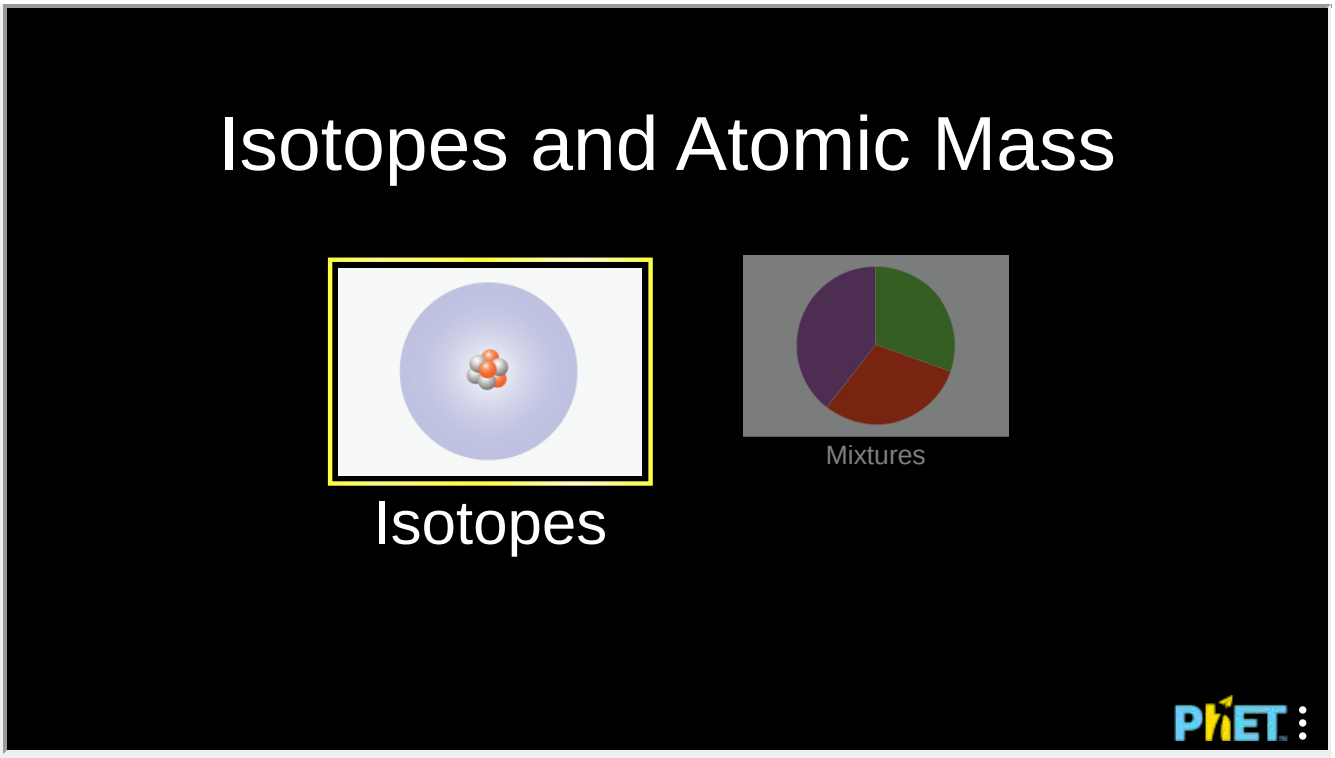
Carbon is normally present in the atmosphere in the form of gaseous compounds like carbon dioxide and methane. Carbon-14 ( $C^{14}$) is a naturally occurring radioisotope that is created in the atmosphere from atmospheric $N^{14}$ (nitrogen) by the addition of a neutron and the loss of a proton because of cosmic rays. This is a continuous process, so more $C^{14}$ is always being created. As a living organism incorporates $C^{14}$ initially as carbon dioxide fixed in the process of photosynthesis, the relative amount of $C^{14}$ in its body is equal to the concentration of $C^{14}$ in the atmosphere. When an organism dies, it is no longer ingesting $C^{14}$, so the ratio between $C^{14}$ and $C^{12}$ will decline as $C^{14}$ decays gradually to $N^{14}$ by a process called beta decay—the emission of electrons or positrons. This decay gives off energy in a slow process.

After approximately 5,730 years, half of the starting concentration of $C^{14}$ will have been converted back to $N^{14}$. The time it takes for half of the original concentration of an isotope to decay back to its more stable form is called its half-life. Because the half-life of $C^{14}$ is long, it is used to date formerly living objects such as old bones or wood. Comparing the ratio of the $C^{14}$ concentration found in an object to the amount of $C^{14}$ detected in the atmosphere, the amount of the isotope that has not yet decayed can be determined. On the basis of this amount, the age of the material, such as the pygmy mammoth shown in Figure **8.1.2.3**, can be calculated with accuracy if it is not much older than about 50,000 years. Other elements have isotopes with different half lives. For example, $K^{40}$ (potassium-40) has a half-life of 1.25 billion years, and $U^{235}$ (Uranium 235) has a half-life of about 700 million years. Through the use of radiometric dating, scientists can study the age of fossils or other remains of extinct organisms to understand how organisms have evolved from earlier species.



Figure **8.1.2.3**: The age of carbon-containing remains less than about 50,000 years old, such as this pygmy mammoth, can be determined using carbon dating. (credit: Bill Faulkner, NPS)

Link to Learning




Video: To learn more about atoms, isotopes, and how to tell one isotope from another, visit this site and run the simulation.

## The Periodic Table

The different elements are organized and displayed in the periodic table. Devised by Russian chemist Dmitri Mendeleev (1834–1907) in 1869, the table groups elements that, although unique, share certain chemical properties with other elements. The properties of elements are responsible for their physical state at room temperature: they may be gases, solids, or liquids. Elements also have specific chemical reactivity, the ability to combine and to chemically bond with each other.

In the periodic table, shown in Figure **8.1.2.4**, the elements are organized and displayed according to their atomic number and are arranged in a series of rows and columns based on shared chemical and physical properties. In addition to providing the atomic number for each element, the periodic table also displays the element's atomic mass. Looking at carbon, for example, its symbol (C) and name appear, as well as its atomic number of six (in the upper left-hand corner) and its atomic mass of 12.11.

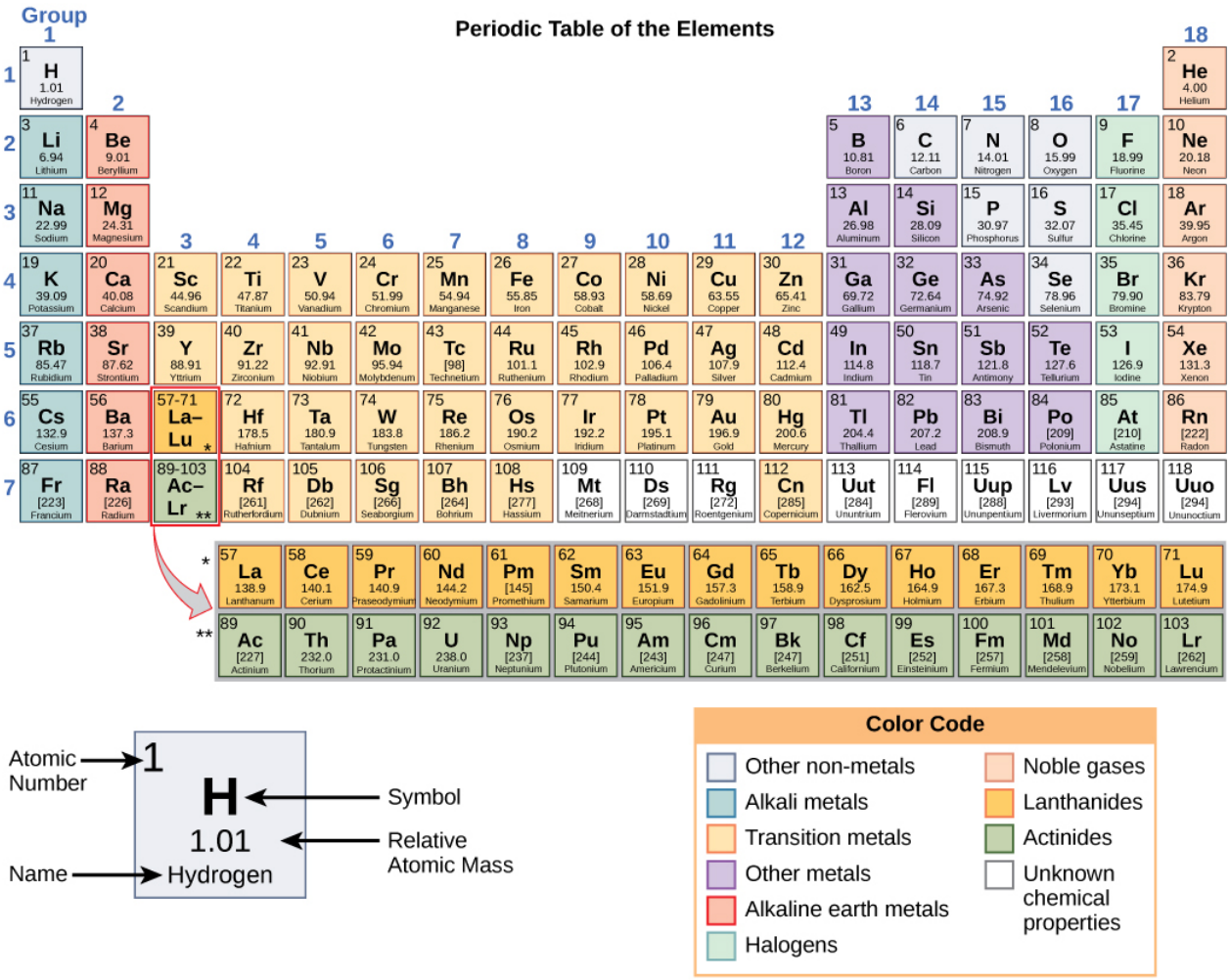



Figure **8.1.2.4**: The periodic table shows the atomic mass and atomic number of each element. The atomic number appears above the symbol for the element and the approximate atomic mass appears below it.

The periodic table groups elements according to chemical properties. The differences in chemical reactivity between the elements are based on the number and spatial distribution of an atom's electrons. Atoms that chemically react and bond to each other form molecules. Molecules are simply two or more atoms chemically bonded together. Logically, when two atoms chemically bond to form a molecule, their electrons, which form the outermost region of each atom, come together first as the atoms form a chemical bond.

## Electron Shells and the Bohr Model

It should be stressed that there is a connection between the number of protons in an element, the atomic number that distinguishes one element from another, and the number of electrons it has. In all electrically neutral atoms, the number of electrons is the same as the number of protons. Thus, each element, at least when electrically neutral, has a characteristic number of electrons equal to its atomic number.

An early model of the atom was developed in 1913 by Danish scientist Niels Bohr (1885–1962). The Bohr model shows the atom as a central nucleus containing protons and neutrons, with the electrons in circular orbitals at specific distances from the nucleus, as illustrated in Figure **8.1.2.5**. These orbits form electron shells or energy levels, which are a way of visualizing the number of electrons in the outermost shells. These energy levels are designated by a number and the symbol "n." For example, 1n represents the first energy level located closest to the nucleus.

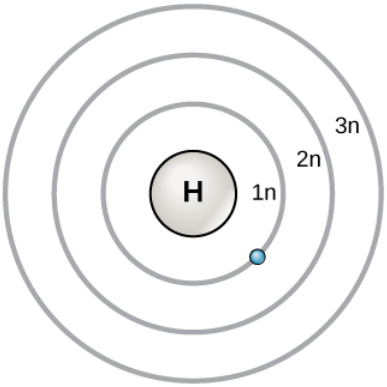



Figure **8.1.2.5**: The Bohr model was developed by Niels Bohrs in 1913. In this model, electrons exist within principal shells. An electron normally exists in the lowest energy shell available, which is the one closest to the nucleus. Energy from a photon of light can bump it up to a higher energy shell, but this situation is unstable, and the electron quickly decays back to the ground state. In the process, a photon of light is released

Electrons fill orbitals in a consistent order: they first fill the orbitals closest to the nucleus, then they continue to fill orbitals of increasing energy further from the nucleus. If there are multiple orbitals of equal energy, they will be filled with one electron in each energy level before a second electron is added. The electrons of the outermost energy level determine the energetic stability of the atom and its tendency to form chemical bonds with other atoms to form molecules.

Under standard conditions, atoms fill the inner shells first, often resulting in a variable number of electrons in the outermost shell. The innermost shell has a maximum of two electrons but the next two electron shells can each have a maximum of eight electrons. This is known as the octet rule, which states, with the exception of the innermost shell, that atoms are more stable energetically when they have eight electrons in their valence shell, the outermost electron shell. Examples of some neutral atoms and their electron configurations are shown in Figure **8.1.2.6**. Notice that in this figure, helium has a complete outer electron shell, with two electrons filling its first and only shell. Similarly, neon has a complete outer 2n shell containing eight electrons. In contrast, chlorine and sodium have seven and one in their outer shells, respectively, but theoretically they would be more energetically stable if they followed the octet rule and had eight.

Art Connection

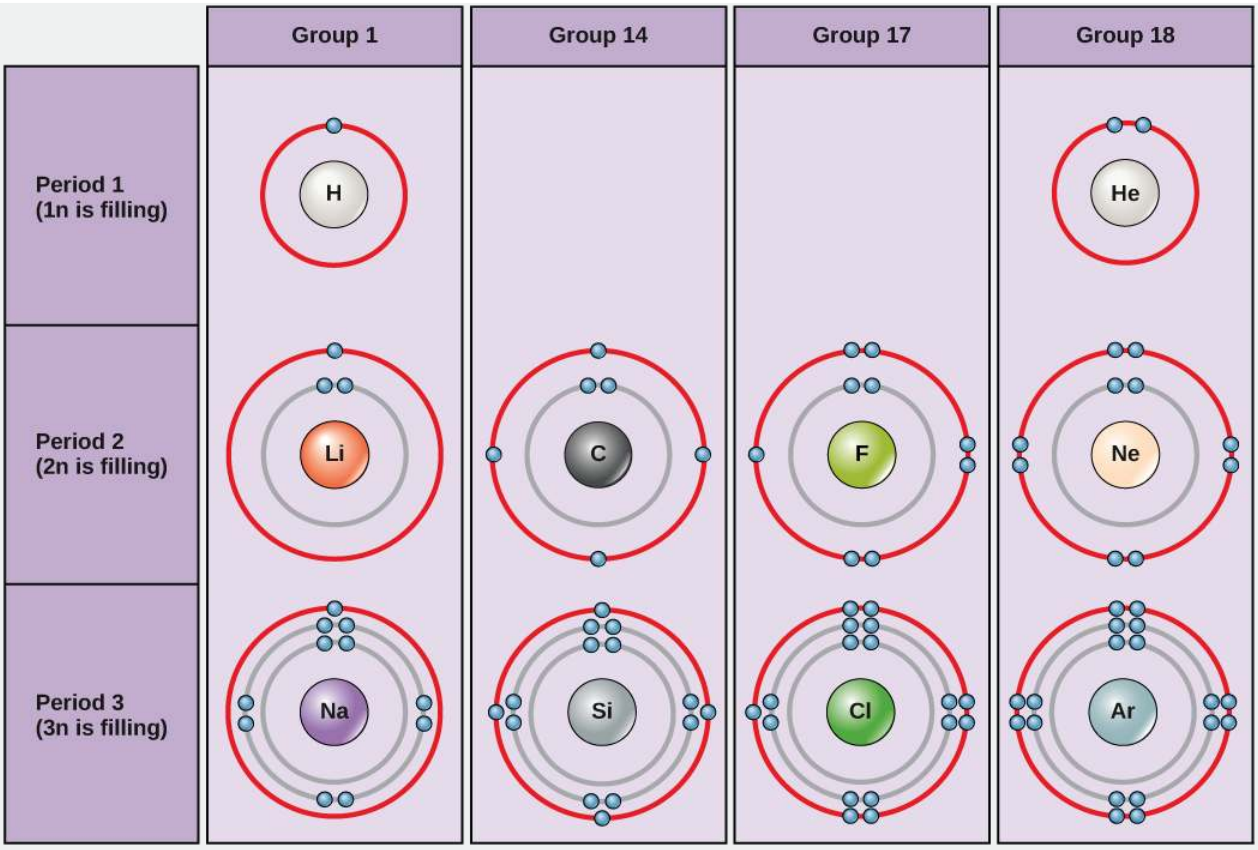



Figure **8.1.2.6**: Bohr diagrams indicate how many electrons fill each principal shell. Group 18 elements (helium, neon, and argon are shown) have a full outer, or valence, shell. A full valence shell is the most stable electron configuration. Elements in other groups have partially filled valence shells and gain or lose electrons to achieve a stable electron configuration.

An atom may give, take, or share electrons with another atom to achieve a full valence shell, the most stable electron configuration. Looking at this figure, how many electrons do elements in group 1 need to lose in order to achieve a stable electron configuration? How many electrons do elements in groups 14 and 17 need to gain to achieve a stable configuration?

Understanding that the organization of the periodic table is based on the total number of protons (and electrons) helps us know how electrons are distributed among the outer shell. The periodic table is arranged in columns and rows based on the number of electrons and where these electrons are located. Take a closer look at the some of the elements in the table's far right column in Figure **8.1.2.6**. The group 18 atoms helium (He), neon (Ne), and argon (Ar) all have filled outer electron shells, making it unnecessary for them to share electrons with other atoms to attain stability; they are highly stable as single atoms. Their non-reactivity has resulted in their being named the inert gases (or noble gases). Compare this to the group 1 elements in the left-hand column. These elements, including hydrogen (H), lithium (Li), and sodium (Na), all have one electron in their outermost shells. That means that they can achieve a stable configuration and a filled outer shell by donating or sharing one electron with another atom or a molecule such as water. Hydrogen will donate or share its electron to achieve this configuration, while lithium and sodium will donate their electron to become stable. As a result of losing a negatively charged electron, they become positively charged ions. Group 17 elements, including fluorine and chlorine, have seven electrons in their outmost shells, so they tend to fill this shell with an electron from other atoms or molecules, making them negatively charged ions. Group 14 elements, of which carbon is the most important to living systems, have four electrons in their outer shell allowing them to make several covalent bonds (discussed below) with other atoms. Thus, the columns of the periodic table represent the potential shared state of these elements' outer electron shells that is responsible for their similar chemical characteristics.

## Electron Orbitals

Although useful to explain the reactivity and chemical bonding of certain elements, the Bohr model of the atom does not accurately reflect how electrons are spatially distributed surrounding the nucleus. They do not circle the nucleus like the earth orbits the sun,

but are found in electron orbitals. These relatively complex shapes result from the fact that electrons behave not just like particles, but also like waves. Mathematical equations from quantum mechanics known as wave functions can predict within a certain level of probability where an electron might be at any given time. The area where an electron is most likely to be found is called its orbital.

Recall that the Bohr model depicts an atom's electron shell configuration. Within each electron shell are subshells, and each subshell has a specified number of orbitals containing electrons. While it is impossible to calculate exactly where an electron is located, scientists know that it is most probably located within its orbital path. Subshells are designated by the letter s, *p*, *d*, and *f*. The *s* subshell is spherical in shape and has one orbital. Principal shell 1n has only a single *s* orbital, which can hold two electrons. Principal shell 2n has one *s* and one *p* subshell, and can hold a total of eight electrons. The *p* subshell has three dumbbell-shaped orbitals, as illustrated in Figure **8.1.2.7**. Subshells *d* and *f* have more complex shapes and contain five and seven orbitals, respectively. These are not shown in the illustration. Principal shell 3n has *s*, *p*, and *d* subshells and can hold 18 electrons. Principal shell 4n has *s*, *p*, *d* and *f* orbitals and can hold 32 electrons. Moving away from the nucleus, the number of electrons and orbitals found in the energy levels increases. Progressing from one atom to the next in the periodic table, the electron structure can be worked out by fitting an extra electron into the next available orbital.

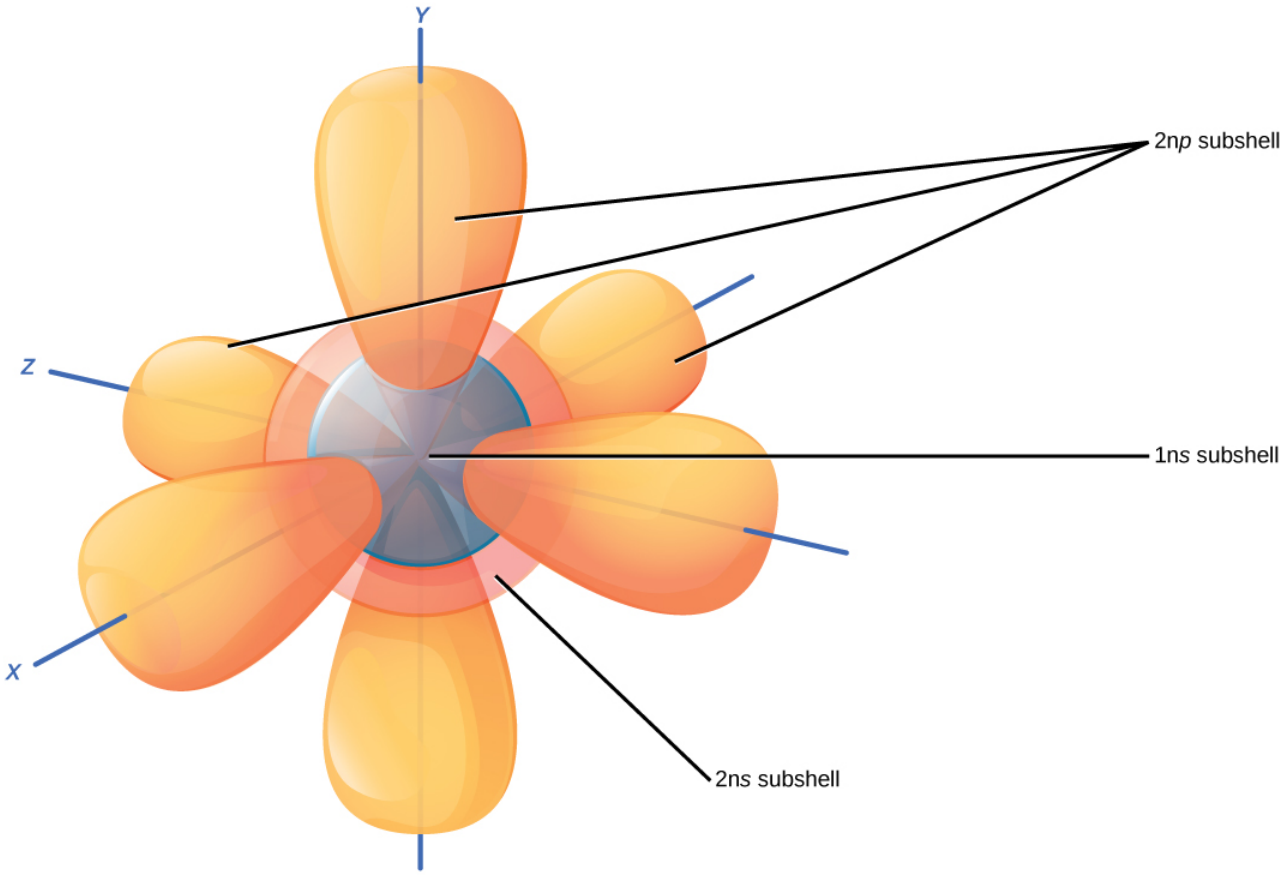



Figure **8.1.2.7**: The *s* subshells are shaped like spheres. Both the 1n and 2n principal shells have an *s* orbital, but the size of the sphere is larger in the 2n orbital. Each sphere is a single orbital. *p* subshells are made up of three dumbbell-shaped orbitals. Principal shell 2n has a *p* subshell, but shell 1 does not.

The closest orbital to the nucleus, called the 1s orbital, can hold up to two electrons. This orbital is equivalent to the innermost electron shell of the Bohr model of the atom. It is called the 1*s* orbital because it is spherical around the nucleus. The 1*s* orbital is the closest orbital to the nucleus, and it is always filled first, before any other orbital can be filled. Hydrogen has one electron; therefore, it has only one spot within the 1*s* orbital occupied. This is designated as $1s^1$, where the superscripted 1 refers to the one electron within the 1*s* orbital. Helium has two electrons; therefore, it can completely fill the 1*s* orbital with its two electrons. This is designated as $1s^2$, referring to the two electrons of helium in the 1*s* orbital. On the periodic table Figure **8.1.2.4**, hydrogen and

helium are the only two elements in the first row (period); this is because they only have electrons in their first shell, the 1*s* orbital. Hydrogen and helium are the only two elements that have the 1*s* and no other electron orbitals in the electrically neutral state.

The second electron shell may contain eight electrons. This shell contains another spherical *s* orbital and three "dumbbell" shaped *p* orbitals, each of which can hold two electrons, as shown in Figure 8.1.2.7. After the 1*s* orbital is filled, the second electron shell is filled, first filling its 2*s* orbital and then its three *p* orbitals. When filling the *p* orbitals, each takes a single electron; once each *p* orbital has an electron, a second may be added. Lithium (Li) contains three electrons that occupy the first and second shells. Two electrons fill the 1*s* orbital, and the third electron then fills the 2*s* orbital. Its electron configuration is $1s^2 2s^1$. Neon (Ne), on the other hand, has a total of ten electrons: two are in its innermost 1*s* orbital and eight fill its second shell (two each in the 2*s* and three *p* orbitals); thus, it is an inert gas and energetically stable as a single atom that will rarely form a chemical bond with other atoms. Larger elements have additional orbitals, making up the third electron shell. While the concepts of electron shells and orbitals are closely related, orbitals provide a more accurate depiction of the electron configuration of an atom because the orbital model specifies the different shapes and special orientations of all the places that electrons may occupy.

Link to Learning



Video: Watch this visual animation to see the spatial arrangement of the *p* and *s* orbitals.

## Chemical Reactions and Molecules

All elements are most stable when their outermost shell is filled with electrons according to the octet rule. This is because it is energetically favorable for atoms to be in that configuration and it makes them stable. However, since not all elements have enough electrons to fill their outermost shells, atoms form chemical bonds with other atoms thereby obtaining the electrons they need to attain a stable electron configuration. When two or more atoms chemically bond with each other, the resultant chemical structure is a molecule. The familiar water molecule, $H_2O$, consists of two hydrogen atoms and one oxygen atom; these bond together to form water, as illustrated in Figure 8.1.2.8. Atoms can form molecules by donating, accepting, or sharing electrons to fill their outer shells.

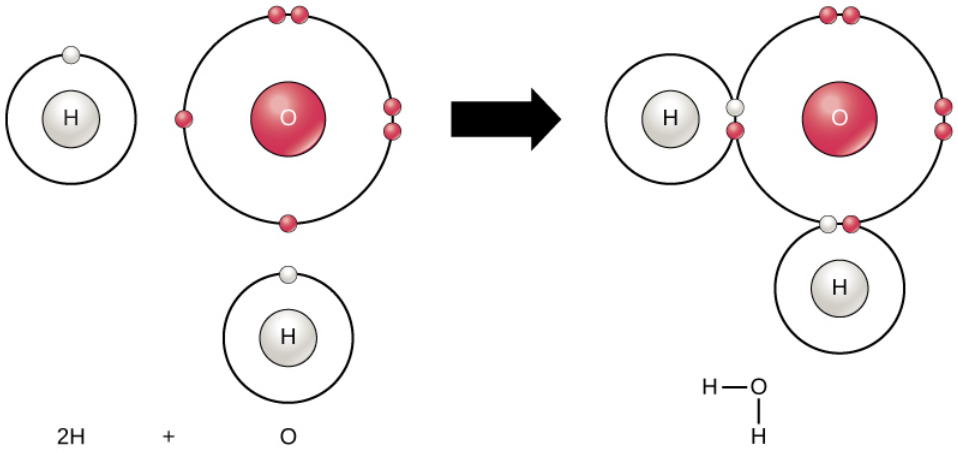



Figure 8.1.2.8: Two or more atoms may bond with each other to form a molecule. When two hydrogens and an oxygen share electrons via covalent bonds, a water molecule is formed.

Chemical reactions occur when two or more atoms bond together to form molecules or when bonded atoms are broken apart. The substances used in the beginning of a chemical reaction are called the reactants (usually found on the left side of a chemical equation), and the substances found at the end of the reaction are known as the products (usually found on the right side of a chemical equation). An arrow is typically drawn between the reactants and products to indicate the direction of the chemical reaction; this direction is not always a "one-way street." For the creation of the water molecule shown above, the chemical equation would be:

$$2\,H + O \rightarrow H_2O$$

An example of a simple chemical reaction is the breaking down of hydrogen peroxide molecules, each of which consists of two hydrogen atoms bonded to two oxygen atoms ($H_2O_2$). The reactant hydrogen peroxide is broken down into water, containing one oxygen atom bound to two hydrogen atoms ($H_2O$), and oxygen, which consists of two bonded oxygen atoms ($O_2$). In the equation below, the reaction includes two hydrogen peroxide molecules and two water molecules. This is an example of a balanced chemical equation, wherein the number of atoms of each element is the same on each side of the equation. According to the law of conservation of matter, the number of atoms before and after a chemical reaction should be equal, such that no atoms are, under normal circumstances, created or destroyed.

$$2\,H_2O_2\ (\text{hydrogen peroxide}) \rightarrow 2\,H_2O\ (\text{water}) + O_2\ (\text{oxygen})$$

Even though all of the reactants and products of this reaction are molecules (each atom remains bonded to at least one other atom), in this reaction only hydrogen peroxide and water are representatives of compounds: they contain atoms of more than one type of element. Molecular oxygen, on the other hand, as shown in Figure 8.1.2.9, consists of two doubly bonded oxygen atoms and is not classified as a compound but as a mononuclear molecule.

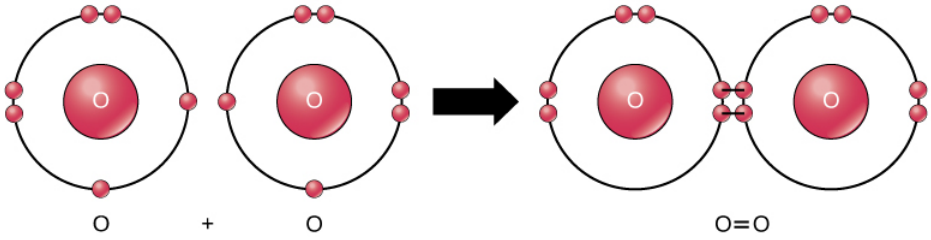



Figure 8.1.2.9: The oxygen atoms in an $O_2$ molecule are joined by a double bond.

Some chemical reactions, such as the one shown above, can proceed in one direction until the reactants are all used up. The equations that describe these reactions contain a unidirectional arrow and are irreversible. Reversible reactions are those that can go in either direction. In reversible reactions, reactants are turned into products, but when the concentration of product goes beyond a certain threshold (characteristic of the particular reaction), some of these products will be converted back into reactants; at this point, the designations of products and reactants are reversed. This back and forth continues until a certain relative balance between

reactants and products occurs—a state called equilibrium. These situations of reversible reactions are often denoted by a chemical equation with a double headed arrow pointing towards both the reactants and products.

For example, in human blood, excess hydrogen ions ($H^+$) bind to bicarbonate ions ($HCO_3^-$) forming an equilibrium state with carbonic acid ($H_2CO_3$). If carbonic acid were added to this system, some of it would be converted to bicarbonate and hydrogen ions.

$$HCO_3^- + H^+ \leftrightarrow H_2CO_3$$

In biological reactions, however, equilibrium is rarely obtained because the concentrations of the reactants or products or both are constantly changing, often with a product of one reaction being a reactant for another. To return to the example of excess hydrogen ions in the blood, the formation of carbonic acid will be the major direction of the reaction. However, the carbonic acid can also leave the body as carbon dioxide gas (via exhalation) instead of being converted back to bicarbonate ion, thus driving the reaction to the right by the chemical law known as law of mass action. These reactions are important for maintaining the homeostasis of our blood.

$$HCO_3^- + H^+ \leftrightarrow H_2CO_3 \leftrightarrow CO_2 + H_2O$$

## Ions and Ionic Bonds

Some atoms are more stable when they gain or lose an electron (or possibly two) and form ions. This fills their outermost electron shell and makes them energetically more stable. Because the number of electrons does not equal the number of protons, each ion has a net charge. Cations are positive ions that are formed by losing electrons. Negative ions are formed by gaining electrons and are called anions. Anions are designated by their elemental name being altered to end in "-ide": the anion of chlorine is called chloride, and the anion of sulfur is called sulfide, for example.

This movement of electrons from one element to another is referred to as electron transfer. As Figure 8.1.2.10 illustrates, sodium (Na) only has one electron in its outer electron shell. It takes less energy for sodium to donate that one electron than it does to accept seven more electrons to fill the outer shell. If sodium loses an electron, it now has 11 protons, 11 neutrons, and only 10 electrons, leaving it with an overall charge of +1. It is now referred to as a sodium ion. Chlorine (Cl) in its lowest energy state (called the ground state) has seven electrons in its outer shell. Again, it is more energy-efficient for chlorine to gain one electron than to lose seven. Therefore, it tends to gain an electron to create an ion with 17 protons, 17 neutrons, and 18 electrons, giving it a net negative (–1) charge. It is now referred to as a chloride ion. In this example, sodium will donate its one electron to empty its shell, and chlorine will accept that electron to fill its shell. Both ions now satisfy the octet rule and have complete outermost shells. Because the number of electrons is no longer equal to the number of protons, each is now an ion and has a +1 (sodium cation) or –1 (chloride anion) charge. Note that these transactions can normally only take place simultaneously: in order for a sodium atom to lose an electron, it must be in the presence of a suitable recipient like a chlorine atom.

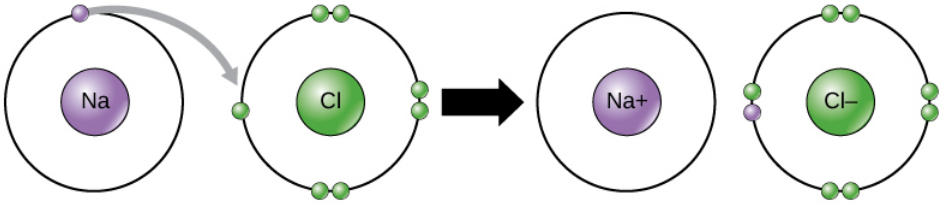



Figure 8.1.2.10: In the formation of an ionic compound, metals lose electrons and nonmetals gain electrons to achieve an octet.

Ionic bonds are formed between ions with opposite charges. For instance, positively charged sodium ions and negatively charged chloride ions bond together to make crystals of sodium chloride, or table salt, creating a crystalline molecule with zero net charge.

Certain salts are referred to in physiology as electrolytes (including sodium, potassium, and calcium), ions necessary for nerve impulse conduction, muscle contractions and water balance. Many sports drinks and dietary supplements provide these ions to replace those lost from the body via sweating during exercise.

## Covalent Bonds and Other Bonds and Interactions

Another way the octet rule can be satisfied is by the sharing of electrons between atoms to form covalent bonds. These bonds are stronger and much more common than ionic bonds in the molecules of living organisms. Covalent bonds are commonly found in

carbon-based organic molecules, such as our DNA and proteins. Covalent bonds are also found in inorganic molecules like $H_2O$, $CO_2$, and $O_2$. One, two, or three pairs of electrons may be shared, making single, double, and triple bonds, respectively. The more covalent bonds between two atoms, the stronger their connection. Thus, triple bonds are the strongest.

The strength of different levels of covalent bonding is one of the main reasons living organisms have a difficult time in acquiring nitrogen for use in constructing their molecules, even though molecular nitrogen, $N_2$, is the most abundant gas in the atmosphere. Molecular nitrogen consists of two nitrogen atoms triple bonded to each other and, as with all molecules, the sharing of these three pairs of electrons between the two nitrogen atoms allows for the filling of their outer electron shells, making the molecule more stable than the individual nitrogen atoms. This strong triple bond makes it difficult for living systems to break apart this nitrogen in order to use it as constituents of proteins and DNA.

The formation of water molecules provides an example of covalent bonding. The hydrogen and oxygen atoms that combine to form water molecules are bound together by covalent bonds, as shown in Figure 8.1.2.8. The electron from the hydrogen splits its time between the incomplete outer shell of the hydrogen atoms and the incomplete outer shell of the oxygen atoms. To completely fill the outer shell of oxygen, which has six electrons in its outer shell but which would be more stable with eight, two electrons (one from each hydrogen atom) are needed: hence the well-known formula $H_2O$. The electrons are shared between the two elements to fill the outer shell of each, making both elements more stable.

Link to Learning



Video: View this short video to see an animation of ionic and covalent bonding.

## Polar Covalent Bonds

There are two types of covalent bonds: polar and nonpolar. In a polar covalent bond, shown in Figure 8.1.2.11, the electrons are unequally shared by the atoms and are attracted more to one nucleus than the other. Because of the unequal distribution of electrons between the atoms of different elements, a slightly positive ($\delta$+) or slightly negative ($\delta$–) charge develops. This partial charge is an important property of water and accounts for many of its characteristics.

Water is a polar molecule, with the hydrogen atoms acquiring a partial positive charge and the oxygen a partial negative charge. This occurs because the nucleus of the oxygen atom is more attractive to the electrons of the hydrogen atoms than the hydrogen nucleus is to the oxygen's electrons. Thus oxygen has a higher electronegativity than hydrogen and the shared electrons spend more time in the vicinity of the oxygen nucleus than they do near the nucleus of the hydrogen atoms, giving the atoms of oxygen and hydrogen slightly negative and positive charges, respectively. Another way of stating this is that the probability of finding a shared electron near an oxygen nucleus is more likely than finding it near a hydrogen nucleus. Either way, the atom's relative electronegativity contributes to the development of partial charges whenever one element is significantly more electronegative than the other, and the charges generated by these polar bonds may then be used for the formation of hydrogen bonds based on the

attraction of opposite partial charges. (Hydrogen bonds, which are discussed in detail below, are weak bonds between slightly positively charged hydrogen atoms to slightly negatively charged atoms in other molecules.) Since macromolecules often have atoms within them that differ in electronegativity, polar bonds are often present in organic molecules.

### Nonpolar Covalent Bonds

Nonpolar covalent bonds form between two atoms of the same element or between different elements that share electrons equally. For example, molecular oxygen ($O_2$) is nonpolar because the electrons will be equally distributed between the two oxygen atoms.

Another example of a nonpolar covalent bond is methane ($CH_4$), also shown in Figure 8.1.2.11. Carbon has four electrons in its outermost shell and needs four more to fill it. It gets these four from four hydrogen atoms, each atom providing one, making a stable outer shell of eight electrons. Carbon and hydrogen do not have the same electronegativity but are similar; thus, nonpolar bonds form. The hydrogen atoms each need one electron for their outermost shell, which is filled when it contains two electrons. These elements share the electrons equally among the carbons and the hydrogen atoms, creating a nonpolar covalent molecule.

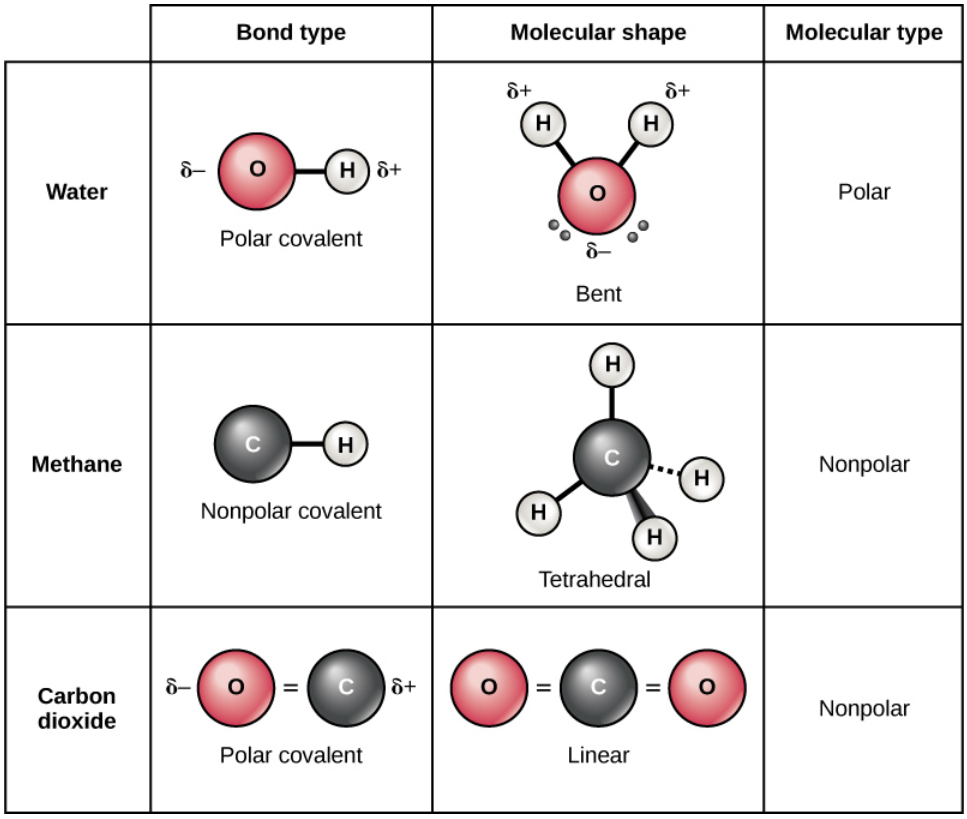



Figure 8.1.2.11: Whether a molecule is polar or nonpolar depends both on bond type and molecular shape. Both water and carbon dioxide have polar covalent bonds, but carbon dioxide is linear, so the partial charges on the molecule cancel each other out.

## Hydrogen Bonds and Van Der Waals Interactions

Ionic and covalent bonds between elements require energy to break. Ionic bonds are not as strong as covalent, which determines their behavior in biological systems. However, not all bonds are ionic or covalent bonds. Weaker bonds can also form between molecules. Two weak bonds that occur frequently are hydrogen bonds and van der Waals interactions. Without these two types of bonds, life as we know it would not exist. Hydrogen bonds provide many of the critical, life-sustaining properties of water and also stabilize the structures of proteins and DNA, the building block of cells.

When polar covalent bonds containing hydrogen form, the hydrogen in that bond has a slightly positive charge because hydrogen's electron is pulled more strongly toward the other element and away from the hydrogen. Because the hydrogen is slightly positive, it will be attracted to neighboring negative charges. When this happens, a weak interaction occurs between the $\delta^+$of the hydrogen from one molecule and the $\delta$– charge on the more electronegative atoms of another molecule, usually oxygen or nitrogen, or within the same molecule. This interaction is called a hydrogen bond. This type of bond is common and occurs regularly between water

molecules. Individual hydrogen bonds are weak and easily broken; however, they occur in very large numbers in water and in organic polymers, creating a major force in combination. Hydrogen bonds are also responsible for zipping together the DNA double helix.

Like hydrogen bonds, van der Waals interactions are weak attractions or interactions between molecules. Van der Waals attractions can occur between any two or more molecules and are dependent on slight fluctuations of the electron densities, which are not always symmetrical around an atom. For these attractions to happen, the molecules need to be very close to one another. These bonds—along with ionic, covalent, and hydrogen bonds—contribute to the three-dimensional structure of the proteins in our cells that is necessary for their proper function.

### Career Connection: Pharmaceutical Chemist

Pharmaceutical chemists are responsible for the development of new drugs and trying to determine the mode of action of both old and new drugs. They are involved in every step of the drug development process. Drugs can be found in the natural environment or can be synthesized in the laboratory. In many cases, potential drugs found in nature are changed chemically in the laboratory to make them safer and more effective, and sometimes synthetic versions of drugs substitute for the version found in nature.

After the initial discovery or synthesis of a drug, the chemist then develops the drug, perhaps chemically altering it, testing it to see if the drug is toxic, and then designing methods for efficient large-scale production. Then, the process of getting the drug approved for human use begins. In the United States, drug approval is handled by the Food and Drug Administration (FDA) and involves a series of large-scale experiments using human subjects to make sure the drug is not harmful and effectively treats the condition it aims to treat. This process often takes several years and requires the participation of physicians and scientists, in addition to chemists, to complete testing and gain approval.

An example of a drug that was originally discovered in a living organism is Paclitaxel (Taxol), an anti-cancer drug used to treat breast cancer. This drug was discovered in the bark of the pacific yew tree. Another example is aspirin, originally isolated from willow tree bark. Finding drugs often means testing hundreds of samples of plants, fungi, and other forms of life to see if any biologically active compounds are found within them. Sometimes, traditional medicine can give modern medicine clues to where an active compound can be found. For example, the use of willow bark to make medicine has been known for thousands of years, dating back to ancient Egypt. It was not until the late 1800s, however, that the aspirin molecule, known as acetylsalicylic acid, was purified and marketed for human use.

Occasionally, drugs developed for one use are found to have unforeseen effects that allow these drugs to be used in other, unrelated ways. For example, the drug minoxidil (Rogaine) was originally developed to treat high blood pressure. When tested on humans, it was noticed that individuals taking the drug would grow new hair. Eventually the drug was marketed to men and women with baldness to restore lost hair.

The career of the pharmaceutical chemist may involve detective work, experimentation, and drug development, all with the goal of making human beings healthier.

## Summary

Matter is anything that occupies space and has mass. It is made up of elements. All of the 92 elements that occur naturally have unique qualities that allow them to combine in various ways to create molecules, which in turn combine to form cells, tissues, organ systems, and organisms. Atoms, which consist of protons, neutrons, and electrons, are the smallest units of an element that retain all of the properties of that element. Electrons can be transferred, shared, or cause charge disparities between atoms to create bonds, including ionic, covalent, and hydrogen bonds, as well as van der Waals interactions.

## Art Connections

Figure **8.1.2.2**: How many neutrons do carbon-12 and carbon-13 have, respectively?

**Answer**

Carbon-12 has six neutrons. Carbon-13 has seven neutrons.

Figure 8.1.2.6: An atom may give, take, or share electrons with another atom to achieve a full valence shell, the most stable electron configuration. Looking at this figure, how many electrons do elements in group 1 need to lose in order to achieve a stable electron configuration? How many electrons do elements in groups 14 and 17 need to gain to achieve a stable configuration?

**Answer**

Elements in group 1 need to lose one electron to achieve a stable electron configuration. Elements in groups 14 and 17 need to gain four and one electrons, respectively, to achieve a stable configuration.

## Glossary

**anion**
negative ion that is formed by an atom gaining one or more electrons

**atom**
the smallest unit of matter that retains all of the chemical properties of an element

**atomic mass**
calculated mean of the mass number for an element's isotopes

**atomic number**
total number of protons in an atom

**balanced chemical equation**
statement of a chemical reaction with the number of each type of atom equalized for both the products and reactants

**cation**
positive ion that is formed by an atom losing one or more electrons

**chemical bond**
interaction between two or more of the same or different atoms that results in the formation of molecules

**chemical reaction**
process leading to the rearrangement of atoms in molecules

**chemical reactivity**
the ability to combine and to chemically bond with each other

**compound**
substance composed of molecules consisting of atoms of at least two different elements

**covalent bond**
type of strong bond formed between two of the same or different elements; forms when electrons are shared between atoms

**electrolyte**
ion necessary for nerve impulse conduction, muscle contractions and water balance

**electron**
negatively charged subatomic particle that resides outside of the nucleus in the electron orbital; lacks functional mass and has a negative charge of –1 unit

**electron configuration**
arrangement of electrons in an atom's electron shell (for example, $1s^2 2s^2 2p^6$)

**electron orbital**
how electrons are spatially distributed surrounding the nucleus; the area where an electron is most likely to be found

**electron transfer**
movement of electrons from one element to another; important in creation of ionic bonds

**electronegativity**
ability of some elements to attract electrons (often of hydrogen atoms), acquiring partial negative charges in molecules and creating partial positive charges on the hydrogen atoms

**element**
one of 118 unique substances that cannot be broken down into smaller substances; each element has unique properties and a specified number of protons

**equilibrium**
steady state of relative reactant and product concentration in reversible chemical reactions in a closed system

**hydrogen bond**
weak bond between slightly positively charged hydrogen atoms to slightly negatively charged atoms in other molecules

**inert gas**
(also, noble gas) element with filled outer electron shell that is unreactive with other atoms

**ion**
atom or chemical group that does not contain equal numbers of protons and electrons

**ionic bond**
chemical bond that forms between ions with opposite charges (cations and anions)

**irreversible chemical reaction**
chemical reaction where reactants proceed uni-directionally to form products

**isotope**
one or more forms of an element that have different numbers of neutrons

**law of mass action**
chemical law stating that the rate of a reaction is proportional to the concentration of the reacting substances

**mass number**
total number of protons and neutrons in an atom

**matter**
anything that has mass and occupies space

**molecule**
two or more atoms chemically bonded together

**neutron**
uncharged particle that resides in the nucleus of an atom; has a mass of one amu

**noble gas**

see inert gas

**nonpolar covalent bond**
type of covalent bond that forms between atoms when electrons are shared equally between them

**nucleus**
core of an atom; contains protons and neutrons

**octet rule**
rule that atoms are most stable when they hold eight electrons in their outermost shells

**orbital**
region surrounding the nucleus; contains electrons

**periodic table**
organizational chart of elements indicating the atomic number and atomic mass of each element; provides key information about the properties of the elements

**polar covalent bond**
type of covalent bond that forms as a result of unequal sharing of electrons, resulting in the creation of slightly positive and slightly negative charged regions of the molecule

**product**
molecule found on the right side of a chemical equation

**proton**
positively charged particle that resides in the nucleus of an atom; has a mass of one amu and a charge of +1

**radioisotope**
isotope that emits radiation composed of subatomic particles to form more stable elements

**reactant**
molecule found on the left side of a chemical equation

**reversible chemical reaction**
chemical reaction that functions bi-directionally, where products may turn into reactants if their concentration is great enough

**valence shell**
outermost shell of an atom

**van der Waals interaction**
very weak interaction between molecules due to temporary charges attracting atoms that are very close together

---

This page titled 8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks is shared under a CC BY 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **2.1: Atoms, Isotopes, Ions, and Molecules - The Building Blocks** by OpenStax is licensed CC BY 4.0.

# 8.1.3: Water

**Skills to Develop**

- Describe the properties of water that are critical to maintaining life
- Explain why water is an excellent solvent
- Provide examples of water's cohesive and adhesive properties
- Discuss the role of acids, bases, and buffers in homeostasis

Why do scientists spend time looking for water on other planets? Why is water so important? It is because water is essential to life as we know it. Water is one of the more abundant molecules and the one most critical to life on Earth. Approximately 60–70 percent of the human body is made up of water. Without it, life as we know it simply would not exist.

The polarity of the water molecule and its resulting hydrogen bonding make water a unique substance with special properties that are intimately tied to the processes of life. Life originally evolved in a watery environment, and most of an organism's cellular chemistry and metabolism occur inside the watery contents of the cell's cytoplasm. Special properties of water are its high heat capacity and heat of vaporization, its ability to dissolve polar molecules, its cohesive and adhesive properties, and its dissociation into ions that leads to the generation of pH. Understanding these characteristics of water helps to elucidate its importance in maintaining life.

## Water's Polarity

One of water's important properties is that it is composed of polar molecules: the hydrogen and oxygen within water molecules ($H_2O$) form polar covalent bonds. While there is no net charge to a water molecule, the polarity of water creates a slightly positive charge on hydrogen and a slightly negative charge on oxygen, contributing to water's properties of attraction. Water's charges are generated because oxygen is more electronegative than hydrogen, making it more likely that a shared electron would be found near the oxygen nucleus than the hydrogen nucleus, thus generating the partial negative charge near the oxygen.

As a result of water's polarity, each water molecule attracts other water molecules because of the opposite charges between water molecules, forming hydrogen bonds. Water also attracts or is attracted to other polar molecules and ions. A polar substance that interacts readily with or dissolves in water is referred to as hydrophilic (hydro- = "water"; -philic = "loving"). In contrast, nonpolar molecules such as oils and fats do not interact well with water, as shown in Figure **8.1.3.1** and separate from it rather than dissolve in it, as we see in salad dressings containing oil and vinegar (an acidic water solution). These nonpolar compounds are called hydrophobic (hydro- = "water"; -phobic = "fearing").

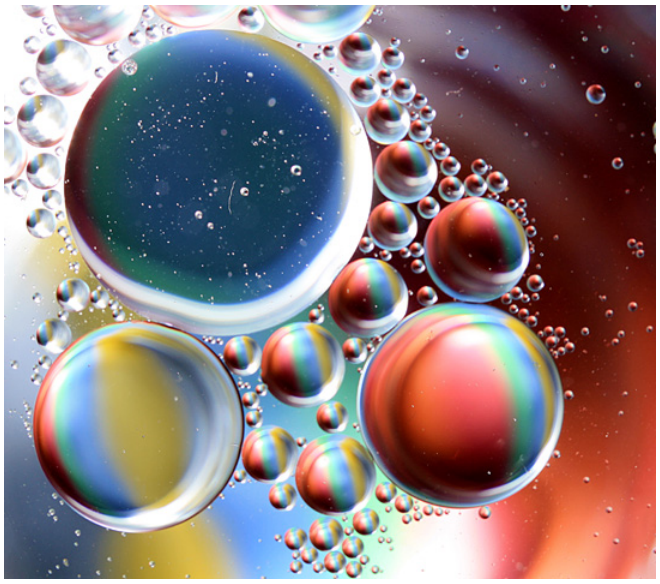


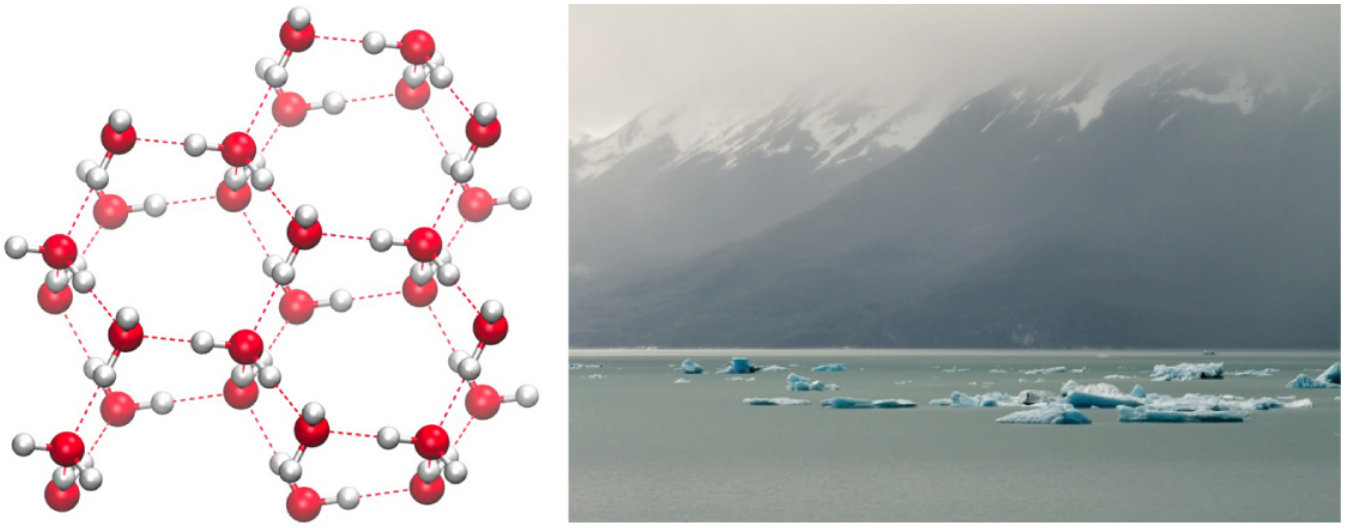
Figure **8.1.3.1**: Oil and water do not mix. As this macro image of oil and water shows, oil does not dissolve in water but forms droplets instead. This is due to it being a nonpolar compound. (credit: Gautam Dogra).

## Water's States: Gas, Liquid, and Solid

The formation of hydrogen bonds is an important quality of the liquid water that is crucial to life as we know it. As water molecules make hydrogen bonds with each other, water takes on some unique chemical characteristics compared to other liquids and, since living things have a high water content, understanding these chemical features is key to understanding life. In liquid water, hydrogen bonds are constantly formed and broken as the water molecules slide past each other. The breaking of these bonds is caused by the motion (kinetic energy) of the water molecules due to the heat contained in the system. When the heat is raised as water is boiled, the higher kinetic energy of the water molecules causes the hydrogen bonds to break completely and allows water molecules to escape into the air as gas (steam or water vapor). On the other hand, when the temperature of water is reduced and water freezes, the water molecules form a crystalline structure maintained by hydrogen bonding (there is not enough energy to break the hydrogen bonds) that makes ice less dense than liquid water, a phenomenon not seen in the solidification of other liquids.

Water's lower density in its solid form is due to the way hydrogen bonds are oriented as it freezes: the water molecules are pushed farther apart compared to liquid water. With most other liquids, solidification when the temperature drops includes the lowering of kinetic energy between molecules, allowing them to pack even more tightly than in liquid form and giving the solid a greater density than the liquid.

The lower density of ice, illustrated and pictured in Figure **8.1.3.2**, an anomaly, causes it to float at the surface of liquid water, such as in an iceberg or in the ice cubes in a glass of ice water. In lakes and ponds, ice will form on the surface of the water creating an insulating barrier that protects the animals and plant life in the pond from freezing. Without this layer of insulating ice, plants and animals living in the pond would freeze in the solid block of ice and could not survive. The detrimental effect of freezing on living organisms is caused by the expansion of ice relative to liquid water. The ice crystals that form upon freezing rupture the delicate membranes essential for the function of living cells, irreversibly damaging them. Cells can only survive freezing if the water in them is temporarily replaced by another liquid like glycerol.



(a) (b)

Figure **8.1.3.2**: Hydrogen bonding makes ice less dense than liquid water. The (a) lattice structure of ice makes it less dense than the freely flowing molecules of liquid water, enabling it to (b) float on water. (credit a: modification of work by Jane Whitney, image created using Visual Molecular Dynamics (VMD) software[1]; credit b: modification of work by Carlos Ponte)

Link to Learning



Video: Click here to see a 3-D animation of the structure of an ice lattice. (Image credit: Jane Whitney. Image created using Visual Molecular Dynamics VMD software.[2])

## Water's High Heat Capacity

Water's high heat capacity is a property caused by hydrogen bonding among water molecules. Water has the highest specific heat capacity of any liquids. Specific heat is defined as the amount of heat one gram of a substance must absorb or lose to change its temperature by one degree Celsius. For water, this amount is one calorie. It therefore takes water a long time to heat and long time to cool. In fact, the specific heat capacity of water is about five times more than that of sand. This explains why the land cools faster than the sea. Due to its high heat capacity, water is used by warm blooded animals to more evenly disperse heat in their bodies: it acts in a similar manner to a car's cooling system, transporting heat from warm places to cool places, causing the body to maintain a more even temperature.

## Water's Heat of Vaporization

Water also has a high heat of vaporization, the amount of energy required to change one gram of a liquid substance to a gas. A considerable amount of heat energy (586 cal) is required to accomplish this change in water. This process occurs on the surface of water. As liquid water heats up, hydrogen bonding makes it difficult to separate the liquid water molecules from each other, which is required for it to enter its gaseous phase (steam). As a result, water acts as a heat sink or heat reservoir and requires much more heat to boil than does a liquid such as ethanol (grain alcohol), whose hydrogen bonding with other ethanol molecules is weaker than water's hydrogen bonding. Eventually, as water reaches its boiling point of 100° Celsius (212° Fahrenheit), the heat is able to break the hydrogen bonds between the water molecules, and the kinetic energy (motion) between the water molecules allows them to escape from the liquid as a gas. Even when below its boiling point, water's individual molecules acquire enough energy from other water molecules such that some surface water molecules can escape and vaporize: this process is known as evaporation.

The fact that hydrogen bonds need to be broken for water to evaporate means that a substantial amount of energy is used in the process. As the water evaporates, energy is taken up by the process, cooling the environment where the evaporation is taking place. In many living organisms, including in humans, the evaporation of sweat, which is 90 percent water, allows the organism to cool so that homeostasis of body temperature can be maintained.

## Water's Solvent Properties

Since water is a polar molecule with slightly positive and slightly negative charges, ions and polar molecules can readily dissolve in it. Therefore, water is referred to as a solvent, a substance capable of dissolving other polar molecules and ionic compounds. The charges associated with these molecules will form hydrogen bonds with water, surrounding the particle with water molecules. This is referred to as a sphere of hydration, or a hydration shell, as illustrated in Figure **8.1.3.3** and serves to keep the particles separated or dispersed in the water.

When ionic compounds are added to water, the individual ions react with the polar regions of the water molecules and their ionic bonds are disrupted in the process of dissociation. Dissociation occurs when atoms or groups of atoms break off from molecules and form ions. Consider table salt (NaCl, or sodium chloride): when NaCl crystals are added to water, the molecules of NaCl dissociate into $Na^+$ and $Cl^-$ ions, and spheres of hydration form around the ions, illustrated in Figure **8.1.3.3**. The positively charged sodium ion is surrounded by the partially negative charge of the water molecule's oxygen. The negatively charged chloride ion is surrounded by the partially positive charge of the hydrogen on the water molecule.

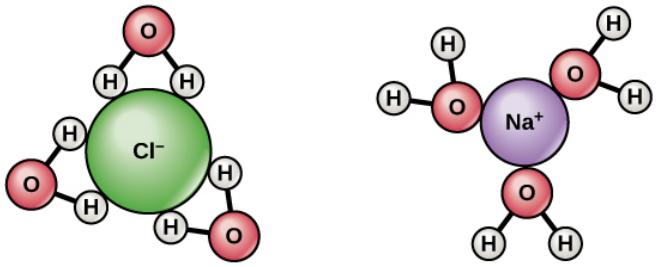



Figure **8.1.3.3**: When table salt (NaCl) is mixed in water, spheres of hydration are formed around the ions.

## Water's Cohesive and Adhesive Properties

Have you ever filled a glass of water to the very top and then slowly added a few more drops? Before it overflows, the water forms a dome-like shape above the rim of the glass. This water can stay above the glass because of the property of cohesion. In cohesion, water molecules are attracted to each other (because of hydrogen bonding), keeping the molecules together at the liquid-gas (water-air) interface, although there is no more room in the glass.

Cohesion allows for the development of surface tension, the capacity of a substance to withstand being ruptured when placed under tension or stress. This is also why water forms droplets when placed on a dry surface rather than being flattened out by gravity. When a small scrap of paper is placed onto the droplet of water, the paper floats on top of the water droplet even though paper is denser (heavier) than the water. Cohesion and surface tension keep the hydrogen bonds of water molecules intact and support the item floating on the top. It's even possible to "float" a needle on top of a glass of water if it is placed gently without breaking the surface tension, as shown in Figure **8.1.3.4**.

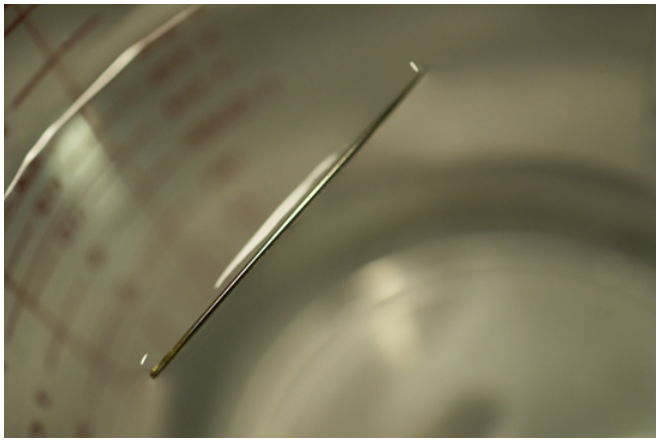


Figure **8.1.3.4**: The weight of the needle is pulling the surface downward; at the same time, the surface tension is pulling it up, suspending it on the surface of the water and keeping it from sinking. Notice the indentation in the water around the needle. (credit: Cory Zanker)

These cohesive forces are related to water's property of adhesion, or the attraction between water molecules and other molecules. This attraction is sometimes stronger than water's cohesive forces, especially when the water is exposed to charged surfaces such as those found on the inside of thin glass tubes known as capillary tubes. Adhesion is observed when water "climbs" up the tube placed in a glass of water: notice that the water appears to be higher on the sides of the tube than in the middle. This is because the water molecules are attracted to the charged glass walls of the capillary more than they are to each other and therefore adhere to it. This type of adhesion is called capillary action, and is illustrated in Figure **8.1.3.5**.

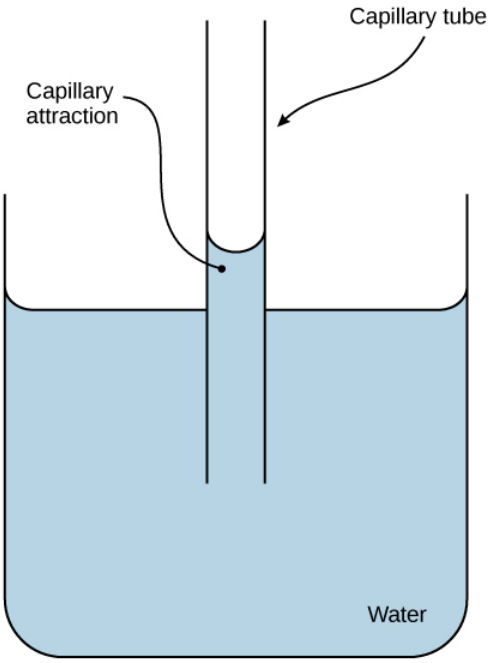



Figure 8.1.3.5: Capillary action in a glass tube is caused by the adhesive forces exerted by the internal surface of the glass exceeding the cohesive forces between the water molecules themselves. (credit: modification of work by Pearson-Scott Foresman, donated to the Wikimedia Foundation)

Why are cohesive and adhesive forces important for life? Cohesive and adhesive forces are important for the transport of water from the roots to the leaves in plants. These forces create a "pull" on the water column. This pull results from the tendency of water molecules being evaporated on the surface of the plant to stay connected to water molecules below them, and so they are pulled along. Plants use this natural phenomenon to help transport water from their roots to their leaves. Without these properties of water, plants would be unable to receive the water and the dissolved minerals they require. In another example, insects such as the water strider, shown in Figure 8.1.3.6, use the surface tension of water to stay afloat on the surface layer of water and even mate there.

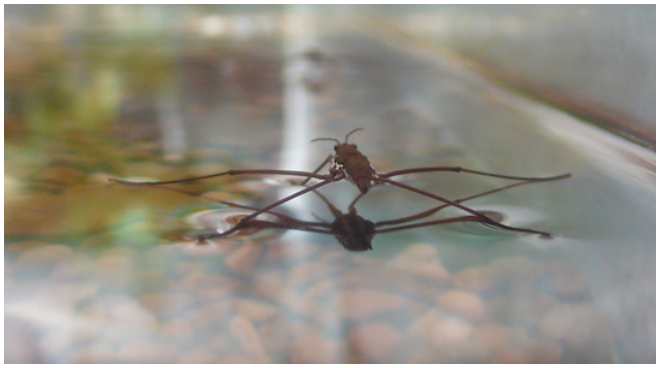


Figure 8.1.3.6: Water's cohesive and adhesive properties allow this water strider (*Gerris* sp.) to stay afloat. (credit: Tim Vickers)

## pH, Buffers, Acids, and Bases

The pH of a solution indicates its acidity or alkalinity.

$$H_2O(l) \rightleftharpoons H^+(aq) + O^-(aq)$$

litmus or pH paper, filter paper that has been treated with a natural water-soluble dye so it can be used as a pH indicator, to test how much acid (acidity) or base (alkalinity) exists in a solution. You might have even used some to test whether the water in a swimming pool is properly treated. In both cases, the pH test measures the concentration of hydrogen ions in a given solution.

Hydrogen ions are spontaneously generated in pure water by the dissociation (ionization) of a small percentage of water molecules into equal numbers of hydrogen ($H^+$) ions and hydroxide ($OH^-$) ions. While the hydroxide ions are kept in solution by their

hydrogen bonding with other water molecules, the hydrogen ions, consisting of naked protons, are immediately attracted to un-ionized water molecules, forming hydronium ions ($H_30^+$). Still, by convention, scientists refer to hydrogen ions and their concentration as if they were free in this state in liquid water.

The concentration of hydrogen ions dissociating from pure water is $1 \times 10^{-7}$ moles $H^+$ ions per liter of water. Moles (mol) are a way to express the amount of a substance (which can be atoms, molecules, ions, etc), with one mole being equal to $6.02 \times 10^{23}$ particles of the substance. Therefore, 1 mole of water is equal to $6.02 \times 10^{23}$ water molecules. The pH is calculated as the negative of the base 10 logarithm of this concentration. The log10 of $1 \times 10^{-7}$ is -7.0, and the negative of this number (indicated by the "p" of "pH") yields a pH of 7.0, which is also known as neutral pH. The pH inside of human cells and blood are examples of two areas of the body where near-neutral pH is maintained.

Non-neutral pH readings result from dissolving acids or bases in water. Using the negative logarithm to generate positive integers, high concentrations of hydrogen ions yield a low pH number, whereas low levels of hydrogen ions result in a high pH. An acid is a substance that increases the concentration of hydrogen ions ($H^+$) in a solution, usually by having one of its hydrogen atoms dissociate. A base provides either hydroxide ions ($OH^–$) or other negatively charged ions that combine with hydrogen ions, reducing their concentration in the solution and thereby raising the pH. In cases where the base releases hydroxide ions, these ions bind to free hydrogen ions, generating new water molecules.

The stronger the acid, the more readily it donates $H^+$. For example, hydrochloric acid (HCl) completely dissociates into hydrogen and chloride ions and is highly acidic, whereas the acids in tomato juice or vinegar do not completely dissociate and are considered weak acids. Conversely, strong bases are those substances that readily donate $OH^–$ or take up hydrogen ions. Sodium hydroxide (NaOH) and many household cleaners are highly alkaline and give up $OH^–$ rapidly when placed in water, thereby raising the pH. An example of a weak basic solution is seawater, which has a pH near 8.0, close enough to neutral pH that marine organisms adapted to this saline environment are able to thrive in it.

The pH scale is, as previously mentioned, an inverse logarithm and ranges from 0 to 14 (Figure **8.1.3.7**). Anything below 7.0 (ranging from 0.0 to 6.9) is acidic, and anything above 7.0 (from 7.1 to 14.0) is alkaline. Extremes in pH in either direction from 7.0 are usually considered inhospitable to life. The pH inside cells (6.8) and the pH in the blood (7.4) are both very close to neutral. However, the environment in the stomach is highly acidic, with a pH of 1 to 2. So how do the cells of the stomach survive in such an acidic environment? How do they homeostatically maintain the near neutral pH inside them? The answer is that they cannot do it and are constantly dying. New stomach cells are constantly produced to replace dead ones, which are digested by the stomach acids. It is estimated that the lining of the human stomach is completely replaced every seven to ten days.

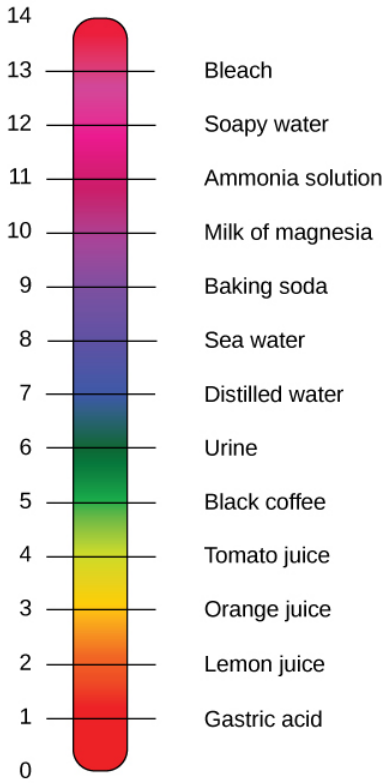



Figure **8.1.3.7**: The pH scale measures the concentration of hydrogen ions ($H^+$) in a solution. (credit: modification of work by Edward Stevens)

Link to Learning



Watch this video for a straightforward explanation of pH and its logarithmic scale.

So how can organisms whose bodies require a near-neutral pH ingest acidic and basic substances (a human drinking orange juice, for example) and survive? Buffers are the key. Buffers readily absorb excess $H^+$ or $OH^-$, keeping the pH of the body carefully maintained in the narrow range required for survival. Maintaining a constant blood pH is critical to a person's well-being. The buffer maintaining the pH of human blood involves carbonic acid ($H_2CO_3$), bicarbonate ion ($HCO_3^-$), and carbon dioxide ($CO_2$). When bicarbonate ions combine with free hydrogen ions and become carbonic acid, hydrogen ions are removed, moderating pH

changes. Similarly, as shown in Figure **8.1.3.8**, excess carbonic acid can be converted to carbon dioxide gas and exhaled through the lungs. This prevents too many free hydrogen ions from building up in the blood and dangerously reducing the blood's pH. Likewise, if too much $OH^-$ is introduced into the system, carbonic acid will combine with it to create bicarbonate, lowering the pH. Without this buffer system, the body's pH would fluctuate enough to put survival in jeopardy.

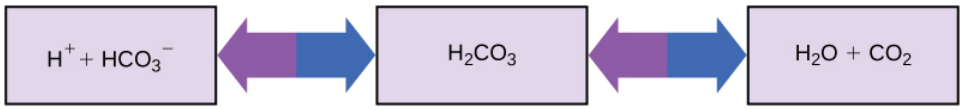



Figure **8.1.3.8**: This diagram shows the body's buffering of blood pH levels. The blue arrows show the process of raising pH as more $CO_2$ is made. The purple arrows indicate the reverse process: the lowering of pH as more bicarbonate is created.

Other examples of buffers are antacids used to combat excess stomach acid. Many of these over-the-counter medications work in the same way as blood buffers, usually with at least one ion capable of absorbing hydrogen and moderating pH, bringing relief to those that suffer "heartburn" after eating. The unique properties of water that contribute to this capacity to balance pH—as well as water's other characteristics—are essential to sustaining life on Earth.

Link to Learning

To learn more about water. Visit the U.S. Geological Survey Water Science for Schools All About Water! website.

## Summary

Water has many properties that are critical to maintaining life. It is a polar molecule, allowing for the formation of hydrogen bonds. Hydrogen bonds allow ions and other polar molecules to dissolve in water. Therefore, water is an excellent solvent. The hydrogen bonds between water molecules cause the water to have a high heat capacity, meaning it takes a lot of added heat to raise its temperature. As the temperature rises, the hydrogen bonds between water continually break and form anew. This allows for the overall temperature to remain stable, although energy is added to the system. Water also exhibits a high heat of vaporization, which is key to how organisms cool themselves by the evaporation of sweat. Water's cohesive forces allow for the property of surface tension, whereas its adhesive properties are seen as water rises inside capillary tubes. The pH value is a measure of hydrogen ion concentration in a solution and is one of many chemical characteristics that is highly regulated in living organisms through homeostasis. Acids and bases can change pH values, but buffers tend to moderate the changes they cause. These properties of water are intimately connected to the biochemical and physical processes performed by living organisms, and life would be very different if these properties were altered, if it could exist at all.

## Footnotes

1. 1 W. Humphrey W., A. Dalke, and K. Schulten, "VMD—Visual Molecular Dynamics," *Journal of Molecular Graphics* 14 (1996): 33-38.
2. 2 W. Humphrey W., A. Dalke, and K. Schulten, "VMD—Visual Molecular Dynamics," *Journal of Molecular Graphics* 14 (1996): 33-38.

## Glossary

**acid**

molecule that donates hydrogen ions and increases the concentration of hydrogen ions in a solution

**adhesion**

attraction between water molecules and other molecules

**base**
molecule that donates hydroxide ions or otherwise binds excess hydrogen ions and decreases the concentration of hydrogen ions in a solution

**buffer**
substance that prevents a change in pH by absorbing or releasing hydrogen or hydroxide ions

**calorie**
amount of heat required to change the temperature of one gram of water by one degree Celsius

**capillary action**
occurs because water molecules are attracted to charges on the inner surfaces of narrow tubular structures such as glass tubes, drawing the water molecules to the sides of the tubes

**cohesion**
intermolecular forces between water molecules caused by the polar nature of water; responsible for surface tension

**dissociation**
release of an ion from a molecule such that the original molecule now consists of an ion and the charged remains of the original, such as when water dissociates into $H^+$ and $OH^-$

**evaporation**
separation of individual molecules from the surface of a body of water, leaves of a plant, or the skin of an organism

**heat of vaporization of water**
high amount of energy required for liquid water to turn into water vapor

**hydrophilic**
describes ions or polar molecules that interact well with other polar molecules such as water

**hydrophobic**
describes uncharged non-polar molecules that do not interact well with polar molecules such as water

**litmus paper**
(also, pH paper) filter paper that has been treated with a natural water-soluble dye that changes its color as the pH of the environment changes so it can be used as a pH indicator

**pH paper**
see litmus paper

**pH scale**
scale ranging from zero to 14 that is inversely proportional to the concentration of hydrogen ions in a solution

**solvent**
substance capable of dissolving another substance

**specific heat capacity**
the amount of heat one gram of a substance must absorb or lose to change its temperature by one degree Celsius

**sphere of hydration**
when a polar water molecule surrounds charged or polar molecules thus keeping them dissolved and in solution

**surface tension**

tension at the surface of a body of liquid that prevents the molecules from separating; created by the attractive cohesive forces between the molecules of the liquid

---

This page titled 8.1.3: Water is shared under a CC BY 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **2.2: Water** by OpenStax is licensed CC BY 4.0.

# 8.1.4: Carbon

**Skills to Develop**

- Explain why carbon is important for life
- Describe the role of functional groups in biological molecules

Cells are made of many complex molecules called macromolecules, such as proteins, nucleic acids (RNA and DNA), carbohydrates, and lipids. The macromolecules are a subset of organic molecules (any carbon-containing liquid, solid, or gas) that are especially important for life. The fundamental component for all of these macromolecules is carbon. The carbon atom has unique properties that allow it to form covalent bonds to as many as four different atoms, making this versatile element ideal to serve as the basic structural component, or "backbone," of the macromolecules.

Individual carbon atoms have an incomplete outermost electron shell. With an atomic number of 6 (six electrons and six protons), the first two electrons fill the inner shell, leaving four in the second shell. Therefore, carbon atoms can form up to four covalent bonds with other atoms to satisfy the octet rule. The methane molecule provides an example: it has the chemical formula $CH_4$. Each of its four hydrogen atoms forms a single covalent bond with the carbon atom by sharing a pair of electrons. This results in a filled outermost shell.

## Hydrocarbons

Hydrocarbons are organic molecules consisting entirely of carbon and hydrogen, such as methane ($CH_4$) described above. We often use hydrocarbons in our daily lives as fuels—like the propane in a gas grill or the butane in a lighter. The many covalent bonds between the atoms in hydrocarbons store a great amount of energy, which is released when these molecules are burned (oxidized). Methane, an excellent fuel, is the simplest hydrocarbon molecule, with a central carbon atom bonded to four different hydrogen atoms, as illustrated in Figure 8.1.4.1. The geometry of the methane molecule, where the atoms reside in three dimensions, is determined by the shape of its electron orbitals. The carbons and the four hydrogen atoms form a shape known as a tetrahedron, with four triangular faces; for this reason, methane is described as having tetrahedral geometry.

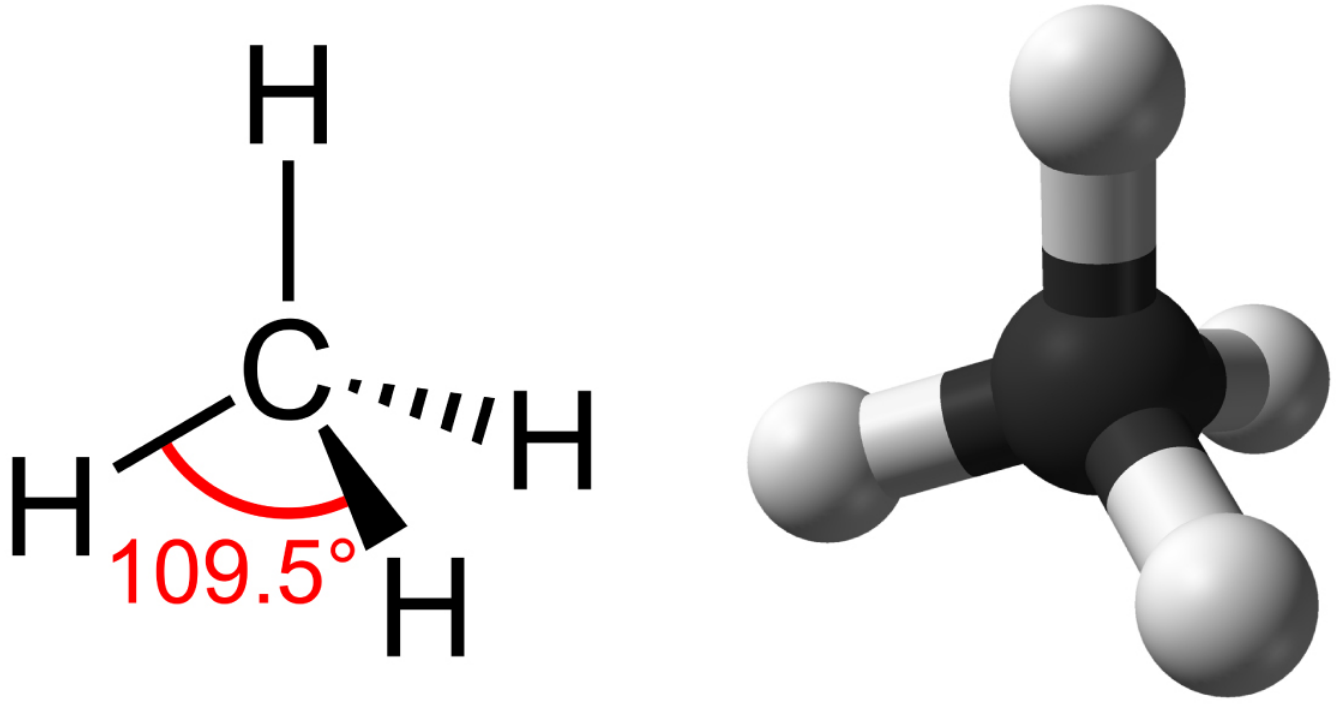



Figure 8.1.4.1: Methane has a tetrahedral geometry, with each of the four hydrogen atoms spaced 109.5° apart.

As the backbone of the large molecules of living things, hydrocarbons may exist as linear carbon chains, carbon rings, or combinations of both. Furthermore, individual carbon-to-carbon bonds may be single, double, or triple covalent bonds, and each

type of bond affects the geometry of the molecule in a specific way. This three-dimensional shape or conformation of the large molecules of life (macromolecules) is critical to how they function.

### Hydrocarbon Chains

Hydrocarbon chains are formed by successive bonds between carbon atoms and may be branched or unbranched. Furthermore, the overall geometry of the molecule is altered by the different geometries of single, double, and triple covalent bonds, illustrated in Figure **8.1.4.2**. The hydrocarbons ethane, ethene, and ethyne serve as examples of how different carbon-to-carbon bonds affect the geometry of the molecule. The names of all three molecules start with the prefix "eth-," which is the prefix for two carbon hydrocarbons. The suffixes "-ane," "-ene," and "-yne" refer to the presence of single, double, or triple carbon-carbon bonds, respectively. Thus, propane, propene, and propyne follow the same pattern with three carbon molecules, butane, butane, and butyne for four carbon molecules, and so on. Double and triple bonds change the geometry of the molecule: single bonds allow rotation along the axis of the bond, whereas double bonds lead to a planar configuration and triple bonds to a linear one. These geometries have a significant impact on the shape a particular molecule can assume.

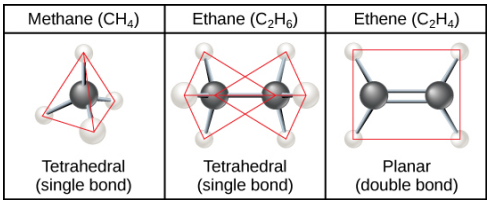



Figure **8.1.4.2**: When carbon forms single bonds with other atoms, the shape is tetrahedral. When two carbon atoms form a double bond, the shape is planar, or flat. Single bonds, like those found in ethane, are able to rotate. Double bonds, like those found in ethene cannot rotate, so the atoms on either side are locked in place.

### Hydrocarbon Rings

So far, the hydrocarbons we have discussed have been aliphatic hydrocarbons, which consist of linear chains of carbon atoms. Another type of hydrocarbon, aromatic hydrocarbons, consists of closed rings of carbon atoms. Ring structures are found in hydrocarbons, sometimes with the presence of double bonds, which can be seen by comparing the structure of cyclohexane to benzene in Figure **8.1.4.3**. Examples of biological molecules that incorporate the benzene ring include some amino acids and cholesterol and its derivatives, including the hormones estrogen and testosterone. The benzene ring is also found in the herbicide 2,4-D. Benzene is a natural component of crude oil and has been classified as a carcinogen. Some hydrocarbons have both aliphatic and aromatic portions; beta-carotene is an example of such a hydrocarbon.

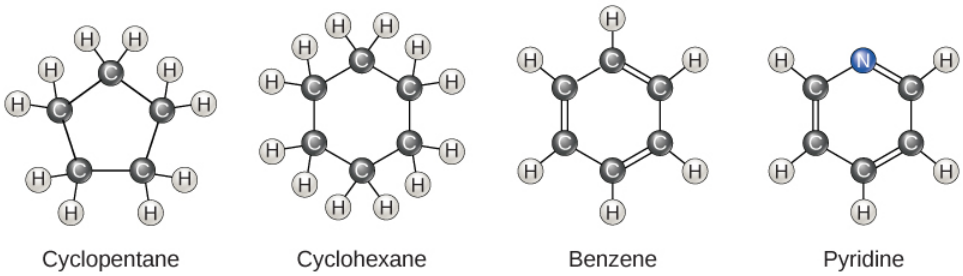



Figure **8.1.4.3**: Carbon can form five-and six membered rings. Single or double bonds may connect the carbons in the ring, and nitrogen may be substituted for carbon.

## Isomers

The three-dimensional placement of atoms and chemical bonds within organic molecules is central to understanding their chemistry. Molecules that share the same chemical formula but differ in the placement (structure) of their atoms and/or chemical bonds are known as isomers. Structural isomers (like butane and isobutene shown in Figure **8.1.4.4**a differ in the placement of their covalent bonds: both molecules have four carbons and ten hydrogens ($C_4H_{10}$), but the different arrangement of the atoms within the molecules leads to differences in their chemical properties. For example, due to their different chemical properties, butane is suited for use as a fuel for cigarette lighters and torches, whereas isobutene is suited for use as a refrigerant and a propellant in spray cans.

Geometric isomers, on the other hand, have similar placements of their covalent bonds but differ in how these bonds are made to the surrounding atoms, especially in carbon-to-carbon double bonds. In the simple molecule butene ($C_4H_8$), the two methyl groups ($CH_3$) can be on either side of the double covalent bond central to the molecule, as illustrated in Figure 8.1.4.4b. When the carbons are bound on the same side of the double bond, this is the *cis* configuration; if they are on opposite sides of the double bond, it is a *trans* configuration. In the *trans* configuration, the carbons form a more or less linear structure, whereas the carbons in the *cis* configuration make a bend (change in direction) of the carbon backbone.

