INTRODUCTION TO PLANT SCIENCE



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Intro to Plant Science

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1: THE PROCESS OF SCIENCE

Learning Objectives

- Develop a strong understanding of the scientific method and its application in plant science.
- Learn how scientists formulate and test hypotheses.
- Understand the difference between inductive and deductive reasoning.
- Explore how experimentation and peer review contribute to scientific progress.

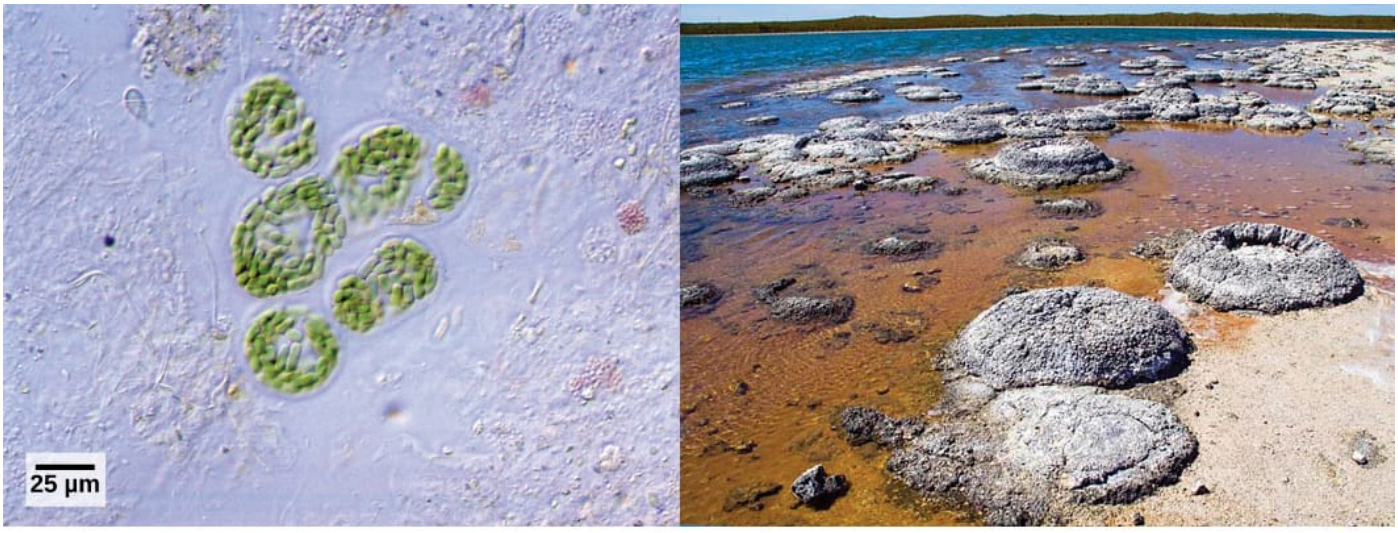
Science isn't just about memorizing facts—it's a way of exploring and understanding the world around us. In Chapter 1, we will learn that science is a process built on curiosity, creativity, and careful thinking. Scientists ask questions, make observations, and test ideas through experiments. They use both inductive reasoning (looking at patterns to form ideas) and deductive reasoning (using general rules to predict outcomes).

1.1: The Process of Science
1.2: Science and Experimentation

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1.1: The Process of Science

Like geology, physics, and chemistry, biology is a science that gathers knowledge about the natural world. Specifically, biology is the study of life. The discoveries of biology are made by a community of researchers who work individually and together using agreed-on methods. In this sense, biology, like all sciences is a social enterprise like politics or the arts.



(a) (b)

Figure 1.1.1**:** Formerly called blue-green algae, the (a) cyanobacteria seen through a light microscope are some of Earth's oldest life forms. These (b) stromatolites along the shores of Lake Thetis in Western Australia are ancient structures formed by the layering of cyanobacteria in shallow waters. (credit a: modification of work by NASA; scale-bar data from Matt Russell; credit b: modification of work by Ruth Ellison)

The methods of science include careful observation, record keeping, logical and mathematical reasoning, experimentation, and submitting conclusions to the scrutiny of others. Science also requires considerable imagination and creativity; a well-designed experiment is commonly described as elegant, or beautiful. Like politics, science has considerable practical implications and some science is dedicated to practical applications, such as the prevention of disease (Figure 1.1.2). Other science proceeds largely motivated by curiosity. Whatever its goal, there is no doubt that science, including biology, has transformed human existence and will continue to do so.

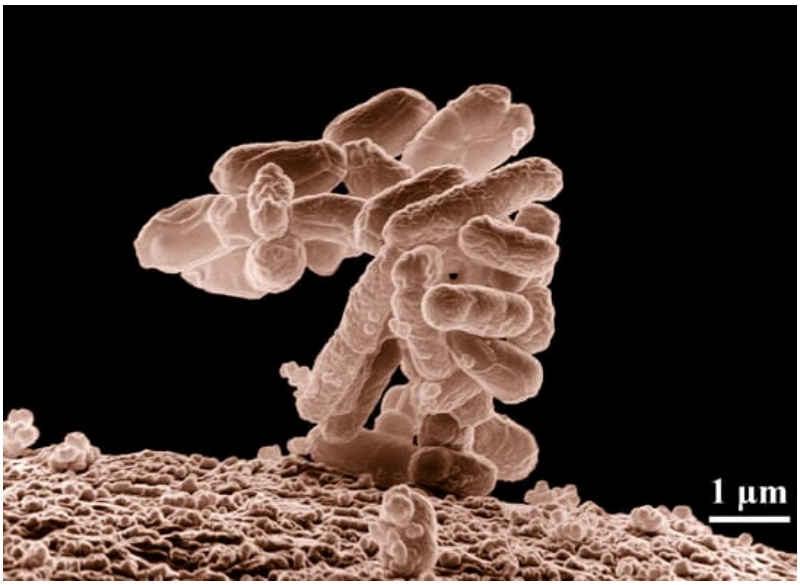


Figure 1.1.2**:** Biologists may choose to study *Escherichia coli* (*E. coli*), a bacterium that is a normal resident of our digestive tracts but which is also sometimes responsible for disease outbreaks. In this micrograph, the bacterium is visualized using a scanning electron microscope and digital colorization. (credit: Eric Erbe; digital colorization by Christopher Pooley, USDA-ARS)

The Nature of Science

Biology is a science, but what exactly is science? What does the study of biology share with other scientific disciplines? Science (from the Latin s*cientia,* meaning "knowledge") can be defined as knowledge about the natural world.

Science is a very specific way of learning, or knowing, about the world. The history of the past 500 years demonstrates that science is a very powerful way of knowing about the world; it is largely responsible for the technological revolutions that have taken place during this time. There are however, areas of knowledge and human experience that the methods of science cannot be applied to. These include such things as answering purely moral questions, aesthetic questions, or what can be generally categorized as spiritual questions. Science has cannot investigate these areas because they are outside the realm of material phenomena, the phenomena of matter and energy, and cannot be observed and measured.

The scientific method is a method of research with defined steps that include experiments and careful observation. The steps of the scientific method will be examined in detail later, but one of the most important aspects of this method is the testing of hypotheses. A hypothesis is a suggested explanation for an event, which can be tested. Hypotheses, or tentative explanations, are generally produced within the context of a scientific theory. A scientific theory is a generally accepted, thoroughly tested and confirmed explanation for a set of observations or phenomena. Scientific theory is the foundation of scientific knowledge. In addition, in many scientific disciplines (less so in biology) there are scientific laws, often expressed in mathematical formulas, which describe how elements of nature will behave under certain specific conditions. There is not an evolution of hypotheses through theories to laws as if they represented some increase in certainty about the world. Hypotheses are the day-to-day material that scientists work with and they are developed within the context of theories. Laws are concise descriptions of parts of the world that are amenable to formulaic or mathematical description.

Natural Sciences

What would you expect to see in a museum of natural sciences? Frogs? Plants? Dinosaur skeletons? Exhibits about how the brain functions? A planetarium? Gems and minerals? Or maybe all of the above? Science includes such diverse fields as astronomy, biology, computer sciences, geology, logic, physics, chemistry, and mathematics (Figure 1.1.3). However, those fields of science related to the physical world and its phenomena and processes are considered natural sciences. Thus, a museum of natural sciences might contain any of the items listed above.

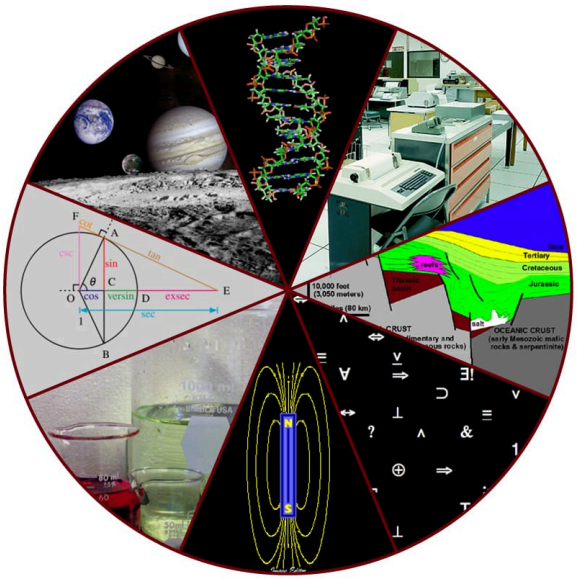


Figure 1.1.3**:** Some fields of science include astronomy, biology, computer science, geology, logic, physics, chemistry, and mathematics. (credit: "Image Editor"/Flickr)

There is no complete agreement when it comes to defining what the natural sciences include. For some experts, the natural sciences are astronomy, biology, chemistry, earth science, and physics. Other scholars choose to divide natural sciences into life sciences, which study living things and include biology, and physical sciences, which study nonliving matter and include astronomy, physics, and chemistry. Some disciplines such as biophysics and biochemistry build on two sciences and are interdisciplinary.

Scientific Inquiry

One thing is common to all forms of science: an ultimate goal “to know.” Curiosity and inquiry are the driving forces for the development of science. Scientists seek to understand the world and the way it operates. Two methods of logical thinking are used: inductive reasoning and deductive reasoning.

Inductive reasoning is a form of logical thinking that uses related observations to arrive at a general conclusion. This type of reasoning is common in descriptive science. A life scientist such as a biologist makes observations and records them. These data can be qualitative (descriptive) or quantitative (consisting of numbers), and the raw data can be supplemented with drawings, pictures, photos, or videos. From many observations, the scientist can infer conclusions (inductions) based on evidence. Inductive reasoning involves formulating generalizations inferred from careful observation and the analysis of a large amount of data. Brain studies often work this way. Many brains are observed while people are doing a task. The part of the brain that lights up, indicating activity, is then demonstrated to be the part controlling the response to that task.

Deductive reasoning or deduction is the type of logic used in hypothesis-based science. In deductive reasoning, the pattern of thinking moves in the opposite direction as compared to inductive reasoning. Deductive reasoning is a form of logical thinking that uses a general principle or law to forecast specific results. From those general principles, a scientist can extrapolate and predict the specific results that would be valid as long as the general principles are valid. For example, a prediction would be that if the climate is becoming warmer in a region, the distribution of plants and animals should change. Comparisons have been made between distributions in the past and the present, and the many changes that have been found are consistent with a warming climate. Finding the change in distribution is evidence that the climate change conclusion is a valid one.

Both types of logical thinking are related to the two main pathways of scientific study: descriptive science and hypothesis-based science. Descriptive (or discovery) science aims to observe, explore, and discover, while hypothesis-based science begins with a specific question or problem and a potential answer or solution that can be tested. The boundary between these two forms of study is often blurred, because most scientific endeavors combine both approaches. Observations lead to questions, questions lead to forming a hypothesis as a possible answer to those questions, and then the hypothesis is tested. Thus, descriptive science and hypothesis-based science are in continuous dialogue.

Hypothesis Testing

Biologists study the living world by posing questions about it and seeking science-based responses. This approach is common to other sciences as well and is often referred to as the scientific method. The scientific method was used even in ancient times, but it was first documented by England's Sir Francis Bacon (1561–1626) (Figure 1.1.4), who set up inductive methods for scientific inquiry. The scientific method is not exclusively used by biologists but can be applied to almost anything as a logical problem-solving method.



Figure 1.1.4: Sir Francis Bacon is credited with being the first to document the scientific method.

The scientific process typically starts with an observation (often a problem to be solved) that leads to a question. Let's think about a simple problem that starts with an observation and apply the scientific method to solve the problem. One Monday morning, a student arrives at class and quickly discovers that the classroom is too warm. That is an observation that also describes a problem: the classroom is too warm. The student then asks a question: "Why is the classroom so warm?"

Recall that a hypothesis is a suggested explanation that can be tested. To solve a problem, several hypotheses may be proposed. For example, one hypothesis might be, "The classroom is warm because no one turned on the air conditioning." But there could be other responses to the question, and therefore other hypotheses may be proposed. A second hypothesis might be, "The classroom is warm because there is a power failure, and so the air conditioning doesn't work."

Once a hypothesis has been selected, a prediction may be made. A prediction is similar to a hypothesis but it typically has the format "If . . . then . . . ." For example, the prediction for the first hypothesis might be, "*If* the student turns on the air conditioning, *then* the classroom will no longer be too warm."

A hypothesis must be testable to ensure that it is valid. For example, a hypothesis that depends on what a bear thinks is not testable, because it can never be known what a bear thinks. It should also be falsifiable, meaning that it can be disproven by experimental results. An example of an unfalsifiable hypothesis is "Botticelli's *Birth of Venus* is beautiful." There is no experiment that might show this statement to be false. To test a hypothesis, a researcher will conduct one or more experiments designed to eliminate one or more of the hypotheses. This is important. A hypothesis can be disproven, or eliminated, but it can never be proven. Science does not deal in proofs like mathematics. If an experiment fails to disprove a hypothesis, then we find support for that explanation, but this is not to say that down the road a better explanation will not be found, or a more carefully designed experiment will be found to falsify the hypothesis.

Each experiment will have one or more variables and one or more controls. A variable is any part of the experiment that can vary or change during the experiment. A control is a part of the experiment that does not change. Look for the variables and controls in the example that follows. As a simple example, an experiment might be conducted to test the hypothesis that phosphate limits the growth of algae in freshwater ponds. A series of artificial ponds are filled with water and half of them are treated by adding phosphate each week, while the other half are treated by adding a salt that is known not to be used by algae. The variable here is the phosphate (or lack of phosphate), the experimental or treatment cases are the ponds with added phosphate and the control

ponds are those with something inert added, such as the salt. Just adding something is also a control against the possibility that adding extra matter to the pond has an effect. If the treated ponds show lesser growth of algae, then we have found support for our hypothesis. If they do not, then we reject our hypothesis. Be aware that rejecting one hypothesis does not determine whether or not the other hypotheses can be accepted; it simply eliminates one hypothesis that is not valid (Figure 1.1.5). Using the scientific method, the hypotheses that are inconsistent with experimental data are rejected.

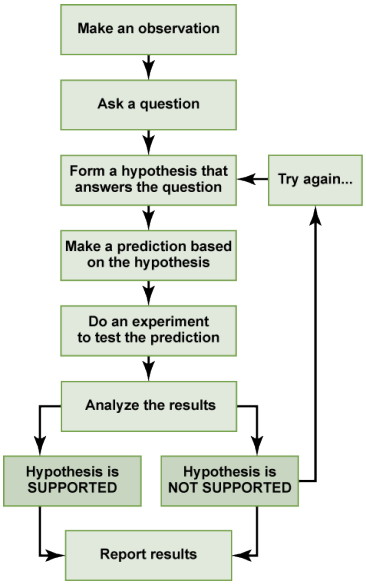


Figure 1.1.5**:** The scientific method is a series of defined steps that include experiments and careful observation. If a hypothesis is not supported by data, a new hypothesis can be proposed.

Example 1.1.1

In the example below, the scientific method is used to solve an everyday problem. Which part in the example below is the hypothesis? Which is the prediction? Based on the results of the experiment, is the hypothesis supported? If it is not supported, propose some alternative hypotheses.

1. My toaster doesn't toast my bread.
2. Why doesn't my toaster work?
3. There is something wrong with the electrical outlet.
4. If something is wrong with the outlet, my coffeemaker also won't work when plugged into it.
5. I plug my coffeemaker into the outlet.
6. My coffeemaker works.

Solution

The hypothesis is #3 (there is something wrong with the electrical outlet), and the prediction is #4 (if something is wrong with the outlet, then the coffeemaker also won't work when plugged into the outlet). The original hypothesis is not supported, as the coffee maker works when plugged into the outlet. Alternative hypotheses may include (1) the toaster might be broken or (2) the toaster wasn't turned on.

In practice, the scientific method is not as rigid and structured as it might at first appear. Sometimes an experiment leads to conclusions that favor a change in approach; often, an experiment brings entirely new scientific questions to the puzzle. Many times, science does not operate in a linear fashion; instead, scientists continually draw inferences and make generalizations, finding patterns as their research proceeds. Scientific reasoning is more complex than the scientific method alone suggests.

Basic and Applied Science

The scientific community has been debating for the last few decades about the value of different types of science. Is it valuable to pursue science for the sake of simply gaining knowledge, or does scientific knowledge only have worth if we can apply it to

solving a specific problem or bettering our lives? This question focuses on the differences between two types of science: basic science and applied science.

Basic science or “pure” science seeks to expand knowledge regardless of the short-term application of that knowledge. It is not focused on developing a product or a service of immediate public or commercial value. The immediate goal of basic science is knowledge for knowledge’s sake, though this does not mean that in the end it may not result in an application.

In contrast, applied science or “technology,” aims to use science to solve real-world problems, making it possible, for example, to improve a crop yield, find a cure for a particular disease, or save animals threatened by a natural disaster. In applied science, the problem is usually defined for the researcher.

Some individuals may perceive applied science as “useful” and basic science as “useless.” A question these people might pose to a scientist advocating knowledge acquisition would be, “What for?” A careful look at the history of science, however, reveals that basic knowledge has resulted in many remarkable applications of great value. Many scientists think that a basic understanding of science is necessary before an application is developed; therefore, applied science relies on the results generated through basic science. Other scientists think that it is time to move on from basic science and instead to find solutions to actual problems. Both approaches are valid. It is true that there are problems that demand immediate attention; however, few solutions would be found without the help of the knowledge generated through basic science.

One example of how basic and applied science can work together to solve practical problems occurred after the discovery of DNA structure led to an understanding of the molecular mechanisms governing DNA replication. Strands of DNA, unique in every human, are found in our cells, where they provide the instructions necessary for life. During DNA replication, new copies of DNA are made, shortly before a cell divides to form new cells. Understanding the mechanisms of DNA replication enabled scientists to develop laboratory techniques that are now used to identify genetic diseases, pinpoint individuals who were at a crime scene, and determine paternity. Without basic science, it is unlikely that applied science would exist.

Another example of the link between basic and applied research is the Human Genome Project, a study in which each human chromosome was analyzed and mapped to determine the precise sequence of DNA subunits and the exact location of each gene. (The gene is the basic unit of heredity; an individual’s complete collection of genes is his or her genome.) Other organisms have also been studied as part of this project to gain a better understanding of human chromosomes. The Human Genome Project (Figure 1.1.6) relied on basic research carried out with non-human organisms and, later, with the human genome. An important end goal eventually became using the data for applied research seeking cures for genetically related diseases.

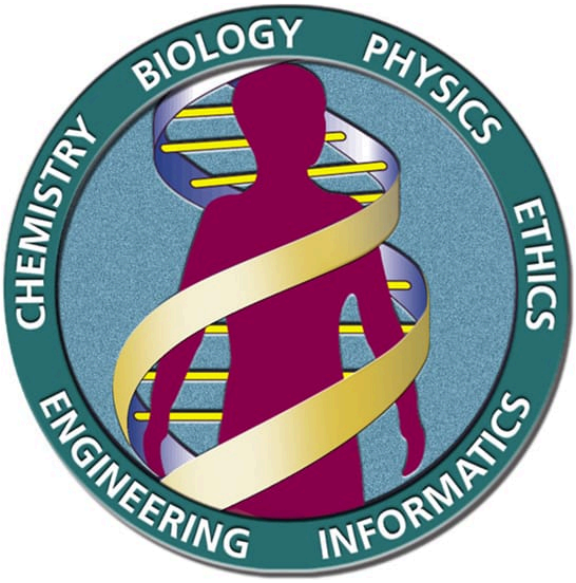


Figure 1.1.6**:** The Human Genome Project was a 13-year collaborative effort among researchers working in several different fields of science. The project was completed in 2003. (credit: the U.S. Department of Energy Genome Programs)

While research efforts in both basic science and applied science are usually carefully planned, it is important to note that some discoveries are made by serendipity, that is, by means of a fortunate accident or a lucky surprise. Penicillin was discovered when biologist Alexander Fleming accidentally left a petri dish of *Staphylococcus* bacteria open. An unwanted mold grew, killing the bacteria. The mold turned out to be *Penicillium*, and a new antibiotic was discovered. Even in the highly organized world of

science, luck—when combined with an observant, curious mind—can lead to unexpected breakthroughs.

Reporting Scientific Work

Whether scientific research is basic science or applied science, scientists must share their findings for other researchers to expand and build upon their discoveries. Communication and collaboration within and between sub disciplines of science are key to the advancement of knowledge in science. For this reason, an important aspect of a scientist's work is disseminating results and communicating with peers. Scientists can share results by presenting them at a scientific meeting or conference, but this approach can reach only the limited few who are present. Instead, most scientists present their results in peer-reviewed articles that are published in scientific journals. Peer-reviewed articles are scientific papers that are reviewed, usually anonymously by a scientist's colleagues, or peers. These colleagues are qualified individuals, often experts in the same research area, who judge whether or not the scientist's work is suitable for publication. The process of peer review helps to ensure that the research described in a scientific paper or grant proposal is original, significant, logical, and thorough. Grant proposals, which are requests for research funding, are also subject to peer review. Scientists publish their work so other scientists can reproduce their experiments under similar or different conditions to expand on the findings. The experimental results must be consistent with the findings of other scientists.

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Summary

Biology is the science that studies living organisms and their interactions with one another and their environments. Science attempts to describe and understand the nature of the universe in whole or in part. Science has many fields; those fields related to the physical world and its phenomena are considered natural sciences.

A hypothesis is a tentative explanation for an observation. A scientific theory is a well-tested and consistently verified explanation for a set of observations or phenomena. A scientific law is a description, often in the form of a mathematical formula, of the behavior of an aspect of nature under certain circumstances. Two types of logical reasoning are used in science. Inductive reasoning uses results to produce general scientific principles. Deductive reasoning is a form of logical thinking that predicts results by applying general principles. The common thread throughout scientific research is the use of the scientific method. Scientists present their results in peer-reviewed scientific papers published in scientific journals.

Science can be basic or applied. The main goal of basic science is to expand knowledge without any expectation of short-term practical application of that knowledge. The primary goal of applied research, however, is to solve practical problems.

Glossary

applied science
: a form of science that solves real-world problems

basic science
: science that seeks to expand knowledge regardless of the short-term application of that knowledge

control
: a part of an experiment that does not change during the experiment

deductive reasoning
: a form of logical thinking that uses a general statement to forecast specific results

descriptive science
: a form of science that aims to observe, explore, and find things out

falsifiable
: able to be disproven by experimental results

hypothesis
a suggested explanation for an event, which can be tested

hypothesis-based science
a form of science that begins with a specific explanation that is then tested

inductive reasoning
a form of logical thinking that uses related observations to arrive at a general conclusion

life science
a field of science, such as biology, that studies living things

natural science
a field of science that studies the physical world, its phenomena, and processes

peer-reviewed article
a scientific report that is reviewed by a scientist's colleagues before publication

physical science
a field of science, such as astronomy, physics, and chemistry, that studies nonliving matter

science
knowledge that covers general truths or the operation of general laws, especially when acquired and tested by the scientific method

scientific law
a description, often in the form of a mathematical formula, for the behavior of some aspect of nature under certain specific conditions

scientific method
a method of research with defined steps that include experiments and careful observation

scientific theory
a thoroughly tested and confirmed explanation for observations or phenomena

variable
a part of an experiment that can vary or change

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1.2: Science and Experimentation

Learning objectives

- Describe why science is considered a discipline of philosophy.
- Summarize the four basic types of experiments.
- Apply the principles of experimental design in this course and in your daily life.

Thinking about science

The primary goal of this section is to help you think about the nature of science. You might be taking this course to fulfill an undergraduate requirement for a biology course. This course fulfills that requirement because we investigate the process behind using science as a way of learning about the natural world around us. If you're starting down the path to becoming a plant scientist, understanding the nature of science will be essential for you in your career

Regardless of whether you're going to pursue a career as a scientist, now is a good time reflect on the nature of science, and to understand how scientific thinking can become a strategy for resolving many issues that you confront during daily life.

Watch this video about connecting science and experimentation to real life:

Scientific inquiry

While "science" is a word commonly used in our culture, in popular use it is rarely spoken of as a philosophy. By identifying science as a philosophy we are taking an epistemic view, one focusing on how knowledge is acquired.

At its core, science is a mode of inquiry: a way of acquiring new knowledge about the world around us and a strategy for understanding the inner workings of elements in that world. Scientists believe that if we follow the principles of this philosophy we will continue to expand our knowledge about how things work in the world around us. This systematic approach is called the "scientific method."

There are two key steps in the scientific method:

- Hypothesis building through reflective observation.
- Hypothesis testing through experimentation.

A "hypothesis" is a question or proposed explanation made on the basis of limited evidence and used as a starting point for experimentation. Experimentation is commonly equated with science—rightly so, because hypotheses evaluated on the basis of evidence generated through experiments. Experimentation, however, isn't the whole story. Science—including the development and testing of new hypotheses—is also a creative endeavor.

Watch this video about scientific inquiry:

Scientific inquiry has generated a vast body of knowledge about the world around us. Your school science classes might have required you to memorize facts and relationships, and pay attention to detail. Sometimes such memorization leads students to believe that science is just an accumulation of facts rather than the process behind discovering all of that information.

Scientific discovery builds on what is already known. Even the most accomplished scientists initially approach a problem by learning what is already known. Armed with that information, they then apply their own creativity to form new hypotheses about something they have observed, and design experiments to test those hypotheses. They also communicate their results publicly so that others can benefit from their work and have the opportunity to challenge conclusions. In this way, science builds on itself.

The foundational knowledge you learn in science classes prepares you to develop and test hypotheses and to make new discoveries of your own. While a good memory may help you pass a science classes, you will absorb a body of knowledge more

effectively when you learn how facts fit and work together in systems rather than learning through the brute force of memorization.

In this section we work from the point of view that science is a way of acquiring knowledge—a mode of inquiry—and that this mode of inquiry follows a process called the scientific method. Those who follow the philosophy of science:

- Use it to understand how the natural world works.
- Start by learning what is already known.
- Carefully observe the subjects of their scientific inquiry and look for details about form, function, and interaction with the environment.
- Develop hypotheses about the inner workings of natural phenomena not yet understood.
- Test their hypotheses by making observations, conducting experiments and collecting and evaluating evidence.
- Communicate with others about their hypotheses, experiments, and the outcomes of their studies so that others can repeat, validate, and build upon their work.

Although science is typically used to understand how the natural world works, it is also regularly applied to the development of new technologies that are based on these natural phenomena and to the solving of problems associated with the natural world.

Putting the scientific method to work

As noted, the scientific method relies on building hypotheses and then testing them through experimentation. In the lab section of this course you will develop hypotheses about the effects of various treatments on propagation success and then conduct experiments to test those hypotheses. Because experimentation is such a key component of the scientific method, we'll spend time characterizing and examining four types of experimentation and explore whether they are part of the scientific method. While each is valuable when applied in the right circumstances, only one clearly follows each step of the scientific method to uncover new knowledge about the natural world.

Types of experiments

The types of experimentation we will cover are:

- Demonstration
- Evaluation
- Exploration
- Discovery

Demonstration experiments



Many experiments conducted in lab courses are demonstration experiments. Photo by Salish Sea Expeditions. CC BY-NC-ND 2.0

Demonstration experiments are a classic method used in educational settings to help students learn and understand known relationships already discovered by others. Learners will usually have had prior exposure to the relationships through preliminary observations, lectures, reading, and discussions, and will have some sense of what the experimental outcome might be.

Good demonstration experiments actively involve the learner, who manipulates the experimental materials, applies the treatments, and observes the outcomes, then gathers, analyzes, and interprets the resulting data. Poor demonstration experiments, in contrast, make learners only passive witnesses to something done by an expert at the front of the classroom.

In the plant propagation labs for this course, you will be actively engaged in demonstration experiments. Although you won't be creating new knowledge, the knowledge will likely be new to you. The hands-on experience of conducting the experiments will help you to learn the concepts more effectively than if you only read a textbook or listened to a lecture. The techniques you learn and use in demonstration experiments often contribute to the learning experience as much as the relationships revealed at the experiment's conclusion. Employing these techniques will help you gain an understanding of many biological functions, such as the production of adventitious roots and mechanisms for seed dispersal.

While demonstration experiments are valuable for actively learning a body of scientific knowledge previously discovered and communicated by others, the experience is specifically orchestrated for teaching and learning, not for the discovery of new information. Yet since the knowledge is new to the learner, it can still bring the joy of personal discovery and a sense of accomplishment.

In summary, demonstration experiments:

- Are designed for teaching and learning.
- Address relationships that may be new to you, but are otherwise known.
- In their best forms, actively involve the learner.
- May emphasize experimental techniques, in addition to outcomes, as part of the learning experience.
- Are not the types of experiments that are at the core of practicing science as a way to uncover new knowledge.

Evaluation experiments

Evaluation experiments are designed to help us make decisions, and to choose from a number of options. They might, for instance, help us determine the efficacy of a new treatment relative to a known treatment, or decide on further experimentation. An evaluation experiment will highlight a compound, a technique, a piece of equipment, or an organism, and will include a control and/or other alternatives.

Evaluation experiments are common in horticultural and agronomic research, where the purpose of the experiment is to identify, for example, the best cultivar, production method, pest control, fertility regime, or light intensity for growing a crop. Correct experimental design is crucial for assuring that conclusions from the experiment are meaningful and credible.



This field experiment is testing different living mulches between rows of strawberries. Photo by University of Minnesota West Central Research and Outreach Center.

These experiments are typically used in the development of new technologies to identify the best method for the desired purpose

(e.g., which pesticides are effective against the target insect, but not harmful to non-target insects). They are not used to discover new knowledge about how the world works, as they typically don't advance our understanding of the natural world. The information from an evaluation experiment might, however, point the way to additional experimentation that does help us discover new knowledge. This is particularly true if the outcome of an evaluation experiment is unexpected or novel.

In summary, evaluation experiments:

- Are used to help in decision-making.
- Help users choose a winner or determine efficacy relative to other alternatives.
- Are commonly used when evaluating and recommending horticultural production methods.
- Can be useful in solving problems and developing technologies.
- Require proper experimental design (e.g., comparison to a control) for credibility and meaningfulness.

Exploration experiments

Some scientists specialize in observing and cataloging nature, and some, like members of the group that discovered a new species of hominid, Homo naledi in a South African cave, aggressively search for previously unknown phenomena. In the botanical realm, such scientists study the diversity of organisms within habitats, discover new species, or are in other ways very skilled in "seeing" nature. Explorer-scientists recognize and appreciate detail and can identify the enormous diversity among plants by comparing characteristics that might be overlooked by others. They may also have the capacity to recognize possible interrelationships among organisms and with habitats, making their work particularly important to science. They might notice, for instance, that a particular species of plant is commonly found in wet areas but not in dry, or that a particular vegetable tastes sweeter when grown at higher altitudes than when grown closer to sea level. They don't confirm the cause of these relationships, but are the first to notice them.



This scientist is collecting plants in Ecuador to identify unknown species and to determine relatedness to other plants. Photo by Dr. Eric Tepe, University of Cincinnati.

Explorers' observations are essential to stimulating the development of sound, testable hypotheses. The possible relationships they propose must be tested to determine whether those relationships actually exist, or are artifacts of other effects. Explorers help develop hypotheses, but the work of exploration, cataloging, and seeing possible relationships don't prove or disprove the hypotheses or necessarily generate new knowledge about relationships. The work does, however, result in new information about the existence of the object or phenomenon itself. An exception is exploration done to test a hypothesis, such as a mission to test the hypothesis that a particular type of ecosystem is required for reproduction of a particular plant species.

Scientists must resist jumping to conclusions based on exploration and observation alone. If you see two people together many times, for example, you might conclude that they are a romantic couple, when in fact they are brother and sister. Relationships hypothesized as a result of exploration and observation must be experimentally tested before they are accepted or rejected.

Exploration experiments uncover new things, many of which can be exciting and eventually change our view of the world. While one of their greatest values is that they lead to the development of new and stronger hypotheses about how the world works, they go so far as to test those hypotheses or fully engage in the cycle of knowledge generation associated with the scientific method. Additional experiments based on this new information are required to put this new information in context and to advance our understanding of how the natural world works.

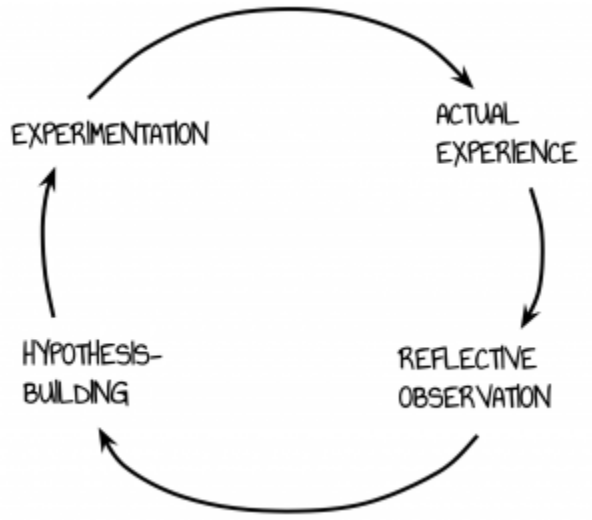
In summary then, exploration experiments:

- Focus on detailed observation of organisms and habitats.
- Increase our knowledge of the natural world.
- Identify potential relationships that need to be tested.
- Are essential to sound and testable hypothesis-building.

Discovery experiments

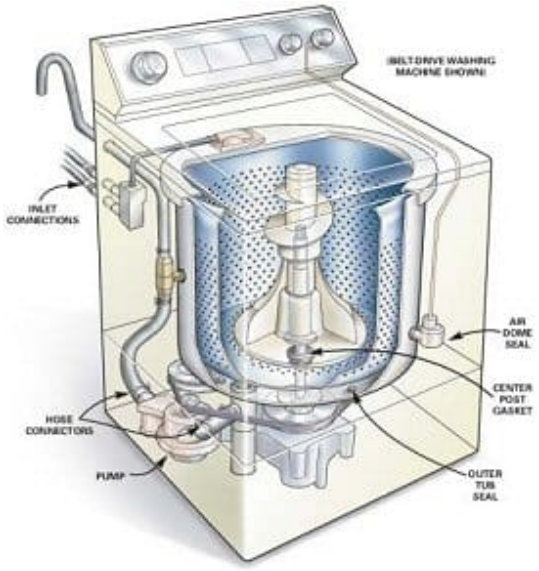
Discovery experiments are central to the use of the scientific method in tasks ranging from problem solving to the discovery of new knowledge. They focus on uncovering new relationships and solving problems, follow the scientific method, test hypotheses and their predicted outcomes, and utilize a careful design in order to maintain meaningfulness and credibility.

The similarity between the scientific method and Kolb's Experiential Learning Cycle is not an accident. The scientific method is a practical strategy based on how we sense and experience the world around us and used to solve problems encountered during those experiences.



The scientific method is a great example of the experiential learning theory. Illustration by Emily Tepe.

The diagram above illustrates a combination of the scientific method and Kolb's four-step experiential learning, describing a cyclic process for solving problems that can be applied to disciplines as diverse as molecular biology, global warming, and even appliance repair. While you might initially think that appliance repair doesn't belong in that list, the difference is one of application, not method. Though far removed from the esoteric scientific discoveries we associate with scientific method, appliance repair follows the same steps. Appliances are often, and quite literally, boxes, where you don't know what is going on inside. But what's going on inside is knowable, and through that knowledge comes repair.



We can apply the scientific method to everyday problems like figuring out why a washing machine isn't working. © HomeTips.com.

The learning/problem solving/scientific process could theoretically start anywhere in Kolb's cycle. But it will likely start with a problem that needs to be solved, something you don't understand but would like to know more about. You become aware that there is a problem or that you lack understanding because you have an experience where you observe something and then step back and said, "I wonder how that works," or perhaps, "why is that broken?" Through observation you develop a sufficiently adequate description of the problem to start doing some research on what is already known.

With a good description of the problem in hand, you can begin to review what is known through the work of others, and think about what might be going on in your situation and how your new understanding can be applied to the problem. This is "reflective observation." It isn't just sitting back and thinking in a vacuum. You need raw material for your mind to work on, and that only comes through the tough task of gathering and engaging with the background information. There is a very important quiet phase in this process when you let your mind assemble and sort through ideas until alternatives begin to emerge that might lead to a solution. Talking with others and sharing ideas is an important part of this quiet phase.

Sometimes the alternatives are no- brainers (blown fuse?), and sometimes they're more creative (residue from the wrong detergent gunking up the water level sensor?). Regardless of their simplicity or complexity, these become hypotheses that need to be tested. The hypothesis-building stage includes both a statement of how something works or why it isn't working, and predictions about what might happen if the hypothesis is true. In appliance repair, for example, the prediction will likely be that the appliance will function normally. In horticultural molecular biology, it might be that you will see accumulation of a particular type of fatty acid in the cotyledons.

You put the hypothesis to the test by designing an experiment that assesses whether your predictions were right. If the outcome doesn't match your prediction, you reject the hypothesis (the fuse was ok, so that wasn't the problem). If the outcome does match your prediction, you tentatively accept the hypothesis pending further observation (when the fuse was replaced the washing machine worked again, so it might have been a blown fuse, but on the other hand maybe it was just because the motor had time to cool down). As with evaluation experimentation, experimental design is important in assuring that the conclusions from the experiment are meaningful and credible.

Experimentation leads to new experiences and an incremental increase in knowledge, and then the cycle begins again.

In summary, discovery experiments:

- Focus on uncovering new relationships and solving problems.
- Follow scientific method.
- Test hypotheses and their predicted outcomes.
- Utilize a careful design in order to maintain meaningfulness and credibility.

Summary

Of the four types of experiments, only the discovery experiments are core to the process of science in the narrow sense of being a way of acquiring new knowledge. The other three types of experimentation are still important; demonstration and evaluation experiments are valuable for learning and decision-making and for technology development, and exploration experiments are essential for developing testable hypotheses. But discovery experiments are core to science.

Remember: the methodology of effective washing machine repair, when applied to what is unknown about the physical world, is the methodology of science. It's not esoteric; it's good appliance repair.

You might argue that, when applied to a broken washing machine, a discovery experiment results in knowledge that is probably already known by those skilled in appliance repair, so it isn't really new knowledge about how the world works. That's a fair criticism. Use of the scientific method can result in new knowledge about how the world works, but whether it uncovers new knowledge depends on the object of experimentation.

Review questions

An interactive H5P element has been excluded from this version of the text. You can view it online here:
https://open.lib.umn.edu/horticulture/?p=94#h5p-3

Experimental design

The methods for designing experiments are carefully studied and often discipline-specific. Methods used in molecular biology, for instance, will be somewhat different from those used in chemistry or in field evaluations of horticultural plants. There are, however, some generalizations we can make about good experimental designs.

Emphasize comparisons

Experiments include more than just one treatment. "Treatment" refers to the factor that you are varying in your experiment—for example, different cultivars of tomato, different fertilizers, or different amounts of light. Experimental designs incorporate comparison of treatments. You usually compare the treatments to one another and often to a control, which is either the application of no treatment or the application of a customary or standard level of treatment.

If you grow a particular type of tomato in your garden, and find that it produces tasty fruit, would you declare it to be the best tomato variety you could grow? Certainly not. You couldn't even say with certainty that it was the best tomato variety you have ever grown (unless it is the only one you have grown). Next year, however, you could grow that tomato as your control, and grow two other varieties that your neighbors like, and compare fruit quality (appearance, flavor, yield, sugar content). You could then say something definitive about the three tomato varieties because you have compared them to each other after growing them next to each other in the same year and environment.

Replicate treatments

The same treatment is applied to more than one "experimental unit"—the object that receives the treatment. In the example above, the tomato plant is the experimental unit, and you would perhaps plant two or three seedlings of each tomato variety rather than just one. Think of a treatment as something like a fertilizer spread on a patch of land. The patch of land is the experimental unit, while the fertilizer is the treatment.

By applying the treatment to more than one experimental unit you can estimate the variation you get when two experimental units are treated the same, and compare this to the variation when experimental units are given different treatments. If the treatments actually differ in their effectiveness, you would expect the variation between experimental units given different treatments to be much greater than the variation between those given the same treatment. This is one of the fundamental ways in which experiments are statistically analyzed and treatments declared significantly different or not.

Randomize treatments

Once you know how many treatments you are going to apply, and how many replications you want, the product of these two quantities (# treatments × # replications) equals the number of experimental units you need. For instance, if you have three fertilizers you want to test, plus a control, you have four treatments. If you want three replications of each treatment, then you 4 treatments x 3 replications = 12 experimental units or patches of land where you will apply the fertilizers. The treatments will be randomly assigned to each experimental unit (patch of land). This is done using a random number table and is not just haphazard picking. Randomization helps minimize any bias you haven't recognized in advance and controlled for in other ways.

Review questions

1. What are two types of control treatments?
2. Does increasing the number of replications increase the number of treatments or the number of experimental units?
3. Can you think of an example of how randomization can protect against bias?

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2: THE IMPORTANCE OF PLANTS

Learning Objectives

- Recognize the vital roles plants play in ecosystems, agriculture, and human society.
- Investigate how plants impact food production and climate regulation.
- Examine the historical and modern significance of plant-based industries.
- Discuss plant adaptations that contribute to environmental resilience.

Plants are essential to human life. This chapter explores how agriculture began, how crops were domesticated, and how plants have shaped human societies. From food and medicine to clothing, shelter, and culture, plants provide the foundation of our daily lives. The chapter highlights the role of women in early farming, the global origins of major crops, and the diversity of edible plant parts we consume. It also explains how how ancient seedless plants contributed to modern energy sources.

2.1: The Origins of Agriculture

2.2: The Origins of Crop Plants

2.3: The Importance of Seed Plants in Human Life

2.4: Plant Parts We Eat

2.5: The Importance of Seedless Vascular Plants

2.6: The importance of plants for mitigating and adapting to the effects of climate change

2.7: Terms

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2.1: The Origins of Agriculture

Hunter-Gatherers

Before the agricultural revolution (10,000–12,000 years ago), hunting and gathering was, universally, our species' way of life. It sustained humanity in a multitude of environments for 200,000 years—95 percent of human history. Why did our ancestors abandon their traditional way of life to pursue agriculture?

For a long time, scientists, including Charles Darwin, assumed that primitive humans invented agriculture by chance, and once the secret was discovered, the transition toward agriculture was inevitable. However, this is only possible if we assume that (i) the biggest obstacle to the adoption of agriculture was a lack of knowledge about plants' life cycles and propagation and (ii) farming was easier than hunting and gathering from its beginnings. We can't verify or refute these hypotheses directly. However, studies of materials (e.g., tools made of stones and bones, fossilized seeds, rock paintings, and engravings) found in many archaeological excavations, as well as anthropological studies on present-day hunters and gatherers—who still live in various corners of the world—have contributed much to our understanding of the early history of agriculture.

Scholars' interest in the contemporary hunters and gatherers was rekindled after the 1966 Man the Hunter conference, organized by Irven DeVore and Richard Lee in Chicago. Richard Lee, a PhD student studying under DeVore, had lived in Botswana with the !Kung, one of the San (Bushman) clans of Kalahari Desert, for three years (1963–1965). He shared his experience at the conference and reported !Kung men hunt and !Kung women gather. He added, "Although hunting involves a great deal of effort and prestige, plant foods provide from 60–80 per cent of the annual diet by weight. Meat has come to be regarded as a special treat; when available, it is welcomed as a break from the routine of vegetable foods, but it is never depended upon as a staple" (1). He further added that the !Kung had a more than adequate diet achieved by a subsistence work effort of only two or three days per week, a far lower level than that required of wage workers in our own industrial society, and working adults easily take responsibility for children, old people, and the disabled. In these groups, starvation, malnutrition, and crime are nil. He argued that the social lives of the people of the Bushmen clans are more dignified than that of civilized society and concluded, "First, life in the state of nature is not necessarily nasty, brutish, and short" (1).

American anthropologist Marshall Sahlins agreed with Richard Lee, stating that Australia's indigenous people also have substantial resources when compared to the common man of industrial society and work fewer hours per day, with more time for leisure. He explained that the hunter-gatherers consume less energy per capita per year than any other group of human beings, and yet all the people's material wants were easily satisfied. Sahlins further adds, "Hunters and gatherers work less than we do, and rather than a *grind* the food quest is intermittent, leisure *is* abundant, and there is a *more* sleep in the daytime per capita than in any other condition of society" (2).

The prevailing belief till then was that in comparison to civilized societies, the hunters and gatherers were impoverished: their way of life precarious, full of hardship, and the life of people in such a state of nature, short and brutish. When the proceedings of this conference were published in 1968, such prejudices were refuted and put to rest, rousing a new interest in researchers worldwide to study contemporary hunters and gatherers.

Over the past fifty years, anthropologists, archeologists, biologists, botanists, demographers, and linguists have studied various tribes of contemporary hunter-gatherers. These studies suggest that hunter-gatherers possess tremendous knowledge about the flora and fauna present in their surroundings. They can identify edible plants from a sea of wild vegetation and know which plants' parts can be eaten raw and which need cooking or further processing. In their memories, they retain a seasonal calendar: they know when new plants sprout, bloom, and are ready for harvest or when animals and birds breed. They extract medicines, drugs, intoxicants, and poisons from various plants and make fibers for clothing, baskets, and other objects. The marks of seasonal variations and their specific geographical surroundings are visible in their diets. For example, people living in Arctic regions are entirely carnivorous; the Hadza of Tanzania are predominantly vegetarians; and the !Kung San of the Kalahari Desert in South Africa are omnivores. Regardless of their locale, hunters and gatherers consume ~500 varieties of food throughout the year and make the best possible use of the resources available to them. In comparison, today's rich urban folks hardly sample food items from fifty unique sources.