Art Connection

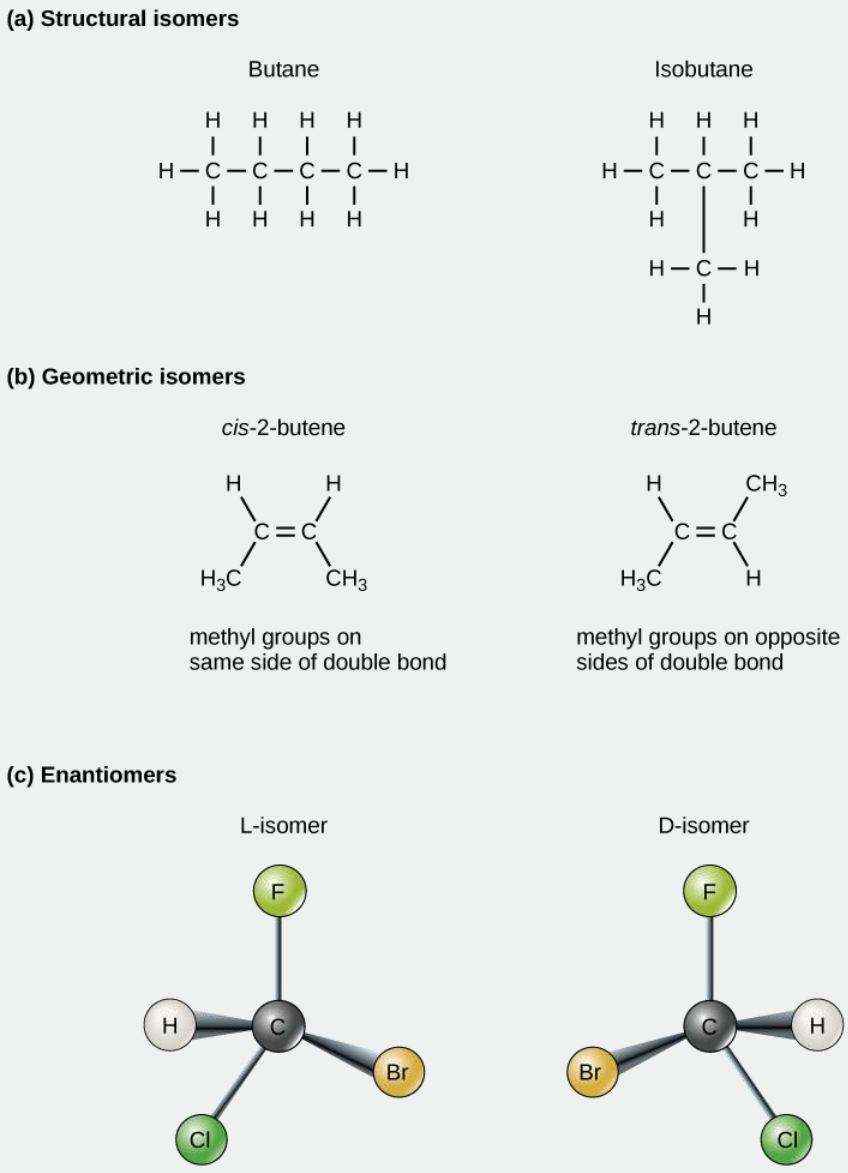
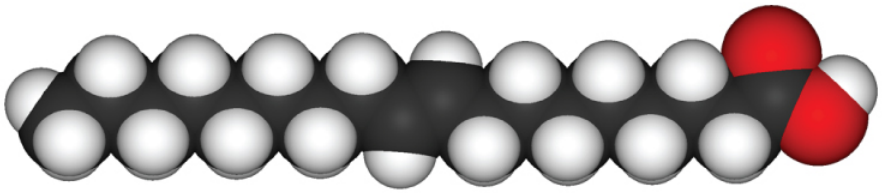



Figure 8.1.4.4: Molecules that have the same number and type of atoms arranged differently are called isomers. (a) Structural isomers have a different covalent arrangement of atoms. (b) Geometric isomers have a different arrangement of atoms around a double bond. (c) Enantiomers are mirror images of each other.

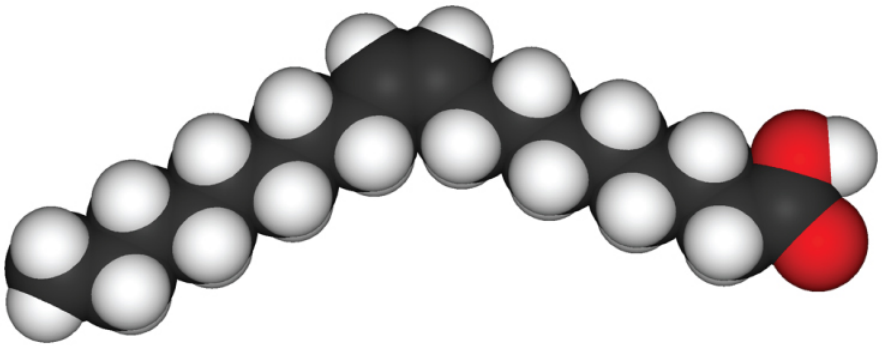
Which of the following statements is false?

A. Molecules with the formulas $CH_3CH_2COOH$ and $C_3H_6O_2$ could be structural isomers.
B. Molecules must have a double bond to be *cis-trans* isomers.
C. To be enantiomers, a molecule must have at least three different atoms or groups connected to a central carbon.
D. To be enantiomers, a molecule must have at least four different atoms or groups connected to a central carbon.

In triglycerides (fats and oils), long carbon chains known as fatty acids may contain double bonds, which can be in either the *cis* or *trans* configuration, illustrated in Figure **8.1.4.5**. Fats with at least one double bond between carbon atoms are unsaturated fats. When some of these bonds are in the *cis* configuration, the resulting bend in the carbon backbone of the chain means that triglyceride molecules cannot pack tightly, so they remain liquid (oil) at room temperature. On the other hand, triglycerides with *trans* double bonds (popularly called trans fats), have relatively linear fatty acids that are able to pack tightly together at room temperature and form solid fats. In the human diet, trans fats are linked to an increased risk of cardiovascular disease, so many food manufacturers have reduced or eliminated their use in recent years. In contrast to unsaturated fats, triglycerides without double bonds between carbon atoms are called saturated fats, meaning that they contain all the hydrogen atoms available. Saturated fats are a solid at room temperature and usually of animal origin.



Eliadic acid



Oleic acid

Figure **8.1.4.5**: These space-filling models show a *cis* (oleic acid) and a *trans* (eliadic acid) fatty acid. Notice the bend in the molecule cause by the *cis* configuration.

## Enantiomers

Enantiomers are molecules that share the same chemical structure and chemical bonds but differ in the three-dimensional placement of atoms so that they are mirror images. As shown in Figure **8.1.4.6**, an amino acid alanine example, the two structures are non-superimposable. In nature, only the L-forms of amino acids are used to make proteins. Some D forms of amino acids are seen in the cell walls of bacteria, but never in their proteins. Similarly, the D-form of glucose is the main product of photosynthesis and the L-form of the molecule is rarely seen in nature.

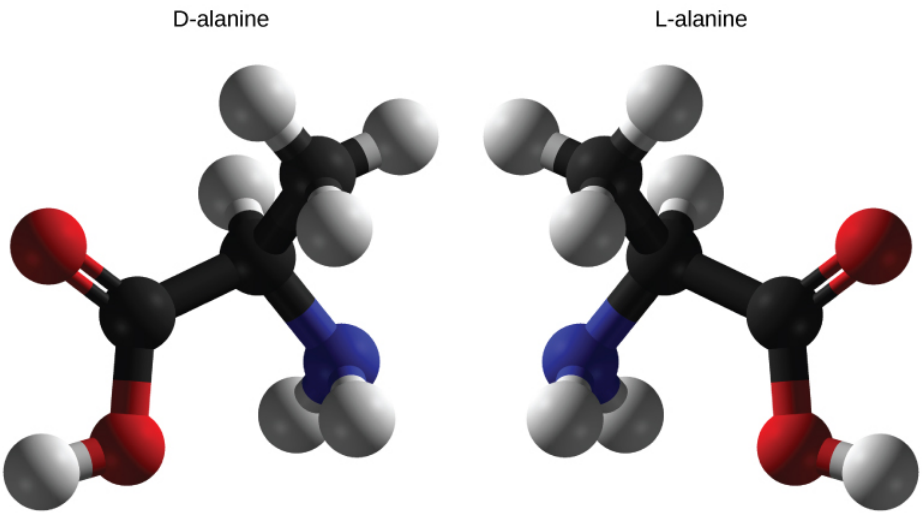



Figure **8.1.4.6**: D-alanine and L-alanine are examples of enantiomers or mirror images. Only the L-forms of amino acids are used to make proteins.

## Functional Groups

Functional groups are groups of atoms that occur within molecules and confer specific chemical properties to those molecules. They are found along the "carbon backbone" of macromolecules. This carbon backbone is formed by chains and/or rings of carbon atoms with the occasional substitution of an element such as nitrogen or oxygen. Molecules with other elements in their carbon backbone are substituted hydrocarbons.

The functional groups in a macromolecule are usually attached to the carbon backbone at one or several different places along its chain and/or ring structure. Each of the four types of macromolecules—proteins, lipids, carbohydrates, and nucleic acids—has its own characteristic set of functional groups that contributes greatly to its differing chemical properties and its function in living organisms.

A functional group can participate in specific chemical reactions. Some of the important functional groups in biological molecules are shown in Figure **8.1.4.7**; they include: hydroxyl, methyl, carbonyl, carboxyl, amino, phosphate, and sulfhydryl. These groups play an important role in the formation of molecules like DNA, proteins, carbohydrates, and lipids. Functional groups are usually classified as hydrophobic or hydrophilic depending on their charge or polarity characteristics. An example of a hydrophobic group is the non-polar methane molecule. Among the hydrophilic functional groups is the carboxyl group found in amino acids, some amino acid side chains, and the fatty acids that form triglycerides and phospholipids. This carboxyl group ionizes to release hydrogen ions ($H^+$) from the COOH group resulting in the negatively charged $COO^-$ group; this contributes to the hydrophilic nature of whatever molecule it is found on. Other functional groups, such as the carbonyl group, have a partially negatively charged oxygen atom that may form hydrogen bonds with water molecules, again making the molecule more hydrophilic.

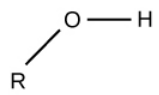
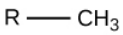
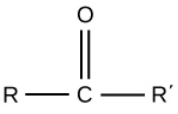
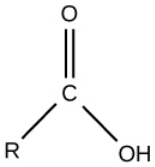
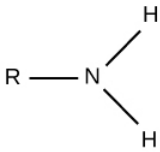
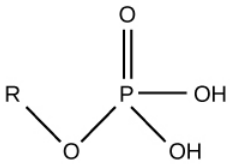
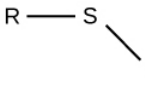
| Functional Group | Structure | Properties |
|---|---|---|
| Hydroxyl |  | Polar |
| Methyl |  | Nonpolar |
| Carbonyl |  | Polar |
| Carboxyl |  | Charged, ionizes to release $H^+$. Since carboxyl groups can release $H^+$ ions into solution, they are considered acidic. |
| Amino |  | Charged, accepts $H^+$ to form $NH_3^+$. Since amino groups can remove $H^+$ from solution, they are considered basic. |
| Phosphate |  | Charged, ionizes to release $H^+$. Since phosphate groups can release $H^+$ ions into solution, they are considered acidic. |
| Sulfhydryl |  | Polar |

Figure 8.1.4.7: The functional groups shown here are found in many different biological molecules.

Hydrogen bonds between functional groups (within the same molecule or between different molecules) are important to the function of many macromolecules and help them to fold properly into and maintain the appropriate shape for functioning. Hydrogen bonds are also involved in various recognition processes, such as DNA complementary base pairing and the binding of an enzyme to its substrate, as illustrated in Figure 8.1.4.8.

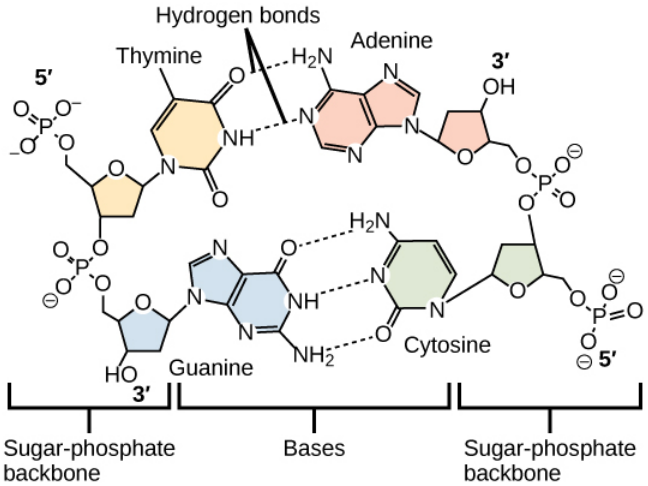



Figure 8.1.4.8: Hydrogen bonds connect two strands of DNA together to create the double-helix structure.

## Summary

The unique properties of carbon make it a central part of biological molecules. Carbon binds to oxygen, hydrogen, and nitrogen covalently to form the many molecules important for cellular function. Carbon has four electrons in its outermost shell and can form four bonds. Carbon and hydrogen can form hydrocarbon chains or rings. Functional groups are groups of atoms that confer specific properties to hydrocarbon (or substituted hydrocarbon) chains or rings that define their overall chemical characteristics and function.

## Art Connections

Figure 8.1.4.4: Which of the following statements is false?

A. Molecules with the formulas $CH_3CH_2COOH$ and $C_3H_6O_2$ could be structural isomers.
B. Molecules must have a double bond to be *cis-trans* isomers.
C. To be enantiomers, a molecule must have at least three different atoms or groups connected to a central carbon.
D. To be enantiomers, a molecule must have at least four different atoms or groups connected to a central carbon.

**Answer**

C

## Glossary

**aliphatic hydrocarbon**
hydrocarbon consisting of a linear chain of carbon atoms

**aromatic hydrocarbon**
hydrocarbon consisting of closed rings of carbon atoms

**enantiomers**
molecules that share overall structure and bonding patterns, but differ in how the atoms are three dimensionally placed such that they are mirror images of each other

**functional group**
group of atoms that provides or imparts a specific function to a carbon skeleton

**geometric isomer**
isomer with similar bonding patterns differing in the placement of atoms alongside a double covalent bond

**hydrocarbon**
molecule that consists only of carbon and hydrogen

**isomers**
molecules that differ from one another even though they share the same chemical formula

**organic molecule**
any molecule containing carbon (except carbon dioxide)

**structural isomers**
molecules that share a chemical formula but differ in the placement of their chemical bonds

**substituted hydrocarbon**
hydrocarbon chain or ring containing an atom of another element in place of one of the backbone carbons

This page titled 8.1.4: Carbon is shared under a CC BY 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **2.3: Carbon** by OpenStax is licensed CC BY 4.0.

# 8.1.E: The Chemical Foundation of Life (Exercises)

## 2.1: Atoms, Isotopes, Ions, and Molecules - The Building Blocks

### Review Questions

If xenon has an atomic number of 54 and a mass number of 108, how many neutrons does it have?

A. 54
B. 27
C. 100
D. 108

**Answer**

A

Atoms that vary in the number of neutrons found in their nuclei are called _____.

A. ions
B. neutrons
C. neutral atoms
D. isotopes

**Answer**

D

Potassium has an atomic number of 19. What is its electron configuration?

A. shells 1 and 2 are full, and shell 3 has nine electrons
B. shells 1, 2 and 3 are full and shell 4 has three electrons
C. shells 1, 2 and 3 are full and shell 4 has one electron
D. shells 1, 2 and 3 are full and no other electrons are present

**Answer**

C

Which type of bond represents a weak chemical bond?

A. hydrogen bond
B. atomic bond
C. covalent bond
D. nonpolar covalent bond

**Answer**

A

### Free Response

What makes ionic bonds different from covalent bonds?

**Answer**

Ionic bonds are created between ions. The electrons are not shared between the atoms, but rather are associated more with one ion than the other. Ionic bonds are strong bonds, but are weaker than covalent bonds, meaning it takes less energy to break an ionic bond compared with a covalent one.

Why are hydrogen bonds and van der Waals interactions necessary for cells?

**Answer**

Hydrogen bonds and van der Waals interactions form weak associations between different molecules or within different regions of the same molecule. They provide the structure and shape necessary for proteins and DNA within cells so that they function properly.

## 2.2: Water

### Review Questions

Which of the following statements is not true?

A. Water is polar.
B. Water stabilizes temperature.
C. Water is essential for life.
D. Water is the most abundant molecule in the Earth's atmosphere.

**Answer**

D

When acids are added to a solution, the pH should _____.

A. decrease
B. increase
C. stay the same
D. cannot tell without testing

**Answer**

A

A molecule that binds up excess hydrogen ions in a solution is called a(n) _____.

A. acid
B. isotope
C. base
D. donator

**Answer**

C

Which of the following statements is true?

A. Acids and bases cannot mix together.
B. Acids and bases will neutralize each other.
C. Acids, but not bases, can change the pH of a solution.
D. Acids donate hydroxide ions ($OH^-$); bases donate hydrogen ions ($H^+$).

**Answer**

B

### Free Response

Discuss how buffers help prevent drastic swings in pH.

**Answer**

Buffers absorb the free hydrogen ions and hydroxide ions that result from chemical reactions. Because they can bond these ions, they prevent increases or decreases in pH. An example of a buffer system is the bicarbonate system in the human body. This system is able to absorb hydrogen and hydroxide ions to prevent changes in pH and keep cells functioning properly.

Why can some insects walk on water?

**Answer**

Some insects can walk on water, although they are heavier (denser) than water, because of the surface tension of water. Surface tension results from cohesion, or the attraction between water molecules at the surface of the body of water (the liquid-air/gas interface).

## 2.3: Carbon

### Review Questions

Each carbon molecule can bond with as many as_____ other atom(s) or molecule(s).

A. one
B. two
C. six
D. four

**Answer**

D

Which of the following is not a functional group that can bond with carbon?

A. sodium
B. hydroxyl
C. phosphate
D. carbonyl

**Answer**

A

### Free Response

What property of carbon makes it essential for organic life?

**Answer**

Carbon is unique and found in all living things because it can form up to four covalent bonds between atoms or molecules. These can be nonpolar or polar covalent bonds, and they allow for the formation of long chains of carbon molecules that combine to form proteins and DNA.

Compare and contrast saturated and unsaturated triglycerides.

**Answer**

Saturated triglycerides contain no double bonds between carbon atoms; they are usually solid at room temperature. Unsaturated triglycerides contain at least one double bond between carbon atoms and are usually liquid at room temperature.

---

This page titled 8.1.E: The Chemical Foundation of Life (Exercises) is shared under a CC BY 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **2.E: The Chemical Foundation of Life (Exercises)** by OpenStax is licensed CC BY 4.0.

# SECTION OVERVIEW

## 8.2: Biological Macromolecules

Food provides the body with the nutrients it needs to survive. Many of these critical nutrients are biological macromolecules, or large molecules, necessary for life. These macromolecules (polymers) are built from different combinations of smaller organic molecules (monomers). What specific types of biological macromolecules do living things require? How are these molecules formed? What functions do they serve? In this chapter, these questions will be explored.


8.2.1: Prelude to Biological Macromolecules

8.2.2: Synthesis of Biological Macromolecules

8.2.3: Carbohydrates

8.2.4: Lipids

8.2.5: Proteins

8.2.6: Nucleic Acids

8.2.E: Biological Macromolecules (Exercises)


---


This page titled 8.2: Biological Macromolecules is shared under a CC BY 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

# 8.2.1: Prelude to Biological Macromolecules



Figure **8.2.1.1**: Foods such as bread, fruit, and cheese are rich sources of biological macromolecules. (credit: modification of work by Bengt Nyman)

Food provides the body with the nutrients it needs to survive. Many of these critical nutrients are biological macromolecules, or large molecules, necessary for life. These macromolecules (polymers) are built from different combinations of smaller organic molecules (monomers). What specific types of biological macromolecules do living things require? How are these molecules formed? What functions do they serve? In this chapter, these questions will be explored.

---

This page titled 8.2.1: Prelude to Biological Macromolecules is shared under a CC BY 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **3.0: Prelude to Biological Macromolecules** by OpenStax is licensed CC BY 4.0.

# 8.2.2: Synthesis of Biological Macromolecules

**Skills to Develop**

- Understand the synthesis of macromolecules
- Explain dehydration (or condensation) and hydrolysis reactions

As you've learned, biological macromolecules are large molecules, necessary for life, that are built from smaller organic molecules. There are four major classes of biological macromolecules (carbohydrates, lipids, proteins, and nucleic acids); each is an important cell component and performs a wide array of functions. Combined, these molecules make up the majority of a cell's dry mass (recall that water makes up the majority of its complete mass). Biological macromolecules are organic, meaning they contain carbon. In addition, they may contain hydrogen, oxygen, nitrogen, and additional minor elements.

## Dehydration Synthesis

Most macromolecules are made from single subunits, or building blocks, called monomers. The monomers combine with each other using covalent bonds to form larger molecules known as polymers. In doing so, monomers release water molecules as byproducts. This type of reaction is known as dehydration synthesis, which means "to put together while losing water."

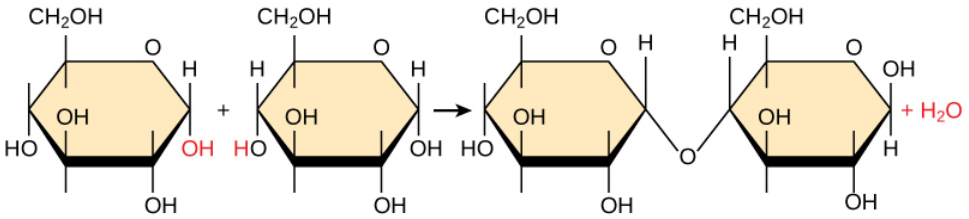



Figure **8.2.2.1**: In the dehydration synthesis reaction depicted above, two molecules of glucose are linked together to form the disaccharide maltose. In the process, a water molecule is formed.

In a dehydration synthesis reaction (Figure **8.2.2.1**), the hydrogen of one monomer combines with the hydroxyl group of another monomer, releasing a molecule of water. At the same time, the monomers share electrons and form covalent bonds. As additional monomers join, this chain of repeating monomers forms a polymer. Different types of monomers can combine in many configurations, giving rise to a diverse group of macromolecules. Even one kind of monomer can combine in a variety of ways to form several different polymers: for example, glucose monomers are the constituents of starch, glycogen, and cellulose.

## Hydrolysis

Polymers are broken down into monomers in a process known as hydrolysis, which means "to split water," a reaction in which a water molecule is used during the breakdown (Figure **8.2.2.2**). During these reactions, the polymer is broken into two components: one part gains a hydrogen atom (H+) and the other gains a hydroxyl molecule (OH–) from a split water molecule.

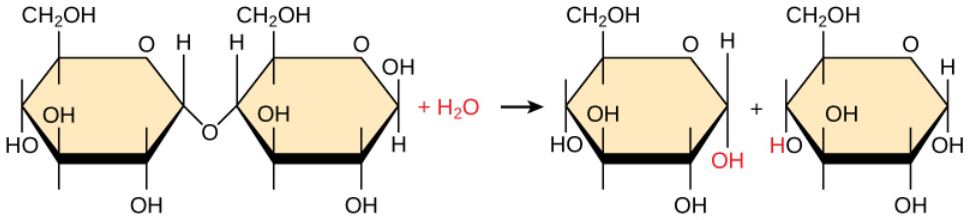



Figure **8.2.2.2**: In the hydrolysis reaction shown here, the disaccharide maltose is broken down to form two glucose monomers with the addition of a water molecule. Note that this reaction is the reverse of the synthesis reaction shown in Figure **8.2.2.1**.

Dehydration and hydrolysis reactions are catalyzed, or "sped up," by specific enzymes; dehydration reactions involve the formation of new bonds, requiring energy, while hydrolysis reactions break bonds and release energy. These reactions are similar for most macromolecules, but each monomer and polymer reaction is specific for its class. For example, in our bodies, food is hydrolyzed, or broken down, into smaller molecules by catalytic enzymes in the digestive system. This allows for easy absorption of nutrients by cells in the intestine. Each macromolecule is broken down by a specific enzyme. For instance, carbohydrates are broken down

by amylase, sucrase, lactase, or maltase. Proteins are broken down by the enzymes pepsin and peptidase, and by hydrochloric acid. Lipids are broken down by lipases. Breakdown of these macromolecules provides energy for cellular activities.

Link to Learning



Visit this site to see visual representations of dehydration synthesis and hydrolysis.

## Summary

Proteins, carbohydrates, nucleic acids, and lipids are the four major classes of biological macromolecules—large molecules necessary for life that are built from smaller organic molecules. Macromolecules are made up of single units known as monomers that are joined by covalent bonds to form larger polymers. The polymer is more than the sum of its parts: it acquires new characteristics, and leads to an osmotic pressure that is much lower than that formed by its ingredients; this is an important advantage in the maintenance of cellular osmotic conditions. A monomer joins with another monomer with the release of a water molecule, leading to the formation of a covalent bond. These types of reactions are known as dehydration or condensation reactions. When polymers are broken down into smaller units (monomers), a molecule of water is used for each bond broken by these reactions; such reactions are known as hydrolysis reactions. Dehydration and hydrolysis reactions are similar for all macromolecules, but each monomer and polymer reaction is specific to its class. Dehydration reactions typically require an investment of energy for new bond formation, while hydrolysis reactions typically release energy by breaking bonds.

## Glossary

**biological macromolecule**
: large molecule necessary for life that is built from smaller organic molecules

**dehydration synthesis**
: (also, condensation) reaction that links monomer molecules together, releasing a molecule of water for each bond formed

**hydrolysis**
: reaction causes breakdown of larger molecules into smaller molecules with the utilization of water

**monomer**
: smallest unit of larger molecules called polymers

**polymer**
: chain of monomer residues that is linked by covalent bonds; polymerization is the process of polymer formation from monomers by condensation

This page titled 8.2.2: Synthesis of Biological Macromolecules is shared under a CC BY 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **3.1: Synthesis of Biological Macromolecules** by OpenStax is licensed CC BY 4.0.

# 8.2.3: Carbohydrates

**Skills to Develop**

- Discuss the role of carbohydrates in cells and in the extracellular materials of animals and plants
- Explain the classifications of carbohydrates
- List common monosaccharides, disaccharides, and polysaccharides

Most people are familiar with carbohydrates, one type of macromolecule, especially when it comes to what we eat. To lose weight, some individuals adhere to “low-carb” diets. Athletes, in contrast, often “carb-load” before important competitions to ensure that they have enough energy to compete at a high level. Carbohydrates are, in fact, an essential part of our diet; grains, fruits, and vegetables are all natural sources of carbohydrates. Carbohydrates provide energy to the body, particularly through glucose, a simple sugar that is a component of starch and an ingredient in many staple foods. Carbohydrates also have other important functions in humans, animals, and plants.

## Molecular Structures

Carbohydrates can be represented by the stoichiometric formula $(CH_2O)_n$, where n is the number of carbons in the molecule. In other words, the ratio of carbon to hydrogen to oxygen is 1:2:1 in carbohydrate molecules. This formula also explains the origin of the term “carbohydrate”: the components are carbon (“carbo”) and the components of water (hence, “hydrate”). Carbohydrates are classified into three subtypes: monosaccharides, disaccharides, and polysaccharides.

### Monosaccharides

Monosaccharides (mono- = “one”; sacchar- = “sweet”) are simple sugars, the most common of which is glucose. In monosaccharides, the number of carbons usually ranges from three to seven. Most monosaccharide names end with the suffix -ose. If the sugar has an aldehyde group (the functional group with the structure R-CHO), it is known as an aldose, and if it has a ketone group (the functional group with the structure RC(=O)R'), it is known as a ketose. Depending on the number of carbons in the sugar, they also may be known as trioses (three carbons), pentoses (five carbons), and or hexoses (six carbons). See Figure **8.2.3.1** for an illustration of the monosaccharides.

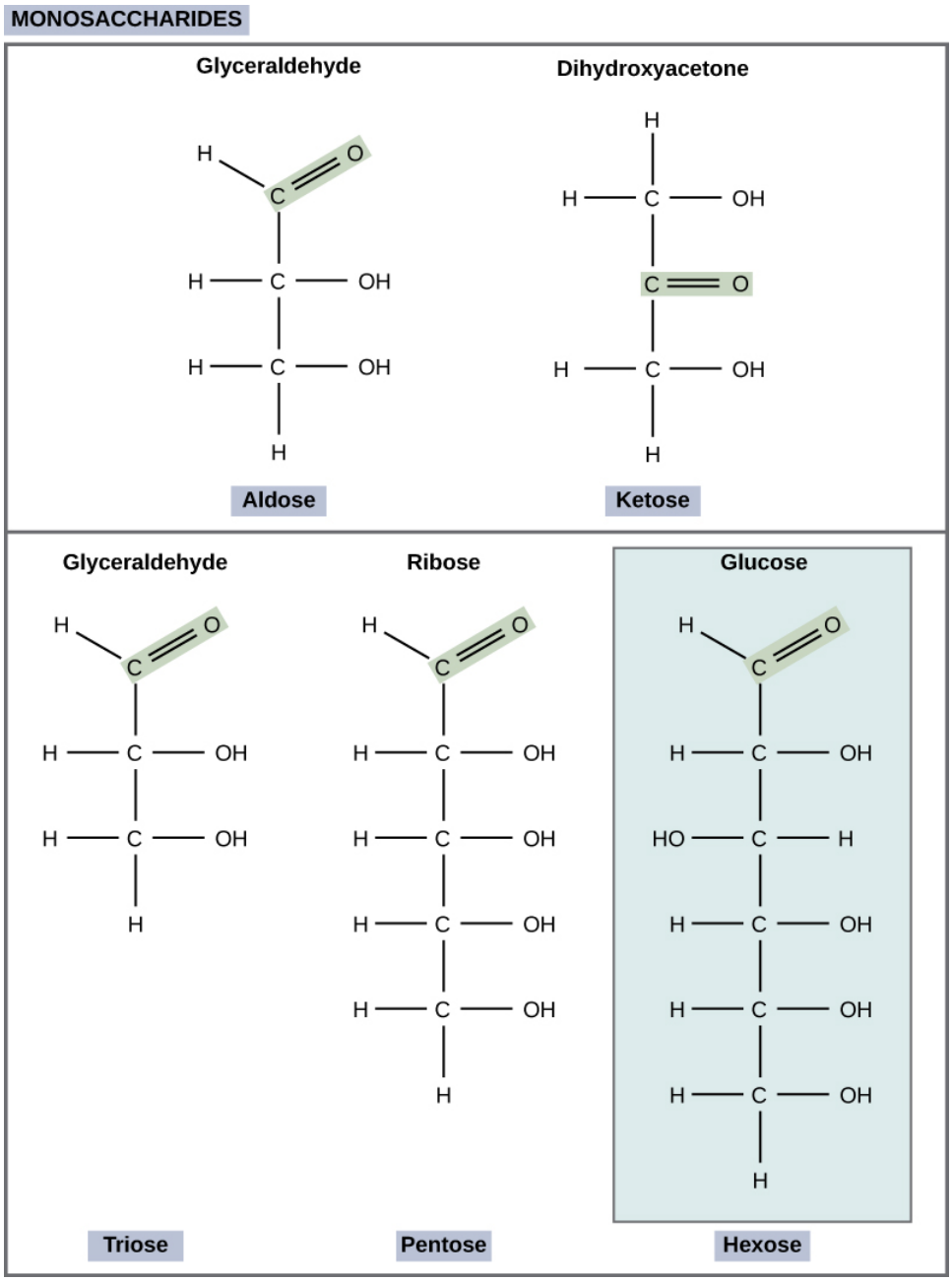



Figure **8.2.3.1**: Monosaccharides are classified based on the position of their carbonyl group and the number of carbons in the backbone. Aldoses have a carbonyl group (indicated in green) at the end of the carbon chain, and ketoses have a carbonyl group in the middle of the carbon chain. Trioses, pentoses, and hexoses have three, five, and six carbon backbones, respectively.

The chemical formula for glucose is $C_6H_{12}O_6$. In humans, glucose is an important source of energy. During cellular respiration, energy is released from glucose, and that energy is used to help make adenosine triphosphate (ATP). Plants synthesize glucose using carbon dioxide and water, and glucose in turn is used for energy requirements for the plant. Excess glucose is often stored as starch that is catabolized (the breakdown of larger molecules by cells) by humans and other animals that feed on plants.

Galactose (part of lactose, or milk sugar) and fructose (found in sucrose, in fruit) are other common monosaccharides. Although glucose, galactose, and fructose all have the same chemical formula ($C_6H_{12}O_6$), they differ structurally and chemically (and are known as isomers) because of the different arrangement of functional groups around the asymmetric carbon; all of these monosaccharides have more than one asymmetric carbon (Figure**8.2.3.2**).

Art Connection

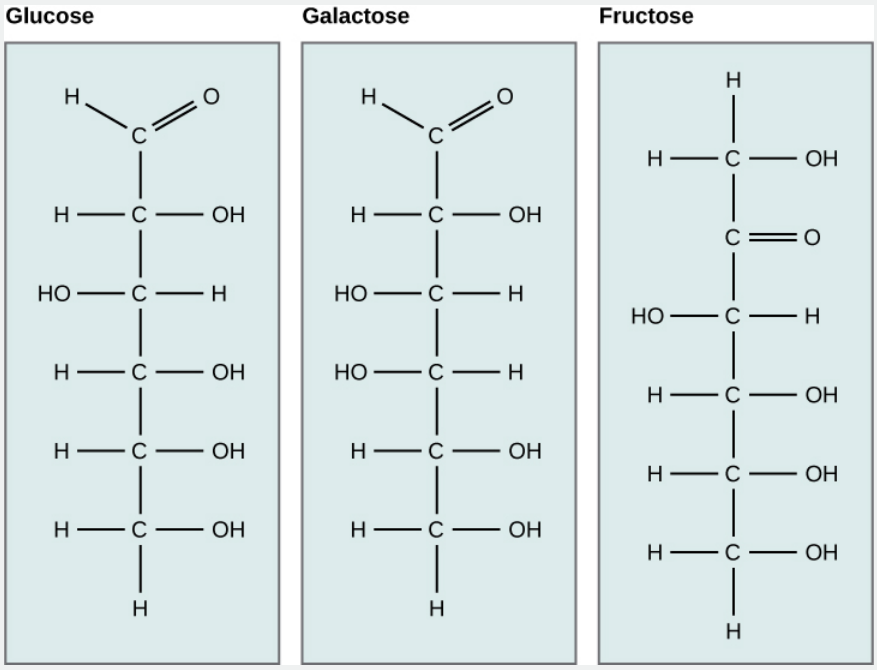



Figure **8.2.3.2**: Glucose, galactose, and fructose are all hexoses. They are structural isomers, meaning they have the same chemical formula ($C_6H_{12}O_6$) but a different arrangement of atoms.

What kind of sugars are these, aldose or ketose?

Glucose, galactose, and fructose are isomeric monosaccharides (hexoses), meaning they have the same chemical formula but have slightly different structures. Glucose and galactose are aldoses, and fructose is a ketose.

Monosaccharides can exist as a linear chain or as ring-shaped molecules; in aqueous solutions they are usually found in ring forms (Figure **8.2.3.3**). Glucose in a ring form can have two different arrangements of the hydroxyl group (OH) around the anomeric carbon (carbon 1 that becomes asymmetric in the process of ring formation). If the hydroxyl group is below carbon number 1 in the sugar, it is said to be in the alpha ($\alpha$) position, and if it is above the plane, it is said to be in the beta ($\beta$) position.

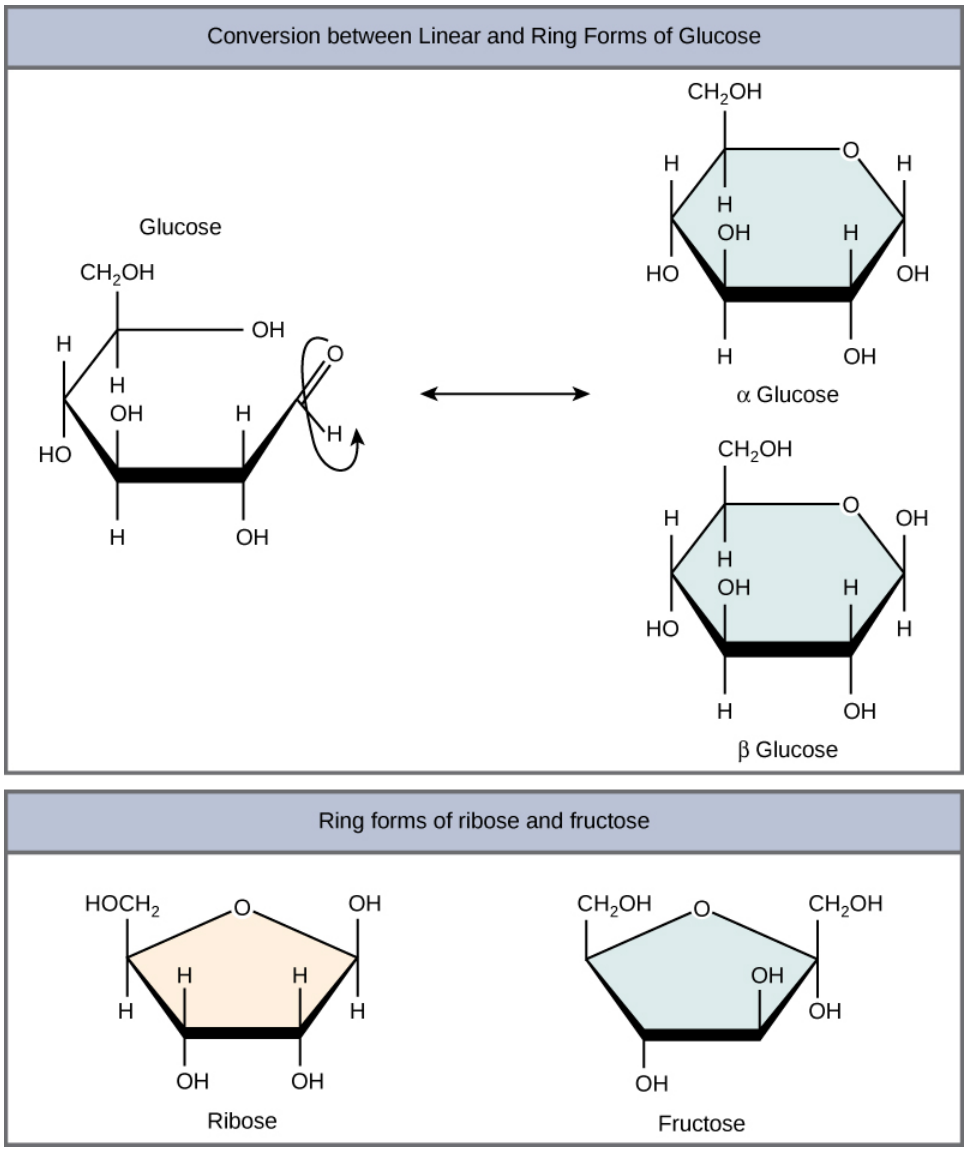



Figure **8.2.3.3**: Five and six carbon monosaccharides exist in equilibrium between linear and ring forms. When the ring forms, the side chain it closes on is locked into an $\alpha$ or $\beta$ position. Fructose and ribose also form rings, although they form five-membered rings as opposed to the six-membered ring of glucose.

## Disaccharides

Disaccharides (di- = "two") form when two monosaccharides undergo a dehydration reaction (also known as a condensation reaction or dehydration synthesis). During this process, the hydroxyl group of one monosaccharide combines with the hydrogen of another monosaccharide, releasing a molecule of water and forming a covalent bond. A covalent bond formed between a carbohydrate molecule and another molecule (in this case, between two monosaccharides) is known as a glycosidic bond (Figure **8.2.3.4**). Glycosidic bonds (also called glycosidic linkages) can be of the alpha or the beta type.

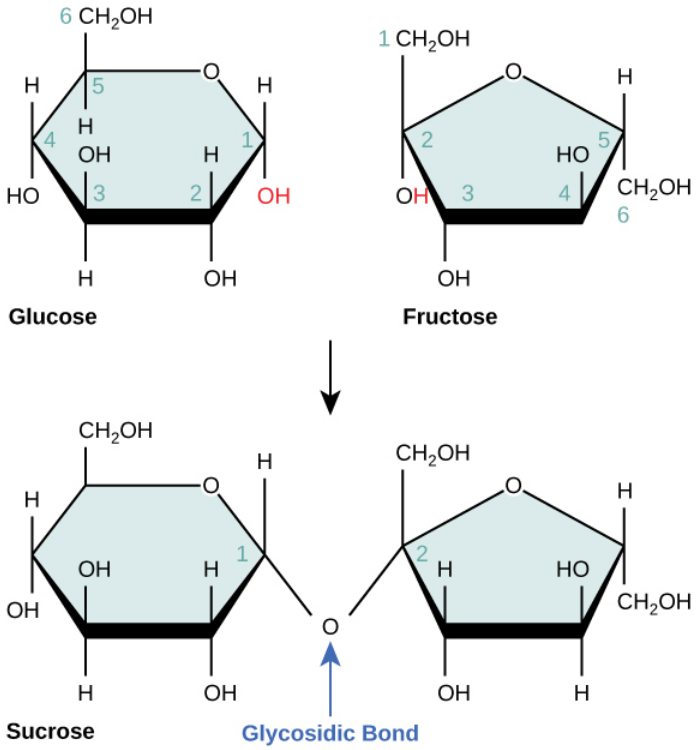



Figure 8.2.3.4: Sucrose is formed when a monomer of glucose and a monomer of fructose are joined in a dehydration reaction to form a glycosidic bond. In the process, a water molecule is lost. By convention, the carbon atoms in a monosaccharide are numbered from the terminal carbon closest to the carbonyl group. In sucrose, a glycosidic linkage is formed between carbon 1 in glucose and carbon 2 in fructose.

Common disaccharides include lactose, maltose, and sucrose (Figure 8.2.3.5). Lactose is a disaccharide consisting of the monomers glucose and galactose. It is found naturally in milk. Maltose, or malt sugar, is a disaccharide formed by a dehydration reaction between two glucose molecules. The most common disaccharide is sucrose, or table sugar, which is composed of the monomers glucose and fructose.

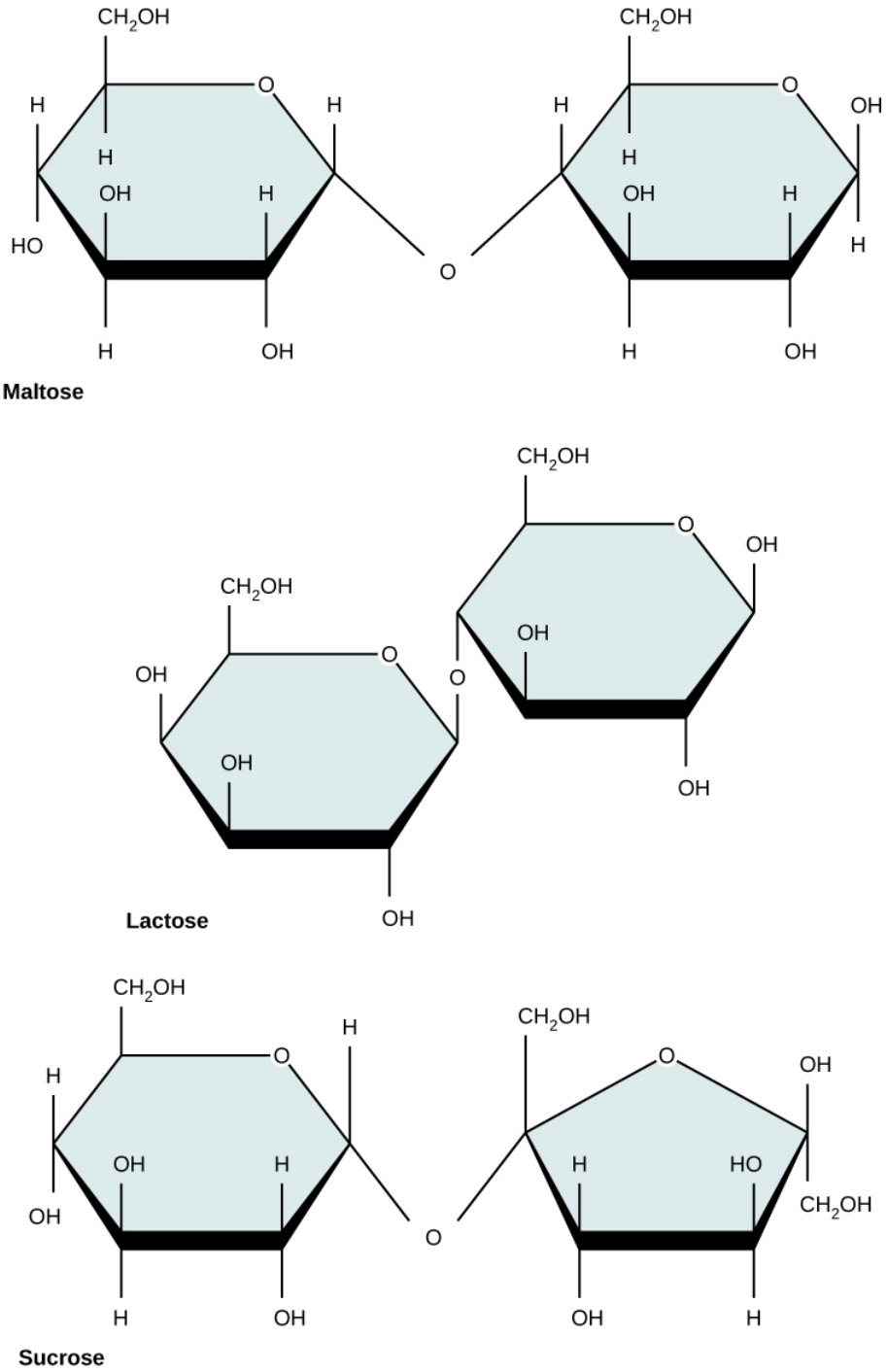



Figure 8.2.3.5: Common disaccharides include maltose (grain sugar), lactose (milk sugar), and sucrose (table sugar).

## Polysaccharides

A long chain of monosaccharides linked by glycosidic bonds is known as a polysaccharide (poly- = “many”). The chain may be branched or unbranched, and it may contain different types of monosaccharides. The molecular weight may be 100,000 daltons or more depending on the number of monomers joined. Starch, glycogen, cellulose, and chitin are primary examples of polysaccharides.

Starch is the stored form of sugars in plants and is made up of a mixture of amylose and amylopectin (both polymers of glucose). Plants are able to synthesize glucose, and the excess glucose, beyond the plant’s immediate energy needs, is stored as starch in different plant parts, including roots and seeds. The starch in the seeds provides food for the embryo as it germinates and can also

act as a source of food for humans and animals. The starch that is consumed by humans is broken down by enzymes, such as salivary amylases, into smaller molecules, such as maltose and glucose. The cells can then absorb the glucose.

Starch is made up of glucose monomers that are joined by $\alpha$ 1-4 or $\alpha$ 1-6 glycosidic bonds. The numbers 1-4 and 1-6 refer to the carbon number of the two residues that have joined to form the bond. As illustrated in Figure **8.2.3.6**, amylose is starch formed by unbranched chains of glucose monomers (only $\alpha$ 1-4 linkages), whereas amylopectin is a branched polysaccharide ($\alpha$ 1-6 linkages at the branch points).

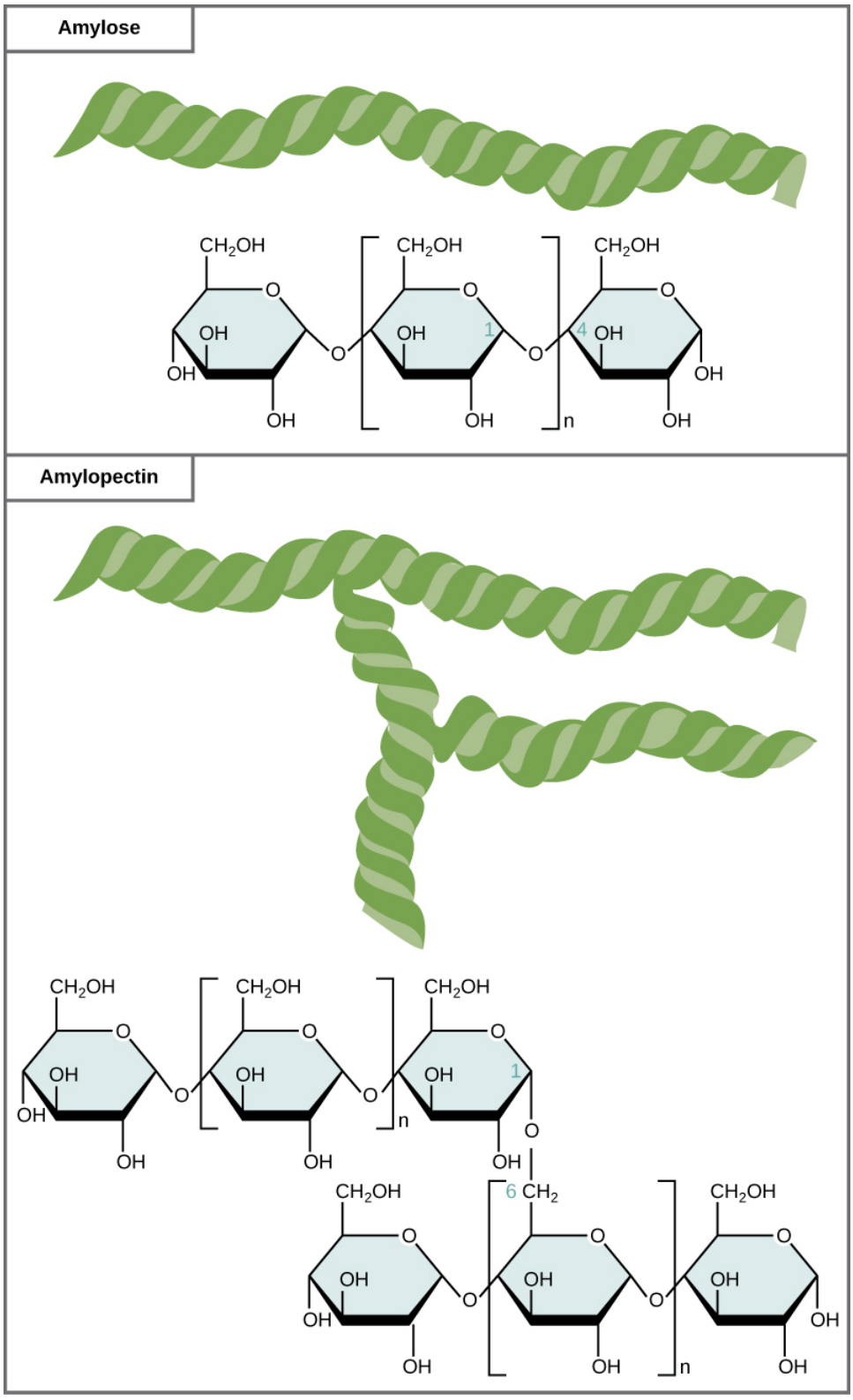



Figure **8.2.3.6**: Amylose and amylopectin are two different forms of starch. Amylose is composed of unbranched chains of glucose monomers connected by $\alpha$ 1,4 glycosidic linkages. Amylopectin is composed of branched chains of glucose monomers connected by $\alpha$ 1,4 and $\alpha$ 1,6 glycosidic linkages. Because of the way the subunits are joined, the glucose chains have a helical structure. Glycogen (not shown) is similar in structure to amylopectin but more highly branched.

Glycogen is the storage form of glucose in humans and other vertebrates and is made up of monomers of glucose. Glycogen is the animal equivalent of starch and is a highly branched molecule usually stored in liver and muscle cells. Whenever blood glucose

levels decrease, glycogen is broken down to release glucose in a process known as glycogenolysis.

Cellulose is the most abundant natural biopolymer. The cell wall of plants is mostly made of cellulose; this provides structural support to the cell. Wood and paper are mostly cellulosic in nature. Cellulose is made up of glucose monomers that are linked by $\beta$ 1-4 glycosidic bonds (Figure **8.2.3.7**).

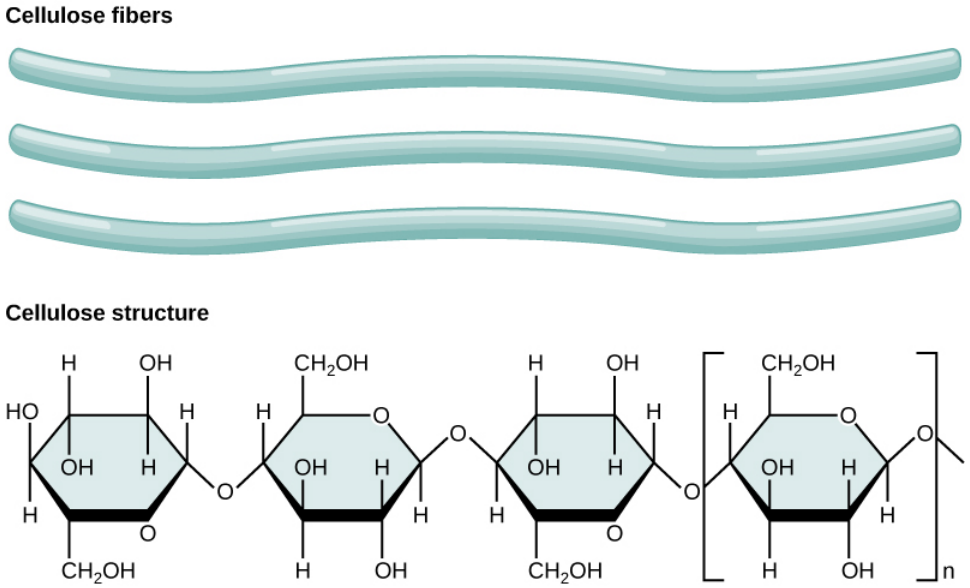



Figure **8.2.3.7**: In cellulose, glucose monomers are linked in unbranched chains by $\beta$ 1-4 glycosidic linkages. Because of the way the glucose subunits are joined, every glucose monomer is flipped relative to the next one resulting in a linear, fibrous structure.

As shown in Figure **8.2.3.7**, every other glucose monomer in cellulose is flipped over, and the monomers are packed tightly as extended long chains. This gives cellulose its rigidity and high tensile strength—which is so important to plant cells. While the $\beta$ 1-4 linkage cannot be broken down by human digestive enzymes, herbivores such as cows, koalas, buffalos, and horses are able, with the help of the specialized flora in their stomach, to digest plant material that is rich in cellulose and use it as a food source. In these animals, certain species of bacteria and protists reside in the rumen (part of the digestive system of herbivores) and secrete the enzyme cellulase. The appendix of grazing animals also contains bacteria that digest cellulose, giving it an important role in the digestive systems of ruminants. Cellulases can break down cellulose into glucose monomers that can be used as an energy source by the animal. Termites are also able to break down cellulose because of the presence of other organisms in their bodies that secrete cellulases.

Carbohydrates serve various functions in different animals. Arthropods (insects, crustaceans, and others) have an outer skeleton, called the exoskeleton, which protects their internal body parts (as seen in the bee in Figure **8.2.3.8**). This exoskeleton is made of the biological macromolecule chitin, which is a polysaccharide-containing nitrogen. It is made of repeating units of N-acetyl-$\beta$-d-glucosamine, a modified sugar. Chitin is also a major component of fungal cell walls; fungi are neither animals nor plants and form a kingdom of their own in the domain Eukarya.



Figure **8.2.3.8**: Insects have a hard outer exoskeleton made of chitin, a type of polysaccharide. (credit: Louise Docker)

**Career Connections: Registered Dietitian**

Obesity is a worldwide health concern, and many diseases such as diabetes and heart disease are becoming more prevalent because of obesity. This is one of the reasons why registered dietitians are increasingly sought after for advice. Registered dietitians help plan nutrition programs for individuals in various settings. They often work with patients in health care facilities, designing nutrition plans to treat and prevent diseases. For example, dietitians may teach a patient with diabetes how to manage blood sugar levels by eating the correct types and amounts of carbohydrates. Dietitians may also work in nursing homes, schools, and private practices.

To become a registered dietitian, one needs to earn at least a bachelor's degree in dietetics, nutrition, food technology, or a related field. In addition, registered dietitians must complete a supervised internship program and pass a national exam. Those who pursue careers in dietetics take courses in nutrition, chemistry, biochemistry, biology, microbiology, and human physiology. Dietitians must become experts in the chemistry and physiology (biological functions) of food (proteins, carbohydrates, and fats).

## Benefits of Carbohydrates

Are carbohydrates good for you? People who wish to lose weight are often told that carbohydrates are bad for them and should be avoided. Some diets completely forbid carbohydrate consumption, claiming that a low-carbohydrate diet helps people to lose weight faster. However, carbohydrates have been an important part of the human diet for thousands of years; artifacts from ancient civilizations show the presence of wheat, rice, and corn in our ancestors' storage areas.

Carbohydrates should be supplemented with proteins, vitamins, and fats to be parts of a well-balanced diet. Calorie-wise, a gram of carbohydrate provides 4.3 Kcal. For comparison, fats provide 9 Kcal/g, a less desirable ratio. Carbohydrates contain soluble and insoluble elements; the insoluble part is known as fiber, which is mostly cellulose. Fiber has many uses; it promotes regular bowel movement by adding bulk, and it regulates the rate of consumption of blood glucose. Fiber also helps to remove excess cholesterol from the body: fiber binds to the cholesterol in the small intestine, then attaches to the cholesterol and prevents the cholesterol particles from entering the bloodstream, and then cholesterol exits the body via the feces. Fiber-rich diets also have a protective role in reducing the occurrence of colon cancer. In addition, a meal containing whole grains and vegetables gives a feeling of fullness. As an immediate source of energy, glucose is broken down during the process of cellular respiration, which produces ATP, the energy currency of the cell. Without the consumption of carbohydrates, the availability of "instant energy" would be reduced. Eliminating carbohydrates from the diet is not the best way to lose weight. A low-calorie diet that is rich in whole grains, fruits, vegetables, and lean meat, together with plenty of exercise and plenty of water, is the more sensible way to lose weight.

Link to Learning

For an additional perspective on carbohydrates, explore “Biomolecules: the Carbohydrates” through this interactive animation.

## Summary

Carbohydrates are a group of macromolecules that are a vital energy source for the cell and provide structural support to plant cells, fungi, and all of the arthropods that include lobsters, crabs, shrimp, insects, and spiders. Carbohydrates are classified as monosaccharides, disaccharides, and polysaccharides depending on the number of monomers in the molecule. Monosaccharides are linked by glycosidic bonds that are formed as a result of dehydration reactions, forming disaccharides and polysaccharides with the elimination of a water molecule for each bond formed. Glucose, galactose, and fructose are common monosaccharides, whereas common disaccharides include lactose, maltose, and sucrose. Starch and glycogen, examples of polysaccharides, are the storage forms of glucose in plants and animals, respectively. The long polysaccharide chains may be branched or unbranched. Cellulose is an example of an unbranched polysaccharide, whereas amylopectin, a constituent of starch, is a highly branched molecule. Storage of glucose, in the form of polymers like starch of glycogen, makes it slightly less accessible for metabolism; however, this prevents it from leaking out of the cell or creating a high osmotic pressure that could cause excessive water uptake by the cell.

## Art Connections

Figure **8.2.3.2**: What kind of sugars are these, aldose or ketose?

**Answer**

Glucose and galactose are aldoses. Fructose is a ketose.

## Glossary

**carbohydrate**
biological macromolecule in which the ratio of carbon to hydrogen and to oxygen is 1:2:1; carbohydrates serve as energy sources and structural support in cells and form the a cellular exoskeleton of arthropods

**cellulose**
polysaccharide that makes up the cell wall of plants; provides structural support to the cell

**chitin**
type of carbohydrate that forms the outer skeleton of all arthropods that include crustaceans and insects; it also forms the cell walls of fungi

**disaccharide**
two sugar monomers that are linked together by a glycosidic bond

**glycogen**
storage carbohydrate in animals

**glycosidic bond**
bond formed by a dehydration reaction between two monosaccharides with the elimination of a water molecule

**monosaccharide**

single unit or monomer of carbohydrates

**polysaccharide**

long chain of monosaccharides; may be branched or unbranched

**starch**

storage carbohydrate in plants

---

This page titled 8.2.3: Carbohydrates is shared under a CC BY 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **3.2: Carbohydrates** by OpenStax is licensed CC BY 4.0.

# 8.2.4: Lipids

**Skills to Develop**

- Describe the four major types of lipids
- Explain the role of fats in storing energy
- Differentiate between saturated and unsaturated fatty acids
- Describe phospholipids and their role in cells
- Define the basic structure of a steroid and some functions of steroids
- Explain the how cholesterol helps to maintain the fluid nature of the plasma membrane

Lipids include a diverse group of compounds that are largely nonpolar in nature. This is because they are hydrocarbons that include mostly nonpolar carbon–carbon or carbon–hydrogen bonds. Non-polar molecules are hydrophobic ("water fearing"), or insoluble in water. Lipids perform many different functions in a cell. Cells store energy for long-term use in the form of fats. Lipids also provide insulation from the environment for plants and animals (Figure **8.2.4.1**). For example, they help keep aquatic birds and mammals dry when forming a protective layer over fur or feathers because of their water-repellant hydrophobic nature. Lipids are also the building blocks of many hormones and are an important constituent of all cellular membranes. Lipids include fats, oils, waxes, phospholipids, and steroids.



Figure **8.2.4.1**: Hydrophobic lipids in the fur of aquatic mammals, such as this river otter, protect them from the elements. (credit: Ken Bosma)

## Fats and Oils

A fat molecule consists of two main components—glycerol and fatty acids. Glycerol is an organic compound (alcohol) with three carbons, five hydrogens, and three hydroxyl (OH) groups. Fatty acids have a long chain of hydrocarbons to which a carboxyl group is attached, hence the name "fatty acid." The number of carbons in the fatty acid may range from 4 to 36; most common are those containing 12–18 carbons. In a fat molecule, the fatty acids are attached to each of the three carbons of the glycerol molecule with an ester bond through an oxygen atom (Figure **8.2.4.2**).

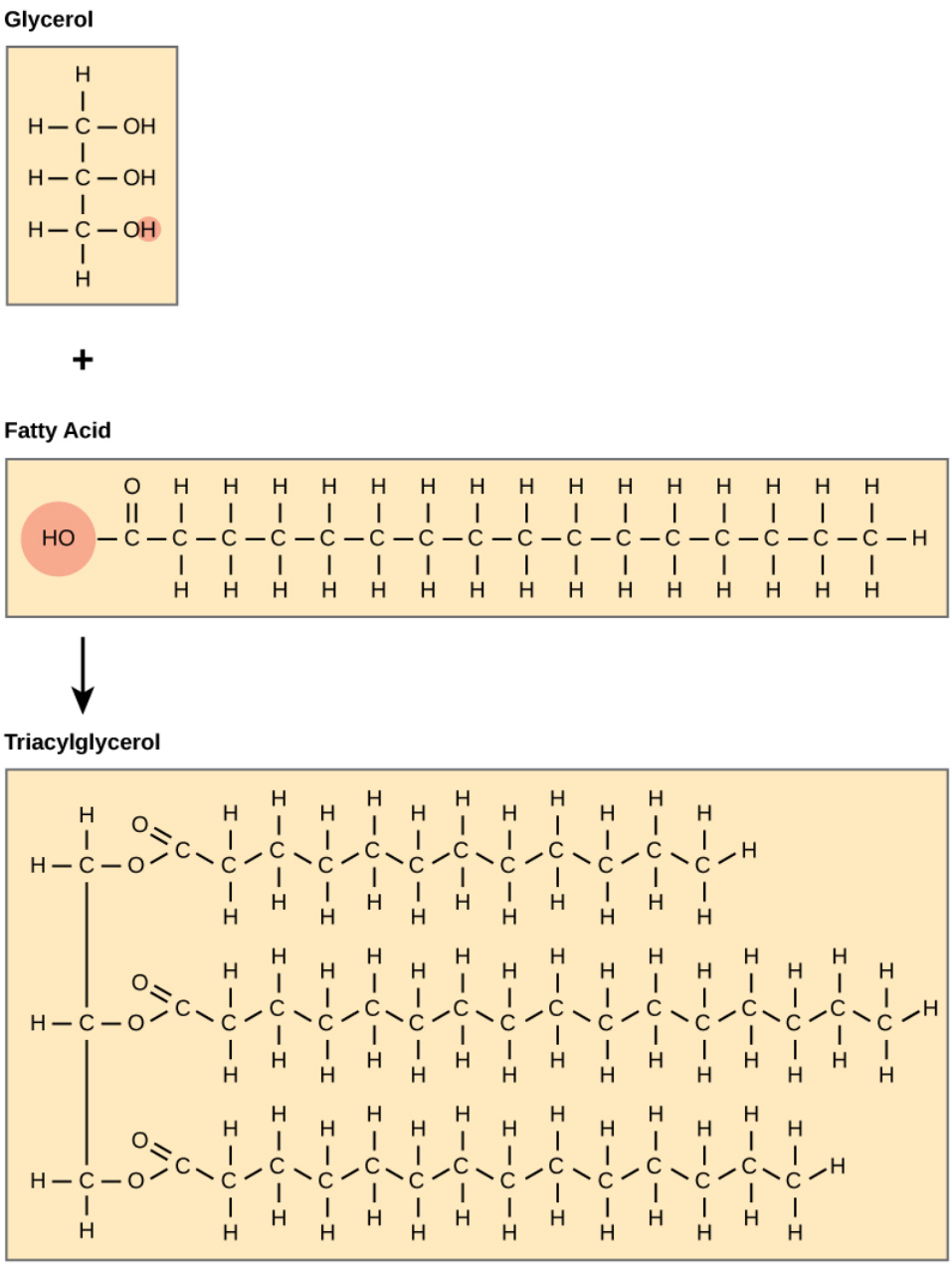



Figure **8.2.4.2**: Triacylglycerol is formed by the joining of three fatty acids to a glycerol backbone in a dehydration reaction. Three molecules of water are released in the process.

During this ester bond formation, three water molecules are released. The three fatty acids in the triacylglycerol may be similar or dissimilar. Fats are also called triacylglycerols or triglycerides because of their chemical structure. Some fatty acids have common names that specify their origin. For example, palmitic acid, a saturated fatty acid, is derived from the palm tree. Arachidic acid is derived from *Arachis hypogea*, the scientific name for groundnuts or peanuts.

Fatty acids may be saturated or unsaturated. In a fatty acid chain, if there are only single bonds between neighboring carbons in the hydrocarbon chain, the fatty acid is said to be saturated. Saturated fatty acids are saturated with hydrogen; in other words, the number of hydrogen atoms attached to the carbon skeleton is maximized. Stearic acid is an example of a saturated fatty acid (Figure **8.2.4.3**)

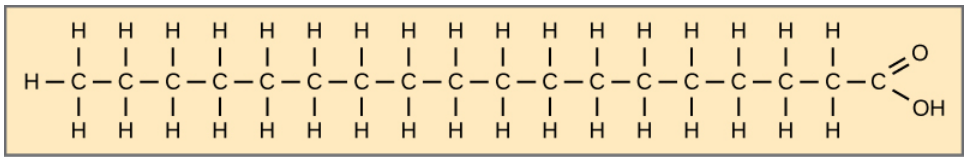


Figure **8.2.4.3**: Stearic acid is a common saturated fatty acid.

When the hydrocarbon chain contains a double bond, the fatty acid is said to be unsaturated. Oleic acid is an example of an unsaturated fatty acid (Figure **8.2.4.4**).

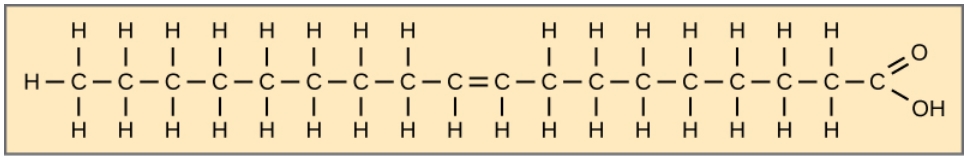


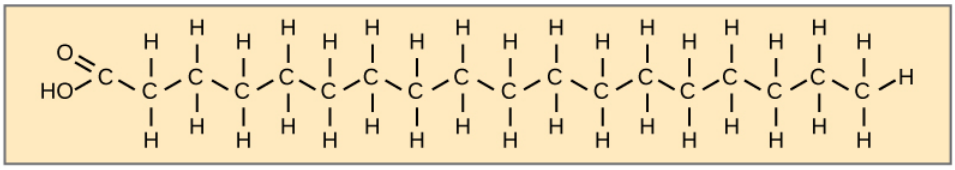
Figure **8.2.4.4**: Oleic acid is a common unsaturated fatty acid.

Most unsaturated fats are liquid at room temperature and are called oils. If there is one double bond in the molecule, then it is known as a monounsaturated fat (e.g., olive oil), and if there is more than one double bond, then it is known as a polyunsaturated fat (e.g., canola oil).

When a fatty acid has no double bonds, it is known as a saturated fatty acid because no more hydrogen may be added to the carbon atoms of the chain. A fat may contain similar or different fatty acids attached to glycerol. Long straight fatty acids with single bonds tend to get packed tightly and are solid at room temperature. Animal fats with stearic acid and palmitic acid (common in meat) and the fat with butyric acid (common in butter) are examples of saturated fats. Mammals store fats in specialized cells called adipocytes, where globules of fat occupy most of the cell's volume. In plants, fat or oil is stored in many seeds and is used as a source of energy during seedling development. Unsaturated fats or oils are usually of plant origin and contain *cis* unsaturated fatty acids. *Cis* and *trans* indicate the configuration of the molecule around the double bond. If hydrogens are present in the same plane, it is referred to as a cis fat; if the hydrogen atoms are on two different planes, it is referred to as a trans fat. The *cis* double bond causes a bend or a "kink" that prevents the fatty acids from packing tightly, keeping them liquid at room temperature (Figure **8.2.4.5**). Olive oil, corn oil, canola oil, and cod liver oil are examples of unsaturated fats. Unsaturated fats help to lower blood cholesterol levels whereas saturated fats contribute to plaque formation in the arteries.

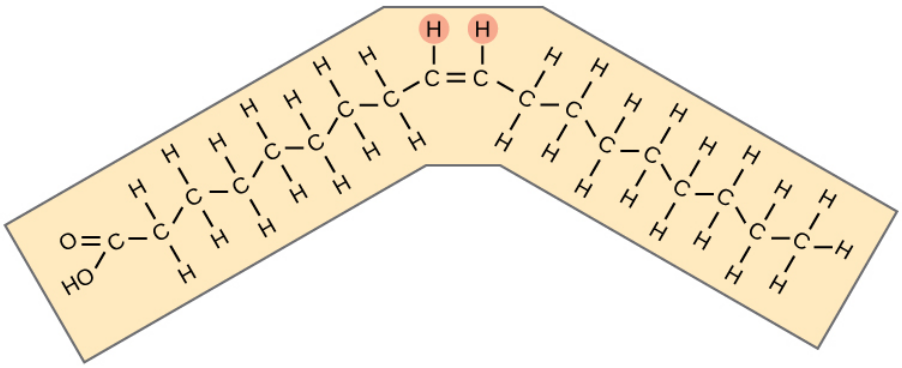
**Saturated fatty acid**

Stearic acid



**Unsaturated fatty acids**

*Cis* oleic acid



*Trans* oleic acid

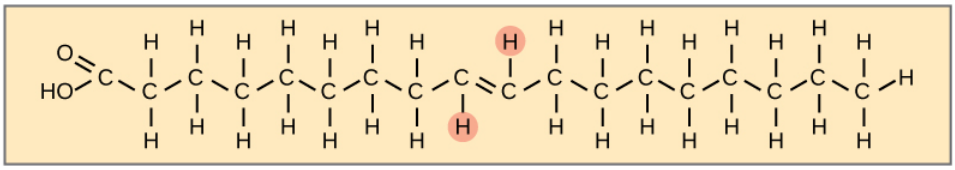


Figure 8.2.4.5: Saturated fatty acids have hydrocarbon chains connected by single bonds only. Unsaturated fatty acids have one or more double bonds. Each double bond may be in a *cis* or *trans* configuration. In the *cis* configuration, both hydrogens are on the same side of the hydrocarbon chain. In the *trans* configuration, the hydrogens are on opposite sides. A *cis* double bond causes a kink in the chain.

## Trans Fats

In the food industry, oils are artificially hydrogenated to make them semi-solid and of a consistency desirable for many processed food products. Simply speaking, hydrogen gas is bubbled through oils to solidify them. During this hydrogenation process, double bonds of the *cis*- conformation in the hydrocarbon chain may be converted to double bonds in the trans- conformation.

Margarine, some types of peanut butter, and shortening are examples of artificially hydrogenated trans fats. Recent studies have shown that an increase in trans fats in the human diet may lead to an increase in levels of low-density lipoproteins (LDL), or “bad” cholesterol, which in turn may lead to plaque deposition in the arteries, resulting in heart disease. Many fast food restaurants have recently banned the use of trans fats, and food labels are required to display the trans fat content.

## Omega Fatty Acids

Essential fatty acids are fatty acids required but not synthesized by the human body. Consequently, they have to be supplemented through ingestion via the diet. Omega-3 fatty acids (like that shown in Figure 8.2.4.6) fall into this category and are one of only two known for humans (the other being omega-6 fatty acid). These are polyunsaturated fatty acids and are called omega-3 because the third carbon from the end of the hydrocarbon chain is connected to its neighboring carbon by a double bond.

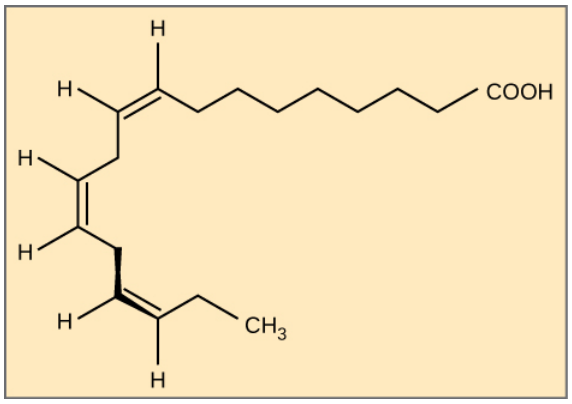



Figure 8.2.4.6: Alpha-linolenic acid is an example of an omega-3 fatty acid. It has three *cis* double bonds and, as a result, a curved shape. For clarity, the carbons are not shown. Each singly bonded carbon has two hydrogens associated with it, also not shown.

The farthest carbon away from the carboxyl group is numbered as the omega ($\omega$) carbon, and if the double bond is between the third and fourth carbon from that end, it is known as an omega-3 fatty acid. Nutritionally important because the body does not make them, omega-3 fatty acids include alpha-linoleic acid (ALA), eicosapentaenoic acid (EPA), and docosahexaenoic acid (DHA), all of which are polyunsaturated. Salmon, trout, and tuna are good sources of omega-3 fatty acids. Research indicates that omega-3 fatty acids reduce the risk of sudden death from heart attacks, reduce triglycerides in the blood, lower blood pressure, and prevent thrombosis by inhibiting blood clotting. They also reduce inflammation, and may help reduce the risk of some cancers in animals.

Like carbohydrates, fats have received a lot of bad publicity. It is true that eating an excess of fried foods and other “fatty” foods leads to weight gain. However, fats do have important functions. Many vitamins are fat soluble, and fats serve as a long-term storage form of fatty acids: a source of energy. They also provide insulation for the body. Therefore, “healthy” fats in moderate amounts should be consumed on a regular basis.

### Waxes

Wax covers the feathers of some aquatic birds and the leaf surfaces of some plants. Because of the hydrophobic nature of waxes, they prevent water from sticking on the surface (Figure 8.2.4.7). Waxes are made up of long fatty acid chains esterified to long-chain alcohols.



Figure 8.2.4.7: Waxy coverings on some leaves are made of lipids. (credit: Roger Griffith)

### Phospholipids

Phospholipids are major constituents of the plasma membrane, the outermost layer of animal cells. Like fats, they are composed of fatty acid chains attached to a glycerol or sphingosine backbone. Instead of three fatty acids attached as in triglycerides, however, there are two fatty acids forming diacylglycerol, and the third carbon of the glycerol backbone is occupied by a modified phosphate group (Figure 8.2.4.8). A phosphate group alone attached to a diaglycerol does not qualify as a phospholipid; it is phosphatidate

(diacylglycerol 3-phosphate), the precursor of phospholipids. The phosphate group is modified by an alcohol. Phosphatidylcholine and phosphatidylserine are two important phospholipids that are found in plasma membranes.

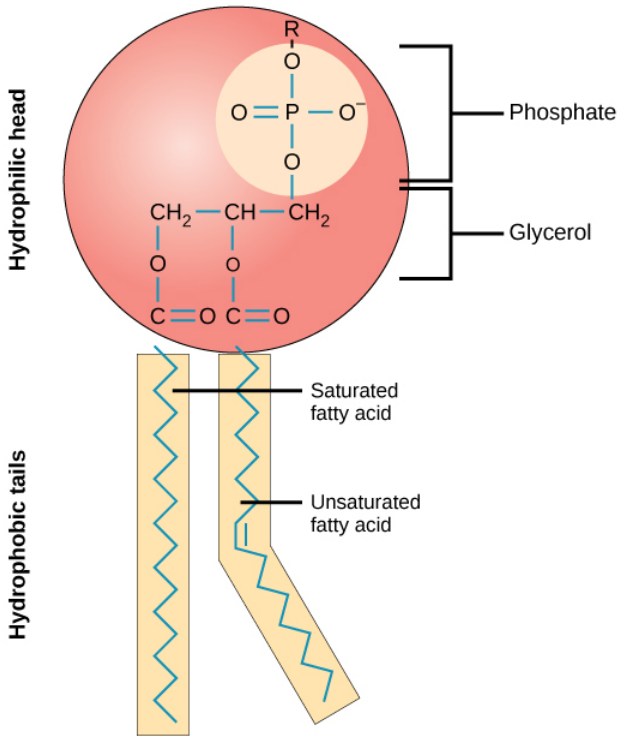



Figure 8.2.4.8: A phospholipid is a molecule with two fatty acids and a modified phosphate group attached to a glycerol backbone. The phosphate may be modified by the addition of charged or polar chemical groups. Two chemical groups that may modify the phosphate, choline and serine, are shown here. Both choline and serine attach to the phosphate group at the position labeled R via the hydroxyl group indicated in green.

A phospholipid is an amphipathic molecule, meaning it has a hydrophobic and a hydrophilic part. The fatty acid chains are hydrophobic and cannot interact with water, whereas the phosphate-containing group is hydrophilic and interacts with water (Figure 8.2.4.9).

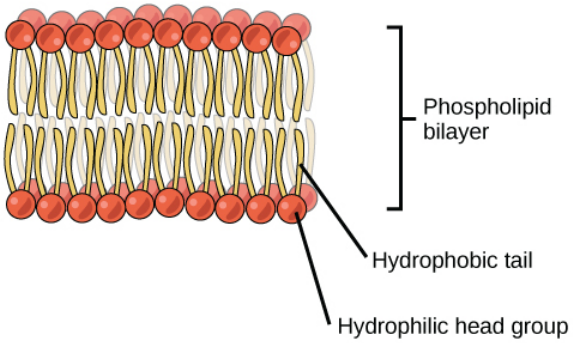


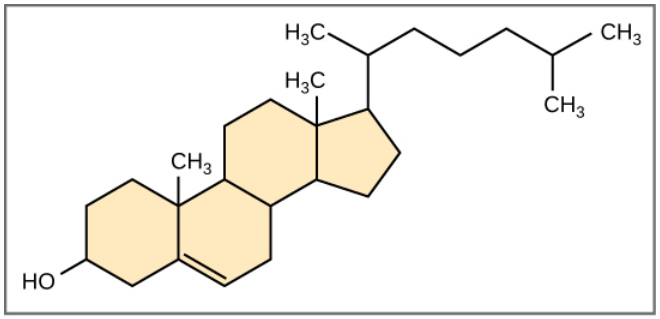

Figure 8.2.4.9: The phospholipid bilayer is the major component of all cellular membranes. The hydrophilic head groups of the phospholipids face the aqueous solution. The hydrophobic tails are sequestered in the middle of the bilayer.

The head is the hydrophilic part, and the tail contains the hydrophobic fatty acids. In a membrane, a bilayer of phospholipids forms the matrix of the structure, the fatty acid tails of phospholipids face inside, away from water, whereas the phosphate group faces the outside, aqueous side (Figure 8.2.4.9).

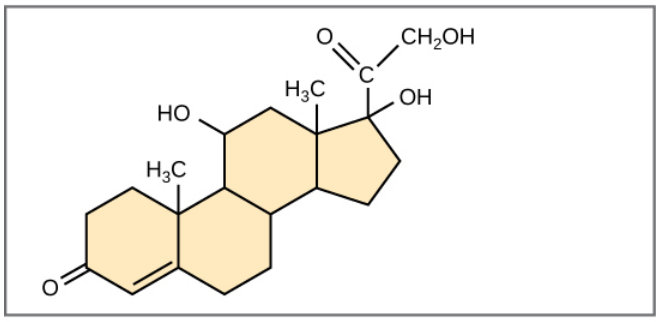
Phospholipids are responsible for the dynamic nature of the plasma membrane. If a drop of phospholipids is placed in water, it spontaneously forms a structure known as a micelle, where the hydrophilic phosphate heads face the outside and the fatty acids face the interior of this structure.

## Steroids

Unlike the phospholipids and fats discussed earlier, steroids have a fused ring structure. Although they do not resemble the other lipids, they are grouped with them because they are also hydrophobicand insoluble in water. All steroids have four linked carbon rings and several of them, like cholesterol, have a short tail (Figure **8.2.4.10**). Many steroids also have the –OH functional group, which puts them in the alcohol classification (sterols).




**Cholesterol**




**Cortisol**

Figure **8.2.4.10**: Steroids such as cholesterol and cortisol are composed of four fused hydrocarbon rings.

Cholesterol is the most common steroid. Cholesterol is mainly synthesized in the liver and is the precursor to many steroid hormones such as testosterone and estradiol, which are secreted by the gonads and endocrine glands. It is also the precursor to Vitamin D. Cholesterol is also the precursor of bile salts, which help in the emulsification of fats and their subsequent absorption by cells. Although cholesterol is often spoken of in negative terms by lay people, it is necessary for proper functioning of the body. It is a component of the plasma membrane of animal cells and is found within the phospholipid bilayer. Being the outermost structure in animal cells, the plasma membrane is responsible for the transport of materials and cellular recognition and it is involved in cell-to-cell communication.

**Link to Learning**

For an additional perspective on lipids, explore the interactive animation "Biomolecules: The Lipids".

## Summary

Lipids are a class of macromolecules that are nonpolar and hydrophobic in nature. Major types include fats and oils, waxes, phospholipids, and steroids. Fats are a stored form of energy and are also known as triacylglycerols or triglycerides. Fats are made up of fatty acids and either glycerol or sphingosine. Fatty acids may be unsaturated or saturated, depending on the presence or absence of double bonds in the hydrocarbon chain. If only single bonds are present, they are known as saturated fatty acids. Unsaturated fatty acids may have one or more double bonds in the hydrocarbon chain. Phospholipids make up the matrix of membranes. They have a glycerol or sphingosine backbone to which two fatty acid chains and a phosphate-containing group are attached. Steroids are another class of lipids. Their basic structure has four fused carbon rings. Cholesterol is a type of steroid and is an important constituent of the plasma membrane, where it helps to maintain the fluid nature of the membrane. It is also the precursor of steroid hormones such as testosterone.

## Glossary

**lipid**
: macromolecule that is nonpolar and insoluble in water

**omega fat**
: type of polyunsaturated fat that is required by the body; the numbering of the carbon omega starts from the methyl end or the end that is farthest from the carboxylic end

**phospholipid**
: major constituent of the membranes; composed of two fatty acids and a phosphate-containing group attached to a glycerol backbone

**saturated fatty acid**
: long-chain of hydrocarbon with single covalent bonds in the carbon chain; the number of hydrogen atoms attached to the carbon skeleton is maximized

**steroid**
: type of lipid composed of four fused hydrocarbon rings forming a planar structure

**trans fat**
: fat formed artificially by hydrogenating oils, leading to a different arrangement of double bond(s) than those found in naturally occurring lipids

**triacylglycerol (also, triglyceride)**
: fat molecule; consists of three fatty acids linked to a glycerol molecule

**unsaturated fatty acid**
: long-chain hydrocarbon that has one or more double bonds in the hydrocarbon chain

**wax**
: lipid made of a long-chain fatty acid that is esterified to a long-chain alcohol; serves as a protective coating on some feathers, aquatic mammal fur, and leaves

---

This page titled 8.2.4: Lipids is shared under a CC BY 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **3.3: Lipids** by OpenStax is licensed CC BY 4.0.

# 8.2.5: Proteins

**Skills to Develop**

- Describe the functions proteins perform in the cell and in tissues
- Discuss the relationship between amino acids and proteins
- Explain the four levels of protein organization
- Describe the ways in which protein shape and function are linked

Proteins are one of the most abundant organic molecules in living systems and have the most diverse range of functions of all macromolecules. Proteins may be structural, regulatory, contractile, or protective; they may serve in transport, storage, or membranes; or they may be toxins or enzymes. Each cell in a living system may contain thousands of proteins, each with a unique function. Their structures, like their functions, vary greatly. They are all, however, polymers of amino acids, arranged in a linear sequence.

## Types and Functions of Proteins

Enzymes, which are produced by living cells, are catalysts in biochemical reactions (like digestion) and are usually complex or conjugated proteins. Each enzyme is specific for the substrate (a reactant that binds to an enzyme) it acts on. The enzyme may help in breakdown, rearrangement, or synthesis reactions. Enzymes that break down their substrates are called catabolic enzymes, enzymes that build more complex molecules from their substrates are called anabolic enzymes, and enzymes that affect the rate of reaction are called catalytic enzymes. It should be noted that all enzymes increase the rate of reaction and, therefore, are considered to be organic catalysts. An example of an enzyme is salivary amylase, which hydrolyzes its substrate amylose, a component of starch.

Hormones are chemical-signaling molecules, usually small proteins or steroids, secreted by endocrine cells that act to control or regulate specific physiological processes, including growth, development, metabolism, and reproduction. For example, insulin is a protein hormone that helps to regulate the blood glucose level. The primary types and functions of proteins are listed in Table **8.2.5.1**.

Table **8.2.5.1**: Protein Types and Functions

| Type | Examples | Functions |
|---|---|---|
| Digestive Enzymes | Amylase, lipase, pepsin, trypsin | Help in digestion of food by catabolizing nutrients into monomeric units |
| Transport | Hemoglobin, albumin | Carry substances in the blood or lymph throughout the body |
| Structural | Actin, tubulin, keratin | Construct different structures, like the cytoskeleton |
| Hormones | Insulin, thyroxine | Coordinate the activity of different body systems |
| Defense | Immunoglobulins | Protect the body from foreign pathogens |
| Contractile | Actin, myosin | Effect muscle contraction |
| Storage | Legume storage proteins, egg white (albumin) | Provide nourishment in early development of the embryo and the seedling |

Proteins have different shapes and molecular weights; some proteins are globular in shape whereas others are fibrous in nature. For example, hemoglobin is a globular protein, but collagen, found in our skin, is a fibrous protein. Protein shape is critical to its function, and this shape is maintained by many different types of chemical bonds. Changes in temperature, pH, and exposure to

chemicals may lead to permanent changes in the shape of the protein, leading to loss of function, known as denaturation. All proteins are made up of different arrangements of the same 20 types of amino acids.

## Amino Acids

Amino acids are the monomers that make up proteins. Each amino acid has the same fundamental structure, which consists of a central carbon atom, also known as the alpha ($\alpha$) carbon, bonded to an amino group ($NH_2$), a carboxyl group (COOH), and to a hydrogen atom. Every amino acid also has another atom or group of atoms bonded to the central atom known as the R group (Figure 8.2.5.1).

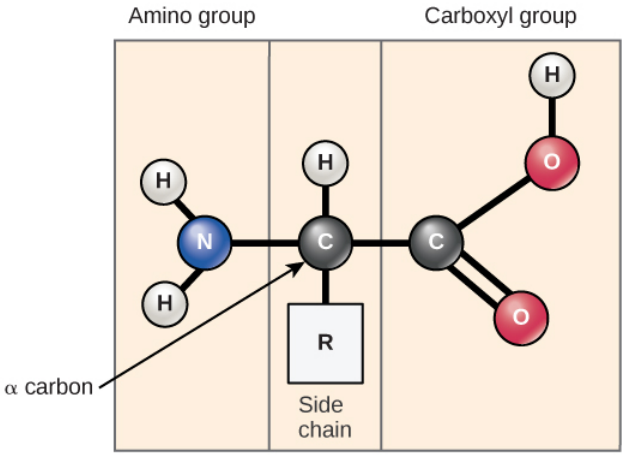



Figure 8.2.5.1: Amino acids have a central asymmetric carbon to which an amino group, a carboxyl group, a hydrogen atom, and a side chain (R group) are attached.

The name "amino acid" is derived from the fact that they contain both amino group and carboxyl-acid-group in their basic structure. As mentioned, there are 20 amino acids present in proteins. Ten of these are considered essential amino acids in humans because the human body cannot produce them and they are obtained from the diet. For each amino acid, the R group (or side chain) is different (Figure 8.2.5.2).