It has also been observed that most hunter-gatherers care about their environment. They do not hunt without need, waste less, and play active roles in managing their resources. For example, natives living in different parts of the world set forest fires at fixed intervals to manage the landscape. Such controlled fires help eliminate weeds and insects and promote the germination

of seeds that are enclosed within hard shells (e.g., pinenuts, chestnuts, and walnuts), thus deliberately increasing the number of seed-producing plants for them to eat. Afterward, when the fire is extinguished, grass grows on the ground, and herbivores are attracted to these pastures for several months, thereby making hunting easy. Such multilevel environmental management is just one example of how these people use their knowledge of the natural world to survive outside of agricultural society.

Many foragers are also aware of how to produce food and occasionally do so in hours of need. For example, New Guinea tribes weed and prune the Sago palms that grow in the forest to increase their yield. The natives of northern Australia bury the tips of taro and eddoes into the ground to propagate new plants and channel rainwater to plains where many wild grasses grow. Subsequently, they harvest tubers and seeds for their consumption.

It is not very difficult to comprehend that compared to foraging, farming is labor-intensive and requires substantial planning to sow, weed, harvest, process, and store crops. Farming must have been a very difficult task in prehistoric times, and crop failures would have been prevalent. Thus as long as needs were fulfilled by hunting and gathering, people likely did not pursue farming despite having the knowledge required for plant propagation. For centuries, humans were sustained instead by a mixed strategy that included hunting, fishing, foraging, and some farming. When resources from the wild were plentiful, farming was abandoned. It was thousands of years before human societies began to completely rely on agriculture. The growth of agriculture was not linear but rather erratic; its adoption was not a coincidence but a slow pursuit full of trials and errors.

Archaeological evidence suggests that nomadic human tribes began farming during the Neolithic period, and so it is often referred to as the Neolithic Revolution. About 12,000 years ago, one of the first attempts at farming began in the Fertile Crescent, the Levant region of the Near East that includes the interior areas of present-day Turkey, Israel, Syria, Jordan, Lebanon, Iran, Iraq, Turkmenistan, and Asia Minor. The ancient inhabitants of the Fertile Crescent, known as Natufians, gathered wild wheat, barley, lentils, almonds, and so on and hunted cattle, gazelle, deer, horses, and wild boars (see figure 1.1).

Throughout this region, thousands of archeological excavations have been conducted and numerous objects—including grinding stones, flint, bone tools, stone sickles, dentalium, shell ornaments, and many fine tools of polished stone—have been unearthed. These show that prior to the adoption of agriculture, the inhabitants of this region had already acquired knowledge about their surrounding vegetation and used tools for cutting, uprooting, and harvesting wild plants, which could have made their transition toward farming easier. The direct descendants of the Natufians, the prepottery Neolithic people, successfully domesticated more than 150 crops, including barley, wheat, pulses, and so on. They also domesticated animals and built the first villages in human history.

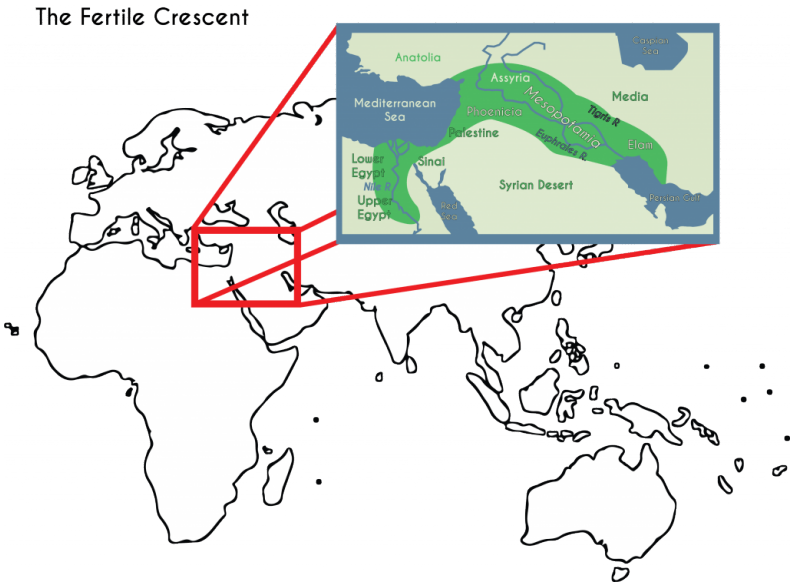


Fig 1.1 “The Fertile Crescent” by OSU OERU is licensed under CC BY 4.0.

Numerous discoveries in recent years indicate that besides the Fertile Crescent, parallel efforts of cultivation began in several other parts of the world. For example, 9,000 years ago, in China’s Yellow River valley, rice cultivation began; 5,000 to 8,000 years ago, in Africa and East Asia, the cultivation of a variety of roots and tubers was underway; and 7,000 to 9,000 years ago, people in South America were growing maize, beans, and squash. Hence the history of agriculture is only 12,000 years old, and it spread around the globe relatively quickly. But how did geographically isolated human groups, unaware of one another’s existence, begin farming within this short period of time, ditching the hunter-gatherer way of life?

Agriculture?

Australian archaeologist Vere Gordon Childe first linked the beginning of agriculture to climate change. He suggests that at the end of the last ice age (6,000–13,000 years ago), the earth's average temperature increased and glaciers moved rapidly northward. Additionally, rainfall progressively decreased in Southwest Asia and Africa; thus year after year, this region suffered spells of drought that caused the loss of vegetation and several animal species. Over a prolonged period, the rainforests turned into savannas, where herbivores dwelled only for a few months. Under the changed circumstances, humans were unable to sustain themselves throughout the year by hunting and foraging. The human groups, living on different continents and unaware of one another's existence, were forced to produce their own food, and farming began within a short span of time all around the globe.

The transition toward farming was not easy. It was not a eureka moment; agriculture was adopted under unpleasant circumstances and the obligation to produce food was indeed a farewell to the heaven for mankind. Consider the story of Eve, who, under the influence of a snake, plucks the forbidden fruit and eats it with Adam; as a consequence, they acquire wisdom and develop a sense of good and evil. The Lord God becomes angry, and as a punishment, Adam and Eve are banished from the Garden of Eden to work the ground and grow their own food to survive. To Adam, God says,

Because you listened to your wife and ate fruit from the tree about which I commanded you, "You must not eat from it,"

> Cursed is the ground because of you;
>
> through painful toil you will eat food from it
>
> all the days of your life.
>
> It will produce thorns and thistles for you,
>
> and you will eat the plants of the field.
>
> By the sweat of your brow
>
> you will eat your food
>
> until you return to the ground,
>
> since from it you were taken;
>
> for dust you are
>
> and to dust you will return.[1]

Farming was not fun. It required tremendous effort and the capacity to endure hardship.

Women's Enterprise

It is believed that agriculture was invented by women. The women of the preagrarian societies collected wild fruits, berries, tubers, and roots and had generational experience in identifying edible plants and knowledge about plants' life cycles and how they grow. It has been suggested that women's extraordinary vision, more developed motor skills, and ability to process finer details evolved due to the importance of their involvement in foraging activities for millions of years. For example, the average woman's eyes can distinguish about 250 shades and hues, while an average man's can only see 40–50.

When droughts became regular, the tribes of our ancestors made temporary encampments along the lakes and ponds where men ambushed animals who came to quench their thirst. Their foraging experience helped womenfolk take the initiative in growing food. They sowed the seeds of wild grasses in the surrounding marshes and planted parts of the tubers to propagate new plants.

In most traditional societies, even today, this historical association of women in agriculture is revered: often, women sow the first seeds to bestow good luck for a bountiful harvest. Invariably, across all cultures, we find a similar feminine influence in stories related to the origin of farming. For example, in ancient Egypt, Isis was deemed the goddess of agriculture: Once upon a time, a severe drought caused a widespread famine on the earth. There was nothing to eat, and cannibalism began. In such a situation,

the goddess Isis offered barley and wheat from the wild to the starving people, and taught them how to produce their own food. Thus farming saved mankind from starvation.

In Greek mythology, Demeter was the goddess of fertility and the harvest. After every harvest, the first loaf of bread was offered to her as a sacrifice. She was called Ceres by the Romans, and thus grains were called “cereal.” The legend of Demeter contains an interesting tale about the origin of agriculture. According to this myth,

> with the blessing of Demeter, the earth was always filled with grains, berries, and fruits. Humans took their share of this bounty and survived happily for a long time. But it came to a sudden end when Hades, the god of the underworld, abducted Demeter’s lovely daughter Persephone. Persephone was Demeter’s only child and the center of all her attention and devotion. Demeter desperately searched everywhere for her daughter, but it was to no avail. She fell into depression, and transformed into an ugly old woman and became unrecognizable. She encountered abuse and ill-treatment from everyone around. Only, Celeus, the king of Eleusis, warmly welcomed her. While she continued her search for Persephone, she ignored her responsibility of making the earth fertile. Her despair had an effect on the crops; famines were prevalent and people starved. Eventually, the gods intervened and plead with Demeter to bless the earth with a good harvest, and in exchange, they forced Hades to free Persephone. However, before releasing Persephone, Hades fed her pomegranate seeds (the food of the underworld) that bound her to the underworld forever. When the gods asked Persephone to choose where she wanted to live, she wished to remain in the underworld. As a result, Demeter was devastated. Finally, Zeus intervened and came up with a compromise that allowed Persephone to spend six months per year on the earth with Demeter and six with Hades in the underworld. When Persephone visits her mother from spring to summer, the earth is full of flowers and fruits, crops grow, and harvests are bountiful. When Persephone heads back underground, Demeter falls into a depressed state, resulting in autumn and winter. Demeter did not get her daughter fully back, so, she did not restore earth’s fertility completely. However, in return for the kindness of King Celeus, she taught his son Triptolemus the art of agriculture for survival, and he later taught it to mankind.

In Mexico, Hispaniola, and Latin America (the sites of the great Mayan and Aztec civilizations), we find stories about the origin of man and corn. For example,

Man is born from maize; maize is the mother of man.

When the gods created man, the Holy Spirits chanted for his well-being and finally maize emerged from the breasts of the mother Earth to sustain humans.

Mother Earth gifted her five daughters—white, red, yellow, spiked, and blue maize—to man.

Similarly, Hindu mythology has several goddesses, including Bhudevi (the earth goddess), Annapurna (the goddess of grains, who provides nutrition to everyone), and Shakti (the creator of the entire plethora of vegetation). According to the legend of Annapurna,

> Once, the Lord Shiva (who represents the male power, the Purush) and his wife Parvati (the creator of nature, a.k.a. Prakriti or Shakti) argued about who was superior between the two and the discussion quickly ended on a sour note. Shiva stressed the superiority of Purush (male) over Prakriti (Mother Nature). Enraged, Parvati deserted her husband and disappeared, which resulted in a widespread famine. Shiva’s followers, who were starving, asked for his help. Shiva took a begging bowl, and his band followed him. They went from door to door, but the people themselves had nothing to eat, so they turned the beggars away. Shiva’s band learned about a charity kitchen in the city of Kashi (also known as Varanasi) that was feeding everyone and decided to visit Kashi. To their surprise, Parvati owned that kitchen, and she had become the goddess Annapurna, wearing celestial purple and brown, and was serving food to the starving gods and mankind. Upon Shiva’s turn, she likewise offered food to him and his followers. Shiva realized that the existence of humanity depends on nature; the brute force of male power is not enough to sustain life on Earth.

The common thread of all these myths is the appearance of the savior female deity who taught mankind to cultivate grains to survive. Although these myths have no literal value, they serve as metaphors or narratives of human experiences and survived through generational memories. They are also, in fact, consistent with the climate change theory of the origin of agriculture.

Slash and Burn: Shifting Cultivation

At the dawn of agriculture, the primitive people of the Neolithic era only had some tools made of stones and animal bones at their disposal. These tools were useless for such a monumental task as embarking on the path to farming. Fortunately, mankind’s knowledge and experience of taming fire came in handy. Long before the origins of modern humans, *Homo erectus*, an ancestor

of the hominid branch, had learned to light and control fire. Afterward, the members of genus *Homo* moved northwards from Africa and survived the cold weather of Europe and Asia with the help of this skill. Humans used their best weapon, fire, to create the first farms. First, they slashed the vegetation, then burned it to clear the small patches in the forests, and finally, sowed seeds in the ashes. This practice of farming, known as slash-and-burn agriculture, still survives in the Amazon rainforests and in many mountainous regions of the world. The plots created by this method are very fertile initially, but with each passing year, they are overtaken by more and more weeds, pests, and parasites, which causes a decline in their fertility. So after three to four years, the people move to another site. Thus this practice is also known as “shifting cultivation” or “swidden agriculture.” In India, it is known as “jhoom” among the native Adivasi tribes (descended from an ancient forest-dwelling people). After people abandon a site, in the fallow field, grass and weeds grow, and it serves as a pasture for herbivores and hunting grounds. Slowly, the fertility of these pastures returns, shrubs and trees grow, and they become part of the forest again. In this way, the field, fallow land, and the surrounding forest are recycled. Also, weeds, insects, and other parasites are kept in balance.

Today, we are farming with highly sophisticated machines and have specialized tools for various tasks, from sowing to harvesting, and yet farming is still a tremendous task. We cannot even grasp how difficult it would have been in prehistoric times. For thousands of years, generations of mankind struggled to make farming productive. They also continued to gather and hunt to make up for the shortfall or crop failures. Since farming required much more time and effort, farming would have been abandoned from time to time if nature was bountiful. It has been suggested by various studies that agriculture did not progress smoothly; it took several thousand years before humanity could fully rely on agriculture.

So to summarize, the history of agriculture is 12,000 years old, and traces back to a time when changes in the earth’s global climate led to widespread drought and a decline in natural resources, forcing our ancestors to produce their own food. For thousands of years, shifting cultivation supplemented their diets while hunting and gathering remained the main source of sustenance. The discovery of agriculture was not an accident but the product of trial and error as well as improvisation that spanned many centuries, a process that still continues today.

Animal husbandry is considered a by-product of agriculture. It has been suggested that during droughts, people survived on stored grains, and they used some grains to feed herbivores to keep them around for easy hunting. The credit to domesticating animals primarily goes to men.

Emergence of the First Agricultural Societies

Even though agriculture started almost simultaneously in many regions of the world, its progress was not uniform. The biodiversity of various geographical regions (e.g., their flora, animals, birds, insects, and microorganisms) influenced the emergence of stable agricultural societies. In some areas of the tropics, particularly in Africa, people had great success in growing tubers like yams, potatoes, eddoe, sweet potatoes, and cassava. These plants can be propagated by burying a small part of the tuber in the ground and so did not require an understanding of the plant’s life cycle. So these groups had an easy head start thanks to vegetative propagation that produced identical plants (clones), which did not differ significantly in yield. They learned to process many types of tubers and invented a very complex process of separating cyanide and starch from cassava to make starchy tapioca pearls. These undertakings helped folks sustain themselves year-round, but did not accumulate enough surplus to free a section of the population from farming, allowing them to pursue other tasks needed for the further advancement of their societies.

In South and Central America, maize was the mainstay of civilization. However, the natural structure of maize plants promotes outcrossing: on this plant, male flowers, known as tassels, hang from the tip, whereas the female flowers (silk) grow on the stem. Maize pollens are very lightweight and reach the female flowers via wind. Thus male flowers can pollinate female flowers of the same plant (self-pollination) or of another plant (cross-pollination). Although in maize, the chances of self-pollination and cross-pollination events are equal, the progeny born of selfing is inferior (gives lower yield) compared to the progeny born of outcrossing. Thus farmers need to plant different varieties of maize in the same fields to ensure maximum yield. In the absence of this knowledge, the productivity of the crop cannot be assured from one year to another. Only after such an understanding developed could people rely fully on maize farming and utilize the surplus to build the great civilizations of the Aztecs and Mayans.

In the Fertile Crescent, about thirty-two species of grass—including the wild species of wheat, barley, sorghum, millet, and oats—grow naturally. Incidentally, most grasses have complete flowers with both male and female organs, and self-pollination rules over cross-pollination. As a result, the characteristics of grasses remain stable, and crop yields do not vary from one year to another. If the plants with large grains are picked and carried forward, then crops with large seeds can be harvested for generations. Additionally, the grass seeds can be stored for a very long period of time and year-round dependence on these grains was easily established. So the early farmers of this region benefitted from growing grasses.

In the Fertile Crescent, animal husbandry began in parallel with farming. Some groups exclusively pursued this path and so

developed a nomadic way of life. They moved with their herds following the availability of grazing grounds and trading the products of one farming community with another. These pastoralists thus further strengthened the stability of farming communities and broadened the region's resource base. Such advances helped the people of the Fertile Crescent settle in one place permanently and establish the first villages.

In China, along the Yellow River, people learned to cultivate rice. Rice is also a self-pollinated grass, and so these early farmers could rely on its harvest for yearlong sustenance and could store surplus seeds. Unlike their contemporaries in the Fertile Crescent, Chinese farmers could harvest two crops of rice per year and so their surplus grew even more rapidly. So they reaped similar advantages and almost simultaneously established permanent settlements.

About 5,500 years ago, an independent initiative of paddy cultivation was undertaken in the Indo-Gangetic plains that are spread across South Asia. In addition to rice, the peoples of South Asia and East Asia independently learned to grow a variety of minor grains, pulses, vegetables, fruits, tubers, roots, and oilseed crops.

As agriculture progressed, many river-valley civilizations—in the Indus Valley, Egypt, Mesopotamia, and China—came into existence. Meanwhile, the populations of hunter-gatherers remained more or less stable. As agriculture developed and productivity increased, the human population grew proportionally (see figure 1.2). The first minor jump occurred after the discovery of metals that made many more tools like plows, available to farmers. The use of a plow powered by domesticated animals resulted in a significant increase in food production. In this way, 5,000 years ago, farming began to seem like a better alternative to the hunter-gatherer's way of life. The surplus grain freed a large section of the population from farming and allowed them to invest energy in other tasks that led to the second major change—the division of labor in human society. Subsequently, the collective sharing of resources was replaced with individual ownership—private property—which gave rise to a need to ensure the succession of one's own bloodline. As a consequence, rules of strict sexual conduct for women were formulated and, like infields and domesticated animals, they became the property of men. As class divisions deepened, the unit of a family, headed by a patriarch, strengthened. Soon, tribes headed by patriarchs began to fight for control over their possessions and to expanding their domains, which gave rise to more complex and organized social and political structures, like states, nations, and religion. In societies dependent on subsistence agriculture—where property has not developed and most of the people remain engaged in agriculture—complex social structures, division of labor, crime, patriarchy, and other sociopolitical structures are also poorly developed.

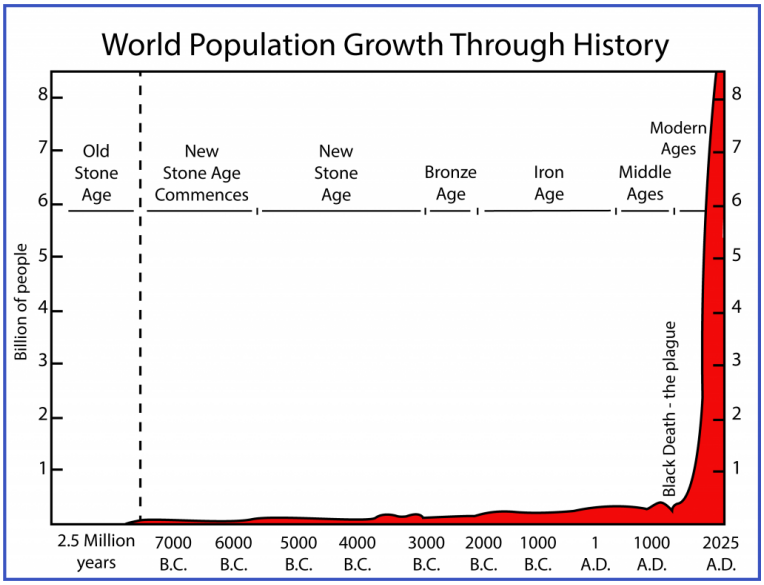


Fig 1.2 "World population growth" by OSU OERU is licensed under CC BY 4.0.

Agriculture transformed human society, but this transformation also, in turn, influenced agricultural practices. While the family, private property, and various institutions were born as by-products of agriculture, these sociopolitical advancements also impacted agriculture. To this day, agriculture continues to be highly entangled with society and human history. In the following chapters, we will review the historical progress of agriculture, advancements in science and technology that influenced farming, and the impact of agriculture on humanity.

References

1. Lee, R. B. (1968). What hunters do for a living, or, how to make out on scarce resources. In R. B. Lee and I. DeVore (Eds.), *Man the hunter* (pp. 40, 43). Aldine. (↵ Return 1) (↵ Return 2)

2. Sahlins, M. (1968). Notes on the original affluent society. In R. B. Lee and I. DeVore (Eds.), *Man the hunter* (pp. 85, 86). Aldine. (↵ Return)

Further Readings

Diamond, J. (1997). *Guns, germs, and steel: The fates of human societies*. W. W. Norton.

Lee, R. B. (1979). *The !Kung San: Men, women and work in a foraging society*. Cambridge University Press.

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2.2: 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.

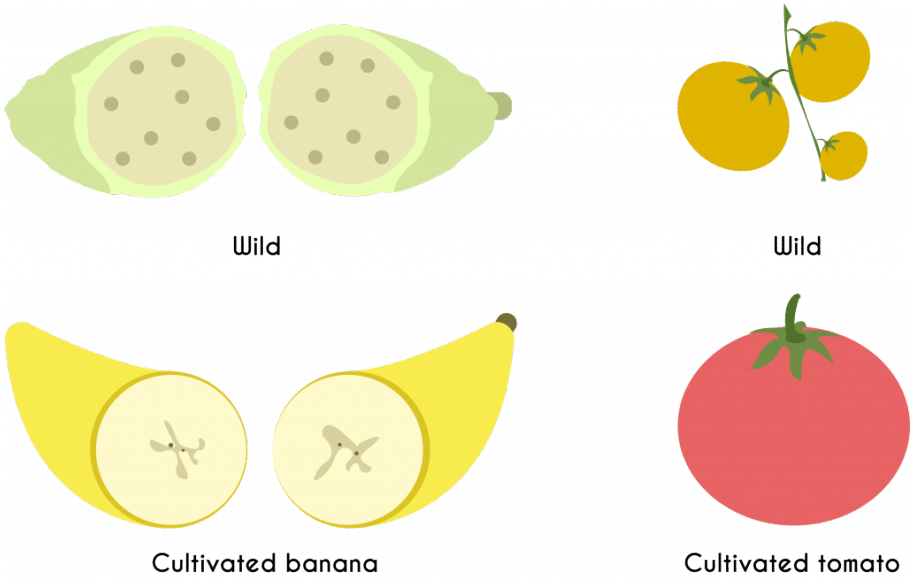


Fig 2.2 “Changes in crop plants as a result of artificial selection” by Sushma Naithani and OSU OERU is licensed under CC BY 4.0.

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.

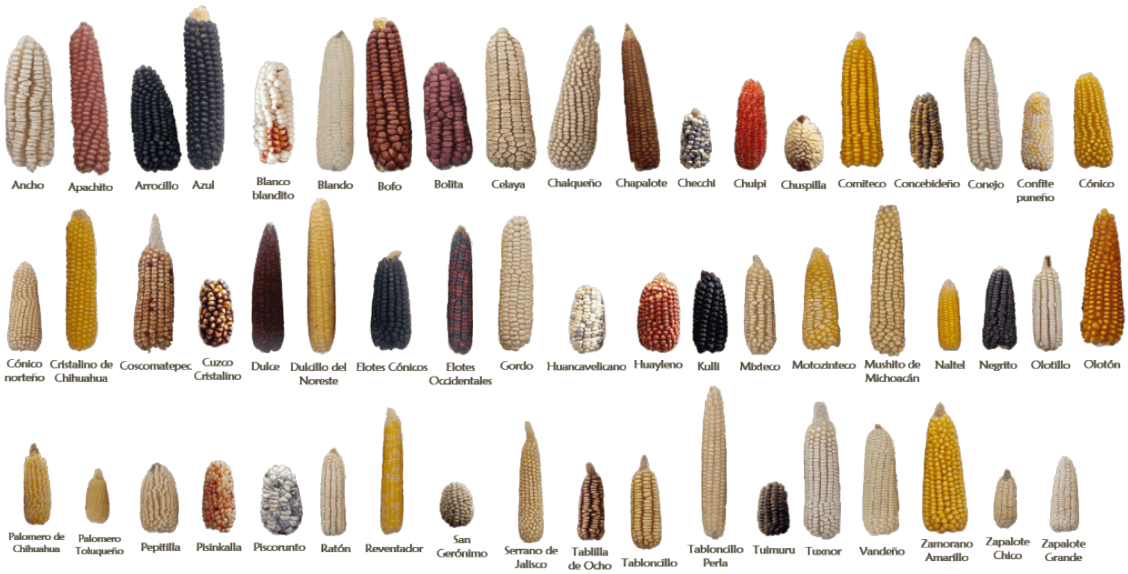


Fig 2.3 Examples of some of the 59 native Mexican maize landraces. Photo of maize by CIMMYT Maize Germplasm Bank is licensed under CC BY 2.0.

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).

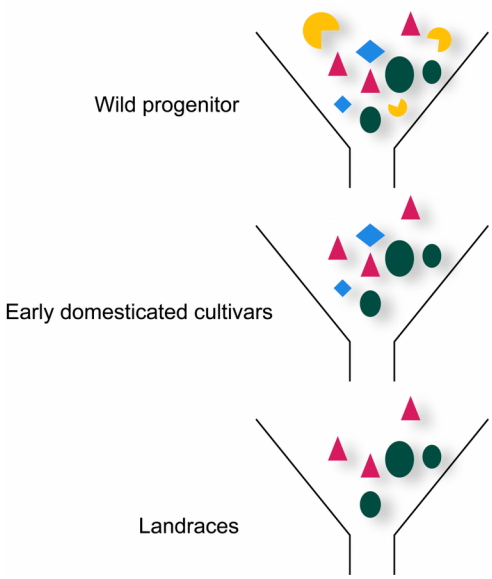


Fig 2.4 Loss of gene pool during crop domestication due to artificial selection. “Loss of gene pool” by Sushma Naithani and OSU OERU is licensed under CC BY 4.0.

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).

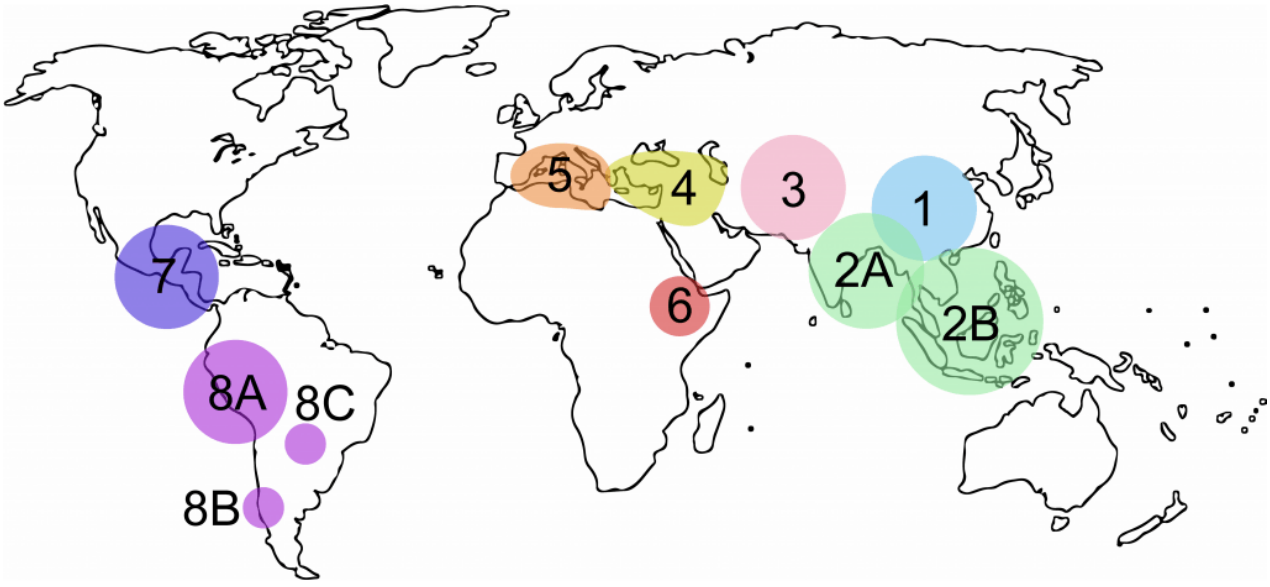


Fig 2.5 The centers of origin of cultivated plants identified by Nikolai Vavilov: 1. China; 2. India; 2a. the Indo-Malayan region; 3. Central Asia (including Pakistan, Punjab, Kashmir, Afghanistan and Turkestan); 4. the Near East (Fertile Crescent); 5. the Mediterranean; 6. Ethiopia; 7. Southern Mexico 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.

Center	Remarks
4. Near East (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 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* (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. *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.

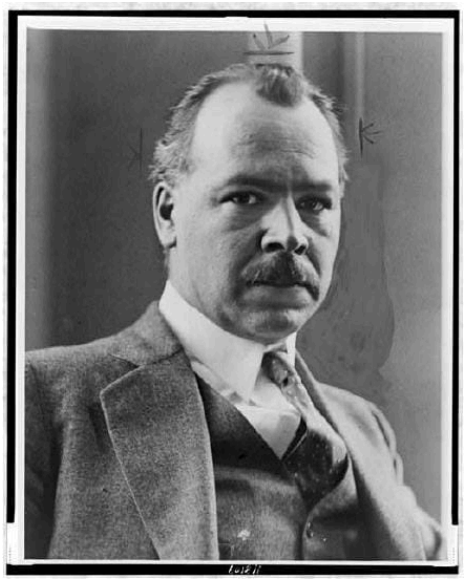


Fig 2.6 Nikolai Vavilov in 1933. "Nikolai Vavilov" by Library of Congress is licensed under no known restrictions on publication.

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.

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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. ↩

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2.3: The Importance of Seed Plants in Human Life

Learning Objectives

- Explain the importance of seed plants to humans

The Importance of Seed Plants in Human Life

Seed plants are cultivated for their beauty and smells, as well as their importance in the development of medicines. Plants are also the foundation of human diets across the world. Many societies eat, almost exclusively, vegetarian fare and depend solely on seed plants for their nutritional needs. A few crops (rice, wheat, and potatoes) dominate the agricultural landscape. Many crops were developed during the agricultural revolution when human societies made the transition from nomadic hunter–gatherers to horticulture and agriculture. Cereals, rich in carbohydrates, provide the staple of many human diets. In addition, beans and nuts supply proteins. Fats are derived from crushed seeds, as is the case for peanut and rapeseed (canola) oils, or fruits such as olives. Animal husbandry also requires large amounts of crops.



Figure 2.3.1: Importance of plants to humans: Humans rely on plants for a variety of reasons. (a) Cacao beans were introduced in Europe from the New World, where they were used by Mesoamerican civilizations. Combined with sugar, another plant product, chocolate is a popular food. (b) Flowers like the tulip are cultivated for their beauty. (c) Quinine, extracted from cinchona trees, is used to treat malaria, to reduce fever, and to alleviate pain. (d) This violin is made of wood.

Staple crops are not the only food derived from seed plants. Fruits and vegetables provide nutrients, vitamins, and fiber. Sugar, to sweeten dishes, is produced from the monocot sugarcane and the eudicot sugar beet. Drinks are made from infusions of tea leaves, chamomile flowers, crushed coffee beans, or powdered cocoa beans. Spices come from many different plant parts: saffron and cloves are stamens and buds, black pepper and vanilla are seeds, the bark of a bush in the Laurales family supplies cinnamon, and the herbs that flavor many dishes come from dried leaves and fruit, such as the pungent red chili pepper. The volatile oils of flowers and bark provide the scent of perfumes. Additionally, no discussion of seed plant contribution to human diet would be complete without the mention of alcohol. Fermentation of plant-derived sugars and starches is used to produce alcoholic beverages in all societies. In some cases, the beverages are derived from the fermentation of sugars from fruit, as with wines, and, in other cases, from the fermentation of carbohydrates derived from seeds, as with beers.

Seed plants have many other uses, including providing wood as a source of timber for construction, fuel, and material to build furniture. Most paper is derived from the pulp of coniferous trees. Fibers of seed plants, such as cotton, flax, and hemp, are woven into cloth. Textile dyes, such as indigo, were mostly of plant origin until the advent of synthetic chemical dyes. Lastly, it is more difficult to quantify the benefits of ornamental seed plants. These grace private and public spaces, adding beauty and serenity to

human lives and inspiring painters and poets alike.

The medicinal properties of plants have been known to human societies since ancient times. There are references to the use of plants' curative properties in Egyptian, Babylonian, and Chinese writings from 5,000 years ago. Many modern synthetic therapeutic drugs are derived or synthesized de novo from plant secondary metabolites. It is important to note that the same plant extract can be a therapeutic remedy at low concentrations, become an addictive drug at higher doses, and can potentially kill at high concentrations.

Ethnobotany

The relatively new field of ethnobotany studies the interaction between a particular culture and the plants native to the region. Seed plants have a large influence on day-to-day human life. Not only are plants the major source of food and medicine, they also influence many other aspects of society, from clothing to industry. The medicinal properties of plants were recognized early on in human cultures. From the mid-1900s, synthetic chemicals began to supplant plant-based remedies.

Pharmacognosy is the branch of pharmacology that focuses on medicines derived from natural sources. With massive globalization and industrialization, there is a concern that much human knowledge of plants and their medicinal purposes will disappear with the cultures that fostered them. This is where ethnobotanists come in. To learn about and understand the use of plants in a particular culture, an ethnobotanist must bring in knowledge of plant life and an understanding and appreciation of diverse cultures and traditions. The Amazon forest is home to an incredible diversity of vegetation and is considered an untapped resource of medicinal plants; yet, both the ecosystem and its indigenous cultures are threatened with extinction.

To become an ethnobotanist, a person must acquire a broad knowledge of plant biology, ecology, and sociology. Not only are the plant specimens studied and collected, but also the stories, recipes, and traditions that are linked to them. For ethnobotanists, plants are not viewed solely as biological organisms to be studied in a laboratory; they are seen as an integral part of human culture. The convergence of molecular biology, anthropology, and ecology make the field of ethnobotany a truly multidisciplinary science.

Key Points

- Providing much of the nutritional values that humans need, seed plants are the foundation of human diets across the world.
- Wood, paper, textiles, and dyes are just a few examples of plant uses in everyday human life.
- Traditionally, humans have also used plants as ornamental species through their use as decorations and as inspiration in the arts.
- As medicinal sources, plants are vital to humans, as many modern drugs have been derived from secondary plant metabolites; ancient societies also depended on them for their curative properties.
- The important relationship that human cultures have developed with plants can be studied through the field of ethnobotany.

Key Terms

- **ethnobotany**: the scientific study of the relationships between people and plants
- **pharmacognosy**: the branch of pharmacology that studies medical substances that are extracted from natural sources, including drugs derived from plants and herbs used for medicinal purposes
- **husbandry**: the raising of livestock and the cultivation of crops; agriculture

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2.4: Plant Parts We Eat

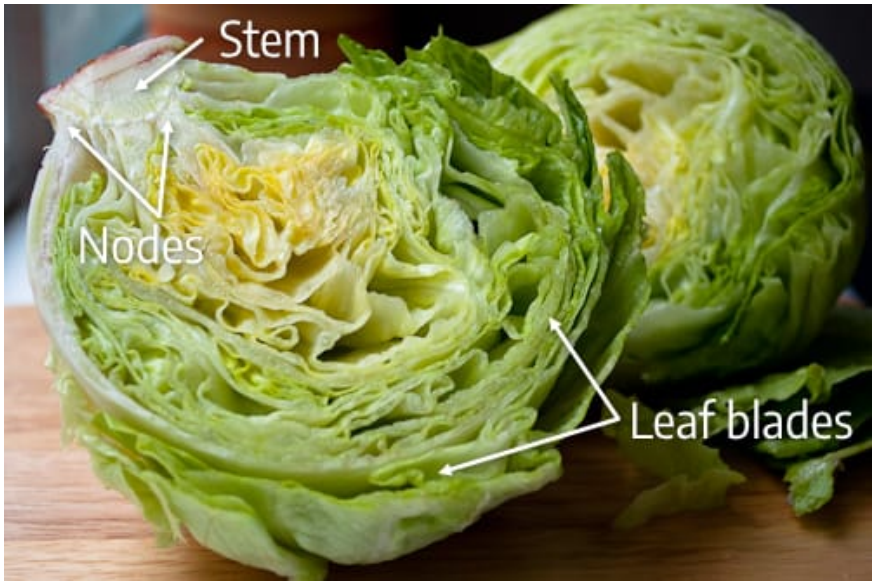
Learning objectives

- Summarize the various above- and below-ground plant parts that contribute to your diet.
- Use the correct language of biology when identifying parts of plants.
- Appreciate the diversity of edible plant parts.

Above-ground plant parts we eat

Edible leaves and petioles

In this image of an iceberg lettuce cut in half, you can see how the leaf blades are packed and folded together tightly in the lettuce head. Lettuce is an example of a plant shoot with very short internodes on the stem. This results in a compact but leafy plant. Iceberg lettuce is a type of heading lettuce where older leaves envelop newer leaves forming a solid or semi-solid ball or head of lettuce leaves.



"Iceberg Lettuce" by Кулинарно, CC BY-NC-SA 2.0

Romaine and leaf lettuces exhibit a more open architecture, with the leaves forming a looser head with upright leaves. Romaine lettuce has elongated leaves. There may be some tendency of older leaves to enclose newer leaves, but it is much less pronounced than in iceberg lettuce, and may be absent altogether in some of the garden types. Leaf lettuce lacks the tendency to form heads.



Image by Peter Drache. Pixabay license

Lettuce leaves generally lack a petiole. The blade narrows a bit, but attaches directly to the node. A leaf lacking a petiole is called a “sessile” leaf. The point of attachment of the leaf to the stem is at a node. If you tear the leaves from a lettuce plant you are left with a short stem made up of many nodes and short internodes.

You can see in the romaine lettuce that its morphology is similar to that of the iceberg lettuce and that it has some tendency to wrap newer leaves within older. However, the nodes are a bit longer than what you see in iceberg lettuce, and that makes the node locations more apparent.

A few examples of leaf parts we eat

An interactive H5P element has been excluded from this version of the text. You can view it online here:
https://open.lib.umn.edu/horticulture/?p=105#h5p-6

Watch this video on edible leaves and petioles:

Modified petioles

Celery is an example of a leaf with a petiole. The parts that you eat are the petioles, while the leaf blades are often not present in the bunch of celery you purchase. If you buy a bunch of celery and pull off the large, outside petioles, inside you will find shorter petioles with the leaf blades still attached.

Celery is a geophyte (covered in a later lesson). Some of the celery petiole — the pale part at the bottom where it attaches to a node on the stem — grows underground. This part is pale because it lacks chlorophyll; the petioles were not exposed to sunlight and chlorophyll failed to develop.

Intentionally covering the petioles to discourage chlorophyll and encourage white, tender stems is called blanching. Blanched celery is more attractive to some cooks and consumers, although it may not be as nutritious.

An interactive H5P element has been excluded from this version of the text. You can view it online here:
https://open.lib.umn.edu/horticulture/?p=105#h5p-7

Edible stems

The photo below shows an asparagus shoot. You can tell it is a shoot by the regular node/internode construction of the stem. Most of the shoot is stem tissue. The triangular growth at each node is colloquially called a “bract” by asparagus growers, but it is actually a very small, scale-like leaf. If the shoots are left unharvested, branches grow from the nodes and then repeatedly branch into soft, feathery green foliage, as shown in the next photo.

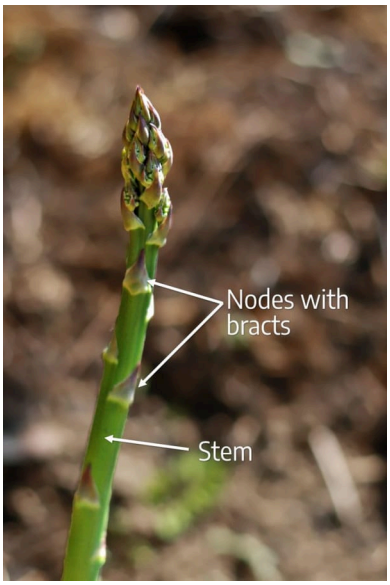


Image by Mark's Postcards from Beloit, CC BY-NC-ND 2.0.



Asparagus shoots that are not harvested grow taller and produce branches and feathery foliage. Photo by Rasbak. CC BY-SA 3.0.

Edible inflorescences

Broccoli and cauliflower are eaten as immature inflorescences. The dark green exterior of the broccoli inflorescence is made up of tight flower (or floret) buds that have not yet opened. The term "floret" is often used for the name of a flower born on a complex inflorescence.



Photo by Fir0002/Flagstaffotos, CC BY-NC.

Inside the inflorescence, the flower buds are supported by short, thin pedicels. The pedicel is attached to a series of increasingly thick internal stalks which make up the rachis structure of the inflorescence. The rachi all connect to the main stem of the inflorescence, which is the peduncle, and which then attaches to a node on the stem. The peduncle is the bit of the stalk that extends from the node where the inflorescence is attached to where the first rachis branches off. Above that, the central axis of the inflorescence is also called the rachis. An inflorescence can contain many rachi.

These plant parts may look similar, but they're in different positions in the inflorescence. The terminology is important for distinguishing between parts, making observations, and describing different aspects of the plant, especially for data collection in experiments.



Nasturtium flowers and leaves are edible. Photo by henna lion. CC BY-NC 2.0.

Nasturtiums, shown above, are also an inflorescence. They can be used as a colorful addition to a salad, and have a pleasant spicy flavor. In this case we are eating a single open flower, instead of a mass of immature rachi, pedicels, and florets as we are with broccoli.

It's important to remember that not all flowers are edible, and some are even poisonous. If you're interested in edible flowers, you must learn which species are safe to eat and how to identify and prepare them.

Review questions

Cauliflower has very tight flower clusters, but otherwise has a very similar morphology to broccoli. Can you identify the pedicel, rachis, peduncle, and florets?



Cauliflower. alsen. Pixabay license

This Chinese cabbage has a morphology similar to that of romaine lettuce. Can you identify the stem, nodes, and leaf blades?



Chinese cabbage. misskursovie2013. Pixabay license

Fruits



"Apple half" EverydayTrish. CC BY-NC 2.0

We will deal with fruits in detail later in the course. Just a bit of introductory information: a fruit is a mature ovary that was part of a flower

Sometimes the botanical and culinary definitions conflict with one another. Botanically speaking, for instance, a nut is a fruit, as are a corn kernel, a pumpkin, a tomato, and an orange. As we'll discuss, you could make a botanical argument that an apple isn't a true fruit because the juicy part we eat isn't ovary tissue; the ovary tissue is the core that we throw in the compost.

Below-ground plant parts we eat: Geophytes

Geophytes are plants with underground organs where the plant stores energy or water. Geophytes are often called bulbs, but they are far more diverse than that. Many of these plants protect buds using structures other than bulbs, such as rhizomes or enlarged roots. These modified parts include:

- Bulbs
- Tubers
- Rhizomes
- Roots, including storage and enlarged tap roots

Underground shoots

Bulb – onion



Half of a purple onion, close-up, by Marco Verch. CC BY 2.0.

A bulb is a specialized, underground organ with a short, fleshy basal stem enclosed by thick, fleshy scales modified for storage. A true bulb consists of both leaf and stem tissue. The compressed stem, or basal plate, has attached to it a set of modified leaves called scales. These scales serve as the primary storage tissue for carbohydrates, nutrients, and water.

The main stem and apical meristem are protected by the layers of leaves. Axillary buds are born at the junction of the scale and basal plate (leaf and stem). Bulbs with a papery outer covering, like onions, are called tunicated. Plants that produce bulbs without this covering, like lilies, are non-tunicated.

Underground stems

Tuber – potato



Russet potato cultivar with sprouts. ZooFari. Public domain

A tuber is a thickened, enlarged underground stem typically produced from a swelling of a stolon or rhizome. The stem tissue serves as the primary storage tissue for carbohydrates, nutrients, and water. The potato tuber is a typical example. Potato tubers are born on stolons that emerge from nodes near the soil surface.

It is common garden and agricultural practice to “hill” potatoes (mound loose soil around the base of the main stem of the plant) so the stolon grows into the mound of soil, where the tip swells into a tuber. Unlike a corm, which is also stem tissue, a tuber has no basal plate, but rather is fleshy throughout. The “eyes” of the potato are the meristems or buds from which new, above-ground growth initiates when conditions are favorable. These eyes are found at nodes on the tuber, which indicates that the tuber is shoot tissue rather than root.

Rhizome – ginger



Organic ginger root, by artizone. CC BY-NC-ND 2.0

Rhizomes are horizontal-growing underground stems that arise from nodes at or below the soil surface. In plants with fleshy rhizomes, these underground stems store nutrients and swell a bit. The stems are not usually as enlarged as a potato tuber, and the node/internode structure typical of stems is usually more obvious than on a potato. The stem tissue itself is the primary storage tissue, and it grows horizontally in the soil.

Ginger “root” (shown at right) isn’t really a root; it’s a rhizome (modified stem). The nodes and internodes, — found on stems, but not roots — are clearly visible.

Modified roots

Storage roots – sweet potato

Storage roots are enlarged fleshy portions of root tissue, and are are the primary storage tissue. There may be a bit of stem — the crown — attached to these roots, where you will find the buds from which new above-ground growth will initiate.



Photo by HarvestPlus, CC BY-NC 2.0.

In plants with storage and fleshy roots, including dahlias and daylilies, it is important to protect the buds on the crown of the root because new shoots originate from there. Roots of some plants can produce shoots directly from the root tissue, Sweet potatoes are propagated this way; roots are cut, new shoots emerge from the cut roots, and these shoots are transplanted into the sweet potato field. Not all plants can produce new shoots from roots.

Tap root – radish, carrot, parsnip, beet, turnip



“Parsnip, Farmers Market” by See-ming Lee (SML), CC BY-SA 2.0

The swollen primary root is the storage organ. New growth initiates from buds at the crown, which is a small area of stem tissue sitting atop the tap root.

Hypocotyl – radish

The below-ground organ of the *Raphinus sativa* (radish) is not a root or shoot, but the continued growth of the hypocotyl — the

part of the embryo arising from the cotyledonary node (where the cotyledons attach to the beginning of the root), and evident when a seed germinates.