Art Connection

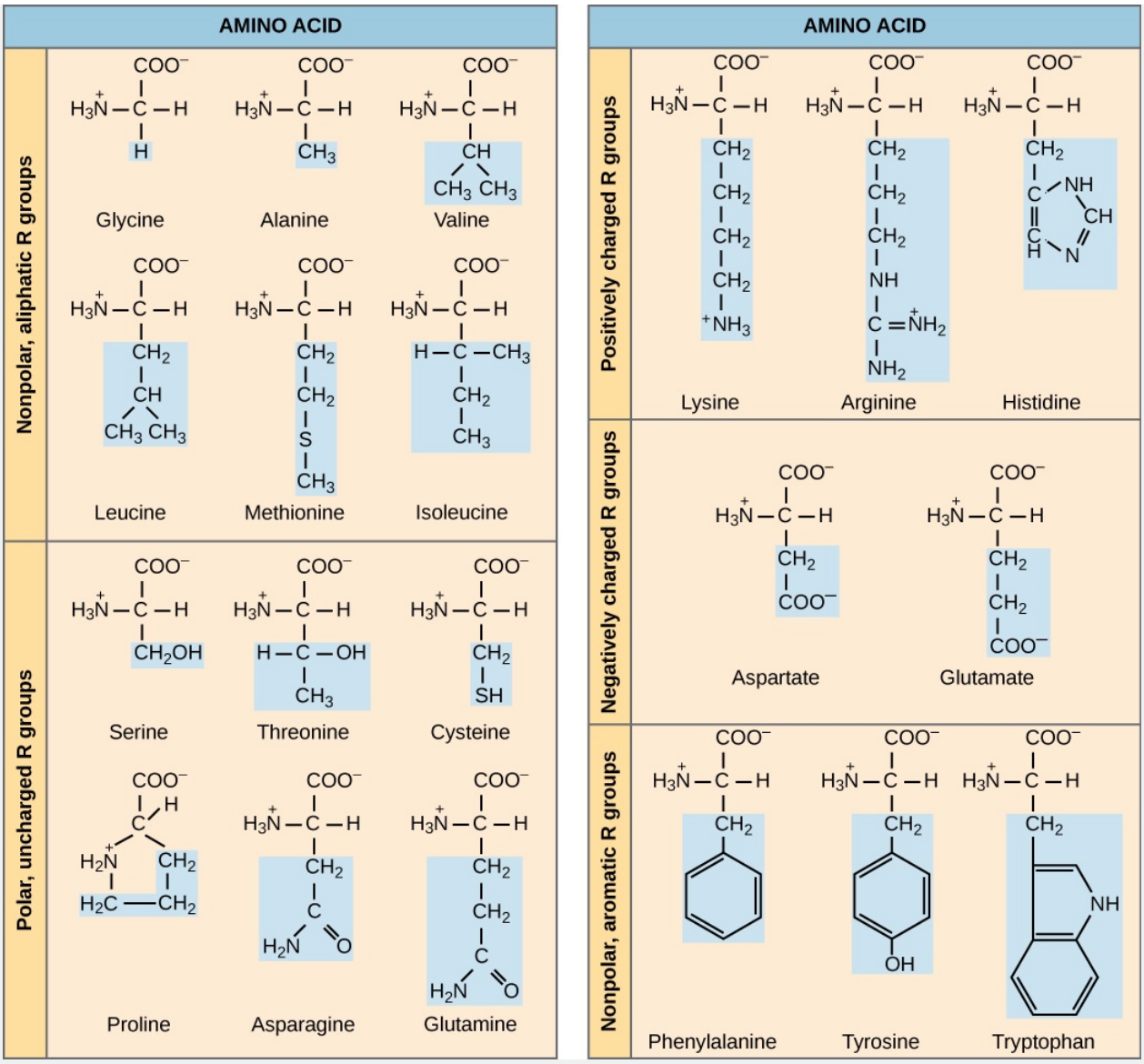



Figure **8.2.5.2**: There are 20 common amino acids commonly found in proteins, each with a different R group (variant group) that determines its chemical nature.

Which categories of amino acid would you expect to find on the surface of a soluble protein, and which would you expect to find in the interior? What distribution of amino acids would you expect to find in a protein embedded in a lipid bilayer?

The chemical nature of the side chain determines the nature of the amino acid (that is, whether it is acidic, basic, polar, or nonpolar). For example, the amino acid glycine has a hydrogen atom as the R group. Amino acids such as valine, methionine, and alanine are nonpolar or hydrophobic in nature, while amino acids such as serine, threonine, and cysteine are polar and have hydrophilic side chains. The side chains of lysine and arginine are positively charged, and therefore these amino acids are also known as basic amino acids. Proline has an R group that is linked to the amino group, forming a ring-like structure. Proline is an exception to the standard structure of an animo acid since its amino group is not separate from the side chain (Figure **8.2.5.2**).

Amino acids are represented by a single upper case letter or a three-letter abbreviation. For example, valine is known by the letter V or the three-letter symbol val. Just as some fatty acids are essential to a diet, some amino acids are necessary as well. They are known as essential amino acids, and in humans they include isoleucine, leucine, and cysteine. Essential amino acids refer to those necessary for construction of proteins in the body, although not produced by the body; which amino acids are essential varies from organism to organism.

The sequence and the number of amino acids ultimately determine the protein's shape, size, and function. Each amino acid is attached to another amino acid by a covalent bond, known as a peptide bond, which is formed by a dehydration reaction. The carboxyl group of one amino acid and the amino group of the incoming amino acid combine, releasing a molecule of water. The resulting bond is the peptide bond (Figure **8.2.5.3**).

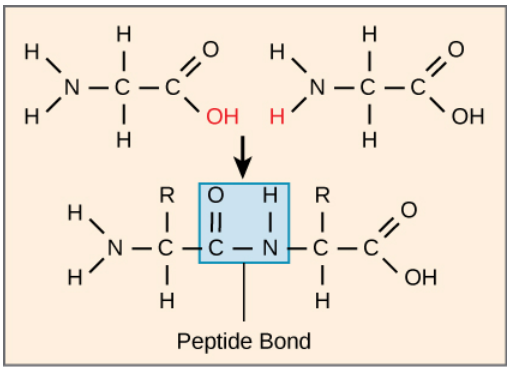



Figure **8.2.5.3**: Peptide bond formation is a dehydration synthesis reaction. The carboxyl group of one amino acid is linked to the amino group of the incoming amino acid. In the process, a molecule of water is released.

The products formed by such linkages are called peptides. As more amino acids join to this growing chain, the resulting chain is known as a polypeptide. Each polypeptide has a free amino group at one end. This end is called the N terminal, or the amino terminal, and the other end has a free carboxyl group, also known as the C or carboxyl terminal. While the terms polypeptide and protein are sometimes used interchangeably, a polypeptide is technically a polymer of amino acids, whereas the term protein is used for a polypeptide or polypeptides that have combined together, often have bound non-peptide prosthetic groups, have a distinct shape, and have a unique function. After protein synthesis (translation), most proteins are modified. These are known as post-translational modifications. They may undergo cleavage, phosphorylation, or may require the addition of other chemical groups. Only after these modifications is the protein completely functional.

**Evolution Connection**

The Evolutionary Significance of Cytochrome cCytochrome c is an important component of the electron transport chain, a part of cellular respiration, and it is normally found in the cellular organelle, the mitochondrion. This protein has a heme prosthetic group, and the central ion of the heme gets alternately reduced and oxidized during electron transfer. Because this essential protein's role in producing cellular energy is crucial, it has changed very little over millions of years. Protein sequencing has shown that there is a considerable amount of cytochrome c amino acid sequence homology among different species; in other words, evolutionary kinship can be assessed by measuring the similarities or differences among various species' DNA or protein sequences.

Scientists have determined that human cytochrome c contains 104 amino acids. For each cytochrome c molecule from different organisms that has been sequenced to date, 37 of these amino acids appear in the same position in all samples of cytochrome c. This indicates that there may have been a common ancestor. On comparing the human and chimpanzee protein sequences, no sequence difference was found. When human and rhesus monkey sequences were compared, the single difference found was in one amino acid. In another comparison, human to yeast sequencing shows a difference in the 44th position.

## Protein Structure

As discussed earlier, the shape of a protein is critical to its function. For example, an enzyme can bind to a specific substrate at a site known as the active site. If this active site is altered because of local changes or changes in overall protein structure, the enzyme may be unable to bind to the substrate. To understand how the protein gets its final shape or conformation, we need to understand the four levels of protein structure: primary, secondary, tertiary, and quaternary.

### Primary Structure

The unique sequence of amino acids in a polypeptide chain is its primary structure. For example, the pancreatic hormone insulin has two polypeptide chains, A and B, and they are linked together by disulfide bonds. The N terminal amino acid of the A chain is

glycine, whereas the C terminal amino acid is asparagine (Figure 8.2.5.4). The sequences of amino acids in the A and B chains are unique to insulin.

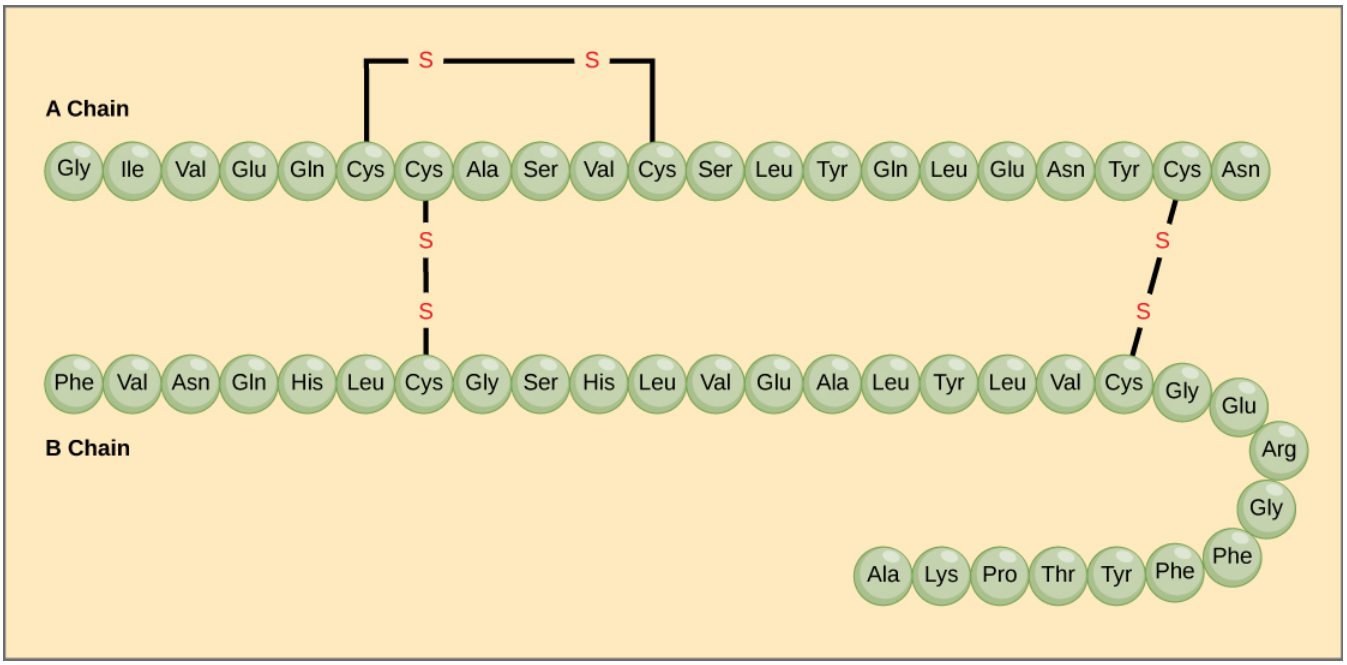



Figure 8.2.5.4: Bovine serum insulin is a protein hormone made of two peptide chains, A (21 amino acids long) and B (30 amino acids long). In each chain, primary structure is indicated by three-letter abbreviations that represent the names of the amino acids in the order they are present. The amino acid cysteine (cys) has a sulfhydryl (SH) group as a side chain. Two sulfhydryl groups can react in the presence of oxygen to form a disulfide (S-S) bond. Two disulfide bonds connect the A and B chains together, and a third helps the A chain fold into the correct shape. Note that all disulfide bonds are the same length, but are drawn different sizes for clarity.

The unique sequence for every protein is ultimately determined by the gene encoding the protein. A change in nucleotide sequence of the gene's coding region may lead to a different amino acid being added to the growing polypeptide chain, causing a change in protein structure and function. In sickle cell anemia, the hemoglobin $\beta$ chain (a small portion of which is shown in Figure 8.2.5.5) has a single amino acid substitution, causing a change in protein structure and function. Specifically, the amino acid glutamic acid is substituted by valine in the $\beta$ chain. What is most remarkable to consider is that a hemoglobin molecule is made up of two alpha chains and two beta chains that each consist of about 150 amino acids. The molecule, therefore, has about 600 amino acids. The structural difference between a normal hemoglobin molecule and a sickle cell molecule—which dramatically decreases life expectancy—is a single amino acid of the 600. What is even more remarkable is that those 600 amino acids are encoded by three nucleotides each, and the mutation is caused by a single base change (point mutation), 1 in 1800 bases.

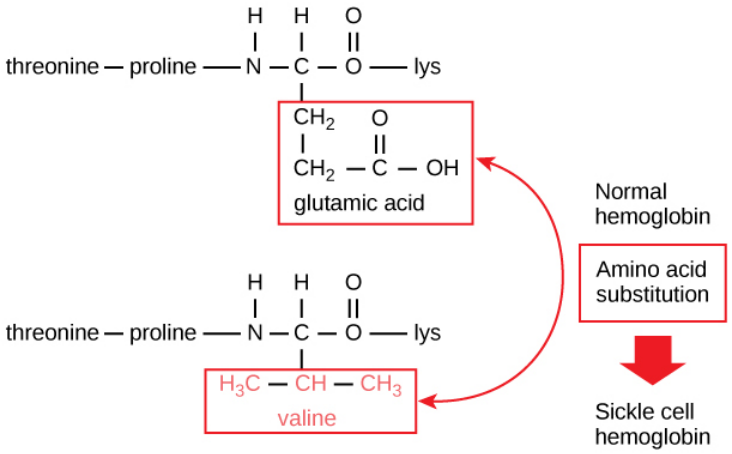



Figure **8.2.5.5**: The beta chain of hemoglobin is 147 residues in length, yet a single amino acid substitution leads to sickle cell anemia. In normal hemoglobin, the amino acid at position seven is glutamate. In sickle cell hemoglobin, this glutamate is replaced by a valine.

Because of this change of one amino acid in the chain, hemoglobin molecules form long fibers that distort the biconcave, or disc-shaped, red blood cells and assume a crescent or "sickle" shape, which clogs arteries (Figure **8.2.5.6**). This can lead to myriad serious health problems such as breathlessness, dizziness, headaches, and abdominal pain for those affected by this disease.

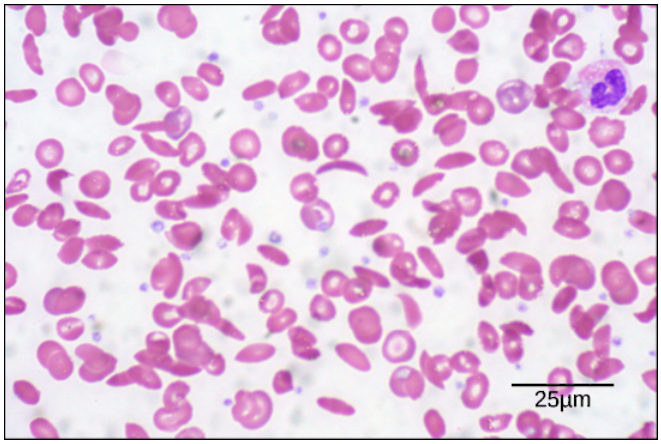



Figure **8.2.5.6**: In this blood smear, visualized at 535x magnification using bright field microscopy, sickle cells are crescent shaped, while normal cells are disc-shaped. (credit: modification of work by Ed Uthman; scale-bar data from Matt Russell)

## Secondary Structure

The local folding of the polypeptide in some regions gives rise to the secondary structure of the protein. The most common are the $\alpha$-helix and $\beta$-pleated sheet structures (Figure **8.2.5.7**). Both structures are the $\alpha$-helix structure—the helix held in shape by hydrogen bonds. The hydrogen bonds form between the oxygen atom in the carbonyl group in one amino acid and another amino acid that is four amino acids farther along the chain.

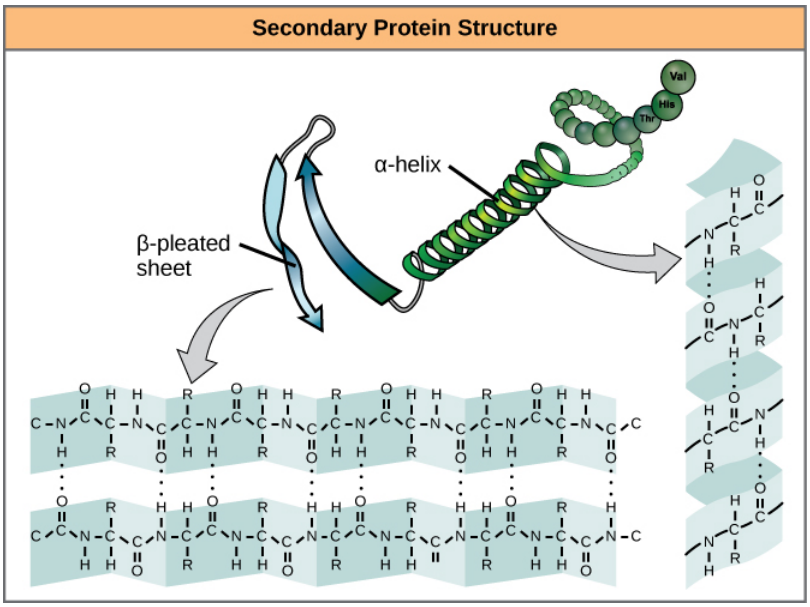



Figure **8.2.5.7**: The $\alpha$-helix and $\beta$-pleated sheet are secondary structures of proteins that form because of hydrogen bonding between carbonyl and amino groups in the peptide backbone. Certain amino acids have a propensity to form an $\alpha$-helix, while others have a propensity to form a $\beta$-pleated sheet.

Every helical turn in an alpha helix has 3.6 amino acid residues. The R groups (the variant groups) of the polypeptide protrude out from the $\alpha$-helix chain. In the $\beta$-pleated sheet, the "pleats" are formed by hydrogen bonding between atoms on the backbone of the polypeptide chain. The R groups are attached to the carbons and extend above and below the folds of the pleat. The pleated segments align parallel or antiparallel to each other, and hydrogen bonds form between the partially positive nitrogen atom in the amino group and the partially negative oxygen atom in the carbonyl group of the peptide backbone. The $\alpha$-helix and $\beta$-pleated sheet structures are found in most globular and fibrous proteins and they play an important structural role.

## Tertiary Structure

The unique three-dimensional structure of a polypeptide is its tertiary structure (Figure **8.2.5.8**). This structure is in part due to chemical interactions at work on the polypeptide chain. Primarily, the interactions among R groups creates the complex three-dimensional tertiary structure of a protein. The nature of the R groups found in the amino acids involved can counteract the formation of the hydrogen bonds described for standard secondary structures. For example, R groups with like charges are repelled by each other and those with unlike charges are attracted to each other (ionic bonds). When protein folding takes place, the hydrophobic R groups of nonpolar amino acids lay in the interior of the protein, whereas the hydrophilic R groups lay on the outside. The former types of interactions are also known as hydrophobic interactions. Interaction between cysteine side chains forms disulfide linkages in the presence of oxygen, the only covalent bond forming during protein folding.

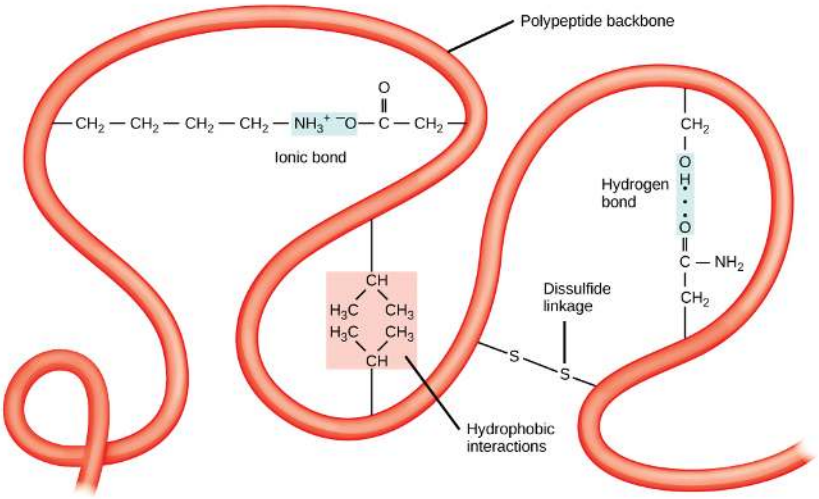



Figure 8.2.5.8: The tertiary structure of proteins is determined by a variety of chemical interactions. These include hydrophobic interactions, ionic bonding, hydrogen bonding and disulfide linkages.

All of these interactions, weak and strong, determine the final three-dimensional shape of the protein. When a protein loses its three-dimensional shape, it may no longer be functional.

## Quaternary Structure

In nature, some proteins are formed from several polypeptides, also known as subunits, and the interaction of these subunits forms the quaternary structure. Weak interactions between the subunits help to stabilize the overall structure. For example, insulin (a globular protein) has a combination of hydrogen bonds and disulfide bonds that cause it to be mostly clumped into a ball shape. Insulin starts out as a single polypeptide and loses some internal sequences in the presence of post-translational modification after the formation of the disulfide linkages that hold the remaining chains together. Silk (a fibrous protein), however, has a $\beta$-pleated sheet structure that is the result of hydrogen bonding between different chains.

The four levels of protein structure (primary, secondary, tertiary, and quaternary) are illustrated in Figure 8.2.5.9.

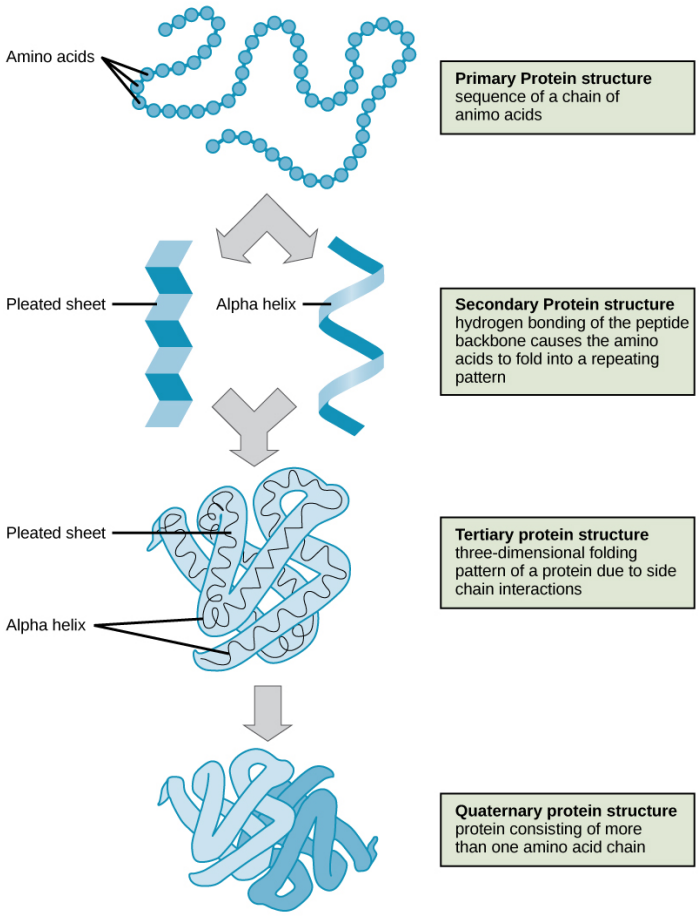



Figure 8.2.5.9: The four levels of protein structure can be observed in these illustrations. (credit: modification of work by National Human Genome Research Institute)

## Denaturation and Protein Folding

Each protein has its own unique sequence and shape that are held together by chemical interactions. If the protein is subject to changes in temperature, pH, or exposure to chemicals, the protein structure may change, losing its shape without losing its primary sequence in what is known as denaturation. Denaturation is often reversible because the primary structure of the polypeptide is conserved in the process if the denaturing agent is removed, allowing the protein to resume its function. Sometimes denaturation is irreversible, leading to loss of function. One example of irreversible protein denaturation is when an egg is fried. The albumin protein in the liquid egg white is denatured when placed in a hot pan. Not all proteins are denatured at high temperatures; for instance, bacteria that survive in hot springs have proteins that function at temperatures close to boiling. The stomach is also very acidic, has a low pH, and denatures proteins as part of the digestion process; however, the digestive enzymes of the stomach retain their activity under these conditions.

Protein folding is critical to its function. It was originally thought that the proteins themselves were responsible for the folding process. Only recently was it found that often they receive assistance in the folding process from protein helpers known as chaperones (or chaperonins) that associate with the target protein during the folding process. They act by preventing aggregation of polypeptides that make up the complete protein structure, and they disassociate from the protein once the target protein is folded.

## Summary

Proteins are a class of macromolecules that perform a diverse range of functions for the cell. They help in metabolism by providing structural support and by acting as enzymes, carriers, or hormones. The building blocks of proteins (monomers) are amino acids. Each amino acid has a central carbon that is linked to an amino group, a carboxyl group, a hydrogen atom, and an R group or side chain. There are 20 commonly occurring amino acids, each of which differs in the R group. Each amino acid is linked to its neighbors by a peptide bond. A long chain of amino acids is known as a polypeptide.

Proteins are organized at four levels: primary, secondary, tertiary, and (optional) quaternary. The primary structure is the unique sequence of amino acids. The local folding of the polypeptide to form structures such as the $\alpha$ helix and $\beta$-pleated sheet constitutes the secondary structure. The overall three-dimensional structure is the tertiary structure. When two or more polypeptides combine to form the complete protein structure, the configuration is known as the quaternary structure of a protein. Protein shape and function are intricately linked; any change in shape caused by changes in temperature or pH may lead to protein denaturation and a loss in function.

## Art Connections

Figure 8.2.5.2: Which categories of amino acid would you expect to find on the surface of a soluble protein, and which would you expect to find in the interior? What distribution of amino acids would you expect to find in a protein embedded in a lipid bilayer?

**Answer**

Polar and charged amino acid residues (the remainder after peptide bond formation) are more likely to be found on the surface of soluble proteins where they can interact with water, and nonpolar (e.g., amino acid side chains) are more likely to be found in the interior where they are sequestered from water. In membrane proteins, nonpolar and hydrophobic amino acid side chains associate with the hydrophobic tails of phospholipids, while polar and charged amino acid side chains interact with the polar head groups or with the aqueous solution. However, there are exceptions. Sometimes, positively and negatively charged amino acid side chains interact with one another in the interior of a protein, and polar or charged amino acid side chains that interact with a ligand can be found in the ligand binding pocket.

## Glossary

**alpha-helix structure ($\alpha$-helix)**
type of secondary structure of proteins formed by folding of the polypeptide into a helix shape with hydrogen bonds stabilizing the structure

**amino acid**
monomer of a protein; has a central carbon or alpha carbon to which an amino group, a carboxyl group, a hydrogen, and an R group or side chain is attached; the R group is different for all 20 amino acids

**beta-pleated sheet ($\beta$-pleated)**
secondary structure found in proteins in which “pleats” are formed by hydrogen bonding between atoms on the backbone of the polypeptide chain

**chaperone**
(also, chaperonin) protein that helps nascent protein in the folding process

**denaturation**
loss of shape in a protein as a result of changes in temperature, pH, or exposure to chemicals

**enzyme**
catalyst in a biochemical reaction that is usually a complex or conjugated protein

**hormone**
chemical signaling molecule, usually protein or steroid, secreted by endocrine cells that act to control or regulate specific physiological processes

**peptide bond**
bond formed between two amino acids by a dehydration reaction

**polypeptide**

long chain of amino acids linked by peptide bonds

**primary structure**

linear sequence of amino acids in a protein

**protein**

biological macromolecule composed of one or more chains of amino acids

**quaternary structure**

association of discrete polypeptide subunits in a protein

**secondary structure**

regular structure formed by proteins by intramolecular hydrogen bonding between the oxygen atom of one amino acid residue and the hydrogen attached to the nitrogen atom of another amino acid residue

**tertiary structure**

three-dimensional conformation of a protein, including interactions between secondary structural elements; formed from interactions between amino acid side chains

---

This page titled 8.2.5: Proteins is shared under a CC BY 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **3.4: Proteins** by OpenStax is licensed CC BY 4.0.

# 8.2.6: Nucleic Acids

**Skills to Develop**

- Describe the structure of nucleic acids and define the two types of nucleic acids
- Explain the structure and role of DNA
- Explain the structure and roles of RNA

Nucleic acids are the most important macromolecules for the continuity of life. They carry the genetic blueprint of a cell and carry instructions for the functioning of the cell.

## DNA and RNA

The two main types of nucleic acids are deoxyribonucleic acid (DNA) and ribonucleic acid (RNA). DNA is the genetic material found in all living organisms, ranging from single-celled bacteria to multicellular mammals. It is found in the nucleus of eukaryotes and in the organelles, chloroplasts, and mitochondria. In prokaryotes, the DNA is not enclosed in a membranous envelope.

The entire genetic content of a cell is known as its genome, and the study of genomes is genomics. In eukaryotic cells but not in prokaryotes, DNA forms a complex with histone proteins to form chromatin, the substance of eukaryotic chromosomes. A chromosome may contain tens of thousands of genes. Many genes contain the information to make protein products; other genes code for RNA products. DNA controls all of the cellular activities by turning the genes “on” or “off.”

The other type of nucleic acid, RNA, is mostly involved in protein synthesis. The DNA molecules never leave the nucleus but instead use an intermediary to communicate with the rest of the cell. This intermediary is the messenger RNA (mRNA). Other types of RNA—like rRNA, tRNA, and microRNA—are involved in protein synthesis and its regulation.

DNA and RNA are made up of monomers known as nucleotides. The nucleotides combine with each other to form a polynucleotide, DNA or RNA. Each nucleotide is made up of three components: a nitrogenous base, a pentose (five-carbon) sugar, and a phosphate group (Figure **8.2.6.1**). Each nitrogenous base in a nucleotide is attached to a sugar molecule, which is attached to one or more phosphate groups.

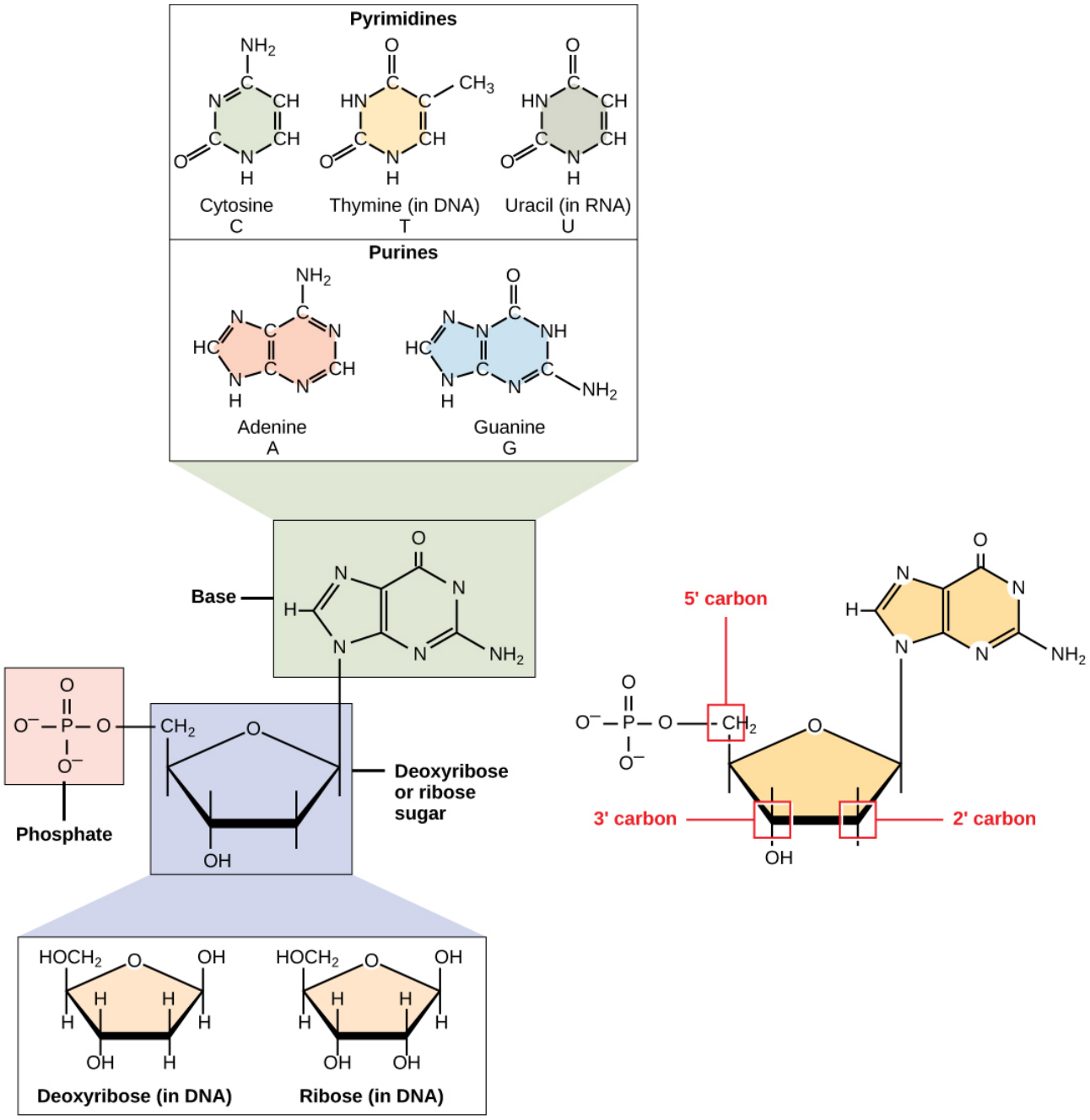



Figure 8.2.6.1: A nucleotide is made up of three components: a nitrogenous base, a pentose sugar, and one or more phosphate groups. Carbon residues in the pentose are numbered 1′ through 5′ (the prime distinguishes these residues from those in the base, which are numbered without using a prime notation). The base is attached to the 1′ position of the ribose, and the phosphate is attached to the 5′ position. When a polynucleotide is formed, the 5′ phosphate of the incoming nucleotide attaches to the 3′ hydroxyl group at the end of the growing chain. Two types of pentose are found in nucleotides, deoxyribose (found in DNA) and ribose (found in RNA). Deoxyribose is similar in structure to ribose, but it has an H instead of an OH at the 2′ position. Bases can be divided into two categories: purines and pyrimidines. Purines have a double ring structure, and pyrimidines have a single ring.

The nitrogenous bases, important components of nucleotides, are organic molecules and are so named because they contain carbon and nitrogen. They are bases because they contain an amino group that has the potential of binding an extra hydrogen, and thus, decreases the hydrogen ion concentration in its environment, making it more basic. Each nucleotide in DNA contains one of four possible nitrogenous bases: adenine (A), guanine (G) cytosine (C), and thymine (T).

Adenine and guanine are classified as purines. The primary structure of a purine is two carbon-nitrogen rings. Cytosine, thymine, and uracil are classified as pyrimidines which have a single carbon-nitrogen ring as their primary structure (Figure 8.2.6.1). Each of

these basic carbon-nitrogen rings has different functional groups attached to it. In molecular biology shorthand, the nitrogenous bases are simply known by their symbols A, T, G, C, and U. DNA contains A, T, G, and C whereas RNA contains A, U, G, and C.

The pentose sugar in DNA is deoxyribose, and in RNA, the sugar is ribose (Figure **8.2.6.1**). The difference between the sugars is the presence of the hydroxyl group on the second carbon of the ribose and hydrogen on the second carbon of the deoxyribose. The carbon atoms of the sugar molecule are numbered as 1′, 2′, 3′, 4′, and 5′ (1′ is read as “one prime”). The phosphate residue is attached to the hydroxyl group of the 5′ carbon of one sugar and the hydroxyl group of the 3′ carbon of the sugar of the next nucleotide, which forms a 5′–3′ phosphodiester linkage. The phosphodiester linkage is not formed by simple dehydration reaction like the other linkages connecting monomers in macromolecules: its formation involves the removal of two phosphate groups. A polynucleotide may have thousands of such phosphodiester linkages.

### DNA Double-Helix Structure

DNA has a double-helix structure (Figure **8.2.6.2**). The sugar and phosphate lie on the outside of the helix, forming the backbone of the DNA. The nitrogenous bases are stacked in the interior, like the steps of a staircase, in pairs; the pairs are bound to each other by hydrogen bonds. Every base pair in the double helivx is separated from the next base pair by 0.34 nm. The two strands of the helix run in opposite directions, meaning that the 5′ carbon end of one strand will face the 3′ carbon end of its matching strand. (This is referred to as antiparallel orientation and is important to DNA replication and in many nucleic acid interactions.)

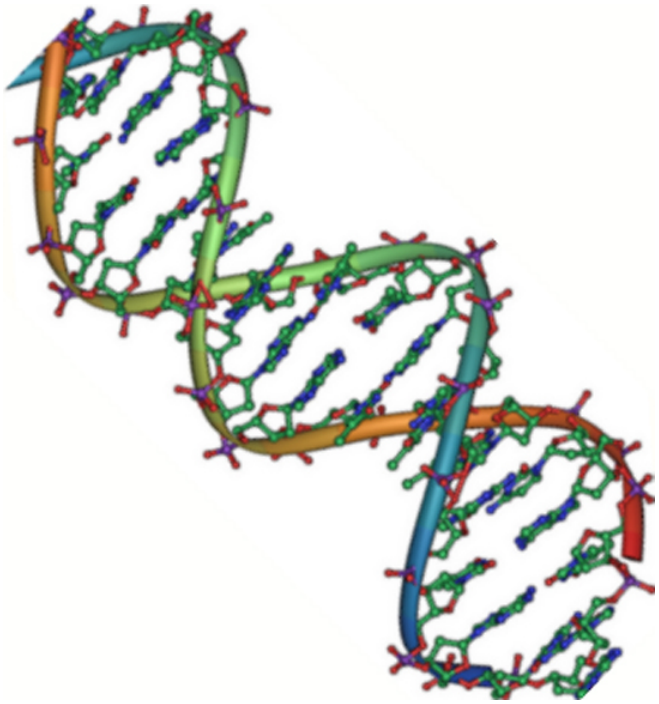


Figure **8.2.6.2**: Native DNA is an antiparallel double helix. The phosphate backbone (indicated by the curvy lines) is on the outside, and the bases are on the inside. Each base from one strand interacts via hydrogen bonding with a base from the opposing strand. (credit: Jerome Walker/Dennis Myts)

Only certain types of base pairing are allowed. For example, a certain purine can only pair with a certain pyrimidine. This means A can pair with T, and G can pair with C, as shown in Figure **8.2.6.3**. This is known as the base complementary rule. In other words, the DNA strands are complementary to each other. If the sequence of one strand is AATTGGCC, the complementary strand would have the sequence TTAACCGG. During DNA replication, each strand is copied, resulting in a daughter DNA double helix containing one parental DNA strand and a newly synthesized strand.

Art Connection

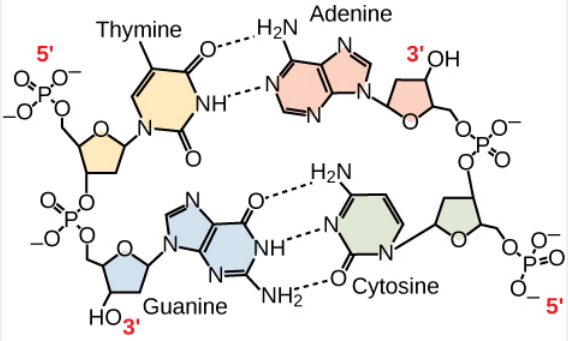



Figure 8.2.6.3: In a double stranded DNA molecule, the two strands run antiparallel to one another so that one strand runs 5′ to 3′ and the other 3′ to 5′. The phosphate backbone is located on the outside, and the bases are in the middle. Adenine forms hydrogen bonds (or base pairs) with thymine, and guanine base pairs with cytosine.

A mutation occurs, and cytosine is replaced with adenine. What impact do you think this will have on the DNA structure?

## RNA

Ribonucleic acid, or RNA, is mainly involved in the process of protein synthesis under the direction of DNA. RNA is usually single-stranded and is made of ribonucleotides that are linked by phosphodiester bonds. A ribonucleotide in the RNA chain contains ribose (the pentose sugar), one of the four nitrogenous bases (A, U, G, and C), and the phosphate group.

There are four major types of RNA: messenger RNA (mRNA), ribosomal RNA (rRNA), transfer RNA (tRNA), and microRNA (miRNA). The first, mRNA, carries the message from DNA, which controls all of the cellular activities in a cell. If a cell requires a certain protein to be synthesized, the gene for this product is turned “on” and the messenger RNA is synthesized in the nucleus. The RNA base sequence is complementary to the coding sequence of the DNA from which it has been copied. However, in RNA, the base T is absent and U is present instead. If the DNA strand has a sequence AATTGCGC, the sequence of the complementary RNA is UUAACGCG. In the cytoplasm, the mRNA interacts with ribosomes and other cellular machinery (Figure 8.2.6.4).

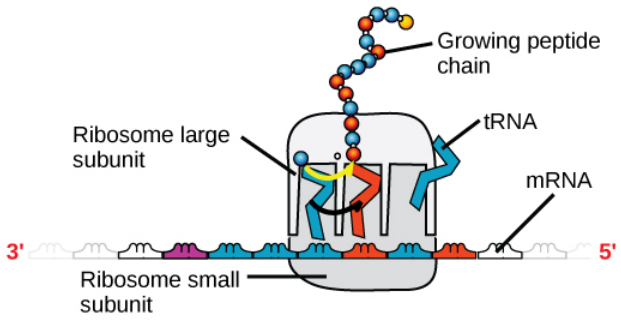



Figure 8.2.6.4: A ribosome has two parts: a large subunit and a small subunit. The mRNA sits in between the two subunits. A tRNA molecule recognizes a codon on the mRNA, binds to it by complementary base pairing, and adds the correct amino acid to the growing peptide chain.

The mRNA is read in sets of three bases known as codons. Each codon codes for a single amino acid. In this way, the mRNA is read and the protein product is made. Ribosomal RNA (rRNA) is a major constituent of ribosomes on which the mRNA binds. The rRNA ensures the proper alignment of the mRNA and the ribosomes; the rRNA of the ribosome also has an enzymatic activity (peptidyl transferase) and catalyzes the formation of the peptide bonds between two aligned amino acids. Transfer RNA (tRNA) is one of the smallest of the four types of RNA, usually 70–90 nucleotides long. It carries the correct amino acid to the site of protein synthesis. It is the base pairing between the tRNA and mRNA that allows for the correct amino acid to be inserted in the polypeptide chain. microRNAs are the smallest RNA molecules and their role involves the regulation of gene expression by interfering with the expression of certain mRNA messages. Table 8.2.6.1 below summarizes features of DNA and RNA.

Table 8.2.6.1: Features of DNA and RNA.

| | DNA | RNA |
|---|---|---|
| Function | Carries genetic information | Involved in protein synthesis |
| Location | Remains in the nucleus | Leaves the nucleus |
| Structure | Double helix | Usually single-stranded |
| Sugar | Deoxyribose | Ribose |
| Pyrimidines | Cytosine, thymine | Cytosine, uracil |
| Purines | Adenine, guanine | Adenine, guanine |

Even though the RNA is single stranded, most RNA types show extensive intramolecular base pairing between complementary sequences, creating a predictable three-dimensional structure essential for their function.

As you have learned, information flow in an organism takes place from DNA to RNA to protein. DNA dictates the structure of mRNA in a process known as transcription, and RNA dictates the structure of protein in a process known as translation. This is known as the Central Dogma of Life, which holds true for all organisms; however, exceptions to the rule occur in connection with viral infections.

Link to Learning

To learn more about DNA, explore the Howard Hughes Medical Institute BioInteractive animations on the topic of DNA.

## Summary

Nucleic acids are molecules made up of nucleotides that direct cellular activities such as cell division and protein synthesis. Each nucleotide is made up of a pentose sugar, a nitrogenous base, and a phosphate group. There are two types of nucleic acids: DNA and RNA. DNA carries the genetic blueprint of the cell and is passed on from parents to offspring (in the form of chromosomes). It has a double-helical structure with the two strands running in opposite directions, connected by hydrogen bonds, and complementary to each other. RNA is single-stranded and is made of a pentose sugar (ribose), a nitrogenous base, and a phosphate group. RNA is involved in protein synthesis and its regulation. Messenger RNA (mRNA) is copied from the DNA, is exported from the nucleus to the cytoplasm, and contains information for the construction of proteins. Ribosomal RNA (rRNA) is a part of the ribosomes at the site of protein synthesis, whereas transfer RNA (tRNA) carries the amino acid to the site of protein synthesis. microRNA regulates the use of mRNA for protein synthesis.

## Art Connections

Figure **8.2.6.3**: A mutation occurs, and cytosine is replaced with adenine. What impact do you think this will have on the DNA structure?

**Answer**

Adenine is larger than cytosine and will not be able to base pair properly with the guanine on the opposing strand. This will cause the DNA to bulge. DNA repair enzymes may recognize the bulge and replace the incorrect nucleotide.

## Glossary

**deoxyribonucleic acid (DNA)**
double-helical molecule that carries the hereditary information of the cell

**messenger RNA (mRNA)**
RNA that carries information from DNA to ribosomes during protein synthesis

**nucleic acid**
biological macromolecule that carries the genetic blueprint of a cell and carries instructions for the functioning of the cell

**nucleotide**
monomer of nucleic acids; contains a pentose sugar, one or more phosphate groups, and a nitrogenous base

**phosphodiester**
linkage covalent chemical bond that holds together the polynucleotide chains with a phosphate group linking two pentose sugars of neighboring nucleotides

**polynucleotide**
long chain of nucleotides

**purine**
type of nitrogenous base in DNA and RNA; adenine and guanine are purines

**pyrimidine**
type of nitrogenous base in DNA and RNA; cytosine, thymine, and uracil are pyrimidines

**ribonucleic acid (RNA)**
single-stranded, often internally base paired, molecule that is involved in protein synthesis

**ribosomal RNA (rRNA)**
RNA that ensures the proper alignment of the mRNA and the ribosomes during protein synthesis and catalyzes the formation of the peptide linkage

**transcription**
process through which messenger RNA forms on a template of DNA

**transfer RNA (tRNA)**
RNA that carries activated amino acids to the site of protein synthesis on the ribosome

**translation**
process through which RNA directs the formation of protein

---

This page titled 8.2.6: Nucleic Acids is shared under a CC BY 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **3.5: Nucleic Acids** by OpenStax is licensed CC BY 4.0.

# 8.2.E: Biological Macromolecules (Exercises)

## 3.1: Synthesis of Biological Macromolecules

### Review Questions

Dehydration synthesis leads to formation of

A. monomers
B. polymers
C. water and polymers
D. none of the above

**Answer**

C

During the breakdown of polymers, which of the following reactions takes place?

A. hydrolysis
B. dehydration
C. condensation
D. covalent bond

**Answer**

A

### Free Response

Why are biological macromolecules considered organic?

**Answer**

Biological macromolecules are organic because they contain carbon.

What role do electrons play in dehydration synthesis and hydrolysis?

**Answer**

In a dehydration synthesis reaction, the hydrogen of one monomer combines with the hydroxyl group of another monomer, releasing a molecule of water. This creates an opening in the outer shells of atoms in the monomers, which can share electrons and form covalent bonds.

## 3.2: Carbohydrates

### Review Questions

An example of a monosaccharide is _____.

A. fructose
B. glucose
C. galactose
D. all of the above

**Answer**

D

Cellulose and starch are examples of:

A. monosaccharides
B. disaccharides
C. lipids
D. polysaccharides

**Answer**

D

Plant cell walls contain which of the following in abundance?

A. starch
B. cellulose
C. glycogen
D. lactose

**Answer**

B

Lactose is a disaccharide formed by the formation of a _____ bond between glucose and _____.

A. glycosidic; lactose
B. glycosidic; galactose
C. hydrogen; sucrose
D. hydrogen; fructose

**Answer**

B

## Free Response

Describe the similarities and differences between glycogen and starch.

**Answer**

Glycogen and starch are polysaccharides. They are the storage form of glucose. Glycogen is stored in animals in the liver and in muscle cells, whereas starch is stored in the roots, seeds, and leaves of plants. Starch has two different forms, one unbranched (amylose) and one branched (amylopectin), whereas glycogen is a single type of a highly branched molecule.

Why is it impossible for humans to digest food that contains cellulose?

**Answer**

The $\beta$ 1-4 glycosidic linkage in cellulose cannot be broken down by human digestive enzymes. Herbivores such as cows, buffalos, and horses are able to digest grass that is rich in cellulose and use it as a food source because bacteria and protists in their digestive systems, especially in the rumen, secrete the enzyme cellulase. Cellulases can break down cellulose into glucose monomers that can be used as an energy source by the animal.

## 3.3: Lipids

### Review Questions

Saturated fats have all of the following characteristics except:

A. they are solid at room temperature
B. they have single bonds within the carbon chain
C. they are usually obtained from animal sources
D. they tend to dissolve in water easily

**Answer**

D

Phospholipids are important components of _____.

A. the plasma membrane of animal cells
B. the ring structure of steroids
C. the waxy covering on leaves
D. the double bond in hydrocarbon chains

**Answer**

A

### Free Response

Explain at least three functions that lipids serve in plants and/or animals.

**Answer**

Fat serves as a valuable way for animals to store energy. It can also provide insulation. Waxes can protect plant leaves and mammalian fur from getting wet. Phospholipids and steroids are important components of animal cell membranes, as well as plant, fungal, and bacterial membranes.

Why have trans fats been banned from some restaurants? How are they created?

**Answer**

Trans fats are created artificially when hydrogen gas is bubbled through oils to solidify them. The double bonds of the *cis* conformation in the hydrocarbon chain may be converted to double bonds in the *trans* configuration. Some restaurants are banning trans fats because they cause higher levels of LDL, or “bad” cholesterol.

## 3.4: Proteins

### Review Questions

The monomers that make up proteins are called _____.

A. nucleotides
B. disaccharides
C. amino acids
D. chaperones

**Answer**

C

The $\alpha$ helix and the $\beta$-pleated sheet are part of which protein structure?

A. primary
B. secondary
C. tertiary
D. quaternary

**Answer**

B

### Free Response

Explain what happens if even one amino acid is substituted for another in a polypeptide chain. Provide a specific example.

**Answer**

A change in gene sequence can lead to a different amino acid being added to a polypeptide chain instead of the normal one. This causes a change in protein structure and function. For example, in sickle cell anemia, the hemoglobin $\beta$ chain has a single amino acid substitution—the amino acid glutamic acid in position six is substituted by valine. Because of this change, hemoglobin molecules form aggregates, and the disc-shaped red blood cells assume a crescent shape, which results in serious health problems.

Describe the differences in the four protein structures.

**Answer**

The sequence and number of amino acids in a polypeptide chain is its primary structure. The local folding of the polypeptide in some regions is the secondary structure of the protein. The three-dimensional structure of a polypeptide is known as its tertiary structure, created in part by chemical interactions such as hydrogen bonds between polar side chains, van der Waals interactions, disulfide linkages, and hydrophobic interactions. Some proteins are formed from multiple polypeptides, also known as subunits, and the interaction of these subunits forms the quaternary structure.

## 3.5: Nucleic Acids

### Review Questions

A nucleotide of DNA may contain _____.

A. ribose, uracil, and a phosphate group
B. deoxyribose, uracil, and a phosphate group
C. deoxyribose, thymine, and a phosphate group
D. ribose, thymine, and a phosphate group

**Answer**

C

The building blocks of nucleic acids are _____.

A. sugars
B. nitrogenous bases
C. peptides
D. nucleotides

**Answer**

D

## Free Response

What are the structural differences between RNA and DNA?

**Answer**

DNA has a double-helix structure. The sugar and the phosphate are on the outside of the helix and the nitrogenous bases are in the interior. The monomers of DNA are nucleotides containing deoxyribose, one of the four nitrogenous bases (A, T, G and C), and a phosphate group. RNA is usually single-stranded and is made of ribonucleotides that are linked by phosphodiester linkages. A ribonucleotide contains ribose (the pentose sugar), one of the four nitrogenous bases (A,U, G, and C), and the phosphate group.

What are the four types of RNA and how do they function?

**Answer**

The four types of RNA are messenger RNA, ribosomal RNA, transfer RNA, and microRNA. Messenger RNA carries the information from the DNA that controls all cellular activities. The mRNA binds to the ribosomes that are constructed of proteins and rRNA, and tRNA transfers the correct amino acid to the site of protein synthesis. microRNA regulates the availability of mRNA for translation.

This page titled 8.2.E: Biological Macromolecules (Exercises) is shared under a CC BY 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **3.E: Biological Macromolecules (Exercises)** by OpenStax is licensed CC BY 4.0.

## 8.3: Unit I- The Chemistry of Life

Our opening unit introduces students to the sciences, including the scientific method and the fundamental concepts of chemistry and physics that provide a framework within which learners comprehend biological processes.

# Contributors

Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

This page titled 8.3: Unit I- The Chemistry of Life is shared under a CC BY 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

# CHAPTER OVERVIEW

## 9: Photosynthesis - carbon reactions


9.1: Discovery of Photosynthesis

9.2: Photosynthesis Overview and Equation

9.3: Light-independent Reactions


---

This page titled 9: Photosynthesis - carbon reactions is shared under a not declared license and was authored, remixed, and/or curated by Tom Buckley.

# 9.1: Discovery of Photosynthesis

**Learning Objective**

Summarize the experimental results that revealed details about the process of photosynthesis.

The history of the studies done on photosynthesis dates back into the 17th century with Jan Baptist van Helmont. He rejected the ancient idea that plants take most of their biomass from the soil. For the proof, he performed an experiment using a willow tree. He started with a willow tree with a mass of 2.27 kg. Over 5 years, it grew to 67.7 kg. However, the mass of the soil only decreased by 57 grams. Van Helmont came to the conclusion that plants must obtain most of their mass from water. He did not know about gases.

Joseph Priestley ran a series of experiments in 1772 (Figure **9.1.1**). He tested a mouse, a candle, and a sprig of mint under hermetically sealed (no air can go in or out) jar. He first observed that a mouse and a candle behave very similarly when covered, in that they both “spend” the air. However, when a plant is placed with either the candle or mouse, the plant “revives” the air for both.

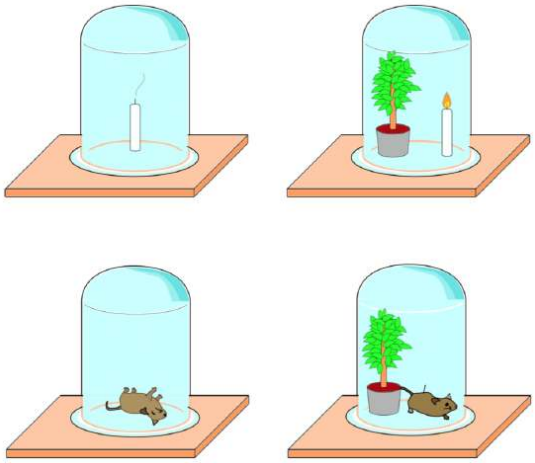


Figure **9.1.1**: Experiments of J. Priestley (1772) demonstrating that plants provided "air" needed for a candle to burn or a mouse to breath.

Further ideas were brought about in the late 1700’s. Jan Ingenhousz and Jean Senebier found that the air is only reviving in the day time and that $CO_2$ is assembled by plants. Antoin-Laurent Lavoiser found that “revived air” is a separate gas, oxygen.

But what is the oxygen “maker”? There are many pigments in plants, and all accept and reflect some parts of rainbow. To identify the culprit, Thomas Engelmann ran an experiment (Figure **9.1.2**) using a crystal prism that shine different wavelengths (colors) of visible light on the algae *Spirogyra* algae. He then measured oxygen production with **aerotactic** bacteria, which move towards areas of high oxygen concentration. A high density of bacteria cells accumulated in the blue and red parts of the spectrum, indicating this was where the most oxygen was produced and the most photosynthesis was conducted. This was a huge find. It tells that the key photosynthetic pigment should accept blue and red rays, and thus reflect green rays. The photosynthetic pigment chlorophyll *a* best fits this description.

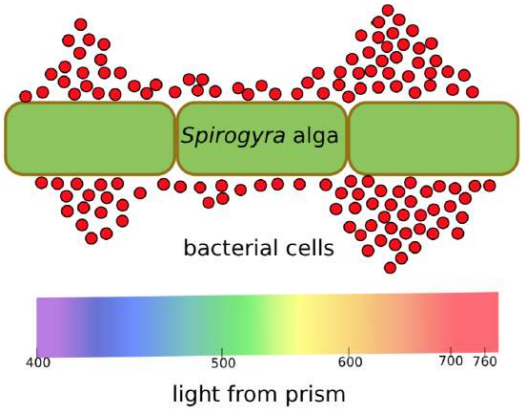



Figure **9.1.2**: The experiment of Thomas Engelmann (1881) involved separating the wavelengths of visible light using a prism. The rainbow of visible light ranges from approximately 400 nm (violet) to 700 nm (red). The algae *Spirogyra* produced the most oxygen bubbles in blue and red parts of the visible light spectrum, and bacterial cells thus accumulated in these regions.

Another important fact was discovered by Frederick Blackman in 1905. He found that if light intensity is low, the increase of temperature actually has very little effect on the rate of photosynthesis. However, the reverse is not exactly true, and light is able to intensify photosynthesis even when it is cold.

This could not happen if light and temperature are absolutely independent factors. If temperature and light are components of the chain, light was first ("ignition") and temperature was second. This ultimately shows that photosynthesis has two stages (now called the light-dependent and light-independent stages). The light-dependent stage relates the to intensity of the light. The light-independent stage relates more with the temperature as it involves many enzymes.

## Attribution

Curated and authored by Melissa Ha using 8.1 Overview of Photosynthesis from *Biology 2e* by OpenStax (licensed CC-BY). Access for free at openstax.org.

---

This page titled 9.1: Discovery of Photosynthesis is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **4.1.4: Discovery of Photosynthesis** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC 4.0.

# 9.2: Photosynthesis Overview and Equation

## Learning Objectives

- Explain the relevance of photosynthesis to other living things.
- Identify the substrates and products of photosynthesis.
- Describe the main structures involved in photosynthesis.
- Relate the light-dependent and light-independent reactions.

Plants, algae, and certain bacteria (cyanobacteria and green and purple sulfur bacteria) are among the organisms capable of performing photosynthesis (Figure 9.2.1). Because they use light to manufacture their own food, they are called **photoautotrophs** (literally, "self-feeders using light"). Other organisms, such as animals, fungi, and most other bacteria, are termed **heterotrophs** ("other feeders"), because they must rely on the sugars produced by photosynthetic organisms for their energy needs. A third very interesting group of bacteria synthesize sugars, not by using sunlight's energy, but by extracting energy from inorganic chemical compounds; hence, they are referred to as **chemoautotrophs**.

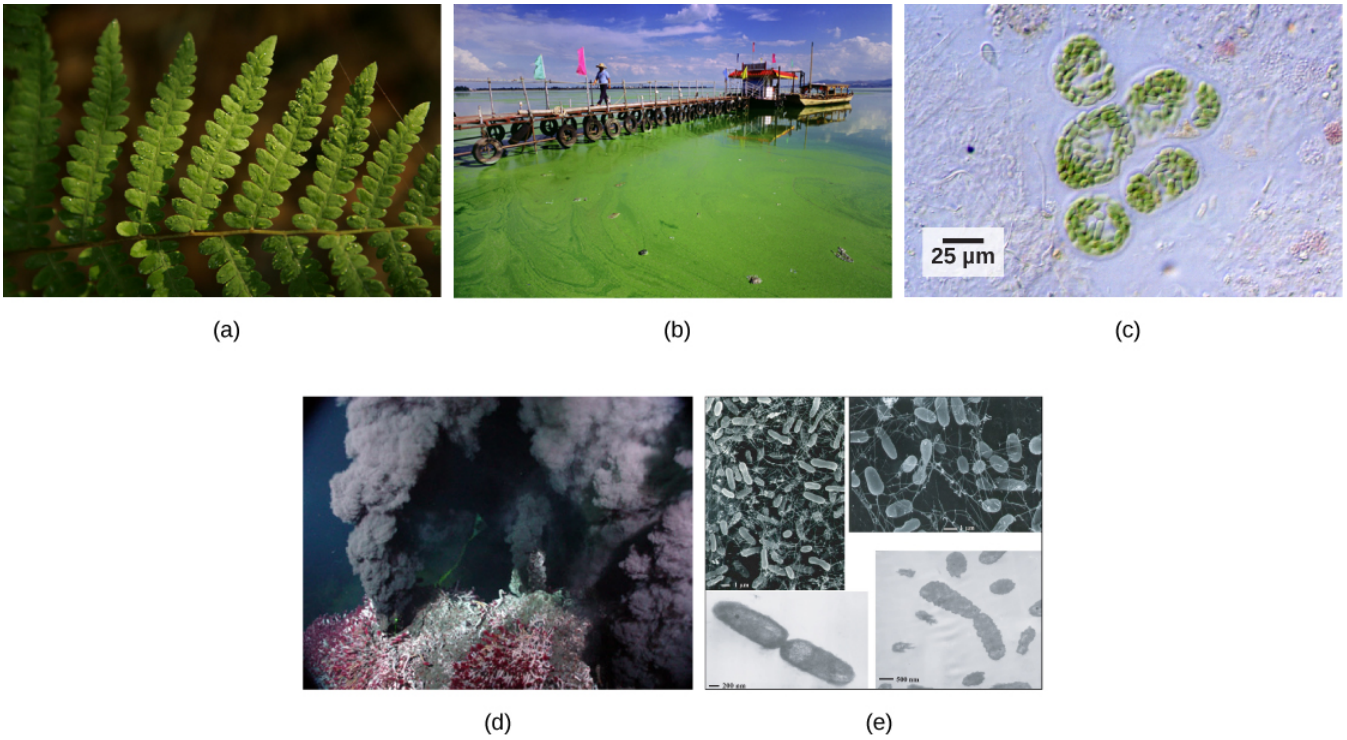



Figure 9.2.1: Photoautotrophs including (a) plants, (b) algae, and (c) cyanobacteria synthesize their organic compounds via photosynthesis using sunlight as an energy source. Cyanobacteria and planktonic algae can grow over enormous areas in water, at times completely covering the surface. In a (d) deep sea vent, chemoautotrophs, such as these (e) thermophilic bacteria, capture energy from inorganic compounds to produce organic compounds. The ecosystem surrounding the vents has a diverse array of animals, such as tubeworms, crustaceans, and octopi that derive energy from the bacteria. (credit a: modification of work by Steve Hillebrand, U.S. Fish and Wildlife Service; credit b: modification of work by "eutrophication&hypoxia"/Flickr; credit c: modification of work by NASA; credit d: University of Washington, NOAA; credit e: modification of work by Mark Amend, West Coast and Polar Regions Undersea Research Center, UAF, NOAA)

The importance of photosynthesis is not just that it can capture sunlight's energy. Photosynthesis is vital because it evolved as a way to store the energy in solar radiation (the "photo-" part) as high-energy electrons in the carbon-carbon bonds of carbohydrate molecules (the "-synthesis" part). Those carbohydrates are the energy source that heterotrophs use to power the synthesis of ATP via celluar respiration. Therefore, photosynthesis powers 99 percent of Earth's ecosystems.

## Photosynthesis Equation

Photosynthesis is a multi-step process that requires sunlight, carbon dioxide (which is low in energy), and water as substrates (Figure **9.2.2**). After the process is complete, it releases oxygen and produces glyceraldehyde-3-phosphate (GA3P), simple carbohydrate molecules (which are high in energy) that can subsequently be converted into glucose, sucrose, or any of dozens of other sugar molecules. These sugar molecules contain energy and the energized carbon that all living things need to survive.

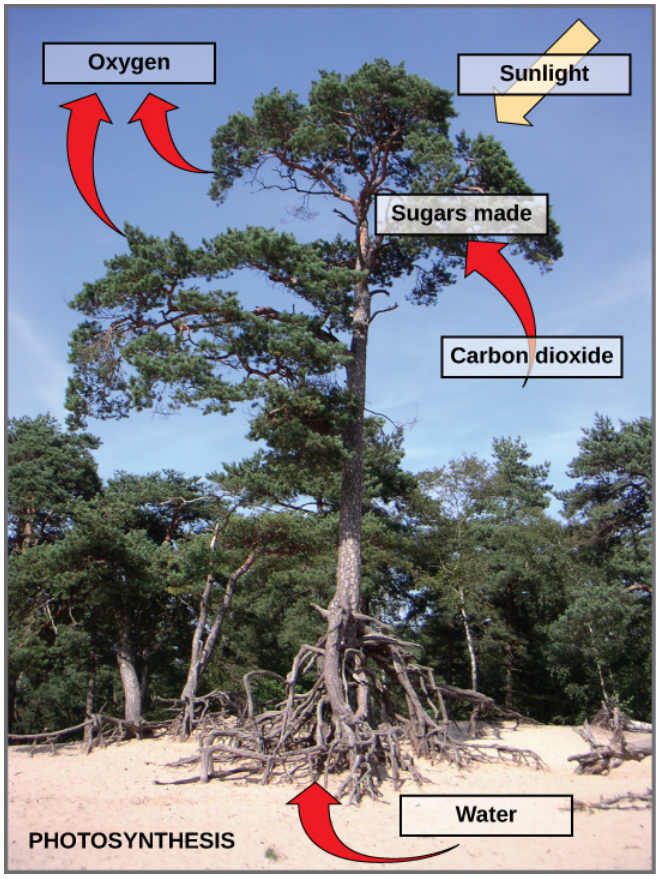



Figure **9.2.2**: Photosynthesis uses solar energy, carbon dioxide, and water to produce energy-storing carbohydrates. Oxygen is generated as a waste product of photosynthesis.

The following is the chemical equation for photosynthesis (Figure **9.2.3**). Although the equation looks simple, the many steps that take place during photosynthesis are actually quite complex.

**Photosynthesis Equation**

| Carbon dioxide | + | Water | SUNLIGHT → | Sugar | + | Oxygen |
|---|---|---|---|---|---|---|
| $6CO_2$ | | $6H_2O$ | | $C_6H_{12}O_6$ | | $6O_2$ |

Figure **9.2.3**: The basic equation for photosynthesis is deceptively simple. In reality, the process takes place in many steps involving intermediate reactants and products. Glucose, the primary energy source in cells, is made from two three-carbon GA3Ps. Technically, water is both reactant and product in photosynthesis, which is not reflected in the balanced chemical equation shown. Sunlight is used as an energy source.

## Structures of Photosynthesis

Before learning the details of how photoautotrophs turn sunlight into food, it is important to review the structures involved. Recall from the Leaves chapter that leaves consist of several layers of cells, and the process of photosynthesis occurs in the **mesophyll** (middle layer). Note that other parts of the plant, such as the stems, are photosynthetic as well. The gas exchange of carbon dioxide

and oxygen occurs through the **stomata** (singular: stoma), which also participate in water balance. The stomata are typically located on the underside of the leaf, which helps to minimize water loss. Each stoma is flanked by **guard cells** that regulate their opening and closing.

In all autotrophic eukaryotes, photosynthesis takes place inside the **chloroplast**. For plants, chloroplast-containing cells exist in the mesophyll. Chloroplasts have a double membrane envelope (composed of an outer membrane and an inner membrane). Within the chloroplast are stacked, disc-shaped structures called **thylakoids**. Embedded in the thylakoid membrane is **chlorophyll**, a **pigment** (molecule that absorbs light) responsible for the initial interaction between light and plant material, and numerous proteins that make up the **electron transport chain**. The thylakoid membrane encloses an internal space called the **thylakoid lumen**. As shown in Figure **9.2.4**, a stack of thylakoids is called a **granum** (plural: grana), and the liquid-filled space surrounding the granum is called **stroma** or "bed" (not to be confused with stoma or "mouth," an opening on the leaf epidermis).

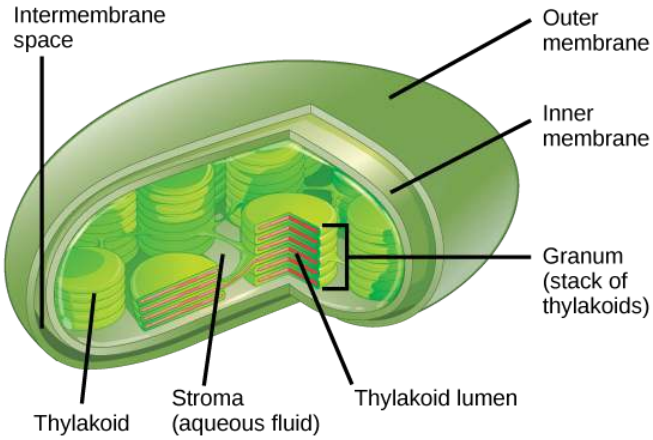



Figure **9.2.4**: Photosynthesis takes place in chloroplasts, which have an outer membrane and an inner membrane. The space between the outer and inner membranes is called the intermembrane space. Stacks of thylakoids called grana form a third membrane layer. The thylakoids form stacks called grana. The liquid inside the inner membrane is called the stroma, and the space inside the thylakoid is called the thylakoid lumen.

## Steps of Photosynthesis

Photosynthesis takes place in two sequential stages: the **light-dependent reactions** and the **light independent-reactions** (Calvin cycle). In the light-dependent reactions, energy from sunlight is absorbed by chlorophyll and that energy is converted into stored chemical energy. Light-dependent reactions require water and produce oxygen and energy in the form of ATP. In the light-independent reactions, the chemical energy harvested during the light-dependent reactions drive the assembly of sugar molecules from carbon dioxide. Therefore, although the light-independent reactions do not use light as a reactant, they require the products of the light-dependent reactions to function. In addition, several enzymes of the light-independent reactions are activated by light.

The light-dependent reactions utilize ATP and **nicotinamide adenine dinucleotide phosphate** (**NADPH**) to temporarily store the energy. Because NADPH carries two high-energy electrons, it is often referred to as an **electron carrier**. It can be thought of as "full" because it is rich in energy in its reduced state. When a molecule is reduced, electrons have been added to it. Electrons have a negative charge, so this is termed "**reduction"**. NAPDH move energy from light-dependent reactions to light-independent reactions. After the energy is released, the "empty" (**oxidized**) version, $NADP^+$, returns to the light-dependent reactions to obtain more high-energy electrons. Likewise, the ATP produced during the light-dependent reactions fuels the light-independent reactions. It then returns in a lower-energy form (ADP) to the light-dependent reactions to become phosphorylated again. Figure **9.2.5** illustrates the components inside the chloroplast where the light-dependent and light-independent reactions take place.

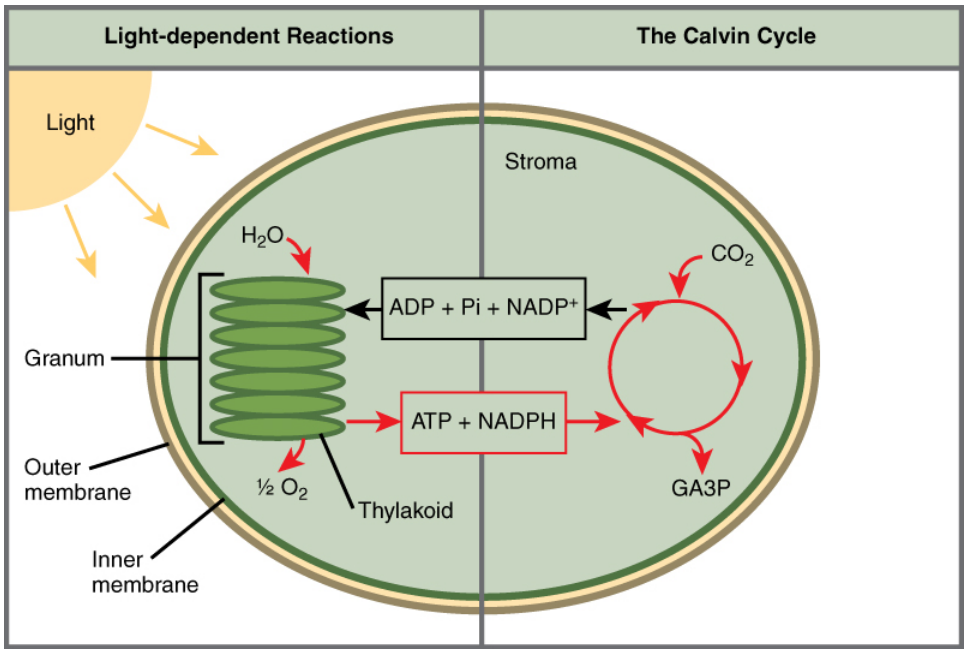



Figure **9.2.5**: Photosynthesis takes place in two stages: light-dependent reactions and the light-independent reactions (Calvin cycle or Calvin-Benson cycle). Light-dependent reactions, which take place in the thylakoid membrane, use light energy to make ATP and NADPH. In the process, water is used and oxygen is produced. Energy from ATP and NADPH are used to power the Calvin cycle, which produces GA3P from carbon dioxide. ATP is broken down to ADP and Pi, and NADPH is oxidized to $NADP^+$. The cycle is completed when the light reactions convert these molecules back into ATP and NADPH.

## Attribution

Curated and authored by Melissa Ha using the following sources:

- 8.1 Overview of Photosynthesis from *Biology 2e* by OpenStax (licensed CC-BY). Access for free at openstax.org.
- 3.1 Discovery of Photosynthesis from *Introduction to Botany* by Alexey Shipunov (public domain)

---

This page titled 9.2: Photosynthesis Overview and Equation is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **4.1.3: Photosynthesis Overview and Equation** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC 4.0.

# 9.3: Light-independent Reactions

## Learning Objectives

- Detail the three steps of the light-independent reactions.
- Define carbon fixation.

After the energy from the sun is converted into chemical energy temporarily stored in the bonds of ATP and NADPH molecules, the cell has the fuel needed to build carbohydrate molecules for long-term energy storage. The products of the light-dependent reactions, ATP and NADPH, have lifespans in the range of millionths of seconds, whereas the products of the light-independent reactions (carbohydrates and other forms of reduced carbon) can survive for hundreds of millions of years. The carbohydrate molecules made will have a backbone of carbon atoms. Where does the carbon come from? It comes from carbon dioxide, the gas that is a waste product of respiration in microbes, fungi, plants, and animals.

In plants, carbon dioxide ($CO_2$) enters the leaves through stomata, where it diffuses over short distances through intercellular spaces until it reaches the mesophyll cells. Once in the mesophyll cells, $CO_2$ diffuses into the stroma of the chloroplast—the site of light-independent reactions of photosynthesis (Figure **9.3.1**). The light-independent reactions (also known as the Calvin cycle) can be organized into three basic stages: fixation, reduction, and regeneration (Video **9.3.1**).

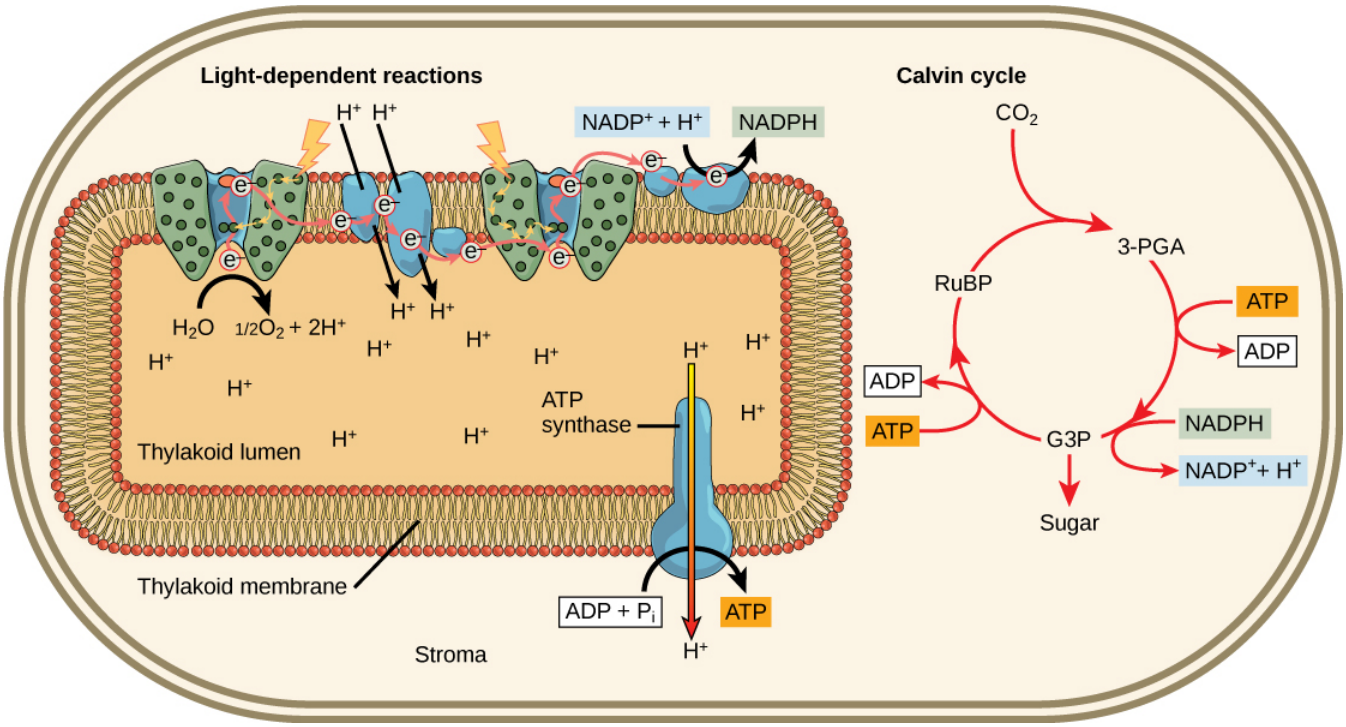



Figure **9.3.1**: Light-dependent reactions harness energy from the sun to produce chemical bonds, ATP, and NADPH. These energy-carrying molecules are made in the stroma where carbon fixation takes place as part of the light-independent reactions (Calvin cycle). The entire image represents the chloroplasts, which is bound by a double membrane. The solution within the chloroplasts is the stroma. A portion of the thylakoid membrane is on the left, and it encloses the thylakoid lumen. Embedded in it are various photosystems (collections of pigments) and protein complexes, which form an electron transport chain. Excited electrons move along the electron transport chain and are ultimately used to reduce $NADP^+$, producing NADPH. The energy from the electrons is used to pump protons into the thylakoid lumen. Protons move down their concentration gradient through ATP synthase, generating ATP. Water is oxidized to replace lost electrons, releasing gaseous oxygen ($O_2$). The Calvin cycle on the right shows how carbon dioxide ($CO_2$) is added to rubulose-1,5,-bisphosphate (RuBP) to produce 3-phosphoglycerate (3-PGA). ATP and NADPH are consumed to reduce 3-PGA to glyceraldehyde-3-phosphate (G3P), which can be used to produce other sugars (glucose). Additional ATP is consumed to regenerate RuBP from G3P, completing the cycle.



Video 9.3.1: Here is an animation of the light-independent reactions (Calvin cycle):

## Stage 1: Fixation

In the stroma, in addition to $CO_2$, two other components are present to initiate the light-independent reactions: an enzyme called **ribulose-1,5-bisphosphate carboxylase/oxygenase** (**RuBisCO**), and three molecules of **ribulose-1,5-bisphosphate** (**RuBP**), as shown in Figure 9.3.2. RuBP has five atoms of carbon, flanked by two phosphates.

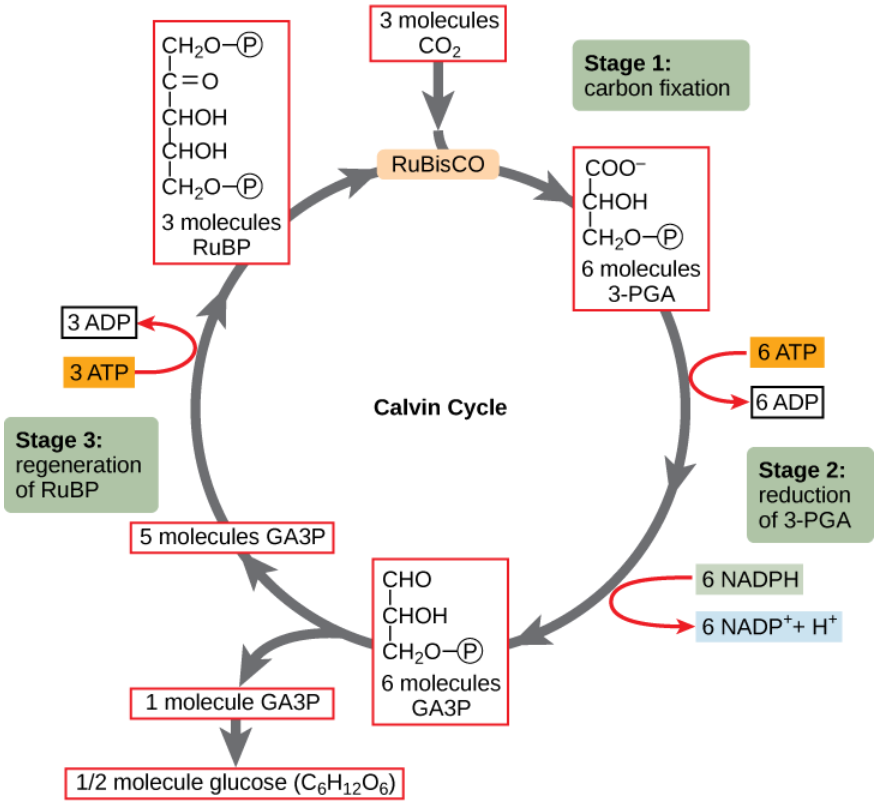



Figure 9.3.2: The light-independent reactions (Calvin cycle) has three stages. In stage 1, the enzyme RuBisCO adds carbon dioxide to RuBP, which immediately splits, producing two three-carbon 3-PGA molecules. In stage 2, two NADPH and two ATP are used to reduce 3-PGA to GA3P. In stage 3, RuBP, the molecule that starts the cycle, is regenerated so that the cycle can continue. One ATP is used in the process. Only one carbon dioxide molecule is incorporated at a time, so the cycle must be completed three times to produce a single three-carbon GA3P molecule, and six times to produce a six-carbon glucose molecule.

RuBisCO catalyzes a reaction between $CO_2$ and RuBP. For each $CO_2$ molecule that reacts with one RuBP, two molecules of another compound, **3-phosphoglycerate** (3-PGA), form. 3-PGA has three carbon atoms and one phosphate. Each turn of the cycle involves only one RuBP and one carbon dioxide and forms two molecules of 3-PGA. The number of carbon atoms remains the

same, as the atoms move to form new bonds during the reactions (3 atoms from 3 $CO_2$ + 15 atoms from 3 RuBP = 18 atoms in 3 atoms of 3-PGA). This process is called **carbon fixation**, because $CO_2$ is "fixed" from an inorganic form into organic molecules.

## Stage 2: Reduction

ATP and NADPH are used to convert the six molecules of 3-PGA into six molecules of a chemical called **glyceraldehyde 3-phosphate** (G3P). That is a reduction reaction because it involves the gain of electrons by 3-PGA. Recall that **reduction** is the gain of an electron by an atom or molecule. Six molecules of both ATP and NADPH are used. For ATP, energy is released with the loss of the terminal phosphate atom, converting it into ADP; for NADPH, both energy and a hydrogen atom are lost, converting it into $NADP^+$. Both of these molecules return to the nearby light-dependent reactions to be reused and re-energized.

## Stage 3: Regeneration

Interestingly, at this point, only one of the G3P molecules leaves the light-independent reactions and is sent to the cytoplasm to contribute to the formation of other compounds needed by the plant. Because the G3P exported from the chloroplast has three carbon atoms, it takes three "turns" of the cycle to fix enough net carbon to export one G3P. But each turn makes two G3P, thus three turns make six G3P. One of these six is exported while the remaining five G3P molecules remain in the cycle and are used to regenerate RuBP, which enables the system to prepare for more $CO_2$ to be fixed. Three more molecules of ATP are used in these regeneration reactions.

### Evolution Connection: Photosynthesis

During the evolution of photosynthesis, a major shift occurred from the bacterial type of photosynthesis that involves only one photosystem and is typically anoxygenic (does not generate oxygen) into modern oxygenic (does generate oxygen) photosynthesis, employing two photosystems. This modern oxygenic photosynthesis is used by many organisms—from giant tropical leaves in the rainforest to tiny cyanobacterial cells—and the process and components of this photosynthesis remain largely the same (Figure **9.3.3**). Photosystems absorb light and use electron transport chains to convert energy into the chemical energy of ATP and NADPH. The subsequent light-independent reactions then assemble carbohydrate molecules with this energy.



Figure **9.3.3**: Cyanobacteria, like *Anabaena circinalis*, do essentially the same type of photosynthesis as plants and algae. Image by Bdcarl (CC-BY-SA).

## Attribution

Curated and authored by Melissa Ha using the following sources:

- 8.3 Using Light Energy to Make Organic Molecules from *Biology 2e* by OpenStax (licensed CC-BY). Access for free at openstax.org.
- 3.3 Enzymatic Stage from *Introduction to Botany* by Alexey Shipunov (public domain)

This page titled 9.3: Light-independent Reactions is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **4.1.6: Light-independent Reactions** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-SA 4.0.

# CHAPTER OVERVIEW

## 10: Photosynthesis - light reactions

10.1: Energy and ATP
10.2: The Light-dependent Reactions

This page titled 10: Photosynthesis - light reactions is shared under a not declared license and was authored, remixed, and/or curated by Tom Buckley.

# 10.1: Energy and ATP

## Learning Objectives

- Describe the different types of energy.
- Describe the structure and function of ATP.

Understanding photosynthesis and aerobic cellular respiration relies on the fundamentals of energy. **Energy** is defined as the ability to do work, and there are several types of energy (Figure **10.1.1**). **Kinetic energy** is the energy of motion. Examples include a ball rolling down a hill, heat energy, and light energy. **Heat energy** is technically energy that is transferred between systems without doing work. The higher the temperature, the faster molecules in matter move. **Potential energy** is the energy that matter possesses but is not currently being used. For example, a ball sitting a the top of the hill that has not yet rolled down the hill possesses potential energy. **Chemical energy** is an example of potential energy that is stored in molecules. When molecules that are higher energy and less stable react to form products that are lower energy and more stable, this stored energy is released.



Figure **10.1.1**: Water stored at the top of a dam has potential energy (left). Water rushing down an incline has kinetic energy (right). Image by OpenStax (CC-BY). Access for free at openstax.org.

**Adenosine triphosphate** (**ATP**) is considered the energy currency of the cell because it provides usable energy. Structurally, ATP resembles a modified nucleotide (the building blocks of DNA and RNA). Specifically, it consists of adenine, ribose, and three phosphate groups (Figure **10.1.2**). The bonds between the phosphate groups are unstable. When these bonds are broken, more stable bonds are formed in their place, releasing energy. **Phosphorylation** refers to adding a phosphate group ($PO_4^{3-}$) to a molecule. However, it often refers specifically to synthesizing ATP by adding a phosphate group to **adenosine diphosphate** (**ADP**).

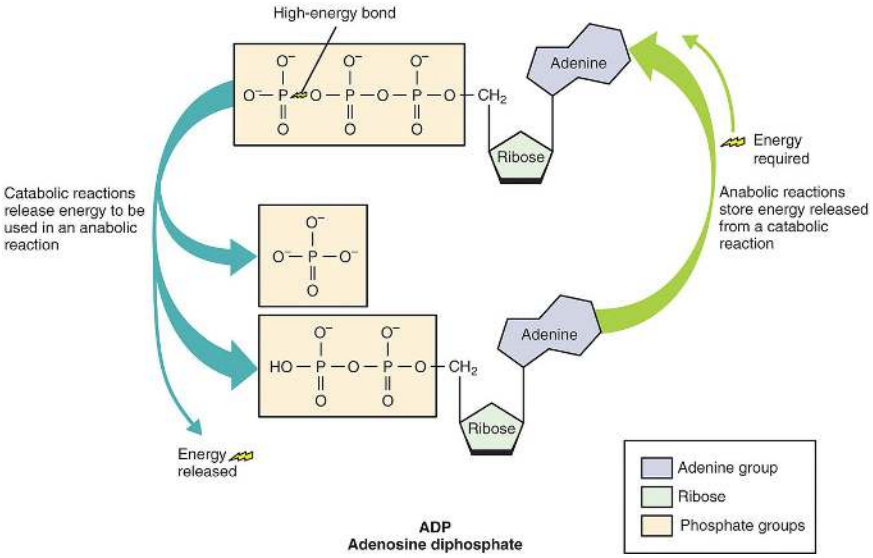



Figure **10.1.2**: ATP consists of adenine, ribose, and three phosphate groups. ADP is similar but only has two phosphate groups. With energy input, adenosine triphoshate (ATP) can be synthesized from adenosine diphosphate (ADP) and a phosphate group. This occurs during anabolic reactions, which store energy. ATP can then be broken down to provide usable energy to the cell. This occurs during catabolic reactions, which release energy. Image by OpenStax (CC-BY). Access for free at openstax.org.

---

This page titled 10.1: Energy and ATP is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Melissa Ha.

# 10.2: The Light-dependent Reactions

**Learning Objectives**

- Relate wavelength, energy, and the type of electromagnetic radiation (and the color of visible light).
- Explain how plants absorb energy from sunlight.
- Detail the steps of the light-dependent interactions.