Image credit: Matt Clark

Review questions

1. Compare and contrast a tuber and a storage root. Which one is actually stem tissue?
2. If ginger isn't a root, what is it and how can you tell?
3. What part of rhubarb and celery do we eat?

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2.5: The Importance of Seedless Vascular Plants

Learning Objectives

- Explain the beneficial roles of seedless vascular plants

The Importance of Seedless Vascular Plants

Mosses and liverworts are often the first macroscopic organisms to colonize an area, both in a primary succession (where bare land is settled for the first time by living organisms) or in a secondary succession (where soil remains intact after a catastrophic event wipes out many existing species). Their spores are carried by the wind, birds, or insects. Once mosses and liverworts are established, they provide food and shelter for other species. In a hostile environment, such as the tundra where the soil is frozen, bryophytes grow well because they do not have roots and can dry and rehydrate rapidly once water is again available. Mosses are at the base of the food chain in the tundra biome. Many species, from small insects to musk oxen and reindeer, depend on mosses for food. In turn, predators feed on the herbivores, which are the primary consumers. Some reports indicate that bryophytes make the soil more amenable to colonization by other plants. Because they establish symbiotic relationships with nitrogen-fixing cyanobacteria, mosses replenish the soil with nitrogen.

At the end of the nineteenth century, scientists observed that lichens and mosses were becoming increasingly rare in urban and suburban areas. Since bryophytes have neither a root system for absorption of water and nutrients, nor a cuticle layer that protects them from desiccation, pollutants in rainwater readily penetrate their tissues; they absorb moisture and nutrients through their entire exposed surfaces. Therefore, pollutants dissolved in rainwater penetrate plant tissues readily and have a larger impact on mosses than on other plants. The disappearance of mosses can be considered a bioindicator for the level of pollution in the environment.

Ferns contribute to the environment by promoting the weathering of rock, accelerating the formation of topsoil, and slowing down erosion by spreading rhizomes in the soil. The water ferns of the genus *Azolla* harbor nitrogen-fixing cyanobacteria and restore this important nutrient to aquatic habitats.

Seedless plants have historically played a role in human life through uses as tools, fuel, and medicine. Dried peat moss, *Sphagnum*, is commonly used as fuel in some parts of Europe and is considered a renewable resource. *Sphagnum* bogs are cultivated with cranberry and blueberry bushes. The ability of Sphagnum to hold moisture makes the moss a common soil conditioner. Florists use blocks of Sphagnum to maintain moisture for floral arrangements.



Figure 2.5.1: Plants as a renewable resource for fuel: Sphagnum acutifolium is dried peat moss and can be used as fuel.

The attractive fronds of ferns make them a favorite ornamental plant. Because they thrive in low light, they are well suited as house plants. More importantly, fiddleheads are a traditional spring food of Native Americans in the Pacific Northwest and are popular as a side dish in French cuisine. The licorice fern, *Polypodium glycyrrhiza*, is part of the diet of the Pacific Northwest coastal tribes, owing in part to the sweetness of its rhizomes. It has a faint licorice taste and serves as a sweetener. The rhizome also figures in the pharmacopoeia of Native Americans for its medicinal properties and is used as a remedy for sore throat.



Figure 2.5.1: Fiddlehead ferns as food: A chicken dish with fiddlehead ferns as a side is shown. Native Americans traditionally cook fiddleheads with meals during the spring.

By far the greatest impact of seedless vascular plants on human life, however, comes from their extinct progenitors. The tall club mosses, horsetails, and tree-like ferns that flourished in the swampy forests of the Carboniferous period gave rise to large deposits of coal throughout the world. Coal provided an abundant source of energy during the Industrial Revolution, which had tremendous consequences on human societies, including rapid technological progress and growth of large cities, as well as the degradation of the environment. Coal is still a prime source of energy and also a major contributor to global warming.



Figure 2.5.1: Carboniferous period plants: This drawing depicts the tall mosses and tree-like ferns of the Carboniferous period that deposited the large amounts of coal throughout the world.

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Key Points

- Mosses and liverworts provide food and shelter for other organisms in otherwise barren or hostile environments.
- The level of pollution in an environment can be determined by the disappearance of mosses, which absorb the pollutants with moisture through their entire surfaces.

- Dried peat moss is used as a renewable resource for fuel.
- Ferns prevent soil erosion, promote topsoil formation, restore nitrogen to aquatic habitats by harboring cyanobacteria, make good house plants, and have been used as food and for medicinal remedies.
- Coal, a major fuel source and contributor to global warming, was deposited by the seedless vascular plants of the Carboniferous period.

Key Terms

- **bioindicator**: any species that acts as a biological indicator of the health of an environment
- **pharmacopoeia**: an official book describing medicines or other pharmacological substances, especially their use, preparation, and regulation
- **sphagnum**: any of various widely-distributed mosses, of the genus Sphagnum, which slowly decompose to form peat; often used for fuel

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2.6: The importance of plants for mitigating and adapting to the effects of climate change

Learning Objectives

- Understand and describe how plants are key to mitigating climate change and helping us adapt to its effects.

Introduction

Plants play a critical role in the global carbon cycle and are key to climate change mitigation and adaptation solutions. Through photosynthesis, plants remove carbon dioxide (CO_2) from the atmosphere and store it as plant biomass. Carbon accumulates in above- or below-ground plant tissues (branches, stems, roots, etc.) and is added to soils through decomposition. The length of time plants store or sequester carbon varies and greatly impacts the global carbon cycle.

Plant-based climate change mitigation

Climate change mitigation involves reducing, preventing, or removing greenhouse gases from the atmosphere. Plant-based approaches that address atmospheric CO_2 include:

1. Protecting high-carbon ecosystems that hold or increase carbon storage (particularly in soils and in plant-rich landscapes such as forests)
2. Practicing agroforestry (incorporating trees and shrubs in crops and pastureland) to improve soil health, ecological diversity, and increase land productivity
3. Using sustainable agricultural approaches that decrease dependency on high-input field production
4. Breeding crops for improved carbon sequestration (e.g., through increased deep root biomass or for biological nitrification inhibition)
5. Developing urban landscapes that minimize water use and sequester carbon

Plant-based adaptation to climate change

Adapting to climate change and its subsequent effects involves making adjustments in response to predicted changes, as well as novel conditions or knowledge. Plants play critical roles in adapting to climate change and plant-based adaptation strategies include:

1. Maintaining diverse forest habitats that offset temperature and moisture extremes
2. Selecting biodiverse cropping systems to retain productivity as a result of a wide range of environmental responses
3. Identifying, developing, and growing a diversity of food plants and agricultural crops
4. Selecting and producing crops/cultivars that reduce the need for inputs and reduce waste at all stages: on the farm, during processing and storage, and by the consumer

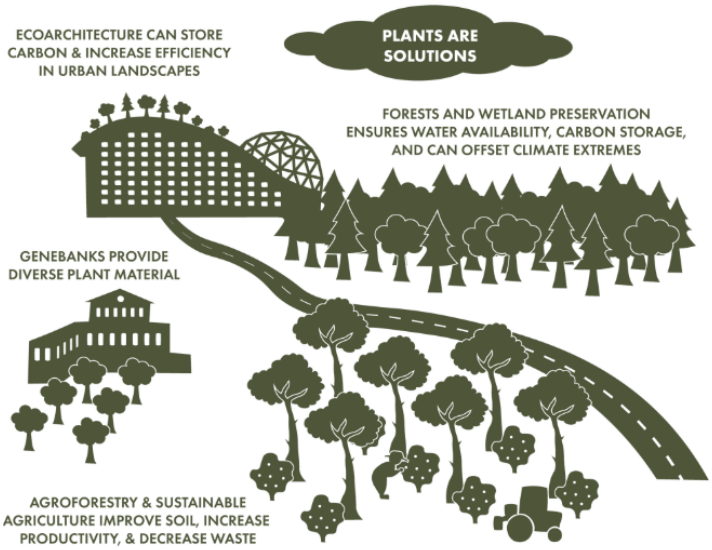


Figure 1. Diagram illustrating examples of how plants play a role in climate change mitigation and adaptation (K. Chen).

Approaches for plant-based mitigation of and adaptation to the effects of climate change

The role of plants in mitigating and adapting to climate change is key. An introduction to some important approaches is highlighted in a few examples below.

Agroecology, agroforestry, and forest ecosystems

Adaptations to climate change that make use of agroecological strategies include crop diversification/biodiversity, maintaining local genetic diversity, soil organic matter management, and water conservation. This could include agroforestry systems that incorporate perennial plants that both capture carbon and provide shade (Altieri et al., 2015). Agroecological methods that incorporate landscape biodiversity can increase resilience to climate-related shocks and disturbances that affect productivity (Queiroz et al., 2021). Biodiversity enhances resilience because crops and cultivars differ in their environmental responses, thus occupying different niches in changing conditions (Vandermeer et al., 1998).



Figure 2. Image of agroforestry setting in Masaka, Uganda (Dan Frendin CC BY-SA 3.0).

Agroforestry is a sustainable land-use system that incorporates trees and shrubs into cropland and pastureland. Agroforestry practices conserve biodiversity, sequester carbon, block wind, and provide food sources (Abbas et al., 2017; Mbow et al., 2014). Forest ecosystems sequester carbon within woody plants and in healthy organic-matter rich soils (Udawatta et al., 2022). These forest ecosystems absorb 15 to 20% of annual human carbon emissions, and thus play an important role in climate change mitigation (Le Quéré et al., 2018; Case et al., 2021). Water is also retained in high quality soils, thereby promoting additional plant growth and reducing the occurrence of wildland fires. Forest ecosystems help buffer the environmental extremes that could be experienced in a changing climate. Shade and moisture-rich microclimates caused by evapotranspiration reduce extreme temperature fluctuations that might occur (De Frenne et al., 2021).

Agriculture

Agricultural production methods play a key role in climate change mitigation and adaptation. For mitigation, adoption of agricultural practices that apply specifically targeted fertilization regimes to single-crop cultivated systems can reduce inputs, decrease water waste, fossil fuels, and unharvested products, which in turn reduce emissions and increase net productivity (Hartin et al., 2014; McPherson et al., 2005; Turner-Skoff and Cavender, 2019). Plant breeding is developing new crops with deep root systems that can sequester carbon (van der Pol et al., 2022). In addition, the choice of plant-based protein sources (such as pulse crops) instead of animal-based proteins reduces agricultural greenhouse gas emissions by reducing methane released in animal production.



Figure 3. Cultivated rice (Oryza sativa) competing with weedy red rice (Oryza sativa spontonea; the taller plants among the rows) near Stuttgart, Arkansas. Weedy red rice has traits that could be used to adapt cultivated rice to climate change such as increased panicle formation with elevated CO2 and resistance to rice blast and sheath blight (USDA-ARS; Hanafiah et al., 2020).

Incorporating climate adaptation action in agriculture aligns with sustainable agriculture practices and can enhance these efforts by considering climate vulnerabilities and potential future threats. For example, organic agriculture practices support soil fertility and pest management and can also enhance the resilience of farms to climate changes. The United Nations Climate-Smart Agriculture program is an example of one approach to develop actions to ensure food security under climate change (Loboguerrero et al., 2019). It aims to develop synergies between climate mitigation, adaptation, and food security, particularly for small farms in developing countries, but it also has implications for large-scale agriculture. The goals of the United Nations Climate-Smart Agriculture program are to:

1. Sustainably and equitably increase agricultural productivity and incomes
2. Help food systems and family livelihoods to be more resilient
3. Minimize agricultural greenhouse gas emissions

Video 1. Video describing the 'Climate-Smart Agriculture' program.

Urban forests and gardens

Gardens and urban forests are important for both mitigating and adapting to climate change. In urban areas, sustainable gardening and landscaping helps minimize water use and sequesters atmospheric carbon both above and below ground (Hartin et al., 2014; McPherson et al., 2005; Turner-Skoff and Cavender, 2019). The Grow Green Guide is a sustainable gardening resource designed for people living in the Metro Vancouver area of Canada. This resource provides over 100 garden designs and information on over 300 plant selections based on criteria including native range, pollinator-friendliness, ability to provide food, water-wise, etc.

Plants are solutions: Principles of resilient food systems

A food system is the network of activities connecting people to their food. According to Schipanski et al. (2016), resilient food systems occur when people produce and access nutritious and culturally acceptable food over time and space in the face of disturbance and change. There are increasing efforts to identify and understand important qualities of resilient food systems. Worstell and Green (2017) use case studies to identify eight qualities common to ecologically resilient food systems and explore how these qualities could be quantified and used.

Qualities common to ecologically resilient food systems:

- Complementary diversity
- Conservative innovation and flexibility (open to new ideas)
- Ecological integration (working with nature)
- Modular connectivity (among farmers, marketers, and suppliers)
- Locally self-organized
- Periodic transformation: Reorganizing, reforming, embracing disturbance
- Physical infrastructure and accumulating reserves
- Responsive redundancy or back-ups

(Worstell and Green, 2017)

Resilient food systems depend on access to diverse plant genetic resources that are made available through conservation efforts. Agricultural production using biodiverse strategies improves ecosystem function because the diversity of species acts as a buffer against failures caused by environmental fluctuations. If one species fails, others can compensate, thus improving the overall health and productivity of the ecosystem (Altieri et al., 2015).

Schipanski et al. (2016) list additional strategies to improve food system resilience, including:

1. Educational gender-equity and women's empowerment, which influences family dietary choices, human nutrition, and can minimize food waste
2. Utilizing ecological, multi-crop systems rather than single-crop production based on intensive external inputs
3. Improving regional food distribution networks
4. Linking human nutrition and food production policies

Conclusions

Plants play a powerful role in mitigating and adapting to climate change. Forest ecosystems store vast quantities of carbon and affect temperature and moisture regimes. Sustainable agricultural methods have the potential of significantly reducing greenhouse gas emissions. Incorporating sustainable gardening and forestry into urban landscapes has the power to reduce water use and activate more regions of the planet for carbon sequestration. Conserving and using biodiversity will be especially important for building food system resilience, if changing climates affect the stability of crop yields. These efforts depend on access to diverse forms of plant genetic resources.

References

Abbas F, Hammad HM, Fahad S, et al. 2017. Agroforestry: a sustainable environmental practice for carbon sequestration under the climate change scenarios—a review. Environmental Science and Pollution Research 24:11177-11191. DOI: 10.1007/s11356-017-8687-0

Altieri M, Nicholls CI, Henao A, Lana MA. 2015. Agroecology and the design of climate change-resilient farming systems. Agronomy for Sustainable Development 35:869-890. DOI: 10.1007/s13593-015-0285-2

Case MJ, Johnson BG, Bartowitz KJ, Hudiburg TW. 2021. Forests of the future: Climate change impacts and implications for carbon storage in the Pacific Northwest, USA. Forest Ecology and Management 482:118886. DOI: 10.1016/j.foreco.2020.118886

De Frenne P, Lenoir J, Luoto M, Scheffers BR, Zellweger F, Aalto J, Ashcroft MB, et al. 2021. Forest microclimates and climate change: Importance, drivers and future research agenda. Global Change Biology 27:2279-2297. DOI: 10.1111/gcb.15569

Hanafiah NM, Mispan MS, Lim PE, Baisakh N, Chen A. 2020. The 21st century agriculture: When rice research draws attention to climate variability and how weedy rice and underutilized grains come in handy. Plants 9:365. DOI: 10.3390/plants9030365

Hartin J, Geisel P, Harivandi A, Elkins R. 2014. Sustainable landscaping in California. University of California. Division of Agriculture and Natural Resources Publication 8504. Available from: escholarship.org/uc/item/2xg41968

Le Quéré C, Andrew RM, Friedlingstein P, Sitch S, Hauck J, Pongratz J, Pickers PA, Korsbakken JI, et al. 2018. Global Carbon Budget 2018, Earth System Science Data 10:2141-2194. DOI: 10.5194/essd-10-2141-2018

Loboguerrero AM, Campbell BM, Cooper PJM, Hansen JW, Rosenstock T, Wollenberg E. 2019. Food and earth systems: Priorities for climate change adaptation and mitigation for agriculture and food systems. Sustainability 11:1372. DOI: 10.3390/su11051372

Mbow C, Van Noordwijk M, Luedeling E, Neufeldt H, Minang PA, Kowero G. 2014. Agroforestry solutions to address food security and climate change challenges in Africa. Current Opinion in Environmental Sustainability 6:61-67. DOI: 10.1016/j.cosust.2013.10.014

McPherson EG, Simpson JR, Peper PJ, Maco SE, Xiao Q. 2005. Municipal forest benefits and costs in five US cities. Journal of Forestry 103:411-416. Available from: fs.usda.gov/research/treesearch/45956

Queiroz C, Norström AV, Downing A, et al. 2021. Investment in resilient food systems in the most vulnerable and fragile regions is critical. Nature Food 2:546-551. DOI: 10.1038/s43016-021-00345-2

Schipanski ME, Macdonald GK, Rosenzweig M, Chappell MJ, Bennett EM, Kerr RB, Blesh J, et al. 2016. Realizing resilient food systems. Bioscience 66:600-610. DOI: 10.1093/biosci/biw052

Turner-Skoff JB, Cavender N. 2019. The benefits of trees for livable and sustainable communities. Plants People Planet 1:323-335. DOI: 10.1002/ppp3.39

Udawatta RP, Walter D, Jose S. 2022. Carbon sequestration by forests and agroforests: a reality check for the United States. Carbon Footprints 1:8. DOI: 10.20517/cf.2022.06

van der Pol LK, Nester B, Schlautman B, Crews TE, Cotrufo MF. 2022. Perennial grain Kernza® fields have higher particulate organic carbon at depth than annual grain fields. Canadian Journal of Soil Science 102:1005-1009. DOI: 10.1139/CJSS-2022-0026

Vandermeer J, van Noordwijk M, Anderson J, Ong C, Perfecto I. 1998. Global change and multi-species agroecosystems: Concepts and issues. Agriculture, Ecosystems & Environment 67:1-22. DOI: 10.1016/S0167-8809(97)00150-3

Worstell J, Green J. 2017. Eight qualities of resilient food systems: Toward a sustainability/resilience index. Journal of Agriculture, Food Systems, and Community Development 7:23-41. DOI: 10.5304/jafscd.2017.073.001

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Citation: Volk GM, Byrne PF, Moreau TL. 2023. Importance of plants for mitigating and adapting to the effects of climate change.

In: Volk GM, Moreau TL, Byrne PF. Conserving and Using Climate-Ready Plant Collections. Fort Collins, Colorado: Colorado State University. Date accessed. Available from:

https://colostate.pressbooks.pub/climatereadyplantcollections/chapter/importance-of-plants/

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2.7: Terms

These are the important terms from this chapter to be sure to know. You might also find these in later chapters.

Agriculture	The science or practice of farming, including cultivation of the soil for the growing of crops and the rearing of animals to provide food, wool, and other products.
Agronomy	The science and technology of producing and using plants for food, fuel, fiber, and land restoration on an extensive scale. The value per acre is lower than for a typical horticultural crop.
Asexual propagation	A form of propagation that results in plants with genetics identical to those of the parent plant.
Bract	A modified leaf or scale, usually small, with a flower or flower cluster in its axil.
Bulb	A specialized, underground organ with a short, fleshy stem axis (basal plate) enclosed by thick, fleshy scales modified for storage.
Control (in an experiment)	Used to verify or regulate a scientific experiment by conducting a parallel experiment or by comparing with another standard.
Demonstration experiment	A method for actively learning the body of scientific knowledge that has been previously discovered and communicated by others; specifically orchestrated for teaching and learning, not for the discovery of new information about the world around us.
Discovery experiment	A method focused on uncovering new relationships and solving problems, following the scientific method, testing hypotheses and their predicted outcomes, and utilizing a careful design in order to maintain meaningfulness and credibility.
Evaluation experiment	A method typically used during the development of new technologies to identify the best products for a desired purpose (e. g., which pesticides are effective against a target insect, but not harmful to non-target insects), but not used to discover new knowledge about how the world works, and thus not typically advancing our understanding of the natural world. Used to pick a winner from among a number of options.
Experimental design	The process of planning an experiment to test a hypothesis.
Experimental unit	The entity to which a specific treatment combination is applied.
Exploration experiment	A method focused on detailed observation of organisms and habitats, used to increase our information about the natural world and to identify potential relationships that need to be tested, and essential to the building of a sound and testable hypothesis.
Floriculture	Discipline of horticulture concerned with the production and marketing of plants valued for their flowers.
Forestry	The science or practice of propagating, planting, managing, and caring for forests; includes harvesting.
Fruit	Ripened ovary together with the seeds within the ovary.
Geophytes	Plants with underground organs in which the plant stores energy or water. New growth begins underground, and the function of this growth is the storage of food, nutrients, and water during adverse environmental conditions.
Horticulture	The art and science of the development, sustainable production, marketing, and use of high-value, intensively cultivated food and ornamental plants.
Hypothesis	Scientific means of forming a question or proposed explanation made on the basis of limited evidence as a starting point for experimentation. In science, a testable statement.
Inflorescence	Complete flower structure of a plant; includes the flower, pedicle, rachis, and peduncle.
Internode	Stem regions between nodes in plants.
Leaf	A usually green, flattened, lateral structure attached to a stem and functioning as a principal organ of photosynthesis and transpiration in most plants.

Leaf blade	Broad portion of a leaf; does not include the petiole.
Monocotyledon	Seed plant that produces an embryo with a single cotyledon and parallel-veined leaves; includes grasses, lilies, palms, and orchids.
Node	Stem region of a plant where one or more leaves attach; location of lateral buds.
Olericulture	Discipline of horticulture concerned with the production and marketing of plants or plant parts valued for culinary use as vegetables.
Pedicel	Short stalk that holds up the flower.
Peduncle	Large, central stalk that attaches the rachi to the stem of the plant.
Petiole	Stalk by which most leaves are attached to a stem; part of the leaf structure, not the stem.
Pomology	Production and marketing of plants or plant parts valued for their culinary use as fruits, including nuts; propagated by cuttings and grafting (asexual propagation).
Rachis	Stalk of a flower that is situated between the peduncle and the pedicel.
Randomization	Act of randomly assigning treatments to experimental units using a random number table or computer-generated randomization to help minimize any bias that has not been recognized in advance and controlled for in other ways.
Replication	Application of the same treatment to more than one experimental unit.
Rhizome	Horizontal stem growing just below the soil surface.
Science	Systematic study of the structure and behavior of the physical and natural world through observation and experiment.
Scientific discovery	Process of scientific inquiry; builds on what is known by testing hypotheses.
Sessile	A leaf that lacks a petiole; called a sessile leaf.
Sexual propagation	Form of propagation that results in plants with genetics that differ from those of the parent plants; also called seed propagation.
Stem	Supporting and conducting organ, usually developed initially from the epicotyl and growing upward; consists of nodes and internodes.
Treatments	Administration or application of agents to a plant to prevent disease or facilitate growth.
Tuber	Swollen, underground, modified stems that store food.

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3: INTRODUCTION TO PLANT SCIENCE

Learning Objectives

- Gain foundational knowledge of plant biology and its applications.
- Understand the basic principles of botany, including plant structure and function.
- Identify key plant physiological processes such as photosynthesis.
- Explore how plant science informs conservation and agricultural practices.

Chapter 3 opens the door to the fascinating field of plant science, or botany—the study of plants and plant-like organisms that shape our ecosystems and support life on Earth. From the duckweed to sequoias, plants are essential for oxygen, food, medicine, and more. We will explore what counts as a plant, dive into their unique life cycles, and the evolutionary processes that shaped them. You'll discover the many branches of plant biology and learn how plants interact with other organisms.

3.1: Organisms Studied in Botany

3.2: Life Cycles

3.3: Intro to Evolution

3.4: Subfields and Applications in Plant Biology

3.5: Plants, Botany, and Kingdoms

3.6: Styles of Life and Basic Chemistry

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3.1: Organisms Studied in Botany

Learning Objectives

Describe the importance of plants in the study of botany and list other organisms that typically included in the study of botany.

Botany is the scientific study of plants and organisms that were historically considered plantlike. It helps us understand why plants are so vitally important to the world. Plants start the majority of food and energy chains, they provide us with oxygen, food and medicine. Most plants are what you typically think of: multicellular eukaryotic organisms that are ancestrally terrestrial and photosynthesize. In the process of photosynthesis, these organisms produce their own food, using sunlight, carbon dioxide, and water into organic molecules, or food. However, some organisms ecologically are considered plant-like due ot their role in nature. For example, green slugs, *Elysia chlorotica* (see Figure 3.1.1) collect chloroplasts from algae and use them for their entire life as food producers. Therefore, green slugs, while technically classified as animals, have plantlike characteristics.



Figure 3.1.1: Green slug *Elysia chlorotica* captures chloroplasts from the alga *Vaucheria litorea*.

Plants are in the domain Eukarya and in the kingdom Plantae. There are about 320,000 species of plants that have been named so far. They fill our terrestrial ecosystem and provide food and shelter for animals. Plants cells contain chloroplasts, which conduct photosynthesis. They are thus **autotrophic**, synthesizing their own organic carbon. In addition, most of the plant cell is filled with a large membrane-bound structure, the central vacuole, which functions in store. Plant cells are surrounded by rigid cell walls containing cellulose. Plants are multicellular, composed of like cells that function as tissue. Their leaves, stems, and roots function as organs. Plants can be small like duckweed or large like the giant sequoia (Figure 3.1.2).



Figure 3.1.2. On top, two species of duckweeds (*Wolffia globosa* and *Spirodela polyrhiza*). . On the bottom, Giant Sequoias from King Canyon National Park. Copyright Eric Guinther (CC BY-SA 3.0) for top image, Kammy Algiers (CC-BY) bottom image.

While fungi are neither closely related to plants, nor do they share key characteristics (like photosynthesis), they are sometimes included in the study of botany. Perhaps this is because the fruiting bodies that some fungi use for reproduction (such as mushrooms) may seem plantlike in the sense that they a stationary structures emerging from the soil. Fungi are **heterotrophic**, meaning that they feed on other organisms to obtain organic carbon. Unlike animals, which ingest their food, fungi secrete digestive enzymes to breakdown large molecules surrounding them. They then absorb the smaller molecules. Fungal cells are surrounded by rigid cell walls that contain the polysaccharide chitin. Some fungi are unicellular while other are multicellular. Although fungi and plants are not closely related, their are intertwined ecologically. For example, mycorrhizae are fungi that grow in or on plant roots and assist with nutrient absorption. Additionally, fungi often decompose dead plant material, releasing nutrients back into the soil and promoting further plant growth.

Other organisms studied in botany are "protists", which have complex, eukaryotic cells but are not plants, animals, or fungi. Some "protists", like slime molds, resembling fungi in the sense that they are heterotrophic. Other "protists" superficially resemble plants in that they conduct photosynthesis and are autotrophic. These are collectively called **algae**, but they arise from many different groups, and some are not closely related to plants at all. Multicellular algae are sometimes called **seaweeds**. Most algae have cell walls, which may or may not contain cellulose.

Photosynthetic prokaryotes, which have simple cells, are sometimes studied in botany as well. For example, **cyanobacteria**, are commonly called blue-green algae, but this is a misnomer because true algae are eukaryotes. Instead, cyanobacteria are photosynthetic bacteria, that often form filaments of cells. Bacteria that are pathogens of plants may also be included in the study of botany. Viruses, which are infectious particles that contain protein and nucleic acid, can also infect plant cells. Unlike plants, fungi, "protists", and prokaryotes, viruses are not technically considered organisms because they are not composed of cells.

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3.2: 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 3.2.1).

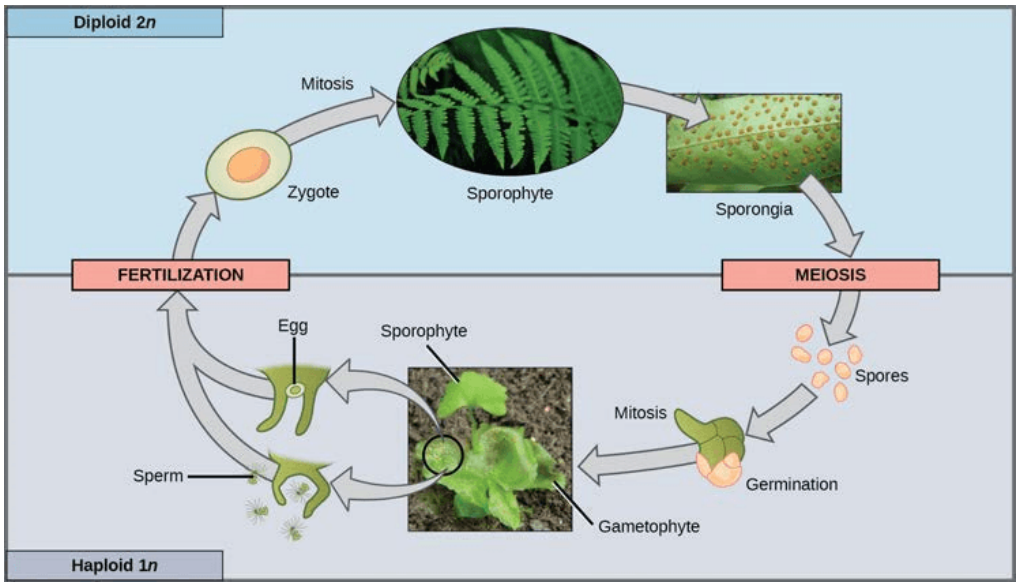


Figure 3.2.1: The plant life cycle is haplodiplontic (alternations of generations). Fern is shown as an example. The haploid (n) multicellular life stage is called the gametophyte as it produces gametes (egg and sperm cells) that fuse during fertilization to form a diploid (2n) zygote. This zygote develops 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.

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3.3: Intro to Evolution

Learning Objectives

- Describe the role of evolution in the history of life.
- Describe the role of natural selection in evolution.

The history of life on Earth goes back more than three and a half billion years. This past serves as a key to understanding the diversity of life. A unifying theme that can be employed throughout this course to boost biology from an overwhelming sea of facts to a coherent study of life is the theory of evolution. Evolution explains both the diversity and unity of life. Through time, some species evolved adaptations that increased their ability to survive and reproduce in their environment. This gave them an evolutionary advantage to other species. **Natural selection**, the most dominant evolutionary force, is a main mechanism that is responsible for the diversity of species on Earth today. Yet, it is through evolution that we also understand the unity of all life. All living organisms today can be followed back to a common ancestor. Scientific evidence from this is extensive and includes data from fossils, genetics, cell biology, and molecular biology, just to name a few. Through descent with modification, our common ancestors gave rise to the species we see on Earth today.



Figure 3.3.1: A glimpse at the diversity of wildflowers in Figueroa Mountain, California. Left: chocolate lily (*Fritillaria biflora*). Middle: California poppies (*Eschscholzia californica*) and lupines (*Lupinus sp.*) Right: shooting stars (*Dodecatheon sp.*). Image by Kammy Algiers (CC-BY)

Evolution

Evolution can be defined as the change in the genetic make up of a population over time (or, for short, change over time). It is important to note that the change happens from one generation to the next. Thus, an individual cannot evolve because their genes do not change throughout their lifetime. However, a population, a community, or an ecosystem can change over time, as can a species or a group of species. The time it takes for evolution to occur is better described as generation time. This can be very short (minutes for a bacterium), or very long (a century or more for a sea turtle). It is the time it takes for one generation of individuals to reproduce and pass their genes down to the next generation. Charles Darwin's book "*On the Origin of Species*" published in 1859 described and popularized the theory of evolution and proposed a mechanism for evolution he called natural selection. Independently, Alfred Russell Wallace also introduced the concept of natural selection.

Natural Selection

There are many forces or mechanisms that cause evolution. However, natural selection is a key mechanism as it is the one that produces adaptive traits. For natural selection to occur, several conditions must be met:

1. The population must contain genetic variation in the trait. This means the differences in the traits of the individuals within the population.
2. The trait must be heritable. This means the individual receives the genetic information for the specific trait from their parent(s).
3. There must be variation in fitness as a result of the trait. This means that some traits result in the individuals with higher reproductive success (they have more offspring) than others.

If these three criteria are met, individuals with the most adaptive trait for the current environment will have more offspring, and thus the adaptive traits will accumulate in the environment.

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3.4: Subfields and Applications in Plant Biology

Learning Objective

Describe the various subdisciplines of plant biology.

Branches of Plant Biology

The scope of biology is broad and therefore contains many branches and subdisciplines. The branch of plant biology can further be divided into many subdisciplines as well. Botanists may pursue one of those subdisciplines and work in a more focused field. Botany's origins come from ancient studies of herbal medicine. Even today, **ethnobotany** focuses on the traditional knowledge and practical uses of plants in medicine, religion, food, etc.

An **agronomist** or **agricultural scientist**, is a scientist who studies crops. Their focus may include crop quality, growth, nutrition, or disease. George Washington Carver (1860-1943) was an American agricultural scientists who revolutionized crop rotation (Figure 3.4.1). He found that by planting different crops in the same location, the nutrients such as nitrogen in the soil are replenished. He promoted planting peanuts as part of the rotation.

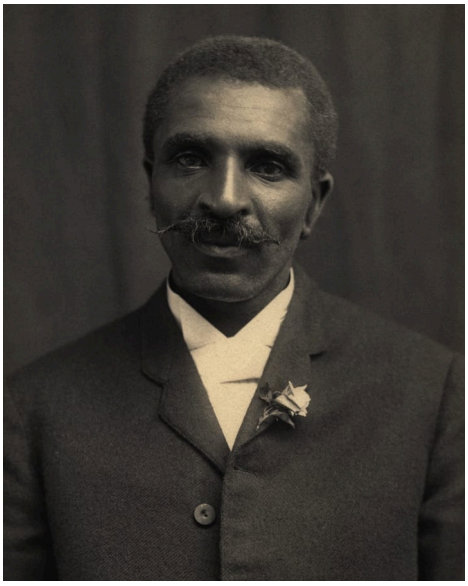


Figure 3.4.1: George Washington Carver was an American agricultural scientist and inventor who promoted crop rotation to prevent soil depletion. He was the most prominent Black scientist of the early 20th century. (Wikipedia; Public Domain)

Phytochemists are plant biochemists who study chemical substances of plants. This is a field that incorporates chemistry as well as biology. These compounds can be studied for medicine, culinary purposes, or as dyes and building material. Some botanists study plant hormones so they can understand the mechanisms of plant growth and regulation. A **plant geneticist** would study plant genes, often working to create new varieties of plants or crops. **Molecular biology** biological processes at the molecular, including interactions among molecules such as DNA, RNA, and proteins, as well as the way they are regulated. A plant molecular biologist would be interested in these aspects of plants. A **plant physiologist** would study the internal chemical and physical activities of plants and plant metabolism. **Plant anatomy** would focus on the structures of plants.

A **systematic botanist** studies the diversity of plants and their evolutionary relationships. **Paleobotanists** study plant fossils and are interested in understanding past environments and ancient plant types. This can also aid in our understanding of the evolution of modern plants.

Plant ecologists are scientists that study the interaction of plants with their environments. Plant ecologists can focus on populations, communities, or ecosystem interactions. **Restoration ecologists** and **conservation biologists** focus on the the

negative impacts of the environment. The restoration ecologist works to reverse environmental impacts caused by human disturbance. Conservation biologists focus on preserving and maintaining existing habitat. There is often a focus on policy change. In many circumstances these two fields overlap with one another and overlap with other disciplines. Many government employees who focus on the environment are involved in restoration, conservation, and promote education, public engagement, and awareness of the environment.

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3.5: Plants, Botany, and Kingdoms

Botany is the scientific study of plants and plant-like organisms. It helps us understand why plants are so vitally important to the world. Plants start the majority of food and energy chains, they provide us with oxygen, food and medicine. Plants can be divided into two groups: plants$_1$ and plants$_2$. Plants$_1$ contain **all photosynthetic organisms** which use light, H_2O, and CO_2 to make organic compounds and O_2. Plants$_1$ are defined *ecologically* (based on their role in nature). Some plants$_1$ can be bacteria or even animals! One example of this a green slug, *Elysia chlorotica* (see Figure 3.5.1). Green slugs collect chloroplasts from algae and use them for their entire life as food producers. Therefore, green slugs are both animals and plants$_1$.



Figure 3.5.1 Green slug Elysia chlorotica caprures chloroplasts from the alga Vaucheria litorea.

Plants$_2$ are **all organisms from Vegetabilia kingdom**. Normally, plants$_2$ are green organisms with a stem and leaves. We can define them also as **multi-tissued, terrestrial, and primarily photosynthetic eukaryotes**. This definition is *taxonomical* (based on evolution).

It is possible for the organism to be plant$_2$ but not plant$_1$ (Figure 3.5.2). Those who fall into that category, are fully parasitic plants (mycoparasites like *Pterospora*, root parasites like *Hydnora*, stem parasites like *Cuscuta*, and internal parasites like Pilostyles) which do not practice photosynthesis but have tissues, terrestrial lifestyle and originated from photosynthetic ancestors. Plants may be understood on several levels of organization: (from top to bottom) (a) ecosystems or taxa, (b) populations, (c) organisms, (d) organs, (e) tissues, (f) cells, (g) organelles, and (h) molecules (Figure 3.5.3). Botany is considered to be a “slice science” because it covers multiple levels of organization.

Taxonomy

Taxonomy, **systematics** and **classification** are terms with similar meanings; they are all about the overwhelming diversity of living organisms, for there are more than 2,000,000 species (and 300,000 of them belong to plants$_2$). **Phylogenetics** is a more fashionable term; it emphasizes the evolutionary history (**phylogeny**) of taxonomic groups (**taxa**). This taxonomic organization is hierarchical. Most scientists accept seven main levels of taxonomy (**ranks**): the highest is **kingdom**, followed by **phylum**, **class**, **order**, **family**, **genus**, and lastly, **species**.

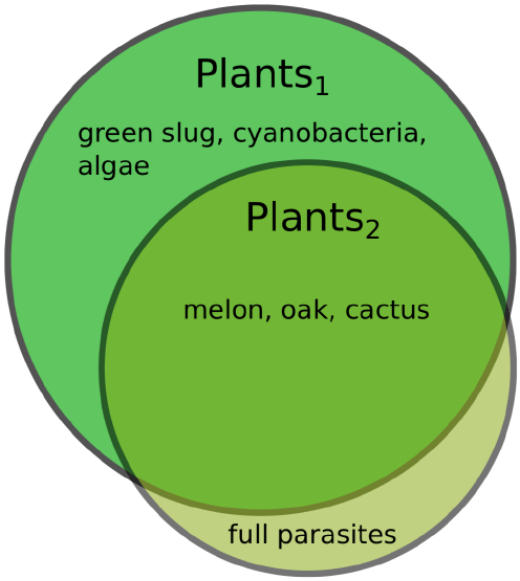


Figure 3.5.2: plants$_1$ and plants$_2$

The highest rank, kingdoms are easy to understand as the *pyramid of life* (Figure 3.5.4) which is divided into four levels—kingdoms. At the bottom is **Monera**, which consists of prokaryotes (Bacteria and Archaea). This is the first level of life: Monera have simplest cells without nucleus. The next level is **Protista**. These are eukaryotes (nuclear cells) without tissues; some examples are algae and fungi. The final level consists of two groups: **Vegetabilia** and **Animalia**. They both have tissues but have obtained them for completely different purposes. Animals have tissues *to hunt and digest*, while plants have tissues mainly *to survive on land*. Viri which are mentioned sideways, are not living things but merely pieces of DNA or RNA which "went astray" out of cells of living organisms of all four kingdoms. Despite of being non-living, viruses are capable of evolution.

Plants$_2$ (kingdom Vegetabilia) contain more than 300,000 species and divided in multiple subgroups (Figure 5.1.1).

Ranks are used to compare taxonomic groups (**taxa**) from different major groups. No precise definitions are available for particular ranks, but it is believed that they are

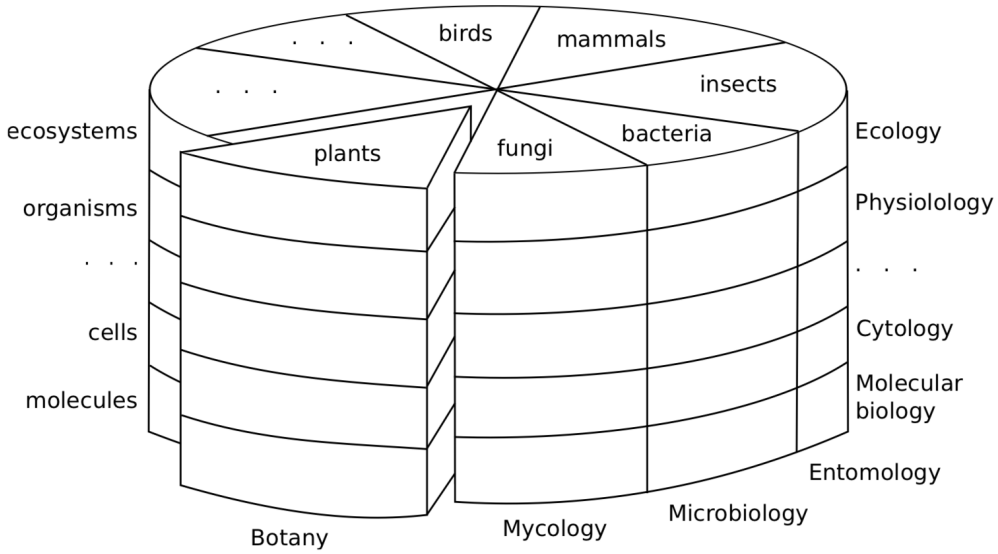


Figure 3.5.3 Layered pie of biology: levels of organization (left), taxonomic groups (top), "slice" sciences (bottom) and "layer" sciences (right).

associated with the time of divergence (separation) between taxa. In addition to seven ranks mentioned above plant taxonomy uses intermediate ranks like **subfamily**, **subclass** or **superorder**—when taxonomic structure is too complicated.

Below is and example of names used for different ranks. Please note that names used for some ranks have standardized endings

(underlined):

English	Latin	Example 1	Example 2
Kingdom	Regnum	Vegetabilia	Animalia
Phylum	Phylum	Spermato	Chordata
Class	Classis	Angiospermae (Magnoli<u>opsida</u>)	Mammalia
Order	Ordo	Lili<u>ales</u>	Primates
Family	Familia	Asparag<u>aceae</u>	Homin<u>idae</u>
Genus	Genus	*Chlorophytum*	*Homo*
Species	Species	*Chlorophytum comosum* (Thunb.) Jacq.	*Homo sapiens* L.

It is frequent when one species has several geographical races without clear borders between them. The example might be the stinging nettle, *Urtica dioica*. In North America, many nettles have narrower leaves and are less stinging than in Eurasia. However, there are many intermediate forms between these races. To reflect this, taxonomists introduced two **subspecies**: in this case, *Urtica diuica* subsp. *dioica* ("Eurasian") and *U.*

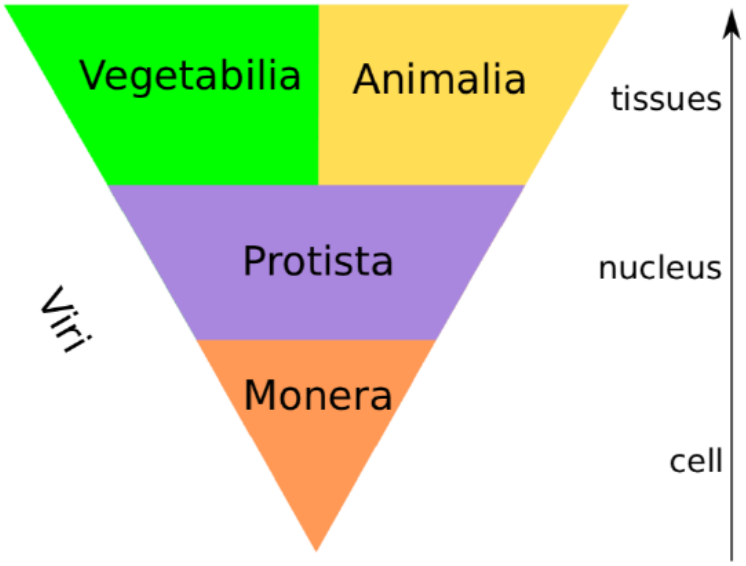


Figure 3.5.4 Pyramid of Life.

dioica subsp. *gracilis* ("North American"). Another frequently used under-species category which is **cultivar**. Cultivars are frequently used in gardening. For example, many roses in cultivation belong to different cultivars of *Rosa banksiae*, and yellow roses are often *Rosa banksiae* cv. 'Lutea' where the last part of name is for the cultivar.

Names of species are **binomials** which consist of the name of genus and **species epithet**:

$$\overbrace{\underbrace{\text{Chlorophytum}}_{\text{Name of genus}}\ \underbrace{\text{comosum}}_{\text{Species epithet}}\ \underbrace{(\text{Thunb.})}_{\text{First author}}\ \underbrace{\text{Jacq.}}_{\text{Second author}}\ \underbrace{1862}_{\text{Year of description}}}^{\text{Name of species}}$$

If one does not know the exact species, "sp." shortcut is used instead of epithet, and "spp." is used as a shortcut for multiple unknown species. It is required to use *slanted font* when one prints a name of species or genus. All scientific names are capitalized, but the second word in a species name (species epithet) always starts from lower case letter. It is a well-known fact that some species have a hybrid origin, and in these cases, botanists use a multiplication sign (×). For example, common plum (*Prunus* ×*domestica*) is a hybrid between blackthorn and cherry plum: *Prunus spinosa* × *Prunus cerasifera*.

The group of plants or animals must have one and only one name. Ideally, the name should be a stable ID for all occasions.

But since biology is a “science of exceptions”, some plant families are allowed to bear two names. As an example, legumes (**Leguminosae**) are frequently named “Fabaceae”, and grasses (**Gramineae**) have the second name “Poaceae”.

Throughout the long history of taxonomy, too many names were given to the same taxa. At the moment, we have almost 20,000,000 names to describe 2,000,000 species. These 18,000,000 “excess names” are **synonyms** which should not be used in science. To regulate the use of names, **nomenclature codes** were created. These codes specify, for example, the **rule of priority**: *when two names are given for the same group, only earlier name is valid*. Consequently, it is recommended to list the author and the year of description along with a name: “*Homo sapiens* L. 1758”, which means that founder of taxonomy, Carolus Linnaeus (“L.” shortcut) described this species in 1758.