How can light be used to make food? When a person turns on a lamp, electrical energy becomes light energy. Like all other forms of kinetic energy, light can travel, change form, and be harnessed to do work. In the case of photosynthesis, light energy is converted into chemical energy, which photoautotrophs use to build carbohydrate molecules (Figure 10.2.1). However, photoautotrophs only use a few specific components of sunlight.



Figure 10.2.1: Photoautotrophs can capture light energy from the sun, converting it into the chemical energy used to build food molecules. (credit: Gerry Atwell)

## What Is Light Energy?

The sun emits an enormous amount of **electromagnetic radiation** (solar energy). Humans can see only a fraction of this energy, which portion is therefore referred to as “visible light”. The manner in which solar energy travels is described as waves. Scientists can determine the amount of energy of a wave by measuring its **wavelength**, the distance between consecutive points of a wave. A single wave is measured from two consecutive points, such as from crest to crest or from trough to trough (Figure 10.2.2). The difference between wavelengths relates to the amount of energy carried by them.

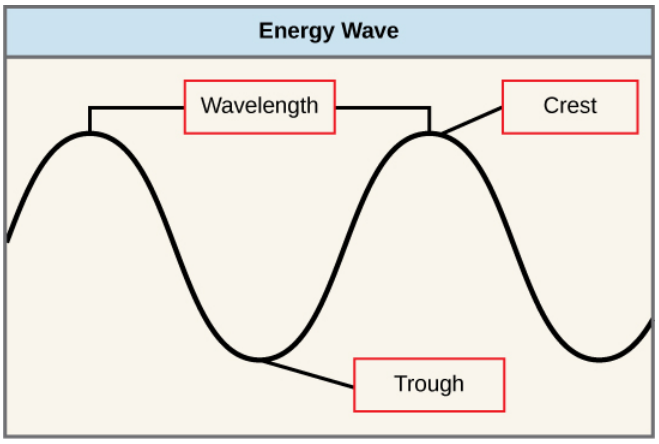



Figure **10.2.2**: The wavelength of a single wave is the distance between two consecutive points of similar position (two crests or two troughs) along the wave.

Visible light constitutes only one of many types of electromagnetic radiation emitted from the sun and other stars. Scientists differentiate the various types of radiant energy from the sun within the electromagnetic spectrum. The electromagnetic spectrum is the range of all possible frequencies of radiation (Figure **10.2.3**). Several types of electromagnetic radiation originate from the sun, including X-rays and ultraviolet (UV) rays. The higher-energy waves can penetrate tissues and damage cells and DNA, explaining why both X-rays and UV rays can be harmful to living organisms.

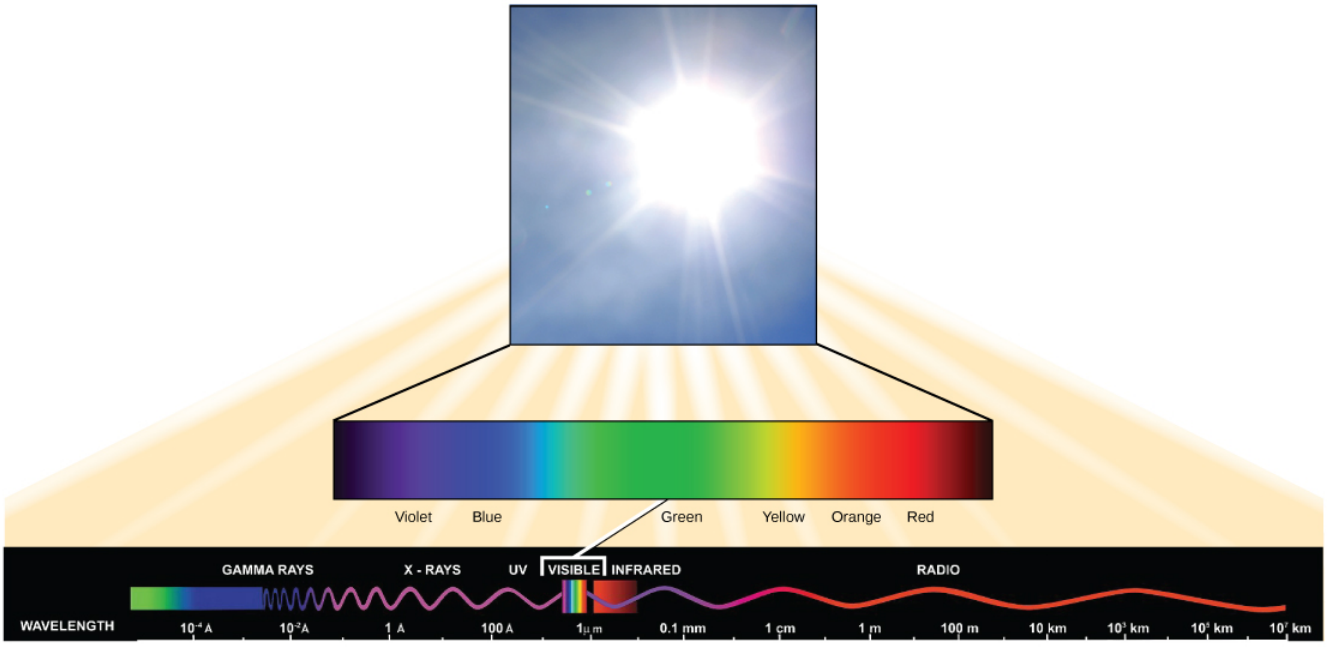



Figure **10.2.3**: The sun emits energy in the form of electromagnetic radiation. This radiation exists at different wavelengths, each of which has its own characteristic energy. All electromagnetic radiation, including visible light, is characterized by its wavelength. Gamma rays have a very short wavelength, on the order of one thousandth of a nanometer (nm). Radio waves have a very long wavelength, on the order of one kilometer. Visible light ranges from violet (380 nm) to blue, green, yellow, orange, and finally red (750 nm) at the end of the spectrum.

Each type of electromagnetic radiation travels at a particular wavelength. The longer the wavelength (or the more stretched out it appears in the diagram), the less energy is carried. Short, tight waves carry the most energy. This may seem illogical, but think of it in terms of a piece of moving a heavy rope. It takes little effort by a person to move a rope in long, wide waves. To make a rope move in short, tight waves, a person would need to apply significantly more energy.

## Absorption of Light

Light energy initiates the process of photosynthesis when pigments absorb the light. Organic pigments, whether in the human retina or the chloroplast thylakoid, have a narrow range of energy levels that they can absorb. Energy levels lower than those represented

by red light are insufficient to excite electrons in the retinal pigments. Energy levels higher than those in blue light will physically tear these molecules apart, called bleaching. So retinal pigments can only "see" (absorb) 700 nm to 400 nm light, which is therefore called visible light. For the same reasons, plants pigment molecules absorb only light in the wavelength range of 700 nm to 400 nm; plant physiologists refer to this range for plants as photosynthetically active radiation.

The visible light seen by humans as white light actually exists in a rainbow of colors. Certain objects, such as a prism or a drop of water, disperse white light to reveal the colors to the human eye. The visible light portion of the electromagnetic spectrum shows the rainbow of colors, with violet and blue having shorter wavelengths, and therefore higher energy. At the other end of the spectrum toward red, the wavelengths are longer and have lower energy (Figure **10.2.4**).

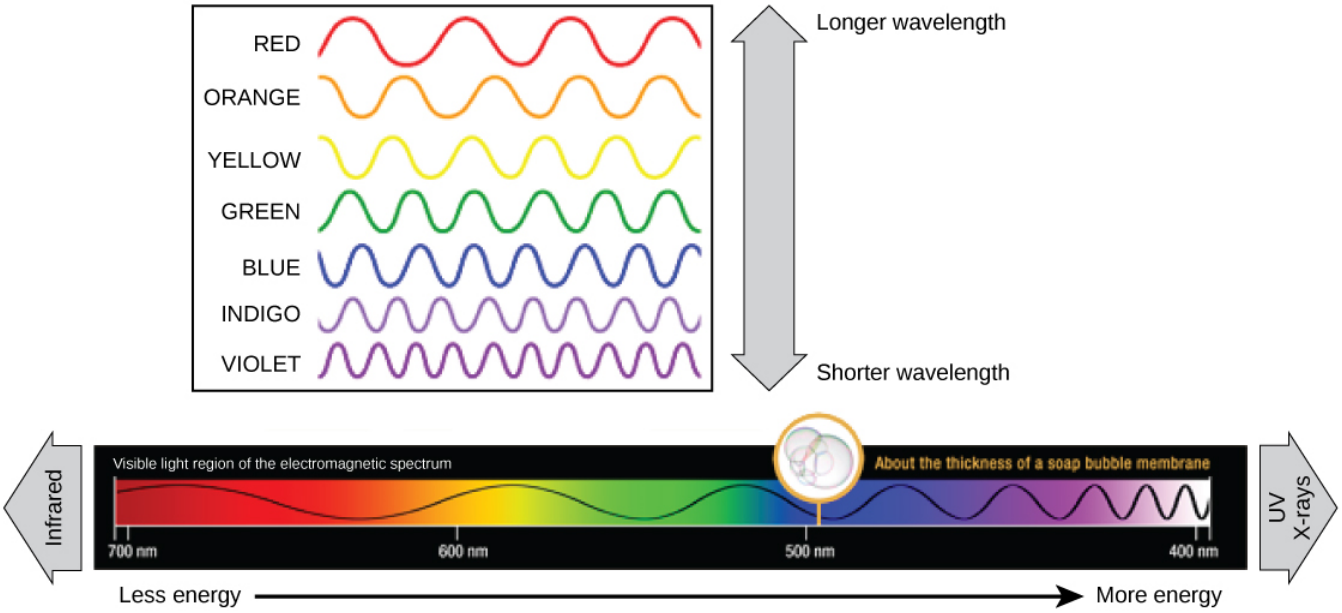



Figure **10.2.4**: The colors of visible light do not carry the same amount of energy. Violet has the shortest wavelength (approximately 400 nm) and therefore carries the most energy. Next is indigo, blue, green, yellow, orange, and finally red, which has the longest wavelength (approximately 700 nm) and carries the least amount of energy. 500 nanometers is about the thickness of a soap bubble membrane. Infrared has longer wavelengths than red light, and UV and X-rays have shorter wavelengths than violet light. (credit: modification of work by NASA)

## Understanding Pigments

Different kinds of pigments exist, and each has evolved to absorb only certain wavelengths (colors) of visible light. Pigments reflect or transmit the wavelengths they cannot absorb, making them appear in the corresponding color.

**Chlorophylls** and **carotenoids** are the two major classes of photosynthetic pigments found in plants and algae; each class has multiple types of pigment molecules. There are five major chlorophylls: *a*, *b*, *c* and *d* and a related molecule found in prokaryotes called bacteriochlorophyll. Chlorophyll *a* and chlorophyll *b* are found in plant chloroplasts and will be the focus of the following discussion.

With dozens of different forms, carotenoids are a much larger group of pigments. The carotenoids found in fruit—such as the red of tomato (lycopene), the yellow of corn seeds (zeaxanthin), or the orange of an orange peel (β-carotene)—are used as advertisements to attract seed dispersers. In photosynthesis, carotenoids function as photosynthetic pigments that are very efficient molecules for the disposal of excess energy. When a leaf is exposed to full sun, the light-dependent reactions are required to process an enormous amount of energy; if that energy is not handled properly, it can do significant damage. Therefore, many carotenoids reside in the thylakoid membrane, absorb excess energy, and safely dissipate that energy as heat.

Each type of pigment can be identified by the specific pattern of wavelengths it absorbs from visible light, which is the absorption spectrum. The graph in Figure **10.2.5** shows the absorption spectra for chlorophyll *a*, chlorophyll *b*, and a type of carotenoid pigment called β-carotene (which absorbs blue and green light). Notice how each pigment has a distinct set of peaks and troughs, revealing a highly specific pattern of absorption. Chlorophyll *a* absorbs wavelengths from either end of the visible spectrum (blue

and red), but not green. Because green is reflected or transmitted, chlorophyll appears green. Carotenoids absorb in the short-wavelength blue region, and reflect the longer yellow, red, and orange wavelengths.

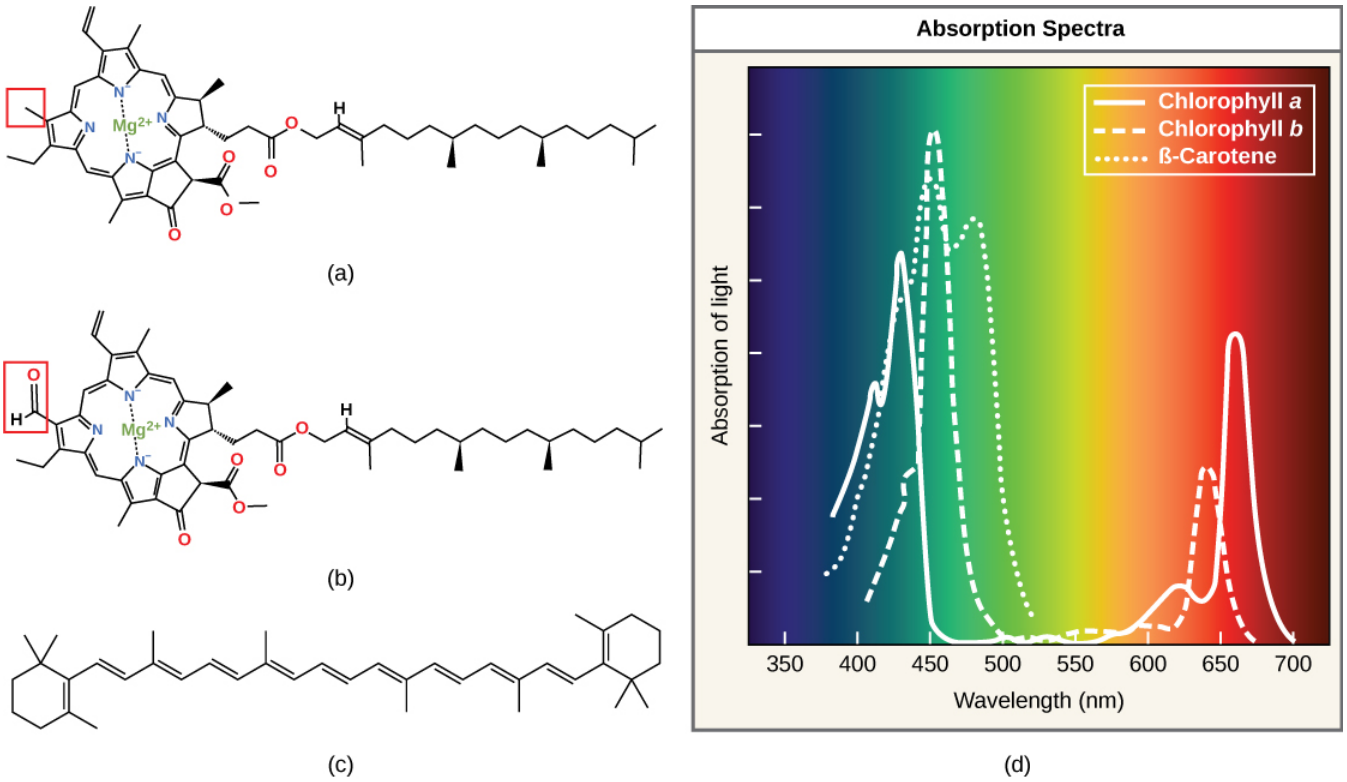



Figure **10.2.5**: (a) Chlorophyll *a*, (b) chlorophyll *b*, and (c) *β*-carotene are hydrophobic organic pigments found in the thylakoid membrane. Chlorophyll a and chlorophyll b are made up of a long hydrocarbon chain attached to a large, complex ring made up of nitrogen and carbon. Magnesium is associated with the center of the ring. Chlorophyll b differs from chlorophyll a in that it has a CHO group instead of a $CH_3$ group associated with one part of the ring (indicated in the red box, are responsible for the green color of leaves). *β*-carotene is a branched hydrocarbon with a six-membered carbon ring at each end. β-carotene is responsible for the orange color in carrots. Each pigment has (d) a unique absorbance spectrum. Chlorophyll *a* peaks around 430 and 660 nm. Chlorophyll *b* peaks around 450 nm and 640 nm. *β*-carotene peaks around 450-500 nm and 640 nm.

Many photosynthetic organisms have a mixture of pigments; using them, the organism can absorb energy from a wider range of wavelengths. Not all photosynthetic organisms have full access to sunlight. Some organisms grow underwater where light intensity and quality decrease and change with depth (Figure **10.2.6**). Other organisms grow in competition for light. Plants on the rainforest floor must be able to absorb any bit of light that comes through, because the taller trees absorb most of the sunlight and scatter the remaining solar radiation (Figure **10.2.7**).

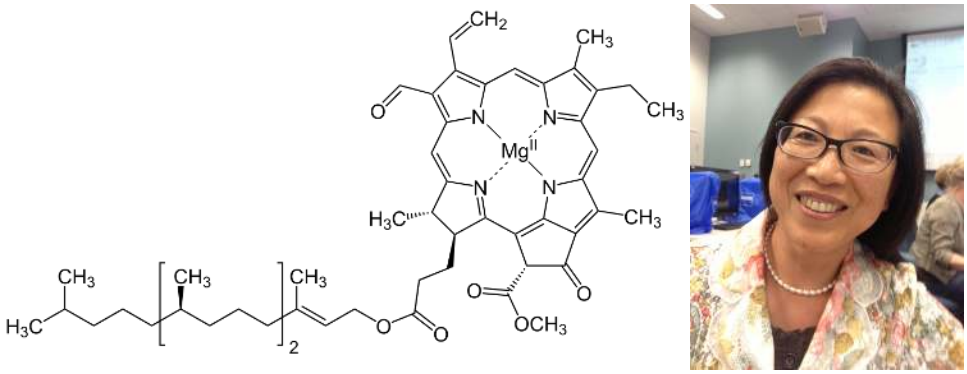


Figure **10.2.6**: In 2010, a new type of chlorophyll, chlorophyll *f* (left), was discovered by Min Chen (right) and colleagues in 2010. It allows cyanobacteria to photosynthesize while deep inside of rocks and absorb infrared light (706 nm) for photosynthesis. Left image by Yikrazuul (public domain), and right image by Ariconte (CC-BY-SA).

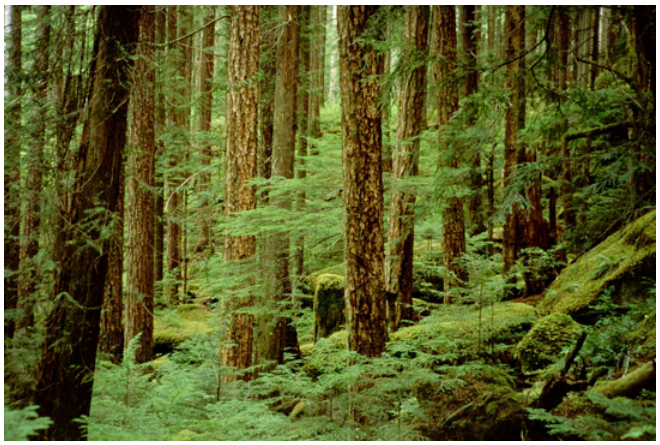


Figure **10.2.7**: Plants that commonly grow in the shade have adapted to low levels of light by changing the relative concentrations of their chlorophyll pigments. (credit: Jason Hollinger)

When studying a photosynthetic organism, scientists can determine the types of pigments present by generating absorption spectra. An instrument called a **spectrophotometer** can differentiate which wavelengths of light a substance can absorb. Spectrophotometers measure transmitted light and compute from it the absorption. By extracting pigments from leaves and placing these samples into a spectrophotometer, scientists can identify which wavelengths of light an organism can absorb. Additional methods for the identification of plant pigments include various types of **chromatography** that separate the pigments by their relative affinities to solid and mobile phases.

## How Light-Dependent Reactions Work

The overall function of light-dependent reactions is to convert solar energy into chemical energy in the form of NADPH and ATP. This chemical energy supports the light-independent reactions and fuels the assembly of sugar molecules. In the light-dependent reactions protein complexes and pigment molecules work together to produce NADPH and ATP (Figure **10.2.8** and Video **10.2.1**).

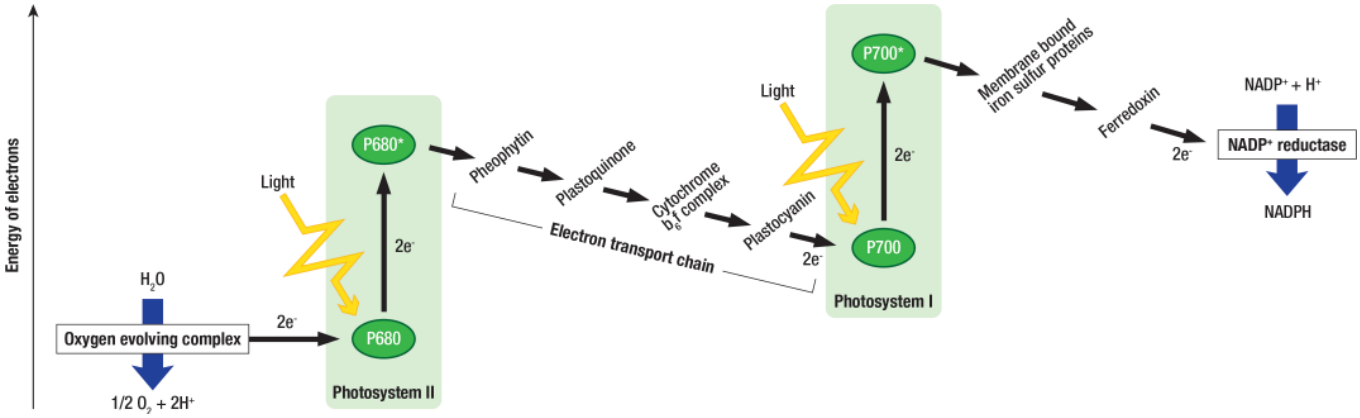



Figure **10.2.8**: The photosynthesis Z-scheme shows the unidirectional flow of electrons from photosystem II ultimately to $NADP^+$. First, photosystem II absorbs light energy. Excited electrons ($2e^-$) are passed to pheophytin, plastoquinone, cytochrome $b_6f$ complex, plastocyanin, and then to photosystem I. This provides energy for ATP synthesis via photophosphorylation (not shown). Photosystem I then absorbs light energy. Excited electrons are passed to membrane sulfur proteins, ferredoxin, and finally to NADP+ reductase, which reduces $NADP^+$ to NADPH. Electrons initially lost from photosystem II are replaced by oxidizing water, producing gaseous oxygen. Image by Jen Valenzuela (CC-BY).



Video **10.2.1**: Here is an animation of the light-dependent reactions.

## Photosystems Absorb Light Energy

The actual step that converts light energy into chemical energy takes place in a multiprotein complex called a **photosystem**, two types of which are found embedded in the thylakoid membrane, **photosystem II** (PSII) and **photosystem I** (PSI) (Figure **10.2.9**). The two complexes differ on the basis of what they oxidize (that is, the source of the low-energy electron supply) and what they reduce (the place to which they deliver their energized electrons).

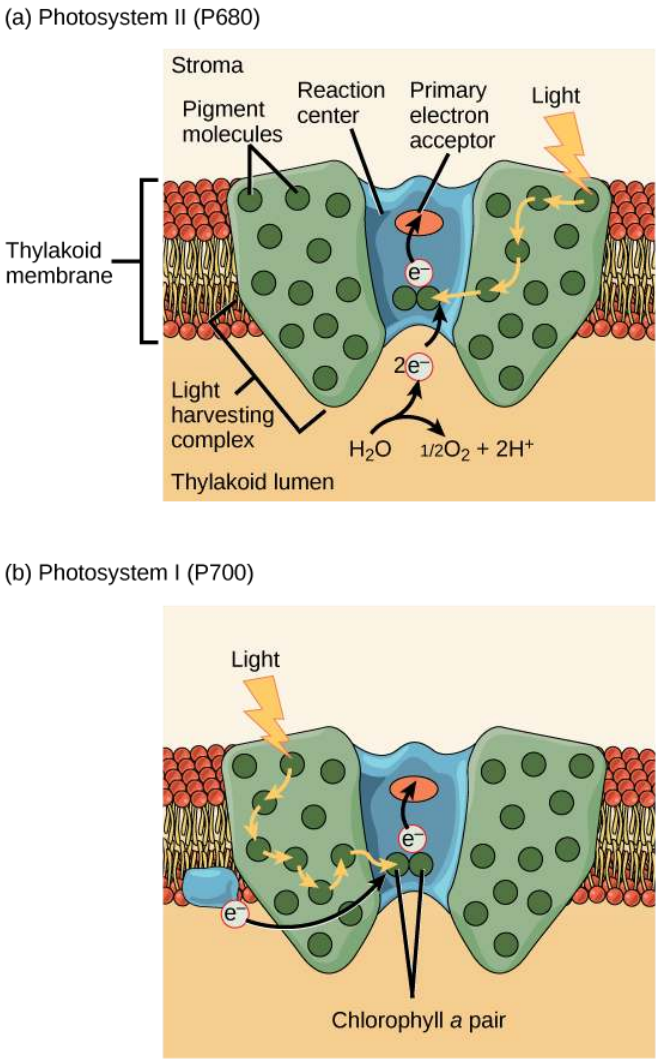



Figure **10.2.9**: A photosystem consists of an antenna complex (labeled as light-harvesting complex) and a reaction center at the core. Pigments in the antenna complex pass light energy to two special chlorophyll a molecules in the reaction center. The light excites an electron from the chlorophyll a pair, which passes to the primary electron acceptor. The excited electron must then be replaced. In (a) photosystem II, the electron comes from the splitting of water, which releases oxygen as a waste product. In (b) photosystem I, the electron comes from the chloroplast electron transport chain discussed below.

Both photosystems have the same basic structure; a number of antenna proteins to which the chlorophyll molecules are bound surround the **reaction center**, where the photochemistry takes place. Each photosystem is serviced antenna complex, which passes energy from sunlight to the reaction center. The **antenna complex** consists of multiple antenna proteins that contain a mixture of 300–400 chlorophyll *a* and *b* molecules as well as other pigments like carotenoids. (Technically, photosystems consist of the reaction center and the antennae complex, and a photosytem plus light-harvesting complexes comprises a photosystem complex, but in Figure **10.2.9**, the light-harvesting complex is labeled as the antennae complex.) The absorption of a single **photon**, or distinct quantity or "packet" of light, by any of the chlorophylls pushes that molecule into an excited state. In short, the light energy has now been captured by biological molecules but is not stored in any useful form yet. The energy is transferred from chlorophyll to chlorophyll until eventually (after about a millionth of a second), it is delivered to the reaction center. Up to this point, only energy has been transferred between molecules, not electrons.

The reaction center contains a pair of chlorophyll *a* molecules with a special property. Those two chlorophylls can undergo oxidation upon excitation; they can actually give up an electron. It is at this step in the reaction center, this step in photosynthesis, that light energy is converted into an excited electron.

## Electrons Move Down the Electron Transport Chain, Providing Energy to Pump Protons into the Thylakoid Lumen

The reaction center of PSII (called P680) delivers its high-energy electrons, one at the time, to the primary electron acceptor, and through the **electron transport chain** (Pq to cytochrome b6f complex to plastocyanine) to PSI (Figure 10.2.10). The **cytochrome b6f complex**, an enzyme composed of two protein complexes, transfers the electrons from the carrier molecule **plastoquinone** (Pq) to the protein **plastocyanin** (Pc), ultimately facilitating the transfer of electrons from PSII to PSI. During this process, cytochrome b6f pumps protons from the stroma into the thylakoid lumen using the energy from electrons moving down the electron transport chain.

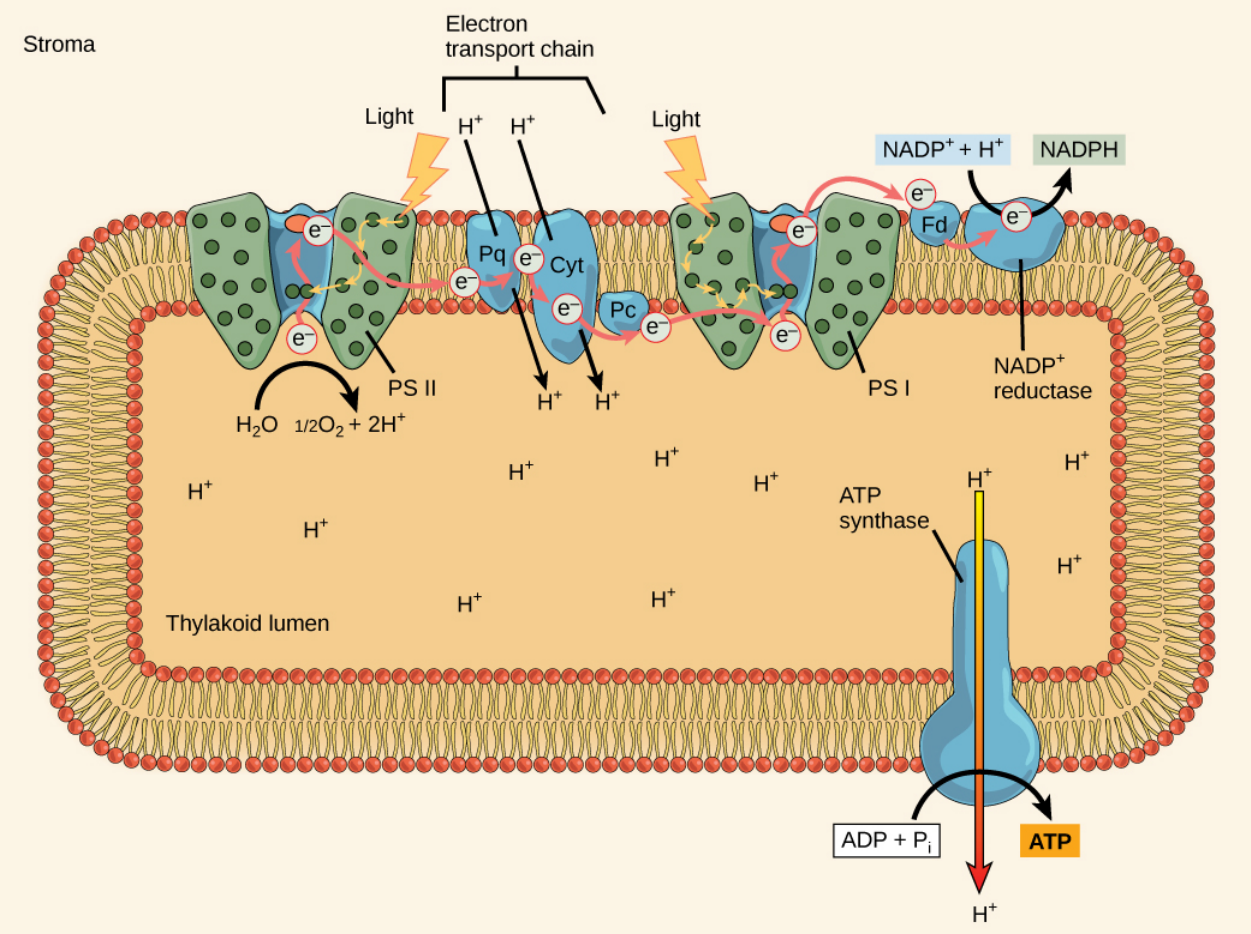



Figure 10.2.10: In the photosystem II (PSII) reaction center, energy from sunlight is used to extract electrons from water, producing half an oxygen molecule and two protons in the process. The electrons travel through the chloroplast electron transport chain to photosystem I (PSI), which passes the electron to NADP+ reductase, which uses it to convert NADP+ and a proton to NADPH. The electron transport chain moves protons ($H^+$) across the thylakoid membrane into the lumen. At the same time, splitting of water adds protons to the lumen, and reduction of NADPH removes protons from the stroma. The net result is a low pH in the thylakoid lumen, and a high pH in the stroma. ATP synthase moves protons down their electrochemical gradient, from the lumen to the stroma, and uses the energy from this gradient to make ATP.

## Photophosphorylation

The synthesis of ATP in the light-dependent reactions is called **photophosphorylation**. The buildup of protons inside the thylakoid lumen creates a concentration gradient. The passive movement (facilitated diffusion) of protons from high concentration (in the thylakoid lumen) to low concentration (in the stroma) is harnessed to create ATP. The protons build up energy at high concentrations because they all have the same electrical charge, repelling each other.

To release this energy, protons will rush through any opening, similar to water jetting through a hole in a dam. In the thylakoid, that opening is a passage through a specialized protein channel called the **ATP synthase**. The energy released by the proton stream allows ATP synthase to attach a third phosphate group to ADP, which forms a molecule of ATP (Figures 10.2.10 – 11). The flow of

protons through ATP synthase is called **chemiosmosis** because the ions move from an area of high to an area of low concentration through a semi-permeable structure.

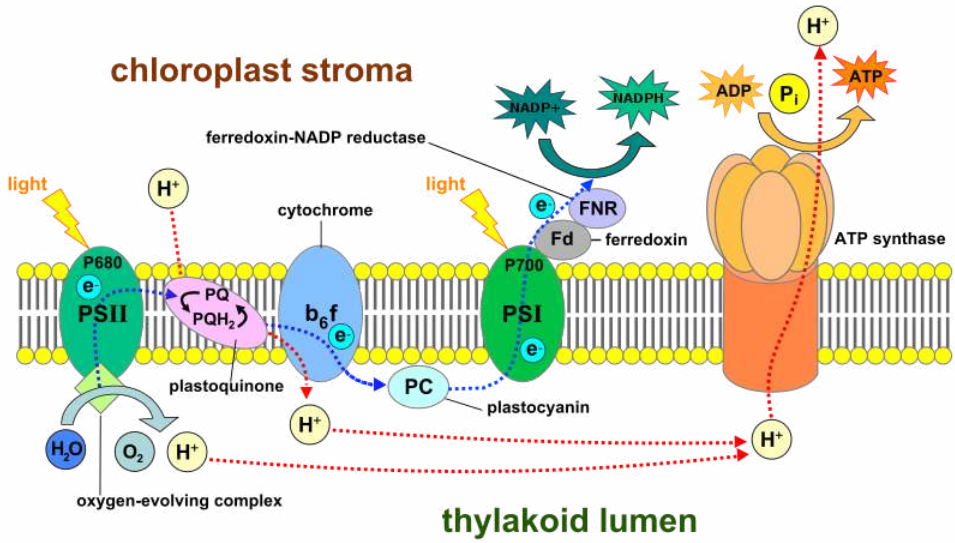



Figure **10.2.11**: The electron transport chain, water photolysis, and photophosphorylation in the light-dependent reactions. Light is first absorbed by photosystem II (PS II) and high-energy electrons ($e^-$) are transferred to pheophytin (not shown), which pass electrons to plastoquinone (PQ) and then to cytochrome $b_6$/f complex, which pumps protons ($H^+$) into the thylakoid lumen. Electrons then are passed to plastocyanin (PC) and then photosystem I (PSI). PS I reabsorbs light energy, and high-energy electrons are passed to ferredoxin (Fd) and then to ferredoxin-$NADP^+$ reductase. Finally, the electrons reduce $NADP^+$ to NADPH. Protons move down their electrochemical gradients through ATP synthase into the stroma, generating ATP. Electrons lost from PS III are replaced by oxidizing water ($H_2O$), releaseing gaseous oxygen ($O_2$) and protons. Image by Somepics (CC-BY-SA).

### Water Photolysis

P680's missing electron is replaced by extracting a low-energy electron from water; thus, water is split (**water photolysis**) and PSII is re-reduced. Splitting one $H_2O$ molecule releases two electrons, two protons, and one atom of oxygen (Figures **10.2.10 – 11**). Those protons, in addition to the ones transported by cytrochrome b6f, accumulate in the thylakoid lumen and fuel photophosphorylation. Splitting two molecules is required to form one molecule of diatomic $O_2$ gas. About 10 percent of the oxygen is used by mitochondria in the leaf to support aerobic cellular respiration, the process of breaking down glucose to generate ATP. The remainder escapes to the atmosphere where it is used by aerobic organisms to support respiration.

### Reduction of $NADP^+$

Because the electrons have lost energy prior to their arrival at PSI, they must be re-energized by PSI, hence, another photon is absorbed by the PSI antenna. That energy is relayed to the PSI reaction center (called P700). P700 is oxidized and sends high-energy electrons to the electron carrier $NADP^+$ to form NADPH. Thus, PSII captures the energy to create proton gradients to make ATP, and PSI captures the energy to reduce $NADP^+$ into NADPH. The two photosystems work in concert, in part, to guarantee that the correct proportions of NADPH and ATP needed for the light-independent reactions are generated. Other mechanisms exist to fine tune that ratio to exactly match the chloroplast's constantly changing energy needs.

## Attribution

Curated and authored by Melissa Ha using 8.2 The Light-Dependent Reactions of Photosynthesis from *Biology 2e* by OpenStax (licensed CC-BY). Access for free at openstax.org.

---

This page titled 10.2: The Light-dependent Reactions is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **4.1.5: The Light-dependent Reactions** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-SA 4.0.

# CHAPTER OVERVIEW

## 11: Plant water relations


11.1: Water Potential

11.2: Transpiration

11.2.1: Adaptations to Reduce Transpiration

11.2.2: Stomatal Opening and Closure

11.3: Cohesion-Tension Theory

11.4: Water Absorption

11.5: Water Transport

11.6: Transport of Water and Solutes in Plants


---

This page titled 11: Plant water relations is shared under a not declared license and was authored, remixed, and/or curated by Tom Buckley.

# 11.1: Water Potential

## Learning Objectives

- Define water potential and explain how it is influenced by solutes, pressure, gravity, and the matric potential.
- Explain which components of water potential plants can manipulate and describe how.

Plants are phenomenal hydraulic engineers. Using only the basic laws of physics and the simple manipulation of potential energy, plants can move water to the top of a tree approaching 116 m (~381 ft, see The Tallest Trees box). Plants can also use hydraulics to generate enough force to split rocks and buckle sidewalks (Figure **11.1.1**). Plants achieve this because of water potential.



Figure **11.1.1**: Plant roots can easily generate enough force to buckle and break concrete sidewalks, much to the dismay of homeowners and city maintenance departments. Image modified from Pedestrians Educating Drivers on Safety, Inc.

**Water potential** is a measure of the potential energy in water. Plant physiologists are not interested in the energy in any one particular aqueous system, but they are very interested in water movement between two systems. In practical terms, therefore, water potential is the difference in potential energy between a given water sample and pure water (at atmospheric pressure and ambient temperature). Water potential is denoted by the Greek letter ψ (*psi*) and is expressed in units of pressure (pressure is a form of energy) called megapascals (MPa). The potential of pure water ($\Psi_w^{\text{pure H2O}}$) is, by convenience of definition, designated a value of zero (although pure water contains plenty of potential energy, that energy is ignored). Water potential values for the water in a plant root, stem, or leaf are therefore expressed relative to $\Psi_w^{\text{pure H2O}}$.

The water potential in plant solutions is influenced by solute concentration, pressure, gravity, and factors called matrix effects. Water potential can be broken down into its individual components using the following equation:

$$\psi_{\text{system}} = \psi_{\text{total}} = \psi_s + \psi_p + \psi_g + \psi_m \tag{11.1.1}$$

where $\Psi_s$, $\Psi_p$, $\Psi_g$, and $\Psi_m$ refer to the solute, pressure, gravity, and matric potentials, respectively. “System” can refer to the water potential of the soil water ($\Psi^{\text{soil}}$), root water ($\Psi^{\text{root}}$), stem water ($\Psi^{\text{stem}}$), leaf water ($\Psi^{\text{leaf}}$) or the water in the atmosphere ($\Psi^{\text{atmosphere}}$): whichever aqueous system is under consideration. As the individual components change, they raise or lower the total water potential of a system. When this happens, water moves to equilibrate, moving from the system or compartment with a higher water potential to the system or compartment with a lower water potential. This brings the difference in water potential between the two systems ($\Delta\Psi$) back to zero ($\Delta\Psi = 0$). Therefore, for water to move through the plant from the soil to the air (a process called transpiration), $\Psi^{\text{soil}}$ must be $> \Psi^{\text{root}} > \Psi^{\text{stem}} > \Psi^{\text{leaf}} > \Psi^{\text{atmosphere}}$.

Water only moves in response to $\Delta\Psi$, not in response to the individual components. However, because the individual components influence the total $\Psi_{\text{system}}$, by manipulating the individual components (especially $\Psi_s$), a plant can control water movement. Solutes, pressure, gravity, and matric potential are all important for the transport of water in plants. Water moves from an area of higher total water potential to an area of lower total water potential.

## Solute Potential

**Solute potential** ($\Psi_s$), also called osmotic potential, is negative in a plant cell and zero in distilled water. Typical values for cell cytoplasm are –0.5 to –1.0 MPa. Solutes reduce water potential (resulting in a negative $\Psi_w$) by consuming some of the potential energy available in the water. Solute molecules can dissolve in water because water molecules can bind to them via hydrogen bonds; a hydrophobic molecule like oil, which cannot bind to water, cannot go into solution. The energy in the hydrogen bonds between solute molecules and water is no longer available to do work in the system because it is tied up in the bond. In other words, the amount of available potential energy is reduced when solutes are added to an aqueous system. Thus, $\Psi_s$ decreases with increasing solute concentration.

Because $\Psi_s$ is one of the four components of $\Psi_{system}$ or $\Psi_{total}$, a decrease in $\Psi_s$ will cause a decrease in $\Psi_{total}$. Water moves towards areas of lower $\Psi_s$ (and thus lower $\Psi_{total}$). In Figure **11.1.2**, the semipermeable membrane that separates the two sides of the tube allows water but not solutes to pass. In the first tube, solute has been added to the right side. Adding solute to the right side lowers $\Psi_s$, causing water to move to the right side of the tube. As a result, the water level is higher on the right side.

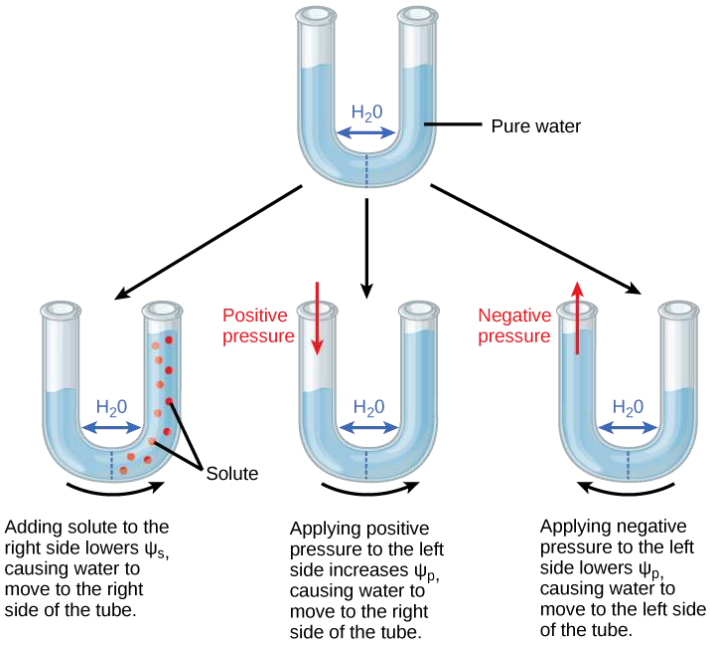



Figure **11.1.2**: In this example with a semipermeable membrane between two aqueous systems, water will move from a region of higher to lower water potential until equilibrium is reached. Solutes ($\Psi_s$), pressure ($\Psi_p$), and gravity ($\Psi_g$) influence total water potential ($\Psi_{total}$ ) for each side of the tube, and therefore, the difference between $\Psi_{total}$ on each side ($\Delta\Psi$). ($\Psi_m$ , the potential due to interaction of water with solid substrates, is ignored in this example.). Water moves in response to the difference in water potential between the left and right sides of the tube. Top image: Pure water is on both sides of the tube. Bottom left image: Adding solute to the the right side lowers $\Psi_s$, causing water to move to the right side fo the tube. Bottom middle image: Applying positive pressure to the left side increases $\Psi_p$, causing water to move to the right side fo the tube. Bottom right image: Applying negative pressure to the left side lowers $\Psi_p$, causing water to move to the left side of the tube.

The internal water potential of a plant cell is more negative than pure water because of the cytoplasm's high solute content. Because of this difference in water potential water will move from the soil into a plant's root cells via the process of osmosis. This is why solute potential is sometimes called osmotic potential. Plant cells can metabolically manipulate $\Psi_s$ (and by extension, $\Psi_{total}$) by adding or removing solute molecules. Therefore, plants have control over $\Psi_{total}$ via their ability to exert metabolic control over $\Psi_s$.

## Pressure Potential

**Pressure potential** ($\Psi_p$), also called turgor potential, may be positive or negative (Figure **11.1.*c***). Because pressure is an expression of energy, the higher the pressure, the more potential energy in a system, and vice versa. Therefore, a positive $\Psi_p$ (compression) increases $\Psi_{total}$, and a negative $\Psi_p$ (tension) decreases $\Psi_{total}$. The second tube in Figure **11.1.2**) has pure water on both sides of the membrane. Positive pressure is applied to the left side. Applying positive pressure to the left side causes $\Psi_p$ to increase. As a results, water moves to the right so that the water level is higher on the right than on the left. The third tube also has pure water, but this time negative pressure is applied to the left side. Applying negative pressure lowers $\Psi_p$, causing water to move to the left side of the tube. As a result, the water level is higher on the left.

Positive pressure inside cells is contained by the cell wall, producing turgor pressure. Pressure potentials are typically around 0.6–0.8 MPa, but can reach as high as 1.5 MPa in a well-watered plant. A $\Psi_p$ of 1.5 MPa equates to 210 pounds per square inch (1.5 MPa x 140 lb $in^{-2}$ $MPa^{-1}$ = 210 $lb/in^{-2}$). As a comparison, most automobile tires are kept at a pressure of 30–34 psi. An example of the effect of turgor pressure is the wilting of leaves and their restoration after the plant has been watered (Figure **11.1.3**). Water is lost from the leaves via transpiration (approaching $\Psi_p$ = 0 MPa at the wilting point) and restored by uptake via the roots.



(a) (b)

Figure **11.1.3**: When (a) total water potential ($\Psi_{total}$) is lower outside the cells than inside, water moves out of the cells, and the plant wilts. When (b) the total water potential is higher outside the plant cells than inside, water moves into the cells, resulting in turgor pressure ($\Psi_p$) and keeping the plant erect. (credit: modification of work by Victor M. Vicente Selvas)

A plant can manipulate $\Psi_p$ via its ability to manipulate $\Psi_s$ and by the process of osmosis. If a plant cell increases the cytoplasmic solute concentration, $\Psi_s$ will decline, $\Psi_{total}$ will decline, the $\Delta\Psi$ between the cell and the surrounding tissue will decline, water will move into the cell by osmosis, and $\Psi_p$ will increase. $\Psi_p$ is also under indirect plant control via the opening and closing of stomata. Stomatal openings allow water to evaporate from the leaf, reducing $\Psi_p$ and $\Psi_{total}$ of the leaf and increasing it between the water in the leaf and the petiole, thereby allowing water to flow from the petiole into the leaf.

## Gravitational Potential

**Gravitational potential** ($\Psi_g$) is always negative to zero in a plant with no height. The force of gravity pulls water downwards to the soil, reducing the difference in water potential between the leaves at the top of the plant and the roots. The taller the plant, the taller the water column, and the more influential $\Psi_g$ becomes. On a cellular scale and in short plants, this effect is negligible and easily ignored. However, over the height of a tall tree like a giant coastal redwood, the gravitational pull of –0.1 MPa $m^{-1}$ is equivalent to an extra 1 MPa of resistance that must be overcome for water to reach the leaves of the tallest trees. Plants are unable to manipulate $\Psi_g$.

## Matric Potential

**Matric potential** ($\Psi_m$) is always negative to zero. In a dry system, it can be as low as –2 MPa in a dry seed, and it is zero in a water-saturated system. The binding of water to a matrix always removes or consumes potential energy from the system. $\Psi_m$ is similar to solute potential because it involves tying up the energy in an aqueous system by forming hydrogen bonds between the water and some other component. However, in solute potential, the other components are soluble, hydrophilic solute molecules,

whereas in $\Psi_m$, the other components are insoluble, hydrophilic molecules of the plant cell wall. Every plant cell has a cellulosic cell wall and the cellulose in the cell walls is hydrophilic, producing a matrix for adhesion of water: hence the name matric potential. $\Psi_m$ is very large (negative) in dry tissues such as seeds or drought-affected soils. However, it quickly goes to zero as the seed takes up water or the soil hydrates. $\Psi_m$ cannot be manipulated by the plant and is typically ignored in well-watered roots, stems, and leaves.

## Attribution

Curated and authored by Melissa Ha using 30.5 Transport of Water and Solutes in Plants from *Biology 2e* by OpenStax (licensed CC-BY). Access for free at openstax.org.

---

This page titled 11.1: Water Potential is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **4.5.1.1: Water Potential** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC 4.0.

# SECTION OVERVIEW

## 11.2: Transpiration

**Learning Objective**

Define transpiration and identify how environmental factors affect transpiration rate.

Less than 1% of the water reaching the leaves is used in photosynthesis and plant growth. Most of it is lost in **transpiration**, the loss of water vapor to the atmosphere through stomata. It is a passive process, meaning that metabolic energy in the form of ATP is not required for water movement. The energy driving transpiration is the difference in water potential between the soil and the atmosphere. Transpiration serve two functions- it provides the force for lifting the water up the stems and it cools the leaves. However, the volume of water lost in transpiration can be very high. It has been estimated that over the growing season, one acre of corn (maize) plants may transpire 400,000 gallons (1.5 million liters) of water. As liquid water, this would cover the field with a lake 15 inches (38 cm) deep.

Transpiration involves several cellular structures in the leaf (Figure 11.2.1). Water on the surface of mesophyll cells saturates the cellulose microfibrils of the primary cell wall. The leaf contains many large intercellular air spaces for the exchange of oxygen for carbon dioxide, which is required for photosynthesis. The wet cell wall is exposed to this leaf internal air space, and the water on the surface of the cells evaporates into the air spaces, decreasing the thin film on the surface of the mesophyll cells.

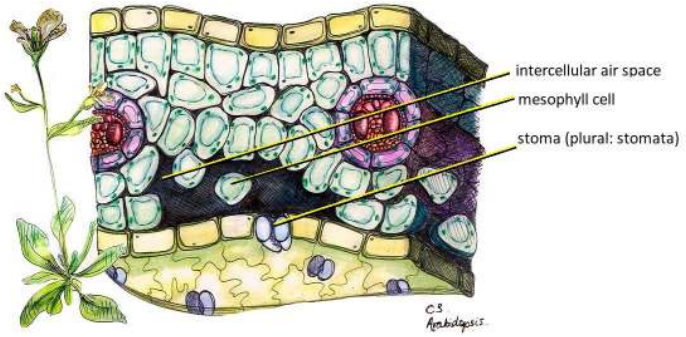



Figure 11.2.1: Intercellular air spaces are found between mesophyll cells in this illustration of an *Arabidopsis thaliana* leaf cross section. During transpiration, water evaporates from mesophyll cells and exits through stomata, the pores in the epidermis, which surrounds the leaf. Image modified from Ninghui Shi (CC-BY-SA).

Several environmental factors influence transpiration rate, which can be measured with a **potometer** (Figure 11.2.2). Light, high temperatures, and wind increase transpiration rate while humidity reduces it. Light stimulates stomatal opening (see Stomatal Opening and Closure), allowing water vapor to easily leave the leaf. Light also speeds up transpiration by warming the leaf. Plants transpire more rapidly at higher temperatures because water evaporates more rapidly as the temperature rises. At 30°C, a leaf may transpire three times as fast as it does at 20°C. Humidity decreases transpiration rate by reducing the difference in water potential between the air and intercellular air spaces. The rate of diffusion of any substance increases as the difference in concentration of the substances in the two regions increases. When the surrounding air is dry, diffusion of water out of the leaf goes on more rapidly. As transpiration occurs, the air surrounding a leaf becomes increasingly humid, reducing the difference in water potential between the intercellular air spaces and the atmosphere and slowing transpiration. When a breeze is present, however, the humid air is carried away and replaced by drier air. Plants can regulate transpiration through opening and closing stomata, and plants that live in especially hot or dry regions have special adaptations to reduce water loss.

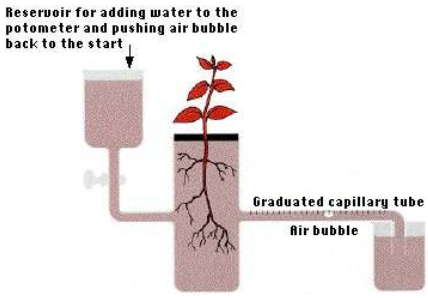



Figure **11.2.2**: This potometer can measure transpiration rate. As water is transpired or otherwise used by the plant, it is replaced from the reservoir on the right. This pushes the air bubble to the left in the graduated capillary tube, providing a precise measure of the volume of water used.

## Attributions

Curated and authored by Melissa Ha using the following sources:

- 30.5 Transport of Water and Solutes in Plants from *Biology 2e* by OpenStax (licensed CC-BY). Access for free at openstax.org.
- 16.2C Transpiration from *Biology* by John. W. Kimball (licensed CC-BY)

**Transpiration**

## 11.2.1: Adaptations to Reduce Transpiration

## 11.2.2: Stomatal Opening and Closure

This page titled 11.2: Transpiration is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

# 11.2.1: Adaptations to Reduce Transpiration

**Learning Objective**

Describe the various adaptations that help plants reduce transpiration rate.

Plants have evolved over time to adapt to their local environment and reduce transpiration. Leaves are covered by a waxy cuticle on the outer surface that prevents the loss of water. Plants that grow in dry environments and plants that grow on other plants (**epiphytes**) have a much thicker waxy cuticle than those growing in more moderate, well-watered environments (Figure **11.2.1.1**). Additionally, they often have a thick covering of **trichomes** or of stomata that are sunken below the leaf's surface (Figure **11.2.1.2**). These adaptations impede air flow across the stomatal pore and reduce transpiration. Multiple epidermal layers are also commonly found in these types of plants .



Figure **11.2.1.1**: Plants are suited to their local environment. Plants adapted to dry conditions such as the prickly pear cactus (*Opuntia* sp., left) and epiphytes like this tropical *Aeschynanthus perrottetii* (right) have adapted to very limited water resources. The leaves of a prickly pear are modified into spines, which lowers the surface area-to-volume ratio and reduces water loss. Photosynthesis takes place in the stem, which also stores water. *A. perottetii* leaves have a waxy cuticle that prevents water loss. The left image is a modification of work by Jon Sullivan, and the right image is a modification of work by L. Shyamal/Wikimedia Commons.

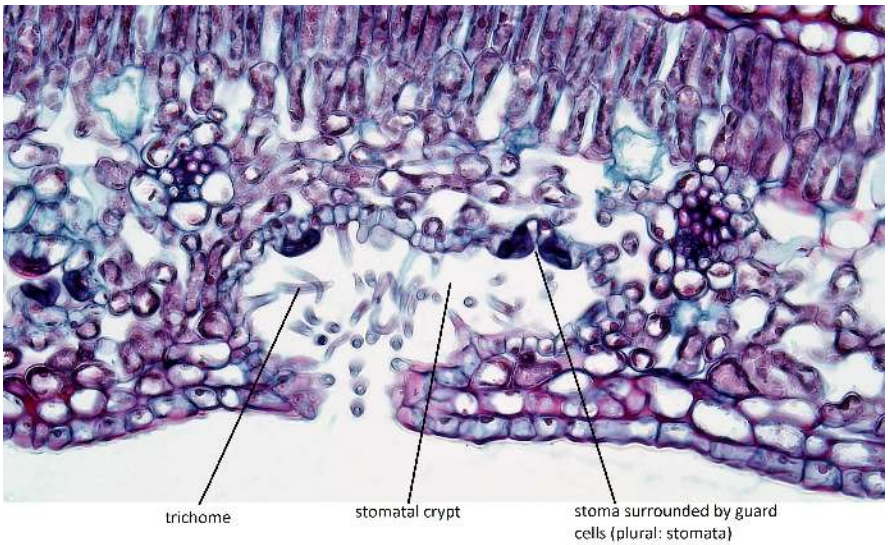



Figure **11.2.1.2**: Cross section of an oleander (*Nerium* sp.) leaf. Oleander is adapted to dry conditions. Stomata are sunken into stomatal crypts and bordered by trichomes, reducing transpiration. Magnified at 400x. Image modified from Berkshire Community College Bioscience Image Library (public domain).

The size and shape of photosynthetic structures also influences transpiration rate. **Succulent** plants, common in deserts, have thick, fleshy leaves or stems (Figure **11.2.1.1**, left). Other plants, such as the evergreen shrubs of the chaparral, have small, thick, tough leaves (Figure **11.2.1.3**). Compared to thin, broad leaves, these shapes reduce surface area-to-volume ratio and decreases the opportunity for water loss. Plants with thin, broad leaves that live in climates with hot, dry seasons (such as chaparral or tropical forests that have a wet and dry season) may be **deciduous**, losing their leaves during these seasons to limit transpiration (Figure **11.2.1.4**).



Figure **11.2.1.3**: (left) The thick, tough leaves of chamise (*Adenostoma fasciculatum*) limit transpiration during dry, hot summers. Image by Tom Hilton (CC-BY). (right) Sal tree (*Shorea robusta*) is a tropical deciduous tree, losing its leaves during the dry season. Image by J.M.Garg (CC-BY-SA).

As discussed in 13.7: Photorespiration and Photosynthetic Pathways, CAM plants close their stomata during the day when light and high temperatures would otherwise increase transpiration rate. $C_4$ plants reduce the need to frequently open stomata by creating a high carbon dioxide concentration in the bundle sheath cells, which conduct the Calvin cycle. Regardless of photosynthetic pathway, plants can open and close stomata to regulate transpiration rate based on environmental conditions.

## Attribution

- Curated and authored by Melissa Ha using 30.5 Transport of Water and Solutes in Plants from *Biology 2e* by OpenStax (licensed CC-BY). Access for free at openstax.org.

---

This page titled 11.2.1: Adaptations to Reduce Transpiration is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **4.5.1.2.1: Adaptations to Reduce Transpiration** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-SA 4.0.

# 11.2.2: Stomatal Opening and Closure

## Learning Objectives

- Relate the pattern of cell wall thickening in guard cells to their function.
- Explain the mechanism by which blue light triggers stomatal opening.
- Explain the mechanism by which water stress, signaled by abscisic acid, triggers stomatal closure.

Regulation of transpiration is achieved primarily through the opening and closing of stomata on the leaf surface. Stomata are surrounded by two specialized cells called guard cells (Figure **11.2.2.1**). Stomata must open to allow the gas exchange of carbon dioxide and oxygen for efficient photosynthesis (see Photorespiration), and light thus typically triggers stomatal opening. When stomata are open, however, water vapor is lost to the external environment, increasing the rate of transpiration. Therefore, plants must maintain a balance between gas exchange and water loss. Water stress, high temperatures, and high carbon dioxide concentration causes stomata to close.

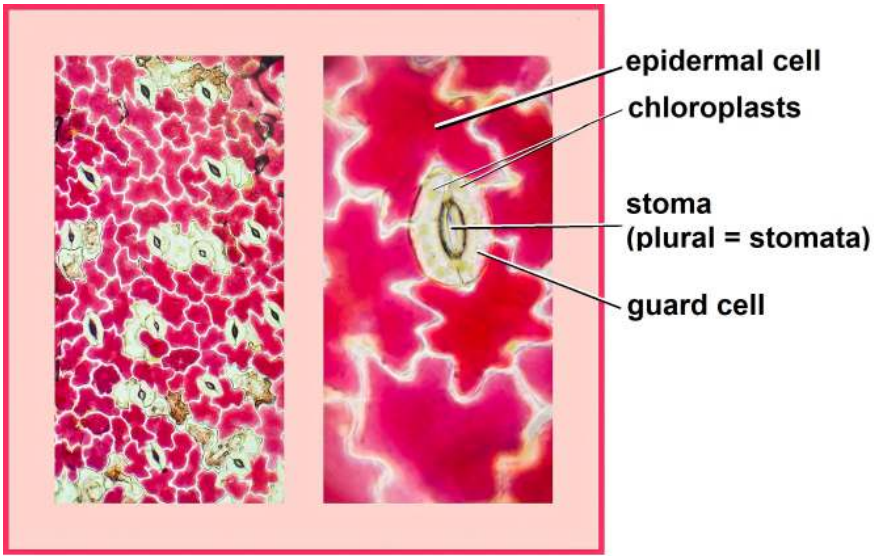



Figure **11.2.2.1**: Italian chicory leaf epidermis showing stomata. The epidermal cells are shaped like puzzle pieces. The stomata (singular = stoma) are pores in the epidermis. Each is bordered by two guard cells, which are filled with oval, green chloroplasts. Image by Umberto Salvagnin (CC-BY).

## Stomatal Opening

Guard cell walls are radially thickened such that the thickenings are concentrated around the stoma (plural: stomata; Figure **11.2.2.2**). When turgor pressure increases in guard cells, the cells swell. However, the thickened inner walls near the stoma cannot expand, so they curve to accommodate the expanding outer walls. The curving of the guard cells opens the stoma.

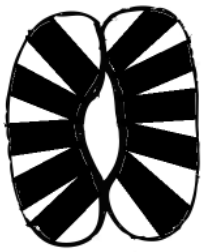


Figure **11.2.2.2**: The guard cells that surround the stoma have radial cell wall thickenings (represented by solid black lines). The portion of the guard cell adjacent to the stoma (ventral side) has a fully thickened cell wall. The outer portion (dorsal side) has alternating bands of thick and thin cell wall. Image modified from Vojtech.dostal (public domain).

How does light cause stomata to open? Phototropins detect blue light, causing a proton pumps to export protons ($H^+$). ATP, generated by the light reactions of photosynthesis, drives the pump. The cytosol usually more negative than the extracellular solution, and this difference in charge (**membrane potential**) increases as protons leave the cell. This increase in membrane potential is called **hyperpolarization**, and it causes potassium ($K^+$) to move down its electrochemical gradient into the cytosol. Protons also move down their electrochemical gradient back into the cytosol, bringing chloride ($Cl^-$) with them through **symport** channels. Meanwhile, starch is broken down, producing sucrose and malate. Nitrate ($NO_3^-$) also enters the cell. The solute potential resulting high concentrations of potassium, chloride, sucrose, malate, and nitrate in the cytosol drives the osmosis of water into the the guard cells. This increases turgor pressure, and the guard cells expand and bend, opening the stoma (Figure **11.2.2.3**).

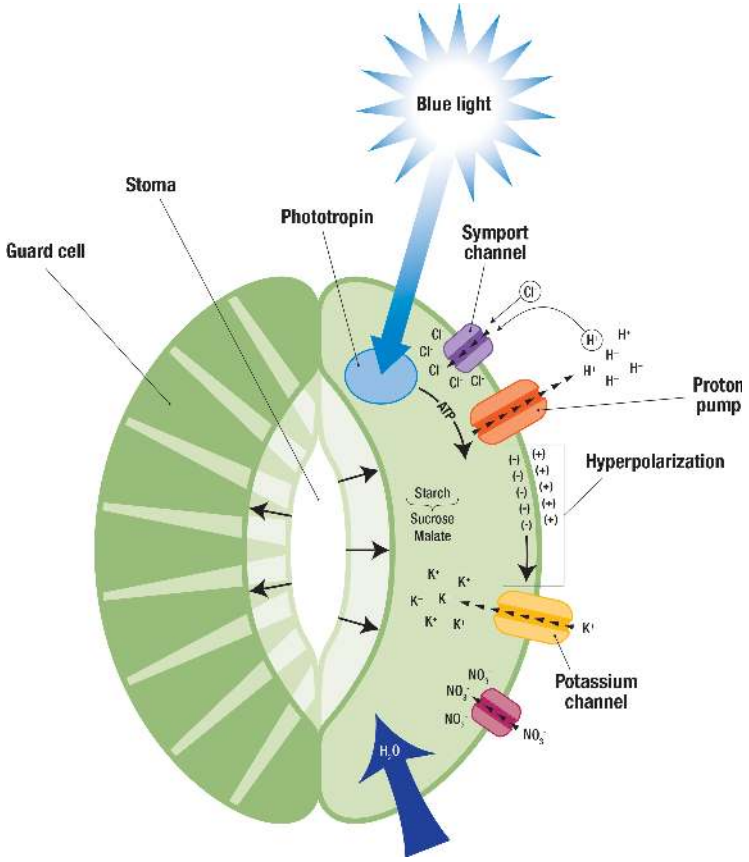



Figure **11.2.2.3**: Phototropins respond to blue light and signal to the proton pump to export protons. This active transport is fueled by the ATP produced in the light-dependent reactions of photosynthesis. This causes the cell to become hyperpolarized, stimulating an influx of potassium ions. At the same time, chloride is symported into the guard cell with protons as they reenter the cell. Nitrate ($NO_3^-$ ) also enters the cell. Starch breaks down, producing sucrose and malate. These, along with the influx of ions, increases the solute concentration inside of the guard cells, driving water into the cells. This increases turgor pressure and causes the guard cells to expand. Due to their radial cell wall thickenings, the guard cells curve when they expand, opening the stoma (plural: stomata). Image by Jen Valenzuela (CC-BY-NC).

Table **11.2.2.1** illustrates how osmotic pressure (which results in turgor pressure) increases with light availability during the day. When the osmotic pressure of the guard cells became greater than that of the surrounding cells, the stomata opened. In the evening, when the osmotic pressure of the guard cells dropped to nearly that of the surrounding cells, the stomata closed.

Table **11.2.2.1**: Osmotic pressure measured at different times of day in typical guard cells. The osmotic pressure within the other cells of the lower epidermis remained constant at ~1 MPa.

| Time | Osmotic Pressure (MPa) |
|---|---|
| 7 A.M. | 1.46 |
| 11 A.M. | 3.14 |
| 5 P.M. | 1.88 |
| 12 Midnight | 1.32 |

## Stomatal Closure

When water is low, roots synthesize **abscisic acid** (ABA), which is transported through the xylem to the leaves. There, abscisic acid causes calcium channels to open. Calcium ($Ca^{2+}$) opens anion channels, and malate, chloride, and nitrate exit the cell. The membrane potential decreases (the difference in charge across the membrane becomes less pronounced) as anions leave the cell. Potassium exits the cell in response to this decrease in membrane potential (called **depolarization**). The loss of these solutes in the cytosol results in water leaving the cell and a decrease in turgor pressure. The guard cells regain their original shape, and the stoma closes (Figure **11.2.2.4**).

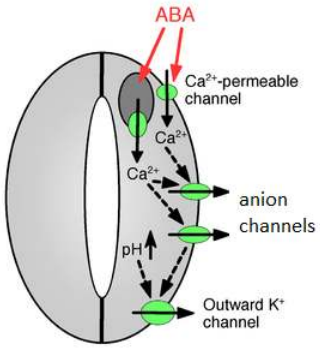



Figure **11.2.2.4**: Stomatal closure is triggered by abscisic acid (ABA), which causes calcium ($Ca^{2+}$) ions to enter the cell. These open anion channels. At this point, the cytoplasm is not as negatively charged as it was before. The change in charge opens potassium ($K^{+}$) channels, and potassium leaves the cell as well. Water leaves the cells, causing them to loose turgor pressure. The stoma then closes. Image modified from June Kwak (public domain).

## Attributions

Curated and authored by Melissa Ha using the following sources:

- 16.2D Gas Exchange from *Biology* by John. W. Kimball (licensed CC-BY)
- 30.2 Stems and 30.5 Transport of Water and Solutes in Plants from *Biology 2e* by OpenStax (licensed CC-BY). Access for free at openstax.org.

---

This page titled 11.2.2: Stomatal Opening and Closure is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **4.5.1.2.2: Stomatal Opening and Closure** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC 4.0.

# 11.3: Cohesion-Tension Theory

## Learning Objectives

- Explain how water moves upward through a plant according to the cohesion-tension theory.
- Provide experimental evidence for the cohesion-tension theory.

In 1895, the Irish plant physiologists H. H. Dixon and J. Joly proposed that water is pulled up the plant by **tension** (negative pressure) from above. As we have seen, water is continually being lost from leaves by transpiration. Dixon and Joly believed that the loss of water in the leaves exerts a pull on the water in the xylem ducts and draws more water into the leaf. But even the best vacuum pump can pull water up to a height of only 10.4 m (34 ft) or so. This is because a column of water that high exerts a pressure of 1.03 MPa just counterbalanced by the pressure of the atmosphere. How can water be drawn to the top of a sequoia, the tallest is 113 m (370 ft) high? Taking all factors into account, a pull of at least ~1.9 MPa is probably needed.

The answer to the dilemma lies the **cohesion** of water molecules; that is the property of water molecules to cling to each through the hydrogen bonds they form (Figure **11.3.1**). When ultrapure water is confined to tubes of very small bore, the force of cohesion between water molecules imparts great strength to the column of water. It has been reported that tensions as great as 21 MPa are needed to break the column, about the value needed to break steel wires of the same diameter. In a sense, the cohesion of water molecules gives them the physical properties of solid wires.

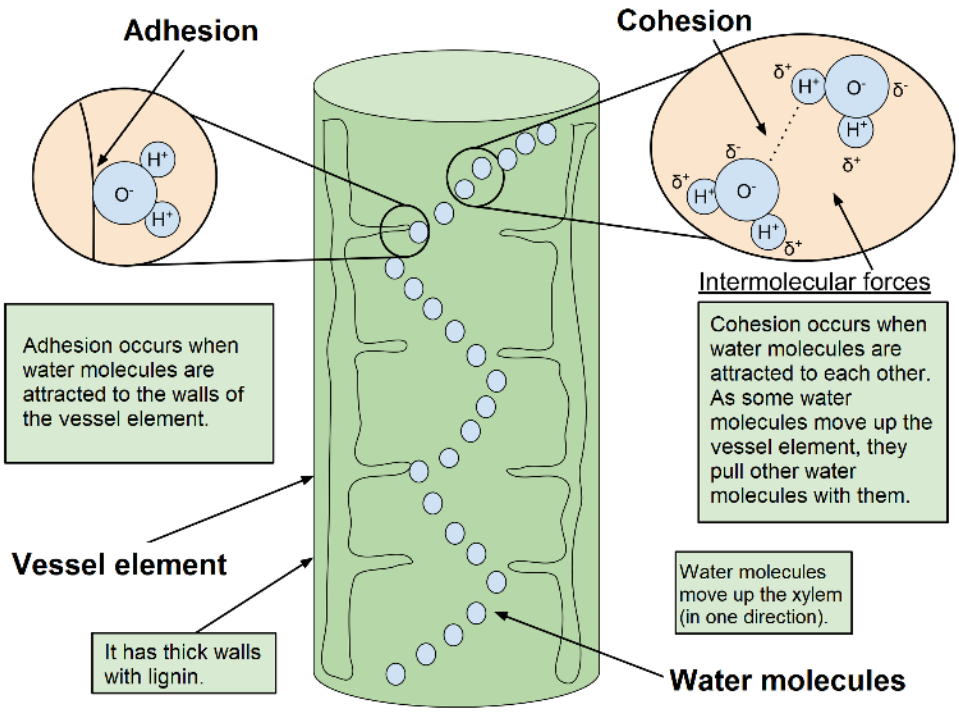



Figure **11.3.1**: The cohesion and adhesion of water in the vessel element helps water move up the vessel without breaking under tension. Adhesion occurs when water molecules are attracted to the walls of the vessel element, which has thick walls with lignin, a stiff substance. Cohesion occurs when water molecules are attracted to each other. This is due to hydrogen bonds, which form between the partially negative oxygen of one molecule and the partially positive hydrogen of another molecule. Hydrogen bonds are a strong intermolecular force. As some water molecules move up the vessel element, they pull other water molecules with them. Water molecules move up the xylem (in one direction). Image modified from FeltyRacketeer6 (CC-BY-SA).

According to the **cohesion-tension theory**, transpiration is the main driver of water movement in the xylem. It creates negative pressure (tension) equivalent to –2 MPa at the leaf surface. Water from the roots is ultimately pulled up by this tension. Negative water potential draws water from the soil into the root hairs, then into the root xylem. Cohesion and adhesion draw water up the xylem. Transpiration draws water from the leaf through the stoma. Water potential becomes increasingly negative from the root cells to the stem to the highest leaves, and finally to the atmosphere (Figure **11.3.2**).

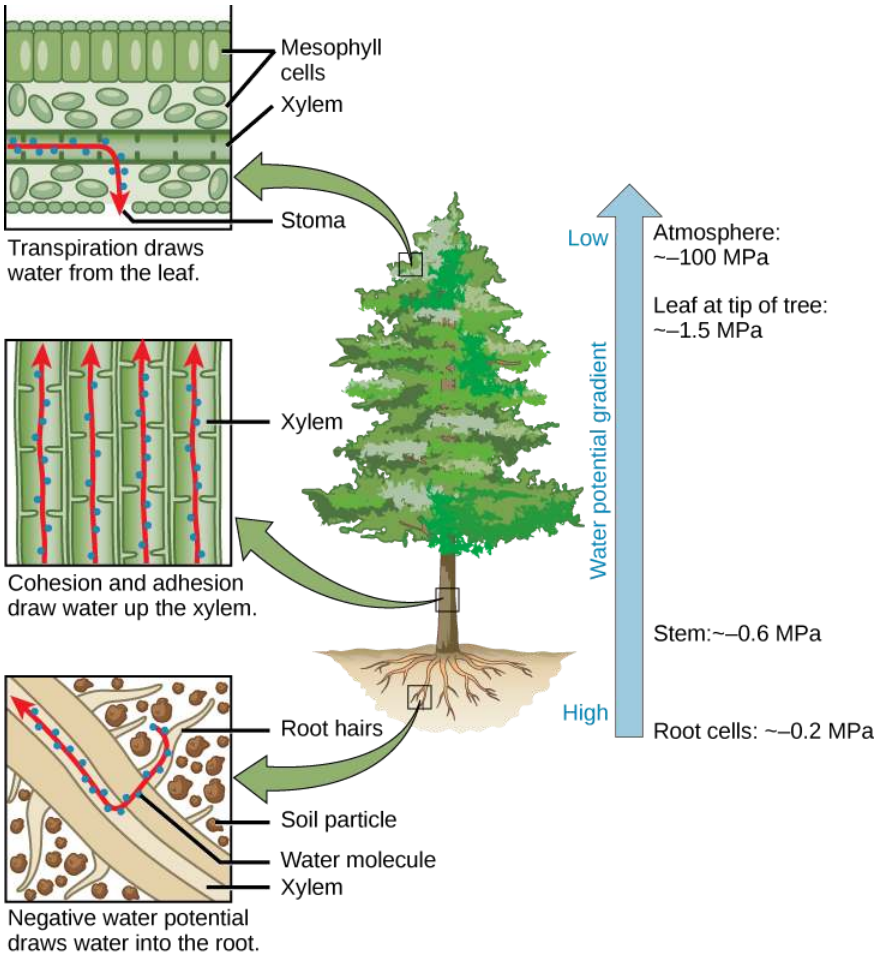



Figure **11.3.2**: The cohesion–tension theory is shown. Evaporation from the mesophyll cells produces a negative water potential gradient that causes water to move upwards from the roots through the xylem. Water potential is measured in megapascals (MPa), which is a measure of pressure. Water potential decreases from the root cells (-0.2 MPa) to the stem (-0.6 MPa) to the leaf at the tip of a tree (-1.5 MPa) to the atmosphere (-100 MPa). Transpiration draws water from the leaf. The water leaves the tube-shaped xylem and enters the air space between mesophyll cells. Finally, it exits through the stoma. Cohesion and adhesion draw water up the xylem. Negative water potential draws water into the root. Water moves from the spaces between soil particles into the root hairs, and into the xylem of the root.

The water potential at the leaf surface varies greatly depending on the **vapor pressure deficit**, which can be negligible at high **relative humidity** (RH) and substantial at low RH. At night, when stomata typically shut and transpiration stops, the water is held in the stem and leaf by the adhesion of water to the cell walls of the xylem vessels and tracheids, and the cohesion of water molecules to each other.

The mechanism of the cohesion-tension theory is based on purely physical forces because the xylem vessels and tracheids are not living at maturity. Evaporation of water into the intercellular air spaces creates a greater tension on the water in the mesophyll cells , thereby increasing the pull on the water in the xylem vessels. The xylem vessels and tracheids are structurally adapted to cope with large changes in pressure. Rings in the vessels maintain their tubular shape, much like the rings on a vacuum cleaner hose keep the hose open while it is under pressure. Small perforations between vessel elements reduce the number and size of gas bubbles that can form via a process called **cavitation**. The formation of gas bubbles in xylem interrupts the continuous stream of water from the base to the top of the plant, causing a break termed an embolism in the flow of xylem sap. The taller the tree, the greater the tension forces needed to pull water, and the more cavitation events. In larger trees, the resulting embolisms can plug xylem vessels, making them non-functional.

The pulling force due to transpiration is so powerful that it enables some trees and shrubs to live in seawater. Seawater is markedly hypertonic to the cytoplasm in the roots of the red mangrove (*Rhizophora mangle*), and we might expect water to leave the cells

resulting in a loss in turgor and wilting. However, the remarkably high tensions in the xylem (~3 to 5 MPa) can pull water into the plant against this osmotic gradient. Mangroves literally desalt seawater to meet their needs.

Experimental evidence supports the cohesion-tension theory. Over a century ago, a German botanist who sawed down a 21-m (70-ft) oak tree and placed the base of the trunk in a barrel of picric acid solution. The solution was drawn up the trunk, killing nearby tissues as it went. If the roots were the driving force, upward water movement would have stopped as soon as the acid killed the roots. However, the solution reached the top of the tree. When the acid reached the leaves and killed them, the water movement ceased, demonstrating that the transpiration in leaves was causing the water the upward movement of water.

According to the cohesion-tension theory, the water in the xylem is under tension due to transpiration. Consistent with this prediction, the diameter of Monterey pines decreases during the day, when transpiration rates are greatest (Figure **11.3.3**). Because the water column is under tension, the xylem walls are pulled in due to adhesion.

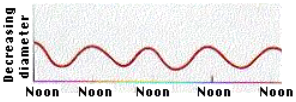



Figure **11.3.3**: This graph shows the diameter of a Monterey pine over time. The diameter fluctuates on a daily basis reaching its minimum when the rate of transpiration reaches its maximum (around noon). Results obtained by D. T. MacDougall.

## The Tallest Trees

By spinning branches in a centrifuge, it has been shown that water in the xylem avoids cavitation at negative pressures exceeding ~1.6 MPa. And the fact that giant redwoods (*Sequoia sempervirens*, Figure **11.3.4**) can successfully lift water 109 m (358 ft), which would require a tension of ~1.9 MPa, indicating that cavitation is avoided even at that value. However, such heights may be approaching the limit for xylem transport. Measurements close to the top of one of the tallest living giant redwood trees, 112.7 m (~370 ft), show that the high tensions needed to transport water have resulted in smaller stomata, causing lower concentrations of $CO_2$ in the needles, reduced photosynthesis, and reduced growth (smaller cells and much smaller needles; Koch et al. 2004). The limits on water transport thus limit the ultimate height which trees can reach. The tallest living tree is a 115.9-m giant redwood, and the tallest tree ever measured, a Douglas fir, was 125.9 m.



Figure **11.3.4**: A giant redwood tree (*Sequoia sempervirens*) 'Sherman' in the Sequoia National Park, California, USA. (Note that this is the same species but a different individual than the trees described in this box.) Image by Nagytibi and Revolus (CC-BY-SA).

Reference: Koch, G., Sillett, S., Jennings, G. *et al.* The limits to tree height. *Nature* **428,** 851–854 (2004). https://doi.org/10.1038/nature02417

## Supplemental Reading

Woodward, I. Tall storeys. *Nature* **428,** 807–808 (2004). https://doi.org/10.1038/428807a

## Attributions

Curated and authored by Melissa Ha using the following sources:

- 30.5 Transport of Water and Solutes in Plants from *Biology 2e* by OpenStax (licensed CC-BY). Access for free at openstax.org.
- 16.2A Xylem from *Biology* by John. W. Kimball (licensed CC-BY)

---

This page titled 11.3: Cohesion-Tension Theory is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **4.5.1.3: Cohesion-Tension Theory** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-SA 4.0.

# 11.4: Water Absorption

**Learning Objectives**

- Explain the function of root hairs.
- Define root pressure and explain its mechanism.
- Contrast the three pathways of water movement through the roots and identify each cell type or tissue involved.

Most plants secure the water and minerals they need from their roots. Water moves from the soil to the roots, stems, and ultimately the leaves, where transpiration occurs. The roots absorb enough water to compensate for water lost to transpiration. Rapid absorption is aided by **root hairs**, which extend from epidermal cells, increasing surface area (Figure 11.4.1). As discussed earlier in this chapter, roots draw water from the soil because they have lower water potential than the soil. Much of this difference in water potential is an indirect result of transpiration, but roots can also water potential by decreasing solute potential.



Figure 11.4.1: The young roots (radicles) of these radish seedlings are covered with fuzzy, white root hairs, which aid with water absorption. Image by Melissa Ha (CC-BY).

## Root Pressure

When a tomato plant is carefully severed close to the base of the stem, sap oozes from the stump (Figure 11.4.2). The fluid comes out because roots are constantly absorbing water, drawing it into the vascular cylinder, and pushing it up the xylem. This is called **root pressure**, and it is created by the osmotic pressure of solutes trapped in the vascular cylinder by the **Casparian strip**.

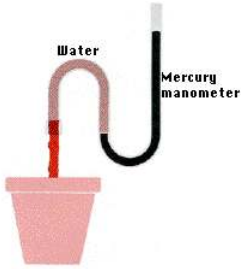



Figure 11.4.2: An experiment illustrating root pressure. The stem of a plant is severed and attached to a tube containing water. Mercury lies on top of the water. Root pressure pushes water out of the stem, moving the mercury up the tube.

Although root pressure plays a small role in the transport of water in the xylem in some plants and in some seasons, it does not account for most water transport. As evidence, few plants develop root pressures greater than ~0.2 kPa, and some develop no root pressure at all. Additionally, the volume of fluid transported by root pressure is not enough to account for the measured movement of water in the xylem of most trees and vines. Furthermore, the highest root pressures occur in the spring, but water moves through the xylem most rapidly in the summer (when transpiration is high).

As discussed in the Cohesion-Tension Theory section, transpiration, rather than root pressure, is typically the driving force for upward water movement in a plant. However, when transpiration rates are very low, such as in cool and humid weather, root pressure pushes water up the xylem faster than water is lost through the stomata. As a result water droplets are forced out of openings on the leaf margin, a phenomenon called **guttation** (Figure 11.4.3). Droplets resulting from guttation are not to be confused with dew droplets, which result from the condensation of water vapor when the air becomes colder and has less capacity

to hold water. In other words, guttation results from water that was inside of the plant, but dew droplets form from water vapor that was in the surrounding air.



Figure 11.4.3: Guttation of a strawberry leaf. Image by Noah Elhardt (public domain).

## Pathways of Water Movement

Water can move through the roots by three separate pathways: apoplast, symplast, and transmembrane (transcellular). In the **apoplast pathway** (apoplastic route), water moves through the spaces between the cells and in the cells walls themselves. In the **symplast pathway** (symplastic route), water passes from cytoplasm to cytoplasm through **plasmodesmata** (Figure 11.4.4). In the **transmembrane pathway**, water crosses plasma membranes, entering and exiting each cell. Water moving through the transmembrane pathway thus moves through both the symplast (interconnected cytoplasms) and apoplast (cell walls and spaces in between cells). Water may also cross the tonoplast, entering the central vacuole as part of the transmembrane pathway.

Water from the soil is absorbed by the root hairs of the epidermis and then moves through the cortex through one of the three pathways. However, the inner boundary of the cortex, the **endodermis**, is impervious to water due to the Casparian strip. Regardless of how the water moved up to this point (apoplast, symplast, transmembrane), it must enter the cytoplasms of the endodermal cells. From here it can pass via plasmodesmata into the cells of the vascular cylinder (stele). Once inside, water is again free to move through the apolast, the symplast, or both (transmembrane).

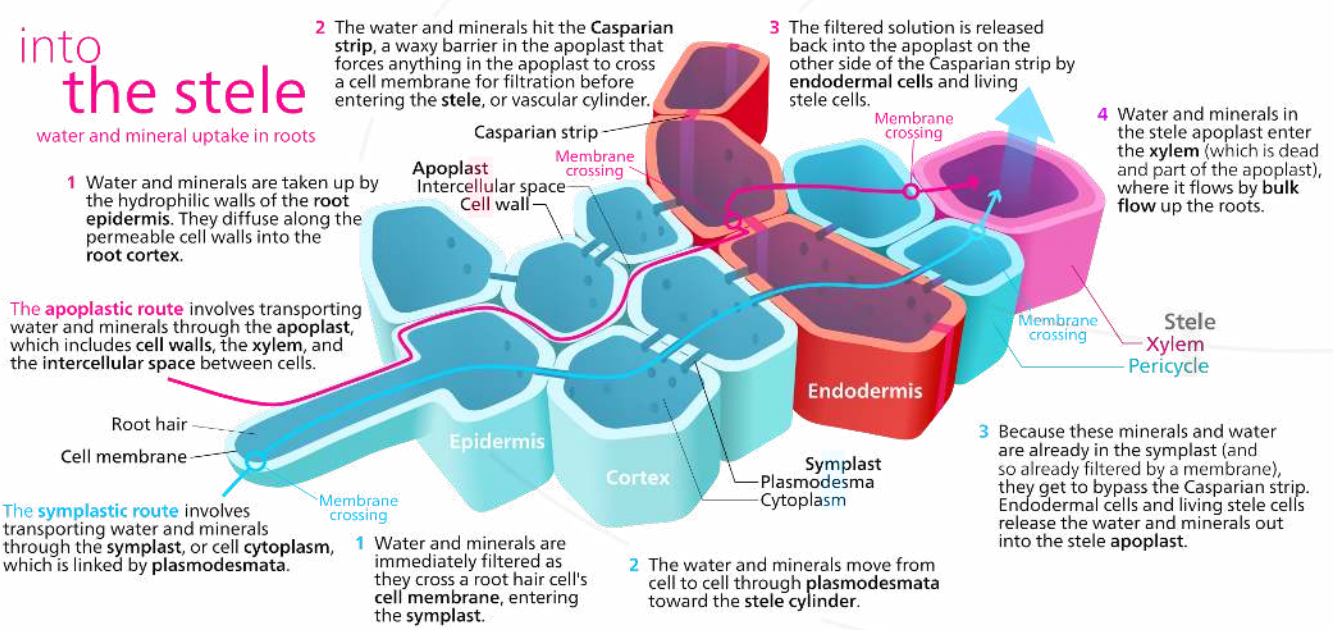



Figure **11.4.4**: Movement of water and minerals through the roots. Water moves through the root hairs of the epidermal cells through the cortex, including the endodermis, before entering the outermost layer of the vascular cylinder, the pericycle. the vascular cylinder (stele). Water ultimately enters the conducting cells of the xylem. Water can move between cells and through the cell walls and intercellular spaces in the apoplast pathway (apoplastic route) or between adjacent cytoplasms through plasmodesmata in the symplast pathway (symplastic route). In both pathways, all water must move through the cytoplasm of the endodermal cells because the Casparian strip blocks apoplastic movement across the Casparian strip. The steps of the apoplastic pathway are as follows: (1) Water and minerals are taken up by the hydrophilic walls of the root epidermis. They diffuse along the permeable cell walls into the root cortex. (2) The water and minerals hit the Casparian strip, a waxy barrier in the apoplast that forces anything in the apoplast to cross a cell membrane for filtration before entering the stele, or vascular cylinder. (3) The filtered solution is released back into the apoplast on the other side of the Casparian strip by endodermal cells and living stele cells. (4) Water and minerals in the stele apoplast enter the xylem (which is dead and part of the apoplast), where it flows by bulk flow up the roots. The steps of the symplastic pathway are as follows: (1) Water and minerals are immediately filtered as they cross a root hair cell's cell membrane, entering the symplast. (2) The water and minerals move from cell to cell through plasmodesmata toward the stele cylinder. (3) Because these minerals and water are already in the symplast (and so already filtered by a membrane), they get to bypass the Casparian strip. Endodermal cells and living stele cells release the water and minerals out into the stele apoplast (the xylem). The transmembrane pathway is not shown. Image by Kelvinsong (CC-BY-SA).

Once in the xylem, water with the minerals that have been deposited in it (as well as occasional organic molecules supplied by the root tissue) move up in the vessel elements and tracheids. At any level, the water can leave the xylem and pass laterally to supply the needs of other tissues. At the leaves, the xylem passes into the petiole and then into the veins of the leaf. Water leaves the finest veins and enters the cells of the spongy and palisade layers. Here some of the water may be used in metabolism, but most is lost in transpiration.

Figure **11.4.4** illustrates minerals moving through the apoplast or symplast, but minerals typically move through the symplast. Minerals enter the root by active transport into the symplast of epidermal cells and move toward and into the vascular cylinder through the plasmodesmata connecting the cells. They enter the conducting cells of the xylem from the pericycle and other parenchyma cells via active transport through specialized transmembrane channels.

## Attributions

Curated and authored by Melissa Ha using the following sources:

- 16.2A Xylem from *Biology* by John. W. Kimball (licensed CC-BY)
- 30.5 Transport of Water and Solutes in Plants from *Biology 2e* by OpenStax (licensed CC-BY). Access for free at openstax.org.

This page titled 11.4: Water Absorption is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **4.5.1.4: Water Absorption** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-SA 4.0.

# SECTION OVERVIEW

## 11.5: Water Transport

Water potential, transpiration, and stomatal regulation influence how water and nutrients are transported in plants. **Water potential** refers to the potential energy in water, and water moves towards the areas with the lowest water potential. Water is ultimately pulled to the top of the plant (**cohesion-tension theory**), and lost through **transpiration** through stomata. Complex mechanisms control stomatal opening and closure. Both adaptations that increase absorption of water through the roots (Figure 11.5.1) and those that limit transpiration ensure that plants collect and retain enough water.

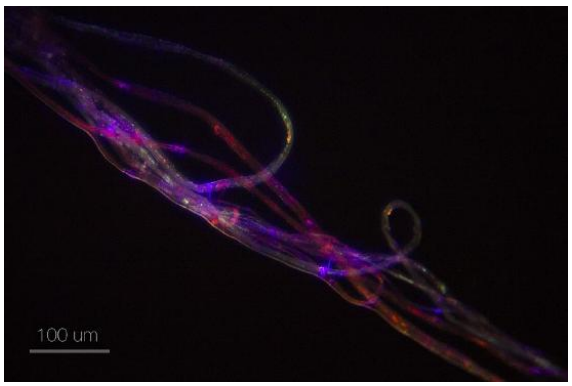



Figure **11.5.1**: Microscope of stained root hairs of the soybean. Roots hairs are an example of an adaptation that increases water absorption. Image by Ihor Panas (CC-BY-SA).

**Topic hierarchy**

### Attribution

Curated and authored by Melissa Ha using 30.5 Transport of Water and Solutes in Plants from *Biology 2e* by OpenStax (licensed CC-BY). Access for free at openstax.org.

This page titled 11.5: Water Transport is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

# 11.6: Transport of Water and Solutes in Plants

**Skills to Develop**

- Define water potential and explain how it is influenced by solutes, pressure, gravity, and the matric potential
- Describe how water potential, evapotranspiration, and stomatal regulation influence how water is transported in plants
- Explain how photosynthates are transported in plants

The structure of plant roots, stems, and leaves facilitates the transport of water, nutrients, and photosynthates throughout the plant. The phloem and xylem are the main tissues responsible for this movement. Water potential, evapotranspiration, and stomatal regulation influence how water and nutrients are transported in plants. To understand how these processes work, we must first understand the energetics of water potential.

## Water Potential

Plants are phenomenal hydraulic engineers. Using only the basic laws of physics and the simple manipulation of potential energy, plants can move water to the top of a 116-meter-tall tree (Figure **11.6.1**a). Plants can also use hydraulics to generate enough force to split rocks and buckle sidewalks (Figure **11.6.1**b). Plants achieve this because of water potential.



(a) (b)

Figure **11.6.1**: With heights nearing 116 meters, (a) coastal redwoods (*Sequoia sempervirens*) are the tallest trees in the world. Plant roots can easily generate enough force to (b) buckle and break concrete sidewalks, much to the dismay of homeowners and city maintenance departments. (credit a: modification of work by Bernt Rostad; credit b: modification of work by Pedestrians Educating Drivers on Safety, Inc.)

Water potential is a measure of the potential energy in water. Plant physiologists are not interested in the energy in any one particular aqueous system, but are very interested in water movement between two systems. In practical terms, therefore, water potential is the difference in potential energy between a given water sample and pure water (at atmospheric pressure and ambient temperature). Water potential is denoted by the Greek letter ψ (*psi*) and is expressed in units of pressure (pressure is a form of energy) called megapascals (MPa). The potential of pure water ($\Psi_w^{\text{pure H2O}}$) is, by convenience of definition, designated a value of zero (even though pure water contains plenty of potential energy, that energy is ignored). Water potential values for the water in a plant root, stem, or leaf are therefore expressed relative to $\Psi_w^{\text{pure H2O}}$.

The water potential in plant solutions is influenced by solute concentration, pressure, gravity, and factors called matrix effects. Water potential can be broken down into its individual components using the following equation:

$$\psi_{system} = \psi_{total} = \psi_s + \psi_p + \psi_g + \psi_m$$

where $\Psi_s$, $\Psi_p$, $\Psi_g$, and $\Psi_m$ refer to the solute, pressure, gravity, and matric potentials, respectively. "System" can refer to the water potential of the soil water ($\Psi^{soil}$), root water ($\Psi^{root}$), stem water ($\Psi^{stem}$), leaf water ($\Psi^{leaf}$) or the water in the atmosphere ($\Psi^{atmosphere}$): whichever aqueous system is under consideration. As the individual components change, they raise or lower the total water potential of a system. When this happens, water moves to equilibrate, moving from the system or compartment with a higher water potential to the system or compartment with a lower water potential. This brings the difference in water potential between the two systems ($\Delta\Psi$) back to zero ($\Delta\Psi = 0$). Therefore, for water to move through the plant from the soil to the air (a process called transpiration), $\Psi^{soil}$ must be $> \Psi^{root} > \Psi^{stem} > \Psi^{leaf} > \Psi^{atmosphere}$.

Water only moves in response to $\Delta\Psi$, not in response to the individual components. However, because the individual components influence the total $\Psi_{system}$, by manipulating the individual components (especially $\Psi_s$), a plant can control water movement.

## Solute Potential

Solute potential ($\Psi_s$), also called osmotic potential, is negative in a plant cell and zero in distilled water. Typical values for cell cytoplasm are –0.5 to –1.0 MPa. Solutes reduce water potential (resulting in a negative $\Psi_w$) by consuming some of the potential energy available in the water. Solute molecules can dissolve in water because water molecules can bind to them via hydrogen bonds; a hydrophobic molecule like oil, which cannot bind to water, cannot go into solution. The energy in the hydrogen bonds between solute molecules and water is no longer available to do work in the system because it is tied up in the bond. In other words, the amount of available potential energy is reduced when solutes are added to an aqueous system. Thus, $\Psi_s$ decreases with increasing solute concentration. Because $\Psi_s$ is one of the four components of $\Psi_{system}$ or $\Psi_{total}$, a decrease in $\Psi_s$ will cause a decrease in $\Psi_{total}$. The internal water potential of a plant cell is more negative than pure water because of the cytoplasm's high solute content (Figure **11.6.2**). Because of this difference in water potential water will move from the soil into a plant's root cells via the process of osmosis. This is why solute potential is sometimes called osmotic potential.

Plant cells can metabolically manipulate $\Psi_s$ (and by extension, $\Psi_{total}$) by adding or removing solute molecules. Therefore, plants have control over $\Psi_{total}$ via their ability to exert metabolic control over $\Psi_s$.

Art Connection

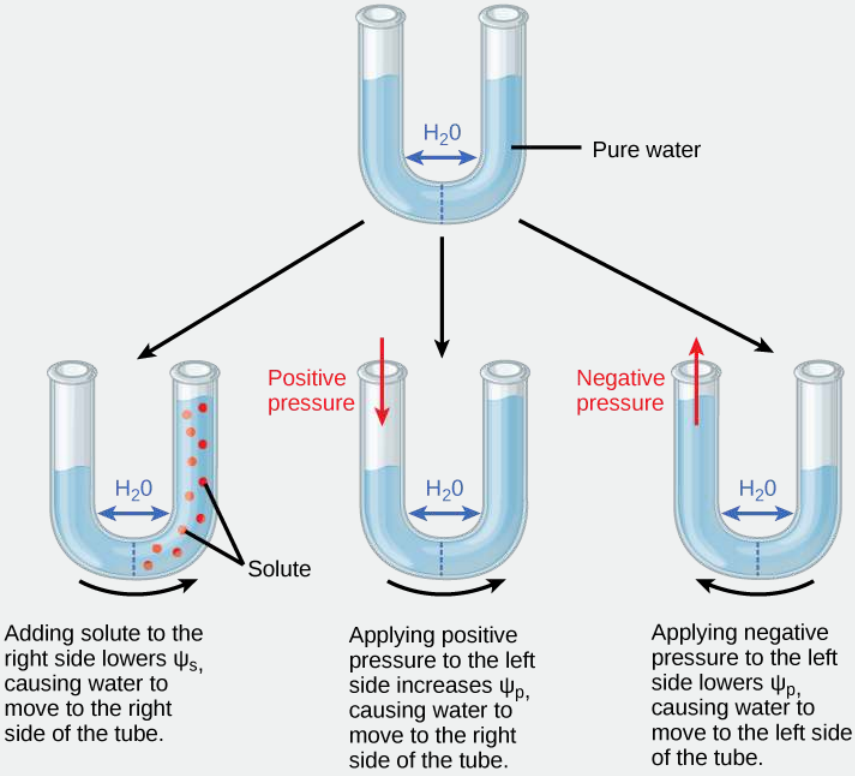



Figure **11.6.2**: In this example with a semipermeable membrane between two aqueous systems, water will move from a region of higher to lower water potential until equilibrium is reached. Solutes ($\Psi_s$), pressure ($\Psi_p$), and gravity ($\Psi_g$) influence total water potential for each side of the tube ($\Psi_{total}$ $^{right\ or\ left}$), and therefore, the difference between $\Psi_{total}$ on each side ($\Delta\Psi$). ($\Psi_m$ , the potential due to interaction of water with solid substrates, is ignored in this example because glass is not especially hydrophilic). Water moves in response to the difference in water potential between two systems (the left and right sides of the tube).

Positive water potential is placed on the left side of the tube by increasing $\Psi_p$ such that the water level rises on the right side. Could you equalize the water level on each side of the tube by adding solute, and if so, how?

## Pressure Potential

Pressure potential ($\Psi_p$), also called turgor potential, may be positive or negative (Figure **11.6.3**). Because pressure is an expression of energy, the higher the pressure, the more potential energy in a system, and vice versa. Therefore, a positive Ψp (compression) increases $\Psi_{total}$, and a negative $\Psi_p$ (tension) decreases $\Psi_{total}$. Positive pressure inside cells is contained by the cell wall, producing turgor pressure. Pressure potentials are typically around 0.6–0.8 MPa, but can reach as high as 1.5 MPa in a well-watered plant. A $\Psi_p$ of 1.5 MPa equates to 210 pounds per square inch (1.5 MPa x 140 lb $in^{-2}$ $MPa^{-1}$ = 210 $lb/in^{-2}$). As a comparison, most automobile tires are kept at a pressure of 30–34 psi. An example of the effect of turgor pressure is the wilting of leaves and their restoration after the plant has been watered (Figure **11.6.3**). Water is lost from the leaves via transpiration (approaching $\Psi_p$ = 0 MPa at the wilting point) and restored by uptake via the roots.

A plant can manipulate $\Psi_p$ via its ability to manipulate $\Psi_s$ and by the process of osmosis. If a plant cell increases the cytoplasmic solute concentration, $\Psi_s$ will decline, $\Psi_{total}$ will decline, the $\Delta\Psi$ between the cell and the surrounding tissue will decline, water will move into the cell by osmosis, and $\Psi_p$ will increase. $\Psi_p$ is also under indirect plant control via the opening and closing of stomata. Stomatal openings allow water to evaporate from the leaf, reducing $\Psi_p$ and $\Psi_{total}$ of the leaf and increasing ii between the water in the leaf and the petiole, thereby allowing water to flow from the petiole into the leaf.



(a) (b)

Figure 11.6.3: When (a) total water potential ($\Psi_{total}$) is lower outside the cells than inside, water moves out of the cells and the plant wilts. When (b) the total water potential is higher outside the plant cells than inside, water moves into the cells, resulting in turgor pressure ($\Psi_p$) and keeping the plant erect. (credit: modification of work by Victor M. Vicente Selvas)

## Gravity Potential

Gravity potential ($\Psi_g$) is always negative to zero in a plant with no height. It always removes or consumes potential energy from the system. The force of gravity pulls water downwards to the soil, reducing the total amount of potential energy in the water in the plant ($\Psi_{total}$). The taller the plant, the taller the water column, and the more influential $\Psi_g$ becomes. On a cellular scale and in short plants, this effect is negligible and easily ignored. However, over the height of a tall tree like a giant coastal redwood, the gravitational pull of –0.1 MPa $m^{-1}$ is equivalent to an extra 1 MPa of resistance that must be overcome for water to reach the leaves of the tallest trees. Plants are unable to manipulate $\Psi_g$.

## Matric Potential

Matric potential ($\Psi_m$) is always negative to zero. In a dry system, it can be as low as –2 MPa in a dry seed, and it is zero in a water-saturated system. The binding of water to a matrix always removes or consumes potential energy from the system. $\Psi_m$ is similar to solute potential because it involves tying up the energy in an aqueous system by forming hydrogen bonds between the water and some other component. However, in solute potential, the other components are soluble, hydrophilic solute molecules, whereas in $\Psi_m$, the other components are insoluble, hydrophilic molecules of the plant cell wall. Every plant cell has a cellulosic cell wall and the cellulose in the cell walls is hydrophilic, producing a matrix for adhesion of water: hence the name matric potential. $\Psi_m$ is very large (negative) in dry tissues such as seeds or drought-affected soils. However, it quickly goes to zero as the seed takes up water or the soil hydrates. $\Psi_m$ cannot be manipulated by the plant and is typically ignored in well-watered roots, stems, and leaves.

## Movement of Water and Minerals in the Xylem

Solutes, pressure, gravity, and matric potential are all important for the transport of water in plants. Water moves from an area of higher total water potential (higher Gibbs free energy) to an area of lower total water potential. Gibbs free energy is the energy associated with a chemical reaction that can be used to do work. This is expressed as $\Delta\Psi$.

Transpiration is the loss of water from the plant through evaporation at the leaf surface. It is the main driver of water movement in the xylem. Transpiration is caused by the evaporation of water at the leaf–atmosphere interface; it creates negative pressure (tension) equivalent to –2 MPa at the leaf surface. This value varies greatly depending on the vapor pressure deficit, which can be negligible at high relative humidity (RH) and substantial at low RH. Water from the roots is pulled up by this tension. At night, when stomata shut and transpiration stops, the water is held in the stem and leaf by the adhesion of water to the cell walls of the xylem vessels and tracheids, and the cohesion of water molecules to each other. This is called the cohesion–tension theory of sap ascent.

Inside the leaf at the cellular level, water on the surface of mesophyll cells saturates the cellulose microfibrils of the primary cell wall. The leaf contains many large intercellular air spaces for the exchange of oxygen for carbon dioxide, which is required for photosynthesis. The wet cell wall is exposed to this leaf internal air space, and the water on the surface of the cells evaporates into

the air spaces, decreasing the thin film on the surface of the mesophyll cells. This decrease creates a greater tension on the water in the mesophyll cells (Figure **11.6.4**), thereby increasing the pull on the water in the xylem vessels. The xylem vessels and tracheids are structurally adapted to cope with large changes in pressure. Rings in the vessels maintain their tubular shape, much like the rings on a vacuum cleaner hose keep the hose open while it is under pressure. Small perforations between vessel elements reduce the number and size of gas bubbles that can form via a process called cavitation. The formation of gas bubbles in xylem interrupts the continuous stream of water from the base to the top of the plant, causing a break termed an embolism in the flow of xylem sap. The taller the tree, the greater the tension forces needed to pull water, and the more cavitation events. In larger trees, the resulting embolisms can plug xylem vessels, making them non-functional.

Art Connection

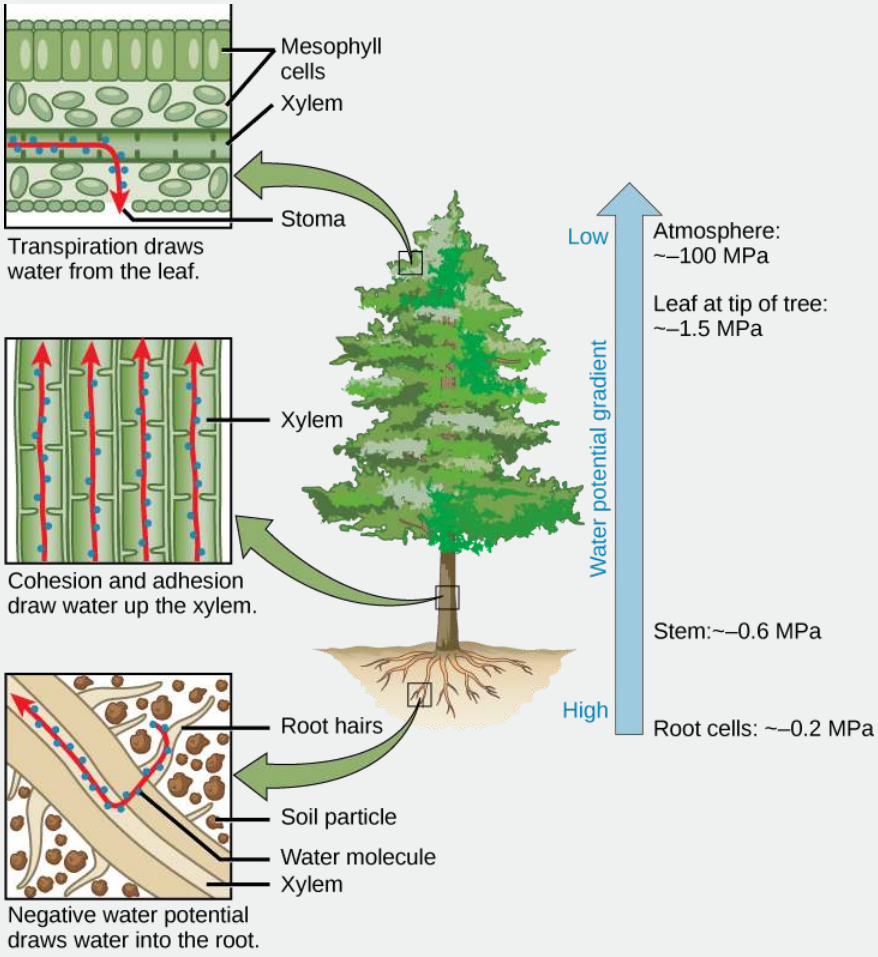



Figure **11.6.4**: The cohesion–tension theory of sap ascent is shown. Evaporation from the mesophyll cells produces a negative water potential gradient that causes water to move upwards from the roots through the xylem.

Which of the following statements is false?

A. Negative water potential draws water into the root hairs. Cohesion and adhesion draw water up the xylem. Transpiration draws water from the leaf.
B. Negative water potential draws water into the root hairs. Cohesion and adhesion draw water up the phloem. Transpiration draws water from the leaf.
C. Water potential decreases from the roots to the top of the plant.
D. Water enters the plants through root hairs and exits through stoma.

Transpiration—the loss of water vapor to the atmosphere through stomata—is a passive process, meaning that metabolic energy in the form of ATP is not required for water movement. The energy driving transpiration is the difference in energy between the water in the soil and the water in the atmosphere. However, transpiration is tightly controlled.

## Control of Transpiration

The atmosphere to which the leaf is exposed drives transpiration, but also causes massive water loss from the plant. Up to 90 percent of the water taken up by roots may be lost through transpiration.

Leaves are covered by a waxy cuticle on the outer surface that prevents the loss of water. Regulation of transpiration, therefore, is achieved primarily through the opening and closing of stomata on the leaf surface. Stomata are surrounded by two specialized cells called guard cells, which open and close in response to environmental cues such as light intensity and quality, leaf water status, and carbon dioxide concentrations. Stomata must open to allow air containing carbon dioxide and oxygen to diffuse into the leaf for photosynthesis and respiration. When stomata are open, however, water vapor is lost to the external environment, increasing the rate of transpiration. Therefore, plants must maintain a balance between efficient photosynthesis and water loss.

Plants have evolved over time to adapt to their local environment and reduce transpiration(Figure 11.6.5). Desert plant (xerophytes) and plants that grow on other plants (epiphytes) have limited access to water. Such plants usually have a much thicker waxy cuticle than those growing in more moderate, well-watered environments (mesophytes). Aquatic plants (hydrophytes) also have their own set of anatomical and morphological leaf adaptations.

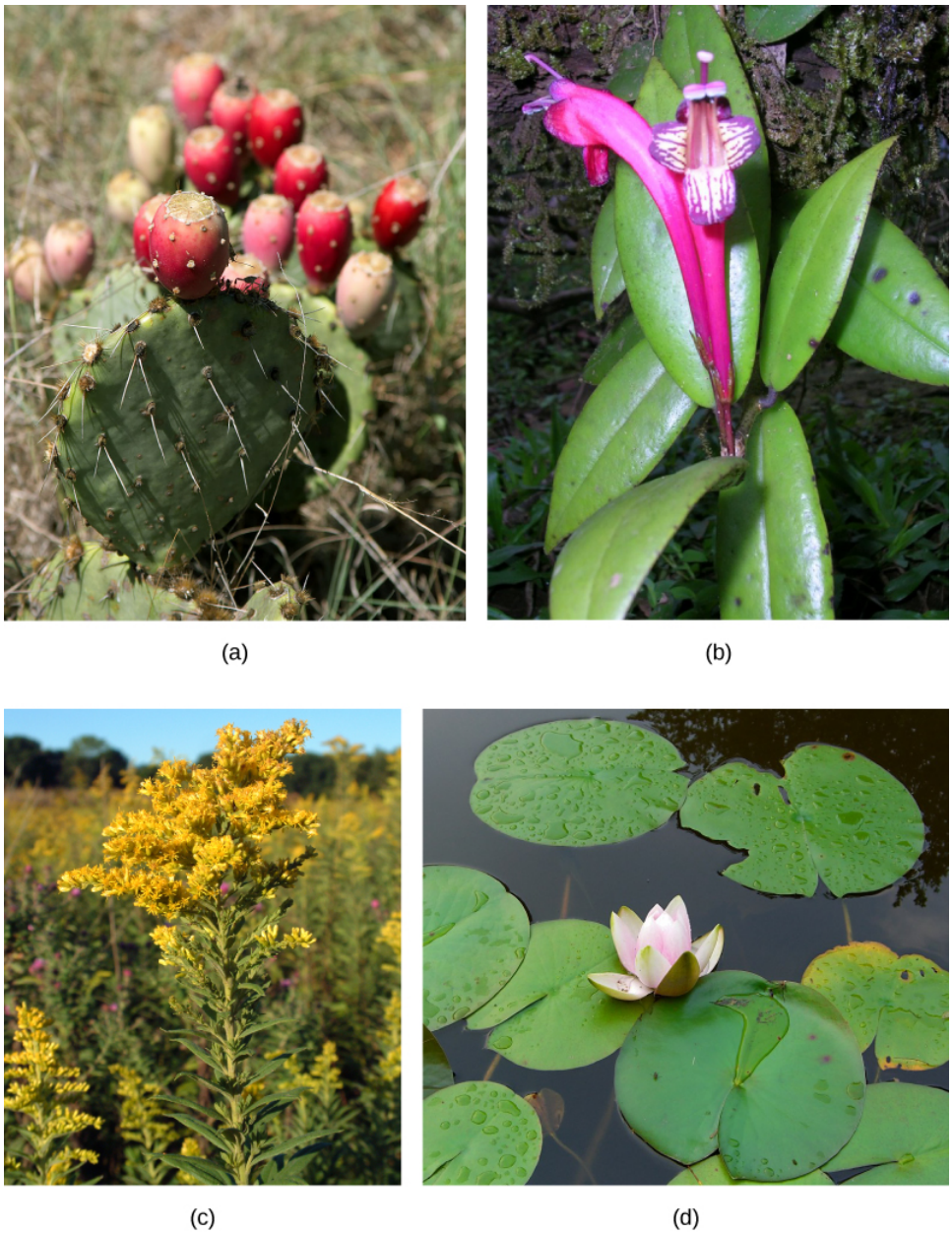



Figure **11.6.5**: Plants are suited to their local environment. (a) Xerophytes, like this prickly pear cactus (*Opuntia* sp.) and (b) epiphytes such as this tropical *Aeschynanthus perrottetii* have adapted to very limited water resources. The leaves of a prickly pear are modified into spines, which lowers the surface-to-volume ratio and reduces water loss. Photosynthesis takes place in the stem, which also stores water. (b) *A. perottetii* leaves have a waxy cuticle that prevents water loss. (c) Goldenrod (*Solidago* sp.) is a mesophyte, well suited for moderate environments. (d) Hydrophytes, like this fragrant water lily (*Nymphaea odorata*), are adapted to thrive in aquatic environments. (credit a: modification of work by Jon Sullivan; credit b: modification of work by L. Shyamal/Wikimedia Commons; credit c: modification of work by Huw Williams; credit d: modification of work by Jason Hollinger)

Xerophytes and epiphytes often have a thick covering of trichomes or of stomata that are sunken below the leaf's surface. Trichomes are specialized hair-like epidermal cells that secrete oils and substances. These adaptations impede air flow across the stomatal pore and reduce transpiration. Multiple epidermal layers are also commonly found in these types of plants.

## Transportation of Photosynthates in the Phloem

Plants need an energy source to grow. In seeds and bulbs, food is stored in polymers (such as starch) that are converted by metabolic processes into sucrose for newly developing plants. Once green shoots and leaves are growing, plants are able to produce

their own food by photosynthesizing. The products of photosynthesis are called photosynthates, which are usually in the form of simple sugars such as sucrose.

Structures that produce photosynthates for the growing plant are referred to as sources. Sugars produced in sources, such as leaves, need to be delivered to growing parts of the plant via the phloem in a process called translocation. The points of sugar delivery, such as roots, young shoots, and developing seeds, are called sinks. Seeds, tubers, and bulbs can be either a source or a sink, depending on the plant's stage of development and the season.

The products from the source are usually translocated to the nearest sink through the phloem. For example, the highest leaves will send photosynthates upward to the growing shoot tip, whereas lower leaves will direct photosynthates downward to the roots. Intermediate leaves will send products in both directions, unlike the flow in the xylem, which is always unidirectional (soil to leaf to atmosphere). The pattern of photosynthate flow changes as the plant grows and develops. Photosynthates are directed primarily to the roots early on, to shoots and leaves during vegetative growth, and to seeds and fruits during reproductive development. They are also directed to tubers for storage.

## Translocation: Transport from Source to Sink

Photosynthates, such as sucrose, are produced in the mesophyll cells of photosynthesizing leaves. From there they are translocated through the phloem to where they are used or stored. Mesophyll cells are connected by cytoplasmic channels called plasmodesmata. Photosynthates move through these channels to reach phloem sieve-tube elements (STEs) in the vascular bundles. From the mesophyll cells, the photosynthates are loaded into the phloem STEs. The sucrose is actively transported against its concentration gradient (a process requiring ATP) into the phloem cells using the electrochemical potential of the proton gradient. This is coupled to the uptake of sucrose with a carrier protein called the sucrose-$H^+$ symporter.

Phloem STEs have reduced cytoplasmic contents, and are connected by a sieve plate with pores that allow for pressure-driven bulk flow, or translocation, of phloem sap. Companion cells are associated with STEs. They assist with metabolic activities and produce energy for the STEs (Figure **11.6.6**).

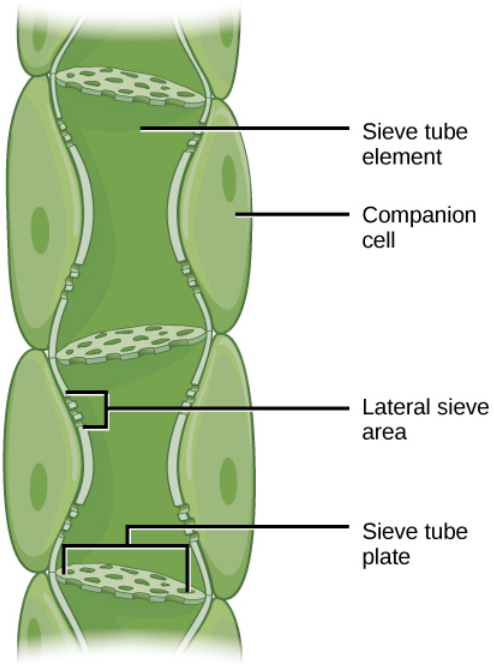



Figure **11.6.6**: Phloem is comprised of cells called sieve-tube elements. Phloem sap travels through perforations called sieve tube plates. Neighboring companion cells carry out metabolic functions for the sieve-tube elements and provide them with energy. Lateral sieve areas connect the sieve-tube elements to the companion cells.

Once in the phloem, the photosynthates are translocated to the closest sink. Phloem sap is an aqueous solution that contains up to 30 percent sugar, minerals, amino acids, and plant growth regulators. The high percentage of sugar decreases $\Psi_s$, which decreases the total water potential and causes water to move by osmosis from the adjacent xylem into the phloem tubes, thereby increasing

pressure. This increase in total water potential causes the bulk flow of phloem from source to sink (Figure **11.6.7**). Sucrose concentration in the sink cells is lower than in the phloem STEs because the sink sucrose has been metabolized for growth, or converted to starch for storage or other polymers, such as cellulose, for structural integrity. Unloading at the sink end of the phloem tube occurs by either diffusion or active transport of sucrose molecules from an area of high concentration to one of low concentration. Water diffuses from the phloem by osmosis and is then transpired or recycled via the xylem back into the phloem sap.

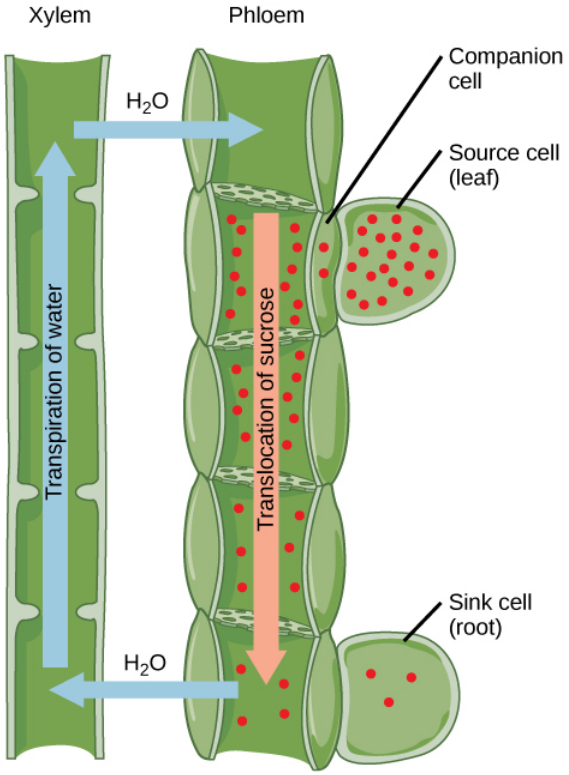



Figure **11.6.7**: Sucrose is actively transported from source cells into companion cells and then into the sieve-tube elements. This reduces the water potential, which causes water to enter the phloem from the xylem. The resulting positive pressure forces the sucrose-water mixture down toward the roots, where sucrose is unloaded. Transpiration causes water to return to the leaves through the xylem vessels.

## Summary

Water potential (Ψ) is a measure of the difference in potential energy between a water sample and pure water. The water potential in plant solutions is influenced by solute concentration, pressure, gravity, and matric potential. Water potential and transpiration influence how water is transported through the xylem in plants. These processes are regulated by stomatal opening and closing. Photosynthates (mainly sucrose) move from sources to sinks through the plant's phloem. Sucrose is actively loaded into the sieve-tube elements of the phloem. The increased solute concentration causes water to move by osmosis from the xylem into the phloem. The positive pressure that is produced pushes water and solutes down the pressure gradient. The sucrose is unloaded into the sink, and the water returns to the xylem vessels.

## Art Connections

Figure **11.6.2**: Positive water potential is placed on the left side of the tube by increasing $\Psi_p$ such that the water level rises on the right side. Could you equalize the water level on each side of the tube by adding solute, and if so, how?

**Answer**

Yes, you can equalize the water level by adding the solute to the left side of the tube such that water moves toward the left until the water levels are equal.

Figure 11.6.4: Which of the following statements is false?

A. Negative water potential draws water into the root hairs. Cohesion and adhesion draw water up the xylem. Transpiration draws water from the leaf.
B. Negative water potential draws water into the root hairs. Cohesion and adhesion draw water up the phloem. Transpiration draws water from the leaf.
C. Water potential decreases from the roots to the top of the plant.
D. Water enters the plants through root hairs and exits through stoma.

**Answer**

B.

## Glossary

**cuticle**
waxy covering on the outside of the leaf and stem that prevents the loss of water

**megapascal (MPa)**
pressure units that measure water potential

**sink**
growing parts of a plant, such as roots and young leaves, which require photosynthate

**source**
organ that produces photosynthate for a plant

**translocation**
mass transport of photosynthates from source to sink in vascular plants

**transpiration**
loss of water vapor to the atmosphere through stomata

**water potential ($\Psi_w$)**
the potential energy of a water solution per unit volume in relation to pure water at atmospheric pressure and ambient temperature

---

This page titled 11.6: Transport of Water and Solutes in Plants is shared under a CC BY 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **30.5: Transport of Water and Solutes in Plants** by OpenStax is licensed CC BY 4.0.

# CHAPTER OVERVIEW

## 12: Photosynthetic adaptations

12.1: Photorespiration and Photosynthetic Pathways
12.2: CO2 uptake - C4 and CAM Pathways

This page titled 12: Photosynthetic adaptations is shared under a not declared license and was authored, remixed, and/or curated by Tom Buckley.

# 12.1: Photorespiration and Photosynthetic Pathways

**Learning Objectives**

- Define photorespiration.
- Explain how C3, C4, and CAM plants reduce photorespiration.
- Outline the $C_4$ pathway and compare its use by $C_4$ plants and CAM plants.

Different plant species have adaptations that allow them to do different variations of the light-independent reactions. These are called **photosynthetic pathways**. Plants are classified as $C_3$, $C_4$, or CAM depending on their use of these pathways, but note that some plants can switch photosynthetic pathways depending on environmental conditions. The process for light-independent reactions described in the previous section was the **$C_3$ pathway**: the compound formed during fixation (3-PGA) has three carbon atoms. Before discussing the details of the $C_4$ pathway, it is important to understand the circumstances that led to these adaptations.

## Photorespiration

As its name suggests, **ribulose-1,5-bisphosphate carboxylase/oxygenase** (**RuBisCO**) catalyzes two different reactions. The first is adding $CO_2$ to ribulose-1,5- bisphosphate (RuBP) — the **carboxylase** activity. The second is adding $O_2$ to RuBP — the **oxygenase** activity.

The oxygenase activity of RuBisCO forms the three-carbon molecule 3-phosphoglycerate (3-PGA), just as in the light-independent reactions, and the two-carbon molecule glycolate. The glycolate enters peroxisomes, where it uses $O_2$ to form intermediates that enter mitochondria where they are broken down to $CO_2$. So this process uses $O_2$ and liberates $CO_2$ as aerobic cellular respiration does, which is why it is called **photorespiration**. It undoes the work of photosynthesis, which is to build sugars.

Which action of RuBisCO predominates depends on the relative concentrations of $O_2$ and $CO_2$ with high $CO_2$, low $O_2$ favoring the carboxylase action and high $O_2$, low $CO_2$ favoring the oxygenase action. The light reactions of photosynthesis liberate oxygen, and more oxygen dissolves in the cytosol of the cell at higher temperatures. Therefore, high light intensities and high temperatures (above ~ 30°C) favor the second reaction and result in photorespiration.

## $C_3$ Plants

One solution to photorespiration is for plants to open their stomata to release $O_2$ and obtain $CO_2$. However, if conditions are hot or dry, this will result in too much water loss (**transpiration**). For this reason, $C_3$ plants, which only do the $C_3$ pathway and do not use the $C_4$ pathway to prevent photorespiration (see below), do best in cool, moist areas. Rice and potatoes are examples of $C_3$ plants.

## $C_4$ Plants

Many angiosperms have developed adaptations which minimize the losses to photorespiration. They all use a supplementary method of $CO_2$ uptake which initially forms a four-carbon molecule compared to the two three-carbon molecules that are initially formed in the $C_3$ pathway. Hence, these plants are called **$C_4$ plants**. Note that $C_4$ plants will eventually conduct the light-independent reactions ($C_3$ pathway), but they form a four-carbon molecule first.

$C_4$ plants have structural changes in their leaf anatomy so that synthesizing the four-carbon sugar (the $C_4$ pathway) and resuming the light-independent reactions ($C_3$ pathways) are separated in different parts of the leaf with RuBisCO sequestered where the $CO_2$ level is high and the $O_2$ level low. After entering through stomata, $CO_2$ diffuses into a mesophyll cell (Figure **12.1.1**). Being close to the leaf surface, these cells are exposed to high levels of $O_2$, but they have no RuBisCO so cannot start photorespiration (nor the light-independent reactions).

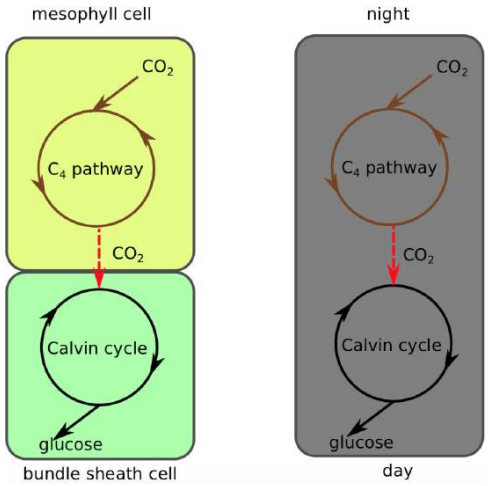



Figure **12.1.1**: $C_4$ plants conduct the C4 pathway in the mesophyll cells and the Calvin cycle ($C_3$ pathway) in the bundle sheath cells, meaning they spatially separate the two (left). CAM plants (right) conduct the C4 pathway at night and the Calvin cycle ($C_3$ pathway) during the day, resulting an a temporal separation of the two.

Instead, the $CO_2$ is inserted into a three-carbon compound called **phosphoenolpyruvic acid** (**PEP**) forming the four-carbon compound **oxaloacetic acid**. Oxaloacetic acid is converted into malic acid or aspartic acid (both have 4 carbons), which is transported through plasmodesmata into a **bundle sheath cell**. Bundle sheath cells are deep in the leaf, so atmospheric oxygen cannot diffuse easily to them (Figure **12.1.2**). Additionally, they often have thylakoids with reduced photosystem II complexes (the one that produces $O_2$). Both of these features keep oxygen levels low in bundle sheath cells, which is where the four-carbon compound is broken down into carbon dioxide, which enters the light-independent reactions ($C_3$ pathway) to form sugars and pyruvic acid, which is transported back to a mesophyll cell where it is converted back into **PEP**.

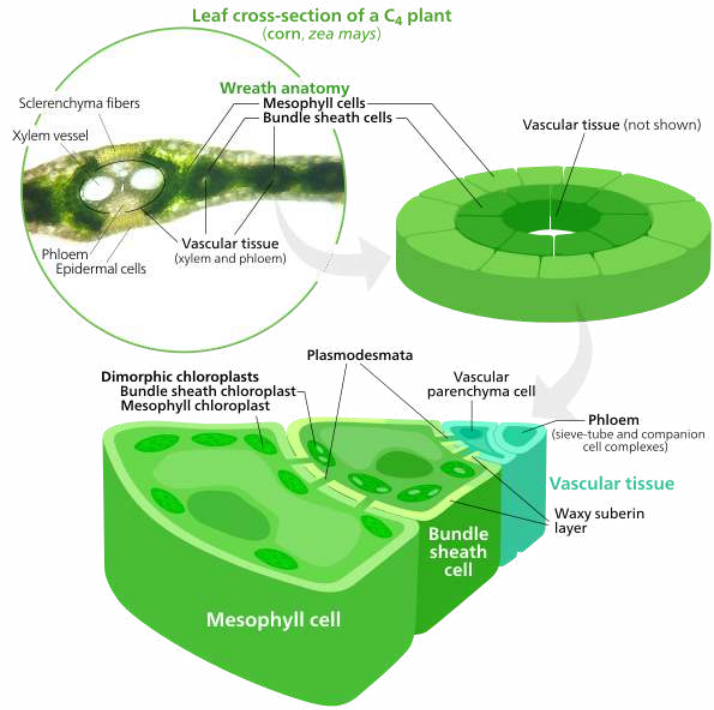



Figure **12.1.2**: Cross section and diagram of a C4 plant, showing mesophyll cells surrounding bundle sheath cells in concentric circles. The bundle sheath cells are larger and have more chloroplasts than in other plants. This arrangement is called Kranz anatomy (wreath anatomy). Vascular bundles contain xylem (vessel elements and tracheids) and phloem (sieve-tube and companion cell complexes). A vascular parenchyma is also shown in the vascular bundle. Waxy suberin borders the bundle sheath cells. The chloroplasts in the mesophyll cells are distinct from those in the bundle sheath cells, and the chloroplasts are thus called dimorphic. Sclerenchyma fibers are just above and below the vascular bundle, and epidermal cells surround the entire leaf. Image by Kelvinsong (CC-BY-SA).

These $C_4$ plants are well adapted to (and likely to be found in) habitats with high daytime temperatures and intense sunlight. Because they use the $C_4$ pathway to prevent photorespiration, they do not have to open their stomata to the same extent as $C_3$ plants and can thus conserve water. Some examples crabgrass, corn (maize), sugarcane, and sorghum. Although comprising only ~3% of the angiosperms by species, $C_4$ plants are responsible for ~25% of all the photosynthesis on land.

## CAM Plants

CAM stands for **c**rassulacean **a**cid **m**etabolism because it was first studied in members of the plant family Crassulaceae. **CAM plants** also do the $C_4$ pathway. However, instead of segregating the $C_4$ and $C_3$ pathways in different parts of the leaf, CAM plants separate them in **time** instead (Table **12.1.1**). As a result, CAM plants do not need to open their stomata in the daytime to reduce photorespiration because they have already formed a four-carbon molecule at night that can be broken down to release carbon dioxide during the day.

Table **12.1.1**: Activities of CAM plants at night and in the morning.

| Night | Morning |
|---|---|
| • CAM plants take in $CO_2$ through their open stomata (they tend to have reduced numbers of them).<br>• The $CO_2$ joins with PEP to form the four-carbon oxaloacetic acid.<br>• This is converted to four-carbon **malic acid** that accumulates during the night in the central vacuole of the cells. | • The stomata close (thus conserving moisture as well as reducing the inward diffusion of oxygen).<br>• The accumulated malic acid leaves the vacuole and is broken down to release $CO_2$.<br>• The $CO_2$ is taken up into the light-independent reactions ($C_3$ pathway). |

CAM plants thus thrive in conditions of high daytime temperatures, intense sunlight, and low soil moisture. Some examples of CAM plants include cacti (Figure **12.1.3**), pineapples, all epiphytic bromeliads, sedums, and the "ice plant" that invade the California coast line.



Figure **12.1.3**: Cultivated cacti in the Singapore Botanic Gardens. Image by Calvin Teo (CC-BY-SA).

## Attribution

Curated and authored by Melissa Ha using 16.2E Photorespiration and C4 Plants from *Biology* by John W. Kimball (licensed CC-BY)

This page titled 12.1: Photorespiration and Photosynthetic Pathways is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **4.1.7: Photorespiration and Photosynthetic Pathways** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-SA 4.0.

# 12.2: CO2 UPTAKE - C4 AND CAM PATHWAYS

## LEARNING GOALS (CHATGPT O3-MINI)

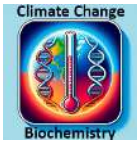
Below are a series of learning goals tailored for junior and senior biochemistry majors based on the provided information about the C4 pathway and associated topics:

- **Distinguish C3 and C4 Photosynthetic Pathways:**
  • Explain how photorespiration in C3 plants, driven by Rubisco's competing oxygenase activity and the glycolate salvage (C2) pathway, reduces photosynthetic efficiency.
  • Describe how the C4 pathway circumvents these inefficiencies by initially capturing $CO_2$ as bicarbonate ($HCO_3^-$) and converting it into a 4-carbon (4C) compound prior to RuBisCo fixation.
- **Outline the Initial Steps of the C4 Pathway:**
  • Describe the role of phosphoenolpyruvate (PEP) carboxylase in mesophyll cells in converting $HCO_3^-$ and PEP into oxaloacetate (OAA), a 4C intermediate.
  • Explain subsequent reactions where OAA is converted either to malate (via malate dehydrogenase) or aspartate (via transamination) and how these intermediates transport $CO_2$ to bundle sheath cells.
- **Examine the Role of Malate Decarboxylation and $CO_2$ Release:**
  • Discuss how, in the bundle sheath cells, malate is decarboxylated by NADP-malic enzyme to release $CO_2$ for fixation by RuBisCo, thereby locally saturating RuBisCo with $CO_2$ and suppressing its oxygenase activity.
- **Understand the Function and Mechanism of Pyruvate Phosphate Dikinase (PPDK):**
  • Describe the reaction catalyzed by PPDK, including its net reaction, formation of high-energy phosphorylated intermediates, and the overall cost of ATP (equivalent to two ATPs per $CO_2$ fixed in the C4 pathway).
  • Analyze the domain organization of PPDK (nucleotide-binding, central catalytic, and PEP/pyruvate binding domains) and explain how conformational "swiveling" enables sequential phosphotransfer events.
- **Compare Energy Costs and Thermodynamic Trade-offs:**
  • Contrast the ATP requirements for fixing $CO_2$ in the C4 pathway (approximately 5 ATPs per $CO_2$ fixed) with those in the C3 pathway (approximately 3 ATPs per $CO_2$ fixed).
  • Discuss how temperature influences Rubisco affinity for $CO_2$ and the relative efficiencies of C3 versus C4 pathways.
- **Explore the Role of Carbonic Anhydrases:**
  • Describe the function and distribution of the three classes of carbonic anhydrase (α, β, and γ) in plants, emphasizing their role in interconverting $CO_2$ and $HCO_3^-$ in different cellular compartments (chloroplast, cytosol, mitochondria) and in the $CO_2$-concentrating mechanisms of C4 and CAM plants.
- **Introduce Crassulacean Acid Metabolism (CAM):**
  • Outline the CAM pathway, highlighting its adaptation to water-limited environments through nocturnal $CO_2$ capture and daytime decarboxylation of stored malic acid, and compare its metabolic organization to that of C3 and C4 plants.
- **Discuss Plastid Diversity and Interconversion:**
  • Explain the various types of plastids (chloroplasts, amyloplasts, etioplasts, chromoplasts) and the processes (e.g., "greening" and "de-greening") by which plastids interconvert in response to environmental and developmental cues.
- **Examine Rubisco Aggregation and Phase Separation Mechanisms:**
  • Describe how the enzyme Rubisco, despite its slow turnover, is present in high concentrations and can undergo phase separation with intrinsically disordered linker proteins (such as EPYC1/LCI5 in algae or CsoS2 in carboxysomes) to enhance local $CO_2$ concentrations. • Understand the roles of protein-protein interactions, tandem repeats, and charge distribution in promoting phase separation and the formation of structures like pyrenoids and carboxysomes.
- **Evaluate the Evolutionary and Ecological Implications:**
  • Discuss the evolutionary history of Rubisco, including its adaptation from a high-$CO_2$, low-$O_2$ environment to current atmospheric conditions, and the strategies (e.g., C4 and CAM pathways) that have evolved to mitigate its inefficiencies.
  • Consider how rising atmospheric $CO_2$ and global warming might impact plant metabolism, photosynthetic efficiency, and ultimately food security through changes in nutrient composition.
- **Relate Plant Photosynthetic Efficiency to Thermodynamic Models:**
  • Compare the thermodynamic efficiencies of C3/C4 photosynthesis with energy conversion in internal combustion engines (e.g.,

the Otto cycle), highlighting how plants use concentration and storage mechanisms to optimize carbon fixation under varying environmental conditions.

These learning goals are designed to help students integrate structural, mechanistic, and regulatory aspects of the C4 pathway and related carbon fixation processes, as well as appreciate their significance in plant physiology and global carbon cycling.

The source for the organization and some of the text derives from Sindayigaya and Longhini. https://www.peoi.org/Courses/Courses...chem/biochem18 CC - https://creativecommons.org/licenses...sa/3.0/deed.en




Everything in the chapter is related to climate change. For more general information on biochemistry and climate change, visit Chapter 32 Biochemistry and Climate Change. For more details on carbon fixation or capture, visit Chapter 32.16: Part 4 - Fixing Carbon Fixation.

## 12.2.1:

## 12.2.2: THE C4 PATHWAY

Photorespiration, caused by the oxygenase activity of RuBisCo/Oxygenase and the ensuing glycolate salvage (C2) pathway, significantly diminishes the efficiency of photosynthesis in C3 plants. Rest assured, some plants have found a way around the problem by adding a few steps before RuBisCo. The altered pathway is known as the C4 pathway, and plants that utilize it are referred to as C4 plants. The initial steps involve the temporary capture of $CO_2$ in the form of $HCO_3^-$, into a 4C, not 3C sugar. Plants that utilize the C4 pathway include maize, sorghum, sugarcane, and many tropical plants. An overview of the pathways emphasizing the steps that precede RuBisCo is shown in Figure **12.2.1**.

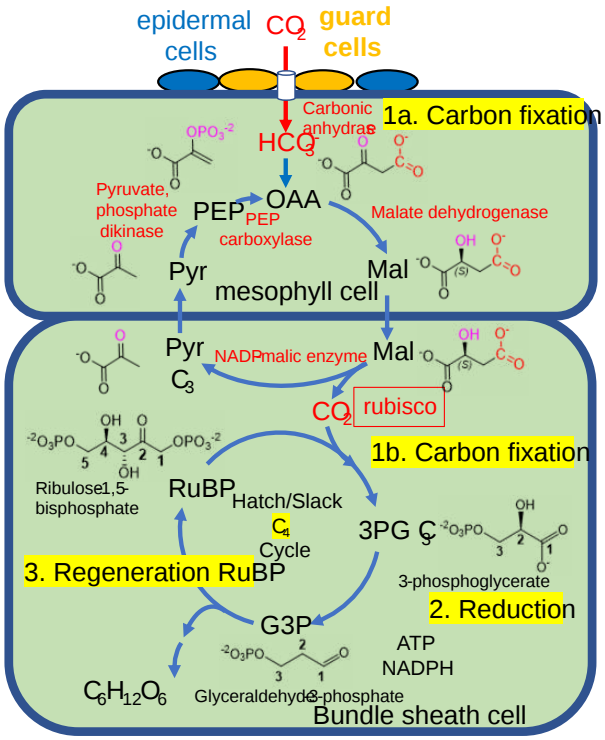



Figure **12.2.1**: Carbon assimilation in C4 plant

This extra step (compared to C3 plants) concentrates $CO_2$ and effectively decrease the competing substrate $O_2$ to increase the efficiency of Rubisco.

Experimental evidence shows that radiolabeled $^{14}CO_2$ is captured into the 4C molecule, oxaloacetate (OAA), a citric acid cycle and gluconeogenic intermediate, through the enzyme phosphoenolpyruvate carboxylase, which uses $HCO_3^-$ as a substrate. The reaction takes place in mesophyll cells. OAA can be reduced by NADPH using malate dehydrogenase or converted to aspartate through a transamination (not shown in the figure). Malate moves into the bundle sheath cell. It is then decarboxylated by the NADP-malic enzyme to pyruvate. Pyruvate can move back into the mesophyll cell and be converted to phosphoenolpyruvate (PEP) and then back to OAA by the **pyruvate phosphate dikinase** and **PEP carboxylase**. $CO_2$ from the decarboxylation of malate is delivered as a substrate to RuBisCo.

Pyruvate dikinase is used in bacteria, protozoa, C4 plants, and another type, Crassulacean, discussed below. Its non-plant function is to produce ATP, similar to pyruvate kinase. The net reaction is:

ATP + phosphate + pyruvate = AMP + $PP_i$ + $H^+$ + phosphoenolpyruvate

Figure **12.2.2** shows a simplified mechanism for the reaction

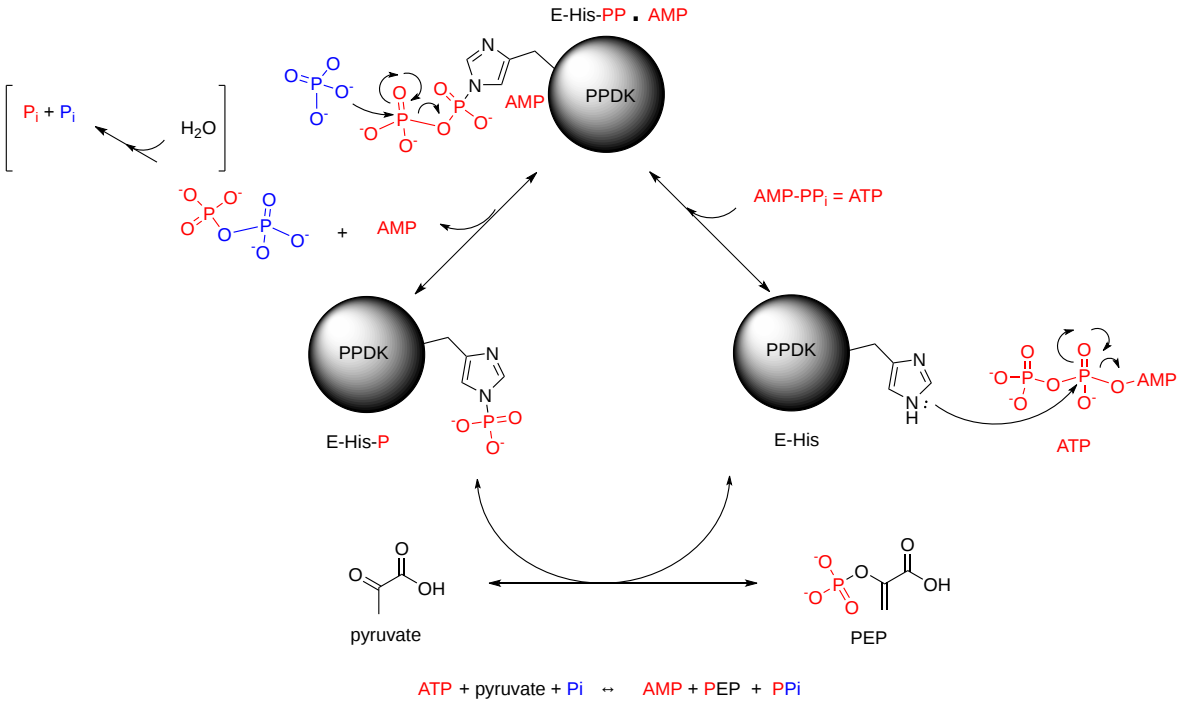



Figure **12.2.2**: Mechanism of pyruvate phosphate dikinase

The net reaction shows that in C4 plants, two molecules are phosphorylated by ATP. One is pyruvate, and the other is inorganic phosphate (Pi). Hence the name dikinase. The reverse reaction of ATP synthesis occurs in bacteria and protozoans. There are two phosphorylated intermediates, an Enz-His-P and an Enz-His-$PP_i$. These are "activated" phosphate carriers in the phosphotransfer reactions to pyruvate and $P_i$, respectively. If $PP_i$ is not hydrolyzed to $2P_i$, as illustrated in the top left of Figure 2 above, the reaction is fully reversible.

In C4 plants, there are three reactions

1. Pyr + E-His-P ↔ PEP + E-His
2. E-His + ATP ↔ E-His-PP ·AMP (· indicates a noncovalent interaction)
3. E-His-PP ·AMP + $P_i$ ↔ E-His-P + AMP + $PP_i$

When $PP_i$ is hydrolyzed, the net input of ATP to phosphorylated pyruvate is two ATP equivalents.

In the next step, PEP is carboxylated in a carbon capture reaction by PEP carboxylase, which, as mentioned above, uses $HCO_3^-$ as a substrate, not $CO_2$ per se. PEP carboxylase also lacks competing oxidase activity. The product is malate, which releases locally high "saturating" concentrations of $CO_2$ in the bundle sheath cells, significantly suppressing the oxygenase activity of RuBisCo.

Pyruvate phosphate dikinase undergoes a very large conformational change in domain organization during the catalytic cycle. The two kinase activities are located at different sites in the enzyme. The phosphorylation of Pi occurs in the N-terminal domain, while the phosphorylation of pyruvate occurs in the C-terminal domain. The central domain, which links to the N- and C-terminal domains via associated "tethers," is the site of the catalytic histidine involved in phosphotransfer. A swiveling of domains occurs to allow sequential phosphotransfers.

Figure **12.2.3** shows the Pfam domain structure for the protein.




Figure **12.2.3**: The green represents the AMP/ATP nucleotide-binding domain (NBD), the blue the PEP/pyruvate binding domain (PBD), and the red the central domain which catalyzes the phosphotransfer from ATP to pyruvate and from PEP to AMP through phosphorylated histidine intermediates. The NBD has three subdomains.

Figure **12.2.4** shows an interactive iCn3D model of an AlphaFold-predicted model of chloroplast pyruvate, phosphate dikinase from *Flaveria brownii (Brown's yellowtops) (*Q39734)

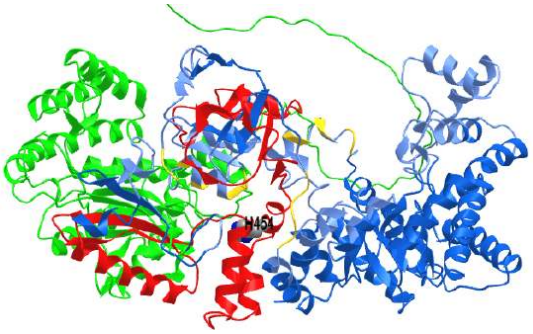



Figure **12.2.4**: AlphaFold-predicted model of chloroplast pyruvate, phosphate dikinase from *Flaveria brownii (Brown's yellowtops) (*Q39734). (Copyright; author via source). Click the image for a popup or use this external link: https://structure.ncbi.nlm.nih.gov/i...VB6Aywuc2bLD38

The green represents the N-terminal NBD, the red is the central domain with the catalytic His (side chain shown as CPK-colored spheres and labeled), and the blue is the PEP/Pyr PBD.

Figure **12.2.5** illustrates the conformation changes that occur in the central domain (yellow in this figure) and the N-terminal nucleotide-binding domain (NBD, green) in various ligand-bound states.

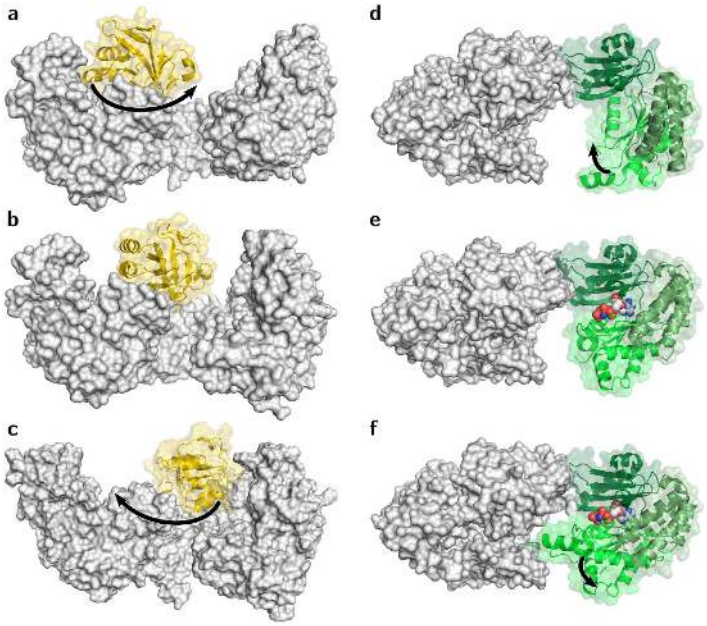



Figure **12.2.5**: **Movement of the PPDK domains**

Panel a–c show movement of the central domain (yellow). In (**a**), it swivels to face the PBD domain (PDB 5JVL/C), and in (**c**), it faces the NBD domain (*Tb*PPDK (PDB 2X0S)). In (**b**) it is in an intermediate position.

Panels d-f show the movement of the NBD (three greens depict the three subdomains). Pane (**d**) is the state without bound nucleotide (PDB 5JVJ/A), while panel (**f**) shows the fully closed, nucleotide-bound state (PDB 5JVL/A). Panel (**e**) shows a semi-closed, nucleotide-bound state (PDB 5JVL/C). Minges, A., Ciupka, D., Winkler, C. *et al.* Structural intermediates and directionality of the swiveling motion of Pyruvate Phosphate Dikinase. *Sci Rep* **7,** 45389 (2017). https://doi.org/10.1038/srep45389. Creative Commons Attribution 4.0 International License. http://creativecommons.org/licenses/by/4.0/

Figure **12.2.6** shows the interactions of bound substrates in different conformation states of PPDK.

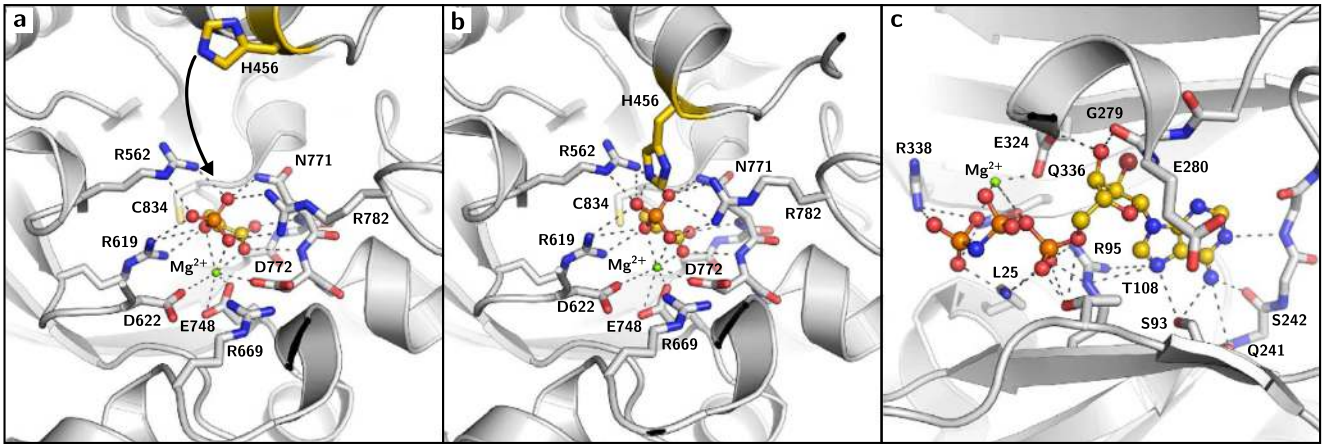



Figure **12.2.6**: **Substrate binding sites of *Ft*PPDK.**

Panel (**a**) shows the semi-closed state of the PEP binding site (PDB 5JVL/A) with the catalytic H456 (yellow) pointing away from PEP.

Panel (**b**) shows the closed state of the PEP binding site (PDB 5JVL/C), showing interactions between PEP and surrounding residues, including the catalytic H456 (yellow).

Panel (**c**) shows the closed state of the nucleotide-binding site of 5JVL/D occupied with 2'-Br-dAppNHp, a nonhydrolyzable ATP analog. Interacting residues are highlighted. Minges, A et al. ibid.

After $CO_2$ is delivered from malate in the bundle sheath cell using RuBisCo, the remaining reactions are the same as in the C3 pathways.

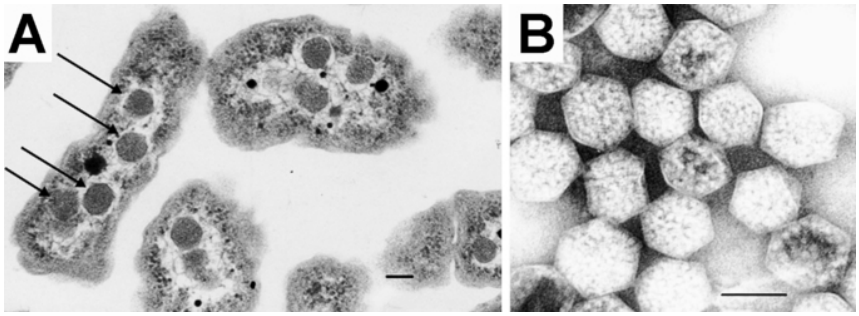
Once $CO_2$ is fixed into 3-phosphoglycerate in the bundle-sheath cells, the Calvin cycle's other reactions occur exactly as described earlier. Overall, the C4 pathways require more ATP. A molecule of PEP is required for each $CO_2$ fixed in the C4 pathway, which takes the equivalent of two ATPs. So, each $CO_2$ fixed in the C4 pathway takes five ATPs compared to three ATPs in the C3 pathway. As mentioned above, the affinity (estimated from the KM) of CO2 for RuBisCo decreases with increasing temperature, thereby decreasing the energetic efficiency of carbon capture. At higher temperatures (28-30 °C), the extra energy cost for the C4 pathway balances out the extra energy cost for the C3 pathway at higher temperatures.

## 12.2.3: CARBONIC ANHYDRASES

We first encountered carbonic anhydrase when we discussed its mechanism in Chapter x.xx. We'll now discuss its function and activity in the C4 pathway in detail. Given that we are facing a climate crisis due to the increasing levels of $CO_2$ in the atmosphere arising from the burning of fossil fuels, removing CO2 from the atmosphere —a process called carbon sequestration for climate purposes —becomes even more important. Understanding the role of carbonic anhydrase in CO2 sequestration also becomes crucial.

Plants have three genes for carbonic anhydrase (α, β, and γ). Each can be differentially spliced, resulting in plants having many different isoforms of this protein. They are most abundant in the chloroplast, cytoplasm, and mitochondria, and they have many additional roles outside of fixing $CO_2$ in C4 (and CAM) plants. In autotrophic (make their own "food") bacteria (such as cyanobacteria, also known as blue-green algae), there are no internal organelles. However, there are **carboxysomes,** which are protein-bounded vesicles (much like a bacteriophage head), which contain not nucleic acid but RuBisCo and carbonic anhydrase in their internal compartment. The carbonic anhydrase converts $HCO_3^-$ to $CO_2$ for reaction with RuBisCo. The carboxysome thus concentrates the $CO_2$-producing and fixing enzymes for photosynthesis.

Figure **12.2.7**:




F

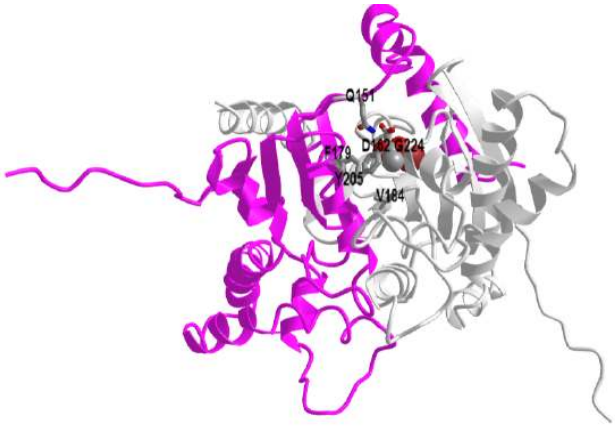
Figure **12.2.7**: **Electron Micrograph of a carboxysome**: (A) A thin-section electron micrograph of H. neapolitanus cells with carboxysomes inside. In one of the cells shown, arrows highlight the visible carboxysomes. (B) A negatively stained image of intact carboxysomes isolated from H. neapolitanus. The features visualized arise from the distribution of stains around proteins that form the shell, as well as around the RuBisCO molecules that fill the carboxysome interior. Scale bars indicate 100 nm. BioLibreText

In C3 plants, $CO_2$ (aq), which is dissolved CO2, is the actual substrate for RuBisCo, so available HCO3—is converted to CO2 by carbonic anhydrase. In C4 and CAM plants, CO2 (aq) is first converted to bicarbonate by carbonic anhydrase. HCO3- (aq) is then used as the actual substrate for the "carbon fixation" step. Hence, carbonic anhydrase has roles in C3, C4, and CAM plants.

All of the carbonic anhydrases have a $Zn^{+2}$ at the active site. The most prominent alpha form in plants was discovered in erythrocytes and is typically active as a monomer. It has one large 10-strand beta sheet surrounded by seven alpha helices. Three histidine side chains and water form a tetrahedral coordination around the $Zn^{2+}$ ion. **Gamma** carbonic anhydrase is a trimer with three active sites at the interface between pairwise monomers with the Zn-coordinating histidine side chains from two different subunits.

**Beta** carbonic anhydrase in plants is typically an octamer of identical subunits. Two cysteines, one histidine, and water coordinate the Zn ion. The monomer has four beta strands in a beta-sheet surrounded by alpha helices. An additional beta-strand is involved in monomer interactions. As the active site is located at the interface of two subunits, the functional biological unit is the dimer; however, a tetramer and even an octamer are typically formed. The substrate binding groups have a one-to-one correspondence with the functional groups in the alpha-carbonic anhydrase active site, with the corresponding residues being closely superimposable by a mirror plane of symmetry. Therefore, despite differing folds, alpha- and beta-carbonic anhydrases have converged upon a similar active site design and are likely to share a common mechanism.

Figure **12.2.8** shows an interactive iCn3D model of beta-carbonic anhydrase from Pisum sativum (pea) with bound acetate (1EKJ).




NCBI iCn3D Figure **12.2.8**: Beta-carbonic anhydrase from Pisum sativum (pea) with bound acetate (1EKJ). (Copyright; author via source). Click the image for a popup or use this external link: https://structure.ncbi.nlm.nih.gov/i...VZTEJPy1hPxK27

For the sake of simplicity, only two subunits (A - gray and B - magenta) of the octamer are shown. Acetate, a proxy for $HCO_3^{-2}$, is shown in spacefill binding between the two subunits in CPK-colored spheres. The side chains involved in $Zn^{2+}$ binding, Cys 160, His 220, and Cys 223 (unlabeled), are on the A chain. The amino acids that bind acetate are distributed between the A chain (Asp 162, Gly 224, Val 184) and the B chain (Gln 151, Phe 169, and Tyr 205) and are labeled. The same groups are involved in substrate binding in alpha carbonic anhydrase, but in a mirror image orientation (with the normal L-amino acids).

Beta carbonic anhydrase is highly expressed in leaves and is found in chloroplasts, mitochondria, and the cytoplasm. Many plants have it in the cytoplasm and chloroplasts.

- β-carbonic anhydrase (βCA) in C3 plants: Most of the βCA in leaves is in chloroplasts in mesophyll cells and may comprise up to 2% of leaf protein. Yet studies have shown that you can delete the gene for it with minimal effect on the maximal rate of photosynthesis. However, by interference, plant development was affected, so the enzyme is probably most needed to produce $HCO_3^-$ for biosynthesis.
- β-carbonic anhydrase (βCA) in C4 plants: Most of the βCA is found in the cytoplasm of mesophyll cells. There, it catalyzes the first reaction of the C4 pathway, $CO_2$ (aq) to $HCO_3^-$ (aq). Mitochondrial (βCA) and γCA probably function to fix $CO_2$ arising from oxidative respiration.

## 12.2.4: CRASSULACEAN ACID METABOLISM (CAM) PATHWAY

Plants that encounter the chronic stress of low water availability have evolved another pathway to adapt to these conditions. Stomata in C3 plants are open during the day to allow carbon capture from $CO_2$, but they can close when water is limited. This obviously will inhibit plant growth. In the CAM pathway, the stomata remain open at night, allowing for carbon capture when water loss through the stomata is lower. The incoming $CO_2$ is fixed through carbonic anhydrase and then a series of several enzymes to form malic acid, which is transported for storage and use during the light in vacuoles. This CAM pathway is described in Figure **12.2.9**.

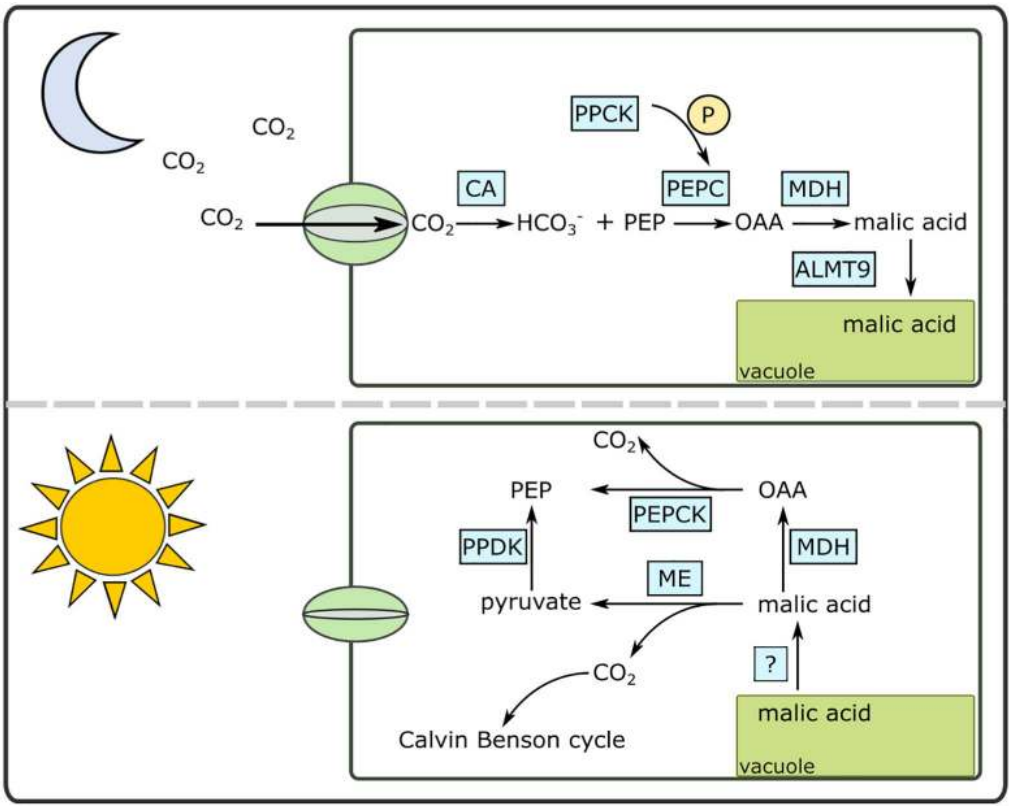



Figure **12.2.9**: A simplified diagram of the Crassulacean acid metabolism (CAM) pathway under day and night conditions. Heyduk Karolina, et al. Frontiers in Plant Science.2019. https://www.frontiersin.org/article/...pls.2018.02000. DOI=10.3389/fpls.2018.02000. **Creative Commons Attribution License (CC BY)**.

The proteins and intermediates in the CAM pathways are ALMT9, aluminum-activated malate transporter; CA, carbonic anhydrase; MDH, malate dehydrogenase; OAA, oxaloacetate; ME, malic enzyme (NAD or NADP); P, phosphate; PEPC, phosphoenolpyruvate carboxylase; PEPCK, PEP carboxykinase; PPCK, PEPC kinase; PPDK, pyruvate, phosphate dikinase.

During the day, malic acid moves back into the cytoplasm, where it is decarboxylated by malic enzyme, releasing locally high $CO_2$ concentrations for use by RuBisCo in the C3 cycle. In plants that use CAM, other changes occur, including modifications to leaf structure and the activation of additional regulatory processes that coordinate metabolic gene expression.

Figure **12.2.10**s shows more details of the CAM cycle.

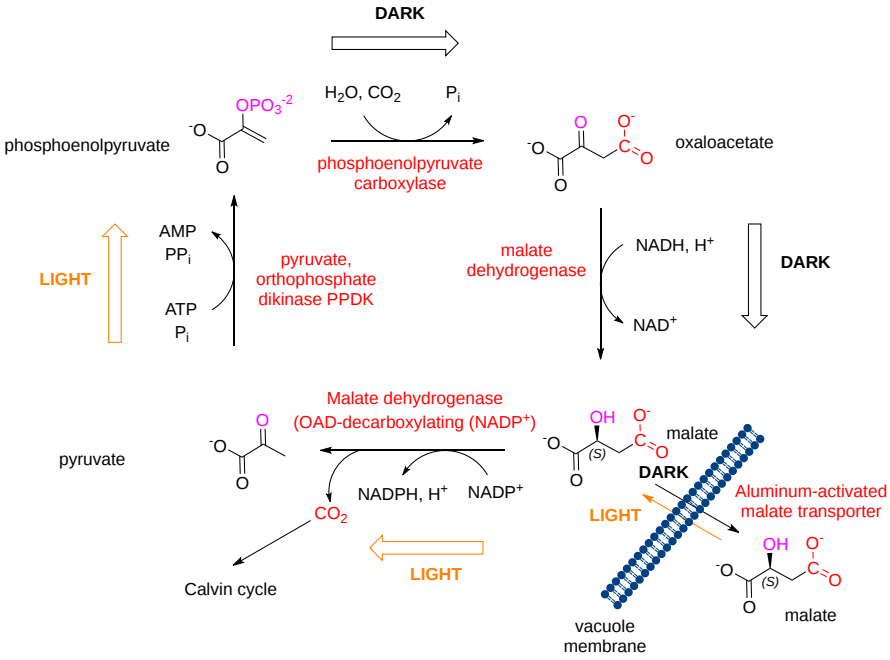



Figure **12.2.10**: Details of the CAM cycle

## 12.2.5: THERMODYNAMIC COMPARISON BETWEEN THE C3/C4 PATHWAYS AND THE OTTO CYCLE

It is interesting to compare the thermodynamic efficiencies of plants to that of the internal combustion engines, which is governed by the thermodynamic Otto cycle. In the cycle, chemical energy in the form of gasoline and $O_2$ is converted to thermal energy, which is then converted into mechanical energy. Both photosynthesis (the conversion of the energy of photons into chemical energy) and the Otto cyclehave limited efficiencies.

- In internal combustion engines, power is partly limited by air uptake and different efficiencies when running at non-constant speeds (like stop-and-go).
- In the C3 pathway, efficiency is limited by the oxygenase activity of RuBisCo/Oxygenase (given the much higher concentration of atmospheric $O_2$ compared to $CO_2$) and the ensuing photorespiration pathway.
- Water availability also plays a role, as the net reaction of photosynthesis and glucose production, in simplified form, is $6CO_2 + 6H_2O \rightarrow 6C(H_2O_6)$, so in high heat and low humidity, the process efficiency decreases.

Figure **12.2.11** shows a comparison of three stages, the storage component, the basic cycle, and a concentration mechanism, in photosynthesis and the internal combustion engine (ICE).

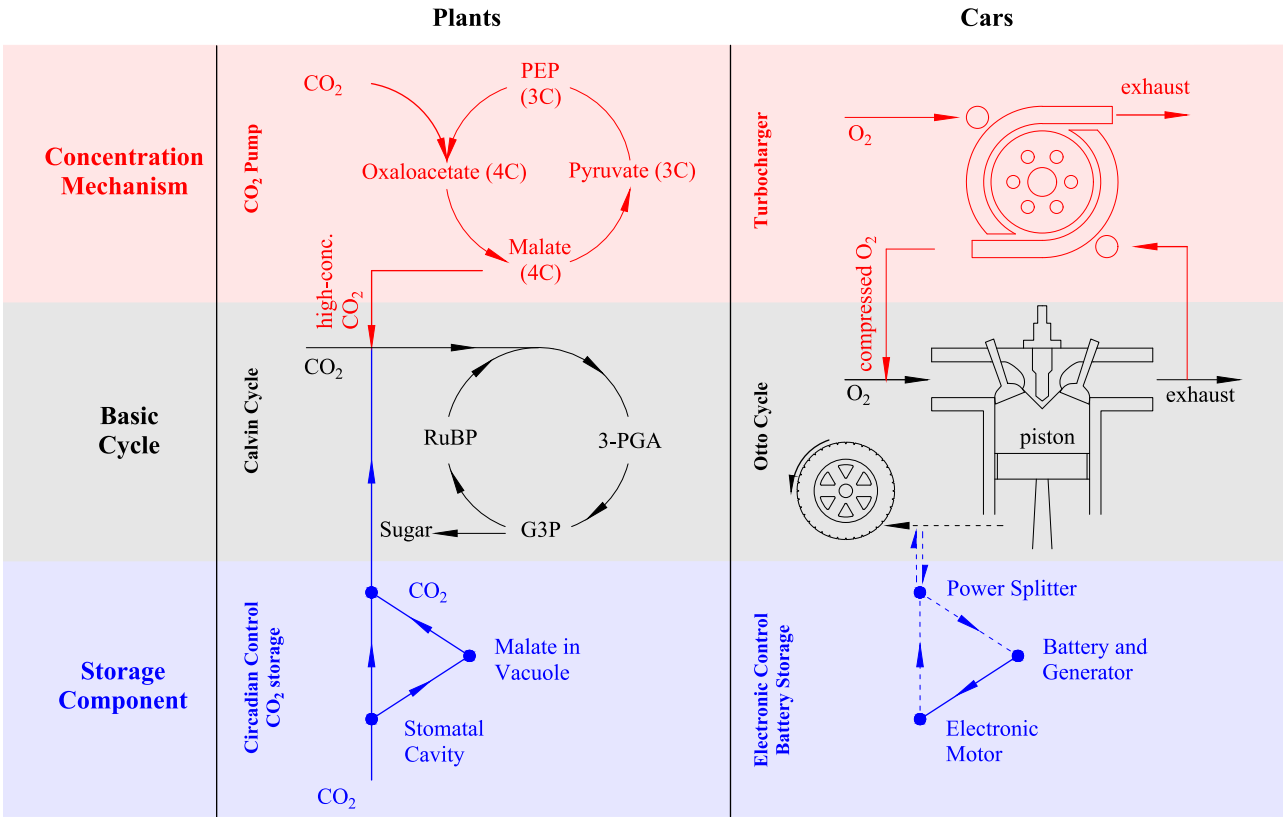



Figure 12.2.11: A comparison of plant photosynthesis and car engine functioning illustrates how the core processes interact with the additional components. Hartzell S, Bartlett M, Yin J, Porporato A (2018). Similarities in the evolution of plants and cars. PLoS ONE 13(6): e0198044. https://doi.org/10.1371/journal.pone.0198044. Creative Commons Attribution License,

A concentrating mechanism in C4 plants and turbocharged cars provides concentrated $CO_2$ and oxygen, respectively, to the core cycle (upper row). A storage mechanism in CAM plants allows carbon dioxide to be stored as malic acid at night and then passed to the Calvin cycle during the day, while a storage mechanism in hybrid electric vehicles (HEVs) allows energy to be stored in the battery during braking and then passed to the motor to power the drivetrain in parallel with the engine (bottom row).

## 12.2.6: SUMMARY

This chapter examines how certain plants overcome the inefficiencies of photorespiration inherent in the C3 pathway by employing the C4 pathway and related adaptations. In C3 plants, Rubisco's dual carboxylase/oxygenase activity leads to significant energy losses due to photorespiration. The C4 pathway, utilized by plants such as maize, sorghum, and sugarcane, introduces additional steps before $CO_2$ fixation to concentrate $CO_2$ and suppress Rubisco's oxygenase activity.

**Key Elements of the C4 Pathway:**

- **Initial $CO_2$ Capture:**
  In mesophyll cells, atmospheric $CO_2$ is first converted to bicarbonate ($HCO_3^-$) and then rapidly fixed by phosphoenolpyruvate (PEP) carboxylase to form a 4-carbon compound, oxaloacetate (OAA). OAA may be reduced to malate or converted to aspartate, which then transports the captured carbon to the bundle sheath cells.
- **$CO_2$ Release and Concentration:**
  Within bundle sheath cells, malate is decarboxylated by NADP-malic enzyme, releasing $CO_2$ near Rubisco. This localized, high concentration of $CO_2$ effectively minimizes Rubisco's competing oxygenase activity and enhances carboxylation efficiency.
- **Role of Pyruvate Phosphate Dikinase (PPDK):**
  PPDK regenerates PEP from pyruvate in the mesophyll cells. This enzyme undergoes significant conformational changes during its catalytic cycle, transferring high-energy phosphate groups via phosphorylated histidine intermediates. The process consumes two ATP equivalents per $CO_2$ fixed, which, while energetically more demanding than the C3 cycle, is offset by improved carbon fixation efficiency under conditions where photorespiration would otherwise dominate.

**Associated Enzymes and Plastid Adaptations:**

- **Carbonic Anhydrases:**
  These enzymes (α, β, and γ forms) facilitate the rapid interconversion between $CO_2$ and $HCO_3^-$, ensuring efficient substrate availability for PEP carboxylase in C4 and CAM plants. In C3 plants, carbonic anhydrases help generate $CO_2$ from dissolved bicarbonate for direct fixation by Rubisco.
- **Crassulacean Acid Metabolism (CAM):**
  As an adaptation to water-limited conditions, CAM plants open their stomata at night to fix $CO_2$ into malic acid, which is stored in vacuoles. During the day, malic acid is decarboxylated to release $CO_2$ for the Calvin cycle, reducing water loss while maintaining photosynthetic activity.
- **Plastid Interconversion:**
  The dynamic nature of plastids, such as the conversion between chloroplasts and amyloplasts, supports the diverse metabolic needs of the plant. These transitions are regulated by light and developmental signals, optimizing both photosynthesis and storage functions.

**Integration with Overall Plant Metabolism and Global Impact:**

- **Energy and Carbon Efficiency:**
  The C4 pathway requires additional ATP (approximately 5 ATP per $CO_2$ fixed compared to 3 ATP in the C3 cycle) due to the extra steps in carbon fixation. However, under high-temperature and high-light conditions, the enhanced $CO_2$ concentration at Rubisco's active site improves overall photosynthetic efficiency, making the C4 pathway advantageous in tropical and arid environments.
- **Evolutionary Adaptation:**
  The evolution of the C4 pathway represents a critical adaptation to declining atmospheric $CO_2$ and increasing $O_2$ levels over geological time, addressing the inherent limitations of Rubisco's carboxylase/oxygenase activity in C3 plants.
- **Implications for Global Climate and Food Security:**
  Changes in atmospheric $CO_2$ levels and global warming can affect the balance between $CO_2$ fixation and photorespiration. Although increased $CO_2$ may boost carbon assimilation in some contexts, rising temperatures and altered water availability can reduce nutrient content in crops, impacting food security worldwide.

In summary, this chapter details the biochemical and structural adaptations that enable C4 plants—and to some extent CAM plants—to more efficiently fix $CO_2$ and overcome the limitations of the C3 pathway. It integrates discussions of enzyme mechanisms (PEP carboxylase, PPDK, carbonic anhydrases), plastid dynamics, and the evolutionary and ecological implications of these pathways, providing a comprehensive view of advanced carbon fixation strategies in plants.

---

This page titled 12.2: CO2 uptake - C4 and CAM Pathways is shared under a not declared license and was authored, remixed, and/or curated by Tom Buckley.

- **20.5: CO2 uptake - C4 and CAM Pathways** by Henry Jakubowski and Patricia Flatt has no license indicated.
- **11.2: Diffusion Across a Membrane - Passive and Facilitated Diffusion** by Henry Jakubowski and Patricia Flatt has no license indicated.
- **20.4: $CO_2$ uptake - Calvin Cycle and C3 organisms** by Henry Jakubowski and Patricia Flatt is licensed CC BY-NC-SA 4.0.

# CHAPTER OVERVIEW

## 13: Respiration and metabolism

13.1: Aerobic Cellular Respiration

This page titled 13: Respiration and metabolism is shared under a not declared license and was authored, remixed, and/or curated by Tom Buckley.

# 13.1: Aerobic Cellular Respiration

**Learning Objectives**

- Identify the reactants and products of aerobic cellular respiration.
- Explain each step of aerobic cellular respiration and where in the cell it occurs.

Not only do plants produce sugars through photosynthesis, but they also break down these sugars to generate usable energy in the form of ATP through **aerobic cellular respiration**. Glucose begins its breakdown outside of the mitochondria in a metabolic pathway called glycolysis. However, the majority of the reactions that produce ATP happen within the mitochondria (in eukaryotic cells; Figure 13.1.1). During these reactions, electron carriers are created and oxygen pulls the electrons through an electron transport chain to create ATP, which powers cellular activity. The oxygen you breathe in combines with electrons to form water, which you breathe out. The carbon dioxide you breathe out comes from the carbon in glucose, which your body metabolized.