Another important concept of nomenclature is the **nomenclature type**. Practically, this means that every species name must be associated with the physical museum specimen. In botany, these museums are collections of dried and pressed plants, called **herbaria**. Type specimens are of immense importance because there are no labels in nature, and only these specimens will “tell” about real plants or animals associated with particular names.

Names of taxa higher than species also have nomenclature types, but in these cases they are other names, not specimens. This example may clarify the use on nomenclature types. Initially, oleaster family (Elaeagnaceae) contained two genera, *Elaeagnus* (oleaster) and *Hippophaë* (sea-buckthorn). The second genus included *Hippophaë rhamnoides* (Siberian sea-buckthorn, **type species**) and *Hippophaë canadensis* (North American plant). Thomas Nuttall decided to split sea-buckthorns in two genera. Since one of them contains *Hippophaë rhamnoides*, the **type species**, it should keep the name *Hippophaë*. The second genus can be named arbitrarily. Nuttall gave it name “*Shepherdia*”. As a result, the species which had name *Hippohaë canadensis* L., became *Shepherdia canadensis* (L.) Nutt.

Plant taxonomy is a science. That means that our understanding of plant groups will always change. It also means that there always are different competing opinions, the *taxonomic hypotheses* which describe plant diversity in different ways. As a result, some groups of plants could be accepted in a broad sense, including as many subgroups as possible. For example, there might be an opinion of *Homo sapiens* s.l. (*sensu lato* = wide sense) including not only contemporary humans but also Neanderthal men. As a contrast, other opinions may accept groups in a strict sense, and *Homo sapiens* s.str. (*sensu stricto* = strict sense) includes only contemporary humans.

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3.6: Styles of Life and Basic Chemistry

Life obtains energy in a few different ways: (1) from sunlight (**phototrophy**); (2) from chemical reactions with inorganic matter (**lithotrophy**); (3) from breaking organic molecules into inorganic molecules, typically carbon dioxide and water (**organotrophy**). To make its body, living beings obtain building blocks either by (a) from the assimilation of carbon dioxide (**autotrophy**), or from other living beings (**heterotrophy**).

These ways combine in six lifestyles. For example, plants$_1$ are by definition **photoautotrophs**. Most plants$_2$ are also photoautotrophs, but there are exceptions: full parasites (see above). Carnivorous plants (like sundew, *Drosera* or the Venus flycatcher, *Dionaea*) are all photoautotrophs. They "eat" animals in order to obtain nitrogen and phosphorus, so the dead bodies serve not as food but as a fertilizer. Note that plants are also **organoheterotrophs** like animals because in addition to photosynthesis, all plant cells can respire.

To understand life of plants, a basic knowledge of chemistry is needed. This includes knowledge of atoms (and its components like protons, neutrons and electrons), atomic weight, isotopes, elements, the periodic table, chemical bonds (ionic, covalent, and hydrogen), valence, molecules, and molecular weight. For example, it is essential to know that protons have a charge of $+1$, neutrons have no charge, and electrons have a charge of -1. The atomic weight is equal to the weight of protons and neutrons. Isotopes have the same number of protons but different number of neutrons; some isotopes are unstable (radioactive).

One of the most outstanding molecules is water. Theoretically, water should boil at much lower temperature, but it boils at 100° C just because of the hydrogen bonds sealing water molecules. These bonds arise because a water molecule is *polar*: hydrogens are slightly positively charged, and oxygen is slightly negatively charged (***Figure*** 3.6.1).

Another important concept related to water is **acidity**. If in a solution of water, the molecule takes out proton (H^+), it is an **acid**. One example of this would be hydrochloric acid (HCl) which dissociates into H^+ and Cl^-. If the molecule takes out OH^- (hydroxide ion), this is a **base**.

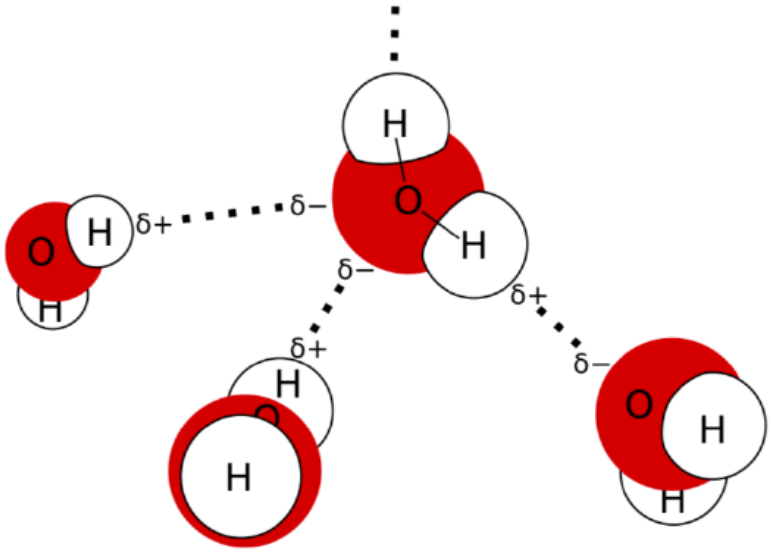


Figure 3.6.1 Hydrogen bonds between water molecules, δ shows the partial charge.

An example of this would be sodium hydroxide (NaOH) which dissociates into Na^+ and hydroxide ion.

To plan chemical reactions properly, we need to know about **molar mass** and **molar concentration**. Molar mass is a gram equivalent of molecular weight. This means that (for example) the molecular weight of salt (NaCl) could be estimated as $23 + 35$, which equals 58 units. Consequently, one mole of salt is approximately 58 **grams**. One mole of any matter (of molecular structure) always contains $6.02214078 \times 10^{23}$ molecules (**Avogadro's number**).

The density of a dissolved substance is the **concentration**. If in 1 liter of distilled water, 58 grams of salt are diluted, we have 1M

(one molar) concentration of salt. Concentration will not change if we take any amount of this liquid (spoon, drop, or half liter).

Depending on the concentration of protons in a substance, a solution can be very acidic. The acidity of a solution can be determined via pH. For example, if the concentration of protons is 0.1 M (1×10^{-1}, which 0.1 grams of protons in 1 liter of water), this is an extremely acidic solution. The pH of it is just 1 (the negative logarithm, or negative degree of ten of protons concentration). Another example is distilled water. The concentration of protons there equals 1×10^{-7} M, and therefore pH of distilled water is 7. Distilled water is much less acidic because water molecules dissociate rarely.

When two or more carbon atoms are connected, they form a **carbon skeleton**. All **organic molecules** are made of some organic skeleton. Apart from C, elements participate in organic molecules (biogenic elements) are H, O, N, P, and S. These six elements make four types of biomolecules: (1) lipids—hydrophobic organic molecules which do not easily dissolve in water; (2) carbohydrates or sugars, such as glucose (raisins contain lots of glucose) and fructose (honey); by definition, carbohydrates have multiple $-$OH group, there are also polymeric carbohydrates (polysaccharides) like cellulose and starch; (3) amino acids (components of proteins) which always contain N, C, O and H; and (4) nucleotides combined from carbon cycle with nitrogen (heterocycle), sugar, and phosphoric acid; polymeric nucleotides are nucleic acids such as DNA and RNA.

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4: TAXONOMY

Learning objectives

- List the seven levels of the plant classification system.
- Recognize the taxonomic diversity of common foods in your diet.
- Summarize the contribution of *Linneaus* to binomial nomenclature.
- Understand how the two-part scientific naming system works and its applications.
- Describe the differences between epigeal and hypogeal seedling emergence.

This chapter addresses the importance of **binomial names**, sometimes referred to as **scientific names**. At a garden center, a plant labeled a bluebill could be *Scilla non-scripta*, from the monocotyledones, or *Mertensia virginica*, from the dicotyledones. Two different plants, both from division Anthophyta, but from different Classes. Common names have their place, but they can be ambiguous. Binomial nomenclature is more precise; its use ensures that you'll get the correct plant and the correct information on how to grow and propagate it. The second section in this chapter addresses seed germination, arguably the most common and important method of propagating plants.

4.1: Plant Taxonomy

4.2: Methods of Taxonomy and Diagnostics

4.2.1: Cladistics

4.2.2: Phenetics

4.2.3: Dichotomous Keys

4.2.4: Glossary

4.3: Terms

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4.1: Plant Taxonomy

Learning objectives

- List the seven levels of the plant classification system.
- Recognize the taxonomic diversity of common foods in your diet.
- Summarize the contribution of *Linneaus* to binomial nomenclature.
- Understand how the two-part scientific naming system works and its applications.

Plant taxonomy

Here are some introductory definitions:

Taxonomy (or systematics): The science of classifying organisms.

Classification: A grouping of plants according to shared qualities or characteristics.

Plant taxonomy: A hierarchical classification system based on morphological (see below) and phylogenetic (see below) similarities among plants.

Nomenclature: A formal system of names attached to taxonomic groupings.

Hierarchy: A system of grouping in which each classification is a subset of a superior grouping, and may contain subordinate categories. As an example: The landmass of the United States (used here as the highest or most inclusive level of classification) is partitioned into states (a middle level of classification). States, in turn, are partitioned into counties (the lowest level in this hierarchy). Counties are subsets of states, which are in turn subsets of the nation. This hierarchical type of grouping system is used in plant taxonomy.

Morphology: The appearance (shape and structure) of a plant. Plant taxonomy is a hierarchy primarily based on grouping together plants that exhibit structural (phenotypic) similarities.

Phylogeny: Ancestral, evolutionary relationships among plants. While plant taxonomy has historically been based on plant morphology, these relationships are currently being verified and expanded using new molecular genetic technologies that uncover genetic similarities through comparisons of shared DNA sequences. In general, plants sharing more DNA are considered more similar from an evolutionary standpoint, and considered to have diverged from each other more recently in evolutionary time than plants that share less DNA.

Taxonomy in the pantry: Classification exercise



"Food on shelf" by Jaranda, CC BY-SA 2.0

To start becoming familiar with taxonomic categories, go to your fridge, cupboard, or pantry and choose a variety of fruits, vegetables, and grains. These might include cans of mushrooms, green peas, black-eyed peas, chickpeas, butter beans, and sweet corn; bags of pine nuts and coconut, and perhaps a banana that was getting a bit too brown.

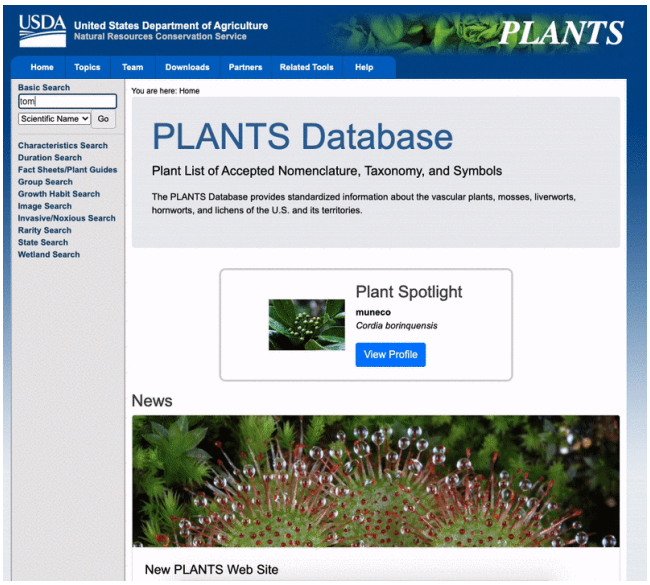
Think about the many ways in which you could group these foods. You might, for instance, categorize a food by whether it is canned or fresh, by size, manufacturer, or color, or by the meal in which you would typically eat it.

Or you could apply a biological, hierarchical classification system, categorizing them by the morphology and phylogeny of the plant on which they grew. The plant systematics hierarchy we will use in this course is as follows, from highest (most inclusive) to lowest level:

- Kingdom
- Division (or Phylum, although Phylum is more commonly associated with animal taxonomy)
- Class
- Order
- Family
- Genus
- Specific epithet (usually a species name)

Memorize this hierarchy, so it rolls off your tongue like a multiplication table.

Now apply this taxonomic system to your foods. An easy way to do this is to search for each food on the U.S. Department of Agriculture's site USDA Plants Database. If you type "tomato" into the search bar, select "Common Name" from the dropdown menu, and click "go," you'll see all the plants with "tomato" in their common name. Click on *Solanum lycopersicum* L. (garden tomato) and you'll get this entry, the description for the common garden tomato. Scroll down to see the "Classification" section, which lists the taxonomic classification and includes Kingdom, Division, Class, Order, Family, Genus, and Specific epithet. Notice that this database has finer divisions of hierarchy than you are required to know, including Subkingdom, Superdivision, and Subclass.



Here's a look at how you can use the USDA Plants Database to find the full classification of plants, like tomato. Try it out!

You can use the information in the database to classify your foods. For products with several ingredients, pick one from the ingredient list, such as wheat in crackers or tomato in spaghetti sauce.

While you can sometimes find this info on Wikipedia, be aware that Wikipedia is not always reliable and you'll want to cross-reference with other sources. If you enter "tomato" into the Wikipedia search bar you'll get this page. The right sidebar includes the taxonomic classification. "Unranked" is used instead of Division and Class, which means there is some disagreement on whether those names are the correct Division or Class names. You might also see several hierarchical terms listed as "Clade," rather than the proper terms. If you can't find complete information on Wikipedia, use the USDA site.

For the foods in our hypothetical pantry — mushrooms, green peas, black-eyed peas, chickpeas, butter beans, sweet corn, pine nuts, coconut, and banana — we can divide them into the following **Kingdoms**: Plantae and Fungi.

We can separate the products within the Plantae kingdom into two **Divisions**:

- Pinophyta: the pine nuts, which come from a conifer
- Magnoliophyta: everything else in this kingdom, which come from flowering plants

The cans and bags in the Magnoliophyta division can be separated into these **Classes**:

- Liliopsida (Monocotyledons — one embryonic leaf in the seed, parallel leaf veins, and petals and sepals in multiples of three): corn, coconut, and banana
- Magnoliopsida (Dicotyledons — two embryonic leaves in seed, and branched leaf veins): green peas, black-eyed peas, chickpeas, and butter beans

In comparison to the other levels, **Order** is a relatively arbitrary set of classifications that were created in part to make subsequent classifications more manageable. Order will be addressed in the section on phylogeny.

Next, the products can be subdivided by **Family**.



"Public Flower Garden in downtown Seattle" by FallenPegasus, CC BY-NC 2.0

Depending on details of the particular plant classification system used, there are approximately 230 plant families. Families are often based on types and organization of flower parts and fruit type, including the number of petals, sepals, stamens, and pistils, and the location of the ovary relative to petals. In this website from the University of California Cooperative Extension (optional) the authors identify many of the characteristics used to group plants into families.

Among our food examples, the Family hierarchy includes:

- Arecaceae (coconut, which comes from a palm tree)
- Poaceae (corn, which is a grass)
- Musaceae (banana)
- Fabaceae (the three peas and the butter beans, which are legumes)

Genus and Specific Epithet are the last two classifications. The pairing of genus and specific epithet to name a plant is called binomial nomenclature. Tthe first letter of the genus is capitalized, and the entire binomial is either underlined or written in italics.

Watch this video for an explanation of plant taxonomy.

Review questions

Think about these questions and be able to discuss the answers or know how to find the them using the resources provided:

1. Where are blue spruce trees (a conifer) taxonomically separated from lilies (flowering plants) at the Kingdom or Division level? (Hint: Use the online resources that were provided in this section.)
2. Are lilies (monocots) separated from beans (dicots) at the Class or Order level?
3. At which taxonomic level are flowering plants separated into different classifications based on flower and fruit characteristics?

Example taxonomy tree

Now that you have the names for each of your plants, you can organize them into a taxonomic tree that more clearly shows their relationships to one another. Below is an example tree based on some of the foods found in our hypothetical pantry:

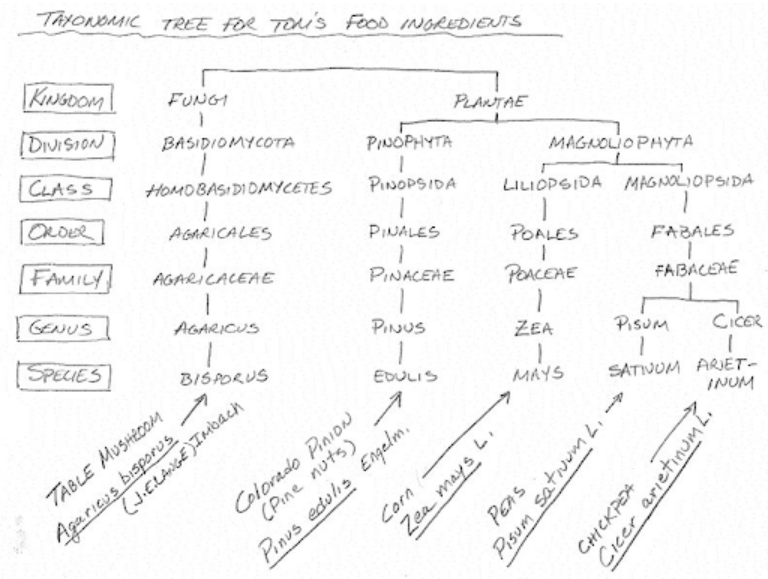


Image credit: Tom Michaels

Now, try it yourself. Determine which plants you want to use, look them up on the USDA Plants Database, write down the Kingdom, Division, Class, and so on for each, and begin constructing the tree to show relationships and points of divergence. In this example, the mushrooms diverge from everything else at the Kingdom level, pine nuts diverge from the other three at the Division level, corn is in a different Class than pea and chickpea, and pea and chickpea diverge at Genus.

The point of this exercise is for you to understand that relationships among plants are known, and are categorized in a sophisticated taxonomic system. Some of the plants we commonly eat have close relationships, like the various plants in the Solenaceae family (tomato, eggplant, potato), but others are much more distant.

Linneaus and plant taxonomy

Binomial nomenclature

Carolus Linnaeus (1707–1778), a Swedish professor, is widely recognized for developing the binomial nomenclature for plants. Binomial nomenclature is a scientific classification in which each organism is given two names. In his 1753 book *Species Plantarum* (kinds of plants), Linnaeus employed this system to describe a great number of plants using Latin polynomials. The first word of the polynomial became the genus, and a marginal note describing the plant became the specific epithet. Several years ago we celebrated Linnaeus' 300th birthday, and you can find a long set of links about him from a simple Google search.

A proper binomial, in addition to the Genus and specific epithet, also includes the initials of the naming authority — the person who proposed the accepted name. Previous naming authorities might also be listed in parentheses. For example:

- *Phaseolus vulgaris* L. — common bean. The "L" stands for Linnaeus.
- *Phaseolus acutifolius* A. Gray — tepary bean. The authority for this one is A. Gray.

Interspecific hybrids (hybrids formed from crossing two different species) may be designated with an "x" separating the two constituent species; the "x" can be read as shorthand for "crossed with" — for example, *Phaseolus vulgaris* L. x *Phaseolus acutifolius* A. Gray. They might also be given a new name incorporating an "x" to show that the plant is the result of an interspecific cross: *Fragaria chiloensis* x *Fragaria virginiana* = *Fragaria x ananassa* (cultivated strawberry)

Notice, from these examples of interspecific crosses, that the ability to cross and to have fertile offspring isn't a firm definition of species. It is generally true that breeding is restricted to within-species boundaries, but there are exceptions.

While some plant names have been updated to reflect the most recent knowledge about their morphology and phylogeny, their older names might still be in common use in some settings. Coleus, for example, has the following binomials, all for the same plant:

- *Ocimum scutellarioides* L.
- *Plectranthus scutellarioides* (L.) R. Br. (Notice that "L" is now in parentheses, showing that Linneaus was the earliest naming authority, but that his original name for the plant has now been superseded.)
- *Coleus scutellarioides* (L.) Benth.
- *Coleus blumei* Benth.

Important notes about binomial naming conventions:

- The Genus is always capitalized and either italicized or underlined.
- The specific epithet is lowercase and either italicized or underlined.
- The naming authority is capitalized and often abbreviated; if the species has been renamed, the first authority is in parentheses.
- An "x" between the Genus and specific epithet denotes an interspecific cross.
- A "x" before the Genus denotes an intergeneric cross.

Future of plant taxonomy and systematics

Taxonomy might first seem an old and dull science, sorting plants into a database using a system developed by someone born more than 300 years ago. But plant exploration experiments and the discovery of previously unknown species can take researchers to the far corners of the world, and taxonomy is important in classifying and naming these new discoveries. Also, for already discovered species, there is continual discussion about the real relationships among these plants and others and whether currently classified plants should be reclassified based on new information. With advances in molecular genetics through techniques that reveal a plant's DNA sequence, for example, taxonomy is moving more and more toward a phylogenetic basis, based on evolutionary relationships established through DNA similarities and differences instead of solely on morphological characteristics (features about the plant that you can see).

- Traditional taxonomy relies on morphological phenotype (the appearance of the plant).
- Molecular taxonomy relies on genotype (the particular combination of alleles of each gene in the organism).

For more information, check out this Wikipedia article about molecular phylogenetics.

The Angiosperm Phylogeny Group (APG) is a group of taxonomists who are working together to modify flowering plant taxonomy using molecular systematics. The APG's work is focused at the taxonomic level of Order and, to some extent, Family. While Order has long been a fairly arbitrary categorization, it may now be based more on molecular relationships.

The utility of classification goes beyond the satisfaction of good organization. Classification can inform us of new or lesser-studied plants that share valuable characteristics with plants already familiar to us. Now we have tools and knowledge that give us increasing control over the transfer of DNA among plants. Plant breeders can use insights from taxonomists to identify DNA sequences in related plants that might provide new sources of resistance to disease and insects, or new quality attributes, if transferred to food crops.

Review questions

An interactive H5P element has been excluded from this version of the text. You can view it online here:
https://open.lib.umn.edu/horticulture/?p=141#h5p-5

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4.2: METHODS OF TAXONOMY AND DIAGNOSTICS

The goal of taxonomy is to describe diversity, provide an insight to the evolutionary history (phylogeny), help to determine organisms (diagnostics) and allow for **taxonomic estimations**. The latter means that if we know features of one plant, the taxonomically close one should have similar features. For example, plants from cabbage family (Cruciferae) contain mustard oil (which is responsible for the horseradish taste of many of them). DNA analysis shows that papaya (*Carica* from Moringaceae family) is taxonomically close to Cruciferae. We may guess that papaya also have mustard oil, and this is true! Papaya seeds have the prominent horseradish taste.

One of the oldest methods of taxonomy is expert-based. Experts produce classifications based of their exclusive knowledge about groups. First taxonomic expert was Carolus Linnaeus (XVIII century). Experts use a variety of methods, including phenetics, cladistics (see below), general evolutionary approach, their ability to reshape available information and their intuition. Their goal is to create the “mind model” of diversity and then convert it to classification, using neighbor groups as a reference (for example, to assign ranks).

4.2.1: Cladistics

4.2.2: Phenetics

4.2.3: Dichotomous Keys

4.2.4: Glossary

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4.2.1: Cladistics

The more contemporary, much more formalized than expert-based is **cladistics**. Below, cladistic procedure is explained using artificial example of three organisms. The goal of the analysis is the creation of a **phylogeny tree** (**cladogram**) which becomes the basis of classification. Below is a short instruction which explains the basics of the cladistic analysis on the artificial example of several "families" of plants.

1. Start with determining the "players"—all subtaxa from bigger group. In our case, it will be these three "families":

Alphaceae

Betaceae

Gammaceae

2. Describe these three groups:

Alphaceae: Flowers red, petioles short, leaves whole, spines absent

Betaceae: Flowers red, petioles long, leaves whole, spines absent

Gammaceae: Flowers green, petioles short, leaves dissected, spines present

3. Determine individual characters (we will need at least $2N + 1$ characters where N is number of studied taxa):

(1) Flower color

(2) Petiole size

(3) Dissection of leaves

(4) Presence of spines

4. **Polarize the characters**: every character should have at least two **character states** where "0" is ancestral, **plesiomorphic** state, and "1" is derived, **apomorphic** state. To decide which state is plesiomorphic and which is apomorphic, use these kinds of arguments:

(a) Historical evidence (e.g., from fossils)

(b) Developmental evidence

(c) Comparative evidence

5. If this information is absent, find the **outgroup** which is the most ancestral, most early divergent taxon related to our groups. In our case, we will employ outgroup:

Omegaceae: Flowers green, petioles short, leaves whole, spines absent.

6. Label characters with "1" (apomorphic) or "0" (plesiomorphic):

(1) Flower color green—0; red—1

(2) Petiole size small—0; big—1

(3) Dissection of leaves absent—0; present—1

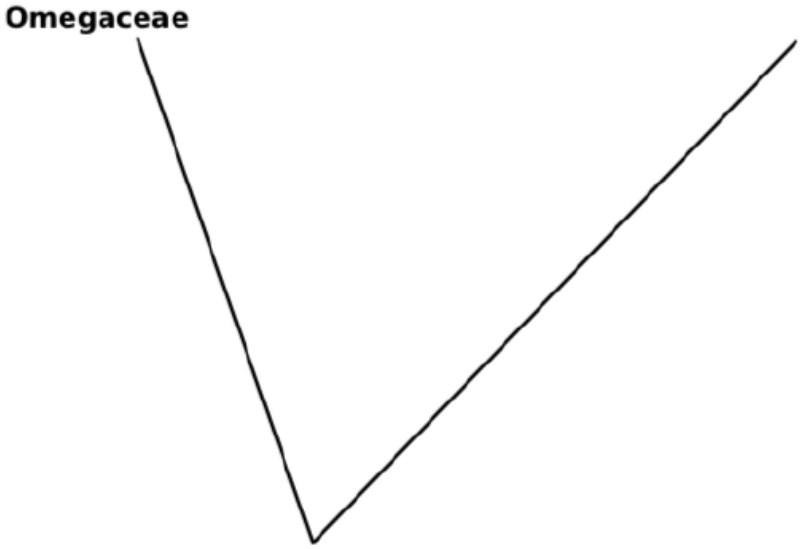
(4) Absence of spines—0; spines present—1

7. Make character table containing both subtaxa and labeled characters:

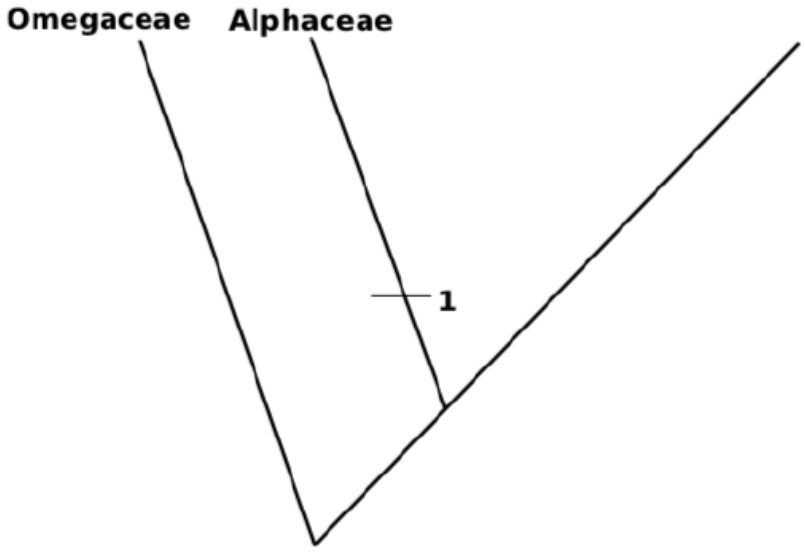
	(1)	(2)	(3)	(4)
Alphaceae	1	0	0	0
Betaceae	1	1	0	0
Gammaceae	0	0	1	1

(Outgroup, Omegaceae evidently has all zeroes.)

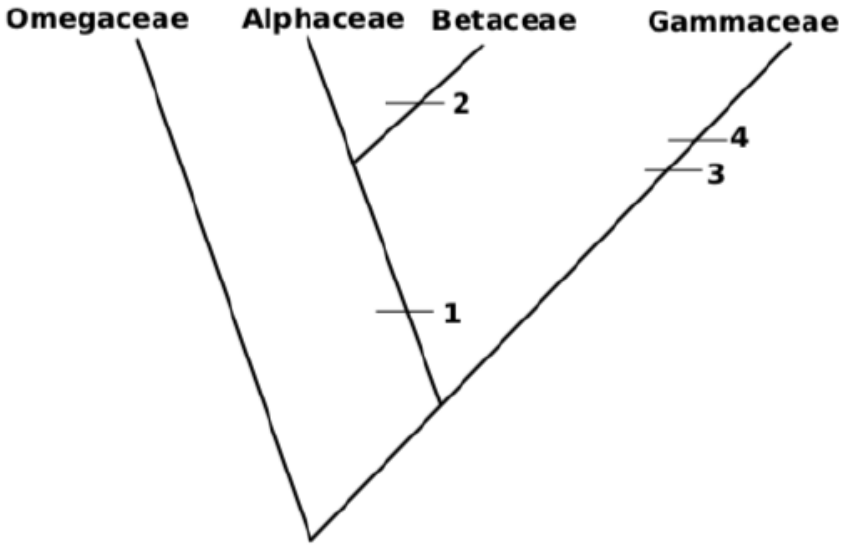
8. Start the tree from outgroup (this step is not absolutely necessary but will make phylogeny more clear):



9. Most ancient ingroup (Alphaceae) is a first branch, label it with bar which shows acquisition of the advanced state of first character (red flower color):

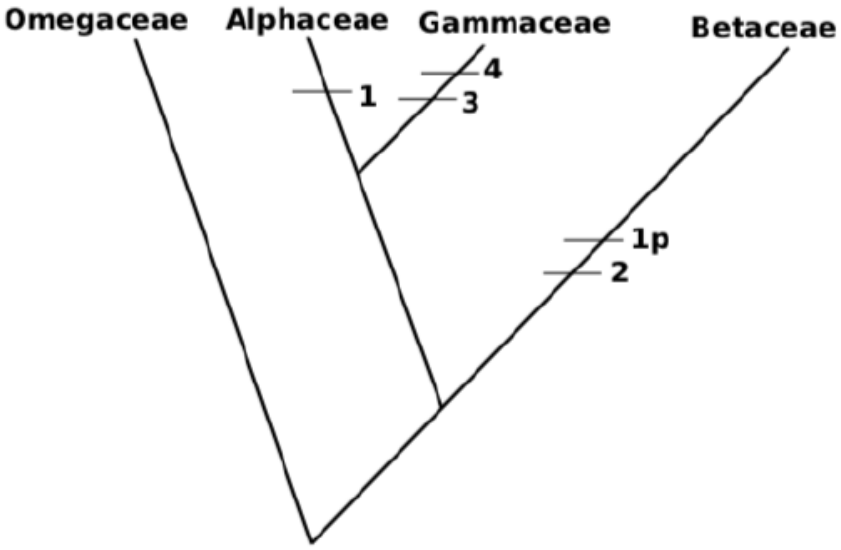


10. Attach more and more sub-taxa. It is possible to do this randomly (like most of phylogeny software), or attach groups to make shortest tree. For example, Betaceae and Gammaceae have equal number of synapomorphies but Betaceae have only one character different from Alphaceae it is sensible to attach it first, and then attach Gammaceae:



This tree has 4 evolutionary events (length $= 4$)

11. If Gammaceae was attached first, then resulted tree will be be one step longer:



There are five evolutionary events; in other words, length of tree $= 5$. ("p" are *parallel* characters (homoplasies); there might be also reversals ("r"), when apomorphic character disappears).

There could be also tree with length $= 6$, or even more if tree includes character reversals, but all of them will be longer than the first one.

12. Choose the shortest, most **parsimonous** tree. Second tree has 5 events, first tree has 4 events, others could be only longer. Consequently, we choose the first tree. By the way, many computer programs do not follow the procedure above strictly and simply produce all possible trees, and finally choose the shortest.

13. Use the chosen tree as a source of classification:

Order Alphales

1. Family Alphaceae

2. Family Betaceae

Order Gammales

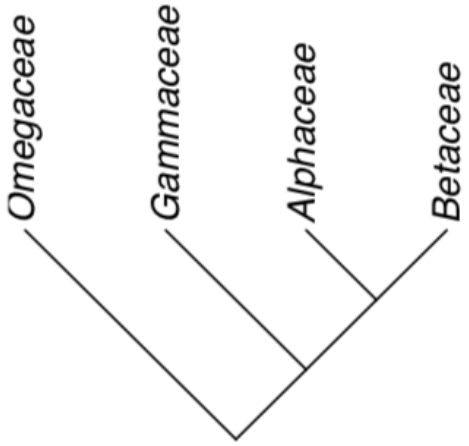
1. Family Gammaceae

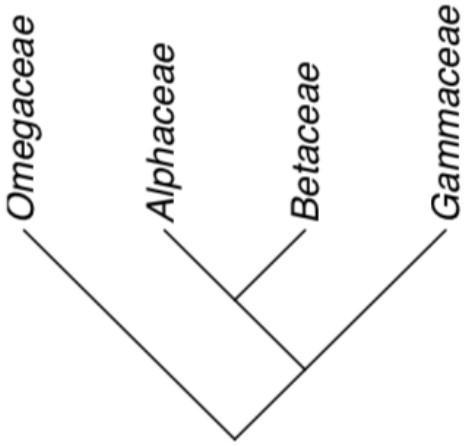
This step is needed only if you wish to convert cladogram into traditional, classification. In fact, cladograms are rank-free and might be used as is.

Cladograms often used as source of *time trees* which are made with genetic information and information from fossils. If we know the age of taxonomic group, we can use it as more objective replacement of rank.

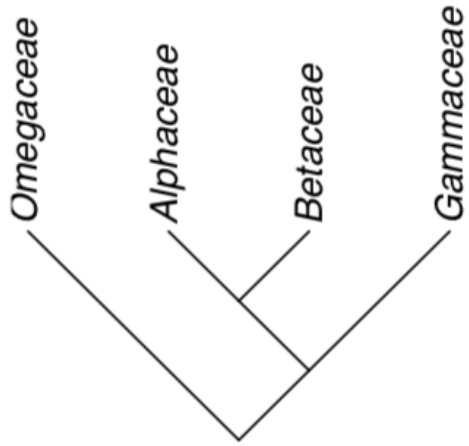
Ability to review and compare phylogenetic trees requires understanding of several basic rules, for example:

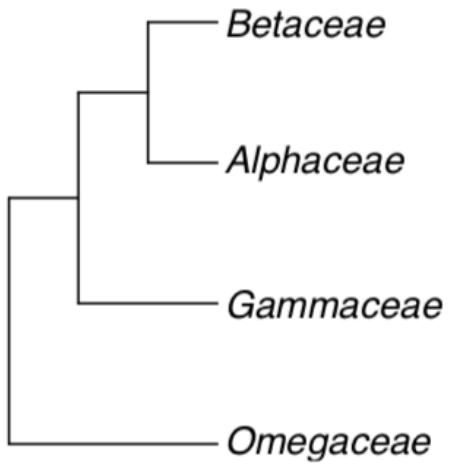
1. Tree edges may be freely rotated in any direction. For example, these trees are same:





2. Direction of branches also does not matter. These trees are same:





It is not always simple to make classification from a tree. On the previous example, we simply designate the whole branch as a taxon (order which contains our three families). There are situations when only middle part of the branch seems to be acceptable as a taxon. In these cases, remaining part is called **paraphyletic** taxon.

Paraphyletic groups include all immediate ancestors of its members but not all descendants of these ancestors. Good example of paraphyletic taxon are reptiles: when we take mammals and birds from amniote branch, reptiles will be what is left. Gymnosperms (all seed plants without angiosperms) is another example, but in this case *some* molecular trees show that gymnosperms is also a natural branch (i.e., **monophyletic** group). Monophyletic groups include all immediate ancestors and all their descendants.

When the group contains taxa from different branches, it is **polyphyletic**. Polyphyletic groups are not allowed.

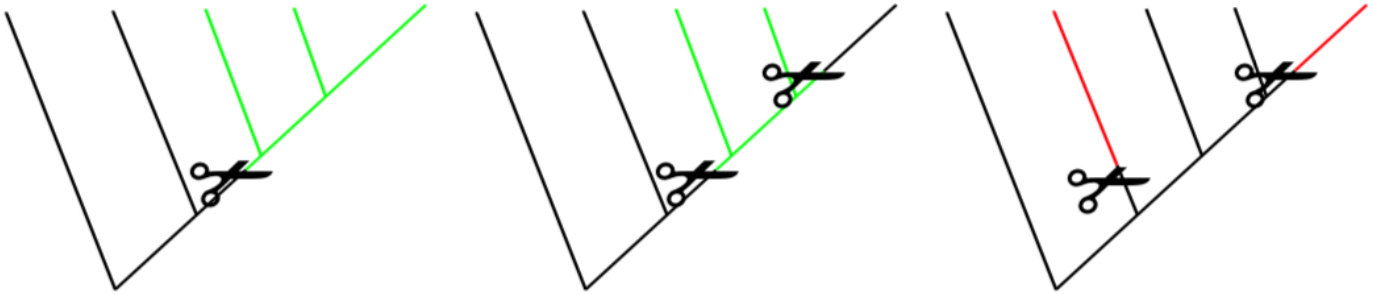


Figure 4.2.1.1: Monophyletic, paraphyletic and polyphyletic groups, respectively.

Another important distinction between groups of the phylogeny tree is stem and crown groups. All extant members together with their immediate ancestors form a **crown** of taxon (Figure 4.2.1.2). If one member of crown went extinct, we can estimate that it was somehow similar to other crown members. In other words, if we find a way ho to re-create mammoth, we probably understand how to feed it because it belongs to the Elephantidae family crown. However, if the fossil, extinct members of taxon branch outside of crown (**stem** groups), there are much less taxonomic estimations. It is hard to guess, for example, how to care for *Archaeopteryx* "dinosaur bird" because such organisms are not exist now and have no living similarities.



Figure 4.2.1.2: Crown (green skull) and stem (red skull) extinct groups among extant groups.

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4.2.2: Phenetics

The other way of making classification is even more mathematical. This is **phenetics** based on multivariate methods of data analysis. One of its methods is **cluster analysis** which is described below.

1. Contrary to cladistics, phenetics considers characters as **all equal** and **does not employ any evolutionary assumptions**.
2. We need to decide which taxa we will need, assess their descriptions, extract characters—all these is similar to cladistics (see above).
3. Character polarization is not needed, character codes may be specified more or less arbitrarily, and there is no need for outgroup.
4. Character table could be the same as in previous example (again, see above).
5. Then, we will need to create the square matrix (or table) of similarity:

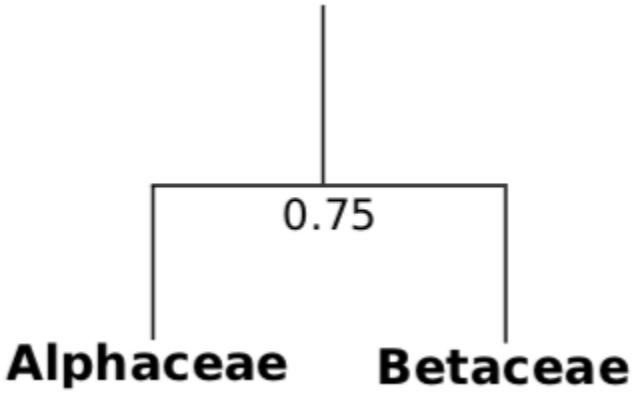
	Alphaceae	Betaceae	Gammaceae
Alphaceae	1		
Betaceae	0.75	1	
Gammaceae	0.25	0	1

Every cell of this matrix contains a value of similarity K:

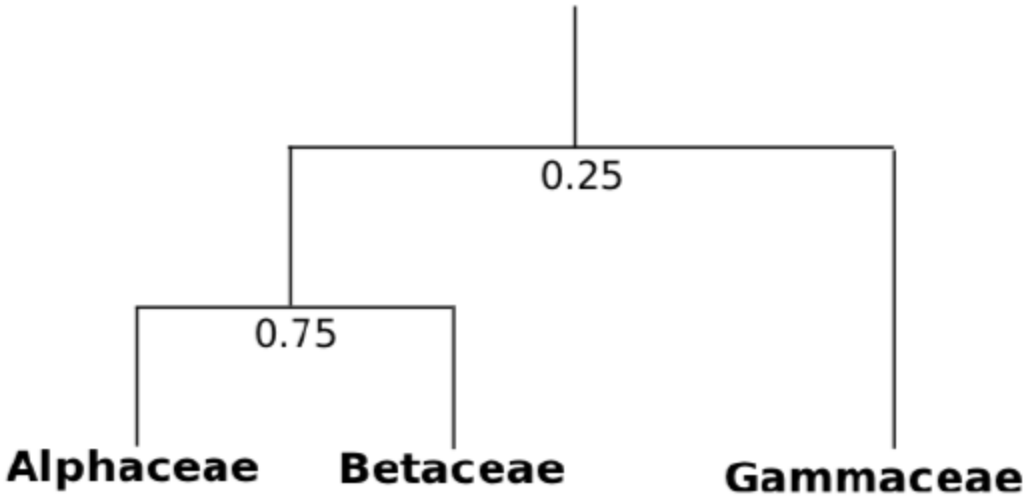
$$K = \frac{\text{number of matching characters}}{\text{number of all characters}} \tag{4.2.2.1}$$

Please note that there are many more relevant coefficients of similarity but they are out of our scope.

6. Then we need to make the dendrogram which is a tree-like structure. Tradi- tionally, dendrogram is built from bottom to top, from more similar to less similar groups. For example, we may start from connecting the closest taxa, Alphaceae and Betaceae:



7. Then we need to attach other taxa which are closest to previous group:



Sometimes, when we have multiple taxa, we end up with several independent groups (clusters). In that case, different clusters could be connected on the base of *average similarity*.

8. Betaceae and Alphaceae are closer, so we can unite them in one order:

Order Alphales

1. Family Alphaceae 2. Family Betaceae

Order Gammales

1. Family Gammaceae

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4.2.3: Dichotomous Keys

Diagnostics is a practical science which helps to determine living organisms. One of the best way of determining was invented in the end of 18 century by famous French naturalist, Jean-Baptiste Lamarck. He created the **dichotomous key** (sometimes called descriptive key, or descriptive table). The legend says that when Lamarck demonstrated this key for the first time, he gave it to the random stranger (who had no idea about plants and their names), and plant were determined without problems! How to make such a key? The example is below:

1.

We need to start with “players”. In this example, it will be same three plant families:

- Alphaceae
- Betaceae
- Gammaceae

2.

Assess descriptions of these three groups (we copy this from the above):

- **Alphaceae**: Flowers red, petioles short, leaves whole, spines absent
- **Betaceae**: Flowers red, petioles long, leaves whole, spines absent
- **Gammaceae**: Flowers green, petioles short, leaves dissected, spines present

3

Start with a character which let to split the list into two nearly equal groups. Then add other character(s). It is always good to use more characters!

1. Petioles long..... **Betaceae**.

-Petioles short .....2.

2. Flowers red, leaves whole, spines absent..... **Alphaceae**.

Flowers green, leaves dissected, spines present .....**Gammaceae**.

As you see here, key consists of steps. Every step has a number and typically two choices. Number is attached to the first choice whereas the second choice is marked with minus “–”. The choice will lead either to the name, or to another step. The choice sentence might contain several phrases, the first is the most important and the last is the least important.

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10.04: Glossary

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4.3: Terms

These are the important terms from this chapter to be sure to know. You might also find these in later chapters.

Binomial nomenclature	System of naming in which two terms are used to denote a species of living organism, the first indicating the Genus and the second the Specific Epithet.
Class	Taxonomic rank below Division and above Order.
Cotyledonary node	Food storage structure used in germination.
Dicotyledon	Seed plant that produces an embryo with paired cotyledons, floral organs arranged in cycles of four or five, and leaves with net-like veins.
Division	Highest taxonomic category, consisting of one or more related classes, and corresponding approximately to a Phylum in zoological classification.
Emergence	Germination, when the embryo becomes active and the radicle grows through the seed coat.
Epicotyl	Portion of the stem of a seedling or embryo located between the cotyledons and the first true leaves.
Epigeal	Type of seedling emergence where cell division in the hypocotyl is initially more active and rapid than cell division in the epicotyl. Cotyledons are brought above the soil surface as the hypocotyl expands.
Family	Taxonomic rank below Order and above Genus.
Genotype	Genetic composition of an organism.
Genus	Group of species possessing fundamental traits in common but differing in other lesser characteristics; taxonomic rank below Family and above Specific Epithet.
Hierarchy	System of grouping where each classification is a subset of a superior grouping, and may contain subordinate categories.
Hypocotyl	Embryonic shoot below the cotyledons.
Hypogeal	Type of seedling emergence where the cotyledons remain below the surface of the ground.
Nomenclature	Formal system of names attached to the taxonomic groupings.
Order	Taxonomic rank below Class and above Family.
Phenotype	Physical appearance of an organism.
Phylum	Taxonomic rank below Kingdom and above Class; used in zoological classification.
Radicle	Embryonic root that breaks through the seed coat during germination and develops into the seedling's root system.
Seed	Ripened ovule containing a seed covering, food storage, and an embryo.
Seed coat	Outer layer of the seed.
Seed germination	Activation of metabolic pathways of the embryo leading to the emergence of a new seedling.
Specific epithet	Uncapitalized Latin adjective or noun that follows a capitalized Genus name in binomial nomenclature and serves to distinguish a species from others in the same genus, as *saccharum* in *Acer saccharum* (sugar maple).
Taxonomy	Science of classifying organisms.

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5: THE PLANT CELL

Learning Objectives

- Understand the structure and function of plant cell organelles
- Explain the unique features of plant cells
- Describe the diversity and specialization of plant cell types
- Understand the evolutionary origins and functions of key organelles

Explore the tiny yet complex world of plant cells! This chapter covers their unique parts—like chloroplasts, vacuoles, and cell walls—and how they work together to support life. Learn about cell types, energy-making organelles, and how plant cells communicate and grow. It's a l journey into the building blocks of all plant life!

5.1: Introduction to Cells

5.2: Mitochondria and Chloroplasts

5.3: Cell wall, Vacuoles, and Plasmodesmata

5.4: Other Parts of the Cell

5.5: Atlas- Cells and Tissues

5.5.1: Plant Cell Structure and Components

5.5.2: Types of Plant Cells

5.5.2.1: The -enchymas

5.5.2.2: Specialized Cells

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5.1: Introduction to Cells

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**.