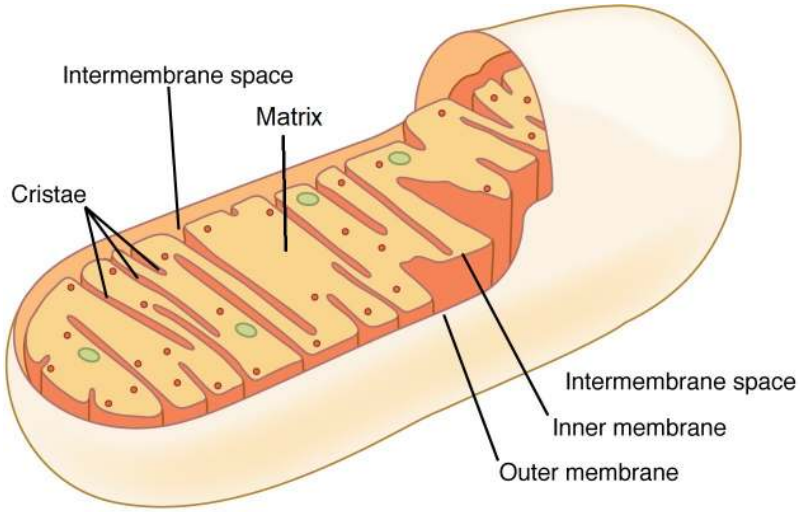



Figure 13.1.1: The mitochondria are the energy-conversion factories of the cell. A mitochondrion is composed of two separate lipid bilayer membranes. The folds of the inner membrane are called cristae, and the space between membranes is the intermembrane space. The matrix is in the center. Along the inner membrane are various molecules that work together to produce ATP, the cell's major energy currency. Image (relabeled) and caption (modified) by OpenStax (CC-BY). Access for free at openstax.org.

Here is a net reaction for cellular respiration:

$$C_6H_{12}O_6 + 6\,O_2 \rightarrow 6\,CO_2 + 6\,H_2O + ATP$$

glucose + oxygen → carbon dioxide + water + energy

## Step 1: Glycolysis

When glucose is transported into the cytoplasm of cells, it is broken down into two molecules of **pyruvate** (Figure 13.1.2). This process is called **glycolysis** (glyco- for glucose and -lysis, meaning to break apart). Glycolysis involves the coordinated action of many different enzymes. As these enzymes start to break the glucose molecule apart, an initial input of energy is required. This initial energy is donated by molecules of ATP.

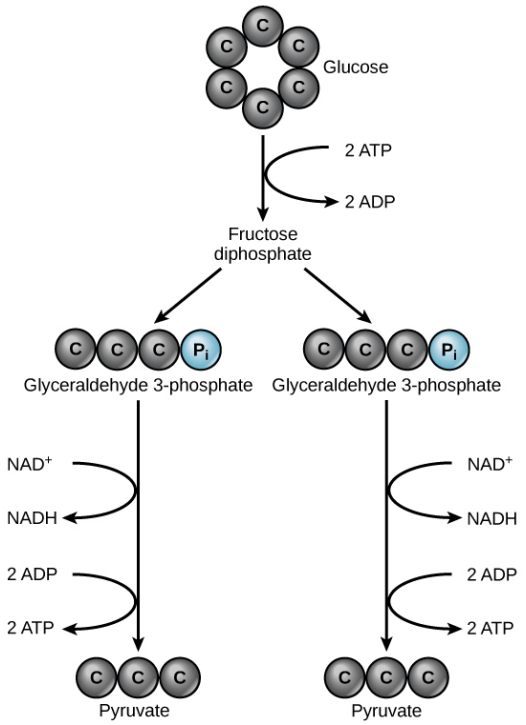
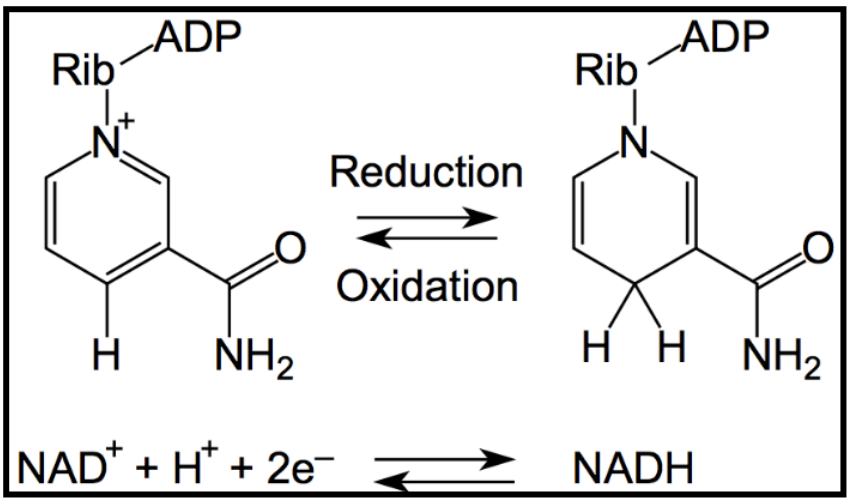



Figure **13.1.2**: In glycolysis, glucose (represented by a ring of six carbons) is converted to fructose-1,6-bisphosphate (labeled fructose diphosphate). This consumes 2 ATP, releasing 2 ADP. Fructose-1,6-bisphosphate is broken into two glyceraldehyde-3-phosphate molecules. Each is represented by a chain of three carbons attached to a phosphate ($P_i$). The phosphate is removed from each of the two glyceraldehyde-3-phosphate molecules, producing 2 pyruvates, 2 NADH, and 4 ATP. Overall, glycolysis consumes 2 ATP, but it then generates 4 ATP and 2 NADH. Image by OpenStax (CC-BY). Access for free at openstax.org.

Though two molecules of ATP are used to get glycolysis going, four more molecules of ATP are produced during the reaction, resulting in the net production of two ATP per molecule of glucose. In addition to ATP, two molecules of **nicotinamide adenine dinucleotide** (**$NAD^+$**) are reduced to form NADH (Figure **13.1.3**). When $NAD^+$ is reduced to NADH, two high energy electrons derived from breaking the bonds of glucose are added to it. One of those negatively charged electrons is balanced by the positive charge (+) on $NAD^+$. The other is balanced by adding a proton ($H^+$) to the molecule.




NAD+ can carry electrons (be reduced) by adding H+ ions

Figure **13.1.3**: When $NAD^+$ is reduced to NADH, it gains one proton ($H^+$) and two electrons ($e^-$). The reverse reaction (oxidation) can also occur. The chemical structure of $NAD^+$ is a modified version of two nucleotides attached together. It is represented by ADP (adenosine diphosphate) attached to ribose (rib, a five-carbon sugar), attached to a ring of carbon and nitrogen.

## Step 2: Pyruvate oxidation

If oxygen is present, aerobic cellular respiration can continue. The two molecules of pyruvate are transported into the matrix of the mitochondrion. During transport, each pyruvate is converted into a 2-carbon molecule called acetyl-CoA. The other carbon atom from each pyruvate molecule exits the cell as $CO_2$. The electrons from this broken bond are captured by another molecule of $NAD^+$, reducing it to NADH. Because two molecules of pyruvate are produced from each glucose molecule during glycolysis, two acetyl CoA molecules are produced (one from each pyruvate) during pyruvate oxidation (Figure 13.1.4).

## Step 3: The Citric Acid (Krebs) Cycle

The two acetyl-CoA molecules enter a cycle which, much like glycolysis, involves the action of many different enzymes to release energy and transport it in energy-carrying molecules, including 2 ATP, 6 NADH, and 2 $FADH_2$, another electron carrier (Figure 13.1.4). This cycle takes place within the matrix of the mitochondrion.

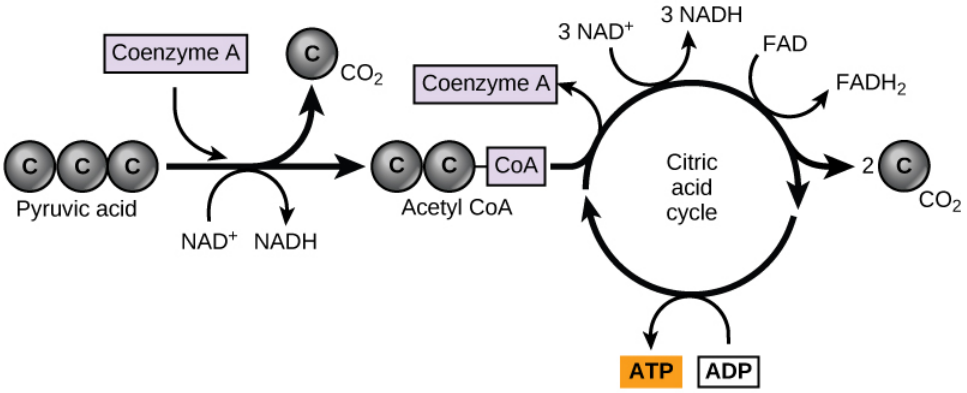



Figure 13.1.4: Combined view of pyruvate oxidation and the citric acid cycle. During pyruvate oxidation, pyurvate/pyruvic acid (three carbons) is converted to acetyl CoA (two carbons). In this process, one carbon dioxide molecule is released and one molecule of $NAD^+$ is reduced to NADH. In the citric acid cycle, acetyl CoA breaks into two carbon dioxide molecules. This process releases 2 NADH, 1 $FADH_2$, and 1 ATP per pyruvate, and double that per glucose. Image by OpenStax (CC-BY). Access for free at openstax.org.

## Step 4: Oxidative Phosphorylation

This stage of cellular respiration has two steps. During the **electron transport chain**, our electron carriers power a series of proton pumps that move $H^+$ ions from the mitochondrial matrix to the space between the inner and outer mitochondrial membranes. During **chemiosmosis**, an enzyme called ATP synthase allows the protons to flow back into the mitochondrial matrix, using the physical flow of the protons to turn ADP into ATP.

### The Electron Transport Chain

NADH and $FADH_2$ drop off their electrons at a protein complex within the **inner mitochondrial membrane.** This effectively "turns on" this protein complex, which pumps a $H^+$ from the mitochondrial matrix to the **intermembrane space**. The electrons are then passed down a line of protein complexes, much like a current of electricity, powering these complexes to each pump a $H^+$ from the matrix into the intermembrane space. This is appropriately named the electron transport chain (Figure 13.1.5).

At the end of the electron transport chain, the low energy electrons need to be picked up to make space for more electrons. An oxygen atom picks up two electrons and, to balance the charge, two $H^+$ from the matrix, forming a water molecule ($H_2O$). In cellular respiration, oxygen is the **terminal electron acceptor**, because it picks up the electrons at the end (the terminus) of the electron transport chain. This job is so important that, as you saw above, if oxygen is not present, this part of cellular respiration will not occur.

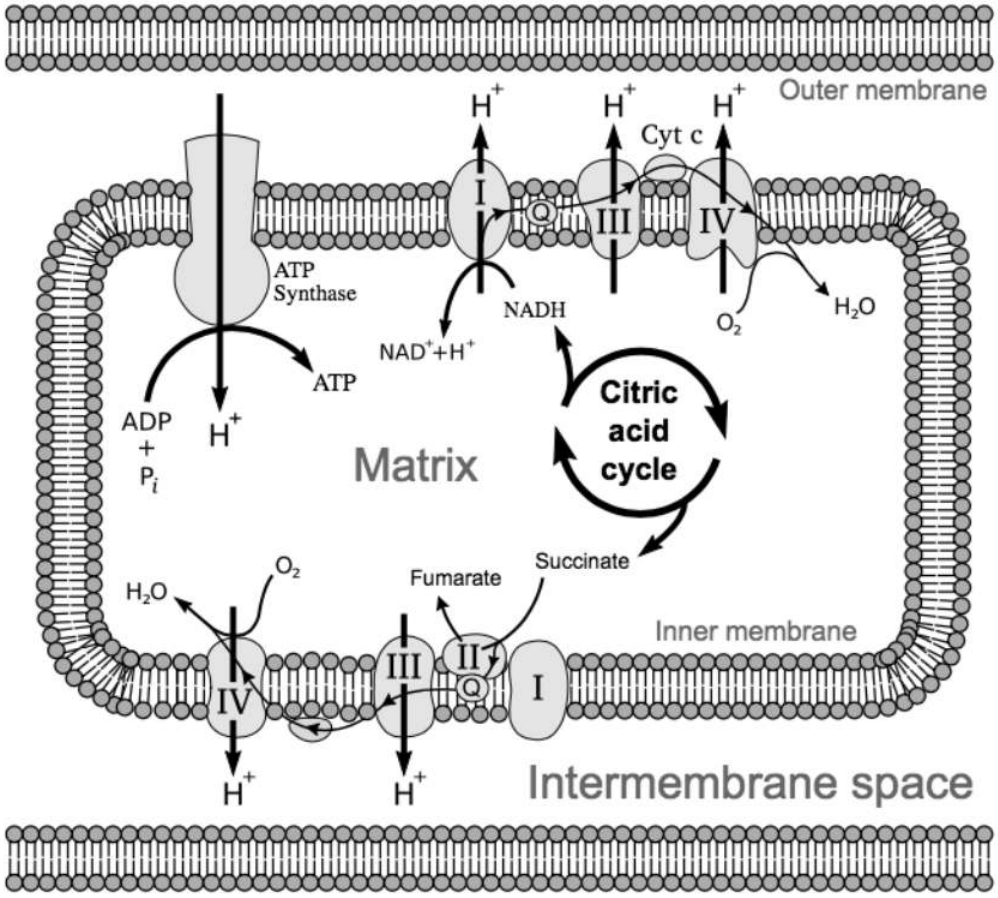



Figure **13.1.5**: This view of the mitochondrion shows the outer membrane and inner membrane, which borders the matrix. The intermembrane space is between the outer and inner membranes. Pyruvate oxidation (not shown) and the citric acid cycle occur in the matrix. The citric acid cycle (along with glycolysis and pyruvate oxidation) supplies NADH to the electron transport chain of oxidative phosphorylation. ($FADH_2$ also provides electrons to the electron transport chain, but it is not shown here.) Electrons from NADH are passed from complex I to coenzyme Q to complex III to cytochrome c to complex IV to gaseous oxygen, which is reduced to form water. The three complexes, which are embedded in the inner membrane pump protons into the intermembrane space. Protons move down their proton gradient through ATP synthase, generating ATP.

## Chemiosmosis

Why are the protein complexes pumping $H^+$ into the intermembrane space? The intermembrane space is relatively small. As more $H^+$ are added to this area, the intermembrane space becomes increasingly positively charged, while the matrix becomes increasingly negatively charged. This is similar to how a battery stores energy--by creating an electrochemical gradient. The positive charges repel each other and would “prefer” to be balanced across both sides of the membrane. However, they cannot directly pass through the membrane. Even though they are small, $H^+$ ions carry a full charge, making them too polar to pass through the nonpolar tails of the phospholipid bilayer that composes the mitochondrial membranes.

An enzyme called **ATP synthase** allows the $H^+$ to move back into the matrix. This enzyme is structured much like a waterwheel or turbine -- the flow of protons through the enzyme physically rotates it, converting the potential energy stored in the electrochemical gradient into kinetic energy (movement)! This kinetic energy is used to force another phosphate group onto ADP, converting the kinetic energy back into chemical energy, which is stored in the bonds of ATP

## Attributions

Curated and authored by Melissa Ha using the following sources:

- Kammy Algiers (CC-BY-NC)
- 13.3: Cellular Respiration in *Botany Lab Manual* by Maria Morrow (CC-BY)

This page titled 13.1: Aerobic Cellular Respiration is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **4.1.8: Chapter Summary** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC 4.0.

# CHAPTER OVERVIEW

## 14: Mineral nutrition


14.1: Prelude to Soil and Plant Nutrition
14.2: Nutritional Requirements of Plants
14.3: The Soil
14.4: Nutritional Adaptations of Plants
14.E: Soil and Plant Nutrition (Exercises)


This page titled 14: Mineral nutrition is shared under a not declared license and was authored, remixed, and/or curated by Tom Buckley.

# 14.1: Prelude to Soil and Plant Nutrition

Cucurbitaceae is a family of plants first cultivated in Mesoamerica, although several species are native to North America. The family includes many edible species, such as squash and pumpkin, as well as inedible gourds. In order to grow and develop into mature, fruit-bearing plants, many requirements must be met and events must be coordinated. Seeds must germinate under the right conditions in the soil; therefore, temperature, moisture, and soil quality are important factors that play a role in germination and seedling development. Soil quality and climate are significant to plant distribution and growth. The young seedling will eventually grow into a mature plant, and the roots will absorb nutrients and water from the soil. At the same time, the aboveground parts of the plant will absorb carbon dioxide from the atmosphere and use energy from sunlight to produce organic compounds through photosynthesis. This chapter will explore the complex dynamics between plants and soils, and the adaptations that plants have evolved to make better use of nutritional resources.



(a) (b)

Figure **14.1.1**: For this (a) squash seedling (*Cucurbita maxima*) to develop into a mature plant bearing its (b) fruit, numerous nutritional requirements must be met. (credit a: modification of work by Julian Colton; credit b: modification of work by "Wildfeuer"/Wikimedia Commons)

This page titled 14.1: Prelude to Soil and Plant Nutrition is shared under a CC BY 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **31.0: Prelude to Soil and Plant Nutrition** by OpenStax is licensed CC BY 4.0.

# 14.2: Nutritional Requirements of Plants

**Skills to Develop**

- Describe how plants obtain nutrients
- List the elements and compounds required for proper plant nutrition
- Describe an essential nutrient

Plants are unique organisms that can absorb nutrients and water through their root system, as well as carbon dioxide from the atmosphere. Soil quality and climate are the major determinants of plant distribution and growth. The combination of soil nutrients, water, and carbon dioxide, along with sunlight, allows plants to grow.

## The Chemical Composition of Plants

Since plants require nutrients in the form of elements such as carbon and potassium, it is important to understand the chemical composition of plants. The majority of volume in a plant cell is water; it typically comprises 80 to 90 percent of the plant's total weight. Soil is the water source for land plants, and can be an abundant source of water, even if it appears dry. Plant roots absorb water from the soil through root hairs and transport it up to the leaves through the xylem. As water vapor is lost from the leaves, the process of transpiration and the polarity of water molecules (which enables them to form hydrogen bonds) draws more water from the roots up through the plant to the leaves (Figure **14.2.1**). Plants need water to support cell structure, for metabolic functions, to carry nutrients, and for photosynthesis.

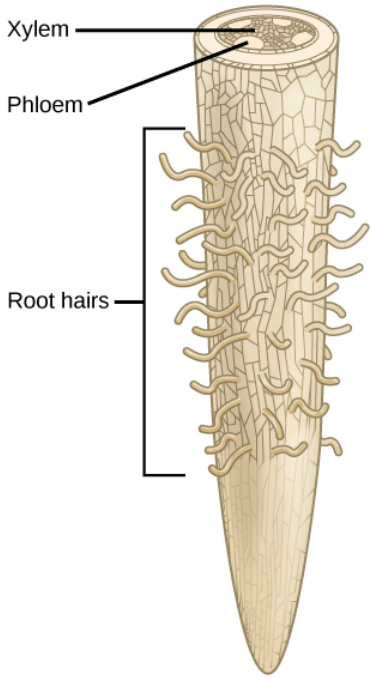



Figure **14.2.1**: Water is absorbed through the root hairs and moves up the xylem to the leaves.

Plant cells need essential substances, collectively called nutrients, to sustain life. Plant nutrients may be composed of either organic or inorganic compounds. An organic compound is a chemical compound that contains carbon, such as carbon dioxide obtained from the atmosphere. Carbon that was obtained from atmospheric $CO_2$ composes the majority of the dry mass within most plants. An inorganic compound does not contain carbon and is not part of, or produced by, a living organism. Inorganic substances, which form the majority of the soil solution, are commonly called minerals: those required by plants include nitrogen (N) and potassium (K) for structure and regulation.

## Essential Nutrients

Plants require only light, water and about 20 elements to support all their biochemical needs: these 20 elements are called essential nutrients. For an element to be regarded as essential, three criteria are required: 1) a plant cannot complete its life cycle without the element; 2) no other element can perform the function of the element; and 3) the element is directly involved in plant nutrition.

**Table 14.2.1:** Essential elements for plant growth

| Macronutrients | Micronutrients |
|---|---|
| Carbon (C) | Iron (Fe) |
| Hydrogen (H) | Manganese (Mn) |
| Oxygen (O) | Boron (B) |
| Nitrogen (N) | Molybdenum (Mo) |
| Phosphorus (P) | Copper (Cu) |
| Potassium (K) | Zinc (Zn) |
| Calcium (Ca) | Chlorine (Cl) |
| Magnesium (Mg) | Nickel (Ni) |
| Sulfur (S) | Cobalt (Co) |
| | Sodium (S) |
| | Silicon (Si) |

### Macronutrients and Micronutrients

The essential elements can be divided into two groups: macronutrients and micronutrients. Nutrients that plants require in larger amounts are called macronutrients. About half of the essential elements are considered macronutrients: carbon, hydrogen, oxygen, nitrogen, phosphorus, potassium, calcium, magnesium and sulfur. The first of these macronutrients, carbon (C), is required to form carbohydrates, proteins, nucleic acids, and many other compounds; it is therefore present in all macromolecules. On average, the dry weight (excluding water) of a cell is 50 percent carbon. As shown in Figure **14.2.2**, carbon is a key part of plant biomolecules.

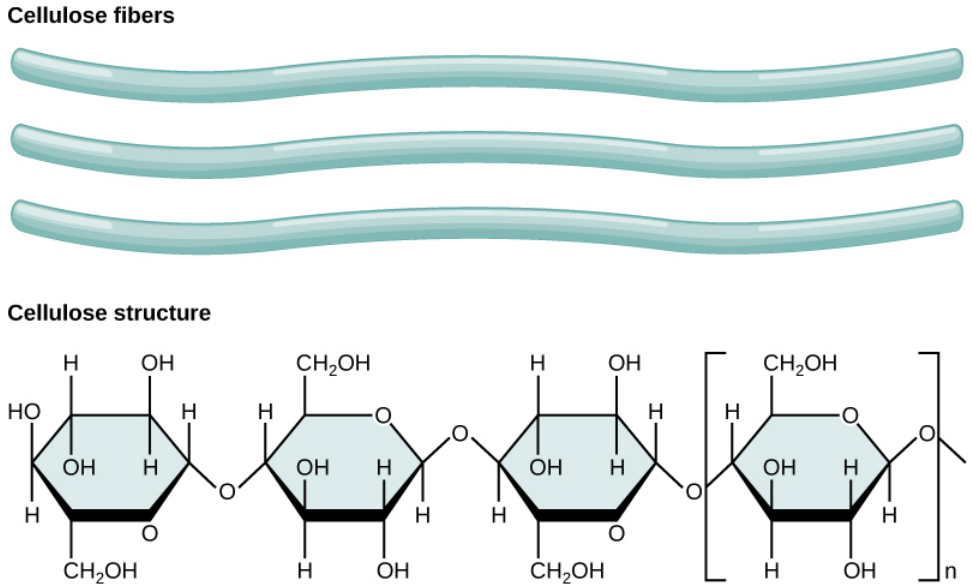



Figure **14.2.2**: Cellulose, the main structural component of the plant cell wall, makes up over thirty percent of plant matter. It is the most abundant organic compound on earth. Plants are able to make their own cellulose, but need carbon from the soil to do so.

The next most abundant element in plant cells is nitrogen (N); it is part of proteins and nucleic acids. Nitrogen is also used in the synthesis of some vitamins. Hydrogen and oxygen are macronutrients that are part of many organic compounds, and also form water. Oxygen is necessary for cellular respiration; plants use oxygen to store energy in the form of ATP. Phosphorus (P), another macromolecule, is necessary to synthesize nucleic acids and phospholipids. As part of ATP, phosphorus enables food energy to be converted into chemical energy through oxidative phosphorylation. Likewise, light energy is converted into chemical energy during photophosphorylation in photosynthesis, and into chemical energy to be extracted during respiration. Sulfur is part of certain amino acids, such as cysteine and methionine, and is present in several coenzymes. Sulfur also plays a role in photosynthesis as part of the electron transport chain, where hydrogen gradients play a key role in the conversion of light energy into ATP. Potassium (K) is important because of its role in regulating stomatal opening and closing. As the openings for gas exchange, stomata help maintain a healthy water balance; a potassium ion pump supports this process.

Magnesium (Mg) and calcium (Ca) are also important macronutrients. The role of calcium is twofold: to regulate nutrient transport, and to support many enzyme functions. Magnesium is important to the photosynthetic process. These minerals, along with the micronutrients, which are described below, also contribute to the plant's ionic balance.

In addition to macronutrients, organisms require various elements in small amounts. These micronutrients, or trace elements, are present in very small quantities. They include boron (B), chlorine (Cl), manganese (Mn), iron (Fe), zinc (Zn), copper (Cu), molybdenum (Mo), nickel (Ni), silicon (Si), and sodium (Na).

Deficiencies in any of these nutrients—particularly the macronutrients—can adversely affect plant growth (Figure **14.2.3**). Depending on the specific nutrient, a lack can cause stunted growth, slow growth, or chlorosis (yellowing of the leaves). Extreme deficiencies may result in leaves showing signs of cell death.



(a)



(b)



(c)



(d)

Figure **14.2.3**: Nutrient deficiency is evident in the symptoms these plants show. This (a) grape tomato suffers from blossom end rot caused by calcium deficiency. The yellowing in this (b) *Frangula alnus* results from magnesium deficiency. Inadequate magnesium also leads to (c) intervenal chlorosis, seen here in a sweetgum leaf. This (d) palm is affected by potassium deficiency. (credit c: modification of work by Jim Conrad; credit d: modification of work by Malcolm Manners)

## Everyday Connection: Hydroponics

Hydroponics is a method of growing plants in a water-nutrient solution instead of soil. Since its advent, hydroponics has developed into a growing process that researchers often use. Scientists who are interested in studying plant nutrient deficiencies can use hydroponics to study the effects of different nutrient combinations under strictly controlled conditions. Hydroponics has also developed as a way to grow flowers, vegetables, and other crops in greenhouse environments. You might find hydroponically grown produce at your local grocery store. Today, many lettuces and tomatoes in your market have been hydroponically grown.

## Summary

Plants can absorb inorganic nutrients and water through their root system, and carbon dioxide from the environment. The combination of organic compounds, along with water, carbon dioxide, and sunlight, produce the energy that allows plants to grow. Inorganic compounds form the majority of the soil solution. Plants access water though the soil. Water is absorbed by the plant root, transports nutrients throughout the plant, and maintains the structure of the plant. Essential elements are indispensable elements for plant growth. They are divided into macronutrients and micronutrients. The macronutrients plants require are carbon, nitrogen, hydrogen, oxygen, phosphorus, potassium, calcium, magnesium, and sulfur. Important micronutrients include iron, manganese, boron, molybdenum, copper, zinc, chlorine, nickel, cobalt, silicon and sodium.

## Glossary

**inorganic compound**
: chemical compound that does not contain carbon; it is not part of or produced by a living organism

**macronutrient**
: nutrient that is required in large amounts for plant growth; carbon, hydrogen, oxygen, nitrogen, phosphorus, potassium, calcium, magnesium, and sulfur

**micronutrient**
: nutrient required in small amounts; also called trace element

**organic compound**
: chemical compound that contains carbon

---

This page titled 14.2: Nutritional Requirements of Plants is shared under a CC BY 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **31.1: Nutritional Requirements of Plants** by OpenStax is licensed CC BY 4.0.

# 14.3: The Soil

**Skills to Develop**

- Describe how soils are formed
- Explain soil composition
- Describe a soil profile

Plants obtain inorganic elements from the soil, which serves as a natural medium for land plants. Soil is the outer loose layer that covers the surface of Earth. Soil quality is a major determinant, along with climate, of plant distribution and growth. Soil quality depends not only on the chemical composition of the soil, but also the topography (regional surface features) and the presence of living organisms. In agriculture, the history of the soil, such as the cultivating practices and previous crops, modify the characteristics and fertility of that soil.

Soil develops very slowly over long periods of time, and its formation results from natural and environmental forces acting on mineral, rock, and organic compounds. Soils can be divided into two groups: organic soils are those that are formed from sedimentation and primarily composed of organic matter, while those that are formed from the weathering of rocks and are primarily composed of inorganic material are called mineral soils. Mineral soils are predominant in terrestrial ecosystems, where soils may be covered by water for part of the year or exposed to the atmosphere.

## Soil Composition

Soil consists of these major components (Figure **14.3.1**):

- inorganic mineral matter, about 40 to 45 percent of the soil volume
- organic matter, about 5 percent of the soil volume
- water and air, about 50 percent of the soil volume

The amount of each of the four major components of soil depends on the amount of vegetation, soil compaction, and water present in the soil. A good healthy soil has sufficient air, water, minerals, and organic material to promote and sustain plant life.

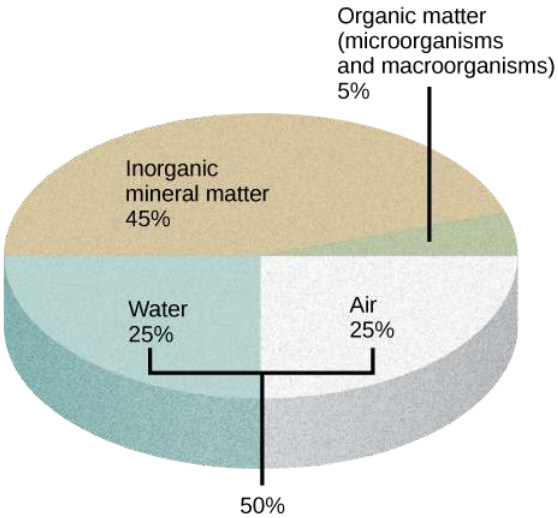



Figure **14.3.1**: The four major components of soil are shown: inorganic minerals, organic matter, water, and air.

**Exercise 14.3.1**

Soil compaction can result when soil is compressed by heavy machinery or even foot traffic. How might this compaction change the soil composition?

**Answer**

> The air content of the soil decreases.

The organic material of soil, called humus, is made up of microorganisms (dead and alive), and dead animals and plants in varying stages of decay. Humus improves soil structure and provides plants with water and minerals. The inorganic material of soil consists of rock, slowly broken down into smaller particles that vary in size. Soil particles that are 0.1 to 2 mm in diameter are sand. Soil particles between 0.002 and 0.1 mm are called silt, and even smaller particles, less than 0.002 mm in diameter, are called clay. Some soils have no dominant particle size and contain a mixture of sand, silt, and humus; these soils are called loams.

## Soil Formation

Soil formation is the consequence of a combination of biological, physical, and chemical processes. Soil should ideally contain 50 percent solid material and 50 percent pore space. About one-half of the pore space should contain water, and the other half should contain air. The organic component of soil serves as a cementing agent, returns nutrients to the plant, allows soil to store moisture, makes soil tillable for farming, and provides energy for soil microorganisms. Most soil microorganisms—bacteria, algae, or fungi—are dormant in dry soil, but become active once moisture is available.

Soil distribution is not homogenous because its formation results in the production of layers; together, the vertical section of a soil is called the soil profile. Within the soil profile, soil scientists define zones called horizons. A horizon is a soil layer with distinct physical and chemical properties that differ from those of other layers. Five factors account for soil formation: parent material, climate, topography, biological factors, and time.

### Parent Material

The organic and inorganic material in which soils form is the parent material. Mineral soils form directly from the weathering of bedrock, the solid rock that lies beneath the soil, and therefore, they have a similar composition to the original rock. Other soils form in materials that came from elsewhere, such as sand and glacial drift. Materials located in the depth of the soil are relatively unchanged compared with the deposited material. Sediments in rivers may have different characteristics, depending on whether the stream moves quickly or slowly. A fast-moving river could have sediments of rocks and sand, whereas a slow-moving river could have fine-textured material, such as clay.

### Climate

Temperature, moisture, and wind cause different patterns of weathering and therefore affect soil characteristics. The presence of moisture and nutrients from weathering will also promote biological activity: a key component of a quality soil.

### Topography

Regional surface features (familiarly called “the lay of the land”) can have a major influence on the characteristics and fertility of a soil. Topography affects water runoff, which strips away parent material and affects plant growth. Steeps soils are more prone to erosion and may be thinner than soils that are relatively flat or level.

### Biological factors

The presence of living organisms greatly affects soil formation and structure. Animals and microorganisms can produce pores and crevices, and plant roots can penetrate into crevices to produce more fragmentation. Plant secretions promote the development of microorganisms around the root, in an area known as the rhizosphere. Additionally, leaves and other material that fall from plants decompose and contribute to soil composition.

### Time

Time is an important factor in soil formation because soils develop over long periods. Soil formation is a dynamic process. Materials are deposited over time, decompose, and transform into other materials that can be used by living organisms or deposited onto the surface of the soil.

## Physical Properties of the Soil

Soils are named and classified based on their horizons. The soil profile has four distinct layers: 1) O horizon; 2) A horizon; 3) B horizon, or subsoil; and 4) C horizon, or soil base (Figure **14.3.2**). The O horizon has freshly decomposing organic matter—humus—at its surface, with decomposed vegetation at its base. Humus enriches the soil with nutrients and enhances soil moisture retention. Topsoil—the top layer of soil—is usually two to three inches deep, but this depth can vary considerably. For instance, river deltas like the Mississippi River delta have deep layers of topsoil. Topsoil is rich in organic material; microbial processes occur there, and it is the "workhorse" of plant production. The A horizon consists of a mixture of organic material with inorganic products of weathering, and it is therefore the beginning of true mineral soil. This horizon is typically darkly colored because of the presence of organic matter. In this area, rainwater percolates through the soil and carries materials from the surface. The B horizon is an accumulation of mostly fine material that has moved downward, resulting in a dense layer in the soil. In some soils, the B horizon contains nodules or a layer of calcium carbonate. The C horizon, or soil base, includes the parent material, plus the organic and inorganic material that is broken down to form soil. The parent material may be either created in its natural place, or transported from elsewhere to its present location. Beneath the C horizon lies bedrock.

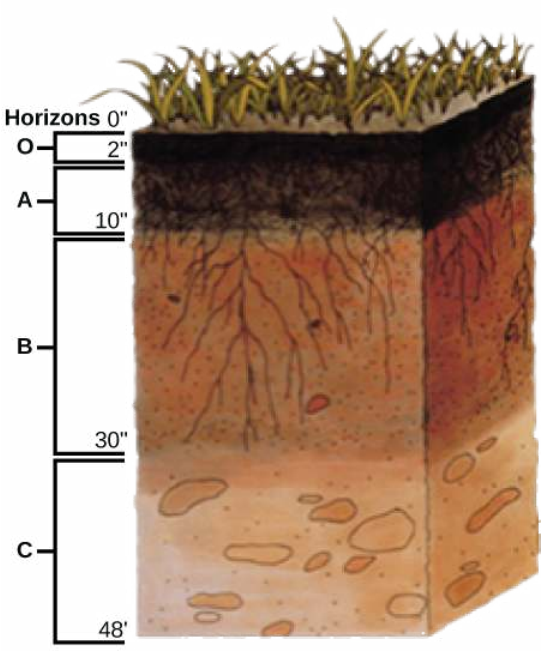



Figure **14.3.2**: This soil profile shows the different soil layers (O horizon, A horizon, B horizon, and C horizon) found in typical soils. (credit: modification of work by USDA)

**Exercise 14.3.2**

Which horizon is considered the topsoil, and which is considered the subsoil?

**Answer**

The A horizon is the topsoil, and the B horizon is subsoil.

Some soils may have additional layers, or lack one of these layers. The thickness of the layers is also variable, and depends on the factors that influence soil formation. In general, immature soils may have O, A, and C horizons, whereas mature soils may display all of these, plus additional layers (Figure **14.3.3**).

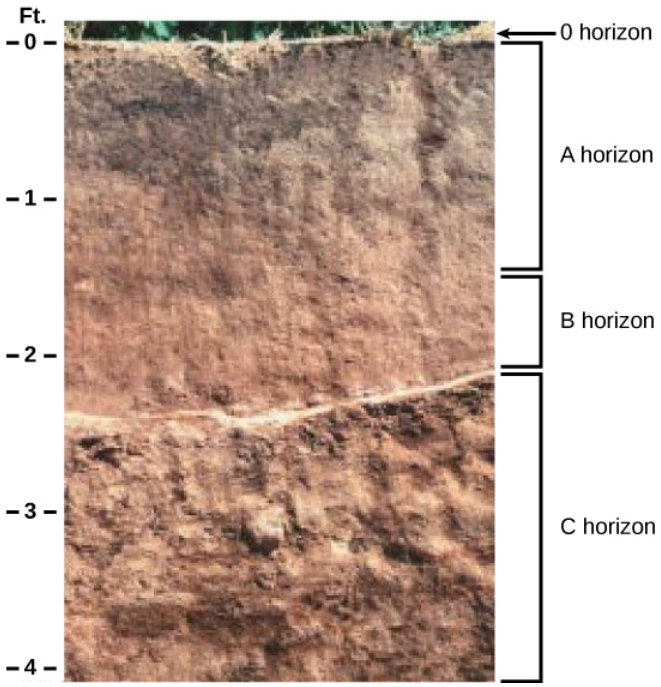



Figure **14.3.3**: The San Joaquin soil profile has an O horizon, A horizon, B horizon, and C horizon. (credit: modification of work by USDA)

## Career Connections: Soil Scientist

A soil scientist studies the biological components, physical and chemical properties, distribution, formation, and morphology of soils. Soil scientists need to have a strong background in physical and life sciences, plus a foundation in mathematics. They may work for federal or state agencies, academia, or the private sector. Their work may involve collecting data, carrying out research, interpreting results, inspecting soils, conducting soil surveys, and recommending soil management programs.



Figure **14.3.4**: This soil scientist is studying the horizons and composition of soil at a research site. (credit: USDA)

Many soil scientists work both in an office and in the field. According to the United States Department of Agriculture (USDA): "a soil scientist needs good observation skills to analyze and determine the characteristics of different types of soils. Soil types are complex and the geographical areas a soil scientist may survey are varied. Aerial photos or various satellite images are often used to research the areas. Computer skills and geographic information systems (GIS) help the scientist to analyze the multiple facets of geomorphology, topography, vegetation, and climate to discover the patterns left on the landscape."[1] Soil scientists play a key role in understanding the soil's past, analyzing present conditions, and making recommendations for future soil-related practices.

## Summary

Plants obtain mineral nutrients from the soil. Soil is the outer loose layer that covers the surface of Earth. Soil quality depends on the chemical composition of the soil, the topography, the presence of living organisms, the climate, and time. Agricultural practice and history may also modify the characteristics and fertility of soil. Soil consists of four major components: 1) inorganic mineral matter, 2) organic matter, 3) water and air, and 4) living matter. The organic material of soil is made of humus, which improves soil structure and provides water and minerals. Soil inorganic material consists of rock slowly broken down into smaller particles that vary in size, such as sand, silt, and loam.

Soil formation results from a combination of biological, physical, and chemical processes. Soil is not homogenous because its formation results in the production of layers called a soil profile. Factors that affect soil formation include: parent material, climate, topography, biological factors, and time. Soils are classified based on their horizons, soil particle size, and proportions. Most soils have four distinct horizons: O, A, B, and C.

## Footnotes

1. 1 National Resources Conservation Service / United States Department of Agriculture. “Careers in Soil Science.” soils.usda.gov/education/facts/careers.html

## Glossary

**A horizon**
consists of a mixture of organic material with inorganic products of weathering

**B horizon**
soil layer that is an accumulation of mostly fine material that has moved downward

**bedrock**
solid rock that lies beneath the soil

**C horizon**
layer of soil that contains the parent material, and the organic and inorganic material that is broken down to form soil; also known as the soil base

**clay**
soil particles that are less than 0.002 mm in diameter

**horizon**
soil layer with distinct physical and chemical properties, which differs from other layers depending on how and when it was formed

**humus**
organic material of soil; made up of microorganisms, dead animals and plants in varying stages of decay

**loam**
soil that has no dominant particle size

**mineral soil**
type of soil that is formed from the weathering of rocks and inorganic material; composed primarily of sand, silt, and clay

**O horizon**
layer of soil with humus at the surface and decomposed vegetation at the base

**organic soil**
type of soil that is formed from sedimentation; composed primarily of organic material

**parent material**
organic and inorganic material in which soils form

**rhizosphere**
area of soil affected by root secretions and microorganisms

**sand**
soil particles between 0.1–2 mm in diameter

**silt**

soil particles between 0.002 and 0.1 mm in diameter

**soil profile**

vertical section of a soil

**soil**

outer loose layer that covers the surface of Earth

---

This page titled 14.3: The Soil is shared under a CC BY 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **31.2: The Soil** by OpenStax is licensed CC BY 4.0.

# 14.4: Nutritional Adaptations of Plants

**Skills to Develop**

- Understand the nutritional adaptations of plants
- Describe mycorrhizae
- Explain nitrogen fixation

Plants obtain food in two different ways. Autotrophic plants can make their own food from inorganic raw materials, such as carbon dioxide and water, through photosynthesis in the presence of sunlight. Green plants are included in this group. Some plants, however, are heterotrophic: they are totally parasitic and lacking in chlorophyll. These plants, referred to as holo-parasitic plants, are unable to synthesize organic carbon and draw all of their nutrients from the host plant.

Plants may also enlist the help of microbial partners in nutrient acquisition. Particular species of bacteria and fungi have evolved along with certain plants to create a mutualistic symbiotic relationship with roots. This improves the nutrition of both the plant and the microbe. The formation of nodules in legume plants and mycorrhization can be considered among the nutritional adaptations of plants. However, these are not the only type of adaptations that we may find; many plants have other adaptations that allow them to thrive under specific conditions.

## Nitrogen Fixation: Root and Bacteria Interactions

Nitrogen is an important macronutrient because it is part of nucleic acids and proteins. Atmospheric nitrogen, which is the diatomic molecule $\mathbf{N_2}$, or dinitrogen, is the largest pool of nitrogen in terrestrial ecosystems. However, plants cannot take advantage of this nitrogen because they do not have the necessary enzymes to convert it into biologically useful forms. However, nitrogen can be "fixed," which means that it can be converted to ammonia ($\mathbf{NH_3}$) through biological, physical, or chemical processes. As you have learned, biological nitrogen fixation (BNF) is the conversion of atmospheric nitrogen ($\mathbf{N_2}$) into ammonia ($\mathbf{NH_3}$), exclusively carried out by prokaryotes such as soil bacteria or cyanobacteria. Biological processes contribute 65 percent of the nitrogen used in agriculture. The following equation represents the process:

$$\mathbf{N_2 + 16\,ATP + 8\,e^- + 8\,H^+ \rightarrow 2\,NH_3 + 16\,ADP + 16\,P_i + H_2}$$

The most important source of BNF is the symbiotic interaction between soil bacteria and legume plants, including many crops important to humans (Figure **14.4.1**). The $NH_3$ resulting from fixation can be transported into plant tissue and incorporated into amino acids, which are then made into plant proteins. Some legume seeds, such as soybeans and peanuts, contain high levels of protein, and serve among the most important agricultural sources of protein in the world.



(a) (b) (c)

Figure **14.4.1**: Some common edible legumes—like (a) peanuts, (b) beans, and (c) chickpeas—are able to interact symbiotically with soil bacteria that fix nitrogen. (credit a: modification of work by Jules Clancy; credit b: modification of work by USDA)

**Exercise 14.4.1**

Farmers often rotate corn (a cereal crop) and soy beans (a legume) planting a field with each crop in alternate seasons. What advantage might this crop rotation confer?

**Answer**

Answer

Soybeans are able to fix nitrogen in their roots, which are not harvested at the end of the growing season. The belowground nitrogen can be used in the next season by the corn.

Farmers often rotate corn (a cereal crop) and soy beans (a legume), planting a field with each crop in alternate seasons. What advantage might this crop rotation confer?

Soil bacteria, collectively called rhizobia, symbiotically interact with legume roots to form specialized structures called nodules, in which nitrogen fixation takes place. This process entails the reduction of atmospheric nitrogen to ammonia, by means of the enzyme nitrogenase. Therefore, using rhizobia is a natural and environmentally friendly way to fertilize plants, as opposed to chemical fertilization that uses a nonrenewable resource, such as natural gas. Through symbiotic nitrogen fixation, the plant benefits from using an endless source of nitrogen from the atmosphere. The process simultaneously contributes to soil fertility because the plant root system leaves behind some of the biologically available nitrogen. As in any symbiosis, both organisms benefit from the interaction: the plant obtains ammonia, and bacteria obtain carbon compounds generated through photosynthesis, as well as a protected niche in which to grow (Figure **14.4.2**).




Figure **14.4.2**: Soybean roots contain (a) nitrogen-fixing nodules. Cells within the nodules are infected with *Bradyrhyzobium japonicum*, a rhizobia or "root-loving" bacterium. The bacteria are encased in (b) vesicles inside the cell, as can be seen in this transmission electron micrograph. (credit a: modification of work by USDA; credit b: modification of work by Louisa Howard, Dartmouth Electron Microscope Facility; scale-bar data from Matt Russell)

## Mycorrhizae: The Symbiotic Relationship between Fungi and Roots

A nutrient depletion zone can develop when there is rapid soil solution uptake, low nutrient concentration, low diffusion rate, or low soil moisture. These conditions are very common; therefore, most plants rely on fungi to facilitate the uptake of minerals from the soil. Fungi form symbiotic associations called mycorrhizae with plant roots, in which the fungi actually are integrated into the physical structure of the root. The fungi colonize the living root tissue during active plant growth.

Through mycorrhization, the plant obtains mainly phosphate and other minerals, such as zinc and copper, from the soil. The fungus obtains nutrients, such as sugars, from the plant root (Figure **14.4.3**). Mycorrhizae help increase the surface area of the plant root system because hyphae, which are narrow, can spread beyond the nutrient depletion zone. Hyphae can grow into small soil pores that allow access to phosphorus that would otherwise be unavailable to the plant. The beneficial effect on the plant is best observed in poor soils. The benefit to fungi is that they can obtain up to 20 percent of the total carbon accessed by plants. Mycorrhizae functions as a physical barrier to pathogens. It also provides an induction of generalized host defense mechanisms, and sometimes involves production of antibiotic compounds by the fungi.



Figure **14.4.3**: Root tips proliferate in the presence of mycorrhizal infection, which appears as off-white fuzz in this image. (credit: modification of work by Nilsson et al., BMC Bioinformatics 2005)

There are two types of mycorrhizae: ectomycorrhizae and endomycorrhizae. Ectomycorrhizae form an extensive dense sheath around the roots, called a mantle. Hyphae from the fungi extend from the mantle into the soil, which increases the surface area for water and mineral absorption. This type of mycorrhizae is found in forest trees, especially conifers, birches, and oaks. Endomycorrhizae, also called arbuscular mycorrhizae, do not form a dense sheath over the root. Instead, the fungal mycelium is embedded within the root tissue. Endomycorrhizae are found in the roots of more than 80 percent of terrestrial plants.

## Nutrients from Other Sources

Some plants cannot produce their own food and must obtain their nutrition from outside sources. This may occur with plants that are parasitic or saprophytic. Some plants are mutualistic symbionts, epiphytes, or insectivorous.

### Plant Parasites

A parasitic plant depends on its host for survival. Some parasitic plants have no leaves. An example of this is the dodder (Figure **14.4.4**), which has a weak, cylindrical stem that coils around the host and forms suckers. From these suckers, cells invade the host stem and grow to connect with the vascular bundles of the host. The parasitic plant obtains water and nutrients through these connections. The plant is a total parasite (a holoparasite) because it is completely dependent on its host. Other parasitic plants (hemiparasites) are fully photosynthetic and only use the host for water and minerals. There are about 4,100 species of parasitic plants.



Figure **14.4.4**: The dodder is a holoparasite that penetrates the host's vascular tissue and diverts nutrients for its own growth. Note that the vines of the dodder, which has white flowers, are beige. The dodder has no chlorophyll and cannot produce its own food. (credit: "Lalithamba"/Flickr)

## Saprophytes

A saprophyte is a plant that does not have chlorophyll and gets its food from dead matter, similar to bacteria and fungi (note that fungi are often called saprophytes, which is incorrect, because fungi are not plants). Plants like these use enzymes to convert organic food materials into simpler forms from which they can absorb nutrients (Figure **14.4.5**). Most saprophytes do not directly digest dead matter: instead, they parasitize fungi that digest dead matter, or are mycorrhizal, ultimately obtaining photosynthate from a fungus that derived photosynthate from its host. Saprophytic plants are uncommon; only a few species are described.



Figure **14.4.5**: Saprophytes, like this Dutchmen's pipe (*Monotropa hypopitys*), obtain their food from dead matter and do not have chlorophyll. (credit: modification of work by Iwona Erskine-Kellie)

## Symbionts

A symbiont is a plant in a symbiotic relationship, with special adaptations such as mycorrhizae or nodule formation. Fungi also form symbiotic associations with cyanobacteria and green algae (called lichens). Lichens can sometimes be seen as colorful growths on the surface of rocks and trees (Figure **14.4.6**). The algal partner (phycobiont) makes food autotrophically, some of which it shares with the fungus; the fungal partner (mycobiont) absorbs water and minerals from the environment, which are made available to the green alga. If one partner was separated from the other, they would both die.



Figure **14.4.6**: Lichens, which often have symbiotic relationships with other plants, can sometimes be found growing on trees. (credit: "benketaro"/Flickr)

## Epiphytes

An epiphyte is a plant that grows on other plants, but is not dependent upon the other plant for nutrition (Figure **14.4.7**). Epiphytes have two types of roots: clinging aerial roots, which absorb nutrients from humus that accumulates in the crevices of trees; and aerial roots, which absorb moisture from the atmosphere.



Figure 14.4.7: These epiphyte plants grow in the main greenhouse of the *Jardin des Plantes* in Paris.

## Insectivorous Plants

An insectivorous plant has specialized leaves to attract and digest insects. The Venus flytrap is popularly known for its insectivorous mode of nutrition, and has leaves that work as traps (Figure 14.4.8). The minerals it obtains from prey compensate for those lacking in the boggy (low pH) soil of its native North Carolina coastal plains. There are three sensitive hairs in the center of each half of each leaf. The edges of each leaf are covered with long spines. Nectar secreted by the plant attracts flies to the leaf. When a fly touches the sensory hairs, the leaf immediately closes. Next, fluids and enzymes break down the prey and minerals are absorbed by the leaf. Since this plant is popular in the horticultural trade, it is threatened in its original habitat.



Figure 14.4.8: A Venus flytrap has specialized leaves to trap insects. (credit: "Selena N. B. H."/Flickr)

## Summary

Atmospheric nitrogen is the largest pool of available nitrogen in terrestrial ecosystems. However, plants cannot use this nitrogen because they do not have the necessary enzymes. Biological nitrogen fixation (BNF) is the conversion of atmospheric nitrogen to ammonia. The most important source of BNF is the symbiotic interaction between soil bacteria and legumes. The bacteria form nodules on the legume's roots in which nitrogen fixation takes place. Fungi form symbiotic associations (mycorrhizae) with plants, becoming integrated into the physical structure of the root. Through mycorrhization, the plant obtains minerals from the soil and the fungus obtains photosynthate from the plant root. Ectomycorrhizae form an extensive dense sheath around the root, while endomycorrhizae are embedded within the root tissue. Some plants—parasites, saprophytes, symbionts, epiphytes, and insectivores—have evolved adaptations to obtain their organic or mineral nutrition from various sources.

## Glossary

**epiphyte**
plant that grows on other plants but is not dependent upon other plants for nutrition

**insectivorous plant**
plant that has specialized leaves to attract and digest insects

**nitrogenase**
enzyme that is responsible for the reduction of atmospheric nitrogen to ammonia

**nodules**
specialized structures that contain *Rhizobia* bacteria where nitrogen fixation takes place

**parasitic plant**
plant that is dependent on its host for survival

**rhizobia**
soil bacteria that symbiotically interact with legume roots to form nodules and fix nitrogen

**saprophyte**
plant that does not have chlorophyll and gets its food from dead matter

**symbiont**
plant in a symbiotic relationship with bacteria or fungi

---

This page titled 14.4: Nutritional Adaptations of Plants is shared under a CC BY 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **31.3: Nutritional Adaptations of Plants** by OpenStax is licensed CC BY 4.0.

# 14.E: Soil and Plant Nutrition (Exercises)

## 31.1: Nutritional Requirements of Plants

Plants are unique organisms that can absorb nutrients and water through their root system, as well as carbon dioxide from the atmosphere. Soil quality and climate are the major determinants of plant distribution and growth. The combination of soil nutrients, water, and carbon dioxide, along with sunlight, allows plants to grow.

### Review Questions

For an element to be regarded as essential, all of the following criteria must be met, except:

A. No other element can perform the function.
B. The element is directly involved in plant nutrition.
C. The element is inorganic.
D. The plant cannot complete its lifecycle without the element.

**Answer**

C

The nutrient that is part of carbohydrates, proteins, and nucleic acids, and that forms biomolecules, is _____.

A. nitrogen
B. carbon
C. magnesium
D. iron

**Answer**

B

Most _____ are necessary for enzyme function.

A. micronutrients
B. macronutrients
C. biomolecules
D. essential nutrients

**Answer**

A

What is the main water source for land plants?

A. rain
B. soil
C. biomolecules
D. essential nutrients

**Answer**

B

### Free Response

What type of plant problems result from nitrogen and calcium deficiencies?

**Answer**

Deficiencies in these nutrients could result in stunted growth, slow growth, and chlorosis.

What did the van Helmont experiment show?

**Answer**

van Helmont showed that plants do not consume soil, which is correct. He also thought that plant growth and increased weight resulted from the intake of water, a conclusion that has since been disproven.

List two essential macronutrients and two essential nutrients.

**Answer**

Answers may vary. Essential macronutrients include carbon, hydrogen, oxygen, nitrogen, phosphorus, potassium, calcium, magnesium, and sulfur. Essential micronutrients include iron, manganese, boron, molybdenum, copper, zinc, chlorine, nickel, cobalt, sodium, and silicon.

## 31.2: The Soil

Soil is the outer loose layer that covers the surface of Earth. Soil quality is a major determinant, along with climate, of plant distribution and growth. Soil quality depends not only on the chemical composition of the soil, but also the topography (regional surface features) and the presence of living organisms. In agriculture, the history of the soil, such as the cultivating practices and previous crops, modify the characteristics and fertility of that soil.

### Review Questions

Which factors affect soil quality?

A. chemical composition
B. history of the soil
C. presence of living organisms and topography
D. all of the above

**Answer**

D

Soil particles that are 0.1 to 2 mm in diameter are called _____.

A. sand
B. silt
C. clay
D. loam

**Answer**

A

A soil consists of layers called _____ that taken together are called a _____.

A. soil profiles : horizon

B. horizons : soil profile
C. horizons : humus
D. humus : soil profile

**Answer**

B

What is the term used to describe the solid rock that lies beneath the soil?

A. sand
B. bedrock
C. clay
D. loam

**Answer**

B

### Free Response

Describe the main differences between a mineral soil and an organic soil.

**Answer**

A mineral soil forms from the weathering of rocks; it is inorganic material. An organic soil is formed from sedimentation; it mostly consists of humus.

Name and briefly explain the factors that affect soil formation.

**Answer**

Parent material, climate, topography, biological factors, and time affect soil formation. Parent material is the material in which soils form. Climate describes how temperature, moisture, and wind cause different patterns of weathering, influencing the characteristics of the soil. Topography affects the characteristics and fertility of a soil. Biological factors include the presence of living organisms that greatly affect soil formation. Processes such as freezing and thawing may produce cracks in rocks; plant roots can penetrate these crevices and produce more fragmentation. Time affects soil because soil develops over long periods.

Describe how topography influences the characteristics and fertility of a soil.

**Answer**

Topography affects water runoff, which strips away parent material and affects plant growth. Steeps soils are more prone to erosion and may be thinner than soils that are on level surfaces.

## 31.3: Nutritional Adaptations of Plants

Plants obtain food in two different ways. Autotrophic plants can make their own food from inorganic raw materials, such as carbon dioxide and water, through photosynthesis in the presence of sunlight. Green plants are included in this group. Some plants, however, are heterotrophic: they are totally parasitic and lacking in chlorophyll. These plants, referred to as holo-parasitic plants, are unable to synthesize organic carbon and draw all of their nutrients from the host plant.

## Review Questions

Which process produces an inorganic compound that plants can easily use?

A. photosynthesis
B. nitrogen fixation
C. mycorrhization
D. Calvin cycle

**Answer**

B

Through mycorrhization, a plant obtains important nutrients such as _____.

A. phosphorus, zinc, and copper
B. phosphorus, zinc, and calcium
C. nickel, calcium, and zinc
D. all of the above

**Answer**

A

What term describes a plant that requires nutrition from a living host plant?

A. parasite
B. saprophyte
C. epiphyte
D. insectivorous

**Answer**

A

What is the term for the symbiotic association between fungi and cyanobacteria?

A. lichen
B. mycorrhizae
C. epiphyte
D. nitrogen-fixing nodule

**Answer**

A

## Free Response

Why is biological nitrogen fixation an environmentally friendly way of fertilizing plants?

**Answer**

Because it is natural and does not require use of a nonrenewable resource, such as natural gas.

What is the main difference, from an energy point of view, between photosynthesis and biological nitrogen fixation?

**Answer**

Photosynthesis harvests and stores energy, whereas biological nitrogen fixation requires energy.

Why is a root nodule a nutritional adaptation of a plant?

**Answer**

A nodule results from the symbiosis between a plant and bacterium. Within nodules, the process of nitrogen fixation allows the plant to obtain nitrogen from the air.

---

This page titled 14.E: Soil and Plant Nutrition (Exercises) is shared under a CC BY 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **31.E: Soil and Plant Nutrition (Exercises)** is licensed CC BY 4.0.

# CHAPTER OVERVIEW

## 15: Functional morphology and anatomy

15.1: Translocation (Assimilate Transport)

This page titled 15: Functional morphology and anatomy is shared under a not declared license and was authored, remixed, and/or curated by Tom Buckley.

# 15.1: Translocation (Assimilate Transport)

## Learning Objectives

- Distinguish between sources and sinks and provide examples of each.
- Explain the process of phloem loading, distinguishing between apoplastic and symplastic pathways.
- Explain how assimilate translocations through the phloem according to the pressure-flow hypothesis.

Plants need an energy source to grow. In seeds and bulbs, food is stored in polymers (such as starch) that are converted by metabolic processes into sucrose for newly developing plants. Once green shoots and leaves are growing, plants are able to produce their own food through photosynthesis. The products of photosynthesis (mainly the sugar sucrose) are a major component of the substance found in the phloem, called **assimilate**. Ions, amino acids, certain hormones, and other molecules are also found in assimilate. The movement of assimilate is called **translocation**, or assimilate transport.

## Sources and Sinks

Structures that produce or release sugars for the growing plant are referred to as **sources**. Examples include mature leaves, which produce sugar through photosynthesis, and storage organs, such bulbs, tubers, or storage roots. Sources produce or store more sugars than they need themselves and can thus export sugars. The points of sugar delivery, such as most roots, young shoots, and developing fruits and seeds, are called **sinks** (Figure **15.1.1**). Because sinks do not produce enough sugars to meet their energy needs, they must import sugars from sources.



Figure **15.1.1**: The mature leaves of this tree are sources, and the apples are sinks. Image by W.carter (public domain).

The pattern of assimilate flow changes as the plant grows and develops. Sugars are directed primarily to the roots early on, to shoots and leaves during vegetative growth, and to seeds and fruits during reproductive development. They are also directed to storage structures. Thus, the same organ may function as a source or a sink depending on the stage of development. For example, a young leaf may initially be a sink, but it will eventually grow and conduct enough photosynthesis to become a source. Similarly, a developing seed is a sink as the embryo develops. Once the seed germinates, however, starches stored in the seed break down, act as a source for the growing seedling structures.

The products from the source are usually translocated to the nearest sink through the phloem. For example, the highest leaves will send sugars upward to the growing shoot tip, whereas lower leaves will direct sugars downward to the roots. Intermediate leaves will send products in both directions, unlike the flow in the xylem, which is always unidirectional (soil to leaf to atmosphere).

## Phloem Loading

Before discussing how sources transport sugars into the phloem (**phloem loading**), let's first review the conducting cells of the phloem. Stacks of these cylindrical cells called **sieve-tube elements** form column-like structures. Each cell is separated by a sieve plate (sieve-tube plate). The sieve plate has holes in it, like a slice of Swiss cheese, allowing for translocation. Lateral sieve areas on the side of the column allow different phloem tubes to interact. Sieve-tube elements have reduced cytoplasmic contents and rely on special parenchyma cells called companion cells, which assist with metabolic activities and provide energy (Figure 15.1.2). In addition to sieve-tube elements and companion cells, the phloem contains other parenchyma cells and may contain sclerenchyma fibers. In leaves, the phloem is found in vascular bundles (leaf veins), which are surrounded by a bundle sheath. Sugars are produced through photosynthesis in the mesophyll cells that fill most of the leaf (see diagram in Transpiration section).

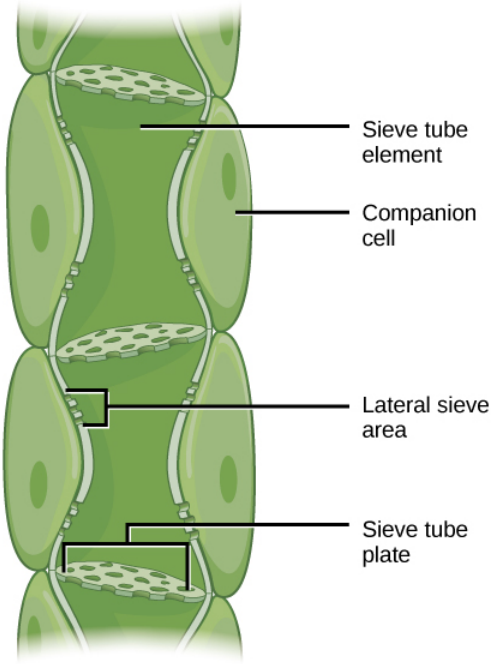



Figure 15.1.2: Sieve-tube elements are the conducting cells of the phloem in angiosperms. Assimilate travels through perforations in sieve plates (labeled sieve-tube plates), which connect stacked sieve-tube elements. Neighboring companion cells carry out metabolic functions for the sieve-tube elements and provide them with energy. Lateral sieve areas connect the sieve-tube elements to the companion cells.

There are two pathways of **phloem loading** (Figure 15.1.3). Both pathways begin the same way. The cytoplasms of most plant cells are interconnected via plasmodesmata.Augars through plasmodesmata from mesophyll cells to bundle sheath cells to the parenchyma cells of the phloem. From there, the pathways differ. The first pathway called **apoplastic phloem loading**, occurs when the regular parenchyma cells of phloem are not connected to the companion cells. In this case, sucrose must exist the regular parenchyma cells and enter the apoplast. It enters the companion cell cytoplasm as well as the inside of the sieve tube through **secondary active transport**. Protons are pumped into the apoplast (outside of the cells), when the protons re-enter the cells (move down their concentration gradient), they bring sucrose with them by flowing through carrier proteins called **sucrose-proton symporters**. In this way, sucrose is actively transported against its concentration gradient, and high sucrose concentrations accumulate in the assimilate of the phloem. The second pathway is **symplastic phloem loading**. When the regular parenchyma cells of the phloem are connected to companion cells via plamodesmata, sucrose can flow through the symplast all the way to the sieve-tube elements. There is no need for sucrose to leave the cytoplasm (enter the apoplast) and re-enter cells via sucrose-proton symport.

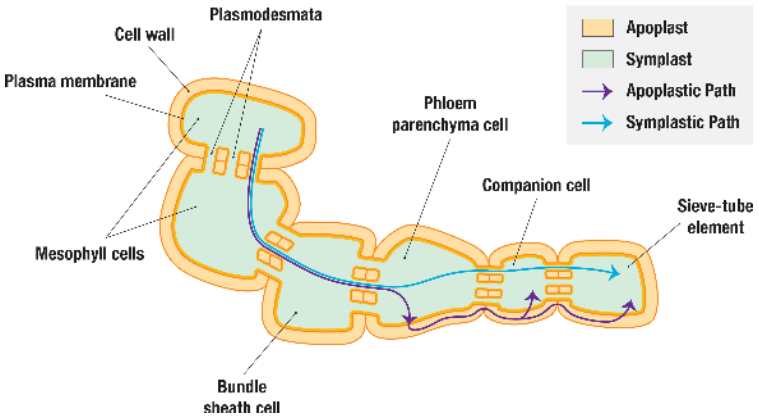



Figure **15.1.3**: Apoplastic and symplastic phloem loading. The apoplast (yellow) consists of the cell wall and spaces between cells. The symplast (green) consists of cytoplasms interconnected via plasmodesmata. Both the apoplastic and symplastic pathways of phloem loading begin the same way, with sugars moving through the plasmodesmata that connect mesophyll cells with each other and bundle sheath cells. In symplastic phloem loading (top line, blue), sugars continue through plasmodesmata (remain in the symplast) to the companion cell and then to the sieve-tube element. In apoplastic phloem loading (bottom line, purple), sugars exit phloem parenchyma cells into the apoplast. They then reenter the symplast when they are actively transported into companion cells and sieve-tube elements. Image by Jen Valenzuela (CC-BY).

# Pressure-Flow Hypothesis

What drives the movement of assimilate in the phloem? According to the **pressure-flow hypothesis**, assimilate moves due to osmosis of water to and from the xylem. While this is a passive process, it ultimately results from the active transport of sugars during phloem loading and unloading. In contrast with transpiration, an entirely passive process, translocation as a passive process that is indirectly driven by active processes.

Assimilate contains up to 30 percent sugar, and this high solute concentration decreases $\Psi_s$, which decreases the total water potential. The sugar concentration of the assimilate near sinks, where phloem loading occurs, is highest. This causes water to move by osmosis from the adjacent xylem into sieve tubes, thereby increasing pressure. The increase in pressure increases in total water potential causes the bulk flow of phloem from source to sink (Figure **15.1.4**). Sugar concentration in the sink cells is lower than in the sieve-tube elements because the sink sucrose has been metabolized for growth, or converted to starch for storage or other polymers, such as cellulose, for structural integrity. Unloading at the sink end of the phloem tube occurs by either diffusion or active transport of sucrose molecules from an area of high concentration to one of low concentration. Unloading reduces the sugar concentration of assimilate near sinks, increasing water potential. As a result, water moves from the phloem by osmosis and is then transpired or recycled via the xylem back into the phloem sap.

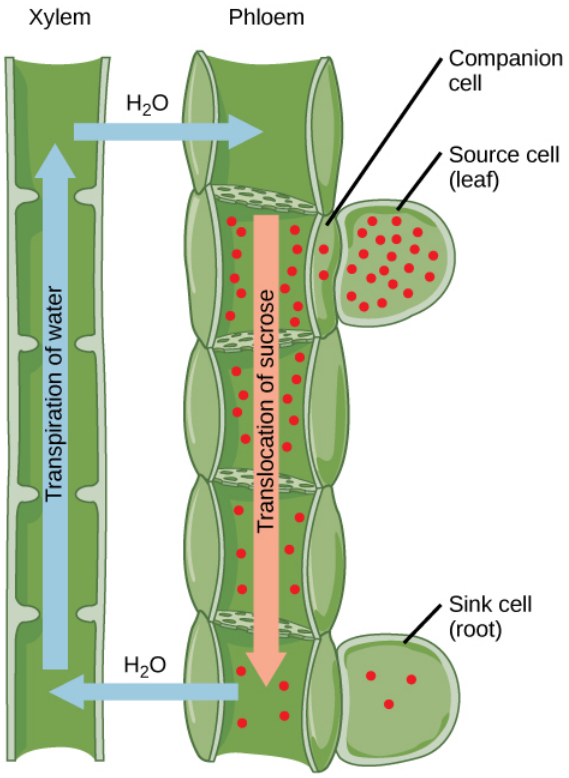



Figure **15.1.4**: The pressure-flow hypothesis of assimilate transport. The assimilate, which is rich in sucrose, is actively transported from source cells into companion cells and then into the sieve-tube elements. This reduces the water potential, which causes water to enter the phloem from the xylem. The resulting positive pressure forces the assimilate down toward the sink cells, where sucrose is unloaded. At this point, there is no longer a high concentration of sucrose, and water returns to the xylem. The leaf is an example of a source, and the root is an example of a sink.

## Attribution

Curated and authored by Melissa Ha using 30.5 Transport of Water and Solutes in Plants from *Biology 2e* by OpenStax (licensed CC-BY). Access for free at openstax.org.

---

This page titled 15.1: Translocation (Assimilate Transport) is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **4.5.2: Translocation (Assimilate Transport)** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC 4.0.

# CHAPTER OVERVIEW

## 16: Environmental plant biology


16.1: Environmental Responses

16.1.1: Tropisms

16.1.2: Flowering

16.1.3: Photoperiodism

16.1.4: Etiolation and Shade Avoidance

16.1.5: Dormancy

16.1.6: Chapter Summary

16.2: Plant Sensory Systems and Responses


---


This page titled 16: Environmental plant biology is shared under a not declared license and was authored, remixed, and/or curated by Tom Buckley.

# SECTION OVERVIEW

## 16.1: Environmental Responses

Animals can respond to environmental factors by moving to a new location. Plants, however, are rooted in place and must respond to the surrounding environmental factors. Plants have sophisticated systems to detect and respond to light, gravity, temperature, and physical touch (Figure **16.1.1**). Plants may grow towards or away from environmental stimuli, and these growth responses are called **tropisms**. Environmental factors, particularly temperature and the hours of light and dark each day, also control flowering in many species. Plants detect the latter through **photoperiodism**. In the absence of light, plants respond physiologically to increase the chance of accessing light. Finally, plants rely on environmental cues to break dormancy in seeds and buds on winter twigs.



Figure **16.1.1**: The first flower to bloom in space. The International Space Station provides a unique opportunity to study the growth of plants under microgravity. Image by NASA (CC-BY-NC).

### Attributions

Curated and authored by Melissa Ha using 30.6: Plant Sensory Systems and Responses from *General Biology* by OpenStax (licensed CC-BY). Access for free at openstax.org.


16.1.1: Tropisms

16.1.2: Flowering

16.1.3: Photoperiodism

16.1.4: Etiolation and Shade Avoidance

16.1.5: Dormancy

16.1.6: Chapter Summary



This page titled 16.1: Environmental Responses is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

# 16.1.1: Tropisms

## Learning Objectives

- Distinguish among phototropism, gravitropism, hydrotropism, and thigmotropism.
- Discuss the adaptive value of tropisms.
- Describe the mechanism of phototropism in shoots.
- Describe the mechanism of gravitropism in shoots and roots.
- Distinguish among thigmotropism, thigmonastic movements, and thigmomorphogenesis.

A **tropism** is directional growth in response to a stimulus. A **positive tropism** occurs when a plant (or a part of the plant) grows towards the stimulus, and a **negative tropism** is growth away from the stimulus.

**Phototropism** is directional growth in response to light (Figure **16.1.1.1**). (More generally, **photomorphogenesis** is the growth and development of plants in response to light.) Stems are positively phototropic, and roots are typically negatively phototropic. **Gravitropism** is directional growth in response to gravity. Stems are negatively gravitropic, and roots are positively gravitropic. The adaptive value of these tropisms is clear. Stems growing upward and/or toward the light will be able to expose their leaves so that photosynthesis can occur. Roots growing downward and/or away from light are more likely to find the soil, water, and minerals they need. Plants can also grow directionally in response to water (**hydrotropism**) and touch (**thigmotropism**).



Figure **16.1.1.1**: Azure bluets (*Houstonia caerulea*) display a phototropic response by bending toward the light. Image by Cory Zanker.

## Phototropism in Shoots

Plants can detect different characteristics of light, such as quantity, quality, duration, and direction. They can tell the time of day and time of year by sensing and using various wavelengths of sunlight. Plants are generally capable of detecting and responding to at least three wavelengths of light: **blue light, red light,** and **far-red light**. The different wavelengths are detected by different **photoreceptors** (Figure **16.1.1.2**), an example of which are phototropins.

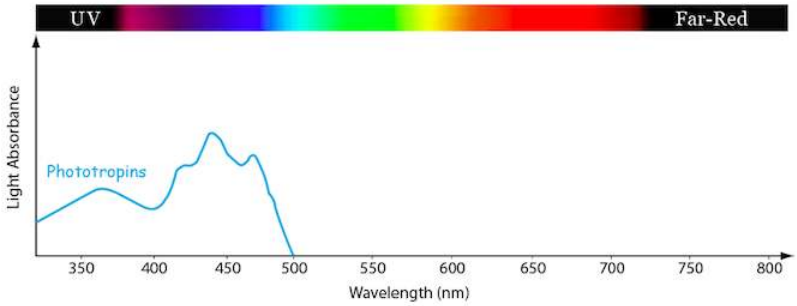



Figure **16.1.1.2**: The absorption spectrum of phototropins, blue-light photoreceptors in plants. They absorb the most light between 400 and 500 nanometers (nm). Visible light ranges from violet (400 nm) to red (700 nm). Ultraviolet light has a shorter wavelength than visible light, and far red light has a longer wavelenth.

## The Shoot Tip Detects Light and Induces Phototropism

In their 1880 treatise *The Power of Movements in Plants*, Charles Darwin and his son Francis first described phototropism as the bending of seedlings toward light. The Darwins used grass seedlings for some of their experiments. When grass seeds germinate, the primary leaf pierces the seed coverings and the soil while protected by the **coleoptile**, a hollow, cylindrical sheath that surrounds it (Figure **16.1.1.3** ).



Figure **16.1.1.3**: The coleoptile is a sheath surrounding the young shoot of some seedlings, including corn (shown above) and grass (studied by the Darwins' phototropism experiment). Image by Melissa Ha (CC-BY)

Once the seedling has grown above the surface, the coleoptile stops growing and the primary leaf pierces it. If they placed an opaque cover over the tip, phototropism failed to occur even though the rest of the coleoptile was illuminated from one side. However, when they buried the plant in fine black sand so that only its tip was exposed, there was no interference with the tropism — the buried coleoptile bent in the direction of the light (Figure **16.1.1.4** ). In conclusion, light was perceived by the tip of the plant (the apical meristem), but that the response (bending) took place in a different part of the plant. The signal had to travel from the apical meristem to the base of the plant.

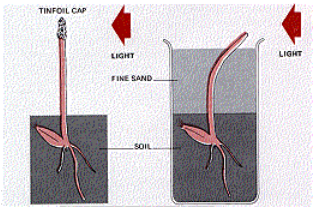



Figure **16.1.1.4**: In the Darwins' experiment, there was not phototropism when the tip of the coleoptile was covered (left). When the tip was exposed, phototropism occured (right).

We now know that phototropism is a response to blue wavelengths of light. The detection of light in the apical meristem occurs via phototropins called **phot1** and **phot2**, which specifically detect **blue light** (Figure **16.1.1.5** ). The aptly-named **phototropins** are

protein-based receptors responsible for mediating the phototropic response. Like all plant photoreceptors, phototropins consist of a protein portion and a light-absorbing portion, called the **chromophore**. Together, the two are called a chromoprotein. In phototropins, the chromophore is a covalently-bound molecule of flavin; hence, phototropins belong to a class of proteins called flavoproteins.

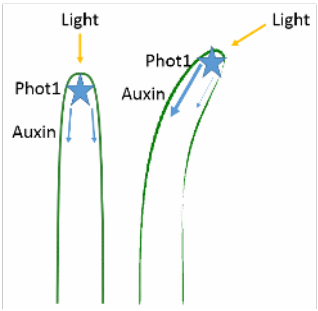



Figure **16.1.1.5**: Blue light activates phot1 and phot2 (not shown). The hormone auxin (see Auxin section) then accumulates on the shaded side of the stem in response to phot1 and phot2 activation. Auxin promotes cell elongation, causing bending toward the light.

## The Hormone Auxin from the Shoot Tip Stimulates Elongation on the Shaded Side of the Stem

In 1913, the Danish plant physiologist Peter Boysen-Jensen demonstrated that a chemical signal produced in the plant tip was responsible for the bending at the base. He cut off the tip of a seedling, covered the cut section with a layer of gelatin, and then replaced the tip. The seedling bent toward the light when illuminated. However, when impermeable mica flakes were inserted between the tip and the cut base, the seedling did not bend. A refinement of the experiment showed that the signal traveled on the shaded side of the seedling. When the mica plate was inserted on the illuminated side, the plant did bend towards the light. When a horizontal incision was made on the illuminated side and the mica inserted in it, phototropism was normal (Figure **16.1.1.6** ). Therefore, the chemical signal was a growth stimulant because the phototropic response involved faster cell elongation on the shaded side than on the illuminated side.

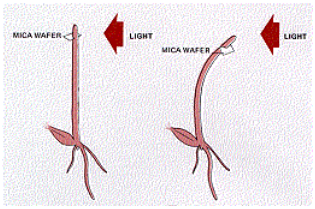



Figure **16.1.1.6**: The Boysen-Jensen experiment showed that a chemical signal (now known to be auxin) passed from the shoot tip to the shaded side of the coleoptile, resulting in positive phototropism.

We now know that **auxin** is the chemical signal that accumulates and stimulates elongation on shaded side of coleoptile. H. W. Went placed a coleoptile that has previously been illuminated from one side on two separated agar blocks. The block on the side that had been shaded accumulated almost twice as much auxin as the block on the previously lighted side (Figure **16.1.1.7** ).

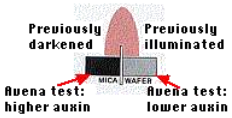



Figure **16.1.1.7**: The Went experiment showed that auxin concentration was greater in the shaded side of the coleoptile.

Auxin stimulates cell elongation on the shady side of the stem through a process called the **acid growth hypothesis**: Auxin causes cells to activate proton pumps, which then pump protons out of the cells and into the space between the plasma membrane and the cell wall. The movement of protons into the extracellular space does two things:

- The lower pH activates **expansin**, which breaks the links between the cellulose fibers in the cell walls, making them more flexible.
- The high concentration of protons causes sugars to move into the cell, which then creates an osmotic gradient where water moves into cell causing the cell to expand.

## Phototropism in Roots

Although roots are underground, they can be exposed to light directly as well. Not only can light penetrate up to a few centimeters in the upper layers of some soils, the plant itself can also guide light through the stem to the roots. Additionally, roots can also be exposed to light shortly after germination in the top layer of the soil or because cracks in the soil emerge that trigger a phototropic reaction. Negative phototropism in roots may be evolutionarily advantageous because it increases root efficiency and enhances seedling survival under dry conditions. As in shoots, phototropin 1 is involved in root phototropism. Directional auxin transport and an auxin gradient are associated with root phototropsim, but it is unclear whether they mediate the process.

## Gravitropism

Whether or not they germinate in the light or in total darkness, shoots usually sprout up from the ground, and roots grow downward into the ground. A plant laid on its side in the dark will send shoots upward when given enough time. Gravitropism also involves the unequal distribution of auxin.

When an oat coleoptile tip is placed on two separated agar blocks, as shown here, there is no difference in the auxin activity picked up by the two blocks. When the preparation is placed on its side, however, the lower block accumulates twice as much auxin activity as the upper block. Under natural conditions, this would cause greater cell elongation on the underside of the coleoptile and the plant would bend upward (Figure **16.1.1.8**).

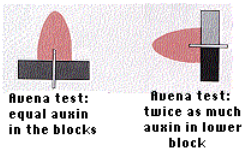



Figure **16.1.1.8**: When a coleoptile is placed on its side, auxin accumulates in the lower side.

Specialized amyloplasts called **statoliths** settle downward in response to gravity. Statoliths are found in the inner part of a stem's cortex (the starch sheath) and in the the central column of the root cap (columella). When a plant is tilted, the statoliths drop to the new bottom cell wall. A few hours later, the shoot or root will show growth in the new vertical direction (Figure **16.1.1.9**).

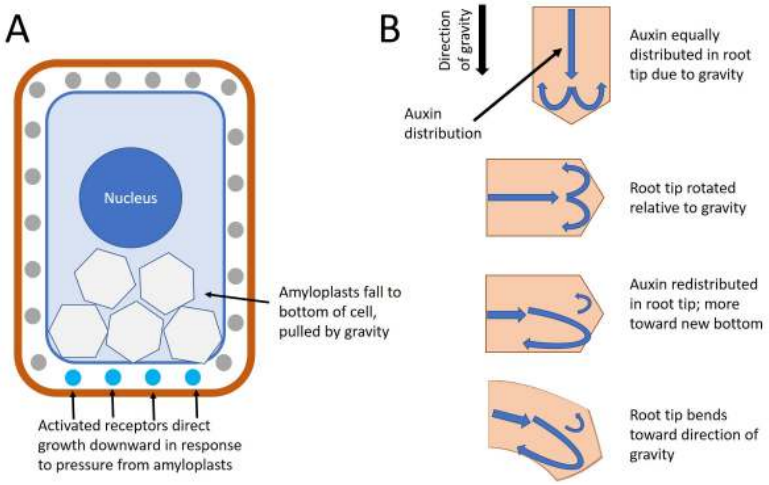



Figure **16.1.1.9**: Auxin and specialized amyloplasts called statoliths together mediate gravitropism. **A** Statoliths (amyloplasts) fall to the bottom of cells and activate pressure-sensitive receptors which direct growth downward. **B** Auxin distribution in the root tip changes as a result of gravity, with auxin accumulating in the direction of gravity. Higher auxin distribution in roots inhibits cell elongation while lower auxin distribution promotes cell elongation. Image credit: A, modeled after Freeman Biological Sciences 5th edition Figure 40.12; B, modeled after Freeman Biological Sciences 5th edition Figure 40.13

The mechanism that mediates gravitropism is reasonably well understood. When amyloplasts settle to the bottom of the gravity-sensing cells in the root or shoot, they physically contact the endoplasmic reticulum (ER), causing the release of calcium ions from inside the ER. Calcium may be released by ion channels sensitive to mechanical stimulation. This calcium signaling in the cells causes auxin transport proteins (**PIN proteins**) to redistribute to the underside of the cell leading to the polar transport of auxin to the bottom of the cell. In roots, a high concentration of indoleacetic acid (IAA) inhibits cell elongation. The effect slows growth on

the lower side of the root, while cells develop normally on the upper side. IAA has the opposite effect in shoots, where a higher concentration at the lower side of the shoot stimulates cell expansion, causing the shoot to grow up. After the shoot or root begin to grow vertically, the amyloplasts return to their normal position. Another hypotheses—involving the entire cell in the gravitropism effect—have been proposed to explain why some mutants that lack amyloplasts may still exhibit a weak gravitropic response.

### Plant Tropisms in Space

Considering the fundamental role of plants in producing fresh food and recycling of air and water, plant tropism research is critical for advancing plant-based life support systems in space. Understanding of the relative strengths of the different root tropisms would be needed to properly guide root growth by technological means, as the gravity vector is absent in space. For example, by exposing roots in microgravity to blue light, they could be induced to develop away from light toward the growth medium. Furthermore, the possibility of performing explorative experiments in the space environment, together with the development of new technologies, is crucial to pave the way toward the goal of deepening our fundamental understanding of plant tropisms and their underlying molecular networks on Earth.

Modified by Melissa Ha from Muthert, L., Izzo, L. G., van Zanten, M., & Aronne, G. (2020). Root Tropisms: Investigations on Earth and in Space to Unravel Plant Growth Direction. *Frontiers in plant science*, *10*, 1807. https://doi.org/10.3389/fpls.2019.01807. CC BY

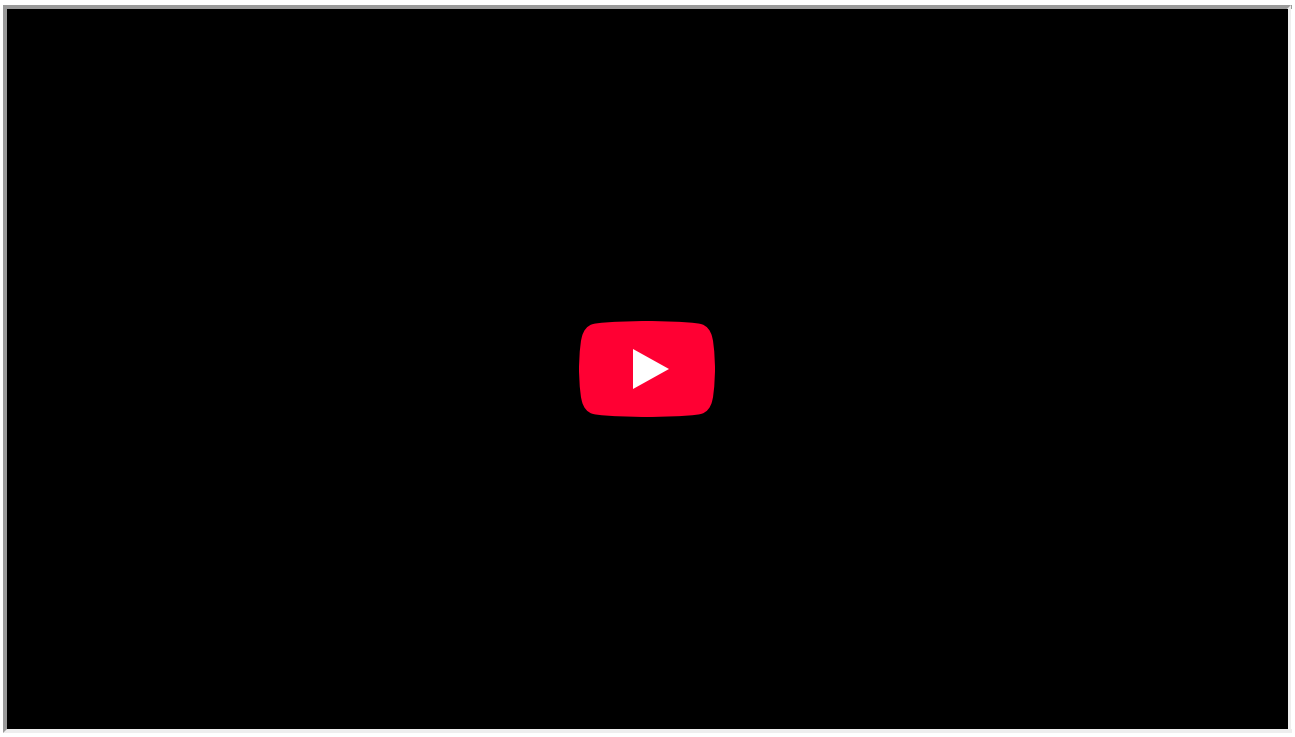
## Hydrotropism

Water acquisition is an important function of plant roots. Because water availability in the soil is often spatially and temporally patchy, roots of many species can exert directional root growth toward water; i.e., positive hydrotropism. The underlying mechanisms of hydrotropism are still being researched. Gravitropism is often dominant over hydrotropic responses, making it difficult to study hydrotropism in isolation. In contrast to phototropism and gravitropism, hydrotropism does not result from an auxin gradient resulting from directional auxin transport. However, auxin still appears to play a role in signaling hydrotropism.

## Thigmotropism, Thigmomorphogensis, and Thigmonastic Movements

The shoot of a pea plant winds around a trellis while a tree grows on an angle in response to strong prevailing winds. These are examples of how plants respond to touch or wind.

The movement of a plant subjected to constant directional pressure is called thigmotropism, from the Greek words *thigma* meaning “touch,” and *tropism* implying “direction.” Tendrils are one example of plants displaying positive thigmotropism (Video **16.1.1.1**). The meristematic region of tendrils is very touch sensitive; light touch will evoke a quick coiling response. Cells in contact with a support surface contract, whereas cells on the opposite side of the support expand. Application of jasmonic acid is sufficient to trigger tendril coiling without a mechanical stimulus.





Video **16.1.1.1**: This video shows an example of positive thigmotropism in morning glory plants, which require a support structure of some type to grow optimally. The time lapse images were taken at 10 minute intervals. This video has no sound. Here is a description: The morning glory stems (which are modified as tendrils) grow in a counterclockwise pattern, widening their radius with each rotation. When they encounter one of the two wooden stakes on either side of the plant, grow in a tight coil around it.

Plant roots exhibit negative thigmotropism when contacting obstacles in the soil. When plant roots encounter an obstacle in their growth path, the root first continues growing in the same direction until it slips sideways. The root bends away from the stimulus and then bends again in the opposite direction, creating a step-like shape. Note that at this point the root "side stepped" the obstacle and is now continuing to grow in the original direction. If the root contacts another part of the obstacle, the same bending pattern will occur. Thigmotropism in roots may be mediated by calcium, but other signaling mechanisms have also been proposed. Following contact, the calcium concentration in the root cap is greater than that of surrounding regions. (Under regular conditions, calcium concentration in the root cap is lower.) Ultimately, the directional transport of auxin results in an auxin gradient. When touching an obstacle during downward growth, the root bends and auxin accumulates at the higher (concave) side of the root suppressing elongation. Greater elongation on the convex (lower) side of the root causes it to bend away from the obstacle.

**Thigmomorphogenesis** is a slow developmental change in the shape of a plant subjected to continuous mechanical stress. When trees bend in the wind, for example, growth is usually stunted and the trunk thickens. Strengthening tissue, especially xylem, is

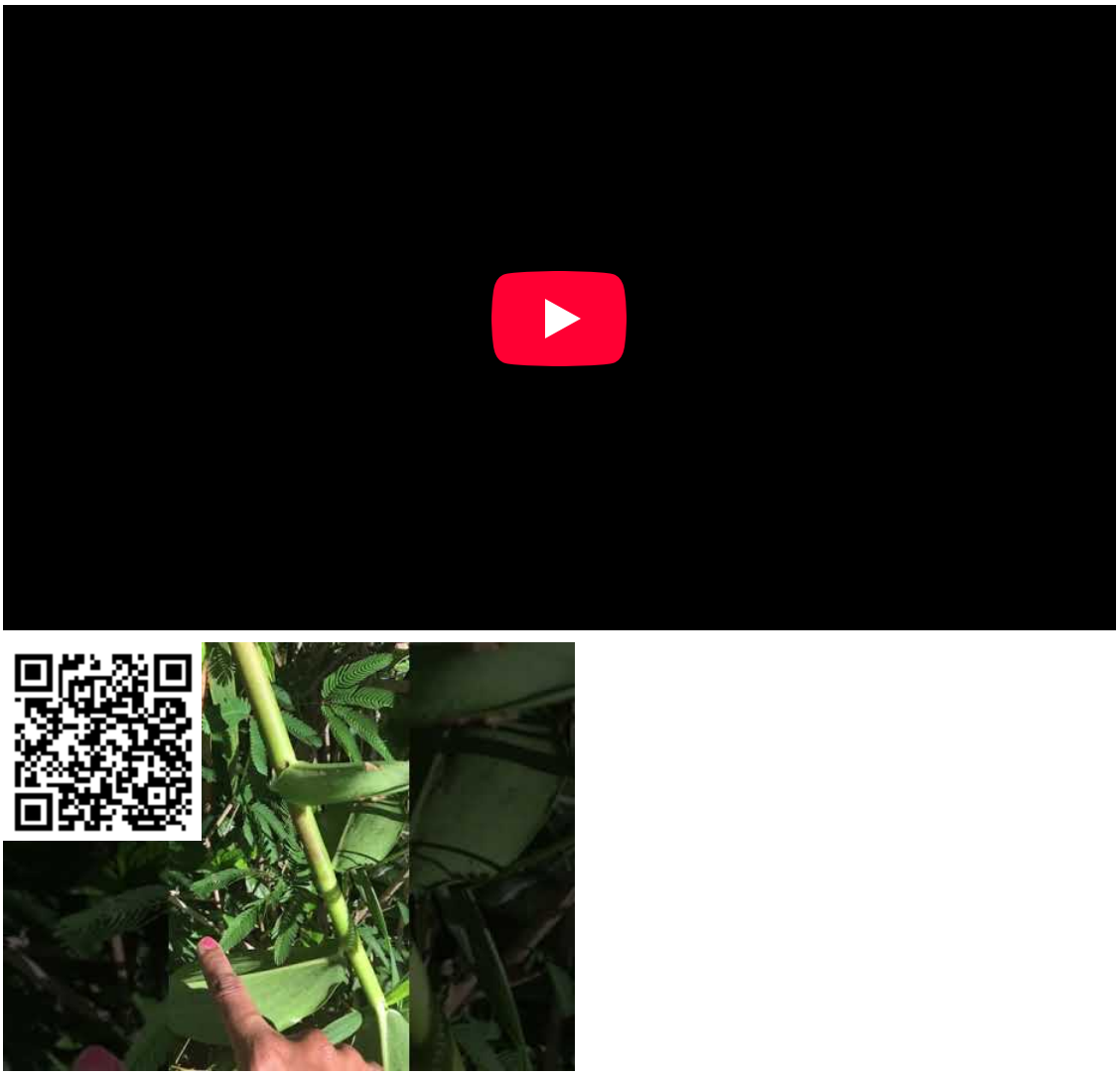
produced to add stiffness to resist the wind's force. Researchers hypothesize that mechanical strain induces growth and differentiation to strengthen the tissues. Ethylene and jasmonate are likely involved in thigmomorphogenesis.

A **thigmonastic movement** is a touch response independent of the direction of stimulus. In the Venus flytrap, two modified leaves are joined at a hinge and lined with thin fork-like tines along the outer edges (Video **16.1.1.2**). Tiny hairs are located inside the trap. When an insect brushes against these trigger hairs, touching two or more of them in succession, the leaves close quickly, trapping the prey. Glands on the leaf surface secrete enzymes that slowly digest the insect. The released nutrients are absorbed by the leaves, which reopen for the next meal.



Video **16.1.1.2**: This video below shows an example of thigmonastic movements in a Venus flytrap. There is no only ambient sound in this video and no speaking. Here is a description. At 0:08, a fly enters the taco-shaped trap of the Venus flytrap. It escapes before the tines (prongs) interlock, as shown in a slow-motion replay. At 0:42, another fly crawls into the trap. It crawls around a bit before the trap closes, locking it inside.

Another example of thigmonastic movement occurs in the sensitive plant (*Mimosa pudica*). Its leaflets and leaves retract in response to touch, and this is thought to be an adaptation that deters herbivores (Video **16.1.1.3**).



Video **16.1.1.3**: The leaflets of the sensitive plant retract when touched. This video has no speaking, but there are natural sounds (such as birds) in the background and laughing when the leaflets retract.

## Attributions

Curated and authored by Melissa Ha using the following sources:

- 16.2F: Tropisms from *Biology* by John. W. Kimball (licensed CC-BY)
- 30.6 Plant Sensory Systems and Responses from *Biology 2e* by OpenStax (licensed CC-BY). Access for free at openstax.org.
- Plant Hormones and Sensory Systems by Biology 1520 Introduction to Organismal Biology (licensed CC-BY-NC-SA)
- Muthert, L., Izzo, L. G., van Zanten, M., & Aronne, G. (2020). Root Tropisms: Investigations on Earth and in Space to Unravel Plant Growth Direction. *Frontiers in plant science*, *10*, 1807. https://doi.org/10.3389/fpls.2019.01807. (licensed CC-BY)

---

This page titled 16.1.1: Tropisms is shared under a CC BY-NC-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **4.2.1: Tropisms** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC-SA 4.0.
- **4.2: Environmental Responses** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC 4.0.

# 16.1.2: Flowering

**Learning Objective**

Describe the environmental conditions that induce flowering.

The flowering plants (angiosperms) go through a phase of **vegetative growth** producing more stems and leaves and a flowering phase where they produce the organs for sexual reproduction. In **annuals** the vegetative phase begins with germination of the seed. Flowering follows and ends with the senescence and death of the plant. In **biennials**, the vegetative phase takes up the first year; flowering followed by death occurs the second year. In **perennials**, flowering typically occurs year after year when conditions are appropriate (Figure **16.1.2.1**)



Figure **16.1.2.1**: Annuals, like snapdragon (*Antirrhinum majus*), complete their life cycles in one year (or less), growing, flowering, and dying (left). Biennials, like mullein (*Verbascum*) form vegetative rosettes in the first year and flower and die the second year (middle). Perennials, like lavender (*Lavendula*), persist and flower each year (right). Images from left to right by Off2riorob (licensed under CC-BY), Dcrjsr (licensed under CC-BY), Lairich Rig (licensed under CC-BY), and Greyspshaw22 (licensed under CC-BY-SA).

Flowering involves the conversion of the apical meristem into a **floral meristem**, from which all the parts of the flower will be produced. Signals that change the fate of the apical meristem include the following:

- maturity of the plant
- temperature
- the plant hormone gibberellin
- for many plants, photoperiod (daylength; see Photoperiodism section)

Many annual plants (e.g., winter wheat) and biennial plants have their time of flowering delayed unless they have undergone a preceding period of wintertime cold. The change brought about by this prolonged exposure to the cold is called **vernalization**.

In *Arabidopsis*, vernalization involves a gene designated *Flowering Locus C* (*FLC*), which encodes a transcription factor that blocks the expression of the genes needed for flowering. Recall that one of the two DNA strands in a gene is called the sense (coding) strand and has the same sequence as the RNA transcript. The other DNA strand is called the antisense (non-coding) strand and has a sequence that is complementary to the RNA transcript. The antisense strand acts as a template during transcription. In the fall, the level of FLC mRNA is high. With the onset of cold temperatures, production of an antisense transcript of *FLC* (called *COOLAIR*) increases as does, later, a sense transcript of part of the *FLC* gene. Both of these transcripts are non-coding; that is, they are not translated into protein. Instead, they cooperate in suppressing the production of FLC mRNA and its translation into FLC protein. With the arrival of spring, there is no FLC protein remaining to suppress flowering so flowering can begin.

The buds of many species of woody angiosperms found in temperate climates, such as apples and lilacs, also need a preceding period of cold weather before they can develop into flowers. So these plants cannot be grown successfully at lower latitudes because the winters never get cold enough (a few days at 0–10°C). This bud dormancy is localized. Prior chilling of one bud on a lilac stem enables it to flower while the other, nonchilled, buds on the stem remain dormant (Figure **16.1.2.2**).

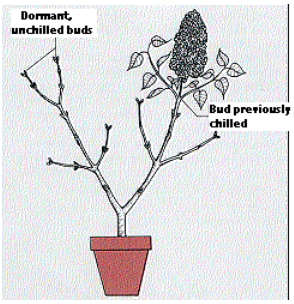



Figure 16.1.2.2: Vernalization (chilling) of lilac buds induces flowering, but the effect is localized. Unchilled buds on the same plant remain dormant.

## Attributions

Curated and authored by Melissa Ha using 16.4D: Flowering from *Biology* by John. W. Kimball (licensed CC-BY)

---

This page titled 16.1.2: Flowering is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **4.2.2: Flowering** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-SA 4.0.

# 16.1.3: Photoperiodism

**Learning Objectives**

- Describe the mechanism of photoperiodism with respect to flowering.
- Distinguish among short-day, long-day, and day-neutral plants.
- Define circadian rhythms and provide examples in plants.

Detection of seasonal changes is crucial to plant survival. Although temperature and light intensity influence plant growth, they are not reliable indicators of season because they may vary from one year to the next. Day length is a better indicator of the time of year. Many angiosperms flower at about the same time every year. This occurs even though they may have started growing at different times. Their flowering is a response to the changing length of day and night as the season progresses. It helps promote cross pollination. The biological response to the timing and duration of day and night is called **photoperiodism**.

## The Phytochrome System and the Red/Far-Red Response

Plants use the phytochrome system to sense the change of season, which can control flowering. The **phytochromes** are a family of photoreceptors. They are chromoproteins with a linear tetrapyrrole chromophore (a molecule that absorbs light), similar to the ringed tetrapyrrole light-absorbing head group of chlorophyll. A phytochrome is a homodimer: two identical protein molecules, each conjugated to a light-absorbing molecule (compare to rhodopsin). Plants make 5 phytochromes: **PhyA**, **PhyB**, as well as C, D, and E. There is some redundancy in function of the different phytochromes, but there also seem to be functions that are unique to one or another. The phytochromes also differ in their absorption spectrum; that is, which wavelengths (e.g., red vs. far-red) they absorb best. Phytochromes have two photo-interconvertible forms: Pr and Pfr. Pr absorbs red light (~667 nm) and is immediately converted to Pfr. Pfr absorbs far-red light (~730 nm) and is quickly converted back to Pr. Absorption of red or far-red light causes a massive change to the shape of the chromophore, altering the conformation and activity of the phytochrome protein to which it is bound. Pfr is the physiologically active form of the protein; therefore, exposure to red light yields physiological activity. Exposure to far-red light inhibits phytochrome activity. Together, the two forms represent the phytochrome system (Figure **16.1.3.1**).

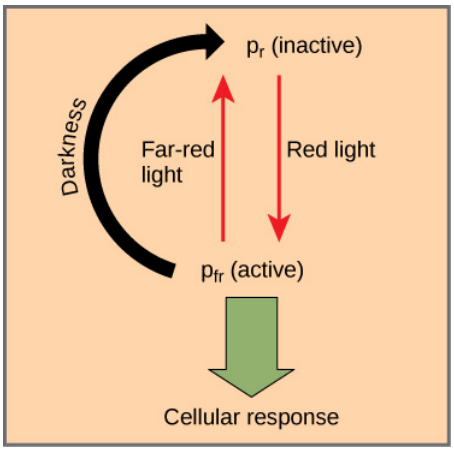



Figure **16.1.3.1**: The biologically inactive form of phytochrome (Pr) is converted to the biologically active form Pfr under illumination with red light. Far-red light and darkness convert the molecule back to the inactive form.

The phytochrome system acts as a biological light switch. It monitors the level, intensity, duration, and color of environmental light. The effect of red light is reversible by immediately shining far-red light on the sample, which converts the chromoprotein to the inactive Pr form. Additionally, Pfr can slowly revert to Pr in the dark, or break down over time. In all instances, the physiological response induced by red light is reversed. The active form of phytochrome (Pfr) can directly activate other molecules in the cytoplasm, or it can be transported to the nucleus, where it directly activates or represses specific gene expression.

Unfiltered sunlight is rich in red light but deficient in far-red light. Therefore, at dawn, all the phytochrome molecules in a leaf quickly convert to the active Pfr form, and remain in that form until sunset. In the dark, the Pfr form takes hours to slowly revert back to the Pr form. If the night is long (as in winter), all of the Pfr form reverts. If the night is short (as in summer), a considerable

amount of Pfr may remain at sunrise. By sensing the Pr/Pfr ratio at dawn, a plant can determine the length of the day/night cycle. In addition, leaves retain that information for several days, allowing a comparison between the length of the previous night and the preceding several nights. Shorter nights indicate springtime to the plant; when the nights become longer, autumn is approaching. This information, along with sensing temperature and water availability, allows plants to determine the time of the year and adjust their physiology accordingly.

In 1920 two employees of the U. S. Department of Agriculture, W. W. Garner and H. A. Allard, discovered a mutation in tobacco - a variety called Maryland Mammoth - that prevented the plant from flowering in the summer as normal tobacco plants do. Maryland Mammoth would not bloom until late December. Experimenting with artificial lighting in winter and artificial darkening in summer, they found that Maryland Mammoth was affected by photoperiod. Because it would flower only when exposed to short periods of light, they called it a **short-day** plant. Examples of other short-day plants include chrysanthemums, rice (*Oryza sativa*), poinsettias, morning glory (*Pharbitis nil*), and cocklebur (*Xanthium*).

Experiments with the cocklebur have shown that the term short-day is something of a misnomer; what the cocklebur needs is a sufficiently **long night** (Figure **16.1.3.2**). Short-day (long-night) plants flower in the late summer and early fall, when nights exceed a critical length (often eight or fewer hours). In short-day plants, the active form of phytochrome (Pfr) suppresses flowering. During long periods of darkness (long nights), Pfr is converted to Pr. With Pfr no longer present, flowering is not suppressed, and short-day plants flower. If a flash of light interrupts the dark period, Pr is converted back to Pfr, and flowering is suppressed.

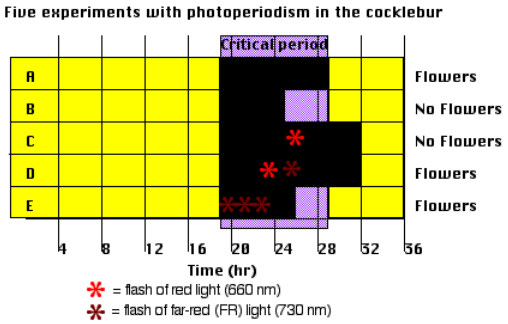



Figure **16.1.3.2**: Cockleburs (adapted to the latitude of Michigan) will flower only if they have been kept in the dark for at least 8.5 hours — the **critical period** (**A** and **B**). Interruption of an otherwise long night by light — **red** (**660 nm**) rays are particularly effective — prevents flowering (**C**). Unless it is followed by irradiation with **far-red** (**730 nm**) light (**D**). An intense exposure to far-red light at the start of the night reduces the dark requirement by two hours (**E**).

**Long-day** (short-night) plants flower during the spring, when darkness is less than a critical length (often eight to 15 hours). Examples include spinach, *Arabidopsis*, sugar beet, and the radish flower.

Flowering in **day-neutral** plants, such as the tomato, is not regulated by photoperiod.

Photoperiodism also explains why some plant species can be grown only in a certain latitude. Spinach, a long-day plant, cannot flower in the tropics because the days never get long enough (14 hours). Ragweed, a short-day plant, fails to thrive in northern Maine because by the time the days become short enough to initiate flowering, a killing frost in apt to occur before reproduction and the formation of seeds is completed.

Some plants do not neatly fit into the categories of short day, long day, or day neutral. In 1941, Marie Taylor Clark found that flowering in scarlet sage did not flower under daylengths longer than 16 hours, suggesting it was a short-day plant; however, days that were too short (6 hours) slowed flower development. Flower development was optimal with daylengths of 10 hours.

The leaves produce a chemical signal called **florigen** that is transmitted to the apical meristems to start their conversion into floral meristems. The chemical nature of florigen has been sought for decades. The most recent evidence suggests that at least one component is the protein encoded by the gene *FLOWERING LOCUS T* (***FT***). Due to florigen signaling, the entire plant will bloom even if only a part of one leaf is exposed to the correct photoperiod (Figure **16.1.3.3**).

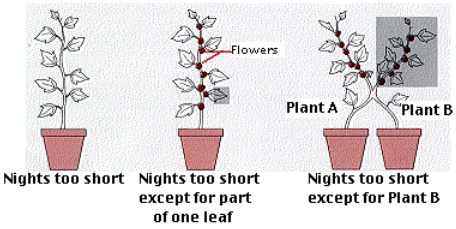



Figure **16.1.3.3**: The cocklebur needs at least 8.5 hours of darkness in order to flower. Grafting a cocklebur (**B**) that receives the required period of darkness to one (**A**) that does not causes flowering in both. Evidently the florigen signal passes from **B** to **A** through their connected vascular systems.

## Career Connection: Horticulturist

The word "horticulturist" comes from the Latin words for garden (hortus) and culture (cultura). This career has been revolutionized by progress made in the understanding of plant responses to environmental stimuli. Growers of crops, fruit, vegetables, and flowers were previously constrained by having to time their sowing and harvesting according to the season. Now, horticulturists can manipulate plants to increase leaf, flower, or fruit production by understanding how environmental factors affect plant growth and development.

Greenhouse management is an essential component of a horticulturist's education. To lengthen the night, plants are covered with a blackout shade cloth. Long-day plants are irradiated with red light in winter to promote early flowering. For example, fluorescent (cool white) light high in blue wavelengths encourages leafy growth and is excellent for starting seedlings. Incandescent lamps (standard light bulbs) are rich in red light, and promote flowering in some plants. The timing of fruit ripening can be increased or delayed by applying plant hormones. Recently, considerable progress has been made in the development of plant breeds that are suited to different climates and resistant to pests and transportation damage. Both crop yield and quality have increased as a result of practical applications of the knowledge of plant responses to external stimuli and hormones.

Horticulturists find employment in private and governmental laboratories, greenhouses, botanical gardens, and in the production or research fields (Figure **16.1.3.4**). They improve crops by applying their knowledge of genetics and plant physiology. To prepare for a horticulture career, students take classes in botany, plant physiology, plant pathology, landscape design, and plant breeding. To complement these traditional courses, horticulture majors add studies in economics, business, computer science, and communications.



Figure **16.1.3.4**: Horticulturalist Anderson Ifui (left) with Jack McGilchrist, the technical adviser for the Australian Volunteer Initiative (right), at Honiara Botanic gardens in the Solomon Islands in 2004. Image by Peter Davis/AusAID (CC-BY).

## Circadian Rhythms

**Circadian rhythms** are changes based on a 24-hour cycle. For example, flowers might open every morning and close every evening or vice versa. In *Oxalis* and silk tree (*Albizia julibrissin*), leaflets expand during the day and retract at night. Circadian

rhythms may also involve physiological processes like photosynthetic rate or the the production of floral scent compounds.

Under constant conditions, circadian rhythms may drift out of phase with the environment (figure 16.1.3.5). However, when exposed to environmental changes (e.g., alternating day and night), the rhythms become **entrained**; that is, they now cycle synchronized with the cycle of day and night with a period of exactly 24 hours. Internal circadian clocks also adjust to changing photoperiods. Suppose a plant that flowers throughout the spring opens its flowers every morning. The sun rises earlier in the late spring compared to the early spring (photoperiod increases in late spring). As time passes and the plant detects the changing photoperiod (technically, plants measure the length of the night rather than daylength; see above), the circadian clock would adjust such that its flowers opened earlier. In *Arabidopsis*, the entrainment of circadian rhythms requires that light is detected by phytochromes (absorb red light) and cryptochromes (absorb blue light).



Figure 16.1.3.5: The leaves and leaflets of the silk tree (*Albizia julibrissin*) expand during the day (left) and retract and night (right). These diurnal (daily) movements are an example of circadian rhythms. Image is public domain.

## Attributions

Curated and authored by Melissa Ha using the following sources:

- 16.4E: Photoperiodism and Phytochrome from *Biology* by John. W. Kimball (licensed CC-BY)
- 30.6 Plant Sensory Systems and Responses from *Biology 2e* by OpenStax (licensed CC-BY). Access for free at openstax.org.

This page titled 16.1.3: Photoperiodism is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **4.2.3: Photoperiodism** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC 4.0.

# 16.1.4: Etiolation and Shade Avoidance

## Learning Objectives

- Contrast etiolated seedlings with those grown in light.
- Describe the adaptive value of etiolation.

Plants grown in the dark have elongated stems, are white or yellow (due to lack of chlorophyll), and have small leaves (Figures **16.1.4.1** and 2). This phenomenon is called **etiolation**, and it is a mechanism that increases the chance that the plant will access light.

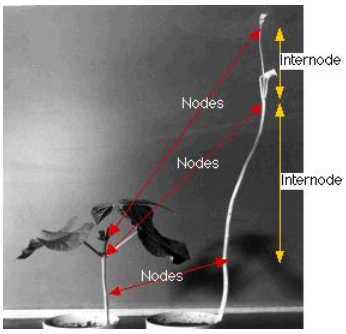



Figure **16.1.4.1**: Common garden bean seedlings grown in the light (left) and in darkness (right). The dark-grown is etiolated, exhibiting elongated internodes, pale coloration, and small leaves. Each seedling has three nodes (the bottom ones where the cotyledons were attached), but the dark-grown seedling is taller because its internodes are greatly elongated. When the food reserves in its seed are exhausted, the dark-grown seedling will die (unless placed in the light).



Figure **16.1.4.2**: Etiolated Spanish blue bells (*Hyacinthoides hispanica*) with elongated, yellow and white stems and leaves. Image by Chiswick Chap (licensed under CC-BY-SA)

The prevention of etiolation in *Arabidopsis* is mediated by **phytochrome B**. When sunlight (660 nm) converts Pr into Pfr, Pfr moves from the cytoplasm into the nucleus. There it stimulates the activity of DELLA proteins, which bind to and inhibit proteins called **PIFs** (phytochrome-interacting factors). PIFs are transcription factors that bind to and turn on promoters of genes that, among other effects, stimulate cell and thus stem elongation. DELLA proteins prevent PIFs from binding to the promoters of their target genes, resulting in reduced cell elongation (no etiolation) in the presence of light.

Gibberellins are plant hormones that promote stem elongation thus mimicking the etiolation response. They do this by triggering the degradation of DELLA proteins, which frees PIFS to bind to the promoters of genes needed for cell elongation.

The shade-avoidance response also involves phytochrome and and PIFs. This response helps ensure that the plant accesses enough sunlight to be able to conduct photosynthesis. Natural sunlight contains about the same amount of red (660 nm) as far-red (735 nm) light. However, chlorophyll absorbs 660 nm light strongly, so that the light that filters through a canopy of foliage is enriched in far-red light. This is absorbed by Pfr, converting it into inactive Pr such that PIFs are no longer inhibited. The now-active PIFs turn on the genes needed for auxin synthesis, and auxin stimulates stem elongation.

## Attributions

Curated and authored by Melissa Ha using 16.4C: Etiolation from *Biology* by John. W. Kimball (licensed CC-BY)

---

This page titled 16.1.4: Etiolation and Shade Avoidance is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **4.2.4: Etiolation and Shade Avoidance** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC 4.0.

# 16.1.5: Dormancy

**Learning Objectives**

- List the environmental factors that break seed dormancy (induce germination) and define the horticultural techniques based on these factors.
- Explain how phytochrome mediates light-induced germination in lettuce.

During certain time periods or environmental circumstances, active growth is not advantageous for a plant. For example, the embryos in seeds must stay dormant for long enough to disperse from the parent plant or until there are suitable conditions for growth (temperature, light availability, water, etc.). In seeds, the phytochrome system is not used to determine direction and quality of light (shaded versus unshaded). Instead, is it used merely to determine if there is any light at all. This is especially important in species with very small seeds, such as lettuce. Because of their size, lettuce seeds have few food reserves. Their seedlings cannot grow for long before they run out of fuel. If they germinated even a centimeter under the soil surface, the seedling would never make it into the sunlight and would die. In the dark, phytochrome is in the Pr (inactive form) and the seed will not germinate; it will only germinate if exposed to light at the surface of the soil. Upon exposure to light, Pr is converted to Pfr, which signals transcription of the gene that encodes **amylase**, an enzyme that breaks down starches stored in the seed into simple sugars. Germination then proceeds. Experimentally exposing lettuce seeds to red light induces germination because this converts Pr to Pfr. Exposure to far red light inhibits germination because this causes the active form of phtochrome (Pfr) to be converted to the inactive form (Pr; Figure **16.1.5.1**).

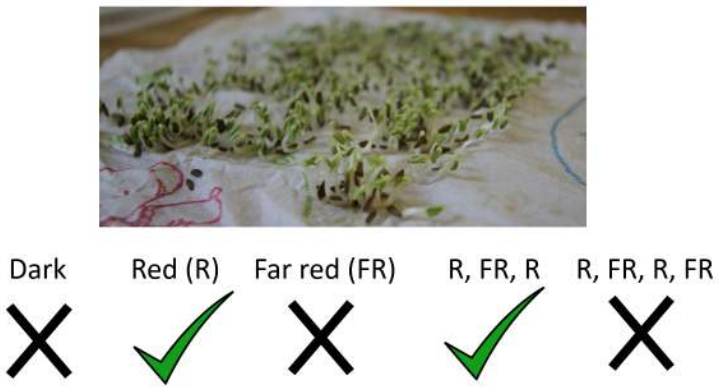



Figure **16.1.5.1**: The germination of lettuce seeds (top) is controlled by light. From left to right: Lettuce seeds do not germinate in the dark, but they do germinate when exposed to red light. When exposed to far red light, lettuce seeds do not germinate. Alternating exposure to red light and far red light results in germination if red light is last in the sequence. If far red light ends the sequence, germination does not occur. Image prepared by Melissa Ha using checkmarks (public domain) and lettuce sprouts by Kanu Hawaii (licensed under CC-BY)

Several additional factors are involved in seed germination. Exposure to a cold period can also induce germination in seeds. Cold **stratification** is a horticultural technique that involves storing seeds in cold conditions to promote germination. Sometimes seeds require mechanical abrasion of the seed coat, facilitated by the soil. **Scarification** is a horticultural technique that simulates this abrasion by cutting the seed coat with a knife or other means. Seeds may also require exposure to water, which can wash chemicals from the seed coat that inhibit germination. Seeds that are dispersed by animals that eat the fruits are adapted to the acids in the digestive tract. To promote germination in these species, horticulturalists may need to bathe these seeds in acid.

Likewise, trees in certain climates become dormant in the winter (setting of winter buds; Figure **16.1.5.2**). Similarly to how it controls flowering, photoperiodism mediated by phytochrome stops vegetative growth and promotes the setting of winter buds. This occurs as the days grow shorter in the autumn. To break dormancy in the spring, the buds may need to first be exposed to cold winter temperatures. In other cases, a certain period of time just needs to pass.



Figure **16.1.5.2**: Dormant bud on twig of Arizona walnut (*Juglans major*). Image by Whitney Cranshaw (licensed under CC-BY).

## Attributions

Curated and authored by Melissa Ha using the following sources:

- 16.4E: Photoperiodism and Phytochrome from *Biology* by John. W. Kimball (licensed CC-BY)
- 30.6 Plant Sensory Systems and Responses and 32.2 Pollination and Fertilization from *Biology 2e* by OpenStax (licensed CC-BY). Access for free at openstax.org.
- Plant Hormones and Sensory Systems by Biology 1520 Introduction to Organismal Biology (licensed CC-BY-NC-SA)

---

This page titled 16.1.5: Dormancy is shared under a CC BY-NC-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **4.2.5: Dormancy** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC-SA 4.0.

# 16.1.6: Chapter Summary

Plants respond to light, gravity, water, physical contact, temperature, and other environmental factors. **Tropisms** are a response involve directional growth toward or away from a stimulus. **Positive phototropism** in stems is mediated by blue-light receptors called **photoreceptors** and an auxin gradient. **Positive gravitropism** in roots and **negative gravitropism** in shoots involves specialized amyloplasts called **statoliths** as well as an auxin gradient. Plants also change biological activities according to a 24-hour cycle maintained by an internal clock. These **circadian rhythms** can be **entrained** to the environment. Flowering is another response to environmental factors, such as temperature and photoperiod. **Photoperiodism** with respect to flowering involves two interconvertible forms of the red-light **phytochrome** with which plants can measure the length of the dark period (night). Seedlings respond to a lack of light by **etiolated** growth, which helps them access light. Light, temperature, rainfall, and other environmental factors can break seed dormancy (induce germination).

## After completing this chapter, you should be able to...

- Distinguish among phototropism, gravitropism, hydrotropism, and thigmotropism.
- Discuss the adaptive value of tropisms.
- Describe the mechanism of phototropism in shoots.
- Describe the mechanism of gravitropism in shoots and roots.
- Distinguish among thigmotropism, thigmonastic movements, and thigmomorphogenesis
- Define circadian rhythms and provide examples in plants.
- Describe the environmental conditions that induce flowering
- Describe the mechanism of photoperiodism with respect to flowering.
- Distinguish among short-day, long-day, and day-neutral plants.
- Contrast etiolated seedlings with those grown in light and describe the adaptive value of etiolation.
- List the environmental factors that break seed dormancy (induce germination) and define the horticultural techniques based on these factors.
- Explain how phytochrome mediates light-induced germination in lettuce.

This page titled 16.1.6: Chapter Summary is shared under a CC BY-NC 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **4.2.6: Chapter Summary** by Melissa Ha, Maria Morrow, & Kammy Algiers is licensed CC BY-NC 4.0.

# 16.2: Plant Sensory Systems and Responses

**Skills to Develop**

- Describe how red and blue light affect plant growth and metabolic activities
- Discuss gravitropism
- Understand how hormones affect plant growth and development
- Describe thigmotropism, thigmonastism, and thigmogenesis
- Explain how plants defend themselves from predators and respond to wounds

Animals can respond to environmental factors by moving to a new location. Plants, however, are rooted in place and must respond to the surrounding environmental factors. Plants have sophisticated systems to detect and respond to light, gravity, temperature, and physical touch. Receptors sense environmental factors and relay the information to effector systems—often through intermediate chemical messengers—to bring about plant responses.

## Plant Responses to Light

Plants have a number of sophisticated uses for light that go far beyond their ability to photosynthesize low-molecular-weight sugars using only carbon dioxide, light, and water. Photomorphogenesis is the growth and development of plants in response to light. It allows plants to optimize their use of light and space. Photoperiodism is the ability to use light to track time. Plants can tell the time of day and time of year by sensing and using various wavelengths of sunlight. Phototropism is a directional response that allows plants to grow towards, or even away from, light.

The sensing of light in the environment is important to plants; it can be crucial for competition and survival. The response of plants to light is mediated by different photoreceptors, which are comprised of a protein covalently bonded to a light-absorbing pigment called a chromophore. Together, the two are called a chromoprotein.

The red/far-red and violet-blue regions of the visible light spectrum trigger structural development in plants. Sensory photoreceptors absorb light in these particular regions of the visible light spectrum because of the quality of light available in the daylight spectrum. In terrestrial habitats, light absorption by chlorophylls peaks in the blue and red regions of the spectrum. As light filters through the canopy and the blue and red wavelengths are absorbed, the spectrum shifts to the far-red end, shifting the plant community to those plants better adapted to respond to far-red light. Blue-light receptors allow plants to gauge the direction and abundance of sunlight, which is rich in blue–green emissions. Water absorbs red light, which makes the detection of blue light essential for algae and aquatic plants.

## The Phytochrome System and the Red/Far-Red Response

The phytochromes are a family of chromoproteins with a linear tetrapyrrole chromophore, similar to the ringed tetrapyrrole light-absorbing head group of chlorophyll. Phytochromes have two photo-interconvertible forms: Pr and Pfr. Pr absorbs red light (~667 nm) and is immediately converted to Pfr. Pfr absorbs far-red light (~730 nm) and is quickly converted back to Pr. Absorption of red or far-red light causes a massive change to the shape of the chromophore, altering the conformation and activity of the phytochrome protein to which it is bound. Pfr is the physiologically active form of the protein; therefore, exposure to red light yields physiological activity. Exposure to far-red light inhibits phytochrome activity. Together, the two forms represent the phytochrome system (Figure **16.2.1**).

The phytochrome system acts as a biological light switch. It monitors the level, intensity, duration, and color of environmental light. The effect of red light is reversible by immediately shining far-red light on the sample, which converts the chromoprotein to the inactive Pr form. Additionally, Pfr can slowly revert to Pr in the dark, or break down over time. In all instances, the physiological response induced by red light is reversed. The active form of phytochrome (Pfr) can directly activate other molecules in the cytoplasm, or it can be trafficked to the nucleus, where it directly activates or represses specific gene expression.

Once the phytochrome system evolved, plants adapted it to serve a variety of needs. Unfiltered, full sunlight contains much more red light than far-red light. Because chlorophyll absorbs strongly in the red region of the visible spectrum, but not in the far-red region, any plant in the shade of another plant on the forest floor will be exposed to red-depleted, far-red-enriched light. The

preponderance of far-red light converts phytochrome in the shaded leaves to the Pr (inactive) form, slowing growth. The nearest non-shaded (or even less-shaded) areas on the forest floor have more red light; leaves exposed to these areas sense the red light, which activates the Pfr form and induces growth. In short, plant shoots use the phytochrome system to grow away from shade and towards light. Because competition for light is so fierce in a dense plant community, the evolutionary advantages of the phytochrome system are obvious.

In seeds, the phytochrome system is not used to determine direction and quality of light (shaded versus unshaded). Instead, is it used merely to determine if there is any light at all. This is especially important in species with very small seeds, such as lettuce. Because of their size, lettuce seeds have few food reserves. Their seedlings cannot grow for long before they run out of fuel. If they germinated even a centimeter under the soil surface, the seedling would never make it into the sunlight and would die. In the dark, phytochrome is in the Pr (inactive form) and the seed will not germinate; it will only germinate if exposed to light at the surface of the soil. Upon exposure to light, Pr is converted to Pfr and germination proceeds.

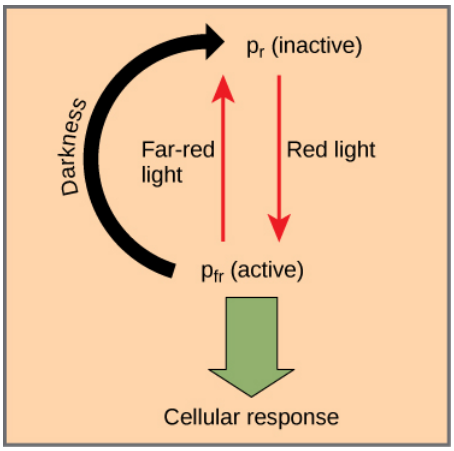



Figure **16.2.1**: The biologically inactive form of phytochrome (Pr) is converted to the biologically active form Pfr under illumination with red light. Far-red light and darkness convert the molecule back to the inactive form.

Plants also use the phytochrome system to sense the change of season. Photoperiodism is a biological response to the timing and duration of day and night. It controls flowering, setting of winter buds, and vegetative growth. Detection of seasonal changes is crucial to plant survival. Although temperature and light intensity influence plant growth, they are not reliable indicators of season because they may vary from one year to the next. Day length is a better indicator of the time of year.

As stated above, unfiltered sunlight is rich in red light but deficient in far-red light. Therefore, at dawn, all the phytochrome molecules in a leaf quickly convert to the active Pfr form, and remain in that form until sunset. In the dark, the Pfr form takes hours to slowly revert back to the Pr form. If the night is long (as in winter), all of the Pfr form reverts. If the night is short (as in summer), a considerable amount of Pfr may remain at sunrise. By sensing the Pr/Pfr ratio at dawn, a plant can determine the length of the day/night cycle. In addition, leaves retain that information for several days, allowing a comparison between the length of the previous night and the preceding several nights. Shorter nights indicate springtime to the plant; when the nights become longer, autumn is approaching. This information, along with sensing temperature and water availability, allows plants to determine the time of the year and adjust their physiology accordingly. Short-day (long-night) plants use this information to flower in the late summer and early fall, when nights exceed a critical length (often eight or fewer hours). Long-day (short-night) plants flower during the spring, when darkness is less than a critical length (often eight to 15 hours). Not all plants use the phytochrome system in this way. Flowering in day-neutral plants is not regulated by daylength.

### Career Connection: Horticulturalist

The word “horticulturist” comes from the Latin words for garden (*hortus*) and culture (*cultura*). This career has been revolutionized by progress made in the understanding of plant responses to environmental stimuli. Growers of crops, fruit, vegetables, and flowers were previously constrained by having to time their sowing and harvesting according to the season. Now, horticulturists can manipulate plants to increase leaf, flower, or fruit production by understanding how environmental factors affect plant growth and development.

Greenhouse management is an essential component of a horticulturist's education. To lengthen the night, plants are covered with a blackout shade cloth. Long-day plants are irradiated with red light in winter to promote early flowering. For example, fluorescent (cool white) light high in blue wavelengths encourages leafy growth and is excellent for starting seedlings. Incandescent lamps (standard light bulbs) are rich in red light, and promote flowering in some plants. The timing of fruit ripening can be increased or delayed by applying plant hormones. Recently, considerable progress has been made in the development of plant breeds that are suited to different climates and resistant to pests and transportation damage. Both crop yield and quality have increased as a result of practical applications of the knowledge of plant responses to external stimuli and hormones.

Horticulturists find employment in private and governmental laboratories, greenhouses, botanical gardens, and in the production or research fields. They improve crops by applying their knowledge of genetics and plant physiology. To prepare for a horticulture career, students take classes in botany, plant physiology, plant pathology, landscape design, and plant breeding. To complement these traditional courses, horticulture majors add studies in economics, business, computer science, and communications.

## The Blue Light Responses

Phototropism—the directional bending of a plant toward or away from a light source—is a response to blue wavelengths of light. Positive phototropism is growth towards a light source (Figure **16.2.2**), while negative phototropism (also called skototropism) is growth away from light.

The aptly-named phototropins are protein-based receptors responsible for mediating the phototropic response. Like all plant photoreceptors, phototropins consist of a protein portion and a light-absorbing portion, called the chromophore. In phototropins, the chromophore is a covalently-bound molecule of flavin; hence, phototropins belong to a class of proteins called flavoproteins.

Other responses under the control of phototropins are leaf opening and closing, chloroplast movement, and the opening of stomata. However, of all responses controlled by phototropins, phototropism has been studied the longest and is the best understood.

In their 1880 treatise *The Power of Movements in Plants*, Charles Darwin and his son Francis first described phototropism as the bending of seedlings toward light. Darwin observed that light was perceived by the tip of the plant (the apical meristem), but that the response (bending) took place in a different part of the plant. They concluded that the signal had to travel from the apical meristem to the base of the plant.



Figure **16.2.2**: Azure bluets (*Houstonia caerulea*) display a phototropic response by bending toward the light. (credit: Cory Zanker)

In 1913, Peter Boysen-Jensen demonstrated that a chemical signal produced in the plant tip was responsible for the bending at the base. He cut off the tip of a seedling, covered the cut section with a layer of gelatin, and then replaced the tip. The seedling bent toward the light when illuminated. However, when impermeable mica flakes were inserted between the tip and the cut base, the seedling did not bend. A refinement of the experiment showed that the signal traveled on the shaded side of the seedling. When the mica plate was inserted on the illuminated side, the plant did bend towards the light. Therefore, the chemical signal was a growth

stimulant because the phototropic response involved faster cell elongation on the shaded side than on the illuminated side. We now know that as light passes through a plant stem, it is diffracted and generates phototropin activation across the stem. Most activation occurs on the lit side, causing the plant hormone indole acetic acid (IAA) to accumulate on the shaded side. Stem cells elongate under influence of IAA.

Cryptochromes are another class of blue-light absorbing photoreceptors that also contain a flavin-based chromophore. Cryptochromes set the plants 24-hour activity cycle, also know as its circadian rhythem, using blue light cues. There is some evidence that cryptochromes work together with phototropins to mediate the phototropic response.

Link to Learning



Use the navigation menu in the left panel of this website to view images of plants in motion.

## Plant Responses to Gravity

Whether or not they germinate in the light or in total darkness, shoots usually sprout up from the ground, and roots grow downward into the ground. A plant laid on its side in the dark will send shoots upward when given enough time. Gravitropism ensures that roots grow into the soil and that shoots grow toward sunlight. Growth of the shoot apical tip upward is called negative gravitropism, whereas growth of the roots downward is called positive gravitropism.

Amyloplasts (also known as statoliths) are specialized plastids that contain starch granules and settle downward in response to gravity. Amyloplasts are found in shoots and in specialized cells of the root cap. When a plant is tilted, the statoliths drop to the new bottom cell wall. A few hours later, the shoot or root will show growth in the new vertical direction.

The mechanism that mediates gravitropism is reasonably well understood. When amyloplasts settle to the bottom of the gravity-sensing cells in the root or shoot, they physically contact the endoplasmic reticulum (ER), causing the release of calcium ions from inside the ER. This calcium signaling in the cells causes polar transport of the plant hormone IAA to the bottom of the cell. In roots, a high concentration of IAA inhibits cell elongation. The effect slows growth on the lower side of the root, while cells develop normally on the upper side. IAA has the opposite effect in shoots, where a higher concentration at the lower side of the shoot stimulates cell expansion, causing the shoot to grow up. After the shoot or root begin to grow vertically, the amyloplasts return to their normal position. Other hypotheses—involving the entire cell in the gravitropism effect—have been proposed to explain why some mutants that lack amyloplasts may still exhibit a weak gravitropic response.

## Growth Responses

A plant's sensory response to external stimuli relies on chemical messengers (hormones). Plant hormones affect all aspects of plant life, from flowering to fruit setting and maturation, and from phototropism to leaf fall. Potentially every cell in a plant can produce

plant hormones. They can act in their cell of origin or be transported to other portions of the plant body, with many plant responses involving the synergistic or antagonistic interaction of two or more hormones. In contrast, animal hormones are produced in specific glands and transported to a distant site for action, and they act alone.

Plant hormones are a group of unrelated chemical substances that affect plant morphogenesis. Five major plant hormones are traditionally described: auxins (particularly IAA), cytokinins, gibberellins, ethylene, and abscisic acid. In addition, other nutrients and environmental conditions can be characterized as growth factors.

## Auxins

The term auxin is derived from the Greek word *auxein*, which means "to grow." Auxins are the main hormones responsible for cell elongation in phototropism and gravitropism. They also control the differentiation of meristem into vascular tissue, and promote leaf development and arrangement. While many synthetic auxins are used as herbicides, IAA is the only naturally occurring auxin that shows physiological activity. Apical dominance—the inhibition of lateral bud formation—is triggered by auxins produced in the apical meristem. Flowering, fruit setting and ripening, and inhibition of abscission (leaf falling) are other plant responses under the direct or indirect control of auxins. Auxins also act as a relay for the effects of the blue light and red/far-red responses.

Commercial use of auxins is widespread in plant nurseries and for crop production. IAA is used as a rooting hormone to promote growth of adventitious roots on cuttings and detached leaves. Applying synthetic auxins to tomato plants in greenhouses promotes normal fruit development. Outdoor application of auxin promotes synchronization of fruit setting and dropping to coordinate the harvesting season. Fruits such as seedless cucumbers can be induced to set fruit by treating unfertilized plant flowers with auxins.

## Cytokinins

The effect of cytokinins was first reported when it was found that adding the liquid endosperm of coconuts to developing plant embryos in culture stimulated their growth. The stimulating growth factor was found to be cytokinin, a hormone that promotes cytokinesis (cell division). Almost 200 naturally occurring or synthetic cytokinins are known to date. Cytokinins are most abundant in growing tissues, such as roots, embryos, and fruits, where cell division is occurring. Cytokinins are known to delay senescence in leaf tissues, promote mitosis, and stimulate differentiation of the meristem in shoots and roots. Many effects on plant development are under the influence of cytokinins, either in conjunction with auxin or another hormone. For example, apical dominance seems to result from a balance between auxins that inhibit lateral buds, and cytokinins that promote bushier growth.

## Gibberellins

Gibberellins (GAs) are a group of about 125 closely related plant hormones that stimulate shoot elongation, seed germination, and fruit and flower maturation. GAs are synthesized in the root and stem apical meristems, young leaves, and seed embryos. In urban areas, GA antagonists are sometimes applied to trees under power lines to control growth and reduce the frequency of pruning.

GAs break dormancy (a state of inhibited growth and development) in the seeds of plants that require exposure to cold or light to germinate. Abscisic acid is a strong antagonist of GA action. Other effects of GAs include gender expression, seedless fruit development, and the delay of senescence in leaves and fruit. Seedless grapes are obtained through standard breeding methods and contain inconspicuous seeds that fail to develop. Because GAs are produced by the seeds, and because fruit development and stem elongation are under GA control, these varieties of grapes would normally produce small fruit in compact clusters. Maturing grapes are routinely treated with GA to promote larger fruit size, as well as looser bunches (longer stems), which reduces the instance of mildew infection (Figure **16.2.3**).



Figure 16.2.3: In grapes, application of gibberellic acid increases the size of fruit and loosens clustering. (credit: Bob Nichols, USDA)

## Abscisic Acid

The plant hormone abscisic acid (ABA) was first discovered as the agent that causes the abscission or dropping of cotton bolls. However, more recent studies indicate that ABA plays only a minor role in the abscission process. ABA accumulates as a response to stressful environmental conditions, such as dehydration, cold temperatures, or shortened day lengths. Its activity counters many of the growth-promoting effects of GAs and auxins. ABA inhibits stem elongation and induces dormancy in lateral buds.

ABA induces dormancy in seeds by blocking germination and promoting the synthesis of storage proteins. Plants adapted to temperate climates require a long period of cold temperature before seeds germinate. This mechanism protects young plants from sprouting too early during unseasonably warm weather in winter. As the hormone gradually breaks down over winter, the seed is released from dormancy and germinates when conditions are favorable in spring. Another effect of ABA is to promote the development of winter buds; it mediates the conversion of the apical meristem into a dormant bud. Low soil moisture causes an increase in ABA, which causes stomata to close, reducing water loss in winter buds.

## Ethylene

Ethylene is associated with fruit ripening, flower wilting, and leaf fall. Ethylene is unusual because it is a volatile gas ($C_2H_4$). Hundreds of years ago, when gas street lamps were installed in city streets, trees that grew close to lamp posts developed twisted, thickened trunks and shed their leaves earlier than expected. These effects were caused by ethylene volatilizing from the lamps.

Aging tissues (especially senescing leaves) and nodes of stems produce ethylene. The best-known effect of the hormone, however, is the promotion of fruit ripening. Ethylene stimulates the conversion of starch and acids to sugars. Some people store unripe fruit, such as avocadoes, in a sealed paper bag to accelerate ripening; the gas released by the first fruit to mature will speed up the maturation of the remaining fruit. Ethylene also triggers leaf and fruit abscission, flower fading and dropping, and promotes germination in some cereals and sprouting of bulbs and potatoes.

Ethylene is widely used in agriculture. Commercial fruit growers control the timing of fruit ripening with application of the gas. Horticulturalists inhibit leaf dropping in ornamental plants by removing ethylene from greenhouses using fans and ventilation.

## Nontraditional Hormones

Recent research has discovered a number of compounds that also influence plant development. Their roles are less understood than the effects of the major hormones described so far.

Jasmonates play a major role in defense responses to herbivory. Their levels increase when a plant is wounded by a predator, resulting in an increase in toxic secondary metabolites. They contribute to the production of volatile compounds that attract natural enemies of predators. For example, chewing of tomato plants by caterpillars leads to an increase in jasmonic acid levels, which in turn triggers the release of volatile compounds that attract predators of the pest.

Oligosaccharins also play a role in plant defense against bacterial and fungal infections. They act locally at the site of injury, and can also be transported to other tissues. Strigolactones promote seed germination in some species and inhibit lateral apical development in the absence of auxins. Strigolactones also play a role in the establishment of mycorrhizae, a mutualistic association of plant roots and fungi. Brassinosteroids are important to many developmental and physiological processes. Signals between these compounds and other hormones, notably auxin and GAs, amplifies their physiological effect. Apical dominance, seed germination, gravitropism, and resistance to freezing are all positively influenced by hormones. Root growth and fruit dropping are inhibited by steroids.

## Plant Responses to Wind and Touch

The shoot of a pea plant winds around a trellis, while a tree grows on an angle in response to strong prevailing winds. These are examples of how plants respond to touch or wind.

The movement of a plant subjected to constant directional pressure is called thigmotropism, from the Greek words *thigma* meaning "touch," and *tropism* implying "direction." Tendrils are one example of this. The meristematic region of tendrils is very touch sensitive; light touch will evoke a quick coiling response. Cells in contact with a support surface contract, whereas cells on the opposite side of the support expand. Application of jasmonic acid is sufficient to trigger tendril coiling without a mechanical stimulus.

A thigmonastic response is a touch response independent of the direction of stimulus. In the Venus flytrap, two modified leaves are joined at a hinge and lined with thin fork-like tines along the outer edges. Tiny hairs are located inside the trap. When an insect brushes against these trigger hairs, touching two or more of them in succession, the leaves close quickly, trapping the prey. Glands on the leaf surface secrete enzymes that slowly digest the insect. The released nutrients are absorbed by the leaves, which reopen for the next meal.

Thigmomorphogenesis is a slow developmental change in the shape of a plant subjected to continuous mechanical stress. When trees bend in the wind, for example, growth is usually stunted and the trunk thickens. Strengthening tissue, especially xylem, is produced to add stiffness to resist the wind's force. Researchers hypothesize that mechanical strain induces growth and differentiation to strengthen the tissues. Ethylene and jasmonate are likely involved in thigmomorphogenesis.

**Link to Learning**

Use the menu at the left to navigate to three short movies: a Venus fly trap capturing prey, the progressive closing of sensitive plant leaflets, and the twining of tendrils.

## Defense Responses against Herbivores and Pathogens

Plants face two types of enemies: herbivores and pathogens. Herbivores both large and small use plants as food, and actively chew them. Pathogens are agents of disease. These infectious microorganisms, such as fungi, bacteria, and nematodes, live off of the

plant and damage its tissues. Plants have developed a variety of strategies to discourage or kill attackers.

The first line of defense in plants is an intact and impenetrable barrier. Bark and the waxy cuticle can protect against predators. Other adaptations against herbivory include thorns, which are modified branches, and spines, which are modified leaves. They discourage animals by causing physical damage and inducing rashes and allergic reactions. A plant's exterior protection can be compromised by mechanical damage, which may provide an entry point for pathogens. If the first line of defense is breached, the plant must resort to a different set of defense mechanisms, such as toxins and enzymes.

Secondary metabolites are compounds that are not directly derived from photosynthesis and are not necessary for respiration or plant growth and development. Many metabolites are toxic, and can even be lethal to animals that ingest them. Some metabolites are alkaloids, which discourage predators with noxious odors (such as the volatile oils of mint and sage) or repellent tastes (like the bitterness of quinine). Other alkaloids affect herbivores by causing either excessive stimulation (caffeine is one example) or the lethargy associated with opioids. Some compounds become toxic after ingestion; for instance, glycol cyanide in the cassava root releases cyanide only upon ingestion by the herbivore.

Mechanical wounding and predator attacks activate defense and protection mechanisms both in the damaged tissue and at sites farther from the injury location. Some defense reactions occur within minutes: others over several hours. The infected and surrounding cells may die, thereby stopping the spread of infection.

Long-distance signaling elicits a systemic response aimed at deterring the predator. As tissue is damaged, jasmonates may promote the synthesis of compounds that are toxic to predators. Jasmonates also elicit the synthesis of volatile compounds that attract parasitoids, which are insects that spend their developing stages in or on another insect, and eventually kill their host. The plant may activate abscission of injured tissue if it is damaged beyond repair.

## Summary

Plants respond to light by changes in morphology and activity. Irradiation by red light converts the photoreceptor phytochrome to its far-red light-absorbing form—Pfr. This form controls germination and flowering in response to length of day, as well as triggers photosynthesis in dormant plants or those that just emerged from the soil. Blue-light receptors, cryptochromes, and phototropins are responsible for phototropism. Amyloplasts, which contain heavy starch granules, sense gravity. Shoots exhibit negative gravitropism, whereas roots exhibit positive gravitropism. Plant hormones—naturally occurring compounds synthesized in small amounts—can act both in the cells that produce them and in distant tissues and organs. Auxins are responsible for apical dominance, root growth, directional growth toward light, and many other growth responses. Cytokinins stimulate cell division and counter apical dominance in shoots. Gibberellins inhibit dormancy of seeds and promote stem growth. Abscisic acid induces dormancy in seeds and buds, and protects plants from excessive water loss by promoting stomatal closure. Ethylene gas speeds up fruit ripening and dropping of leaves. Plants respond to touch by rapid movements (thigmotropy and thigmonasty) and slow differential growth (thigmomorphogenesis). Plants have evolved defense mechanisms against predators and pathogens. Physical barriers like bark and spines protect tender tissues. Plants also have chemical defenses, including toxic secondary metabolites and hormones, which elicit additional defense mechanisms.

## Glossary

**abscisic acid (ABA)**
plant hormone that induces dormancy in seeds and other organs

**abscission**
physiological process that leads to the fall of a plant organ (such as leaf or petal drop)

**auxin**
plant hormone that influences cell elongation (in phototropism), gravitropism, apical dominance and root growth

**chromophore**
molecule that absorbs light

**cryptochrome**

protein that absorbs light in the blue and ultraviolet regions of the light spectrum

**cytokinin**
plant hormone that promotes cell division

**ethylene**
volatile plant hormone that is associated with fruit ripening, flower wilting, and leaf fall

**gibberellin (GA)**
plant hormone that stimulates shoot elongation, seed germination, and the maturation and dropping of fruit and flowers

**jasmonates**
small family of compounds derived from the fatty acid linoleic acid

**negative gravitropism**
growth away from Earth's gravity

**oligosaccharin**
hormone important in plant defenses against bacterial and fungal infections

**photomorphogenesis**
growth and development of plants in response to light

**photoperiodism**
occurrence of plant processes, such as germination and flowering, according to the time of year

**phototropin**
blue-light receptor that promotes phototropism, stomatal opening and closing, and other responses that promote photosynthesis

**phototropism**
directional bending of a plant toward a light source

**phytochrome**
plant pigment protein that exists in two reversible forms (Pr and Pfr) and mediates morphologic changes in response to red light

**positive gravitropism**
growth toward Earth's gravitational center

**statolith**
(also, **amyloplast**) plant organelle that contains heavy starch granules

**strigolactone**
hormone that promotes seed germination in some species and inhibits lateral apical development in the absence of auxins

**thigmomorphogenesis**
developmental response to touch

**thigmonastic**
directional growth of a plant independent of the direction in which contact is applied

**thigmotropism**
directional growth of a plant in response to constant contact

This page titled 16.2: Plant Sensory Systems and Responses is shared under a CC BY 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **30.6: Plant Sensory Systems and Responses** by OpenStax is licensed CC BY 4.0.

# CHAPTER OVERVIEW

## 17: Measuring and analyzing plants

This page titled 17: Measuring and analyzing plants is shared under a not declared license and was authored, remixed, and/or curated by Tom Buckley.

# CHAPTER OVERVIEW

## 18: Predicting plants

This page titled 18: Predicting plants is shared under a not declared license and was authored, remixed, and/or curated by Tom Buckley.

# CHAPTER OVERVIEW

## 19: Biotic interactions

19.1: Industrial Agriculture
19.2: Sustainable Agriculture

This page titled 19: Biotic interactions is shared under a not declared license and was authored, remixed, and/or curated by Tom Buckley.

# 19.1: Industrial Agriculture

Also known as conventional agriculture, **industrial agriculture** is a method of farming that involves use of synthetic fertilizer, synthetic pesticides, and machinery. Industrial agriculture is dependent on large investments in mechanized equipment powered mostly by fossil fuels. In the case of livestock, most production comes from systems where animals are highly concentrated and confined.

## Synthetic Pesticides

**Pests** are organisms that occur where they are not wanted or that cause damage to crops, humans or other animals (figure **19.1.*a***). Thus, the term "pest" is a highly subjective term. A **pesticide** is a term for any substance intended for preventing, destroying, repelling, or mitigating any pest. Though often misunderstood to refer only to insecticides, the term pesticide also applies to **herbicides** (weed killers), fungicides, and various other substances used to control pests. Chemical pesticides can be effective, fast acting, adaptable to all crops and situations. When first applied, pesticides can result in impressive production gains of crops. However, despite these initial gains, excessive use of pesticides can be ecologically unsound (see Disadvantages of Industrial Agriculture). By their very nature, most pesticides create some risk of harm—pesticides can cause harm to humans, animals, and/or the environment because they are designed to kill or otherwise adversely affect living things. At the same time, pesticides are useful to society because they can kill potential disease-causing organisms and control insects, weeds, worms, and fungi.



Figure **19.1.*a***: The cotton boll weevil is considered a major pest because of the damage it does to cotton plants. Image by ARS USDA (public domain).

## Monoculture Farming

Industrial agriculture employs **monoculture** farming, which involves growing only one species of crop in a large area (figure **19.1.*b***). The plants in a monoculture are evenly spaced and have the same planting, irrigation, fertilizer, harvesting, etc. requirements, and this uniformity results in efficient use of farming machinery. Often, the crop is a **high yield variety** (high yielding variety; HYV), which is produced through selectively breeding individual plants with desirable characteristics. Compared to traditional crops, HYVs can produce more per unit area of land. Monoculture farming compromises genetic and species diversity in agriculture, however, promoting the spread of pests and risking that all the plants for hundreds of acres could be susceptible to the same disease (see Genetic Diversity).



Figure 19.1.*b*: Monocultures like this potato farm (left) and cotton farm (right) make it easier to use farming equipment; however, this reduces genetic diversity and consumes fossil fuels. Left image by NightThree (CC-BY) and right image by Kimberly Vardeman (CC-BY).

## Advantages of Industrial Agriculture

Industrial agriculture has delivered tremendous gains in productivity and efficiency. Food production worldwide has overall risen since the 1940s (figure 19.1.*c*); the World Bank estimates that between 70 percent and 90 percent of the recent increases in food production are the result of industrial agriculture rather than greater acreage under cultivation (figure 19.1.*d*). United States consumers have come to expect abundant and inexpensive food. Additionally, the use of synthetic pesticides ensures that produce is relatively free of blemishes (figure 19.1.*e*).

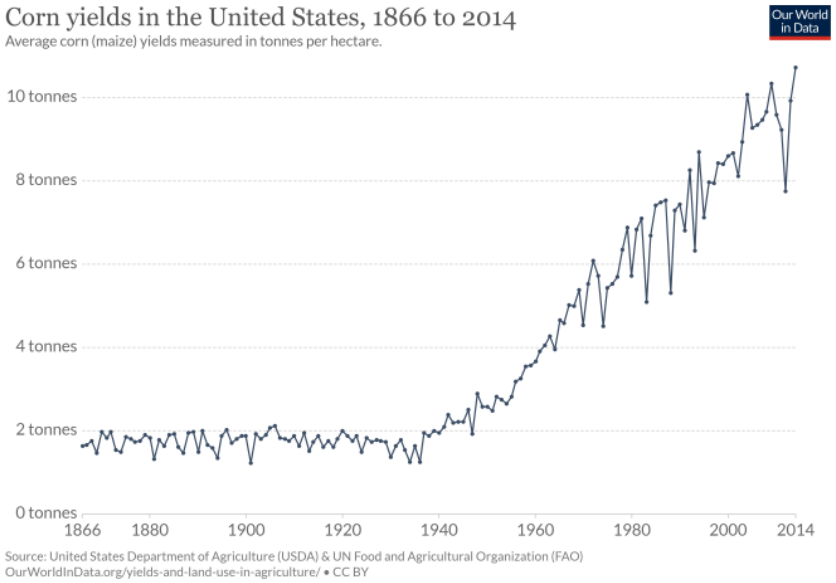



Figure **19.1.*c***: Corn yields in metric tons (tonnes; 1000 kilograms) per hectare over time. While yields have fluctuated from year to year, they have overall increased since the 1940s. This improving agricultural efficiency is partly due to industrial agricultural practices. Image by Hannah Ritchie and Max Roser/Our World in Data (CC-BY).

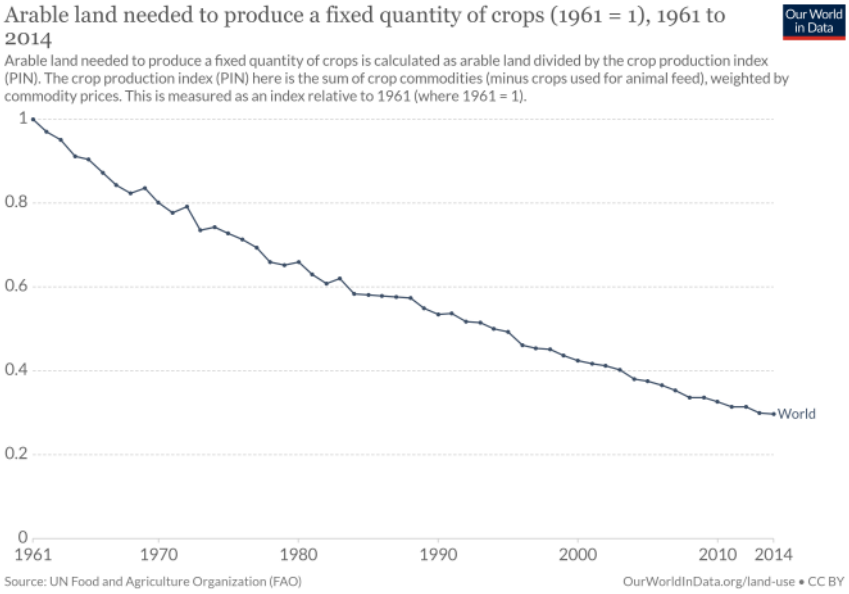



**Figure 19.1.*d*:** The arable (farmable) land required to produce a fixed amount of a crop has decreased over time due to improved agricultural efficiency. Image by Hannah Ritchie and Max Roser/Our World in Data (CC-BY).



Figure **19.1.*e***: Many of us carefully inspect produce at the grocery store and select those without blemishes. This visually appealing produce results from synthetic pesticides use. Image by Amanda Mills (public domain).

Industrial agriculture expands where crops can be cultivated. Applying synthetic fertilizers to poor soils can make them fertile. Additionally, irrigation systems promote high agricultural productivity in regions and during seasons that would otherwise only support the most drought-tolerant species. For example, about 25% of the food consumed in the United States is produced in California's Central Valley, which receives little rain in the summer months (figure **19.1.*f***).

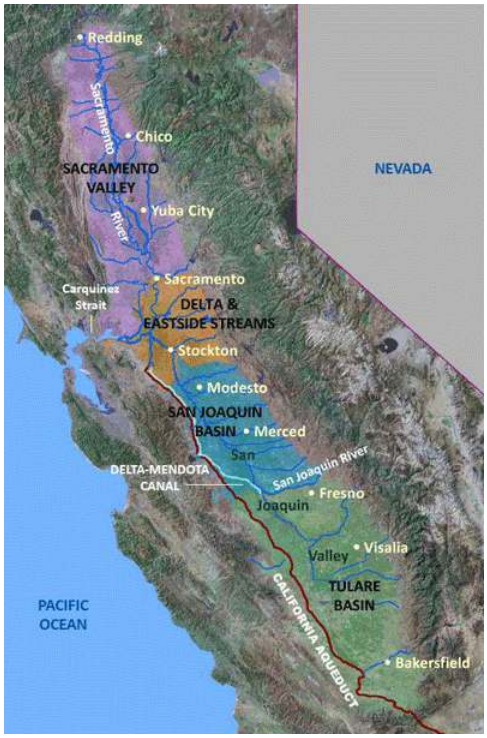



Figure **19.1.*f***: The four regions of California's Central Valley from north to south are the Sacramento Valley, Delta and Eastside Streams, San Joaquin Basin, and Tulare Basin. Image by USGS (public domain).

## Disadvantages of Industrial Agriculture

Economically, the U.S. agricultural sector includes a history of increasingly large federal expenditures. Also observed is a widening disparity among the income of farmers and the escalating concentration of **agribusiness**—industries involved with manufacture,

processing, and distribution of farm products—into fewer and fewer hands. Market competition is limited and farmers have little control over prices of their goods, and they continue to receive a smaller and smaller portion of consumer dollars spent on agricultural products.

Economic pressures have led to a tremendous loss to the number of farms, particularly small farms, and farmers during the past few decades. More than 155,000 farms were lost from 1987 to 1997. Economically, it is very difficult for potential farmers to enter the business today because of the high cost of doing business. Farming equipment is expensive, and the industrial agricultural system favors large corporate farms, which can more easily invest in this equipment. While this equipment promotes efficiency, it also reduces the number of jobs in agriculture (figure **19.1.*g***).

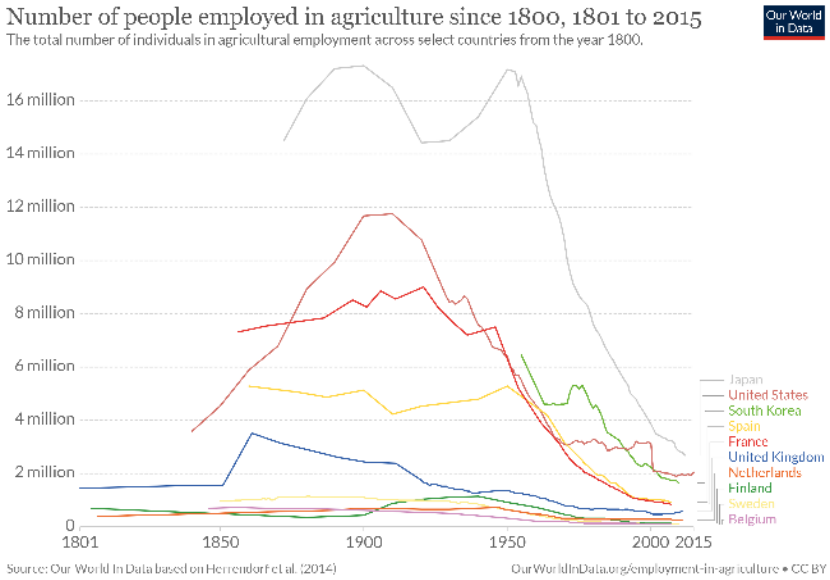



Figure **19.1.*g***: The number of people working in agriculture in selected countries over time (from 1801-2015). Generally, the number of agricultural workers has declined as farming practices increased in efficiency and as farming machinery completed tasks that were once manual. This is both an advantage because people are free to pursue other careers and a disadvantage because of the reduction in jobs. In Japan, the number of agricultural workers peaked above 16 million around 1900 and again around 1960. In the United States, it peaked to nearly 12 million around 1900. France followed a similar pattern, peaking around 1925 at approximately 9 million workers. There were over 6 million agricultural workers in South Korea in 1950, and this has overall declined (although there was a spike around 1980). In Spain the number of workers was over 5 million in 1950 and has since decreased. In the United Kingdom, the number of agricultural workers peaked around 1960 at about 3.5 million. The other countries shown (Netherlands, Finland, Sweden, and Belgium) have consistently had under 1 million agricultural workers. Image by Max Roser/Our World in Data (CC-BY).

The mechanical farming equipment required for industrial agriculture relies on fossil fuels. Burning fossil fuels releases air pollution, including greenhouse gases, which cause climate change. Additionally, the synthetic fertilizers and pesticides used in industrial agriculture are produced from fossil fuels. Furthermore, agriculture areas rarely contain as much biomass (organic matter that comprises living things) as biodiverse, intact ecosystems. Biomass is an important carbon sink because its organic molecules store carbon that could otherwise be in the atmosphere as carbon dioxide or methane, both greenhouse gases. Soils with a substantial organic component are also carbon sinks. Industrial agricultural practices that deplete these soils (see below) contribute to climate change, but alternative practices can promote this benefit of healthy soils (see Sustainable Agriculture).

While synthetic fertilizers provide crops with the necessary nutrients for high productivity, excess nutrients from fertilizers can enter bodies of water through runoff. This can lead to a bloom of algae or photosynthetic bacteria in lakes, rivers, and bays in a process called **eutrophication**. These photosynthetic microorganisms sometimes produce toxins that kill aquatic animals and can even harm the humans who consume these animals. Furthermore, they block aquatic plants from accessing light. Eventual decomposition of algal blooms requires oxygen, which results in **hypoxia** (low levels of dissolved oxygen), further harming aquatic species. Additionally, industrial agriculture pollutes water with pesticides and sediments. Pesticides are not only widespread in surface waters, but pesticides from every chemical class have been detected in groundwater.

Industrial agricultural practices often deplete soil quality. For example, wind and water erosion of exposed topsoil removes particles and nutrients from the soil (which also contributes to eutrophication and sediment pollution). Tilling (mixing the soil) and overgrazing of livestock exacerbates erosion. When livestock remove too much vegetation from an area, plant roots no longer anchor the soil in place, and erosion ensues. Farming equipment compacts the soil. This limits infiltration of water into the soil (decreases soil permeability), makes it more difficult for roots to penetrate the soil, and hinders gas exchange in roots. In extreme cases, soil has eroded and lost its ability to retain water that once arable (farmable) land becomes a desert-like (**desertification**; see Soil Degradation; figure **19.1.*h***).



Figure **19.1.*h***: Overgrazing depleted the soil in the Rukwa Plains of southwestern Tanzania. Image by Lichinga (CC-BY-SA).

Irrigation can lead to **salinization** (increased salinity). While the water itself eventually evaporates, is transpired, or drains from the soil, the minerals dissolved in the water may remain in the soil. Over time, these minerals can accumulate to levels that are toxic for most plants. As discussed in Water Usage, irrigation for agriculture accounts for 69% of global water usage. Withdrawal of sufficient water for irrigation contributes to water shortages and diverts water from ecosystems (see Aqueducts).

Repeated pesticide application exerts selective pressure on insects, fungi, and other crop pests to evolve pesticide resistance. By chance, some individuals in a pest population may carry gene versions that confer pesticide resistance. When these populations are exposed to pesticides, individuals with these gene versions are the most likely to survive and reproduce. They then pass these genes to their offspring, and pesticide resistance becomes more and more common in the population over time (figure **19.1.*i***). At this point, pesticides may need to be applied at greater concentrations or more frequently to achieve the same effect. If pesticide that was initially used is no longer effective at all, the farmer would be forced to find a different pesticide. Over 400 insects and mite pests and more than 70 fungal pathogens have become resistant to one or more pesticides.

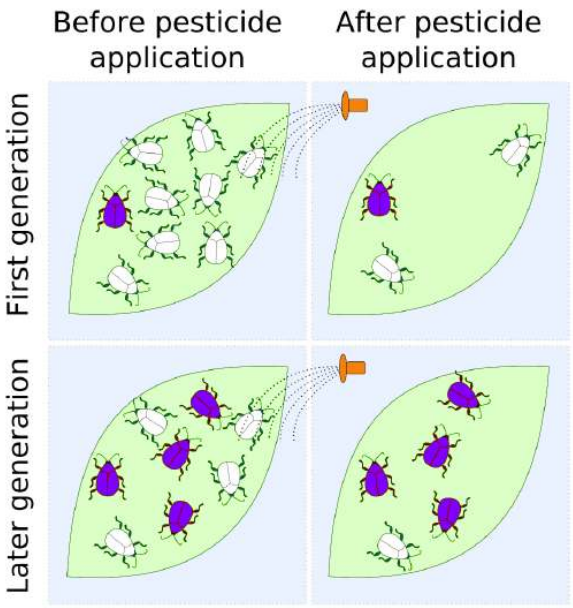



Figure **19.1.*i***: Pesticide application can exert selection for the evolution of pesticide resistance. In this hypothetical example, the purple beetle has a gene version that makes it resistant to pesticides (upper left). Pesticides are applied, killing most of the susceptible individuals (white beetles; upper right). In a later generation, purple, resistant beetles are more common because they had a better chance of surviving and reproducing (lower left). Upon another pesticide application, an even greater proportion of the population is resistant. Image modified from Delldot (CC-BY-SA).

The human health and environmental costs of pesticide use have been unevenly distributed. Despite the fact that the lion's share of chemical pesticides are applied in developed countries, 99 percent of all pesticide poisoning cases occur in developing countries where regulatory, health and education systems are weakest. Many farmers in developing countries overuse pesticides and do not take proper safety precautions because they do not understand the risks and fear smaller harvests. Making matters worse, developing countries seldom have strong regulatory systems for dangerous chemicals; pesticides banned or restricted in industrialized countries are used widely in developing countries. Farmers' perceptions of appropriate pesticide use vary by setting and culture. Prolonged exposure to pesticides has been associated with several chronic and acute health effects like non-Hodgkin's lymphoma, leukemia, as well as cardiopulmonary disorders, neurological and hematological symptoms, and skin diseases.

Pesticides have also placed stresses on pollinators and other beneficial insect species. They can lead to the destruction of natural enemies, which would regulate pest populations in an intact ecosystem. For example, once apple growers began controlling pests with the pesticide dichlorodiphenyltrichloroethane (DDT), which has since been banned, they quickly found their orchards being attacked by scale insects and mites. The reason: DDT had killed off their natural enemies. More generally, pollution from industrial agriculture along with habitat loss due to converting healthy ecosystems into agricultural fields is a major threat to biodiversity. As mentioned previously, monoculture farming limits biodiversity in crops.

With respect to animal agriculture, keeping livestock are kept in close quarters increases the risk of disease spread among them. For these reason, food animals are commonly given antibiotics, either preventatively or to treat existing infections. As discussed in the Infectious Diseases section, the overuse of antibiotics (whether in humans or farm animals) increases selection for the evolution of antibiotic-resistant strains of bacteria or other disease-causing organisms. Infections by antibiotic-resistant strains are more difficult to treat.

As with many industrial practices, potential health hazards are often tied to farming practices. Under research and investigation currently is the sub-therapeutic use of antibiotics in animal production, and pesticide and nitrate contamination of water and food. Farm worker health is also a consideration in all farming practices.

## Attributions

Modified by Melissa Ha from the following sources:

- Conventional Agriculture and Pests and Pesticides from *Environmental Biology* by Matthew R. Fisher (licensed under CC-BY)

- Insecticides from *Biology* by John W. Kimball (licensed under CC-BY)
- Sustainable Agriculture: Definitions and Terms by Mary V. Gold, Alternative Farming Systems Information Center from National Agricultural Library, USDA (public domain)

---

This page titled 19.1: Industrial Agriculture is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **14.2: Industrial Agriculture** by Melissa Ha and Rachel Schleiger is licensed CC BY-SA 4.0.

# 19.2: Sustainable Agriculture

**Sustainable agriculture** is a method of farming that does not deplete natural resources or degrade the environment and can therefore be continued indefinitely. Sustainable farms often rely on components of local ecosystems. For example, they might promote conditions for natural decomposition of wastes or employ natural enemies to control pests through predation or competition. More specifically, the 1977 and 1990 “Farm Bills” describe sustainable agriculture as "an integrated system of plant and animal production practices having a site-specific application that will, over the long term:

- satisfy human food and fiber needs;
- enhance environmental quality and the natural resource base upon which the agricultural economy depends;
- make the most efficient use of nonrenewable resources and on-farm resources and integrate, where appropriate, natural biological cycles and controls;
- sustain the economic viability of farm operations;
- enhance the quality of life for farmers and society as a whole."

Promoting biodiversity is key to sustainable agriculture, and high biodiversity results intact ecosystem services such as nutrient cycling and regulation of pest populations. This is consistent with the goal of sustainable agriculture: to mimic the processes found in natural ecosystems. In contrast to the monocultures of industrial agriculture, **polyculture** farming (growing different species together) is a common practice in sustainable agriculture. This assists with regulating pests and maintaining soil fertility (see below). **Seed banks**, locations at which many different types of seeds are stored, are key to conserving the genetic diversity of crops. These storage sites are cold enough to keep seeds frozen naturally (figure **19.2.*a***).



Figure **19.2.*a***: The Svalbard Global Seed Vault in Norway. Image by Miksu (CC-BY-SA).

## Integrated Pest Management

**Integrated Pest Management** (IPM) refers to a mix of farmer-driven, ecologically-based pest control practices that seek to reduce reliance on synthetic chemical pesticides. It uses several methods simultaneously to control pest populations. The steps of integrated pest management are to (1) identify true pests, (2) set thresholds and monitor (figure **19.2.*b***), and (3) develop an action plan. As many insects, microbes, and other organisms found in an agricultural area have a neutral or beneficial effect, it is not necessary to remove them. True pests are those that are causing economic harm, and they are managed (kept below economically damaging levels) rather than eradicated.



Figure 19.2.*b*: A retired Navy commander and landowner inspect an insect trap as part of an Integrated Pest Management (IPM) conservation practice. Image by NRCS (public domain).

An IPM Action Plan draws on four types of control: cultural, mechanical, biological, and chemical. These methods are listed in order of least to most environmental impact and are thus applied in this order. For example, cultural control is attempted first. If that is not effective, mechanical control is added to the plan, and so on. Chemical control is used as a last resort and is deemphasized in an IPM plan. When pesticides must be used, they are selected and applied in a way that minimizes adverse effects on beneficial organisms, humans, and the environment. It is commonly understood that applying an IPM approach does not necessarily mean eliminating pesticide use, although this is often the case because pesticides are often over-used for a variety of reasons.

### An Alternative to Spraying: Bollworm Control in Shandong

Farmers in Shandong (China) have been using innovative methods to control bollworm infestation in cotton when this insect became resistant to most pesticides. Among the control measures implemented were:

1. The use of pest resistant cultivars and interplanting of cotton with wheat or maize.
2. Use of lamps and poplar twigs to trap and kill adults to lessen the number of adults.
3. If pesticides were used, they were applied on parts of the cotton plant's stem rather than by spraying the whole field (to protect natural enemies of the bollworm).

These and some additional biological control tools have been effective in controlling insect populations and insect resistance, protecting surroundings and lowering costs.

## Cultural Control

**Cultural control** refers to minimizing the conditions that allow pests to thrive and spread. Examples include alternating which crops are planted each year (**crop rotation**), planting multiple types of crops near each other (**intercropping**; figure 19.2.*c*), selecting pest-resistant varieties, and planting pest-free rootstock (underground plant parts). Crop rotation prevents pests that are specialized to a particular type of crop from continuing year after year because their host plants are only available in certain years. Similarly, intercropping spatially limits the spread of pests. **Strip cropping** is a type of intercropping that involves growing different types of crops in alternating rows. Pests may infest one (or several) rows of their host species, but they would have to move past multiple rows of non-hosts to access additional host plants. Additionally, cultural control can involve optimizing irrigation and fertilizer application to promote plant defense and limit disease spread. Cultural control methods can be very effective and cost-efficient and present little to no risk to people or the environment.



Figure 19.2.*c*: *Momordica charantia* (bitter melon) intercropped with rice in the Philippines (cultural control). Bitter melon plants emerge from holes in plastic, which is used for mechanical control of weeds. Image by Judgefloro (CC-BY-SA).

## Mechanical Control

**Mechanical control** refers to physically removing pests or excluding them with barriers (figure 19.2.*d*). Mechanical controls that remove pests include sticky insect traps, mole traps, and removing weeds by hand. Netting to exclude birds, deer fencing, and weed cloth, plastic weed barriers (figure 19.2.*c*) or mulch are additional examples of mechanical control.



Figure 19.2.*d*: This solar insect trap is an example of mechanical control. It emits ultraviolet light to attract insects and is recharged using small solar panels. Image by MGK Solar Trap (CC-BY-SA).

## Biological Control

**Biological control** is the use of organisms to reduce pest populations (also see Invasive Species). One biological control strategy involves releasing natural enemies, such as predators, parasites, or parasitoids of the pest organisms (parasitoids are similar to parasites, but they consistently kill their hosts). Home gardeners can also rely on natural enemies by purchasing preying mantises, ladybugs (ladybird beetles), or lacewings for release (figure 19.2.*e*). Successful examples include ladybird beetles to depress aphid populations, parasitoid wasps to control whiteflies, and fungi, such as *Trichoderma*, to suppress fungal-caused plant diseases.



Figure **19.2.*e***: Lacewings are natural predators of garden and crop pests. Image by artsehn/Pixabay (Pixabay license).

If not used carefully, chemical control can have unintended negative consequences for biological control. In 1887, the cottony cushion scale (native to Australia) was devastating the citrus groves of California. A U.S. entomologist went to Australia to find a natural enemy and came back with the **vedalia beetle**, a species of ladybird beetle. Released in California, the beetle quickly brought the scale under control, at least until 1946. In that year, the pest made a dramatic comeback. This coincided with the first use of the now-banned pesticide dichlorodiphenyltrichloroethane (DDT) in the groves. Not only did DDT kill the target pest insects, but it killed the vedalia beetle as well. Only by altering spray procedures and reintroducing the beetle was the scale insect again controlled.

Another strategy for biological control involves releasing sterile males, which compete with fertile males for mates, ultimately decreasing pest population size. This technique was first applied against the screwworm fly, a serious pest of cattle (figure **19.2.*f***). The female flies lay their eggs in sores or other open wounds on the animals. After hatching, the larvae eat the tissues of their host. As they do so, they expose a still larger area to egg laying, often finally killing the host.



Figure **19.2.*f***: Thought to be eradicated in the United States by 1966, the screwworm fly, a cattle pest, reemerged in deer at Key Deer National Refuge in Florida in 2016. Sterile males were again released, and the pest was eradicated from Florida in 2017. Image by Judy Gallagher (CC-BY).

Prior to its eradication from the southeastern United States, the screwworm was causing huge annual livestock losses. The sterile male technique involves releasing factory-reared and sterilized flies into the natural population. Sterilization is done by exposing the factory flies to just enough gamma radiation to make them sterile but not enough to reduce their general vigor.

Starting in early 1958, up to 50 million sterilized flies were released each week from aircraft flying over Florida and parts of the adjoining states. Each time a fertile female in the natural population mated with a sterile male, the female layed sterile eggs. Since the females mate only once, her reproductive career was at an end. By early 1959, the pest was totally eliminated east of the Mississippi River. The problem in southwestern states was more challenging because the fly winters in Mexico and could move across the border with each new season. Even so, by expanding the program to include Mexico as well, the screwworm fly was finally eliminated from Mexico in 1991.

The sterile male technique also successfully controlled the Mediterranean fruit fly ("medfly"), a destructive fruit fly of citrus, peaches, pears, and apples in California.

### Chemical Control

**Chemical control** refers to the use of pesticides. If chemical control is needed, IPM favors highly targeted chemicals, such as pheromones to disrupt pest mating. **Pheromones** are chemical signals released by animals to communicate with other members of their species. Humans and many insect species alike release pheromones that function in attracting mates. Releasing the pheremones of insect pests can confuse males seeking mates and ultimately hinder them from reproducing (figure **19.2.*g***). This "male confusion" has been successful against the pink bollworm that infests cotton and reduced the need for conventional chemical insecticides by 90%. Pheromones have also been successful against pests that attack tomatoes, grapes, and peaches. If targeted chemicals are not effective, IPM may employ conventional pesticides, ideally only applying them to the spots that they are needed and at the lowest effective concentration. Broadcast spraying of non-specific pesticides is a last resort.



Figure **19.2.*g***: This pheromone trap is used to control the Asiatic rice borer. The caterpillars of this moth species infest rice stems. Image by Mehdi (CC-BY-SA).

## Sustainable Practices to Maintain Soil Fertility

A variety of sustainable practices can maintain soil quality. Many of these strategies have additional benefits such as regulating pests, limiting climate change, and preventing water pollution. These methods enrich the soil with nutrients, ensure proper water holding capacity (ability of the soil to retain water), and limit soil-degrading processes such as erosion and compaction.

### Crop Rotation

As previously mentioned, **crop rotations** are planned sequences of different crops over time on the same field (figure **19.2.*h***). Rotating crops provides productivity benefits by improving soil nutrient levels and breaking crop pest cycles. Farmers may also choose to rotate crops in order to reduce their production risk through diversification or to manage scarce resources, such as labor, during planting and harvesting. This strategy reduces the pesticide costs by naturally breaking the cycle of weeds, insects and diseases. Also, grass and legumes in a rotation protect water quality by preventing excess nutrients or chemicals from entering water supplies.



Figure 19.2.*h*: Crop rotation can be used at a large agricultural scale (left) or in a smaller garden (right). In each situation, which crop species are planted in each location changes year to year. Left image by USDA (public domain) and right image by Sten Porse (CC-BY-SA).

## Intercropping

**Intercropping** means growing two or more crops in close proximity to each other during part or all of their life cycles to promote soil improvement, biodiversity, and pest management. Incorporating intercropping principles into an agricultural operation increases diversity and interaction between plants, arthropods, mammals, birds and microorganisms resulting in a more stable crop-ecosystem and a more efficient use of space, water, sunlight, and nutrients (figure 19.2.*i*). This collaborative type of crop management mimics nature and is subject to fewer pest outbreaks, improved nutrient cycling and crop nutrient uptake, and increased water infiltration and moisture retention. Soil quality, water quality and wildlife habitat all benefit.



Figure 19.2.*i*: Intercropping of beans and maize (corn). Beans have root nodules that house nitrogen-fixing bacteria, enriching the soil. Image by AnnaJB (CC-BY-SA).

A common example of strip cropping (a type of intercropping; see above) involves alternating a row crop such as corn with a ground-covering crop such as alfalfa. The ground-covering crop helps reduce water runoff and traps soil eroded from the row crop. If this ground-covering crop is a member of the legume family such as alfalfa or soybeans and is associated with nitrogen-fixing bacteria, then alternating the strips from one planting to the next can also help maintain topsoil fertility.

### Cover Crops

**Cover crops** are those that are planted in the off-season to avoid leaving the soil bare. They can prevent soil and wind erosion, improve soil's physical and biological properties, supply nutrients, suppress weeds, improve the availability of soil water, and break pest cycles along with various other benefits. Cover crops are often members of the legume family and help enrich the soil with usable nitrogen. A single species or mix of cover crop species may be planted (figure **19.2.*j***).



Figure **19.2.*j***: A roller (crimper) on a tractor being used to roll down a rye and hairy vetch cover crop in April in the United States. While hairy vetch can limit soil erosion and add nitrogen to the soil, it is also an invasive species that must be carefully managed. Image and caption (modified) from Mr. 1032 (CC-BY-SA).

### Agroforestry

**Agroforestry** is the process of planting rows of trees interspersed with a cash crop (figure **19.2.*k* – *l***). Besides helping to prevent wind and water erosion of the soil, the trees provide shade which helps promote soil moisture retention. Decaying tree litter also provides some nutrients for the interplanted crops. The trees themselves may provide a cash crop. For example, fruit or nut trees may be planted with a grain crop. You can learn more about agroforestry using this interactive site by the United States Department of Agriculture and Forest Service.



Figure 19.2.*k*: Through agroforestry, high-value non-timber crops (food, medicinal plants, woody florals, and crafts) can be cultivated under the protection of a forest canopy that has been managed to provide a favorable crop environment. Image and caption (modified) from USDA/UFS (public domain).

## Contour and Terrace Farming

**Contour farming** involves plowing and planting crop rows along the natural contours of gently sloping land (figure 19.2.*l*). The lines of crop rows perpendicular to the slope help to slow water runoff, inhibit the formation of channels of water, and limit soil erosion (and the resultant loss of nutrients). **Terracing** is a common technique used to control water erosion on more steeply sloped hills and mountains (figure 19.2.*l*). Broad, level terraces are constructed along the contours of the slopes, and these act as dams trapping water for crops, reducing runoff, and limiting erosion.



Figure 19.2.*l*: Contour farming (left) and terracing (right). In contour farming, rows of crops wave perpendicular to the slopes of the land. This example (left) also employs agroforestry. Terrace farming involves making step-like structures (terraces) perpendicular to the incline of a slope to reduce erosion. Left image by Pixture2016 (CC-BY-SA). Right image by USDA (public domain).

## Minimal Tillage and No-till Agriculture

In modern agricultural practices, heavy machinery is used to prepare the seedbed for planting, to control weeds, and to harvest the crop. The use of heavy equipment has many advantages in saving time and labor, but can cause compaction of soil and disruption of the natural soil organisms. The problem with soil compaction is that increased soil density limits root penetration depth and may inhibit proper plant growth. Another aspect of soil tillage (mixing the soil) is that it may lead to more rapid decomposition of organic matter due to greater soil aeration. Over large areas of farmland, this has the unintended consequence of releasing more carbon and nitrous oxides (greenhouse gases) into the atmosphere, thereby contributing to climate change.