Discovery of cells is tightly connected with the development of microscopy. Nowadays, there are basically three kinds of microscopy: light microscopy, transmission electron microscopy (TEM), and scanning electron microscopy (SEM). Light microscopes use normal light, it can magnify transparent things 1,000 times. Transmission electron microscopes give a more detailed view of the internal organization of cells and organelles. They use an electronic beam, which kills objects as it passes through. In addition, for examination under a TEM, objects are often stained with heavy metals like osmium, and for SEM with gold which is highly reflective for electronic rays. A TEM can magnify things 10,000,000 times. Scanning electron microscopes show an image of the surface of cells and organisms using reflected electronic beam. It can magnify things 1,000,000 times. It is possible to see atoms on these photographs!

The minimal cell should have three things: protein-synthesizing apparatus (from DNA to RNA and proteins), space designated for all other chemical reactions (jelly-like cytoplasm) and the oily film separating cell from its environment (membrane). This is like fruit jelly covered with thin layer of butter; “fruit pieces” are protein-synthesizing parts.

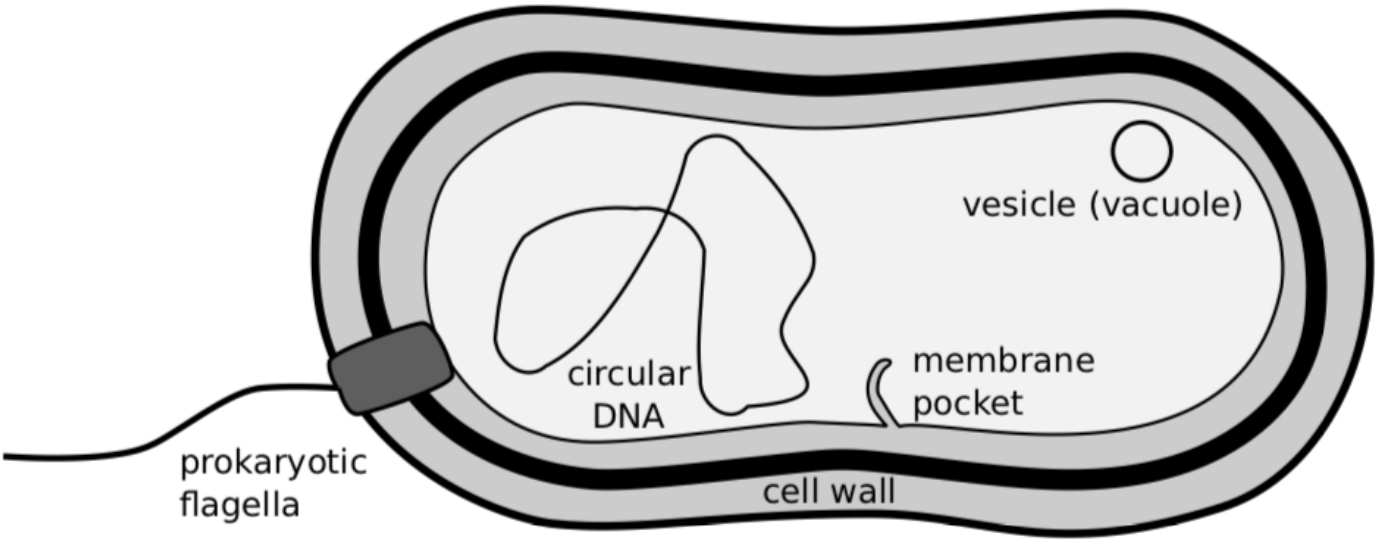


Figure 5.1.1 Prokaryotic cell.

The cell membrane of all cells has two layers. One end of each layer is polar and hydrophilic, while the other end is hydrophobic. These layers are made with **phospholipids** which are similar to typical lipids but have polar head with phosphoric acid, and two hydrophobic, non-polar tails (Figure 5.1.2). Apart from phospholipinds, membrane contains embedded other lipids like cholesterol (in animal cells only) and chlorophyll (in some plant membranes), proteins and carbohydrates. Proteins are extremely important because without them, membrane does not allow large hydrophylic molecules and ions to came trough.

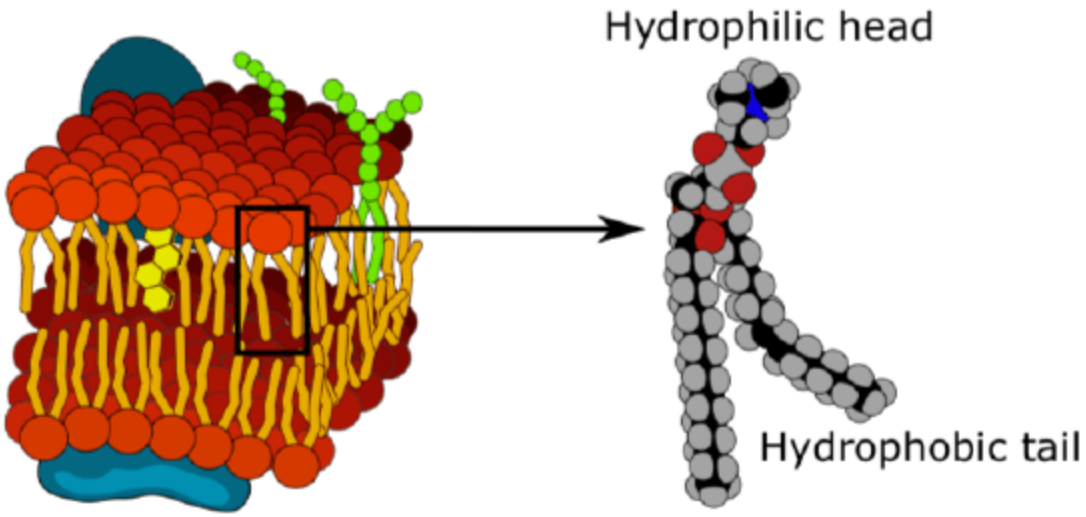


Figure 5.1.2 Membrane and phospholipids.

Cells which have DNA in a membrane-bound nucleus are known as **eukaryotic**, while those which do not are known as **prokaryotic**. Prokaryotic cells have their DNA surrounded by the cytoplasm. Some have also prokaryotic flagella (rotating protein structure), a cell wall, vesicles and membrane folds/pockets (Figure 5.1.1). Eukaryotic cells have their DNA in a nucleus which separates it from the cytoplasm.

There are many other parts of the eukaryotic cell (Figure 3.2.1). The nucleus of the cell contains DNA and proteins. Nucleoli are in the nucleoplasm, this is the place where ribosomal RNAs are assembling. Ribosomes, found in the cytoplasm, help to synthesize proteins. The **endoplasmic reticulum** (ER), usually found near edge of the cell, is where proteins are synthesized, packaged and transported. In many cells, ER is connected with nucleus membrane. The **Golgi apparatus** directs proteins and other substances to the part of the cell where they need to go. Eukaryotic cells must have **mitochondria** and might have **chloroplasts**, both originated via symbiogenesis (see below). Mitochondria are covered with two membranes, the inner membrane has intrusions called **cristae**. Mitochondria break down organic molecules into carbon dioxide and water in a process known as oxidative **respiration**.

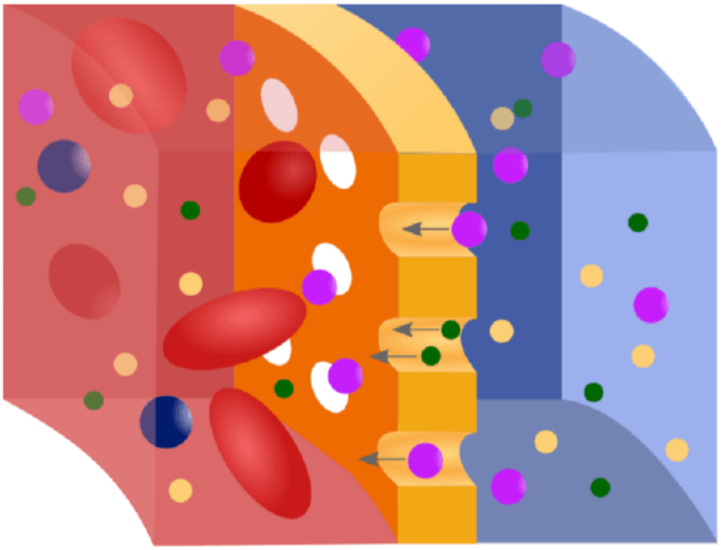


Figure 5.1.3 Semi-permeable membrane: how it works. Big “red” molecules are larger then pores so they are not allowed to go. Other molecules are smaller then pores and they are allowed to equalize their concentrations which are always *lower* in places where “red” molecules present. This is why they go from right to left and not otherwise.

Cell membranes are semi-permeable (Figure 5.1.3), they allow some molecules (typically small and/or non-polar) to go through but others (big and/or polar) will stay outside or inside forever, or until specific pore opens. Water always “wants” to equalize

concentrations on both sides of membrane and water molecules typically flow through the membrane to where concentration of other molecules (salts, acids) is *higher* (and, naturally, concentration of water is *lower*). This is **osmosis**.



Figure 5.1.4 Osmosis in (from left to right) hypertonic (high salt), isotonic and hypotonic (low salt) environments. Blue color is for the vacuole. Red arrows on the right image show turgor—combined pressure of the vacuole and the cell wall.

Cell wall (common in plants and fungi) surrounds the cell and limits how far the cell can expand due to osmosis (Figure 5.1.4). Since osmosis may result in uncontrollable expansion of cell, cells without cell walls must find a way to pump out the excess water. **Vacuole**(s) is the large vesicle(s) which can do a variety of things for the cell, for instance store nutrients, accumulate ions, or become a place to store wastes. It plays an important role in the *turgor* (Figure 5.1.4).

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5.2: Mitochondria and Chloroplasts

To escape from competition, cells which were prokaryotic became larger. To facilitate communication between all parts of this larger cell, they developed cytoplasm mobility using *actin* protein. In turn, this mobility resulted in acquiring **phagocytosis**, which is when a large cell changes shape and can engulf ("eat") other cells. This way, cells that used to be prey became predators. These predators captured prey by phagocytosis and digested bacteria in *lysosomes*, which use enzymes that destroy the cytoplasmic components of the bacterial cells.

The threat of predators result in cells became even larger, and these cells will need a better supply of ATP. Some prey which were not digested, and turned out to be useful in providing ATP. Of course, predator cells should also invent a proper transport through the resulted double membrane! Due to natural selection, those prey, which were purple bacteria, became the cell's mitochondria. This is **symbiogenesis**, or the formation of two separate organisms into a single organism (Figure 5.2.2).

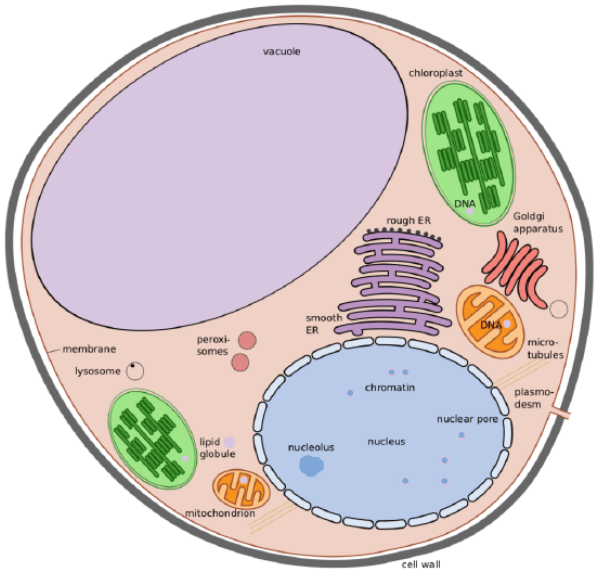


Figure 5.2.1 Schematic overview of the eukaryotic (plant_1) cell.

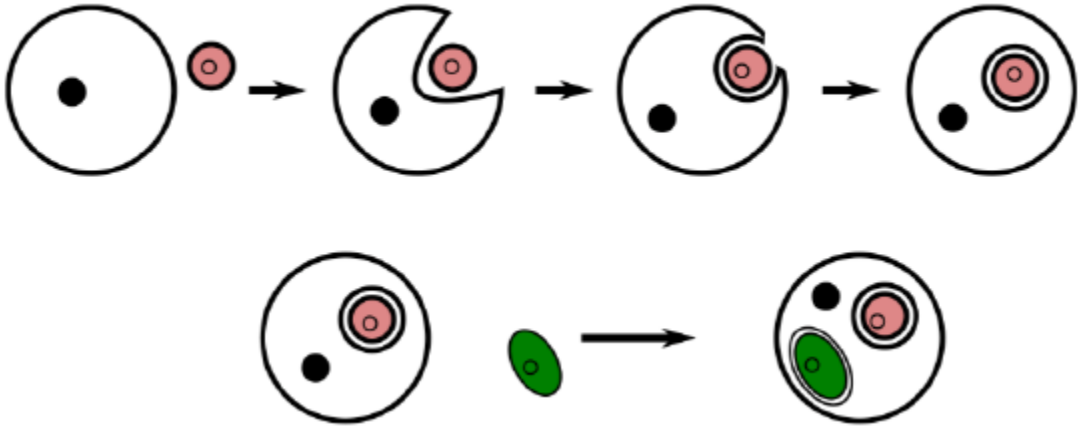


Figure 5.2.2 Symbiogenetic origin of eukaryotic cell (top row) and algal cell (bottom row).

Another result of a larger cell (eukatyotic cells are typically 10–100 fold larger than prokaryotic) is that the size of DNA will increase, and to hold it, the cell will form a nucleus. The new predator cells also needed to prevent alien organisms from transferring their genes which will delay the evolution.

The other reason is that the nucleus protects the DNA by enclosing it; in case if DNA virus comes into the cell and tries to mock up cell DNA, eukaryotic cell immediately destroys any DNA found in the cytoplasm. One more reason to make nucleus is pressure

of antibiotics: nucleus improves isolation from these harmful chemicals. Nucleus formation and symbiogenesis leaded cells to become eukaryotic.

To be called an eukaryote, it is more important to have phagocytosis and mitochondria then nucleus because (1) nucleus is not always exists, it could disappear during the division of cell and (2) some prokaryotes (planctobacteria) also have membrane compartments containing DNA.

On next step, some eukaryotes also captured cyanobacteria (or another photosynthetic eukaryote), which became chloroplasts. These photosynthetic protists are called **algae**.

In all, eukaryotic cells are “second-level cells” because they are cells made up of multiple cells. Cells of all eukaryotes have two genomes, nuclear usually has biparental origin whereas mitochondial genome normally originates only from mother. Plant cells, in turn, have *three genomes*, and chloroplast genome is usually also inherited maternally.

Chloroplasts synthesize organic compounds whereas mitochondria produce most of the cytoplasmic ATP. Both organells are covered with two membranes and contain circular DNA and ribosomes similar to bacterial. Chloroplasts have thylakoids, or inner membrane pockets and vesicles. Chloroplast thylakoids could be long (**lamellae**) or short and stacked (**granes**). In turn, mitochondria could be branched and inter-connecting.

Chloroplasts are normally green because of chlorophyll which converts light energy into chemical energy. Some chloroplasts lose chlorophyll and become transparent, “white”, they are called **leucoplasts**. Other chloroplasts could be red and/or orange (**chromoplasts**), because they are rich of carotenes and xanthophyls. These pigments facilitate photosynthesis and are directly responsible for the fall colors of leaves. Since starch is a more compact way of storing energy than glucose, chloroplasts store carbohydrates as starch grains. Transparent **amyloplasts** contain large granules of starch. Storage tissues of potato tubers, carrot roots, sweet potato roots, and grass seeds are examples of tissues rich in amyloplasts.

Having chloroplasts and cell walls are not directly connected, but almost all organisms with chloroplasts have also cell walls. Probably, this is because cell walls do not facilitate cell motility, and for those protists which already have cell walls, obtaining chloroplast will be the nice way for coming out of competition with organotrophic beings.

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5.3: Cell wall, Vacuoles, and Plasmodesmata

Among eukaryotic cells, plant cells are largest. Some of them (for example, cells from green pepper and grapefruit) are well visible with the naked eye. Plant cells do not have well-developed internal cytoskeleton, but **cell wall** provides an external one. There are two kinds (or, better, two stages of development) of cell walls, the **primary** and the **secondary**. The primary cell wall is typically flexible, frequently thin and is made of cellulose, different carbohydrates and proteins. The secondary cell wall contains also **lignin** and highly hydrophobic **suberin**. These chemicals completely block the exchange between the cell and the environment which means that the cell with secondary wall will soon die. Dead cells can still be useful to plants in many ways, for example as a defense against herbivores, support and water transport. In fact, more than 90% of wood is dead.

Since every plant cell is surrounded with a cell wall, they need a specific way of communication. This is done through **plasmodestata**—thin cytoplasmic bridges between neighbor cells. A **symplast** is the name of continuous cytoplasm inside of cells. An **apoplast** is cell walls and space outside the cell where communication and considerable metabolic activity take place. Both the symplast and apoplast are important to the transportation of nutrients needed by the cell (Figure 5.3.1).

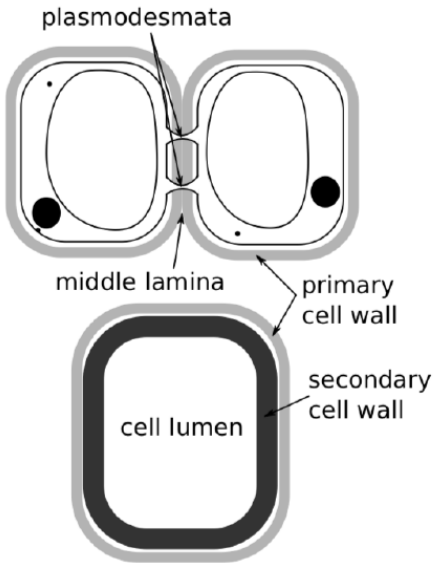


Figure 5.3.1: Living cells with primary cell walls (top) and dead cell with primary and secondary cell walls (bottom). Apoplast colored with shades of gray, symplast with dots.

If cells are surrounded by a smaller concentration of salts than in the cytoplasm, the water will flow into the cell. This process is called **osmosis**. In plant cells, most of the water with diluted chemicals is concentrated in vacuole(s). **Turgor** pressure is the combined pressure of the cell and vacuoles wall that supports the shape of cell (Figure 3.1.4).

You may think of plant tissue as about staked cardboard boxes where every box is made from wet cardboard paper (cell wall) but has the inflated balloon (vacuole) inside, and when the pressure of vacuole decreases (water deficit), plant organs droop. Please see the video http://ashipunov.info/shipunov/school/biol_154/mov/balloon.mp4 to understand this better.

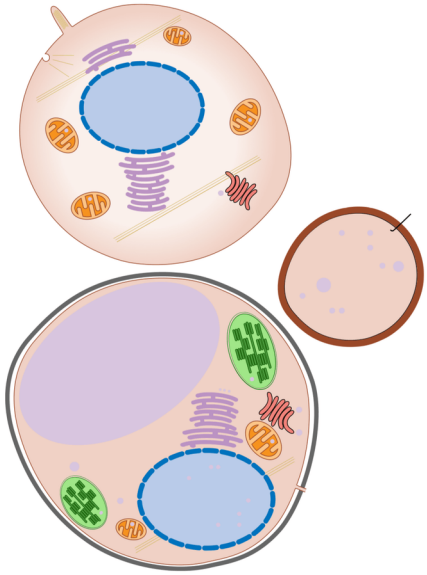


Figure 5.3.2 Animal, bacterial and plant cell.

Comparing with animal cells, plant cells have chloroplasts, vacuoles, cell walls, and plasmodesmata but they hardly have any phagocytosis and true cytoskeleton (Figure 5.3.2). They are easy to explain: animals do not photosynthesize (no chloroplasts), instead, they need to move quickly (no cell walls and plasmodesmata); animals will support the shape of cell from cytoskeleton (no need for vacuole turgor system) and use molecular pumps to counterpart the osmosis.

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5.4: Other Parts of the Cell

Protein Synthesis: from the Nucleus to the Ribosomes

The central dogma of molecular biology states that DNA will be converted into RNA by a process called **transcription** and RNA will be converted to protein by a process called **translation**. Translation in non-reversible whereas transcription could be reverted: there are viruses, such as HIV, that can make DNA from RNA with the enzyme called *reverse transcriptase*. The nuclear envelope is built from a double-layered membrane. The inner and outer membranes of the nuclear envelope connect to form pores which are complicated structures controlling travel between the nucleus and the cytoplasm. Inside of the nuclear envelope there is the nucleoplasm.

Nuleoplasm contains chromatin (chromosomes). **Chromosomes** store genetic information in the form of DNA molecules. Each chromosome consists of a chain of nucleosomes, which are condensed long DNA molecules and their associated **histone** proteins. Chromatin is just another word for non-condensed chromosomes. Visible parts of chromatin (globules, filaments) correspond with non-functional DNA.

Ribosomes, which are particles that contain RNA and proteins, synthesize proteins. The **rough endoplasmic reticulum** (RER) has ribosomes along its surface, and the proteins they create are either secreted or incorporated into membranes in the cell. The **Golgi apparatus** (AG) is made of membranous sacs which are flattened and stacked, it modifies, packages, and sorts proteins and carbohydrates for the cell; this is not an essential component of cell.

Other Vesicles

Plant cells frequently have smaller vesicles: **lysosomes** which digest organic compounds and **peroxisomes** which, among other functions, help in photosynthesis (see above). In addition, many plant cells accumulate lipids as oil drops located directly in cytoplasm.

Cellular Skeleton

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 and are guides for the construction of the cell wall. 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.

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5.5: ATLAS- CELLS AND TISSUES

5.5.1: Plant Cell Structure and Components

5.5.2: Types of Plant Cells

5.5.2.1: The -enchymas

5.5.2.2: Specialized Cells

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5.5.1: Plant Cell Structure and Components

Plant Cells

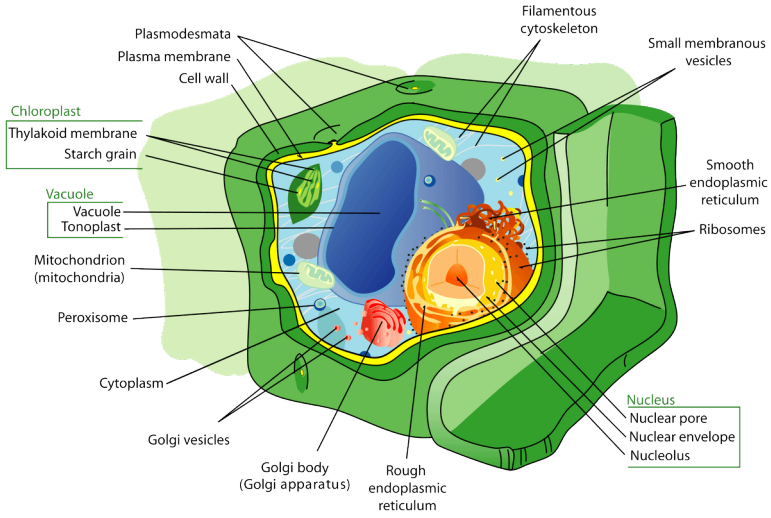


Figure 5.5.1.1: A diagram of a plant cell. Plants cells differ from animal cells in that they have a cell wall (which is glued to adjacent cells by the middle lamellae), a large central vacuole, and chloroplasts. Image by LadyofHats, Public domain, via Wikimedia Commons.

Plant Cell Components

Cell Wall, Plasma Membrane, and Middle Lamella

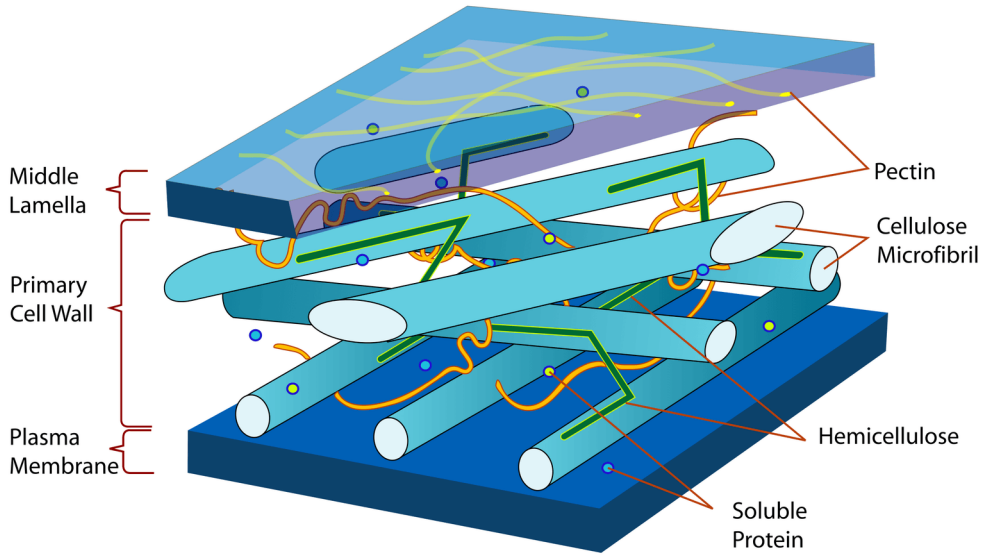


Figure 5.5.1.2: A diagram of the **primary cell wall**, including the plasma membrane and middle lamella. The primary wall is composed of crisscrossing cellulose and hemicellulose microfibrils. Strands of pectin and some soluble proteins are also in the mix. Diagram by LadyofHats, Public domain, via Wikimedia Commons.

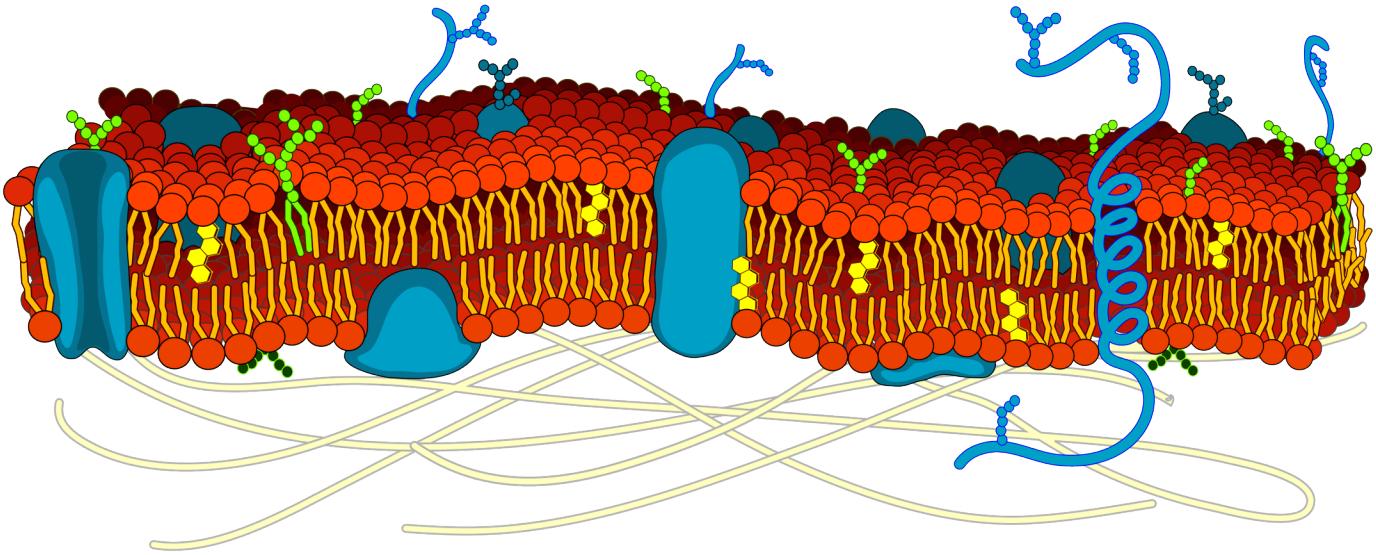


Figure 5.5.1.3: A generalized diagram of a plasma membrane. The cell membrane, also called the plasma membrane or plasmalemma, is a semipermeable lipid bilayer common to all living cells. It contains a variety of biological molecules, primarily proteins and lipids, which are involved in a vast array of cellular processes. It also serves as the attachment point for both the intracellular cytoskeleton and, if present, the cell wall. Diagram by LadyofHats, Public domain, via Wikimedia Commons.

Plasmodesmata are channels through the cell wall and middle lamella where the plasma membrane of adjacent cells (and therefore the cytoplasm) is connected.



Figure 5.5.1.4: The image above shows cells in the epidermis of a red pepper. Two locations are circled and labeled as plasmodesmata. In each of these circles, there is a section of the cell wall that appears to be missing. This is where a section of the plasma membrane traverses through a channel in the middle lamella and cell walls of both cells. Photo by Maria Morrow, CC BY-NC.

The Nucleus

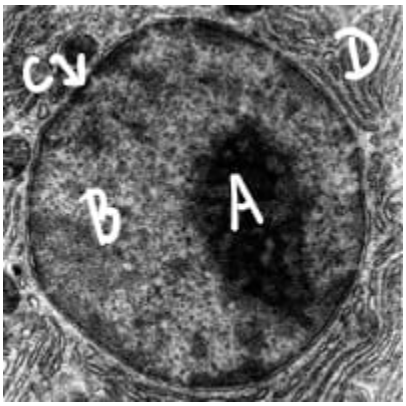


Figure 5.5.1.5: A micrograph of a cell nucleus. The nucleolus (A) is a condensed region within the nucleus (B) where ribosomes are synthesized. The nucleus is surrounded by the nuclear envelope (C). Just oustide the nucleus, the rough endoplasmic reticulum (D) is composed of many layers of folded membrane. Image from the public domain, via Wikimedia Commons, labels added by Maria Morrow.

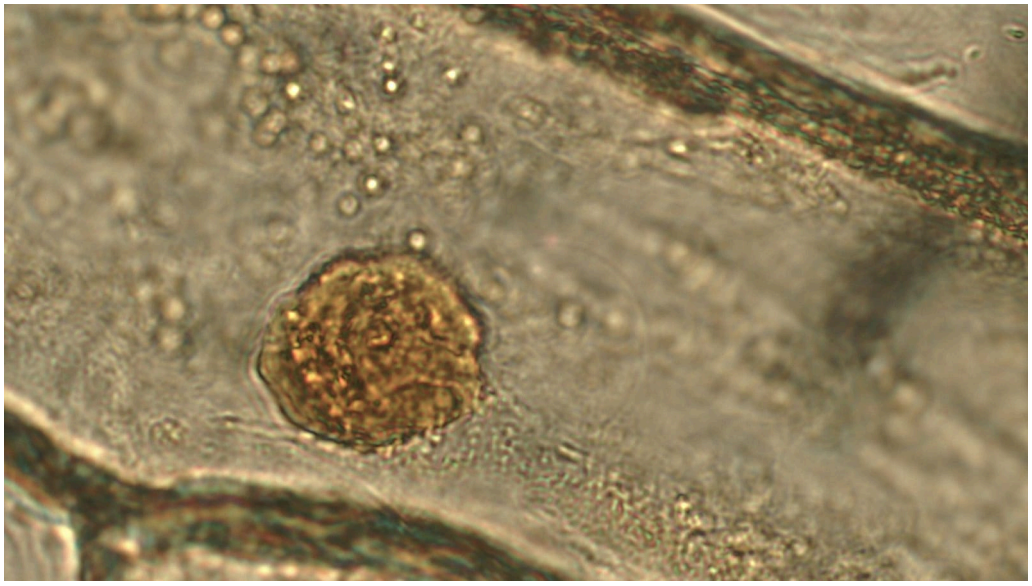


Figure 5.5.1.6: The large, golden, globose structure is an onion cell nucleus, magnification 3000x. Berkshire Community College Bioscience Image Library, CC0, via Wikimedia Commons.

Plastids

Plastids are organelles that are the result of an endosymbiotic event in the evolutionary history of plants. In plants, plastids have two membranes.

Chloroplasts

Chloroplasts are plastids that contain green pigments called chlorophylls.

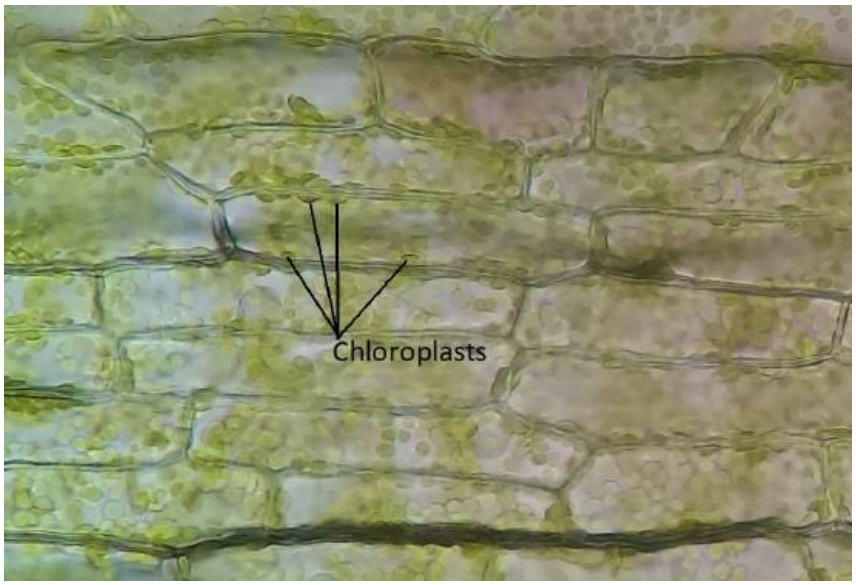


Figure 5.5.1.7: This image shows cells in the leaf of an aquatic plant, *Elodea*. Each cell is filled with small green discs which often appear to line the edges of the cell. These are chloroplasts (four are indicated and labeled in the image). Photo credit: Melissa Ha, CC BY-NC .

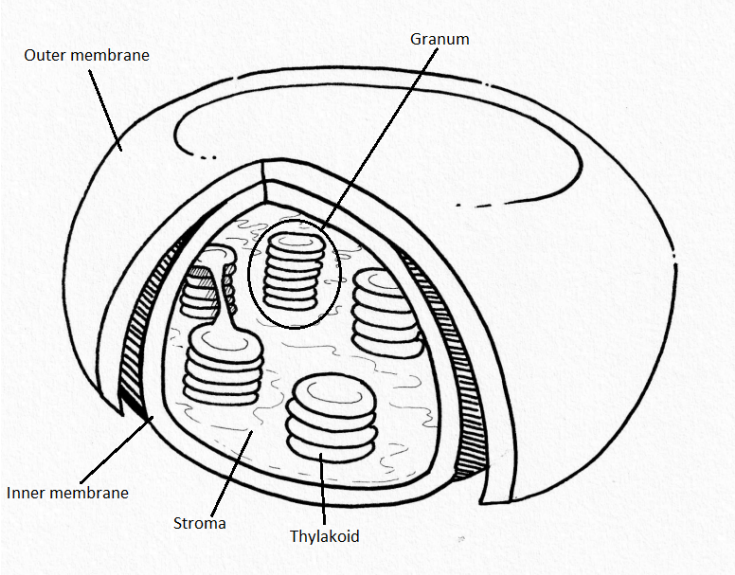


Figure 5.5.1.8: A diagram of chloroplast anatomy. There are two membranes, the outer and inner membrane, that enclose this structure. Within, there are stacks of flat discs. Each stack is called a granum and each individual disc is a thylakoid. The grana float within a jelly-like matrix called the stroma. Artwork by Nikki Harris, CC BY-NC .

Chromoplasts

Chromoplasts are plastids that do not contain chlorophyll, but do contain other pigments, such as carotenoids. Carotenoid pigments reflect colors like yellow, orange, and red.

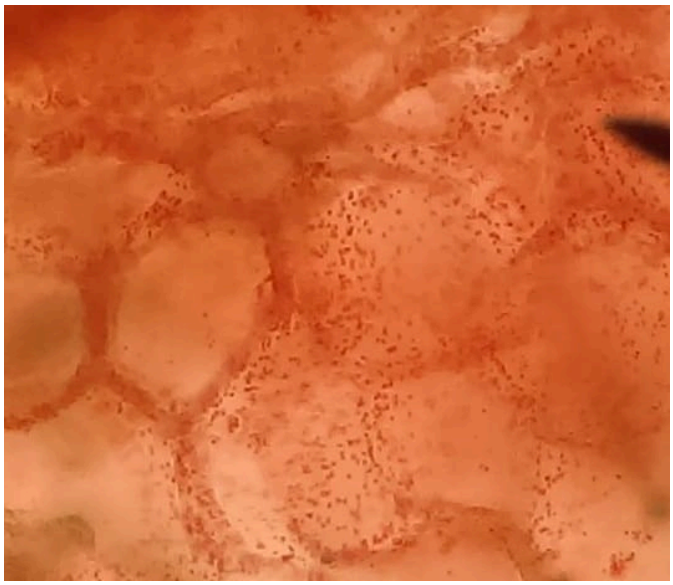


Figure 5.5.1.9: This image shows the cells of a red pepper. There are many small red dots floating within the cells. These dots are chromoplasts that contain carotenoids. The chromoplasts give the pepper its red color. Photo credit: Melissa Ha, CC BY-NC .

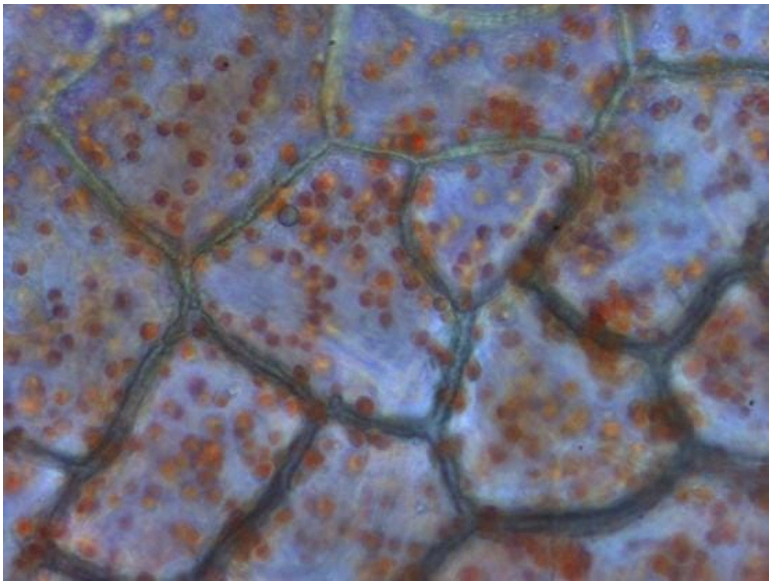


Figure 5.5.1.10: In this image of red pepper epidermal cells, the chromoplasts are larger and easier to distinguish. Each cell is filled with circular, red discs. These are chromoplasts that contain carotenoids. Photo by Maria Morrow, CC BY-NC.

Leucoplasts

Leucoplasts are plastids that do not contain pigments. The main function of leucoplasts is to store starches and oils. Leucoplasts that store starch are called **amyloplasts** (as in amylose).

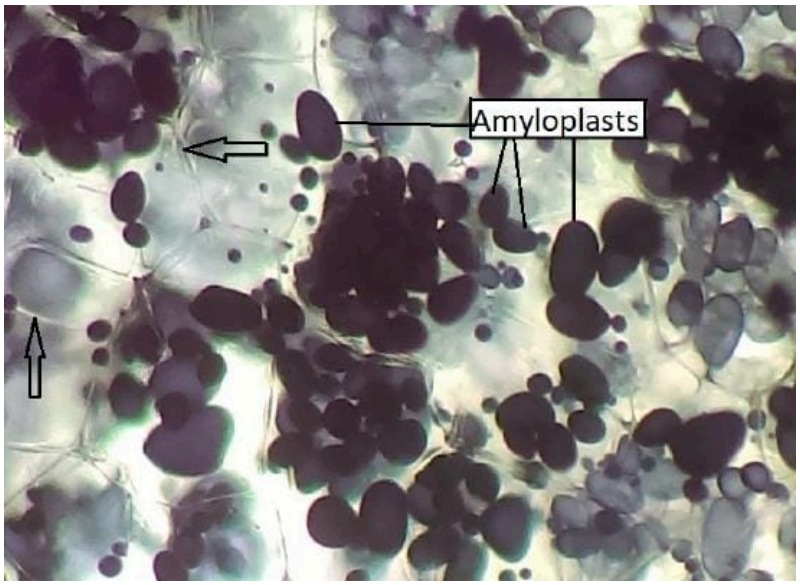


Figure 5.5.1.11: This image shows cells from a potato tuber that have been stained with iodine. When iodine interacts with starch, it turns a blue-black color. This helps us see the amyloplasts inside the cells, which would normally be transparent due to their lack of pigment. In the image, the cell walls of the potato cells can be seen as lighter lines (indicated by the arrows in two places). The amyloplasts are dark, pebble-like structures within the cells. Some of these are less opaque because they have not been in contact with as much of the iodine stain. Photo credit: Melissa Ha, CC BY-NC.

The Central Vacuole

The **central vacuole** is a large organelle that often fills most of the plant cell. It is filled with liquid and surrounded by a membrane called the **tonoplast**. Plants can alter the solute concentration in the central vacuole to influence cell structure and movement of water. It is also a place to store pigments, such as anthocyanins, or other secondary metabolites, such as phytotoxins.

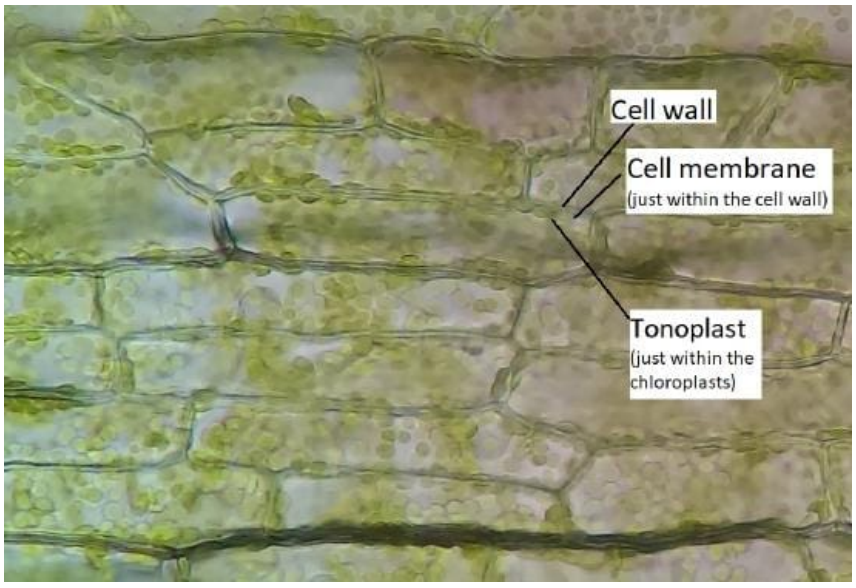


Figure 5.5.1.12: This image shows the same Elodea leaf cells again, this time with the cell wall, cell membrane, and tonoplast of one of the cells labeled. The cell walls are visible as thicker lines between the cells. The plasma membrane and tonoplast locations must be inferred. The plasma membrane is pushed against the cell wall, just to the inside of it. The tonoplast can be seen as the border between the chloroplasts the "empty space" within the cell, as the central vacuole pushes the cytoplasm to the edges of the cell. Photo credit: Melissa Ha, CC BY-NC .

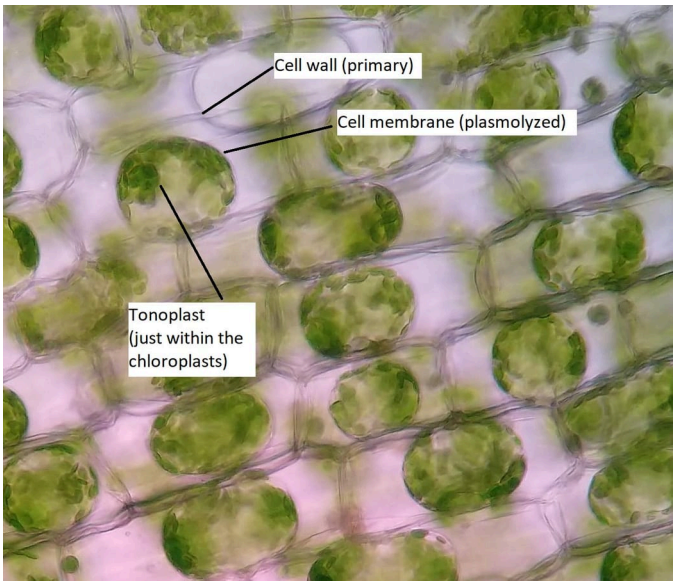


Figure 5.5.1.13: In this image, the *Elodea* leaf has been exposed to salt water. This helps us see the plasma membrane and tonoplast more distinctly, as much of the water has left the cell and the central vacuole has shrunk, causing plasmolysis. As the central vacuole shrinks, the plasma membrane collapses inward but the rigid cell wall remains in place. The plasma membrane is surrounding the outside of the chloroplasts, which have been clustered into a ball inside each cell. Just inside the shell of chloroplasts is the tonoplast. The nucleus will also be squished in there somewhere, though it is also transparent. Photo by Maria Morrow, CC BY-NC.

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5.5.2: TYPES OF PLANT CELLS

Plants have three primary cell types and these cell types compose tissues within the plant. These cells, as well as specialized cells formed from these general types, will be described in the pages of this chapter.

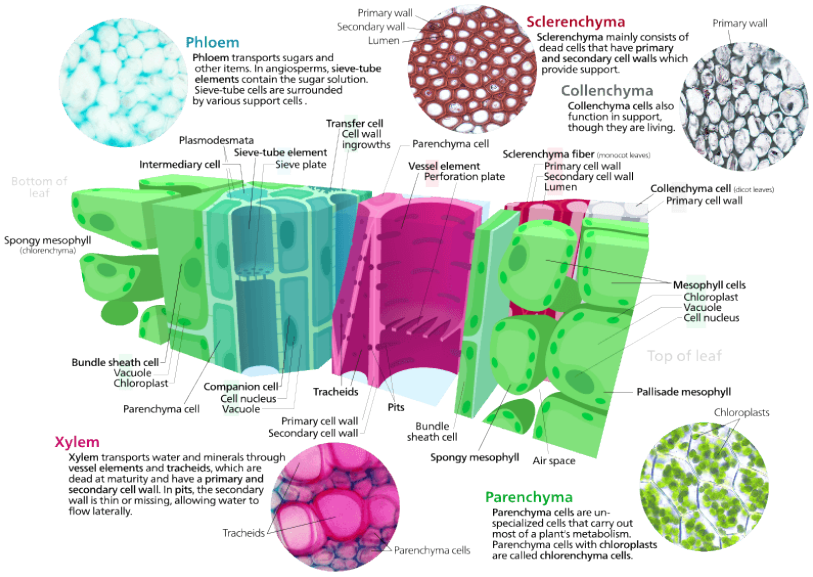


Figure 5.5.2.1: An amazing diagram of the cells and tissues present within a leaf. Image from Kelvinsong, CC BY-SA 3.0, via Wikimedia Commons.

- Types of Plant Cells

5.5.2.1: The -enchymas

5.5.2.2: Specialized Cells

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5.5.2.1: The -enchymas

There are three major cell types in plants that we can distinguish by differences in their cell walls. These three cell types are **parenchyma**, **collenchyma**, and **sclerenchyma**.

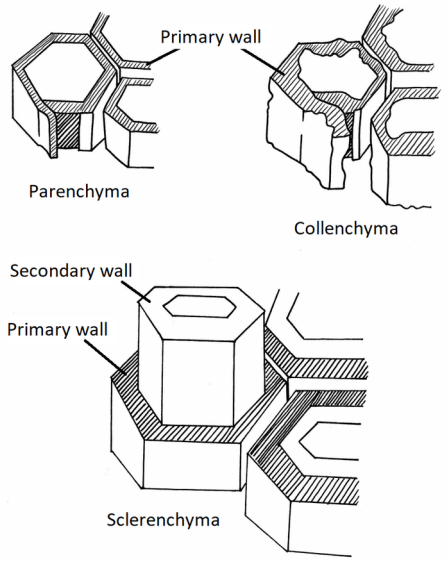


Figure 5.5.2.1.1: This diagram shows the three major cell types found in plants. In the upper left, parenchyma cells have an evenly thickened primary wall (shaded with stripes in the illustration). The primary wall of parenchyma cells is quite thin, though it has been widened in the diagram to make it easier to see. To the right of the parenchyma, collenchyma cells also have only a primary wall, but it is unevenly thickened, giving them a chunky appearance. Unlike parenchyma cells, the primary wall of a collenchyma cell is often quite thick. On the bottom half of the diagram, sclerenchyma cells are shown with a thick secondary wall (unshaded) that develops within the primary wall (shaded). Eventually, the primary wall of the sclerenchyma cells will die away. Artwork by Nikki Harris, CC-BY 4.0 with labels added by Maria Morrow.

Parenchyma

Parenchyma cells are characterized by an even, relatively thin primary wall.

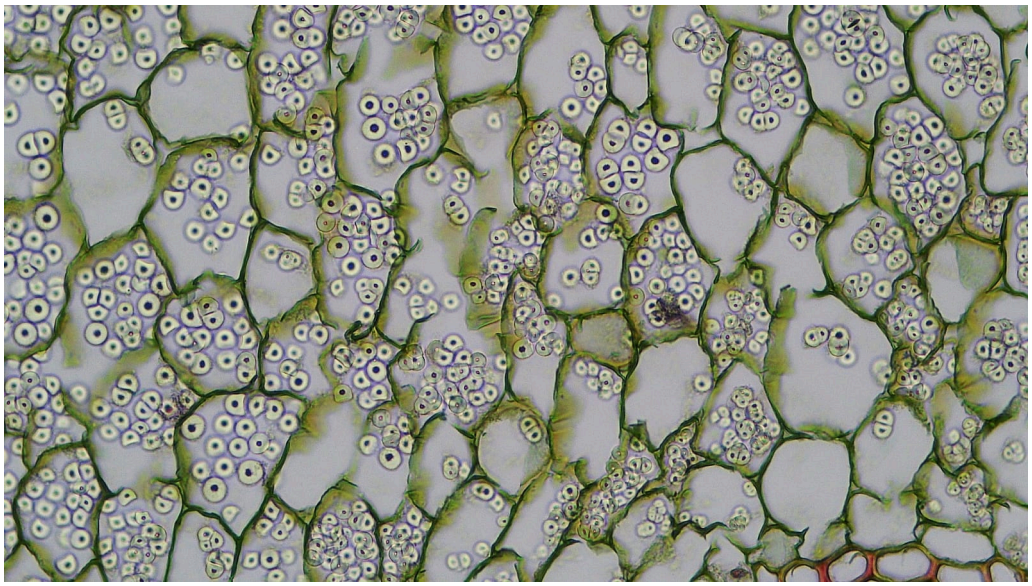


Figure 5.5.2.1.2: A cross section of a Ranunculus root showing parenchyma cells filling the cortex. Note the evenly thin cell walls. These cortex cells contain many starch grains. Photo by Berkshire Community College Bioscience Image Library, CC0, via Wikimedia Commons.

Collenchyma

Collenchyma cells are characterized by an uneven, relatively thick primary wall.

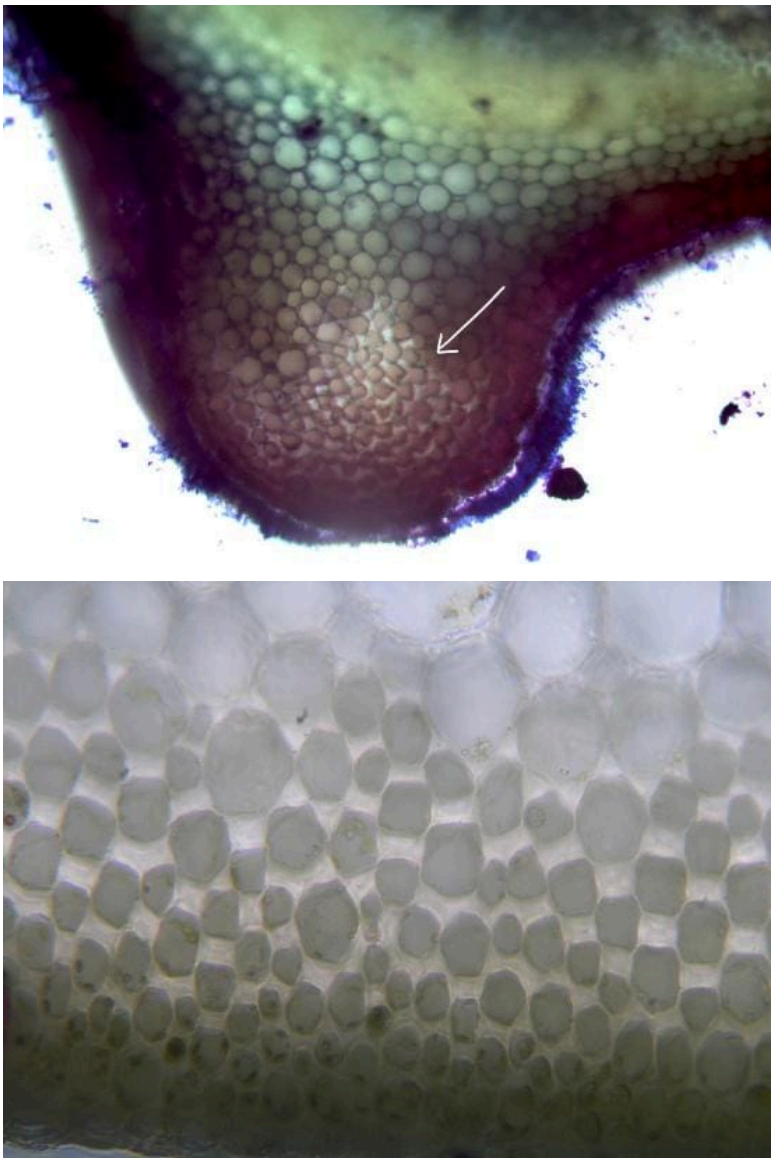


Figure 5.5.2.1.3: Collenchyma cells. Left: Angular collenchyma is a supportive tissue found in peppermint and other species like celery. 200X magnification. Taken in the Plant Lab at CU:Boulder. Photo by Spencer Llerandi, CC BY 4.0, via Wikimedia Commons with an added arrow by Maria Morrow. Right: Collenchyma tissue from celery. Photo from Clematis, CC BY-SA 3.0, via Wikimedia Commons.

Sclerenchyma

Sclerenchyma cells are characterized by the formation of a secondary wall composed of lignin. This secondary wall forms within the primary wall and eventually leads to the death of the cell. Sclerenchyma cells are dead at functional maturity.

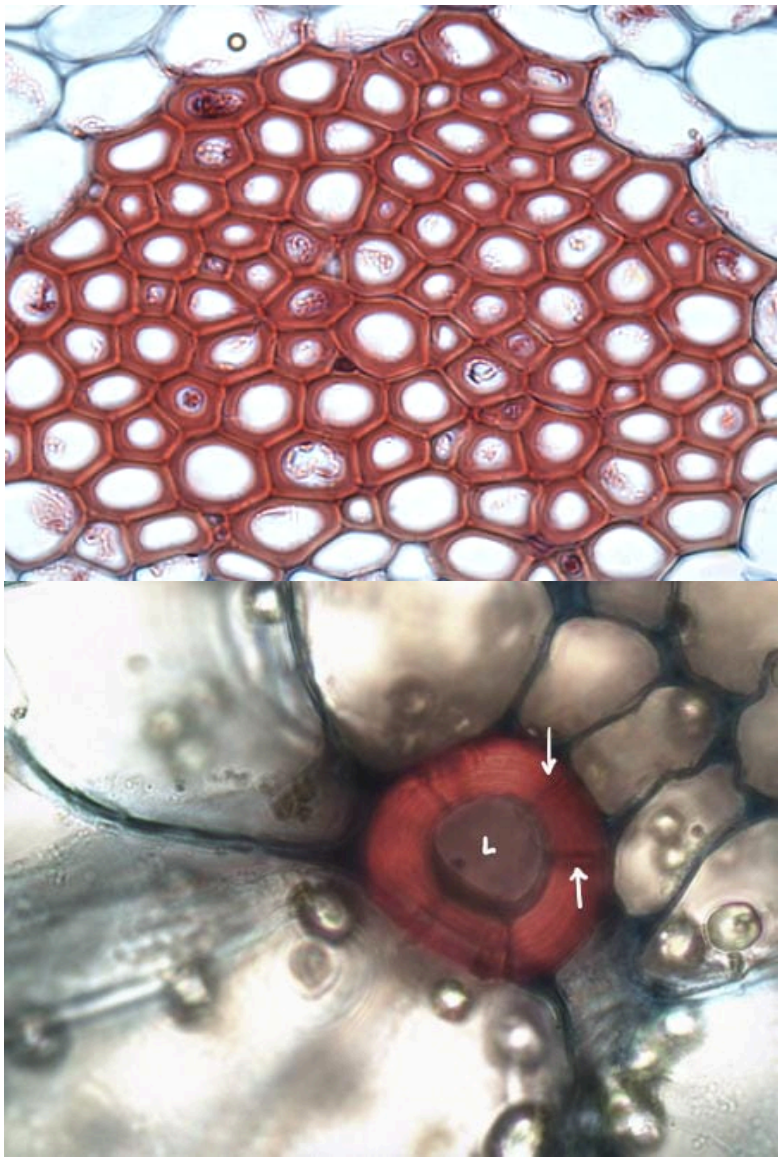


Figure 5.5.2.1.4: The first image is a cross section through a cluster of fiber cells (sclerenchyma). These cells have relatively evenly thick secondary walls that have stained red due to lignin. In the second image, there is a single fiber cell. The reddish donut is formed by its secondary wall. There are several gaps in this wall called pits, two are indicated by arrows. These are pits where plasmodesmata used to traverse the cell walls. The center (L) is the lumen, a now empty region where the cytoplasm used to be. First image: Snowman frosty at en.Wikipedia, Public domain, via Wikimedia Commons. Second image: Roland Gromes, CC BY-SA 4.0, via Wikimedia Commons with labels added by Maria Morrow.

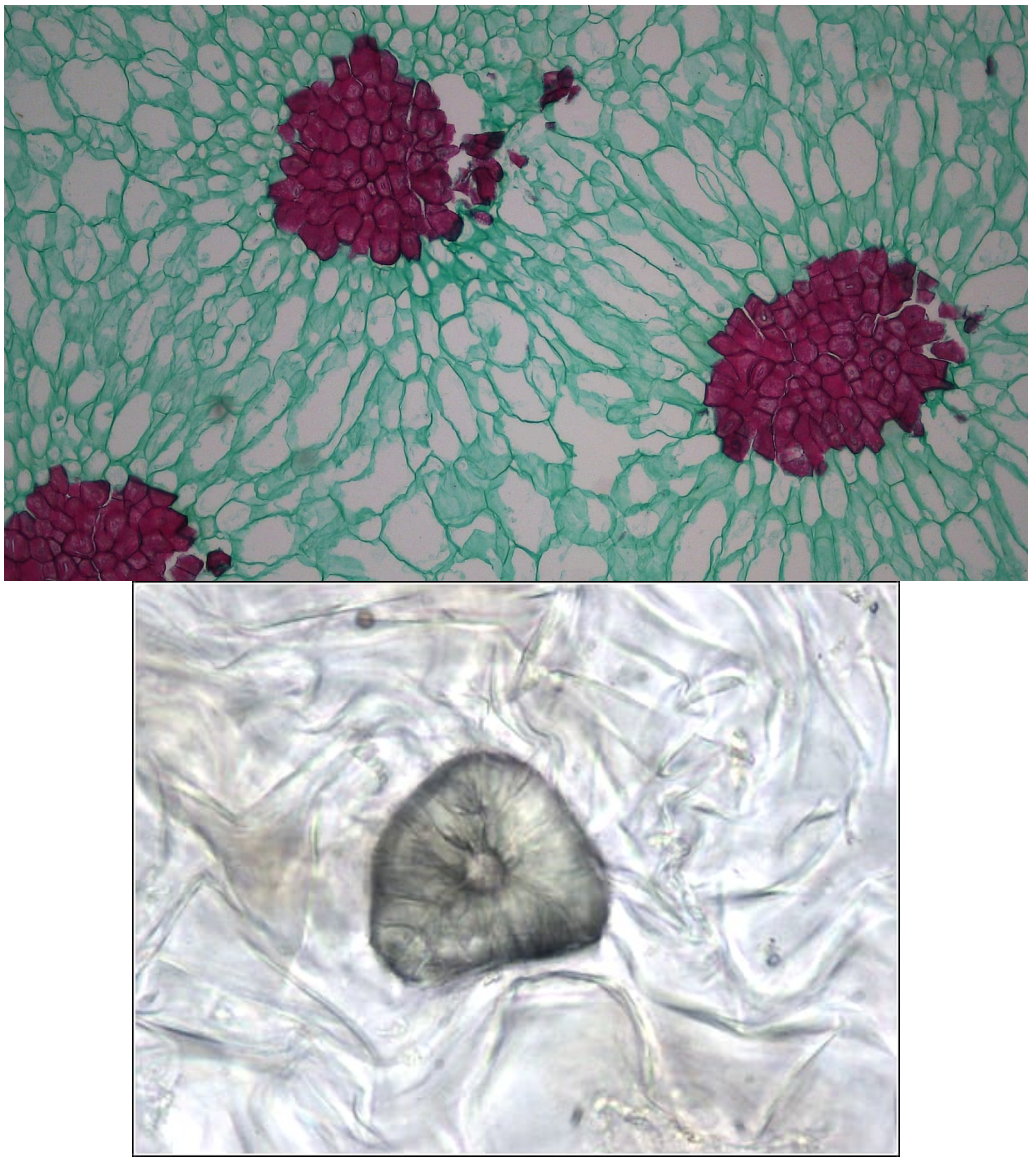


Figure 5.5.2.1.5: Sclereids are sclerenchyma cells found in pears. These woody cells give pears a gritty texture. In the first photo, the sclereids are stained a dark pink color and clustered into large groups, surrounded by parenchyma cells. In the second photo, a single sclereid is visible. It has a thick secondary wall with the channels of former plasmodesmata visible running through it, forming pits. First: Berkshire Community College Bioscience Image Library, CC0, via Wikimedia Commons. Second: Snowman frosty at en.Wikipedia, Public domain, via Wikimedia Commons.

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5.5.2.2: Specialized Cells

Specialized Cells From the Protoderm

Guard Cells

Stomata are pores (holes) in the epidermis of plants. **Guard cells** are the pairs of cells, shaped a bit like parentheses or two sides of a donut, that flank the stoma. The guard cells regulate when the stoma is open or closed, which in turn regulates gas exchange with the environment and the rate of transpiration.

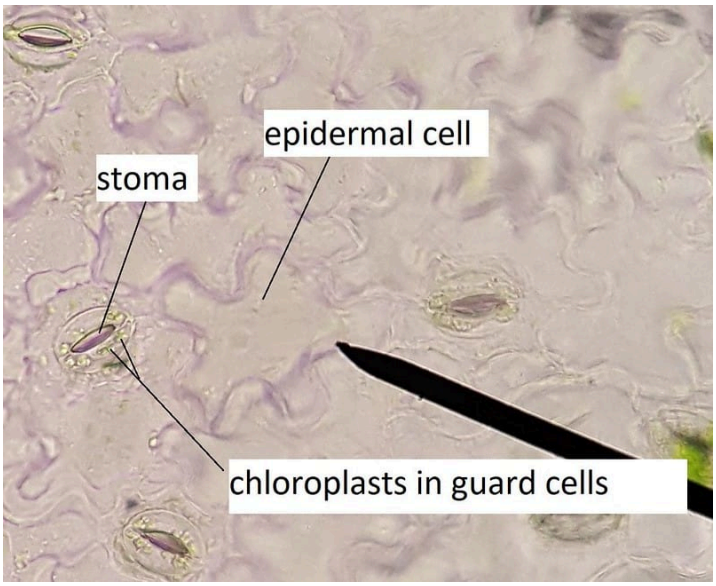


Figure 5.5.2.2.1: This image is of an epidermal peel. The epidermal cells look like transparent, interlocking puzzle pieces. Interspersed between these cells, there are stomata with guard cells. Each stoma looks a bit like a mouth, with one guard cell acting as the upper lip and another guard cell acting as the lower. Chloroplasts are visible within the guard cells. Photo by Melissa Ha, CC BY-NC .



Figure 5.5.2.2.2: There are two images above. The one on the left shows an open stoma, while the one on the right shows a closed stoma. Photo by Melissa Ha, CC BY-NC.

Trichomes

Trichomes are hairs composed of cells on the epidermis of a plant.



Figure 5.5.2.2.2: Trichomes on the underside (abaxial) of a leaf (left) and on a leaf margin (right). The trichomes in the photo on the left are long, fuzzy, and intertwining. The trichomes in the photo on the right are straight, separate from each other, and rigid-looking. The different appearance and texture of trichomes is one of the characteristics used to identify plants. Photos by Maria Morrow, CC BY-NC.



Figure 5.5.2.2.3: These nettle trichomes are structured much like a hypodermic needle. The long silica tip breaks off to inject a cocktail of stinging chemicals into any animal that brushes by it. Photo by Maria Morrow, CC BY-NC.

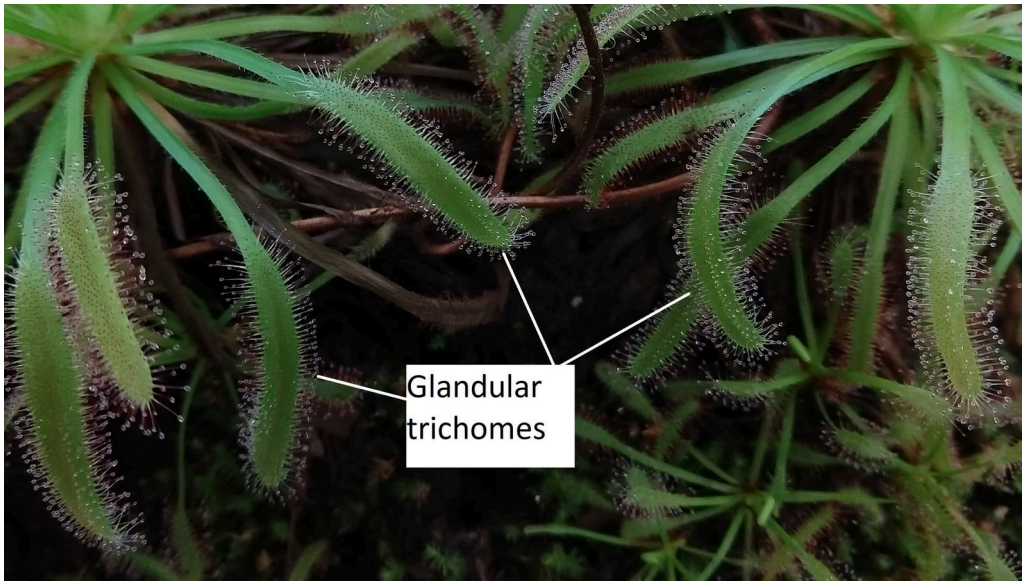


Figure 5.5.2.2.4: The ends of sundew (*Drosera* sp.) leaves are covered with glandular trichomes. Each trichome has a blob of sticky fluid at the tip. Insects are attracted to the fluid, becoming trapped in it, and the plant can slowly digest their bodies for the mineral nutrients that are lacking in their environment. Photo by Maria Morrow, CC BY-NC.



Figure 5.5.2.2.5: The underside (abaxial surface) of this sage leaf has two types of trichomes: glandular trichomes and peltate trichomes. The glandular trichomes are in tufts on raised bumps of the epidermis. Scattered amongst them are small white pearl-like structures (one is indicated by a black arrow). These are the peltate trichomes, which are disc-like instead of hair-like. Photo by Maria Morrow, CC BY-NC.

Specialized Cells From the Ground Meristem

Two types of specialized sclerenchyma cells that can be produced by the ground meristem are **sclereids** and **fibers**.

Sclereids

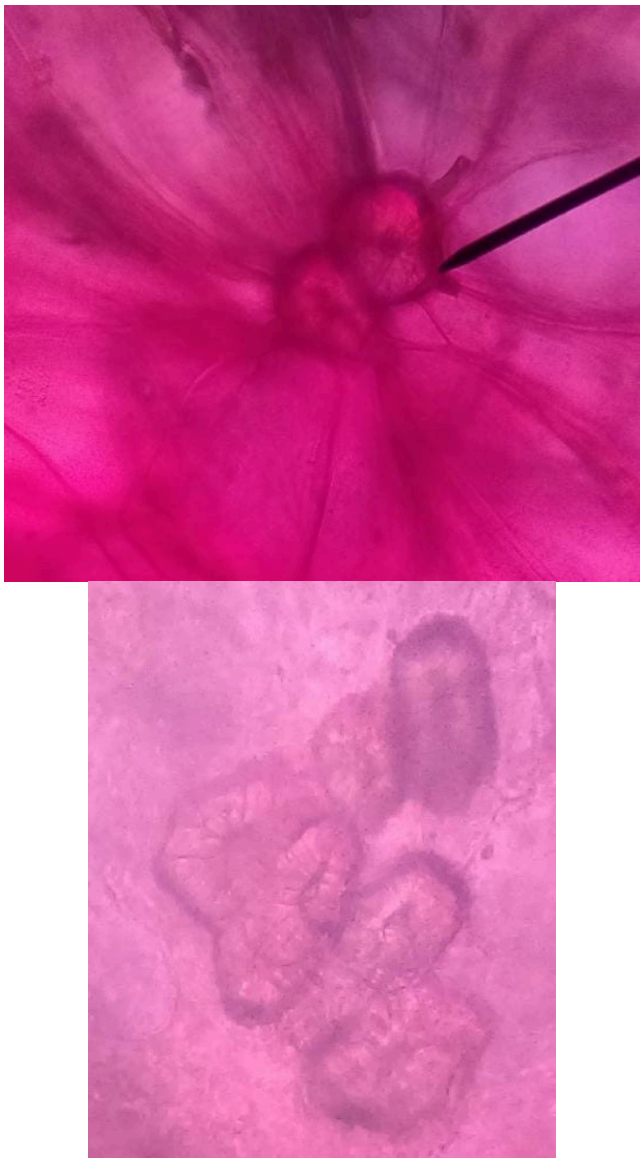


Figure 5.5.2.2.6: Sclereids are a type of sclerenchyma cell. These sclereids, called stone cells, are produced in the fruits of pears. In the image on the left, two stone cells are surrounded by many large parenchyma cells. There are plasmodesmata (not distinguishable) connecting the sclereids to these parenchyma cells. In the image on the right, there are 6 or 7 stone cells. They have a thick secondary wall with channels running through it (pits). These pits are the former locations of the plasmodesmata. Photos by Maria Morrow, CC BY-NC.

Fibers

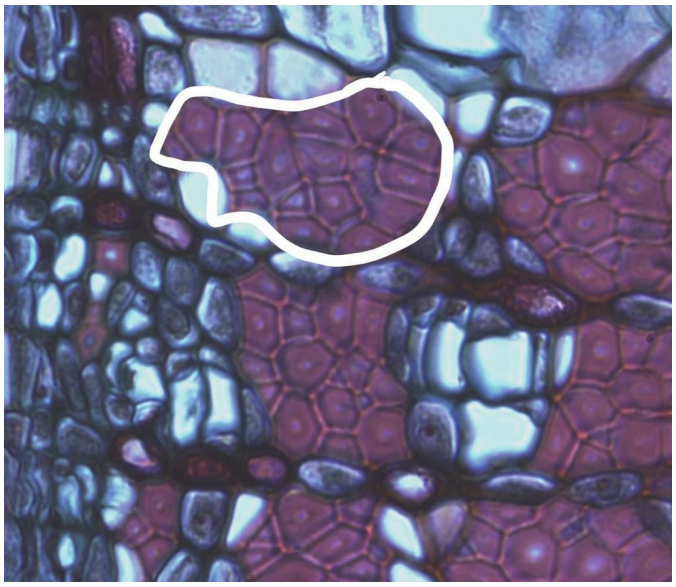


Figure 5.5.2.2.7: Clusters of fibers in the secondary phloem of a *Tilia* stem. Phloem cells are parenchyma, so they are not as rigid as xylem cells. A way for plants to strengthen and protect phloem tissue is to include bundles of fibers. One of these bundles has been circled in the image. Photo by Maria Morrow, CC BY-NC.

Specialized Cells From the Procambium

Tracheids and Vessel Elements

Tracheids and **vessel elements** are cells in the xylem that transport water. They have secondary walls with lignin and are dead at functional maturity.



Figure 5.5.2.2.8: All of these cells are dead and have secondary walls with lignin. The cell labeled A is a vessel element, with larger perforation plates on its ends and strange wall thickenings. B is a tracheid, thinner than a vessel element with rows of holes lining its sides (no perforation plates). C is a fiber, long and thin. Photo by Maria Morrow, CC BY-NC.

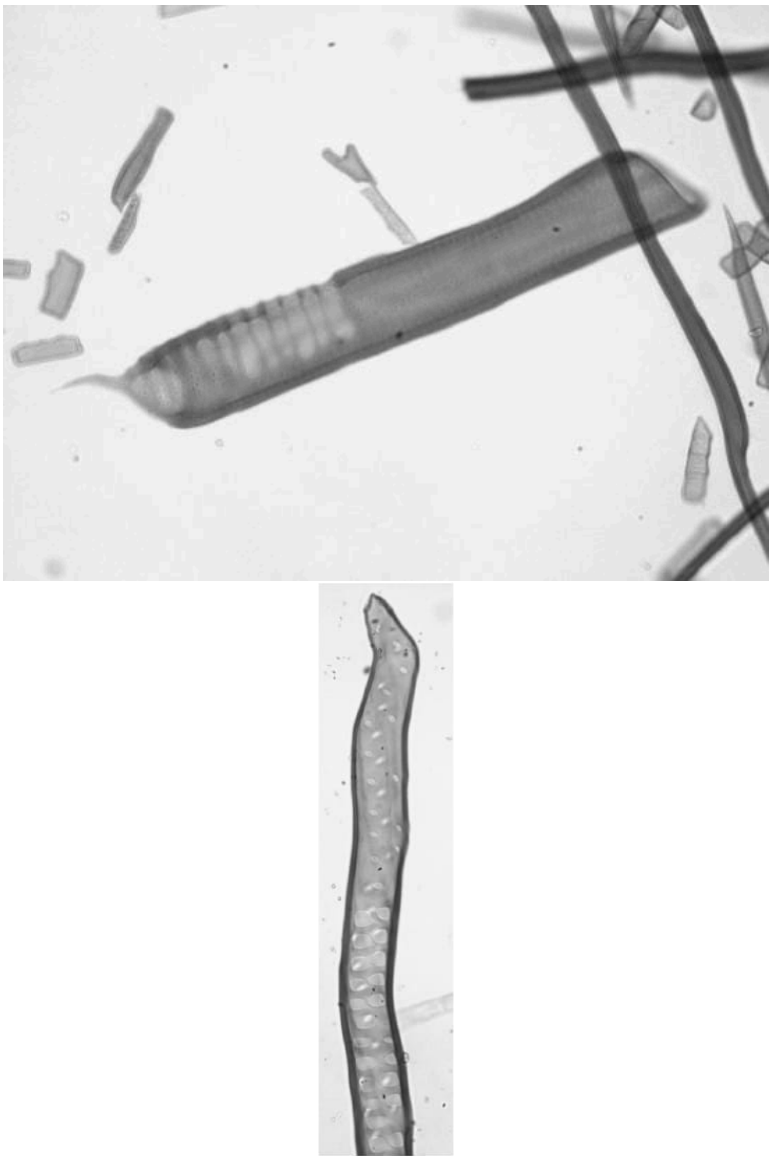


Figure 5.5.2.2.9: Conducting cells from the xylem. The first photo shows a vessel element with large openings at the ends. The second photo shows a tracheid, with tapered ends and sets of bordered pits along the length of it. Photos by Maria Morrow, CC BY-NC.

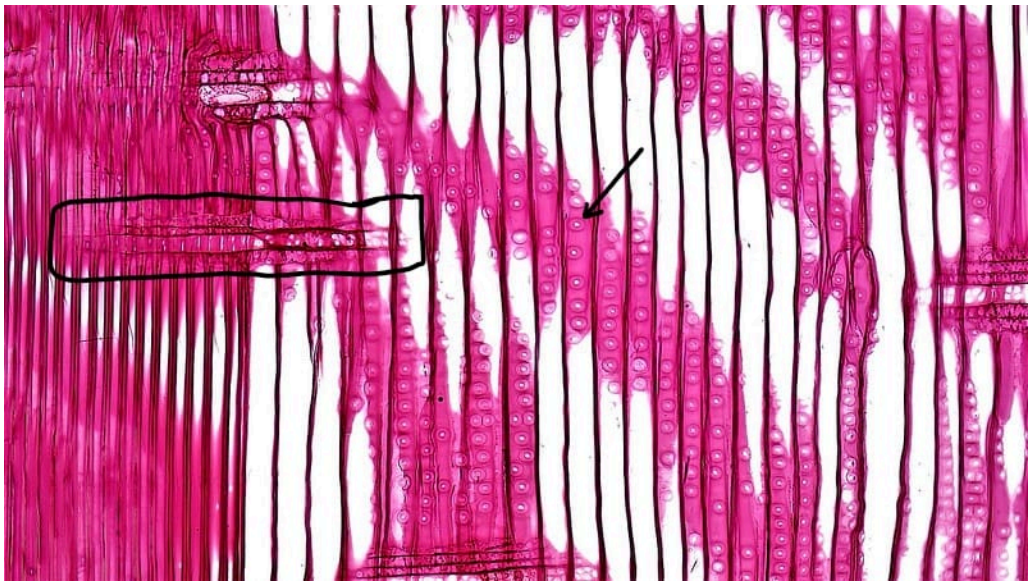


Figure 5.5.2.2.10: A longitudinal section through pine wood. "Gymnosperms like Pinus rely entirely on tracheids for water flow and mechanical support. True xylem vessels and wood parenchyma are lacking. While fibers are generally absent older stems may contain some fiber tracheids. The uniform wood of Pinus consists almost entirely of longitudinally oriented bands of narrow, pale staining tracheids interrupted by short bands of horizontally oriented xylem rays (indicated by box). Xylem rays, usually one cell thick and a few cells high, are composed of clear, thin walled parenchyma cells. The lumen of many tracheids is crossed by branched trabeculae. Tracheid side walls contain large circular bordered pits (indicated by arrow) that function to move water from tracheid to tracheid while preventing air flow from embolized tracheids. The membrane of each bordered pit is marked by a pale, thin, porous outer margo and a thicker, darker, inner torus. Large horizontally oriented resin ducts are lined with living secretory parenchyma that produce resins and many toxic terpenes including turpentines." Image and caption text from Berkshire Community College Bioscience Image Library, CC0, via Wikimedia Commons. Labels added by Maria Morrow.

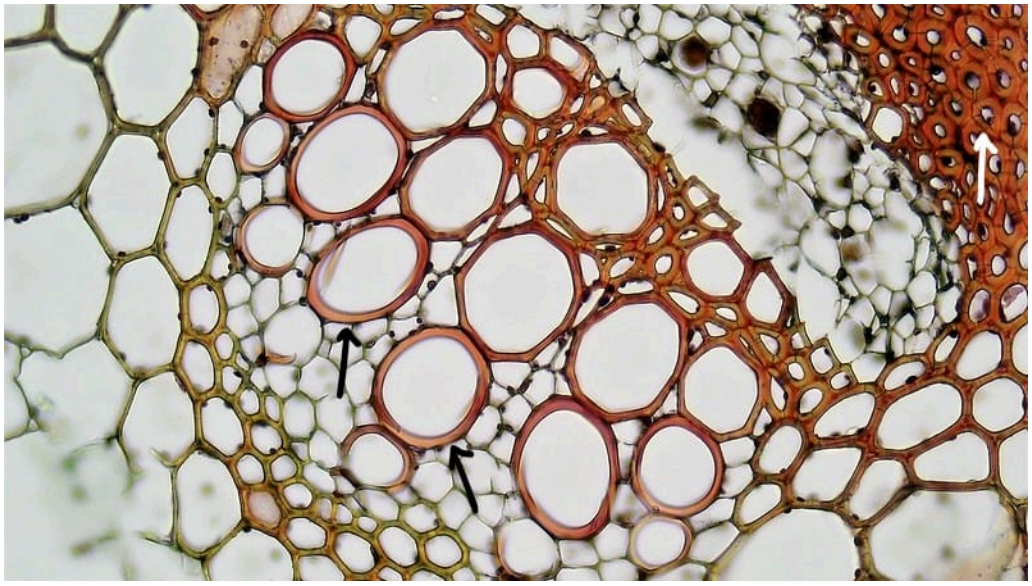


Figure 5.5.2.2.11: A cross section through a vascular bundle of *Helianthus*, 400x. "The highly lignified cells walls of xylem (black arrows indicate vessel elements) and mature sclerenchyma (white arrow indicates fibers) are stained red orange. These cells are dead at maturity and can also be distinguished by a heavy cell wall and absence of cytoplasm." Image and caption text from Berkshire Community College Bioscience Image Library, CC0, via Wikimedia Commons. Labels added by Maria Morrow.

Sieve cells, Sieve Tube Elements, and Companion Cells

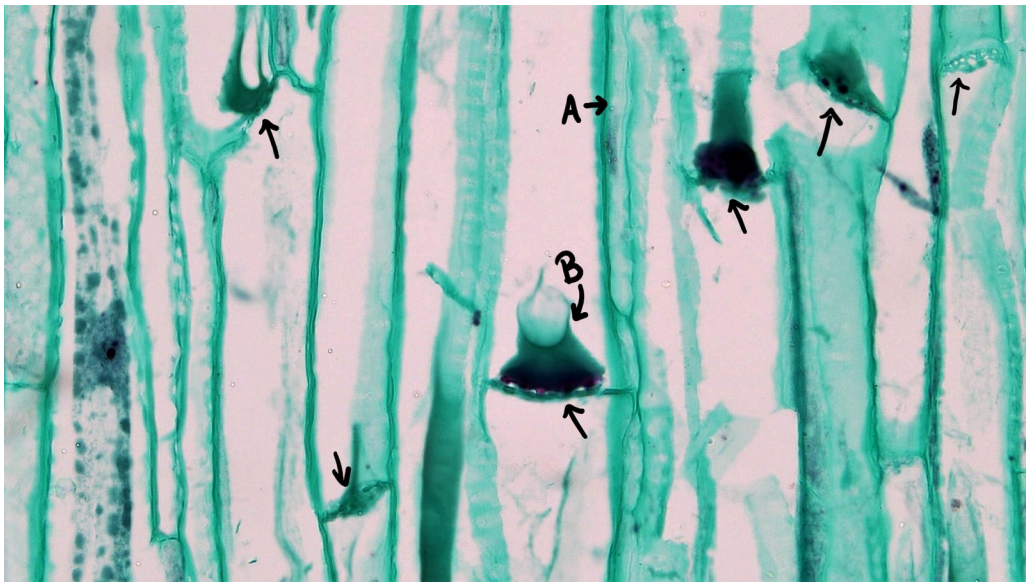


Figure 5.5.2.2.12: Longitudinal section through phloem. Most of the cells are sieve tube elements. The cells have sieve plates at the ends (marked by arrows). In the event of an injury, P-protein rushes to form a slime plug (B) and close the wound. Sieve tubes are alive but contain very little cell contents, they do not even have a nucleus. Instead, they are controlled by smaller companion cells (A). Photo by Berkshire Community College Bioscience Image Library, CC0, via Wikimedia Commons. Labels added by Maria Morrow.

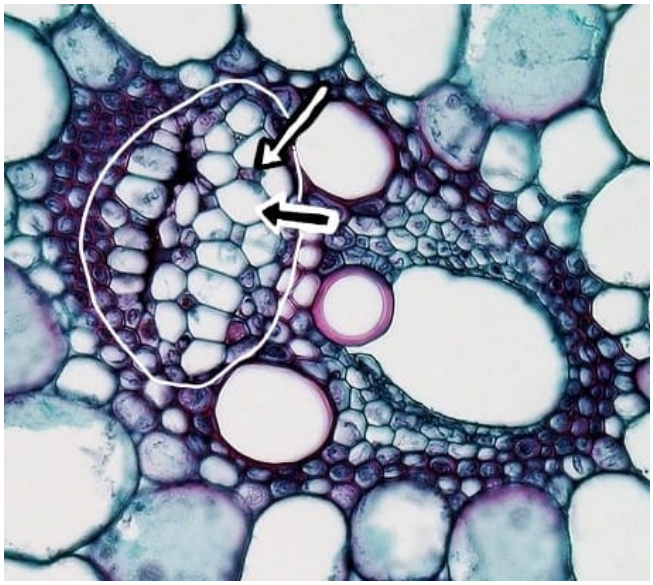


Figure 5.5.2.2.13: A cross section through a vascular bundle with the phloem circled (white). Within the phloem, there are two types of specialized parenchyma cells: the larger sieve tube elements (black arrow with white border) and the much smaller companion cells (white arrow with black border). Photo by Berkshire Community College Bioscience Image Library, CC0, via Wikimedia Commons. Labels added by Maria Morrow.

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6: CELL DIVISION, AND SEXUAL REPRODUCTION

Learning objectives

- Identify the source and mechanisms that produce gametes.
- Explain double fertilization and the production of a zygote, embryo, and other seed structures.
- Contrast the difference between simple/qualitative and complex/quantitative inheritance and the basis of that difference.
- Predict the types of F_1 and F_2 offspring expected when crossing two parents with known genotypes and phenotypes.
- Understand how heritability is a measure of genetic influence, relative to other non-genetic influences.

Plant propagation relies on gametogenesis for fertilization and the formation of fruit and seeds. Unlike asexual propagation, seeds from a single pollination can generation tremendous variation, depending on the diversity that exists within each parent. Geneticists take advantage of this diversity to understand how genes control the plant's phenotypes and to make improved varieties that are tastier and have improved disease resistance.

6.1: Sexual Reproduction

6.1.1: DNA

6.1.2: Mitosis

6.1.3: Meiosis

6.1.4: Terms

6.1.5: Atlas- Life Cycle

6.2: Gametogenesis

6.3: Inheritance of Big Differences

6.4: Linkage and Inheritance of Small Differences

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6.1: SEXUAL REPRODUCTION

Learning objectives

- Understand the structure of DNA.
- Compare the different states of ploidy and which process of cell division — mitosis or meiosis — they are produced from.
- Recognize what happens to the chromosomes, cell wall, cell membrane, and nuclear membrane in each of the stages of mitosis and meiosis.
- Compare the similarities and differences in the outcomes of mitosis and meiosis.

Mitosis is essential to all plant propagation. It produces the mighty oak from a single zygote cell and makes all forms of propagation possible. The adventitious rooting process of any cutting begins with mitosis and continues through many mitotic divisions to produce a root meristem. Meiosis is also fundamental to plant propagation for the production of gametes that fuse, producing diversity for evolution and plant breeding.

6.1.1: DNA

6.1.2: Mitosis

6.1.3: Meiosis

6.1.4: Terms

6.1.5: Atlas- Life Cycle

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6.1.1: DNA

Learning objectives

By the end of this lesson you will be able to:

- Discuss how ribose, phosphate, purine, and pyrimidine molecules are combined to make up a strand of DNA.
- Summarize how the strand of DNA is coiled and packed to become a chromosome.
- List the steps in the cell cycle and describe where in the cycle you would find particular types of cells.

Introduction to chromosomes

Watch this video for an introduction to chromosomes (2:16)

You have learned about two types of meristems: apical meristems, that result in primary growth, and lateral meristems, like vascular cambium and cork cambium, that result in secondary growth. Meristems are sites of cell division in plants. These new cells may themselves divide once or twice, but then they begin to enlarge and differentiate into cells with specialized function depending upon the type of tissue in which they occur. (Parenchyma cells are an exception because they remain undifferentiated. They can become meristematic and divide to form plant parts like lateral roots, to form interfascicular cambium, and to respond to wounds by filling in space with new cells called callus tissue.)

For a cell to divide into two identical cells, it is critical that all the components of the original cell are duplicated prior to cell division and then distributed between the two sister cells before they separate. It is also critical that the hereditary material, the DNA in the nuclear chromosomes, be exactly duplicated and equally distributed between sister cells. Exact duplication and equal distribution ensure that each cell in the organism has all the genetic instructions it needs to carry on its metabolic processes, and that every cell in the organism has the same instructions.

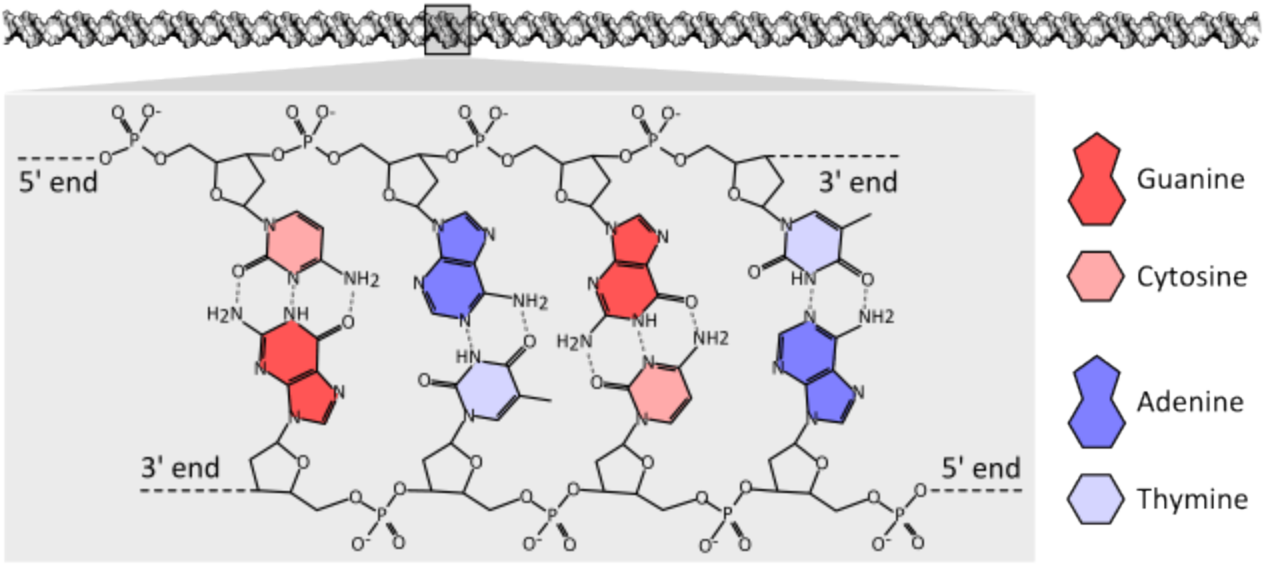
The type of cell division that takes place in meristems, which is the type where one cell divides into two identical sister cells, is called **mitosis**.

Mitotic cell division was first observed under light microscopes well over 150 years ago. Microscopists, scientists who use microscopes, noticed dark-staining cell bodies lined up in the middle of a cell that was about to divide. They called these cells **chromosomes** (based on the Latin for dark staining, “khrôma,” and bodies, “sôma”). Once lined up in the middle of the cell, the chromosomes divided and moved to opposite poles in the cell just prior to the actual division of the cell into two sister cells. It was clear to those scientists that the process of cell division ensured that the chromosomes were specially and carefully handled during cell division. In 1902, Water Sutton, studying grasshoppers, provided proof (optional reading) that chromosomes contained the hereditary material for the organism. That’s why cell division includes such careful division of the chromosomes — the organism needs to ensure that every cell has an exact copy of all of the hereditary material associated with that organism.

What makes up these chromosomes? The short answer is that chromosomes found in the nucleus of plant cells are composed of chromatin (optional reading). Chromatin is made up of DNA wrapped around proteins, called **histones**. These proteins around which the DNA wraps are called histones. We’ll start with the structure of DNA and build up to a chromosome.

DNA structure

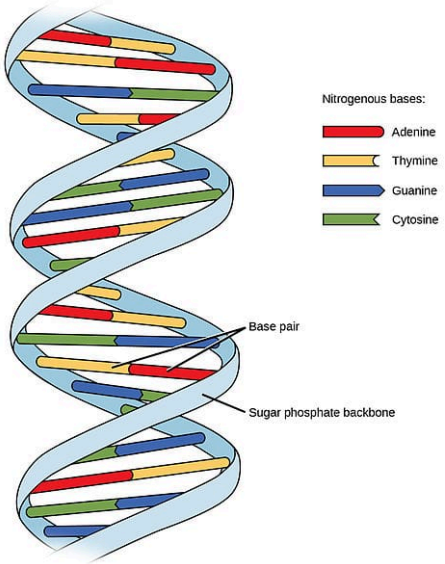
Watch this video for an explanation of DNA structure (4:35)



DNA molecular diagram. Thomas Shafee. CC BY 4.0

DNA is a double-stranded chemical polymer (a polymer is several types of molecules bonded together) that looks like a flexible ladder twisted on its long axis. Each side, or single strand of the ladder, is made up of a chain of alternating ribose and phosphate molecules. Ribose is a sugar molecule composed of a ring of five carbons. These molecules are linked to each other by a phosphate molecule made up of one phosphorus atom and two oxygen atoms. This sequence of ribose and phosphate molecules constitutes what is called the DNA's ribose-phosphate backbone.