One of the easiest ways to prevent these problems is to minimize the amount of **tillage**, or turning over of the soil. In **minimal tillage** (conservation tillage) or **no-till agriculture**, the land is disturbed as little as possible by leaving crop residue in the fields (figure 19.2.*m*). Special seed drills inject new seeds and fertilizer into the unplowed soil. Tillage of fields does help to break up clods that were previously compacted, so best practices may vary at sites with different soil textures and composition. With proper planning, minimal tillage and no-till agriculture can simultaneously limit soil erosion and compaction, protect soil organisms, reduce costs (if performed correctly), and promote water infiltration. Furthermore, carbon can actually become sequestered into the soil with these methods, thus mitigating climate change. Minimal or no-till agriculture have proved a major success in Latin America and are being used in South Asia and Africa. However, a drawback of this method is that the crop residue can serve as a good habitat for insect pests and plant diseases.



Figure 19.2.*m*: No-till agriculture is an important tool to prevent loss of soil moisture. Image by USDA (public domain).

### Windbreaks

Creating **windbreaks** by planting tall trees along the perimeter of farm fields can help control the effects of wind erosion of soil (figure 19.2.*n*). Windbreaks reduce wind speed at ground level, an important factor in wind erosion. They also help trap snow in the winter months, leaving soil less exposed. As a side benefit, windbreaks also provide a habitat for birds and animals. One drawback is that windbreaks can be costly to farmers because they reduce the amount of available cropland.



Figure 19.2.*n*: Windbreaks are rows of trees and shrubs that reduce wind speed. They improve crop yields, reduce soil erosion, improve water-efficiency, protect livestock, and conserve energy. Image and caption (modified) from USDA/UFS (public domain).

## Organic Agriculture

**Organic agriculture** is often incorporated into sustainable agriculture (figure 19.2.*o*). To be certified as organic, farms must avoid using synthetic pesticides, synthetic fertilizers, and genetically modified organisms (figure 19.2.*p*). Organic meat, poultry, eggs, and dairy products come from animals that are given no antibiotics or growth hormones. Pests may instead be controlled by natural enemies or naturally produced substances such as neem oil or diatomaceous earth. Some organic alternatives to synthetic pesticides have relatively low environmental impact (such as salt spray), but there are many naturally produced compounds that are still toxic to people or cause ecological harm when widely used. Interestingly, external application of Bt toxin is approved for organic farming, but use of genetically engineered Bt crops is not. The latter results in lower concentrations of Bt toxin in the environment because it is locally produced directly by the plants themselves. In summary, although many practices of organic agriculture benefit the environment and meet sustainability goals, some organic farms are not sustainable and some sustainable farms are not organic.




Figure **19.2.*o***: United States Department of Agriculture (USDA) Conservationist Shemekia Mosley (right) works with Nuri Icgoren (left) who operates Urban Sprout Farms, a biodynamic, certified organic urban farm Lakewood Heights, Georgia. Image and caption (modified) by Preston Keres/USDA (public domain).




Figure **19.2.*p***: The USDA certified organic label. Modified from image by nikoretro (CC-BY-SA).

## Consumer Choices that Support Sustainable Agriculture

Even if you're not a farmer or lawmaker, you have the power to promote sustainable agriculture as a consumer. As discussed in Food Chains and Food Webs, it generally requires more land and more energy to produce meat compared to plant-based foods due to the inefficient transfer of energy from one trophic level to the next. For this reason, plant-based diets tend to be more sustainable, but this depends on the types of foods consumed and how they were produced.

**Local food** is not only fresher, but it requires fewer food miles (figure **19.2.*q***). In some ways, **organic food** causes less environmental degradation, but note that organic does not necessarily mean sustainable (see above). Because it limits machinery, synthetic pesticides, and synthetic fertilizers, it has a smaller **carbon footprint** (meaning it minimizes contribution to climate change). The Clean 15 is a list of produce that is low in pesticide residues. If you can't afford all organic foods, these are the best items to purchase non-organic. Examples include avocados, sweet corn, and pineapple. The Dirty Dozen lists produce that has the most pesticide residues. If you can only afford a few organic items, these are best to purchase organic. Examples include strawberries, spinach, and nectarines. Finally, some foods, such as beef, have higher **carbon footprint** and **water footprint** than others.



Figure **19.2.*q***: Farmers' markets are one option for purchasing locally grown foods. Image by NatalieMaynor (CC-BY).

## The Future of the Sustainable Agriculture Concept

Many in the agricultural community have adopted the sense of urgency and direction pointed to by the sustainable agriculture concept (figure **19.2.*r***). Sustainability has become an integral component of many government, commercial, and non-profit agriculture research efforts, and it is beginning to be woven into agricultural policy. Increasing numbers of farmers and ranchers have embarked on their own paths to sustainability, incorporating integrated and innovative approaches into their own enterprises.

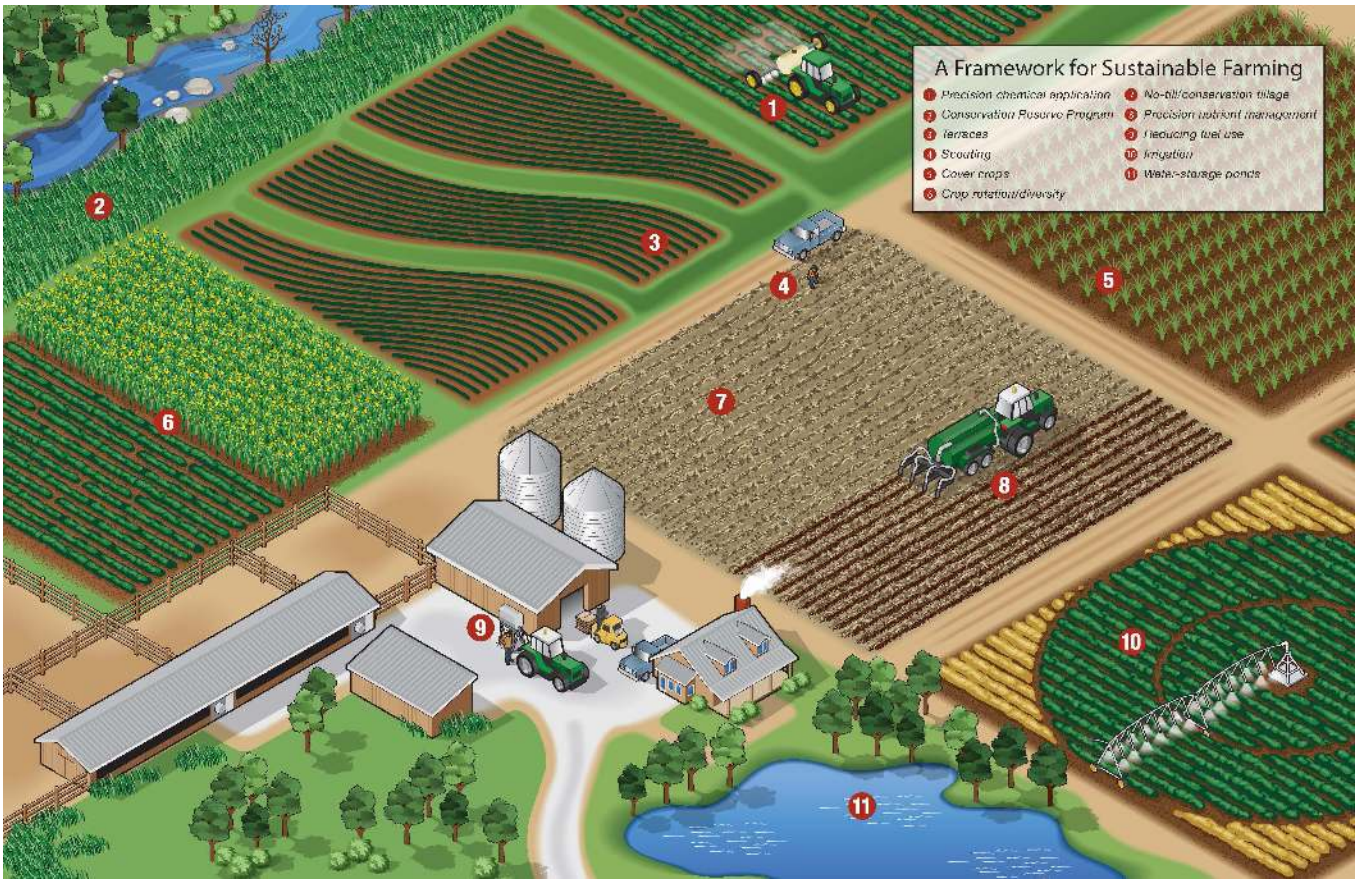



Figure 19.2.7: Sustainable agriculture combines many approaches. (1) If chemical are used, they are applied only where needed. (2) Through the Conservation Reserve Program, the most ecologically important patches are left intact. (3) Terraces on slopes reduce soil erosion. (4) Crops are scouted for pests as part of monitoring, a component of integrated pest management. (5) Cover crops prevent erosion and enrich the soil during off-seasons. (6) Different types of crops are included are planted in close proximity (intercropping) or in different years (crop rotation). (7) Land is either not tilled at all or tilled minimally (conservation tillage). (8) Through precision nutrient management, soil is sampled at different locations, and fertilizer is only applied where needed. (9) Heavy equipment is used only as needed and in such a way that conserves fuel. (10) Irrigation is precisely timed to conserve water. (11) Water storage ponds help recharge groundwater. Image by the United Soybean Board (CC-BY).

## Attributions

Modified by Melissa Ha from the following sources:

- Sustainable Agriculture from *Environmental Biology* by Matthew R. Fisher (licensed under CC-BY)
- Soils from *AP Environmental Science* by University of California College Prep, University of California (licensed under CC-BY). Download for free at CNX.
- Sustainability Definitions. USDA. Accessed 01-05-2021. (public domain)
- Biological Control from *Biology* by John W. Kimball (licensed under CC-BY)
- Integrated Pest Management (IPM) Principles. EPA. Accessed 01-05-2021 (public domain)
- Cover Crops and Soil Health. Natural Resources Conservation Service, USDA. Accessed 01-06-2021. (public domain)

This page titled 19.2: Sustainable Agriculture is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **14.4: Sustainable Agriculture** by Melissa Ha and Rachel Schleiger is licensed CC BY-SA 4.0.

# CHAPTER OVERVIEW

## 20: Climate change and plants


20.1: Earth's Energy Budget

20.2: The Greenhouse Effect

20.3: Climate and the Effects of Global Climate Change

20.4: Soil and Water Conservation


---

This page titled 20: Climate change and plants is shared under a not declared license and was authored, remixed, and/or curated by Tom Buckley.

# 20.1: Earth's Energy Budget

To understand the global climate of Earth, it is important to understand the energy budget of the Earth, which drives the overall climate of the globe. The biodiversity section discusses how the sun's energy is unevenly distributed across the Earth's surface (which leads to the distribution of biomes and the pattern of the seasons); however, here we will consider the totality of energy the Earth receives from the sun across its entire surface (Fig 3.1.1). The majority of energy received from the sun (70%) is absorbed by the Earth's surface or atmosphere while the rest (30%) is reflected directly back out to space. The Earth's surface radiates a large amount of energy back up to the atmosphere (this value includes both the energy absorbed from the sun and the energy reabsorbed by the Earth's surface from the atmosphere), some of which is radiated back out to space, and much of which is retained in the atmosphere and reabsorbed by the Earth's surface.

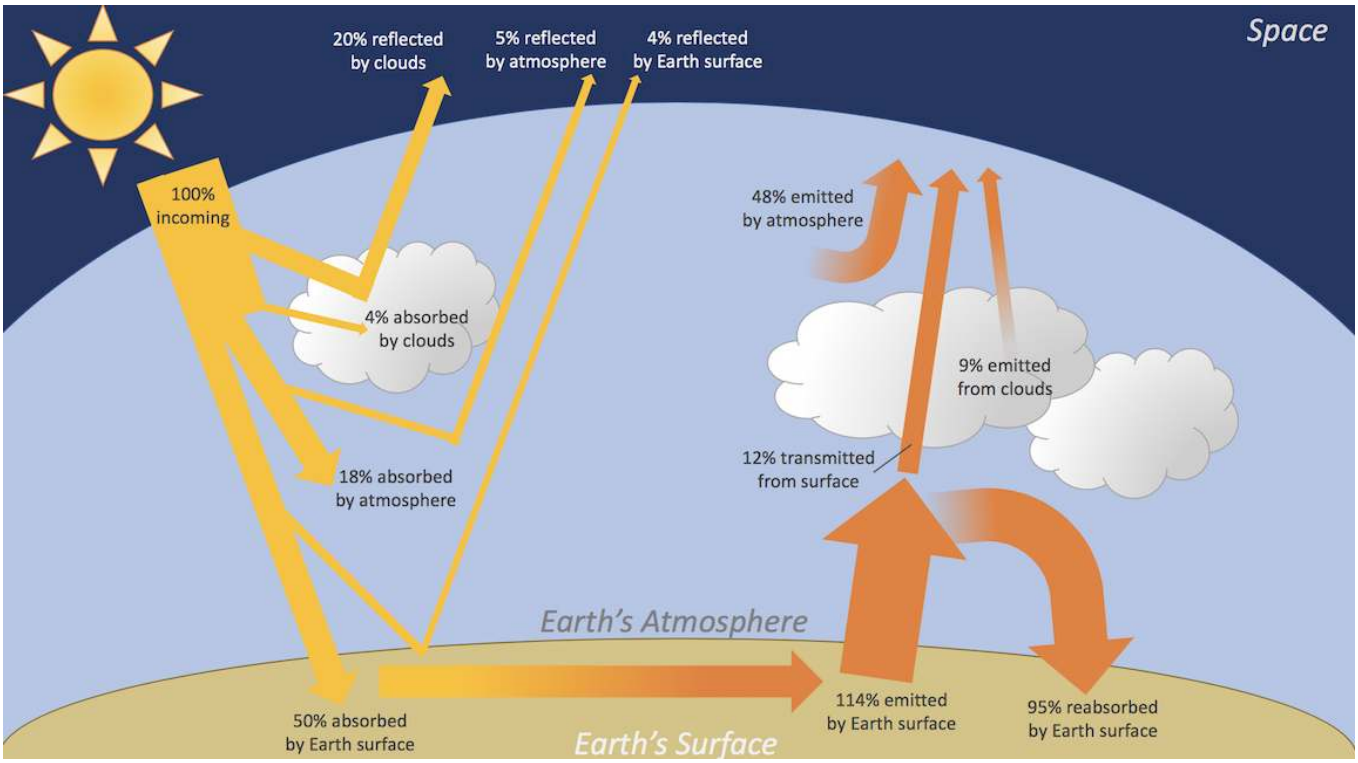



Figure by L Gerhart-Barley

This page titled 20.1: Earth's Energy Budget is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **3.1: Earth's Energy Budget** by Laci M. Gerhart-Barley is licensed CC BY-SA 4.0.

# 20.2: The Greenhouse Effect

The process by which the atmosphere absorbs the sun's energy and prevents it from being radiated back out to space has often been compared to that of a greenhouse, leading to the nickname the **greenhouse effect**. It is the same process that occurs when you leave your car sitting in the sun with the windows rolled up. The sun's rays are powerful enough to pass through the glass of the windows (or through the Earth's atmosphere) and be absorbed by the dashboard and seats (or the Earth's surface); however, when these surfaces emit energy, it is not powerful enough to pass back out through the window glass (or atmosphere) and in so doing becomes trapped within the car (or atmosphere) causing it to warm. There are certain atmospheric gases, termed **greenhouses gases (or GHGs)** that behave like the car windows, increasing the amount of energy retained in the atmosphere, and increasing the amount of warming that occurs. In Figure 3.1.1 the greenhouse effect is represented by the curved arrow showing 95% of the energy emitted by the Earth's surface that is reabsorbed, and the amount of GHGs in the atmosphere drive the size of this arrow.

The primary GHGs considered in this section are carbon dioxide ($CO_2$), methane ($CH_3$), and nitrous oxide ($N_2O$). Scientists at the National Oceanic and Atmospheric Administration (NOAA) have been tracking concentrations of these and other GHGs in the atmosphere for decades (Fig 3.2.1) and have found that all three continue to steadily increase.

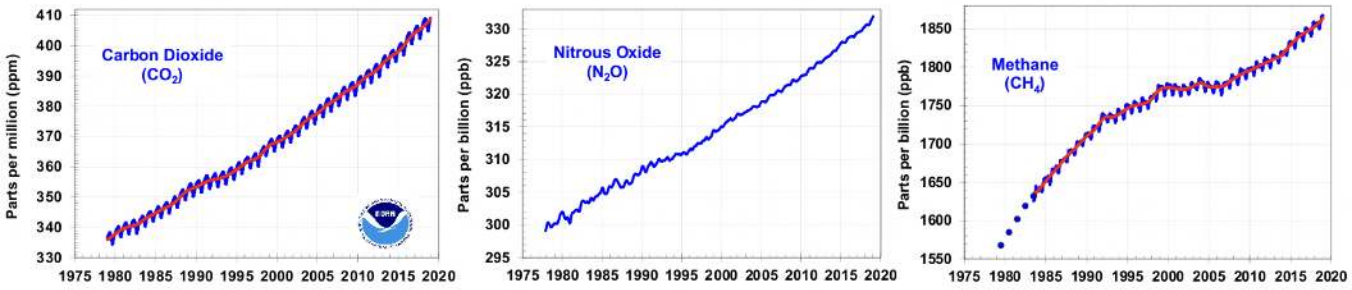



Figure **20.2.1**: Global average concentrations of greenhouse gases carbon dioxide ($CO_2$), nitrous oxide ($N_2O$), and methane ($CH_3$) in the atmosphere since 1978. Image from NOAA[1].

These increases are particularly pronounced when compared to past GHG concentrations. Scientists can measure past atmospheric composition in ice sheets in Greenland and Antarctica. As the ice sheets formed, small bubbles of air were trapped in the ice, and coring deep into the ice sheet (Fig 3.2.2a) allows scientists to reconstruct atmospheric composition from direct measurements as far back as 800,000 years (Fig 3.2.2b). From these measurements, we can see that atmospheric $CO_2$ levels (and temperature, as estimated from oxygen isotope composition of the ice itself) have fluctuated significantly throughout the past. The ice sheets document a clear pattern of periodic increases and decreases in $CO_2$, which are coupled with increases and decreases in temperature. Periods of low $CO_2$ and low temperatures are glacial periods (also referred to as 'ice ages'), and periods of high $CO_2$ and high temperature are inter-glacial periods. For the past 800,000 years, Earth has oscillated between glacial and inter-glacial periods roughly every 100,000 years. The maximum level that $CO_2$ concentrations reached in the last 800,000 years was approximately 300 parts per million (ppm). Global $CO_2$ levels are now over 400 ppm, a level that scientists estimate has not occurred on Earth since the Pliocene Epoch, approximately 3 million years ago.

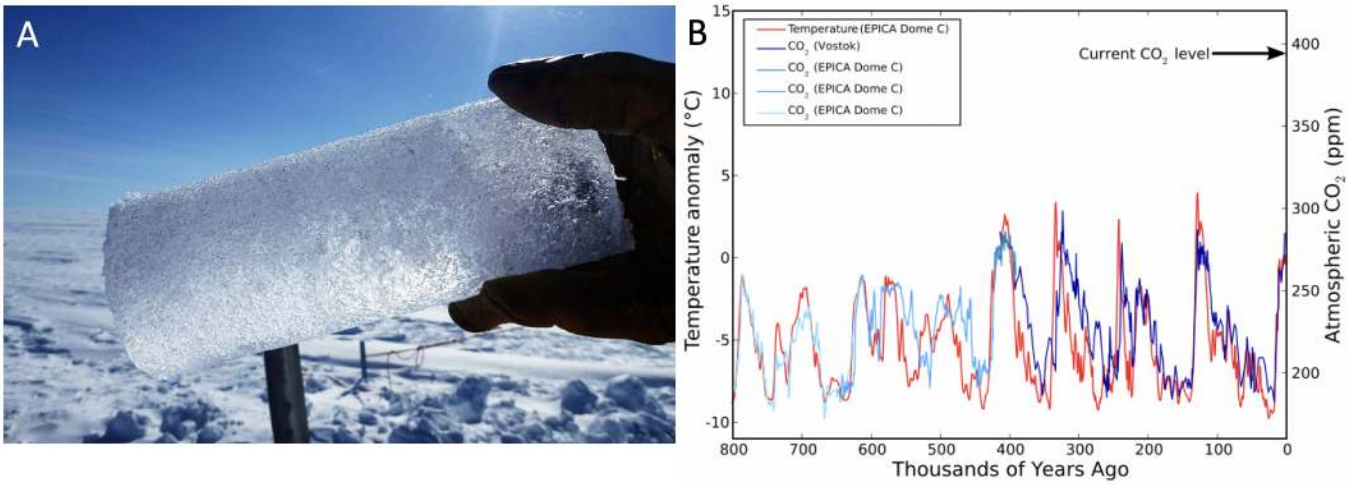



Figure **20.2.2**: A) a section of ice core taken from the Greenland ice sheet and B) carbon dioxide concentration (blue) and temperature reconstruction (red) composites from EPICA Dome C ice cores (light blue and teal) in Greenland and Vostok ice cores (dark blue) in Antarctica. Global $CO_2$ *level as of 2006 is marked with the 'Current* $CO_2$ *level' arrow. Images from Wikimedia Commons*[2,3].

This increase in $CO_2$ (as well as other GHGs) increases the amount of solar energy that is retained in the atmosphere as opposed to radiated back out to space, which increases the temperature of the Earth's surface. Figure 3.2.3 shows the temperature anomaly for the decade 2014-2018 as compared to the average from 1951-1980. The National Aeronautics and Space Administration (NASA) reports that the global average temperature has increased approximately 1.4° Fahrenheit (0.8° C) since 1880, though that warming has not been evenly distributed across the Earth. As can be seen in Figure 3.2.3, the polar regions, particularly the Arctic, have warmed much more than other areas. This pattern is particularly concerning given the feedbacks that warming in polar regions may have on the melting of ice sheets and sea ice.

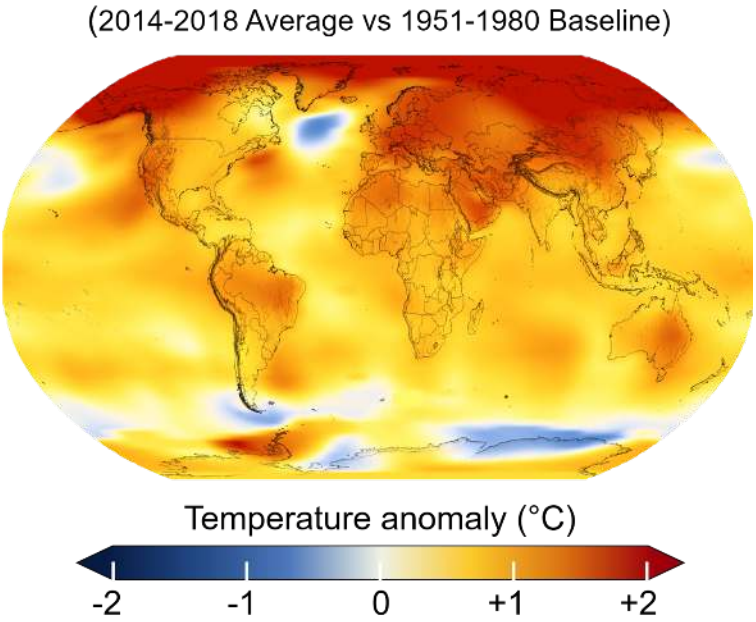



Figure **20.2.3**: *temperature anomaly for 2014-2018, compared to the average temperatures from 1951-1980. Image from Wikimedia Commons*[4].

In 2018, the state of California released its Fourth Climate Change Assessment report, which outlines the impact that global climatic changes are having and will have on the state (Fig 3.2.4). Some regions, most notably southern California, have already experienced nearly 3°F increases in annual average temperatures since the beginning of the 20th century.

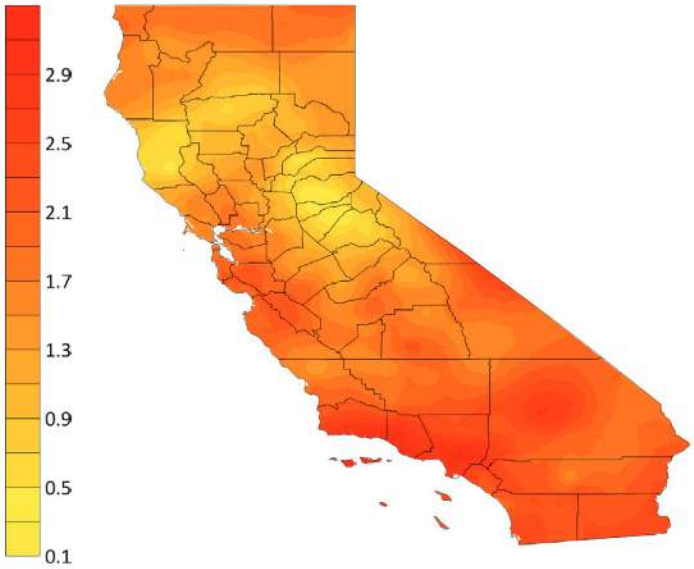



Figure 20.2.4 Observed changes in annual temperature across the state of California. Color bar represents the difference between the recent annual average temperature (1986-2016) and the annual average from 1901-1960 in degrees Fahrenheit. Positive values indicate recent averages are warmer than historical averages with higher values (darker red regions) experiencing more warming than lower values (yellow regions)

## Image Credits

1.
2.
3.
4.

---

This page titled 20.2: The Greenhouse Effect is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **3.2: The Greenhouse Effect** by Laci M. Gerhart-Barley is licensed CC BY-SA 4.0.

# 20.3: Climate and the Effects of Global Climate Change

**Skills to Develop**

- Define global climate change
- Summarize the effects of the Industrial Revolution on global atmospheric carbon dioxide concentration
- Describe three natural factors affecting long-term global climate
- List two or more greenhouse gases and describe their role in the greenhouse effect

All biomes are universally affected by global conditions, such as climate, that ultimately shape each biome's environment. Scientists who study climate have noted a series of marked changes that have gradually become increasingly evident during the last sixty years. Global climate change is the term used to describe altered global weather patterns, including a worldwide increase in temperature, due largely to rising levels of atmospheric carbon dioxide.

## Climate and Weather

A common misconception about global climate change is that a specific weather event occurring in a particular region (for example, a very cool week in June in central Indiana) is evidence of global climate change. However, a cold week in June is a weather-related event and not a climate-related one. These misconceptions often arise because of confusion over the terms climate and weather.

Climate refers to the long-term, predictable atmospheric conditions of a specific area. The climate of a biome is characterized by having consistent temperature and annual rainfall ranges. Climate does not address the amount of rain that fell on one particular day in a biome or the colder-than-average temperatures that occurred on one day. In contrast, weather refers to the conditions of the atmosphere during a short period of time. Weather forecasts are usually made for 48-hour cycles. Long-range weather forecasts are available but can be unreliable.

To better understand the difference between climate and weather, imagine that you are planning an outdoor event in northern Wisconsin. You would be thinking about *climate* when you plan the event in the summer rather than the winter because you have long-term knowledge that any given Saturday in the months of May to August would be a better choice for an outdoor event in Wisconsin than any given Saturday in January. However, you cannot determine the specific day that the event should be held on because it is difficult to accurately predict the weather on a specific day. Climate can be considered "average" weather.

## Global Climate Change

Climate change can be understood by approaching three areas of study:

- current and past global climate change
- causes of past and present-day global climate change
- ancient and current results of climate change

It is helpful to keep these three different aspects of climate change clearly separated when consuming media reports about global climate change. It is common for reports and discussions about global climate change to confuse the data showing that Earth's climate is changing with the factors that drive this climate change.

### Evidence for Global Climate Change

Since scientists cannot go back in time to directly measure climatic variables, such as average temperature and precipitation, they must instead indirectly measure temperature. To do this, scientists rely on historical evidence of Earth's past climate.

Antarctic ice cores are a key example of such evidence. These ice cores are samples of polar ice obtained by means of drills that reach thousands of meters into ice sheets or high mountain glaciers. Viewing the ice cores is like traveling backwards through time; the deeper the sample, the earlier the time period. Trapped within the ice are bubbles of air and other biological evidence that can reveal temperature and carbon dioxide data. Antarctic ice cores have been collected and analyzed to indirectly estimate the temperature of the Earth over the past 400,000 years (Figure **20.3.1**a). The 0 °C on this graph refers to the long-term average. Temperatures that are greater than 0 °C exceed Earth's long-term average temperature. Conversely, temperatures that are less than 0

°C are less than Earth's average temperature. This figure shows that there have been periodic cycles of increasing and decreasing temperature.

Before the late 1800s, the Earth has been as much as 9 °C cooler and about 3 °C warmer. Note that the graph in Figure **20.3.1**b shows that the atmospheric concentration of carbon dioxide has also risen and fallen in periodic cycles; note the relationship between carbon dioxide concentration and temperature. Figure **20.3.1**b shows that carbon dioxide levels in the atmosphere have historically cycled between 180 and 300 parts per million (ppm) by volume.

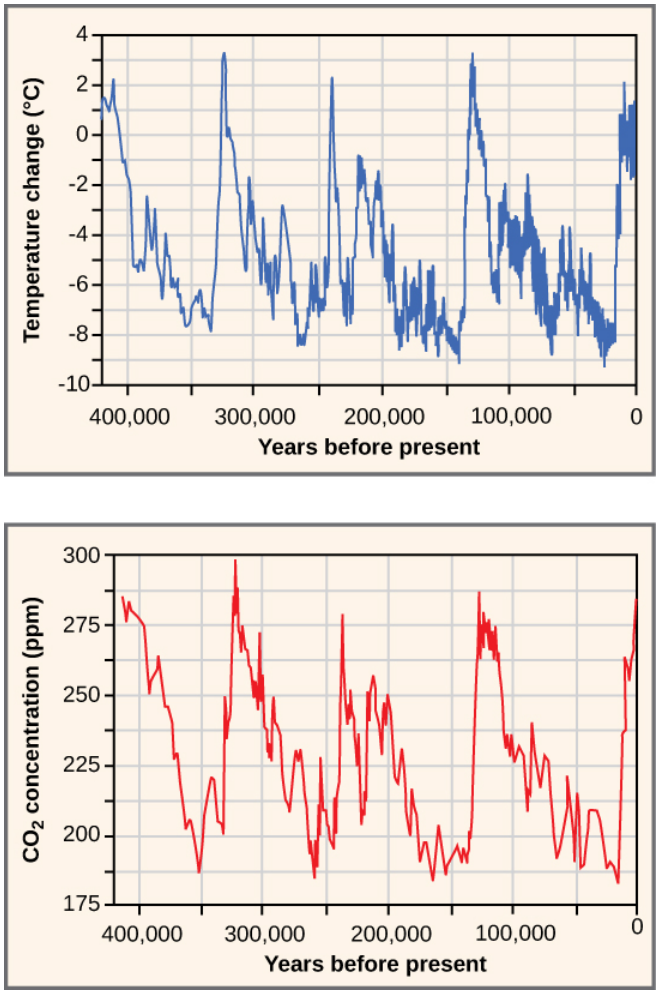



Figure **20.3.1:** Ice at the Russian Vostok station in East Antarctica was laid down over the course of 420,000 years and reached a depth of over 3,000 m. By measuring the amount of $CO_2$ trapped in the ice, scientists have determined past atmospheric $CO_2$ concentrations. Temperatures relative to modern day were determined from the amount of deuterium (an isotope of hydrogen) present.

Figure **20.3.1**a does not show the last 2,000 years with enough detail to compare the changes of Earth's temperature during the last 400,000 years with the temperature change that has occurred in the more recent past. Two significant temperature anomalies, or irregularities, have occurred in the last 2000 years. These are the Medieval Climate Anomaly (or the Medieval Warm Period) and the Little Ice Age. A third temperature anomaly aligns with the Industrial Era. The Medieval Climate Anomaly occurred between 900 and 1300 AD. During this time period, many climate scientists think that slightly warmer weather conditions prevailed in many parts of the world; the higher-than-average temperature changes varied between 0.10 °C and 0.20 °C above the norm. Although 0.10 °C does not seem large enough to produce any noticeable change, it did free seas of ice. Because of this warming, the Vikings were able to colonize Greenland.

The Little Ice Age was a cold period that occurred between 1550 AD and 1850 AD. During this time, a slight cooling of a little less than 1 °C was observed in North America, Europe, and possibly other areas of the Earth. This 1 °C change in global temperature is

a seemingly small deviation in temperature (as was observed during the Medieval Climate Anomaly); however, it also resulted in noticeable changes. Historical accounts reveal a time of exceptionally harsh winters with much snow and frost.

The Industrial Revolution, which began around 1750, was characterized by changes in much of human society. Advances in agriculture increased the food supply, which improved the standard of living for people in Europe and the United States. New technologies were invented and provided jobs and cheaper goods. These new technologies were powered using fossil fuels, especially coal. The Industrial Revolution starting in the early nineteenth century ushered in the beginning of the Industrial Era. When a fossil fuel is burned, carbon dioxide is released. With the beginning of the Industrial Era, atmospheric carbon dioxide began to rise (Figure **20.3.2**).

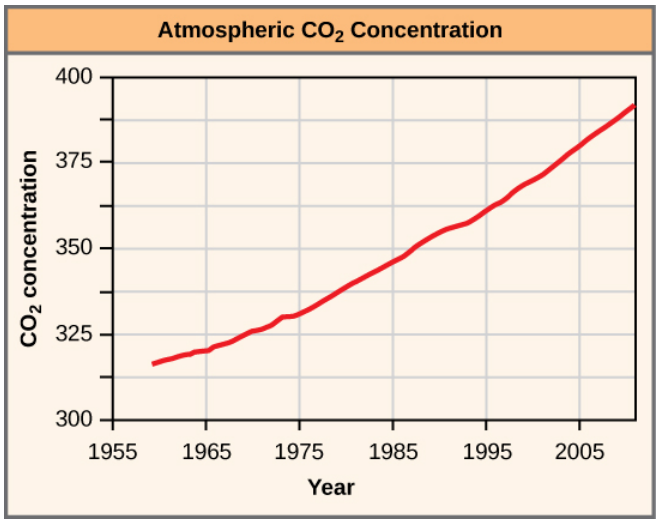



Figure **20.3.2**: The atmospheric concentration of $CO_2$ has risen steadily since the beginning of industrialization.

## Current and Past Drivers of Global Climate Change

Since it is not possible to go back in time to directly observe and measure climate, scientists use indirect evidence to determine the drivers, or factors, that may be responsible for climate change. The indirect evidence includes data collected using ice cores, boreholes (a narrow shaft bored into the ground), tree rings, glacier lengths, pollen remains, and ocean sediments. The data shows a correlation between the timing of temperature changes and drivers of climate change: before the Industrial Era (pre-1780), there were three drivers of climate change that were not related to human activity or atmospheric gases. The first of these is the Milankovitch cycles. The Milankovitch cycles describe the effects of slight changes in the Earth's orbit on Earth's climate. The length of the Milankovitch cycles ranges between 19,000 and 100,000 years. In other words, one could expect to see some predictable changes in the Earth's climate associated with changes in the Earth's orbit at a minimum of every 19,000 years.

The variation in the sun's intensity is the second natural factor responsible for climate change. Solar intensity is the amount of solar power or energy the sun emits in a given amount of time. There is a direct relationship between solar intensity and temperature. As solar intensity increases (or decreases), the Earth's temperature correspondingly increases (or decreases). Changes in solar intensity have been proposed as one of several possible explanations for the Little Ice Age.

Finally, volcanic eruptions are a third natural driver of climate change. Volcanic eruptions can last a few days, but the solids and gases released during an eruption can influence the climate over a period of a few years, causing short-term climate changes. The gases and solids released by volcanic eruptions can include carbon dioxide, water vapor, sulfur dioxide, hydrogen sulfide, hydrogen, and carbon monoxide. Generally, volcanic eruptions cool the climate. This occurred in 1783 when volcanos in Iceland erupted and caused the release of large volumes of sulfuric oxide. This led to haze-effect cooling, a global phenomenon that occurs when dust, ash, or other suspended particles block out sunlight and trigger lower global temperatures as a result; haze-effect cooling usually extends for one or more years. In Europe and North America, haze-effect cooling produced some of the lowest average winter temperatures on record in 1783 and 1784.

Greenhouse gases are probably the most significant drivers of the climate. When heat energy from the sun strikes the Earth, gases known as greenhouse gases trap the heat in the atmosphere, as do the glass panes of a greenhouse keep heat from escaping. The greenhouse gases that affect Earth include carbon dioxide, methane, water vapor, nitrous oxide, and ozone. Approximately half of

the radiation from the sun passes through these gases in the atmosphere and strikes the Earth. This radiation is converted into thermal radiation on the Earth's surface, and then a portion of that energy is re-radiated back into the atmosphere. Greenhouse gases, however, reflect much of the thermal energy back to the Earth's surface. The more greenhouse gases there are in the atmosphere, the more thermal energy is reflected back to the Earth's surface. Greenhouse gases absorb and emit radiation and are an important factor in the greenhouse effect: the warming of Earth due to carbon dioxide and other greenhouse gases in the atmosphere.

Evidence supports the relationship between atmospheric concentrations of carbon dioxide and temperature: as carbon dioxide rises, global temperature rises. Since 1950, the concentration of atmospheric carbon dioxide has increased from about 280 ppm to 382 ppm in 2006. In 2011, the atmospheric carbon dioxide concentration was 392 ppm. However, the planet would not be inhabitable by current life forms if water vapor did not produce its drastic greenhouse warming effect.

Scientists look at patterns in data and try to explain differences or deviations from these patterns. The atmospheric carbon dioxide data reveal a historical pattern of carbon dioxide increasing and decreasing, cycling between a low of 180 ppm and a high of 300 ppm. Scientists have concluded that it took around 50,000 years for the atmospheric carbon dioxide level to increase from its low minimum concentration to its higher maximum concentration. However, starting recently, atmospheric carbon dioxide concentrations have increased beyond the historical maximum of 300 ppm. The current increases in atmospheric carbon dioxide have happened very quickly—in a matter of hundreds of years rather than thousands of years. What is the reason for this difference in the rate of change and the amount of increase in carbon dioxide? A key factor that must be recognized when comparing the historical data and the current data is the presence of modern human society; no other driver of climate change has yielded changes in atmospheric carbon dioxide levels at this rate or to this magnitude.

Human activity releases carbon dioxide and methane, two of the most important greenhouse gases, into the atmosphere in several ways. The primary mechanism that releases carbon dioxide is the burning of fossil fuels, such as gasoline, coal, and natural gas (Figure **20.3.3**). Deforestation, cement manufacture, animal agriculture, the clearing of land, and the burning of forests are other human activities that release carbon dioxide. Methane ($CH_4$) is produced when bacteria break down organic matter under anaerobic conditions. Anaerobic conditions can happen when organic matter is trapped underwater (such as in rice paddies) or in the intestines of herbivores. Methane can also be released from natural gas fields and the decomposition that occurs in landfills. Another source of methane is the melting of clathrates. Clathrates are frozen chunks of ice and methane found at the bottom of the ocean. When water warms, these chunks of ice melt and methane is released. As the ocean's water temperature increases, the rate at which clathrates melt is increasing, releasing even more methane. This leads to increased levels of methane in the atmosphere, which further accelerates the rate of global warming. This is an example of the positive feedback loop that is leading to the rapid rate of increase of global temperatures.



Figure **20.3.3**: The burning of fossil fuels in industry and by vehicles releases carbon dioxide and other greenhouse gases into the atmosphere. (credit: “Pöllö”/Wikimedia Commons)

## Documented Results of Climate Change: Past and Present

Scientists have geological evidence of the consequences of long-ago climate change. Modern-day phenomena such as retreating glaciers and melting polar ice cause a continual rise in sea level. Meanwhile, changes in climate can negatively affect organisms.

### Geological Climate Change

Global warming has been associated with at least one planet-wide extinction event during the geological past. The Permian extinction event occurred about 251 million years ago toward the end of the roughly 50-million-year-long geological time span known as the Permian period. This geologic time period was one of the three warmest periods in Earth’s geologic history. Scientists estimate that approximately 70 percent of the terrestrial plant and animal species and 84 percent of marine species became extinct, vanishing forever near the end of the Permian period. Organisms that had adapted to wet and warm climatic conditions, such as annual rainfall of 300–400 cm (118–157 in) and 20 °C–30 °C (68 °F–86 °F) in the tropical wet forest, may not have been able to survive the Permian climate change.

Link to Learning



Watch this NASA video to discover the mixed effects of global warming on plant growth. While scientists found that warmer temperatures in the 1980s and 1990s caused an increase in plant productivity, this advantage has since been counteracted by more frequent droughts.

## Present Climate Change

A number of global events have occurred that may be attributed to climate change during our lifetimes. Glacier National Park in Montana is undergoing the retreat of many of its glaciers, a phenomenon known as glacier recession. In 1850, the area contained approximately 150 glaciers. By 2010, however, the park contained only about 24 glaciers greater than 25 acres in size. One of these glaciers is the Grinnell Glacier (Figure **20.3.4**) at Mount Gould. Between 1966 and 2005, the size of Grinnell Glacier shrank by 40 percent. Similarly, the mass of the ice sheets in Greenland and the Antarctic is decreasing: Greenland lost 150–250 $km^3$ of ice per year between 2002 and 2006. In addition, the size and thickness of the Arctic sea ice is decreasing.




Figure **20.3.4:** The effect of global warming can be seen in the continuing retreat of Grinnel Glacier. The mean annual temperature in the park has increased 1.33 °C since 1900. The loss of a glacier results in the loss of summer meltwaters, sharply reducing seasonal water supplies and severely affecting local ecosystems. (credit: modification of work by USGS)

This loss of ice is leading to increases in the global sea level. On average, the sea is rising at a rate of 1.8 mm per year. However, between 1993 and 2010 the rate of sea level increase ranged between 2.9 and 3.4 mm per year. A variety of factors affect the volume of water in the ocean, including the temperature of the water (the density of water is related to its temperature) and the amount of water found in rivers, lakes, glaciers, polar ice caps, and sea ice. As glaciers and polar ice caps melt, there is a significant contribution of liquid water that was previously frozen.

In addition to some abiotic conditions changing in response to climate change, many organisms are also being affected by the changes in temperature. Temperature and precipitation play key roles in determining the geographic distribution and phenology of

plants and animals. (Phenology is the study of the effects of climatic conditions on the timing of periodic lifecycle events, such as flowering in plants or migration in birds.) Researchers have shown that 385 plant species in Great Britain are flowering 4.5 days sooner than was recorded earlier during the previous 40 years. In addition, insect-pollinated species were more likely to flower earlier than wind-pollinated species. The impact of changes in flowering date would be mitigated if the insect pollinators emerged earlier. This mismatched timing of plants and pollinators could result in injurious ecosystem effects because, for continued survival, insect-pollinated plants must flower when their pollinators are present.

## Summary

The Earth has gone through periodic cycles of increases and decreases in temperature. During the past 2000 years, the Medieval Climate Anomaly was a warmer period, while the Little Ice Age was unusually cool. Both of these irregularities can be explained by natural causes of changes in climate, and, although the temperature changes were small, they had significant effects. Natural drivers of climate change include Milankovitch cycles, changes in solar activity, and volcanic eruptions. None of these factors, however, leads to rapid increases in global temperature or sustained increases in carbon dioxide. The burning of fossil fuels is an important source of greenhouse gases, which plays a major role in the greenhouse effect. Long ago, global warming resulted in the Permian extinction: a large-scale extinction event that is documented in the fossil record. Currently, modern-day climate change is associated with the increased melting of glaciers and polar ice sheets, resulting in a gradual increase in sea level. Plants and animals can also be affected by global climate change when the timing of seasonal events, such as flowering or pollination, is affected by global warming.

## Glossary

**clathrates**
: frozen chunks of ice and methane found at the bottom of the ocean

**climate**
: long-term, predictable atmospheric conditions present in a specific area

**global climate change**
: altered global weather patterns, including a worldwide increase in temperature, due largely to rising levels of atmospheric carbon dioxide

**greenhouse effect**
: warming of Earth due to carbon dioxide and other greenhouse gases in the atmosphere

**greenhouse gases**
: atmospheric gases such as carbon dioxide and methane that absorb and emit radiation, thus trapping heat in Earth’s atmosphere

**haze-effect cooling**
: effect of the gases and solids from a volcanic eruption on global climate

**Milankovitch cycles**
: cyclic changes in the Earth's orbit that may affect climate

**solar intensity**
: amount of solar power energy the sun emits in a given amount of time

**weather**
: conditions of the atmosphere during a short period of time

This page titled 20.3: Climate and the Effects of Global Climate Change is shared under a CC BY 4.0 license and was authored, remixed, and/or curated by Tom Buckley.

- **44.5: Climate and the Effects of Global Climate Change** by OpenStax is licensed CC BY 4.0.

# 20.4: Soil and Water Conservation

Biodiversity is also important for global soil and water protection. Terrestrial vegetation in forests and other upland habitats maintain water quality and quantity, and controls soil erosion.

In watersheds where vegetation has been removed, flooding prevails in the wet season and drought in the dry season. Soil erosion is also more intense and rapid, causing a double effect: removing nutrient-rich topsoil and leading to siltation in downstream riverine and ultimately oceanic environments. This siltation harms riverine and coastal fisheries as well as damaging coral reefs (Turner and Rabalais 1994; van Katwijk et al. 1993).

One of the most productive ecosystems on earth, wetlands have water present at or near the surface of the soil or within the root zone, all year or for a period of time during the year, and the vegetation there is adapted to these conditions. Wetlands are instrumental for the maintenance of clean water and erosion control. Microbes and plants in wetlands absorb nutrients and in the process filter and purify water of pollutants before they can enter coastal or other aquatic ecosystems.

Wetlands also reduce flood, wave, and wind damage. They retard the flow of floodwaters and accumulate sediments that would otherwise be carried downstream or into coastal areas. Wetlands also serve as breeding grounds and nurseries for fish and support thousands of bird and other animal species.

## Glossary

**watersheds**

land areas drained by a river and its tributaries

**wetlands**

areas where water is present at or near the surface of the soil or within the root zone, all year or for a period of time during the year, and where the vegetation is adapted to these conditions

---

This page titled 20.4: Soil and Water Conservation is shared under a CC BY 3.0 license and was authored, remixed, and/or curated by Tom Buckley via source content that was edited to the style and standards of the LibreTexts platform.

- **1.3: Soil and Water Conservation** by Nora Bynum is licensed CC BY 3.0. Original source: https://cnx.org/contents/AK5sUWpu1.1:GNNbYBSX1.

# Index


## A

A horizon
14.3: The Soil
abscisic acid
16.2: Plant Sensory Systems and Responses
abscission
16.2: Plant Sensory Systems and Responses
absorption spectrum
10.2: The Light-dependent Reactions
accessory fruit
5.2: Pollination and Fertilization
acid
8.1.3: Water
adhesion
8.1.3: Water
aggregate fruit
5.2: Pollination and Fertilization
aleurone
5.2: Pollination and Fertilization
aliphatic hydrocarbon
8.1.4: Carbon
alternation of generations
5.1: Reproductive Development and Structure
amino acid
8.2.5: Proteins
amyloplast
16.1: Environmental Responses
16.2: Plant Sensory Systems and Responses
amyloplasts
2.1.2: Plant Cell Structure
analogy
3.2.1.3: Determining Evolutionary Relationships
androecium
5.1: Reproductive Development and Structure
angiosperms
5.1: Reproductive Development and Structure
anion
8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
antenna protein
10.2: The Light-dependent Reactions
antipodals
5.1: Reproductive Development and Structure
apomixis
4: Asexual reproduction
4.1: Asexual Reproduction
aromatic hydrocarbon
8.1.4: Carbon
artificial selection
7.2.1: Introduction
atom
8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
atomic mass
8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
atomic number
8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
auxin
16.2: Plant Sensory Systems and Responses

## B

B horizon
14.3: The Soil
balanced chemical equation
8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
basal taxon
3.2.1.2: Organizing Life on Earth
base
8.1.3: Water
bedrock
14.3: The Soil
binomial nomenclature
3.2.1.2: Organizing Life on Earth
biological macromolecule
8.2.2: Synthesis of Biological Macromolecules
botany
3.2.2: Early Land Plants
branch point
3.2.1.2: Organizing Life on Earth
bryophytes
3.2.2.2: Bryophytes
buffer
8.1.3: Water

## C

C horizon
14.3: The Soil
C3 plants
12.1: Photorespiration and Photosynthetic Pathways
C4 plants
12.1: Photorespiration and Photosynthetic Pathways
Calvin cycle
9.2: Photosynthesis Overview and Equation
CAM plants
12.1: Photorespiration and Photosynthetic Pathways
capillary action
8.1.3: Water
carbohydrate
8.2.3: Carbohydrates
carotenoid
10.2: The Light-dependent Reactions
Casparian strip
11.5: Water Transport
cation
8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
cellulose
8.2.3: Carbohydrates
chaperones
8.2.5: Proteins
chemical bond
8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
chemical reaction
8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
chemical reactivity
8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
chemoautotroph
9.2: Photosynthesis Overview and Equation
chitin
8.2.3: Carbohydrates
chlorophyll a
10.2: The Light-dependent Reactions
chlorophyll b
10.2: The Light-dependent Reactions
chloroplast
9.2: Photosynthesis Overview and Equation
chromophore
16.1: Environmental Responses
16.2: Plant Sensory Systems and Responses
cladistics
3.2.1.3: Determining Evolutionary Relationships
cladophylls
2.3.4: Stem Modifications
class
3.2.1.2: Organizing Life on Earth
clathrates
20.3: Climate and the Effects of Global Climate Change
clay
14.3: The Soil
climate
20.3: Climate and the Effects of Global Climate Change
Cocklebur chart
16.1.3: Photoperiodism
cohesion
8.1.3: Water
cohesion theory
11.5: Water Transport
coleoptile
5.2: Pollination and Fertilization
coleorhiza
5.2: Pollination and Fertilization
collenchyma cell
2.1.3: Plant Tissues
compound
8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
conservation of energy
1.1: Potential Energy in Biology
corms
2.3.4: Stem Modifications
cotyledon
5.2: Pollination and Fertilization
covalent bond
8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
Crop rotations
19.2: Sustainable Agriculture
cryptochrome
16.1: Environmental Responses
16.2: Plant Sensory Systems and Responses
cuticle
11.6: Transport of Water and Solutes in Plants
cutting
4: Asexual reproduction
4.1: Asexual Reproduction
Cycadopsida
3.2.3.2: Gymnosperms

cytochrome complex
10.2: The Light-dependent Reactions
cytokinin
16.2: Plant Sensory Systems and Responses

## D

dehydration synthesis
8.2.2: Synthesis of Biological Macromolecules
denaturation
8.2.5: Proteins
deoxyribonucleic acid
8.2.6: Nucleic Acids
disaccharide
8.2.3: Carbohydrates
dissociation
8.1.3: Water
DNA
8.2.6: Nucleic Acids
dormancy
5.2: Pollination and Fertilization
double fertilization
5.2: Pollination and Fertilization

## E

electrolyte
8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
electromagnetic spectrum
10.2: The Light-dependent Reactions
electron configuration
8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
electron orbital
8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
electron transfer
8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
electron transport chain
10.2: The Light-dependent Reactions
electronegativity
8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
element
8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
Elysia chlorotica
3.2.2: Early Land Plants
enantiomers
8.1.4: Carbon
endergonic
1.1: Potential Energy in Biology
endocarp
5.2: Pollination and Fertilization
endosperm
5.2: Pollination and Fertilization
endospermic dicot
5.2: Pollination and Fertilization
enzyme
8.2.5: Proteins
epicotyl
5.2: Pollination and Fertilization
epidermis (plants)
2.1.3: Plant Tissues
epiphyte
14.4: Nutritional Adaptations of Plants
ethylene
16.2: Plant Sensory Systems and Responses
etiolation
16.1.4: Etiolation and Shade Avoidance
evaporation
8.1.3: Water
exergonic
1.1: Potential Energy in Biology
exine
5.1: Reproductive Development and Structure
exocarp
5.2: Pollination and Fertilization

## F

family
3.2.1.2: Organizing Life on Earth
ferns
3.2.2.3: Seedless Vascular Plants
florigen
16.1.2: Flowering
flowering
16.1.2: Flowering
free energy
1.1: Potential Energy in Biology
functional group
8.1.4: Carbon

## G

gametophyte
5.1: Reproductive Development and Structure
gene transfer agent
3.2.1.4: Perspectives on the Phylogenetic Tree
genome fusion
3.2.1.4: Perspectives on the Phylogenetic Tree
genus
3.2.1.2: Organizing Life on Earth
geometric isomer
8.1.4: Carbon
gibberellin
16.2: Plant Sensory Systems and Responses
Gibbs energy
1.1: Potential Energy in Biology
Ginkgoopsida
3.2.3.2: Gymnosperms
global climate change
20.3: Climate and the Effects of Global Climate Change
glycogen
8.2.3: Carbohydrates
glycosidic bond
8.2.3: Carbohydrates
glyphosate
7.2.1: Introduction
grafting
4: Asexual reproduction
4.1: Asexual Reproduction
granum
9.2: Photosynthesis Overview and Equation
gravitropism
5.2: Pollination and Fertilization
greenhouse effect
20.2: The Greenhouse Effect
20.3: Climate and the Effects of Global Climate Change
greenhouse gases
20.3: Climate and the Effects of Global Climate Change
greenhouses gases
20.2: The Greenhouse Effect
GTA
3.2.1.4: Perspectives on the Phylogenetic Tree
guard cells
11.2.2: Stomatal Opening and Closure
gynoecium
5.1: Reproductive Development and Structure

## H

heat of vaporization of water
8.1.3: Water
heterotroph
9.2: Photosynthesis Overview and Equation
HGT
3.2.1.4: Perspectives on the Phylogenetic Tree
horizon
14.3: The Soil
horizontal gene transfer
3.2.1.4: Perspectives on the Phylogenetic Tree
hormone
8.2.5: Proteins
humus
14.3: The Soil
hydrocarbon
8.1.4: Carbon
hydrogen bond
8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
hydrolysis
8.2.2: Synthesis of Biological Macromolecules
hydrophilic
8.1.3: Water
hydrophobic
8.1.3: Water
hypocotyl
5.2: Pollination and Fertilization

## I

incompatibility genes
5.2: Pollination and Fertilization
inert gas
8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
Inorganic Compound
14.2: Nutritional Requirements of Plants
insectivorous plant
14.4: Nutritional Adaptations of Plants
integrated pest management
19.2: Sustainable Agriculture
intercropping
19.2: Sustainable Agriculture
intine
5.1: Reproductive Development and Structure
ionic bond
8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks

irreversible chemical reaction
8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
isomers
8.1.4: Carbon
isotope
8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks

J

jasmonates
16.2: Plant Sensory Systems and Responses

K

kingdom
3.2.1.2: Organizing Life on Earth

L

layering
4: Asexual reproduction
4.1: Asexual Reproduction
leucoplasts
2.1.2: Plant Cell Structure
light harvesting complex
10.2: The Light-dependent Reactions
lipid
8.2.4: Lipids
litmus paper
8.1.3: Water
loam
14.3: The Soil
lycophytes
3.2.2.3: Seedless Vascular Plants

M

macronutrient
14.2: Nutritional Requirements of Plants
matter
8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
maximum parsimony
3.2.1.3: Determining Evolutionary Relationships
megagametogenesis
5.1: Reproductive Development and Structure
megapascal
11.6: Transport of Water and Solutes in Plants
megasporangium
5.1: Reproductive Development and Structure
megasporogenesis
5.1: Reproductive Development and Structure
megasporophyll
5.1: Reproductive Development and Structure
Merosity
3.2.4.2: Pollination Syndromes
3.2.4.3: Fruits and Dispersal
mesocarp
5.2: Pollination and Fertilization
mesophyll
9.2: Photosynthesis Overview and Equation
messenger RNA
8.2.6: Nucleic Acids
micronutrient
14.2: Nutritional Requirements of Plants
micropropagation
4: Asexual reproduction
4.1: Asexual Reproduction
micropyle
5.1: Reproductive Development and Structure
microsporangium
5.1: Reproductive Development and Structure
microsporophyll
5.1: Reproductive Development and Structure
Milankovitch cycles
20.3: Climate and the Effects of Global Climate Change
mineral soil
14.3: The Soil
minimal tillage
19.2: Sustainable Agriculture
molecular systematics
3.2.1.3: Determining Evolutionary Relationships
monocarpic
4: Asexual reproduction
4.1: Asexual Reproduction
monomer
8.2.2: Synthesis of Biological Macromolecules
monophyletic group
3.2.1.3: Determining Evolutionary Relationships
Monosaccharide
8.2.3: Carbohydrates
mosses
3.2.2.2: Bryophytes
multiple fruit
5.2: Pollination and Fertilization
muscle contraction
1.1: Potential Energy in Biology

N

nectar guide
5.2: Pollination and Fertilization
negative gravitropism
16.1: Environmental Responses
16.2: Plant Sensory Systems and Responses
neutron
8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
nitrogenase
14.4: Nutritional Adaptations of Plants
noble gas
8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
nodules
14.4: Nutritional Adaptations of Plants
nonpolar covalent bond
8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
nucleic acid
8.2.6: Nucleic Acids
nucleotide
8.2.6: Nucleic Acids

O

O horizon
14.3: The Soil
oligosaccharin
16.1: Environmental Responses
16.2: Plant Sensory Systems and Responses
omega fat
8.2.4: Lipids
order
3.2.1.2: Organizing Life on Earth
Organic Compound
14.2: Nutritional Requirements of Plants
organic farming
19.2: Sustainable Agriculture
organic molecule
8.1.4: Carbon

P

P680
10.2: The Light-dependent Reactions
P700
10.2: The Light-dependent Reactions
parasitic plant
14.4: Nutritional Adaptations of Plants
parenchyma cell
2.1.3: Plant Tissues
parent material
14.3: The Soil
peptide bond
8.2.5: Proteins
perianth
5.1: Reproductive Development and Structure
pericarp
5.2: Pollination and Fertilization
periodic table
8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
pH paper
8.1.3: Water
pH scale
8.1.3: Water
phagocytosis
2.1.2: Plant Cell Structure
phosphodiester
8.2.6: Nucleic Acids
phosphoenolpyruvic acid (PEP)
12.1: Photorespiration and Photosynthetic Pathways
phospholipid
8.2.4: Lipids
photoact
10.2: The Light-dependent Reactions
photoautotroph
9.2: Photosynthesis Overview and Equation
photomorphogenesis
16.1: Environmental Responses
16.2: Plant Sensory Systems and Responses
photon
10.2: The Light-dependent Reactions
photoperiodism
16.1: Environmental Responses
16.1.3: Photoperiodism
16.2: Plant Sensory Systems and Responses
photosynthesis
3.1: A Brief History of Life on Earth
3.1.1: A Brief History of Life on Earth
photosystem
10.2: The Light-dependent Reactions
photosystem I
10.2: The Light-dependent Reactions

photosystem II
10.2: The Light-dependent Reactions
phototropin
16.1: Environmental Responses
16.2: Plant Sensory Systems and Responses
phototropism
16.1: Environmental Responses
16.2: Plant Sensory Systems and Responses
phylogenetic tree
3.2.1.2: Organizing Life on Earth
phylogeny
3.2.1.2: Organizing Life on Earth
phylum
3.2.1.2: Organizing Life on Earth
phytochrome
16.1: Environmental Responses
16.1.3: Photoperiodism
16.1.4: Etiolation and Shade Avoidance
16.2: Plant Sensory Systems and Responses
pigment
9.2: Photosynthesis Overview and Equation
Pinopsida
3.2.3.2: Gymnosperms
plasmodesmata
11.5: Water Transport
plumule
5.2: Pollination and Fertilization
poikilohydricity
2.1.3: Plant Tissues
polar nuclei
5.1: Reproductive Development and Structure
pollination
5.2: Pollination and Fertilization
polycarpic
4: Asexual reproduction
4.1: Asexual Reproduction
polymer
8.2.2: Synthesis of Biological Macromolecules
polynucleotide
8.2.6: Nucleic Acids
polypeptide
8.2.5: Proteins
polysaccharide
8.2.3: Carbohydrates
polytomy
3.2.1.2: Organizing Life on Earth
positive gravitropism
16.1: Environmental Responses
16.2: Plant Sensory Systems and Responses
potential energy
1.1: Potential Energy in Biology
primary electron acceptor
10.2: The Light-dependent Reactions
primary stems
2.3: Stems
primary structure
8.2.5: Proteins
product
8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
protein
8.2.5: Proteins
proton
8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
Pteridophyta
3.2.2.3: Seedless Vascular Plants
pyrimidine
8.2.6: Nucleic Acids

## Q

quaternary structure
8.2.5: Proteins

## R

radicle
5.2: Pollination and Fertilization
radioisotope
8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
reaction center
10.2: The Light-dependent Reactions
rhizobia
14.4: Nutritional Adaptations of Plants
rhizomes
2.3.4: Stem Modifications
rhizosphere
14.3: The Soil
ribonucleic acid
8.2.6: Nucleic Acids
ribosomal RNA
8.2.6: Nucleic Acids
ring of life
3.2.1.4: Perspectives on the Phylogenetic Tree
RNA
8.2.6: Nucleic Acids
Root Pressure
11.5: Water Transport
root system
2.2: Roots
rooted
3.2.1.2: Organizing Life on Earth
rubisco
12.1: Photorespiration and Photosynthetic Pathways

## S

sand
14.3: The Soil
saprophyte
14.4: Nutritional Adaptations of Plants
Saturated fatty acid
8.2.4: Lipids
scarification
5.2: Pollination and Fertilization
scion
4: Asexual reproduction
4.1: Asexual Reproduction
sclerenchyma cell
2.1.3: Plant Tissues
scutellum
5.2: Pollination and Fertilization
secondary structure
8.2.5: Proteins
seed plants
3.2.3.2: Gymnosperms
senescence
4: Asexual reproduction
4.1: Asexual Reproduction
shared ancestral character
3.2.1.3: Determining Evolutionary Relationships
shared derived character
3.2.1.3: Determining Evolutionary Relationships
silt
14.3: The Soil
simple fruit
5.2: Pollination and Fertilization
sink
11.6: Transport of Water and Solutes in Plants
sister taxa
3.2.1.2: Organizing Life on Earth
soil
14.3: The Soil
soil profile
14.3: The Soil
solar intensity
20.3: Climate and the Effects of Global Climate Change
solvent
8.1.3: Water
specific heat capacity
8.1.3: Water
spectrophotometer
10.2: The Light-dependent Reactions
sphere of hydration
8.1.3: Water
spines
2.3.4: Stem Modifications
sporophyte
5.1: Reproductive Development and Structure
starch
8.2.3: Carbohydrates
statolith
16.1: Environmental Responses
16.2: Plant Sensory Systems and Responses
stem traps
2.3.4: Stem Modifications
steroid
8.2.4: Lipids
stolons
2.3.4: Stem Modifications
stoma
9.2: Photosynthesis Overview and Equation
stomata
11.2.2: Stomatal Opening and Closure
strigolactone
16.1: Environmental Responses
16.2: Plant Sensory Systems and Responses
stroma
9.2: Photosynthesis Overview and Equation
structural isomers
8.1.4: Carbon
substituted hydrocarbon
8.1.4: Carbon
succulent
2.4.3: Leaf Modifications
surface tension
8.1.3: Water
suspensor
5.2: Pollination and Fertilization
sustainable agriculture
19.2: Sustainable Agriculture

symbiont
14.4: Nutritional Adaptations of Plants
symplast
11.5: Water Transport
synergid
5.1: Reproductive Development and Structure

## T

taxon
3.2.1.2: Organizing Life on Earth
taxonomy
3.2.1.2: Organizing Life on Earth
3.2.2: Early Land Plants
tegmen
5.2: Pollination and Fertilization
tertiary structure
8.2.5: Proteins
testa
5.2: Pollination and Fertilization
thigmomorphogenesis
16.1: Environmental Responses
16.2: Plant Sensory Systems and Responses
thigmonastic
16.1: Environmental Responses
16.2: Plant Sensory Systems and Responses
thigmotropism
16.1: Environmental Responses
16.2: Plant Sensory Systems and Responses
thylakoid
9.2: Photosynthesis Overview and Equation
thylakoid lumen
9.2: Photosynthesis Overview and Equation
trans fat
8.2.4: Lipids
transcription
8.2.6: Nucleic Acids
transfer RNA
8.2.6: Nucleic Acids
translation
8.2.6: Nucleic Acids
translocation
11.6: Transport of Water and Solutes in Plants
transpiration
11.6: Transport of Water and Solutes in Plants
triacylglycerol
8.2.4: Lipids
triglyceride
8.2.4: Lipids
tubers
2.3.4: Stem Modifications

## U

unsaturated fatty acid
8.2.4: Lipids

## V

van der Waals interaction
8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
vernalization
5.2: Pollination and Fertilization

## W

water potential
11.6: Transport of Water and Solutes in Plants
watersheds
20.4: Soil and Water Conservation
wavelength
10.2: The Light-dependent Reactions
wax
8.2.4: Lipids
weather
20.3: Climate and the Effects of Global Climate Change
web of life
3.2.1.4: Perspectives on the Phylogenetic Tree
wetlands
20.4: Soil and Water Conservation

## X

xylem
11.5: Water Transport

# Glossary

**Sample Word 1** | Sample Definition 1

# Detailed Licensing

## Overview

**Title:** PLS 002: Botany and Physiology of Cultivated Plants

**Webpages:** 158

**Applicable Restrictions:** Noncommercial

**All licenses found:**

- CC BY-NC 4.0: 31% (49 pages)
- Undeclared: 21.5% (34 pages)
- CC BY-SA 4.0: 19.6% (31 pages)
- CC BY 4.0: 19% (30 pages)
- CC BY-NC-SA 4.0: 7% (11 pages)
- CC BY 3.0: 1.9% (3 pages)

## By Page

- PLS 002: Botany and Physiology of Cultivated Plants - *CC BY 4.0*
  - Front Matter - *Undeclared*
    - TitlePage - *Undeclared*
    - InfoPage - *Undeclared*
    - Table of Contents - *Undeclared*
    - Licensing - *Undeclared*
  - 1: Intro - what is life - *Undeclared*
    - 1.1: Potential Energy in Biology - *Undeclared*
  - 2: Plant structure - *CC BY-NC 4.0*
    - 2.1: Cells and Tissues - *CC BY-NC 4.0*
      - 2.1.1: Introduction to Cells - *CC BY-NC 4.0*
      - 2.1.2: Plant Cell Structure - *CC BY-NC 4.0*
      - 2.1.3: Plant Tissues - *CC BY-SA 4.0*
      - 2.1.4: Chapter Summary - *CC BY 4.0*
    - 2.2: Roots - *CC BY-SA 4.0*
      - 2.2.1: Organs and Organ Systems - *CC BY-NC 4.0*
      - 2.2.2: External Root Structure - *CC BY-NC 4.0*
      - 2.2.3: Internal Root Structure - *CC BY 4.0*
      - 2.2.4: Root Modifications - *CC BY-SA 4.0*
      - 2.2.5: Chapter Summary - *CC BY-NC 4.0*
    - 2.3: Stems - *CC BY-SA 4.0*
      - 2.3.1: Stem Morphology (External Structure) - *CC BY-SA 4.0*
      - 2.3.2: Internal Anatomy of the Primary Stem - *CC BY-SA 4.0*
      - 2.3.3: Secondary Stem - *CC BY-NC 4.0*
      - 2.3.4: Stem Modifications - *CC BY-SA 4.0*
      - 2.3.5: Chapter Summary - *CC BY-NC 4.0*
    - 2.4: Leaves - *CC BY-NC 4.0*
      - 2.4.1: External Structure of Leaves - *CC BY-SA 4.0*
      - 2.4.2: Internal Leaf Structure - *CC BY-NC 4.0*
      - 2.4.3: Leaf Modifications - *CC BY-SA 4.0*
      - 2.4.4: Chapter Summary - *Undeclared*
    - 2.5: Meristems - *CC BY-NC 4.0*
  - 3: Origin and evolution of land plants - *Undeclared*
    - 3.1: A Brief History of Life on Earth - *CC BY 3.0*
      - 3.1.1: A Brief History of Life on Earth - *CC BY 3.0*
    - 3.2: Biodiversity (Organismal Groups) - *CC BY-NC 4.0*
      - 3.2.1: Systematics - *CC BY-NC 4.0*
        - 3.2.1.1: Introduction - *CC BY-NC 4.0*
        - 3.2.1.2: Organizing Life on Earth - *CC BY-NC 4.0*
        - 3.2.1.3: Determining Evolutionary Relationships - *CC BY-SA 4.0*
        - 3.2.1.4: Perspectives on the Phylogenetic Tree - *CC BY-NC 4.0*
        - 3.2.1.5: Chapter Summary - *CC BY-NC 4.0*
      - 3.2.2: Early Land Plants - *CC BY-NC 4.0*
        - 3.2.2.1: Introduction to Early Land Plants - *Undeclared*
        - 3.2.2.2: Bryophytes - *CC BY-NC-SA 4.0*
          - 3.2.2.2.1: Anthocerotophyta - *CC BY-NC-SA 4.0*
          - 3.2.2.2.2: Marchantiophyta - *CC BY-NC-SA 4.0*
          - 3.2.2.2.3: Bryophyta - *CC BY-NC-SA 4.0*

- 3.2.2.3: Seedless Vascular Plants - *CC BY-SA 4.0*
  - 3.2.2.3.1: Lycopodiopsida - *CC BY-SA 4.0*
  - 3.2.2.3.2: Polypodiopsida - *CC BY-SA 4.0*
- 3.2.2.4: Chapter Summary - *CC BY-NC 4.0*
- 3.2.3: Seed Plants - *CC BY-NC 4.0*
  - 3.2.3.1: Introduction to Seed Plants - *Undeclared*
  - 3.2.3.2: Gymnosperms - *CC BY-NC-SA 4.0*
    - 3.2.3.2.1: Cycads and Ginkos - *CC BY-NC-SA 4.0*
    - 3.2.3.2.2: Conifers and Gnetophytes - *CC BY-SA 4.0*
  - 3.2.3.3: Angiosperms - *CC BY-SA 4.0*
    - 3.2.3.3.1: Flowers - *CC BY-NC 4.0*
    - 3.2.3.3.2: Angiosperm Life Cycle - *CC BY-NC 4.0*
  - 3.2.3.4: Chapter Summary - *CC BY-NC 4.0*
- 3.2.4: Angiosperm Diversity - *CC BY-SA 4.0*
  - 3.2.4.1: Monocots and Eudicots - *Undeclared*
  - 3.2.4.2: Pollination Syndromes - *CC BY-SA 4.0*
  - 3.2.4.3: Fruits and Dispersal - *CC BY-SA 4.0*
  - 3.2.4.4: Angiosperm Families - *CC BY-NC 4.0*
  - 3.2.4.5: Chapter Summary - *CC BY-NC 4.0*
- 3.3: Life Cycles - *CC BY-NC 4.0*
- 3.4: The Origins of Crop Plants - *CC BY-NC 4.0*

4: Asexual reproduction - *CC BY 4.0*
- 4.1: Asexual Reproduction - *CC BY 4.0*
- 4.2: Grafting - *CC BY-NC 4.0*
  - 4.2.1: Grafts and Wounds - *CC BY-NC 4.0*
  - 4.2.2: Unique Storage Organs - *CC BY-NC 4.0*
  - 4.2.3: Terms - *CC BY-NC 4.0*

5: Sexual reproduction - *Undeclared*
- 5.1: Reproductive Development and Structure - *CC BY 4.0*
- 5.2: Pollination and Fertilization - *CC BY 4.0*

6: Plant genetics and breeding - *Undeclared*
- 6.1: The Early History of Genetics - *CC BY-NC 4.0*
- 6.2: Cataloging, Classification, and Deliberate Hybridizations - *CC BY-NC 4.0*
- 6.3: Plant Breeding - *CC BY-NC 4.0*
- 6.4: Genetic Improvement in Cereal Crops and the Green Revolution - *CC BY-NC 4.0*

7: Biotechnology - *Undeclared*
- 7.1: Genetically Engineered Crops - *CC BY-NC 4.0*
- 7.2: Genetic Modification - *CC BY-NC-SA 4.0*
  - 7.2.1: Introduction - *CC BY-NC-SA 4.0*
  - 7.2.2: GMO Food (Activity) - *CC BY-NC-SA 4.0*
- 7.3: GMOs - *CC BY-NC 4.0*

8: Basic chemistry and biochemistry - *Undeclared*
- 8.1: The Chemical Foundation of Life - *CC BY 4.0*
  - 8.1.1: Prelude to The Chemical Foundation of Life - *CC BY 4.0*
  - 8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks - *CC BY 4.0*
  - 8.1.3: Water - *CC BY 4.0*
  - 8.1.4: Carbon - *CC BY 4.0*
  - 8.1.E: The Chemical Foundation of Life (Exercises) - *CC BY 4.0*
- 8.2: Biological Macromolecules - *CC BY 4.0*
  - 8.2.1: Prelude to Biological Macromolecules - *CC BY 4.0*
  - 8.2.2: Synthesis of Biological Macromolecules - *CC BY 4.0*
  - 8.2.3: Carbohydrates - *CC BY 4.0*
  - 8.2.4: Lipids - *CC BY 4.0*
  - 8.2.5: Proteins - *CC BY 4.0*
  - 8.2.6: Nucleic Acids - *CC BY 4.0*
  - 8.2.E: Biological Macromolecules (Exercises) - *CC BY 4.0*
- 8.3: Unit I- The Chemistry of Life - *CC BY 4.0*

9: Photosynthesis - carbon reactions - *Undeclared*
- 9.1: Discovery of Photosynthesis - *CC BY-NC 4.0*
- 9.2: Photosynthesis Overview and Equation - *CC BY-NC 4.0*
- 9.3: Light-independent Reactions - *CC BY-SA 4.0*

10: Photosynthesis - light reactions - *Undeclared*
- 10.1: Energy and ATP - *CC BY-NC 4.0*
- 10.2: The Light-dependent Reactions - *CC BY-SA 4.0*

11: Plant water relations - *Undeclared*
- 11.1: Water Potential - *CC BY-NC 4.0*
- 11.2: Transpiration - *CC BY-SA 4.0*
  - 11.2.1: Adaptations to Reduce Transpiration - *CC BY-SA 4.0*
  - 11.2.2: Stomatal Opening and Closure - *CC BY-NC 4.0*
- 11.3: Cohesion-Tension Theory - *CC BY-SA 4.0*
- 11.4: Water Absorption - *CC BY-SA 4.0*
- 11.5: Water Transport - *CC BY-SA 4.0*
- 11.6: Transport of Water and Solutes in Plants - *CC BY 4.0*

12: Photosynthetic adaptations - *Undeclared*

- 12.1: Photorespiration and Photosynthetic Pathways - *CC BY-SA 4.0*
- 12.2: CO2 uptake - C4 and CAM Pathways - *Undeclared*

13: Respiration and metabolism - *Undeclared*
- 13.1: Aerobic Cellular Respiration - *CC BY-NC 4.0*

14: Mineral nutrition - *Undeclared*
- 14.1: Prelude to Soil and Plant Nutrition - *CC BY 4.0*
- 14.2: Nutritional Requirements of Plants - *CC BY 4.0*
- 14.3: The Soil - *CC BY 4.0*
- 14.4: Nutritional Adaptations of Plants - *CC BY 4.0*
- 14.E: Soil and Plant Nutrition (Exercises) - *CC BY 4.0*

15: Functional morphology and anatomy - *Undeclared*
- 15.1: Translocation (Assimilate Transport) - *CC BY-NC 4.0*

16: Environmental plant biology - *Undeclared*
- 16.1: Environmental Responses - *CC BY-NC 4.0*
  - 16.1.1: Tropisms - *CC BY-NC-SA 4.0*
  - 16.1.2: Flowering - *CC BY-SA 4.0*
  - 16.1.3: Photoperiodism - *CC BY-NC 4.0*
  - 16.1.4: Etiolation and Shade Avoidance - *CC BY-NC 4.0*
  - 16.1.5: Dormancy - *CC BY-NC-SA 4.0*
  - 16.1.6: Chapter Summary - *CC BY-NC 4.0*
- 16.2: Plant Sensory Systems and Responses - *CC BY 4.0*

17: Measuring and analyzing plants - *Undeclared*

18: Predicting plants - *Undeclared*

19: Biotic interactions - *Undeclared*
- 19.1: Industrial Agriculture - *CC BY-SA 4.0*
- 19.2: Sustainable Agriculture - *CC BY-SA 4.0*

20: Climate change and plants - *Undeclared*
- 20.1: Earth's Energy Budget - *CC BY-SA 4.0*
- 20.2: The Greenhouse Effect - *CC BY-SA 4.0*
- 20.3: Climate and the Effects of Global Climate Change - *CC BY 4.0*
- 20.4: Soil and Water Conservation - *CC BY 3.0*

Back Matter - *Undeclared*
- Index - *Undeclared*
- Glossary - *Undeclared*
- Detailed Licensing - *Undeclared*
- Detailed Licensing - *Undeclared*

# Detailed Licensing

## Overview

**Title:** PLS 002: Botany and Physiology of Cultivated Plants

**Webpages:** 158

**Applicable Restrictions:** Noncommercial

**All licenses found:**

- CC BY-NC 4.0: 31% (49 pages)
- Undeclared: 21.5% (34 pages)
- CC BY-SA 4.0: 19.6% (31 pages)
- CC BY 4.0: 19% (30 pages)
- CC BY-NC-SA 4.0: 7% (11 pages)
- CC BY 3.0: 1.9% (3 pages)

## By Page

- PLS 002: Botany and Physiology of Cultivated Plants - *CC BY 4.0*
  - Front Matter - *Undeclared*
    - TitlePage - *Undeclared*
    - InfoPage - *Undeclared*
    - Table of Contents - *Undeclared*
    - Licensing - *Undeclared*
  - 1: Intro - what is life - *Undeclared*
    - 1.1: Potential Energy in Biology - *Undeclared*
  - 2: Plant structure - *CC BY-NC 4.0*
    - 2.1: Cells and Tissues - *CC BY-NC 4.0*
      - 2.1.1: Introduction to Cells - *CC BY-NC 4.0*
      - 2.1.2: Plant Cell Structure - *CC BY-NC 4.0*
      - 2.1.3: Plant Tissues - *CC BY-SA 4.0*
      - 2.1.4: Chapter Summary - *CC BY 4.0*
    - 2.2: Roots - *CC BY-SA 4.0*
      - 2.2.1: Organs and Organ Systems - *CC BY-NC 4.0*
      - 2.2.2: External Root Structure - *CC BY-NC 4.0*
      - 2.2.3: Internal Root Structure - *CC BY 4.0*
      - 2.2.4: Root Modifications - *CC BY-SA 4.0*
      - 2.2.5: Chapter Summary - *CC BY-NC 4.0*
    - 2.3: Stems - *CC BY-SA 4.0*
      - 2.3.1: Stem Morphology (External Structure) - *CC BY-SA 4.0*
      - 2.3.2: Internal Anatomy of the Primary Stem - *CC BY-SA 4.0*
      - 2.3.3: Secondary Stem - *CC BY-NC 4.0*
      - 2.3.4: Stem Modifications - *CC BY-SA 4.0*
      - 2.3.5: Chapter Summary - *CC BY-NC 4.0*
    - 2.4: Leaves - *CC BY-NC 4.0*
      - 2.4.1: External Structure of Leaves - *CC BY-SA 4.0*
      - 2.4.2: Internal Leaf Structure - *CC BY-NC 4.0*
      - 2.4.3: Leaf Modifications - *CC BY-SA 4.0*
      - 2.4.4: Chapter Summary - *Undeclared*
    - 2.5: Meristems - *CC BY-NC 4.0*
  - 3: Origin and evolution of land plants - *Undeclared*
    - 3.1: A Brief History of Life on Earth - *CC BY 3.0*
      - 3.1.1: A Brief History of Life on Earth - *CC BY 3.0*
    - 3.2: Biodiversity (Organismal Groups) - *CC BY-NC 4.0*
      - 3.2.1: Systematics - *CC BY-NC 4.0*
        - 3.2.1.1: Introduction - *CC BY-NC 4.0*
        - 3.2.1.2: Organizing Life on Earth - *CC BY-NC 4.0*
        - 3.2.1.3: Determining Evolutionary Relationships - *CC BY-SA 4.0*
        - 3.2.1.4: Perspectives on the Phylogenetic Tree - *CC BY-NC 4.0*
        - 3.2.1.5: Chapter Summary - *CC BY-NC 4.0*
      - 3.2.2: Early Land Plants - *CC BY-NC 4.0*
        - 3.2.2.1: Introduction to Early Land Plants - *Undeclared*
        - 3.2.2.2: Bryophytes - *CC BY-NC-SA 4.0*
          - 3.2.2.2.1: Anthocerotophyta - *CC BY-NC-SA 4.0*
          - 3.2.2.2.2: Marchantiophyta - *CC BY-NC-SA 4.0*
          - 3.2.2.2.3: Bryophyta - *CC BY-NC-SA 4.0*

- 3.2.2.3: Seedless Vascular Plants - *CC BY-SA 4.0*
  - 3.2.2.3.1: Lycopodiopsida - *CC BY-SA 4.0*
  - 3.2.2.3.2: Polypodiopsida - *CC BY-SA 4.0*
- 3.2.2.4: Chapter Summary - *CC BY-NC 4.0*
- 3.2.3: Seed Plants - *CC BY-NC 4.0*
  - 3.2.3.1: Introduction to Seed Plants - *Undeclared*
  - 3.2.3.2: Gymnosperms - *CC BY-NC-SA 4.0*
    - 3.2.3.2.1: Cycads and Ginkos - *CC BY-NC-SA 4.0*
    - 3.2.3.2.2: Conifers and Gnetophytes - *CC BY-SA 4.0*
  - 3.2.3.3: Angiosperms - *CC BY-SA 4.0*
    - 3.2.3.3.1: Flowers - *CC BY-NC 4.0*
    - 3.2.3.3.2: Angiosperm Life Cycle - *CC BY-NC 4.0*
  - 3.2.3.4: Chapter Summary - *CC BY-NC 4.0*
- 3.2.4: Angiosperm Diversity - *CC BY-SA 4.0*
  - 3.2.4.1: Monocots and Eudicots - *Undeclared*
  - 3.2.4.2: Pollination Syndromes - *CC BY-SA 4.0*
  - 3.2.4.3: Fruits and Dispersal - *CC BY-SA 4.0*
  - 3.2.4.4: Angiosperm Families - *CC BY-NC 4.0*
  - 3.2.4.5: Chapter Summary - *CC BY-NC 4.0*
- 3.3: Life Cycles - *CC BY-NC 4.0*
- 3.4: The Origins of Crop Plants - *CC BY-NC 4.0*

4: Asexual reproduction - *CC BY 4.0*
- 4.1: Asexual Reproduction - *CC BY 4.0*
- 4.2: Grafting - *CC BY-NC 4.0*
  - 4.2.1: Grafts and Wounds - *CC BY-NC 4.0*
  - 4.2.2: Unique Storage Organs - *CC BY-NC 4.0*
  - 4.2.3: Terms - *CC BY-NC 4.0*

5: Sexual reproduction - *Undeclared*
- 5.1: Reproductive Development and Structure - *CC BY 4.0*
- 5.2: Pollination and Fertilization - *CC BY 4.0*

6: Plant genetics and breeding - *Undeclared*
- 6.1: The Early History of Genetics - *CC BY-NC 4.0*
- 6.2: Cataloging, Classification, and Deliberate Hybridizations - *CC BY-NC 4.0*
- 6.3: Plant Breeding - *CC BY-NC 4.0*
- 6.4: Genetic Improvement in Cereal Crops and the Green Revolution - *CC BY-NC 4.0*

7: Biotechnology - *Undeclared*
- 7.1: Genetically Engineered Crops - *CC BY-NC 4.0*
- 7.2: Genetic Modification - *CC BY-NC-SA 4.0*
  - 7.2.1: Introduction - *CC BY-NC-SA 4.0*
  - 7.2.2: GMO Food (Activity) - *CC BY-NC-SA 4.0*
- 7.3: GMOs - *CC BY-NC 4.0*

8: Basic chemistry and biochemistry - *Undeclared*
- 8.1: The Chemical Foundation of Life - *CC BY 4.0*
  - 8.1.1: Prelude to The Chemical Foundation of Life - *CC BY 4.0*
  - 8.1.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks - *CC BY 4.0*
  - 8.1.3: Water - *CC BY 4.0*
  - 8.1.4: Carbon - *CC BY 4.0*
  - 8.1.E: The Chemical Foundation of Life (Exercises) - *CC BY 4.0*
- 8.2: Biological Macromolecules - *CC BY 4.0*
  - 8.2.1: Prelude to Biological Macromolecules - *CC BY 4.0*
  - 8.2.2: Synthesis of Biological Macromolecules - *CC BY 4.0*
  - 8.2.3: Carbohydrates - *CC BY 4.0*
  - 8.2.4: Lipids - *CC BY 4.0*
  - 8.2.5: Proteins - *CC BY 4.0*
  - 8.2.6: Nucleic Acids - *CC BY 4.0*
  - 8.2.E: Biological Macromolecules (Exercises) - *CC BY 4.0*
- 8.3: Unit I- The Chemistry of Life - *CC BY 4.0*

9: Photosynthesis - carbon reactions - *Undeclared*
- 9.1: Discovery of Photosynthesis - *CC BY-NC 4.0*
- 9.2: Photosynthesis Overview and Equation - *CC BY-NC 4.0*
- 9.3: Light-independent Reactions - *CC BY-SA 4.0*

10: Photosynthesis - light reactions - *Undeclared*
- 10.1: Energy and ATP - *CC BY-NC 4.0*
- 10.2: The Light-dependent Reactions - *CC BY-SA 4.0*

11: Plant water relations - *Undeclared*
- 11.1: Water Potential - *CC BY-NC 4.0*
- 11.2: Transpiration - *CC BY-SA 4.0*
  - 11.2.1: Adaptations to Reduce Transpiration - *CC BY-SA 4.0*
  - 11.2.2: Stomatal Opening and Closure - *CC BY-NC 4.0*
- 11.3: Cohesion-Tension Theory - *CC BY-SA 4.0*
- 11.4: Water Absorption - *CC BY-SA 4.0*
- 11.5: Water Transport - *CC BY-SA 4.0*
- 11.6: Transport of Water and Solutes in Plants - *CC BY 4.0*

12: Photosynthetic adaptations - *Undeclared*

- 12.1: Photorespiration and Photosynthetic Pathways - *CC BY-SA 4.0*
- 12.2: CO2 uptake - C4 and CAM Pathways - *Undeclared*

13: Respiration and metabolism - *Undeclared*
- 13.1: Aerobic Cellular Respiration - *CC BY-NC 4.0*

14: Mineral nutrition - *Undeclared*
- 14.1: Prelude to Soil and Plant Nutrition - *CC BY 4.0*
- 14.2: Nutritional Requirements of Plants - *CC BY 4.0*
- 14.3: The Soil - *CC BY 4.0*
- 14.4: Nutritional Adaptations of Plants - *CC BY 4.0*
- 14.E: Soil and Plant Nutrition (Exercises) - *CC BY 4.0*

15: Functional morphology and anatomy - *Undeclared*
- 15.1: Translocation (Assimilate Transport) - *CC BY-NC 4.0*

16: Environmental plant biology - *Undeclared*
- 16.1: Environmental Responses - *CC BY-NC 4.0*
  - 16.1.1: Tropisms - *CC BY-NC-SA 4.0*
  - 16.1.2: Flowering - *CC BY-SA 4.0*
  - 16.1.3: Photoperiodism - *CC BY-NC 4.0*
  - 16.1.4: Etiolation and Shade Avoidance - *CC BY-NC 4.0*
  - 16.1.5: Dormancy - *CC BY-NC-SA 4.0*
  - 16.1.6: Chapter Summary - *CC BY-NC 4.0*
- 16.2: Plant Sensory Systems and Responses - *CC BY 4.0*

17: Measuring and analyzing plants - *Undeclared*

18: Predicting plants - *Undeclared*

19: Biotic interactions - *Undeclared*
- 19.1: Industrial Agriculture - *CC BY-SA 4.0*
- 19.2: Sustainable Agriculture - *CC BY-SA 4.0*

20: Climate change and plants - *Undeclared*
- 20.1: Earth's Energy Budget - *CC BY-SA 4.0*
- 20.2: The Greenhouse Effect - *CC BY-SA 4.0*
- 20.3: Climate and the Effects of Global Climate Change - *CC BY 4.0*
- 20.4: Soil and Water Conservation - *CC BY 3.0*

Back Matter - *Undeclared*
- Index - *Undeclared*
- Glossary - *Undeclared*
- Detailed Licensing - *Undeclared*
- Detailed Licensing - *Undeclared*