The steps, or rungs, of the ladder are constructed from pairs of bases. Four types of these bases compose both strands of DNA. Two of the bases, collectively called purines — Adenine (A) and Guanine (G) — contain two rings of carbon atoms. The other two, collectively called pyrimidines — Cytosine (C) and Thymine (T) — have only one ring of carbon atoms. There is enough space between the sides of the ladder (or ribose-phosphate backbone) to fit two bases with a total of three carbon rings, so each rung of the ladder always has one purine bonded to one pyrimidine.



Structure of DNA. OpenStax. CC BY 3.0

There isn't enough space for two purines, and there is too much space for two pyrimidines. And because of the molecular structures of the bases, Adenine (A) always bonds with Thymine (T), because they each can share two hydrogen bonds, and Cytosine (C) always bonds with Guanine (G), because they each can share three hydrogen bonds.

As a consequence, the rungs on the ladder are always made up of AT, TA, GC, or CG. And the sequence or order of As, Ts, Gs, and

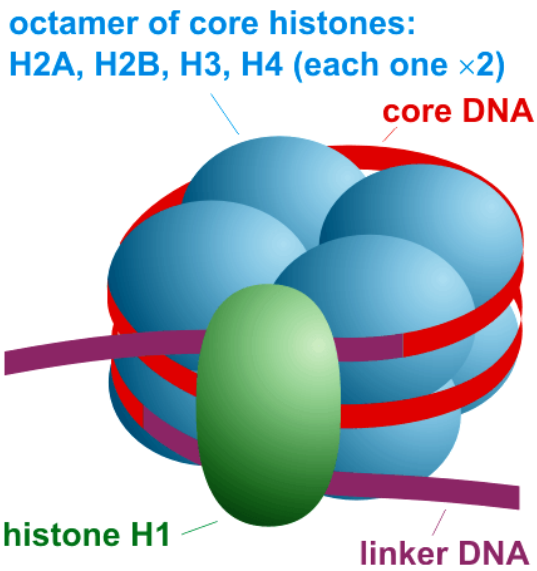
Cs making up the rungs along one strand of the ladder is the genetic code carried in the DNA. With only rare exceptions, the code is read three-bases at a time and encodes all of the information for a plant's life cycle.

Review questions

1. If you know that a rung of the DNA ladder has the base Adenine, then the other base to which it is bonded is Thymine. Why not Guanine? Why not Cytosine?
2. We take for granted now that chromosomes are the hereditary material in plants. When was this proven? A) about 15 years ago when the first genetically modified foods were developed, B) around the time the atom bomb was developed, C) just before WWI, or D) back when Mendel was doing experiments with peas and discovering his principles of inheritance.
3. Why is the shape of DNA called a double helix?

Nucleosomes

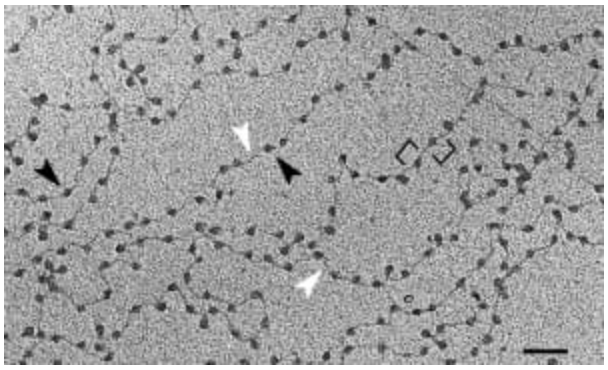
Watch this video for a description of nucleosomes (2:46)



Nucleosome. Darekk2. CC BY-SA 3.0

We now have a DNA helix made up of alternating ribose and phosphate rails with rungs containing a purine and a pyrimidine. The DNA helix strand next loops around nucleosomes (optional reading) which are made up of histone proteins (illustration above). The histone proteins are essentially the spools around which the DNA thread wraps, except that DNA doesn't wrap continuously around one histone protein the way thread wraps around one spool. It makes a couple of loops and then moves on to the next histone protein.

The loops of DNA around these nucleosomes are separated by portions of naked DNA called **linker DNA**, so the effect is called "beads on a string" (see micrograph below). where the beads are the DNA loops and histone protein, and the string is the strand of linker DNA. This description dates back to the early days of exploring DNA using light microscopy. Chromosomes could be observed with the aid of the microscope and described, but their composition was unknown.

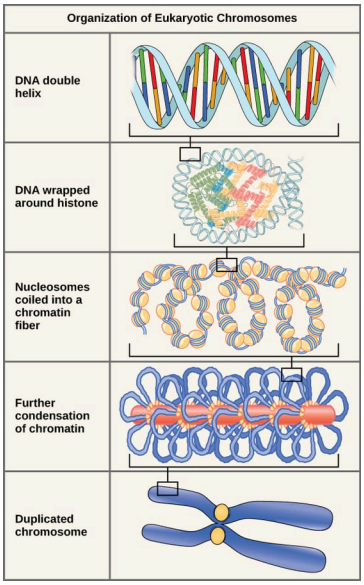


Black brackets highlight individual nucleosomes; black arrowheads point to nucleosome core particles (the beads), white arrowheads to linker DNA (the string). Scale bar: 50 nm. Chris Woodcock. CC BY-SA 3.0

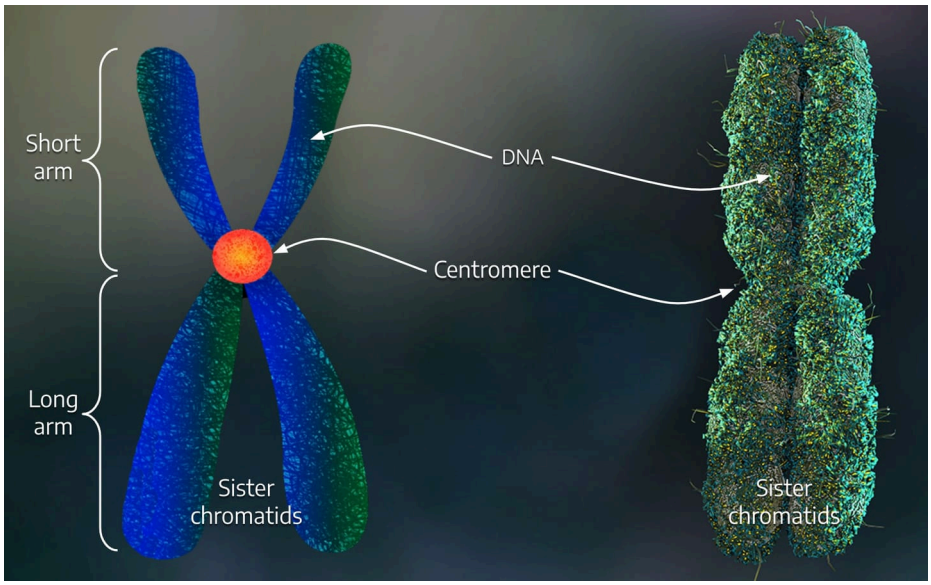
The “beads on a string” structure is further coiled into a 30 nm (nm=nanometer, one billionth of a meter) chromatin fiber, which further folds even more, with the association of other proteins, to form the chromosome.

A chromosome, then, is made up of DNA that has looped around histone proteins, then coiled, then folded. Think of a chromosome as a tightly and carefully packed long thread of DNA that is associated with histone proteins to help with the packing.

Here’s a diagram of this coiling:



Chromosome coiling. OpenStax. CC BY 4.0



Sister chromatids. 3D Rendering X and Y Chromosome with Telomeres © Shutterstock, used with permission. Simple chromosome illustration by Prateek Pattanaik. CC BY-SA. Images adapted by Emily Tepe.

Above is a rendering of a micrograph of a chromosome at the cell division stage, when the chromosome is most highly condensed (which is during a phase of mitosis called metaphase, as we will see later) and compactly packed. At this phase there is extensive coiling (DNA coiling is called “condensation”) of the chromatin (DNA + histone proteins). Note that there are two sister chromatids. Just prior to cell division these sister chromatids will separate at the centromere (the constricted spot where they are attached) and move to opposite sides of the cell.

It is helpful to have this detail so you can recognize where the genetic code sits in the DNA molecule, and how DNA is folded up and condensed into a tight package during cell division. When a cell is not dividing, parts of the chromosome relax, unfold, and uncoil so that the DNA base pairs in specific parts of the chromosome that provide the code for specific cellular functions can open up, be copied, and the code can be translated into proteins that do the cell’s metabolic business — a phase called “interphase“). During cell division, however, the package is tightly condensed (metaphase).

This interactive site has a feature that allows you to rotate the DNA helix (optional). Look for the following:

- 5-carbon ribose ring making up part of the backbone
- phosphate linking the ribose rings completing the backbone
- 2-ring purine base (one per rung)
- 1-ring pyrimidine base (one per rung)
- hydrogen bonds (two or three per rung depending on the composition)

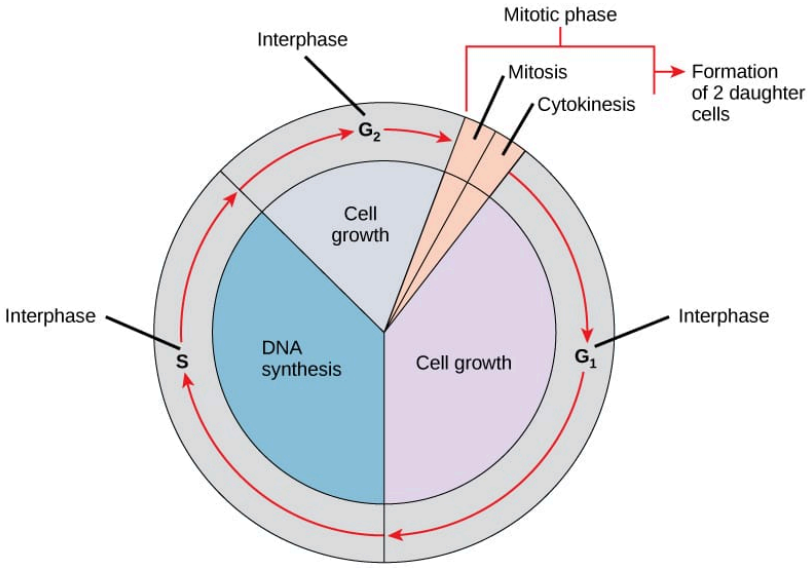
Review questions

1. Why do you think the chromosome is so highly condensed (meaning wrapped and folded) during metaphase, which is in the middle of cell division? Think about why a chromosome might need to be very tightly packed during cell division.
2. What is the connection among nucleosomes, linker DNA, and beads on a string?

The cell cycle

Watch this video about the cell cycle (3:38)

Below is a diagrammatic summary of the cell cycle, the cycle a cell goes through during its lifetime. You’ll see that about 3/4 of the cycle is called **Interphase** and the other 1/4 is called **M** (for mitosis). As noted, during interphase the cell isn’t dividing (but may be preparing to divide); the cell divides during M. Interphase is divided into three parts: G1 (the “G” is short for “Gap” or “Growth”), S (S for DNA “Synthesis”), and G2.



Cell cycle. OpenStax. CC BY 4.0

Consult this page on the cell cycle (optional reading) for additional information about the cell cycle.

The stages in the cell cycle are:

- G1 — cells are enlarging, and some are differentiating into specialized cells like epidermis, collenchyma, sclerenchyma, and cells in the xylem and phloem tissue that will no longer divide. These differentiated cells stay in G1 until death.
- S — chromosomes in cells like apical meristem cells, vascular and cork cambium, or undifferentiated parenchyma cells prepare to divide by replicating their chromosomes. To prepare for division, the cell makes a complete copy of all of its DNA, so in the process of copying the DNA there is DNA Synthesis. Once a chromosome has been replicated, the two copies are called sister chromatids and they are held together at a spot called the centromere. The sister chromatids are exactly alike, down to the exact order of AT, TA, CG, and GC bases in the rungs of the DNA backbone.
- G2 — the cell builds up the chemical machinery that it needs for division.
- M — finally, the cell heads into mitosis (M), addressed next.

Note that the size of the slices of pie in the diagram above are not indicative of the actual time duration.

Review questions

1. Where would you place leaf spongy mesophyll cells on the cell cycle? Why?
2. Where would you place cork cambium cells? Why?

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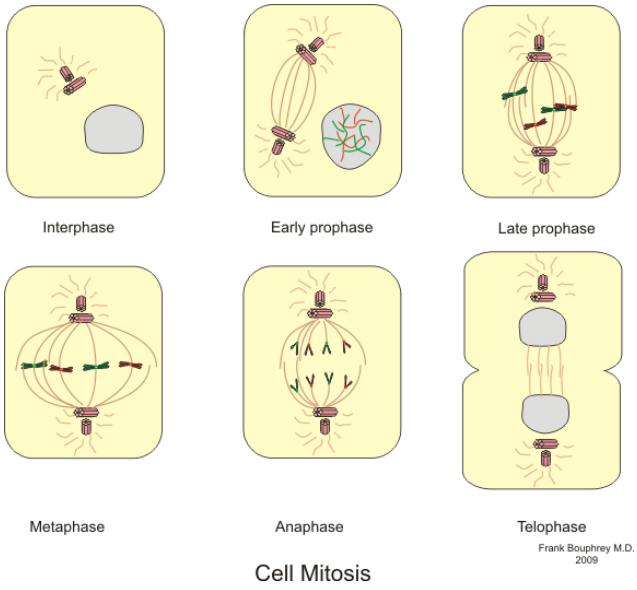
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6.1.2: Mitosis

Learning objectives

By the end of this lesson you will be able to:

- Compare diploid and haploid and identify which cells in the plant are which.
- Understand why cells undergo mitosis.
- Explain how the chromosomes prepare for cell division in the S phase of interphase.
- Recognize what happens to the chromosomes, cell wall, cell membrane, and nuclear membrane in each stage of mitosis.



Phases of mitosis. Boumphreyfr. CC BY-SA 3.0

Ploidy

The previous lesson focused on DNA's ribose-phosphate backbone, on the purine and pyrimidine bases, and on how DNA complexes with protein and coils to form chromatin. Here we'll look more closely at the synthesis (S) phase of interphase and at the mitosis (M) phase. Recall that the mitosis phase of the cell cycle "pie" is divided into four stages; we'll look now at what happens in each of those stages and how it contributes to the outcome of mitosis, the equal division of chromosomes into two daughter cells.

Ploidy refers to the number of sets of homologous (identical) chromosomes in a cell.

- In higher organisms like plants (and animals, including humans), gamete cells (egg and sperm) typically each contain one set of each of the chromosomes found in that particular species. When cells contain one set of chromosomes characteristic of the species, this state is called haploid and is abbreviated n.
- When the sperm and egg, each of which are n, unite to form a zygote, the zygote cell now has two sets of chromosomes, one from the male parent's sperm and one from the female parent's egg. When cells contain two sets of chromosomes, they are described as diploid, abbreviated 2n.
- Recall that one result of double fertilization in plants is that one sperm cell unites with two female polar bodies to create the endosperm found in seeds. Endosperm cells have three sets of chromosomes, two from the female parent's polar nuclei (n + n) and one from the male parent's sperm (n), so this tissue is triploid, abbreviated 3n.

Most of the cells of flowering plants that we have studied so far, like the cells making up the epidermis, cortex, and vascular tissues

(but not the sperm and eggs cells), are called somatic cells, and are diploid (2n). Each cell carries two sets of chromosomes: one from the male parent and one from the female parent.

Each species of plant has a characteristic number of chromosomes in its somatic cells. Bur oak has 24. The garden petunia has 14. Green bean has 22. Half of those chromosomes came from the egg and half from the sperm, so the plant has two sets of chromosomes. In the bean, the 22 chromosomes can be numbered from 1 to 11 based on their morphology (chromosomes have different lengths). The numbering only goes to 11, even though there are 22 chromosomes, because each diploid cell has two copies of chromosome 1, two copies of chromosome 2, and so on.

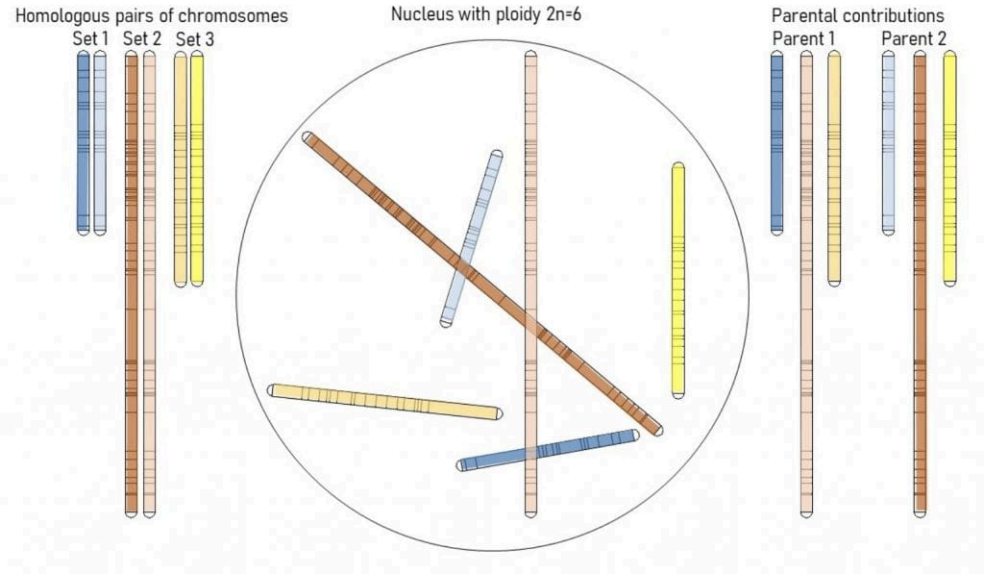


Illustration by Dr. Matt Clark, University of Minnesota

The illustration above shows this for a hypothetical plant's somatic cell's nucleus containing 6 chromosomes. On the left side, the chromosomes are rearranged into three pairs of homologs. The matching chromosomes from the two different sets (for instance, the two copies of chromosome 1) are called **homologous chromosomes** or **homologs**. Homologs carry, at the same location on the chromosome, the genetic information that affects the same characteristic or function. The version of the information can be different between the homologous chromosomes — that is, the sequence of base pairs may be somewhat different because one homolog came from the female and the other from the male.

The homologs look identical and carry genetic information about particular cell functions at identical places on the chromosome (shown using dark bands at specific locations on the chromosome), but the exact base pair sequences at those locations may differ, resulting in different alleles and gene function. The parental combinations are shown at the right, and are the haploid contribution that resulted from meiosis. The 50% reduction in the sex cells ensures that offspring have the proper diploid chromosome number and matching homologs that are the full compliment of the plants genome.

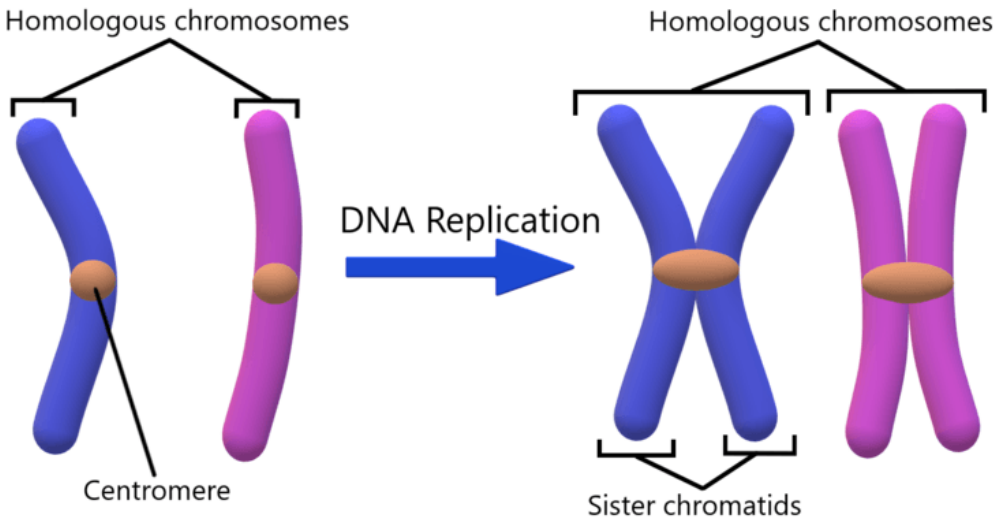
A cell in the plant's apical meristem that is preparing to divide is a somatic cell, so it is diploid, and contains two sets of chromosomes. When it undergoes mitosis, the outcome will be two identical diploid sister cells. Each of these sister cells will also be diploid, and will contain exact copies of the two sets of chromosomes that were in the original cell. "Daughter" and "sister" cells refer to the same thing — the new cells that arise as the result of mitosis.

From our study of meristems, you know that growth is the result of the formation of new cells, and the subsequent elongation of those cells. Mitosis is the process that results in the formation of new cells. Cells undergo mitosis, therefore, as part of plant growth.

Review questions

1. Somatic cells of beans have 22 chromosomes. How many chromosomes in a bean sperm cell?
2. Corn egg cells have 10 chromosomes. How many chromosomes are found in a corn seed's endosperm cells?
3. Why do cells undergo mitosis? Is it important?

Synthesis



Outcome of S phase. Christinelmiller. CC BY-SA 4.0

If a cell that undergoes mitosis divides into two cells, how can both of these new cells be identical to each other and to the original cell? Won't the chromosomes in the original parent cell be divided in half during division? Won't the resulting cells be haploid instead of diploid? No. The number of chromosomes isn't reduced during mitotic cell division because, prior to division, each of the chromosomes replicates (duplicates), meaning that the cell makes an exact copy of each chromosome. This replication process happens during the synthesis (S) phase of the cell cycle.

Remember that G1, S, and G2 phases of the cell cycle are collectively called interphase. Most cells in the plant go about their business in the G1 phase. Only those cells called upon to divide make the next step, which is to replicate their chromosomes in the S phase. Once the chromosomes are replicated, the cell moves into the G2 phase of interphase and awaits mitosis. The S phase is called **synthesis** because making a copy of the chromosome requires new DNA production, or synthesis.

The two chromosomes that are exact copies are called sister chromatids and remain connected at one spot along their length; this spot is called the **centromere**, as shown in the illustration.

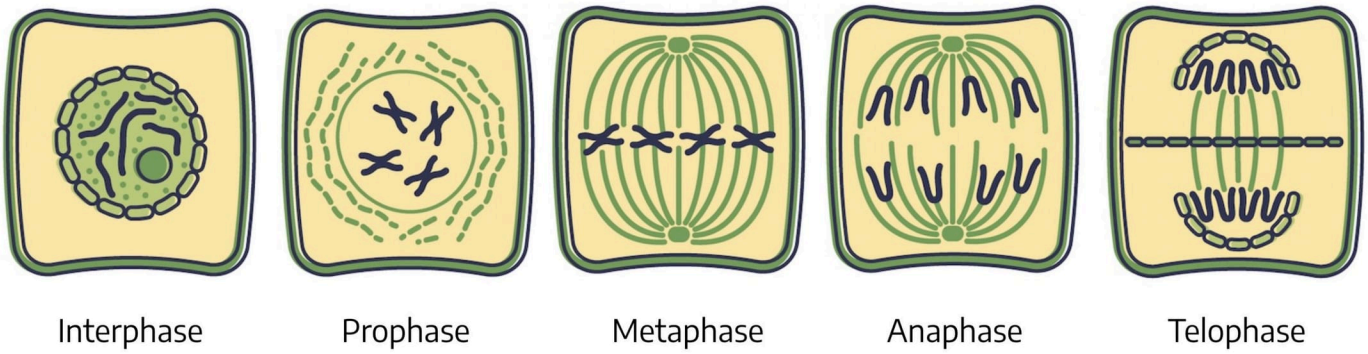
Review questions

1. If a diploid cell enters S phase with 2n=20 chromosomes, how many sister chromatids are in the cell when it enters G2?
2. Are the replicated sister chromatids independent or are they connected in some physical way?

Stages of mitosis

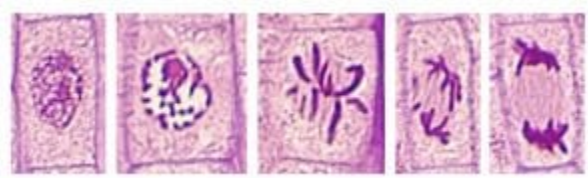
This video provides a view of the fluidity of mitosis in a cell where 2N = 8 chromosomes, 4 pairs = 4 paternal + 4 maternal.

Below is an illustration and a corresponding micrograph for each stage in mitosis, showing a hypothetical plant cell where 2n=4 (two sets of chromosomes, two chromosomes per set).



Stages of mitosis. © VectorMine | Dreamstime.com. Used with permission.

The micrographs below are onion (*Allium cepa*) root tip cells. Onion has 2n=16 chromosomes. Each of the cells has two sets of chromosomes where each set is made up of eight chromosomes. The micrographs are real examples of the illustrations above.



Stages of mitosis in onion root tip. Melissa Ha. CC BY-NC-SA 2.0

Interphase



The lefthand frame of the illustration shows interphase cells. The deep red stained structures in the center of the onion cell micrograph are the chromosomes. They are corralled together within the nuclear membrane. Recall that during interphase the chromosomes are relaxed rather than highly condensed (that is, not extensively coiled or folded), and during the S phase of interphase each chromosome replicates. It makes sense that the chromosomes are relaxed because they can't go through the replication process if they are tightly coiled, and because chromosomes only need to be coiled so that they can withstand movement and not break. They aren't moving, just replicating, so being in a relaxed state is perfect. The two identical copies are called sister chromatids and they are held together at a site called the centromere. Note that sister chromatids are not the same as homologs. Homologs are corresponding chromosomes, one contributed through the sperm, the other through the egg. Sister chromatids are chromosomes that have replicated, are identical to each other, and are held together at centromeres. You can't distinguish individual chromosomes in the picture because they are relaxed rather than tightly coiled and folded, making them so fine that they are difficult to see.

Prophase



Prophase is the first stage of the M phase. In prophase the chromatin begins to coil and condense to form chromosomes. They are coiling because they are preparing to move around. You can begin to notice that each chromosome appears to have two strands (sister chromatids) and that these sister chromatids are attached to each other at a centromere. In prophase the nuclear membrane disappears and the chromosomes spread out to fill up much of the cell. During this phase, the spindle apparatus begins to appear. The spindles are microtubules associated with movement of the chromosomes during division.

Metaphase



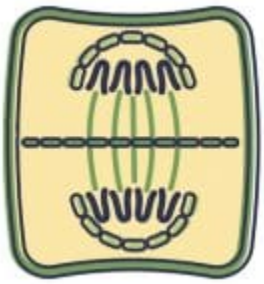
In metastage the spindle grows and forms attachments to the pairs of sister chromatids at the centromere that connects the sister chromatids. This point of attachment is called the kinetochore. The sister chromatids move to an imaginary equatorial plate (called the metaphase plate), which is formed along the midline of the cell between the poles. The sister chromatids are in their most condensed state at metaphase.

Anaphase



The sister chromatids begin to separate at anaphase. When the sister chromatids separate, the centromeres divide so that one sister chromatid migrates to one pole, and the other migrates to the opposite pole. The chromatids that formed back in the S phase of interphase, when the chromosome replicated, now separate, and the spindle fibers shorten. With the sister chromatids separated, we can return to calling them chromosomes. Anaphase is the stage where the chromosomes carrying the DNA code are divided precisely so that each of the resulting cells has exactly the same chromosomes that were in the mother cell prior to division. One complete diploid complement of chromosomes (two sets) is delivered to each daughter cell.

Telophase



In telophase, the nuclear membrane forms around the chromosomes in each of the daughter cells, a cell plate forms between these cells, and cell walls separate the newly formed cells in a process called cytokinesis. The chromosomes decondense and again become relaxed chromatin. Telophase is the last stage of the M phase. After telophase and cytokinesis, the cells return to G1 of interphase.

Review questions

1. When do the sister chromatids separate from each other?
2. Do the chromosomes replicate during mitosis or during interphase?
3. Why are the chromosomes in their most condensed state during metaphase and retain this condensed state through chromatid migration in anaphase?

Review

Recall that the outcome of mitosis is two cells with DNA identical to that in the original cell. There are three keys to understanding how two cells are formed from one, both with the same DNA as the original cell:

1. The DNA is completely replicated during the S stage of interphase. This replication results in twice as many sister chromatids as there were chromosomes, and once these sister chromatids separate and are evenly allocated to the two new sister cells, both sister cells have the diploid number of chromosomes, just like the original cell prior to division.
2. As the cell prepares to divide, the DNA condenses. This packaging helps keep the very thin DNA helices from being broken, and keeps the DNA organized into a tight package so that the cell can keep track of it and move it around.
3. The process is very organized. For instance, the sister chromatids all line up in the middle of the cell at metaphase, split at the centromere, and half the chromatids go to one side of the cell, half to the other. This orderly separation of the sister chromatids ensures that the right number of chromosomes is packaged into each of the new sister cells.

There are many sites online that illustrate mitosis, but particularly relevant here are ones that show micrographs of plant cells. You may discover that there are some details about the spindles and their apparent site of origin that differ between descriptions of mitosis in animal and plant cells; not everything online pertains to plants. Any mention of a structure called a “centriole” refers to animal cell mitosis, not plants (as plants don’t have centrioles).

John H. Wahlert and Mary Jean Holland, of Baruch College, authored this site showing stages of mitosis in onion. (You can ignore the stages of whitefish mitosis in the second half of the site unless you are interested in the differences between plant and animal mitosis.)

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6.1.3: Meiosis

Learning objectives

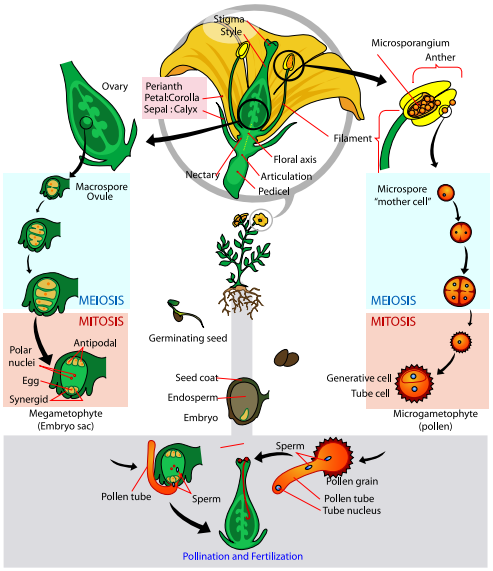
By the end of this lesson you will:

- Understand how meiosis starts with one diploid cell and results in four haploid cells.
- Know how meiosis produces gametes that are genetically diverse.
- Be able to model the stages of meiosis.
- Be able tompare the similarities and differences in the mechanics of mitosis and meiosis.

Review of sexual and asexual propagation

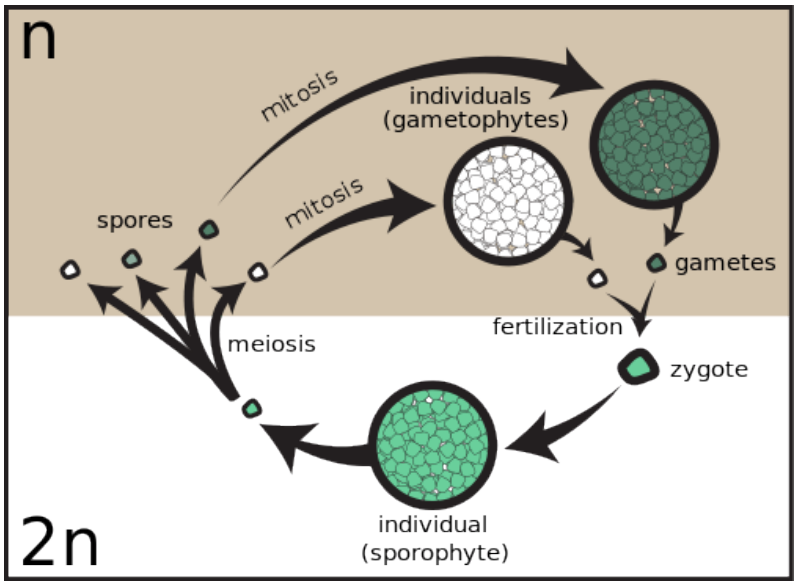
As seen earlier, there are two broad categories of plant propagation: sexual and asexual. When new plants are produced from existing plant parts, like pieces of leaf, stem, or root, reproduction is asexual and the only type of cell division that has taken place is mitosis, where one diploid cell produces two identical diploid cells.

If new plants are instead produced from seeds, this is a strong indication (but not a certainty...optionally read about apomixis) that reproduction was sexual. Plants that practice sexual reproduction use mitotic cell division when increasing the diploid vegetative parts of the plant like stem, leaf, and root, but use meiotic cell division to initiate the haploid stage of the plant that ultimately results in production of egg and sperm cells central to sexual reproduction. Instead of two diploid cells from one diploid cell (the outcome of mitosis), the outcome of meiosis is four haploid cells from one diploid cell.



Sexual reproduction of an angiosperm. LadyofHats, Public domain, via Wikimedia Commons.

Plant growth is divided into two generations that are diploid (2n) and haploid (1n). Higher plants (angiosperms) have a long-lived sporophytic generation that is the diploid sporophyte. The sporophyte is the growth you would easily recognize as a plant. Through the process of meiosis, the sporophyte produces haploid spores in the flower. The spores are the gametophytic generation. Meiosis occurs in the male flower parts to produce pollen (represented by the green circle) and the female floral organs produce egg cells (represented by the white circle). Spores grow by mitosis producing more haploid cells, this is the gametophytic generation. We get a brief glimpse of the gametophytic generation when pollen is released from the flower, the female gametes are hidden from direct view in the ovary. When the haploid gametes (male pollen and female egg cells) unite they reform the sporophytic generation producing a diploid (2n) zygote. The zygote grows into the embryo of the seed and eventually into the plant we see. Lower plants, mosses and ferns that are not flowering plants, also alternate generations, but the gametophytic generation is longer lived and separate from the sporophytic generation.



Mitosis/meiosis cycle. Menchi. CC BY-SA 3.0

The plant doesn't magically transition to being haploid, but instead particular parts of the flower in the androecium and gynoecium develop and protect a limited number of haploid cells, called the **male gametophyte** and **female gametophyte**. A later chapter addresses how the male and female gametophyte include the haploid egg and sperm cells that must unite to form the diploid embryo in seeds. For now, know that meiosis is the gateway into the haploid phase. Meiosis is the type of cell division that starts with diploid cells and results in haploid cells. Without meiosis there is no egg and sperm, and thus no sexual reproduction.

Propagation and natural selection

From the natural selection perspective, how do asexual and sexual reproduction differ?

In asexual reproduction, the plants are genetic copies of the parent plant. Cell division is strictly mitosis. Except for rare mutations, the resulting progeny are identical to the parents. The fitness of the progeny will mirror the fitness of the parent. The downside of this type of propagation is that there is no genetic variance among progeny that might result in selection for plants that have greater fitness than the parent for characteristics such as increased cold hardiness, drought tolerance, or disease resistance. The upside is that if the parent has high fitness to begin with (and it must have had reasonable fitness to reach reproductive age), all progeny will also have that high level of fitness. If the environment remains the same as it was for the parent, the progeny will stand a good chance of reproductive success. But if the environment changes, the fitness of the progeny may no longer be optimum.

In sexual reproduction, since one gamete comes from the male parent and one from the female, and because in a population of cross-pollinating wild plants there are many potential parents, each with different genotypes, there are many potential genetic combinations of male and female gametes. Not only are the plants producing the gametes each genetically different, but each gamete from each plant is potentially unique. The many combinations of male and female gametes, and the uniqueness of gametes from the same plant, result in a substantial genetic variation among the progeny of plants that sexually reproduce. Some of these progeny will have greater fitness than others, and will be favored by natural selection — some will survive to reproductive age and have more progeny than other plants, while the rest will either not survive to reproduce or, if they do reproduce, it will be with low frequency. The DNA of the fittest plants will thus be represented more frequently in the next generation of plants than the DNA of the least fit plants, which may never survive to reproduce and pass on their DNA. This is the process of natural selection. The DNA of reproductively successful parents is passed on the next generation, while the DNA of reproductively unsuccessful parents is not.

Sex generates genetic variation. Genetic variation, generated by meiosis and sexual reproduction, is the fuel for the engine of natural selection.

Ploidy review

To review: if you count the number of chromosomes in a somatic cell, for instance a root tip cell, you will find that there is always an even number. These are diploid 2*n* cells that arose from mitotic cell divisions tracking all the way back to the zygote that formed the embryo of the seed. Listed below are the numbers of chromosomes found in somatic, diploid, 2*n* cells of a few commonly grown plants. Note that the number of chromosomes is even, never odd, and that it doesn't imply anything about the size or type of plant:

- Corn = 20
- Rice = 24
- Soybean = 40
- Green bean = 22
- Tomato = 24
- Potato = 48
- Apple = 34
- Rose = 14

Diploid cells always contain an even number of chromosomes because there are two copies of each chromosome, one contributed by the male sperm and one by the female egg. If you number each type of corn chromosome 1 through 10, there would be two 1s (a maternal and a paternal), two 2s, etc. Recall that the two (donated from the male and female) versions of the same chromosome in a diploid cell are called homologous chromosomes or homologs. In a diploid cell like corn where 2*n*=20, there are 10 pairs of homologous chromosomes.

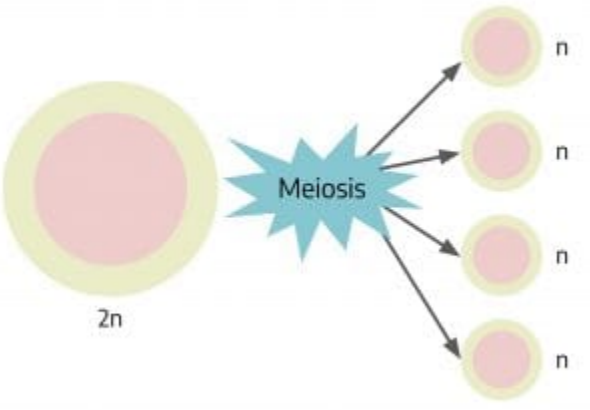
Also recall that the number of chromosomes in a gamete is half the number of chromosomes found in a somatic cell of the same plant. The gamete cells are haploid, abbreviated *n*. There may be an even or odd number of haploid chromosomes, depending on the diploid chromosome number. Beans have a diploid number of 22, so the gametes have an odd number of chromosomes (11). Tomato has a diploid number of 24, so the gametes have an even number of chromosomes (12).

When two gametes fuse and form a zygote, the zygote has the 2*n* chromosome number restored. From then on, the cell divisions that allow a plant to grow from zygote to full size are all mitosis, and all the cells are copies of the zygote formed by fusion of the two gametes.

Review questions

1. In what sense is meiosis the gateway into the haploid or gametophytic stage of alternation of generations?
2. Why does a diploid plant cell always have an even number of chromosomes?
3. A diploid rose cell has 14 chromosomes. How many pairs of homologous chromosomes will you find in that diploid cell?

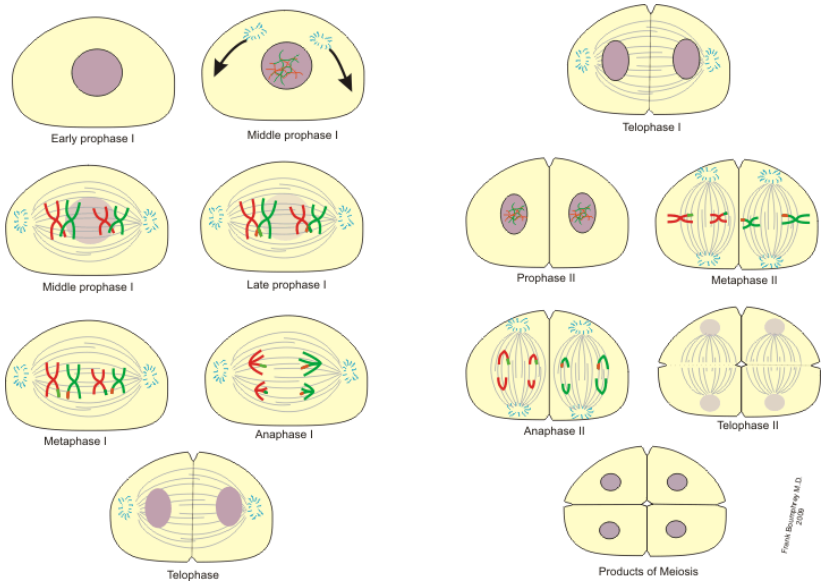
Meiosis mechanics



Meiosis. Emily Tepe

Meiosis starts with a diploid cell and results in haploid (n) cells that we could correctly call spores. In the illustration above, note that starting with one diploid cell and meiosis yields four haploid cells.

Below are the stages of meiosis. It won't be difficult to memorize them because you already know the stages of mitosis, and meiosis builds on mitosis. The illustration shows a hypothetical species with two pairs of chromosomes (2*n*=4) in the starting cell and *n*=2 in the resulting gamete cells. Meiosis has **two** chromosome divisions, so the stages are labeled I for those stages associated with the first division (e.g., Metaphase I) and II for those associated with the second division (e.g., Metaphase II).



Stages of meiosis. Boumphreyfr. CC BY-SA 3.0

As in mitosis, the cell division process starts when the chromosomes replicate in the S phase of interphase.

Prophase I — the nuclear membrane disintegrates, and we see that the chromosomes have already replicated (in "S" of interphase) so that the now condensed chromosomes are made up of two sister chromatids attached at the centromere. New, however, is that in this stage the homologous chromosomes pair up and form structures called tetrads because they are groupings of four sister chromatids (two sister chromatids per homolog). This process of pairing and tetrad formation promotes chiasma (seen under the microscope as the point where sister chromatids of homologs lay over each other, forming an "X" shape) and crossing over between sister chromatids of homologous chromosomes. Crossing over results in an exchange of DNA between homologs and is another contributor to genetic variation in the gametes and resulting organisms.

Reread the preceding paragraph, making sure you understand how homologs pair, form chiasma, and cross over between sister chromatids. This type of pairing of homologs and subsequent chiasma formation doesn't happen in mitosis — a very important and essential difference between the two types of cell division.

Metaphase I — the tetrads are lining up on the metaphase plate, ready to divide. Recall that they are called tetrads because they are made up of four sister chromatids.

Anaphase I — the tetrads divide and homologs go to opposite poles. Note that sister chromatids stay intact and the centromeres do not divide yet. It is the homologous chromosomes that separate at Anaphase I. The sister chromatids may differ in some places along their arms due to crossing over that causes exchange of DNA between homologs.

Telophase I — the nuclear membrane reappears to separate the products of the first division.

The DNA relaxes in Interphase I, but no replication occurs. DNA condenses again in Prophase II, and we can see the chromosomes.

Metaphase II — the chromosomes (which are in the form of sister chromatids still connected at the centromere) line up at the metaphase plate, as in metaphase of mitosis.

Anaphase II — also like anaphase in mitosis, the centromeres split and sister chromatids are pulled to opposite poles.

Telophase II — nuclear membrane reforms, cytokinesis takes place, just like the telophase of mitosis. Note that the "II" stages of meiosis are just like the corresponding stages of mitosis, making them easy to remember.

Review questions

1. Do the chromosomes replicate prior to meiosis?
2. What happens during crossing over?
3. The illustration above shows that some of the sister chromatids are combinations of red and blue rather than being all red or all blue. What does that represent?
4. What separates in Anaphase I?
5. What separates in Anaphase II?

Division

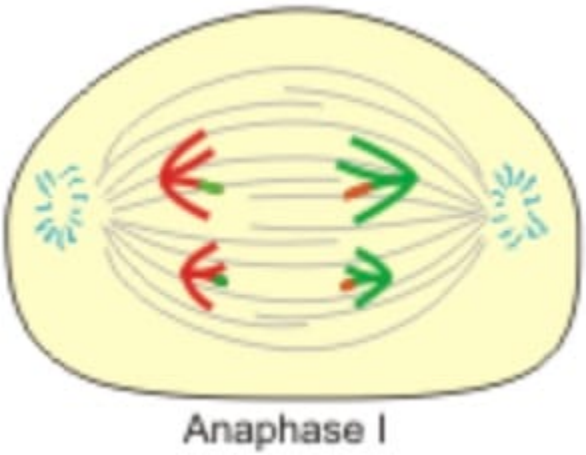
Watch this video for a detailed explanation of division (8:19)

Memorizing this process helps you focus on clearly understanding the mechanics of the process, and recognize how it is that meiosis results in four *n* haploid cells instead of the two 2*n* cells that result from mitosis. You get four *n* haploid cells because the initial cell undergoes two divisions. The cell first divides into two nuclei, then those two divide again into four. The chromosome number drops from 2*n* in the original cell to n in each of the four haploid cells because the number of sets of chromosomes is reduced from 2 to 1 (that is, homologs separated to opposite poles) in the first meiotic division, and then the sister chromatids separated in the mitosis-like second meiotic division. There was chromosome replication before the first division, but no replication before the second division.

Here's a summary of what is dividing and when:

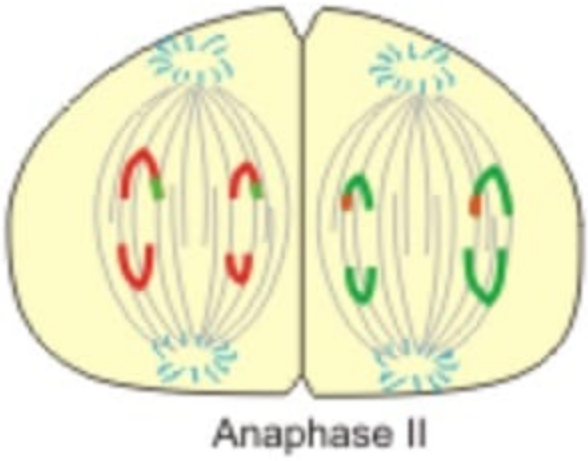
Two divisions:

Homologs separate in Anaphase I. Centromeres holding the chromatids do not split.



Anaphase I. Boumphreyfr. CC BY-SA 3.0

Chromatids separate in Anaphase II. Centromeres holding the chromatids do split.



Anaphase II. Boumphreyfr. CC BY-SA 3.0

Genetic variation among gametes

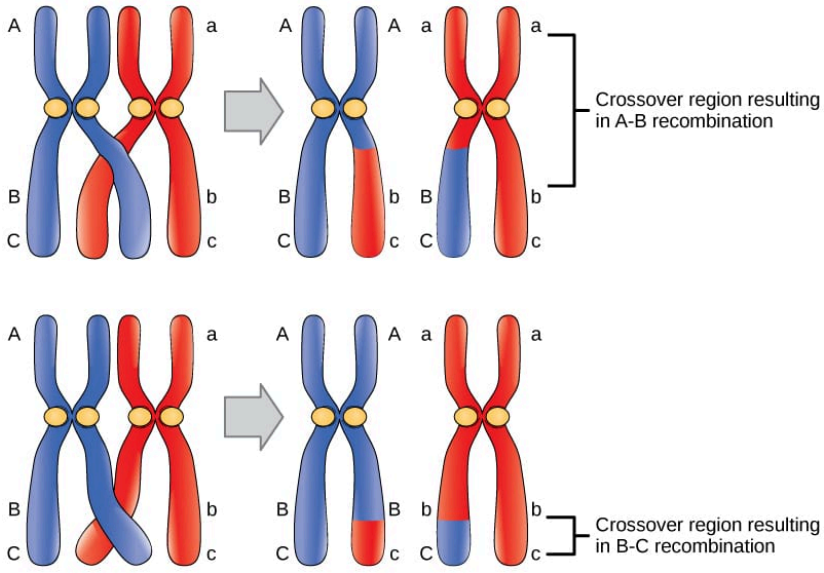
Watch this video to see how meiosis contributes to genetic variation. (9:26)

Each gamete ends up with one of the homologs of the pair, not both.

- Imagine that there are two or three or even 30 pairs of homologous chromosomes. Each homolog pair making up the tetrad in Metaphase I separates in Anaphase I. One homolog from the pair heads to one pole and the other heads to the opposite pole. Each pair of homologs moves independently of all the other homolog pairs that are also separating. That is, all the paternal-source chromosomes making up the homologous pairs don't go to one pole and all the maternal-source go to the other pole (this is possible, but since it would be by chance the probability is very low). Instead, paternal-source homologs of some chromosomes and maternal-source homologs of the other chromosomes are pulled to the poles, so that eventually there is a mix of maternal- and paternal-source chromosomes in the gametes, and that mix of maternal and paternal is generally thought to be random.
- This principle, where homologs move to poles independently, is called **independent assortment**, and leads to differences in the genotype of the gametes — one source of genetic variation among gametes.

Crossing over and exchange of DNA between homologous sister chromatids in Prophase I is another source of variation in gametes. If two cells in the sporangia are undergoing meiosis, the crossing over in each cell will probably happen in different places on the chromosome in each cell, resulting in exchanges taking place at different locations on the DNA backbone so that the gametes resulting from different cells going through meiosis will all be unique.

What is crossing over?



Crossing over. OpenStax. CC BY 4.0

The illustration above shows a tetrad where the red and blue homologous chromosomes of the same chromosome type are pairing. Each homolog here consists of two sister chromatids joined at the centromere. Note that the chromosomes have already replicated in interphase prior to the start of Prophase I.

In Prophase I, homologous chromosome pairs come together (synapsis).

Arms of sister chromatids from different homologs overlap (chiasma) and exchange DNA (crossing over).

Note that all four of the resulting sister chromatids are now genetically different, with each potentially having a different DNA sequence.

Summary

- Meiosis is a type of cell division that starts with a diploid, 2*n* cell.
- The process includes two chromosome divisions and produces four haploid, *n* cells.
- The haploid cells are genetically different from each other due to crossing over in Prophase I and independent assortment in Anaphase I.
- Homologs separate in Anaphase I while sister chromatids separate (the centromeres divide) in Anaphase II.

Review questions

1. Why does independent assortment during meiosis contribute to genetic variability of gametes?
2. Why does crossing over contribute to genetic variability of gametes?

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6.1.4: Terms

These are the important terms from this chapter to be sure to know. You might also find these in later chapters.

Alternation of generations	Cycle of diploid, asexual, vegetative generation alternating with the haploid, sexual generation.
Anaphase	Third phase of mitosis; the sister chromatids separate (now chromosomes) and the centromeres divide, pulling the chromosomes to opposite poles.
Antipodal cells	Three cells sequestered at the opposite end of the mature female gametophyte from the egg and synergid cells.
Cell cycle	Cycle which cells go through in their lifetime; consists of interphase and mitosis.
Centromere	Constricted spot where sister chromatids attach.
Chiasma	Point where sister chromatids of homologs lay over each other, forming an “X” shape.
Chromosome	Structure within the nucleus of a cell that contains the genes; made up of DNA that has looped around histone proteins and then coils and folds.
Crossing over	Exchange of arms of DNA between sister chromatids of homologous chromosomes that can take place at the point of chiasma formation.
Cytokinesis	Occurs directly after telophase; the cell plate forms between the two daughter cells and the cell walls separate the newly formed cells.
Diploid	Term used for zygote cells, where the cell has two sets of chromosomes; abbreviated 2n.
DNA	Basic biochemical compound that makes up the gene.
G1 stage of interphase	First stage of interphase; “G” stands for Gap/Growth.
G2 stage of interphase	Third and final stage of interphase; “G” stands for Gap/Growth.
Genetic code	Order of the four different combinations of the bases in DNA; AT, TA, GC, or CG.
Haploid	Term used for gamete cells that typically contain one set of each of the chromosomes; abbreviated n.
Histone protein	Protein around which the DNA surrounds.
Homologous chromosomes (homologs)	Matching chromosomes from the two different sets; carry the genetic information that affects the same characteristic or function at the same location on the chromosome; from sperm and egg cells.
Interphase	One of the two major parts of the cell cycle; consists of G1, S, and G2 stages.
Kinetochore	Point of attachment of the spindle and the centromere.
Metaphase	Second stage of mitosis; the spindle fibers grow and form attachments to the pairs of sister chromatids at the centromeres.
Metaphase plate	Equatorial plate formed along the midline of the cell between the poles.
Nucleosome	Made up of eight histone proteins and wrapped by a segment of DNA.
Ploidy	Number of sets of homologous chromosomes in a cell.
Polar nuclei	Two haploid nuclei contained within one cell membrane in the mature female gametophyte. One sperm cell will unite with these two polar nuclei to establish the triploid endosperm tissue.
Prophase	First stage of mitosis; chromatin begins to coil and condense to form chromosomes.
Purine	Consists of the base pairs Adenine and Guanine and contains two rings of carbon atoms.

Pyrimidine	Consists of the base pairs Cytosine and Thymine and contains one ring of carbon atoms.
Ribose-phosphate backbone	Chain of alternating ribose and phosphate that make up the sides of the DNA structure.
S stage of interphase	Second stage of interphase where the chromosomes replicate (DNA replicated).
Sister chromatids	Two chromosomes that are exact copies and are created during the S stage of interphase.
Somatic cells	Cells of flowering plants, other than the reproductive cells; always 2n.
Spindle apparatus	Microtubules associated with movement of the chromosomes during division.
Sporangia	Structures in the androecium and gynoecium where meiosis takes place and the gametophyte generation develops.
Spore	Haploid single cell produced by meiosis in the sporangium of a diploid sporophyte.
Telophase	Fourth and final stage of mitosis; the nuclear membrane forms around the chromosomes in each of the daughter cells.
Tetrads	Groupings of four sister chromatids.
Triploid	Term used for endosperm that has three sets of chromosomes; abbreviated 3n.

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6.1.5: Atlas- Life Cycle

Watch Video 6.1.5.1 to help untangle this complex life cycle.

YouTube Video

This interactive element is not available in this format. Visit the link or scan the QR code to access it online.

View this YouTube Video online

Video 6.1.5.1: A digital, narrated rendition of the angiosperm life cycle. https://youtu.be/0UEpq1W9C_E

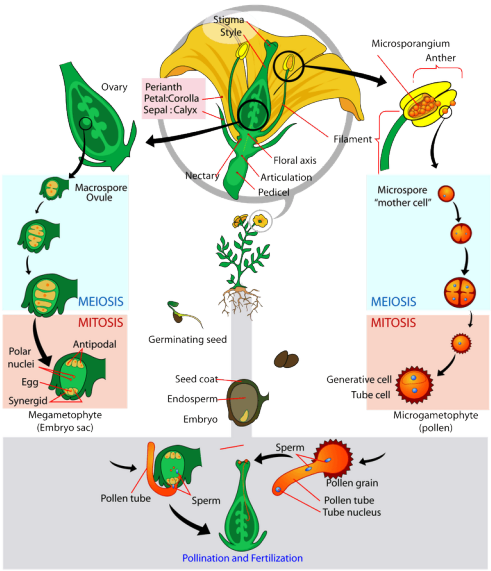


Figure 6.1.5.1: A diagram of the angiosperm life cycle. The formation of the ovule takes place on the left hand side, moving from top to bottom. The formation of the pollen grain takes place on the right hand side, again moving from top to bottom. At the center bottom of the image, pollination and double fertilization occurs, where the sperm cells fuse with the egg (forming a zygote) and polar nuclei (forming the triploid endosperm). The seed develops through the center of the image, transitioning into a mature sporophyte (the flowering plant). Diagram by LadyofHats, Public domain, via Wikimedia Commons.

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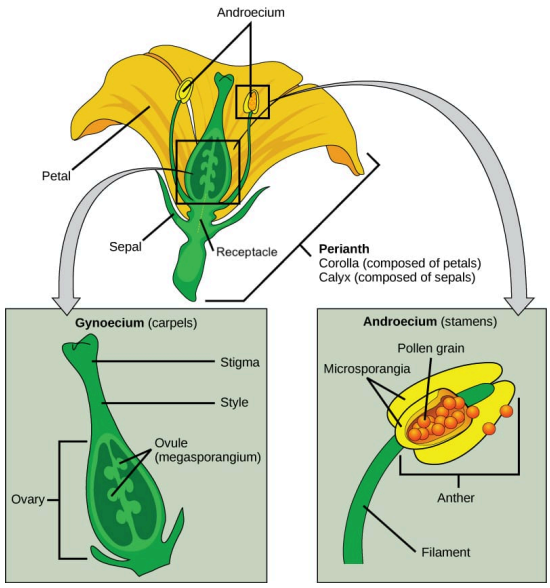
- 8.6: Life Cycle by Maria Morrow is licensed CC BY-NC 4.0.

6.2: Gametogenesis

Learning objectives

- Identify where sporangia are found in the angiosperm flower.
- Describe how the male gametophyte is formed.
- Describe how the female gametophyte is formed.
- List which cells unite during double fertilization.
- Explain how the embryo goes through developmental stages that are identified according to the developing embryo's shape.

Recall, as shown below, that the flower is made up of a compressed, four-node stem called the **receptacle** that supports four whorls of modified leaves: calyx (sepals), corolla (petals), androecium (stamens), and gynoecium (carpels). The two whorls nearest the tip of the receptacle, the androecium and gynoecium, contain structures housing the (micro- and mega-) sporangia, where meiosis takes place and the gametophyte generations develop.



Parts of a flower. OpenStax Biology. CC BY 4.0

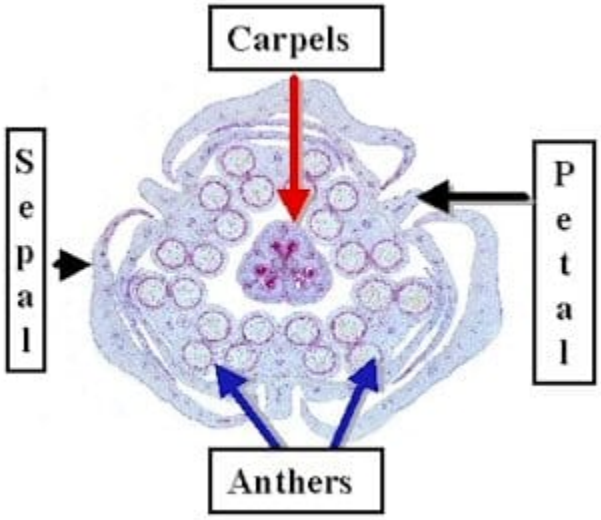
Watch this video for a chalkboard demonstration of gametogenesis (4:49)

Sporangia

The sporangia of angiosperm plants are found in two places within the flower depending, on whether they lead to a female or male gametophyte. The sporangium in the anther (where the male gametophyte will be formed) is called the microsporangium. The sporangium in the ovary (where the female gametophyte will be formed) is called the **megasporangium**. Diploid microspore mother cells in the microsporangium and diploid megaspore mother cells in the megasporangium divide by meiosis to form four haploid micro- or mega- spores. These spores initiate the gametophyte phase. Two (male) to three (female) mitotic divisions later, the mature micro- and mega- gametophytes have been formed. Note how few divisions take place to form the gametophyte after the meiotic division of the microspore or megaspore mother cell, and that those two or three additional divisions are mitotic divisions. One round of meiosis is sufficient to generate haploid cells. From there on the divisions are mitotic, but in this case mitosis starts with one haploid cell and generates two haploid cells.



Helleborus foetidus cross-section. Simon Garbutt. Public domain



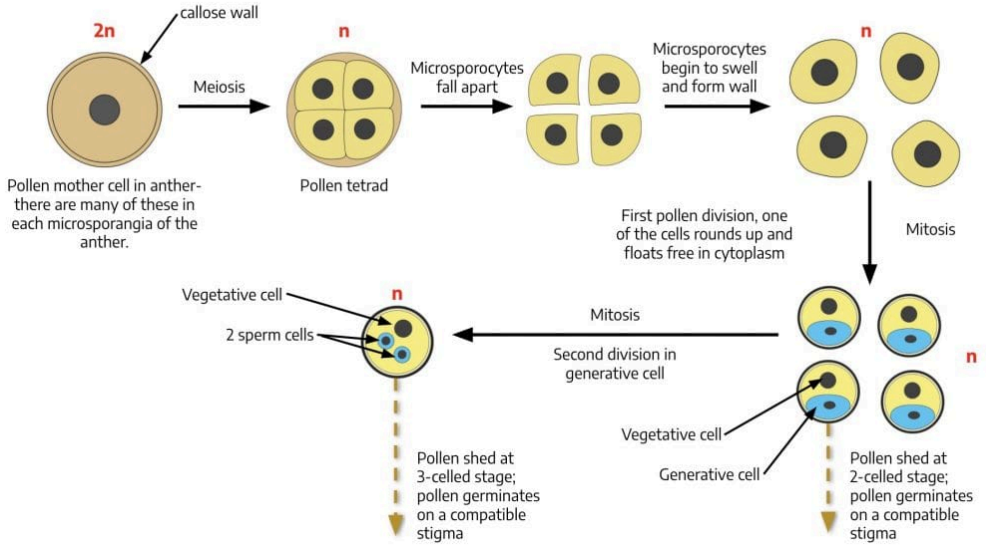
Lilium flower bud cross section. Photomicrograph by Michael W. Clayton, used with permission. © Board of Regents of the University of Wisconsin System.

The images above provide a visual orientation to the micro- and megasporangia. In the photo, the bud in the horizontal cross section shows the three chambers in the fused carpels as well as a number of anther cross sections. In the center of the vertical cross section of the flower bud you'll see a carpel with ovary, locule (interior chamber), and ovule within the locule. Also note the anther cross sections containing pollen.

Microsporogenesis

Watch this video for a chalkboard demonstration of microsporogenesis (5:35)

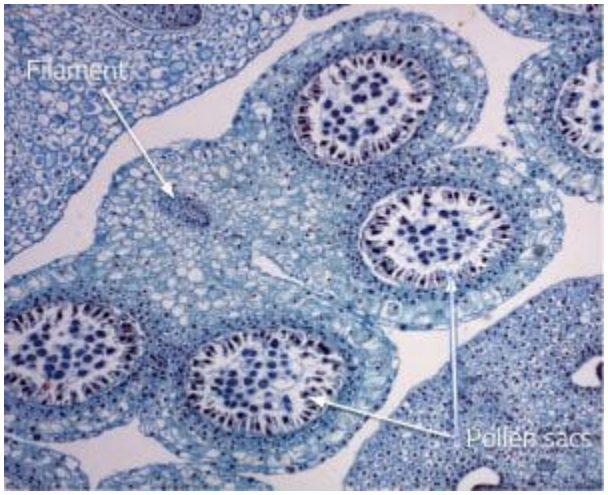
The illustration below shows the development of the male gametophyte within the anther. The process, called **microsporogenesis**, or **male gametogenesis**, starts in the top left hand corner. Study these steps and be able to draw them. Red "2*n*" or "*n*" notations indicate the ploidy of the nuclei and blue notations show where the mitotic cell divisions occur. To this point we've learned that mitosis starts with one diploid cell and results in two diploid cells. We'll modify that now to say that mitosis starts with a cell and results in two cells that are exact copies of the original cell. If the starting cell is diploid, there will be two diploid copies. If the starting cell is haploid, there will be two haploid copies.



Pollen development and growth. Pollen can be shed at either the two-celled or three-celled stage; it varies from species to species. Image labeled and adapted by Emily Tepe. © Shutterstock. Used with permission.

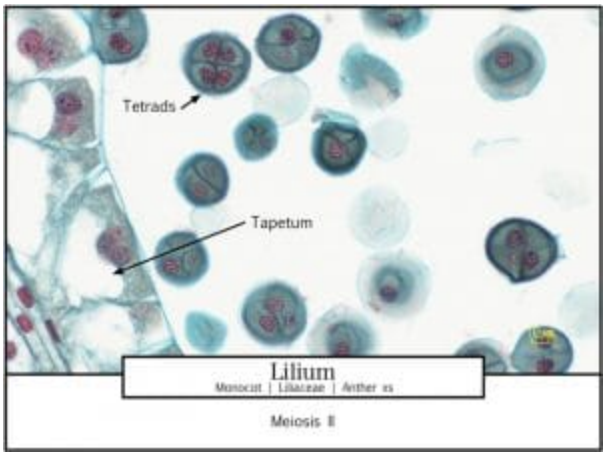
The result of microsporogenesis, shown on the bottom row of the illustration above, is either a male gametophyte that is a two-celled pollen grain (with vegetative and generative cells), where the generative cell will later undergo another mitotic division to produce two sperm cells (shown to the right of the box), or, following mitosis of the generative cell and shown to the left of the box, a three-celled pollen grain with a vegetative (or tube) cell plus two sperm cells.

Below is a cross section of young anther showing the developing pollen grains in four chambers.



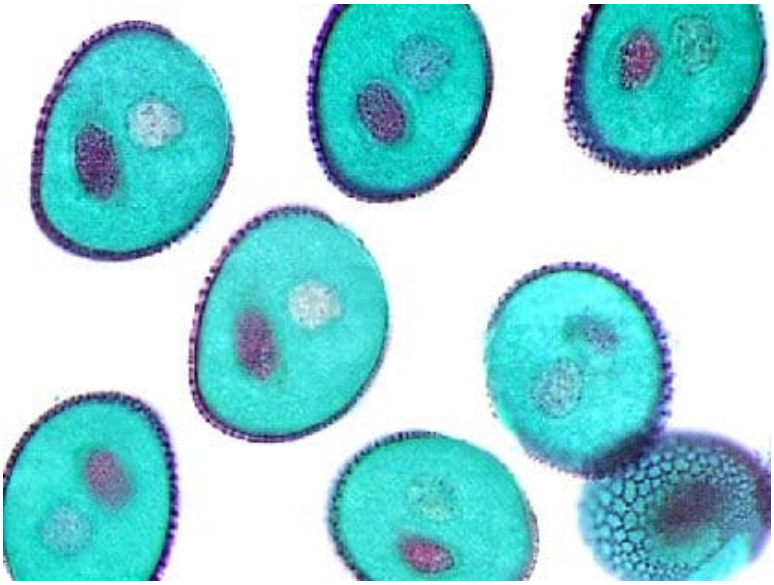
Lilium anther cross-section. Marc Perkins. CC BY-NC 2.0

Below are tetrads of cells following meiosis of the microspore mother cell. Note the sets of four cells still attached together.



Lilium tetrads. Jen Dixon. CC BY-NC-SA 2.0

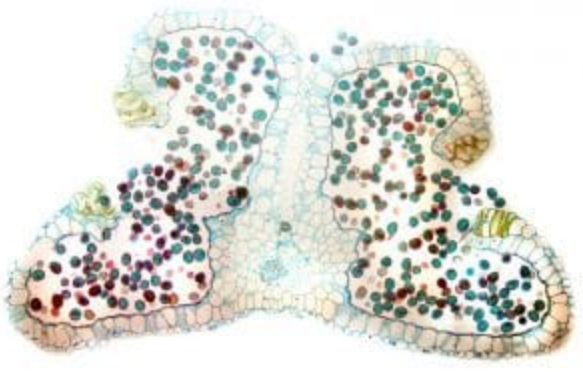
Below are nearly mature, two-celled pollen grains with the start of an exine coat. The exine coat is made up of protein and other compounds deposited by the inside wall of the anther, and it forms a protective coat around the three-celled microgametophyte.



2-celled pollen grain of lily. Photomicrograph by Michael W. Clayton, used with permission. © Board of Regents of the University of Wisconsin System.

In this micrograph the exine coat looks like rough, geometrically shaped plates on the surface of the pollen. The exine coat patterns are characteristic of the species and can be used to identify the species of plant that produced the pollen. For more forensic botany, see this optional link from the Botanical Society of America.

Below is a mature, dehiscing (split and releasing pollen) anther.



Lilium – cross section of dehiscing anther with two-nucleated pollen grains. Photomicrograph by Michael W. Clayton, used with permission. © Board of Regents of the University of Wisconsin System.

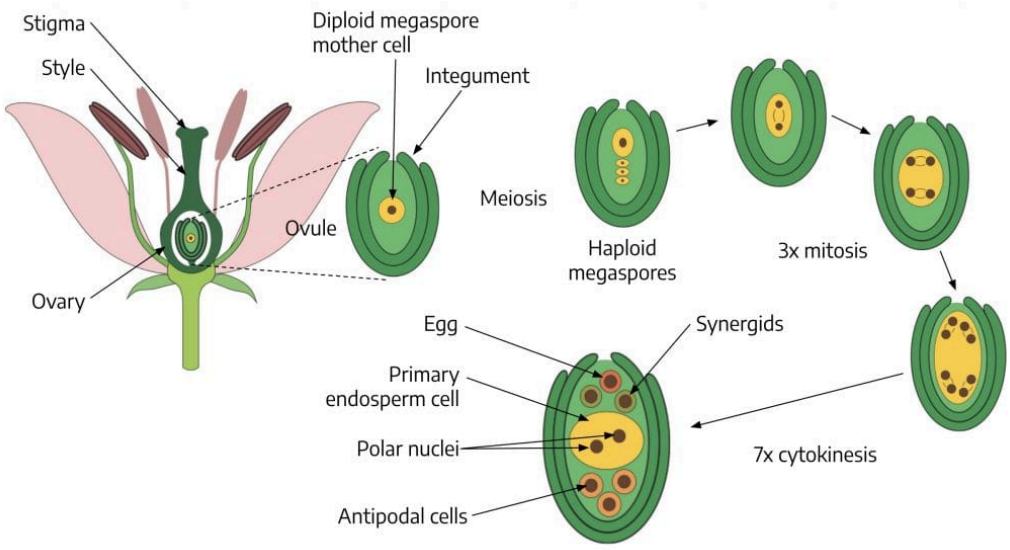
Review questions

- Where are the microsporangia located?
- Where is the mature male gametophyte in the Pollen Development and Growth illustration above?
- Starting with the microspore mother cell, how many meiotic and mitotic cell divisions are required to produce the mature male gametophyte?

Megasporogenesis

Watch this video for a chalkboard demonstration of megagametogenesis (4:28)

The illustration below shows the development of the female gametophyte, a process is called **megasporogenesis** or **female gametogenesis**. Study this diagram and be able to draw it.



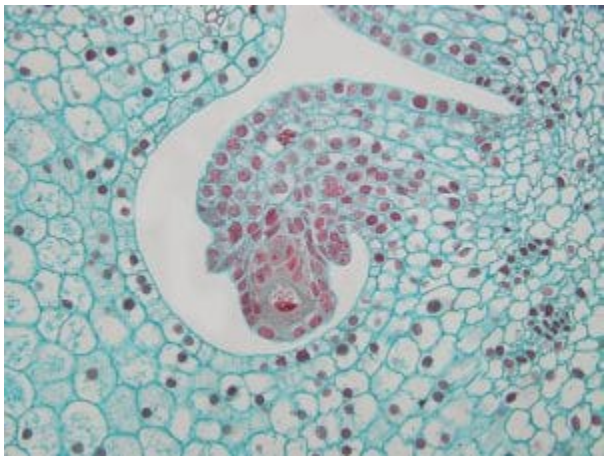
Development of the female gametophyte. Image labeled and adapted by Emily Tepe. Original image by Kazakova Maryia via Shutterstock. Used and adapted with permission.

The chambers within the ovary are the locules, and within the locules are the ovules. The ovule wall is made up of integument tissue, and it is from this integument tissue that diploid megaspore mother cells form. A diploid megaspore mother cell undergoes meiosis and initially produces four haploid megaspores. Three of the four spores formed through meiotic division of the megaspore mother cell disintegrate, as indicated by the “X” through three of the spores in the illustration. The lone surviving

megaspore subsequently undergoes three mitotic divisions to form eight haploid cells that are held within the ovule in an embryo sac. These eight cells comprise the female gametophyte.

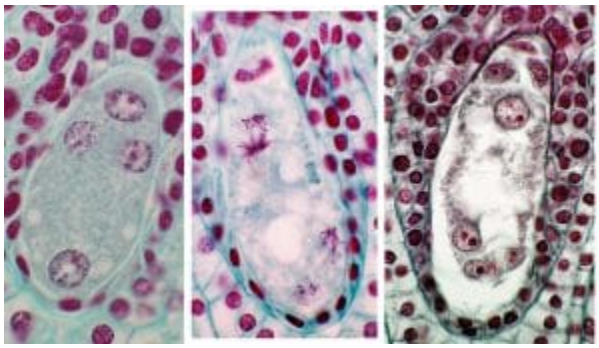
Only six of the nuclei are surrounded by their own cell membrane after the three rounds of mitosis. The two remaining nuclei are surrounded by one cell membrane. These two nuclei in one membrane become the polar nuclei and contribute two of the three nuclei to the endosperm tissue, with the other nucleus contributed by a sperm cell.

The megaspore mother cell is the swollen cell shown in the micrograph below. Note the linear tetrad of haploid megaspores resulting from meiosis of the megaspore mother cell. Three will disintegrate and one will undergo three rounds of mitosis.

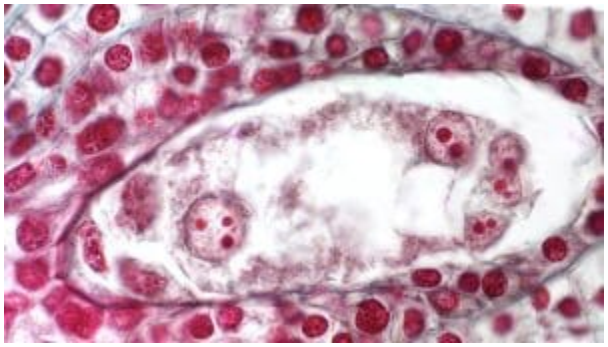


Lilium – ovule with megaspore mother cell. Photomicrograph by Micheal W. Clayton, used with permission. © Board of Regents of the University of Wisconsin System.

The four cells in the embryo sac in the left-hand image below are from two mitotic divisions of the one surviving megaspore. After one more mitotic division (center image below), the embryo sac, or female gametophyte, contains 7 cells (with 8 nuclei), and their arrangement is shown in the rightmost image below. The egg and two synergids are positioned on the bottom, two polar nuclei are shown in the center, and three antipodal cells are positioned at the top.



Composite of Lilium megagametophyte, 1. four-nucleated embryo sac, 2. final mitotic division, and 3. mature eight-nucleated, seven-celled embryo sac. Photomicrograph by Micheal W. Clayton, used with permission. © Board of Regents of the University of Wisconsin System.



Mature embryo sac of Lilium. Photomicrograph by Michael W. Clayton, used with permission. © Board of Regents of the University of Wisconsin System.

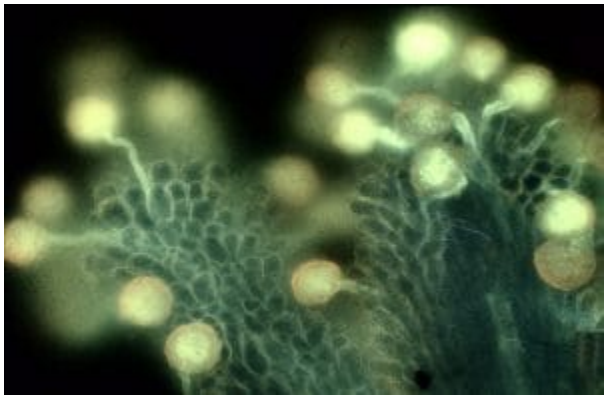
Review questions

1. Where are the megasporangia located?
2. Where is the mature female gametophyte in the Development of the Female Gametophyte illustration above?
3. Is the female gametophyte diploid or haploid? Is the integument tissue diploid or haploid?
4. Starting with the megaspore mother cell, how many meiotic and mitotic cell divisions are required to produce the mature female gametophyte?

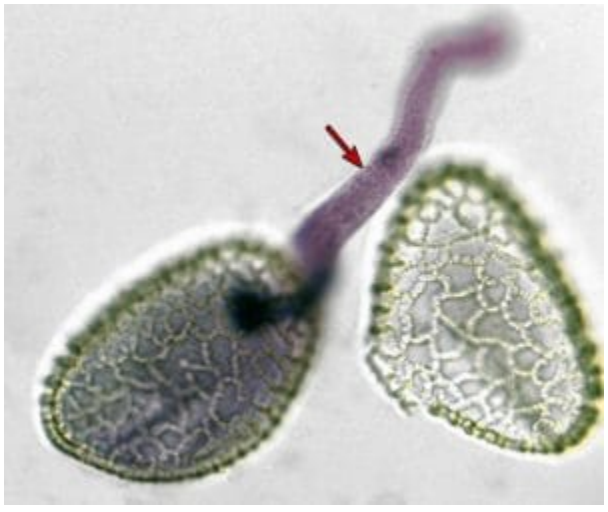
Fusion or fertilization

In the image below, pollen has fallen on the stigma and some grains are germinating. The next image shows the germination of pollen and tube growth in an artificial medium.

Think of the pollen tube as an extension of the cell membrane and cell wall of the pollen grain. The pollen tube isn't a long string of cells, but is one long skinny cell with two or three nuclei (one vegetative and either one generative or two sperm depending when the generative cell undergoes mitosis). The tube grows down the style through the intercellular (between cell) spaces rather than through cells. Pollen tube growth is an active area of study, with some work showing that the style cells are important for providing nutrients to the pollen tube and also apparently provide directional guidance to tube growth.



Stigmas and pollen tubes. George Shepherd. CC BY-NC-SA 2.0

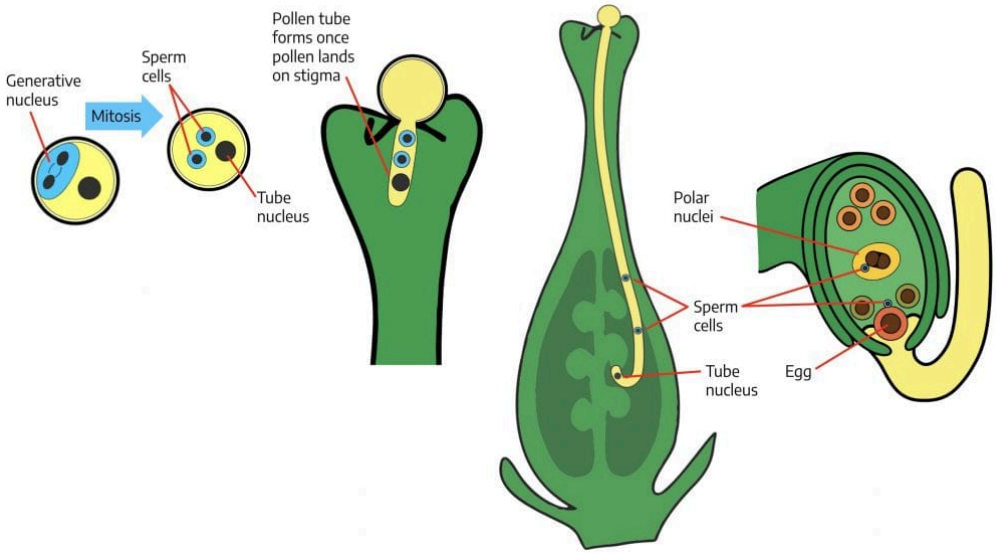


Pollen grain and pollen tube (indicated by red arrow). Bruce Kirchoff. CC BY 2.0

In the illustration below we see a generative nucleus in a pollen grain. This subsequently undergoes mitosis to form two sperm cells. As noted earlier, in some species this happens during pollen development before it is shed from the plant; in other species it occurs in the pollen tube. The image on the far left below identifies all of the cells in both the female and male gametophyte: in the female gametophyte are three antipodal cells at the top of the ovule, the polar nuclei in the middle, and at the bottom are

two synergid cells flanking the egg. There are eight cells or nuclei in total.

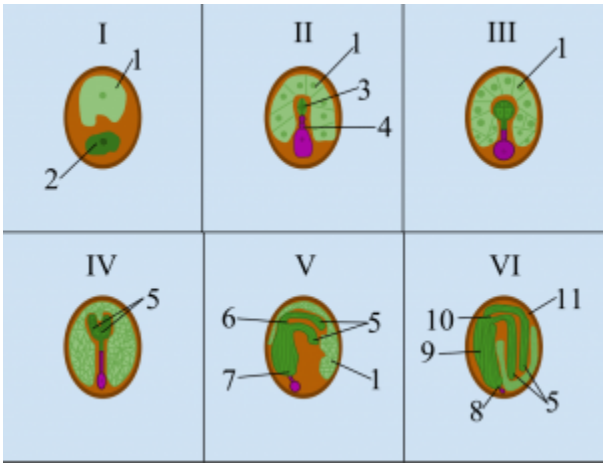
In the illustration, you can see the three cells within the pollen tube: two sperm and one tube or vegetative nucleus. The tube finds its way to the embryo sac through the **micropyle** and ruptures, and the sperm are delivered to the egg and polar nuclei. The rightmost section of the illustration is a closeup of the ovule and shows double fertilization. One sperm nucleus has fused with the egg nucleus to form a 2*n* zygote. The other sperm nucleus has fused with the two polar nuclei to form the 3*n* endosperm.



Pollen tube growth and double fertilization. Image labeled and adapted by Emily Tepe. Original image by Kazakova Maryia via Shutterstock. Used and adapted with permission.

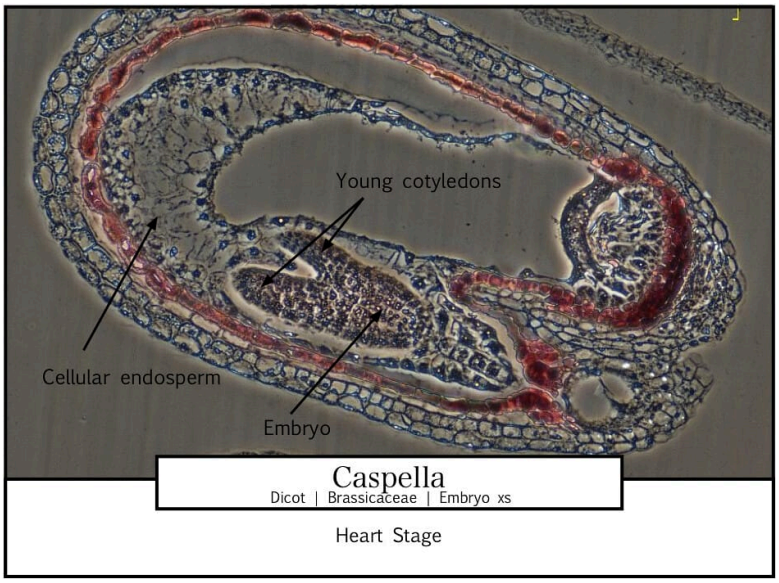
Embryo growth

Embryo development is initiated when the zygote divides once mitotically to form an apical and a basal cell. The basal cell undergoes several additional mitotic divisions to form a suspensor that anchors the apical cell to the nucellus tissue on the inner surface of the maturing ovule wall (seed coat). Next, the apical cell begins to divide mitotically to form the embryo. The embryo goes through distinctive phases that look like particular shapes. This image shows the early embryo heart shape (second from right), and the torpedo shape (far right) stages. The lobes will become cotyledons. Between the lobes is the stem or shoot apical meristem, and at the base near the suspensor is the root apical meristem.



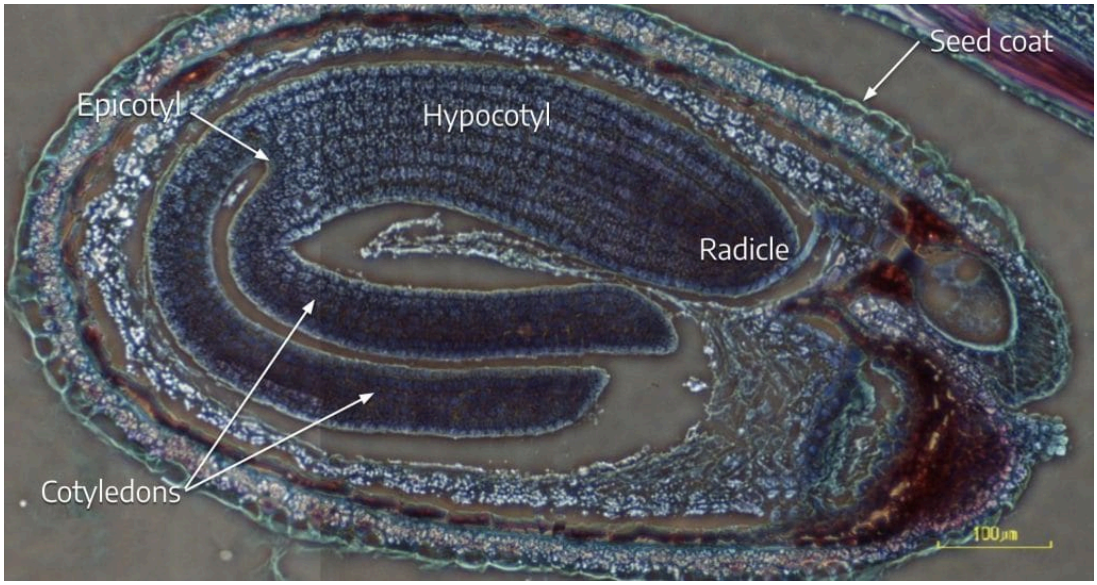
Seed development in plants consists of six stages. TheLAW14. CC BY-SA 3.0

Below is a heart stage embryo. Note the endosperm developing in another part of the embryo sac.



Heart stage embryo. Jen Dixon. CC BY-NC-SA 2.0

Finally, a later stage embryo with cotyledons readily apparent. This lesson has brought you from flower to seed.



Micrograph of late stage Capsella embryo, mature with cotyledons. Botanical Voyeur, CC BY-NC-SA

Review questions

1. How many nuclei are in the pollen tube?
2. Where is the egg cell of the embryo and what does it do?
3. A heart-shaped embryo has two swollen lobes that give it the shape of a heart. What will those lobes become when the embryo is mature?
4. You may recall that the ovule is attached to the placenta of the ovary by a stalk called the funiculus. What is the difference between the funiculus and the suspensor that is produced by mitotic divisions of the basal cell?

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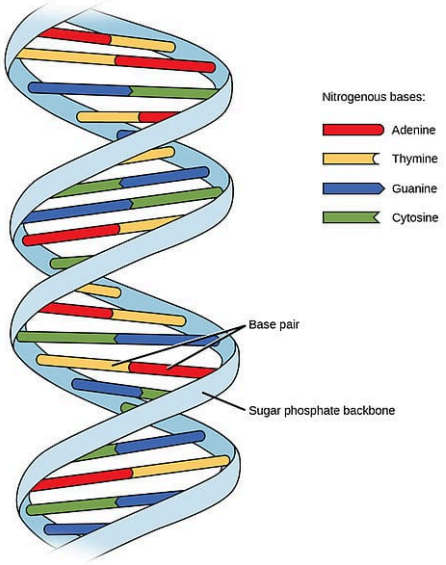
6.3: Inheritance of Big Differences

Learning objectives

- Compare the difference between simple and complex inheritance and explain how that difference is based on the number of genes involved and on the influence of the environment.
- Predict the types of offspring expected when crossing two parents that differ for their alleles at one locus, or when self-pollinating an F_1 hybrid.
- Predict the types of offspring expected when crossing two parents that differ for their alleles at two loci.
- Use a Punnett square to calculate the expected frequencies of different types of offspring.

Quantitative or qualitative differences?

This lesson and the next focus on the inheritance of characteristics that are passed down from parents to their offspring (also called **progeny**). This lesson focuses on the inheritance of large differences among plants that you can easily see or measure and can report in qualitative terms, such as red vs, yellow flowers, tall vs, short plants, or early vs, late maturity. The next addresses the inheritance of comparatively small differences that require more meticulous measurement and are reported in quantitative terms, such as seed yield in kg/ha, or milligrams of sucrose per gram of grape tissue. The expression of characteristics that are qualitatively inherited (larger, discrete differences) is influenced primarily by the plant's genes. The environment has little effect on the plant for these characteristics. In contrast to qualitative inheritance, plant characteristics that are quantitatively inherited are influenced by the environment, and sometimes the influence of the environment overshadows that of the genes themselves.



Structure of DNA. OpenStax. CC BY 3.0

Recall that the genetic code lies in the order of the purine (Adenine and Guanine) and pyrimidine (Cytosine and Thymine) bases in the DNA double helix. Some of these base sequences don't appear to have a function, but others are translated into structural and enzymatic proteins that influence cell and plant growth. The sequences that are translated into proteins that influence cell and plant growth are called **genes**. In corn, for example, the sucrose manufactured in the leaves through photosynthesis is transported through the phloem to the ear and into the developing seed or kernel. There the sucrose is broken down to simpler sugars like glucose that are linked together into starch for storage in the corn kernel's endosperm. The starch synthesis process is catalyzed by a series of enzymes that are produced as a result of expression of a set of corn genes. If even one of those genes is defective and doesn't produce an enzyme used in the sequence of reactions leading to starch, starch production could be halted.

Shrunken-2 (Sh_2) corn contains a DNA sequence (gene) mutation that renders nonfunctional an enzyme that is key to normal

starch biosynthesis. Starch biosynthesis is interrupted at an early stage of kernel growth, so instead of accumulating starch, the kernel accumulates sucrose in the endosperm. Shrunken-2 (sh_2) corn has high kernel sucrose levels and is one of the common types of "supersweet" sweet corn. This is an example of a large difference (a qualitative trait), because you can easily distinguish the difference between a bite of starchy field corn from a bite of sweet corn, and because the difference in sweetness is the result of just one mutant gene. This mutation is not, however, good for the vigor of the plant in the early spring. A seed that has accumulated sucrose rather than starch is very susceptible to fungus infection at planting time in comparison to the starchy seed of field (commonly called dent) corn. Sweet corn is not nearly as vigorous during germination as regular dent corn, as the dent corn has stored high amounts of starch in its endosperm while the sweet corn has not.

The principles of qualitative inheritance are consistent with the concepts of DNA structure, with genes and meiotic divisions resulting in segregation, and independent assortment of chromosomes. These principles of inheritance were actually worked out **before** knowledge of DNA, genes, and meiosis, using carefully controlled experimentation, crosses between contrasting parents, observation of progeny, and genius in developing and testing hypotheses.

Review questions

- Let's say a carrot breeder is showing us one of her carrot experiments. She planted 20 different types of carrots. If we see that some of the varieties have red tap roots, some have white roots, and others have the usual orange roots, do we suspect that the genetic control of red, orange, and white root colors is qualitatively (large, discrete differences) or quantitatively (smaller differences requiring measurement) inherited?
- If, later in the season, we inspect the data on root yield for each of these 20 varieties, and see that all of the varieties have a fairly similar yield in kilograms per hectare (the highest yielding carrot is perhaps 20% higher than that of the lowest yielding carrot), do we suspect that the genetic control of root yield is qualitatively or quantitatively inherited?

Phenotype, genotype, and environment

This simple arithmetic expression highlights a central concept of how genes and environment combine to influence a plant's appearance:

Phenotype = Genotype + Environment

Phenotype means the characteristics we actually observe about the plant. Is it tall? Short? Green? Yellow? Starchy? Sweet? The starchiness or sweetness of corn from a garden is one example of a phenotype. Phenotype is the actual expression of a characteristic in the plant that can be measured or expressed in some way.

Genotype is the genetic composition of a plant, including chromosomes of the nucleus and the DNA in chloroplasts and mitochondria. The genotype of a plant is subdivided into genes, which are the hereditary units consisting of a sequence of DNA that occupies a specific location on a chromosome (locus) and determines a particular characteristic in an organism. Genes undergo mutation when their DNA sequence changes, which results in changes in a gene, for example a flower color gene that mutates from red to white in color. The alternative versions of the DNA sequences making up the gene are called alleles. Shrunken-2, introduced above, is a gene. That gene is found at a particular location of a chromosome, and that location is called the gene's locus. At that locus will be one of the gene's alleles. It will either be the allele for the normal enzyme that facilitates starch formation, or the mutant allele that blocks starch formation and leads to supersweet corn. The sequence of the purine (A, G) and pyrimidine (C, T) bases along the DNA strand and the differences the sequence imparts to the genetic code produce differences among gene alleles.

Environment is the total influence of known and unknown factors, other than genotype, that might affect this trait, like rainfall, soil type and fertility, temperature, insect predation, and other influences that we may not recognize, but might still affect the phenotype.

Phenotype is then the sum of the genotypic and environmental effects. If you are a sociologist, then you might be familiar with arguments about whether a certain type of human behavior is due to "nature" or "nurture." Roughly, "nature" corresponds to genotype while "nurture" corresponds to environment. A shorthand representation for the equation introduced above is **P = G + E**, which roughly corresponds to

Behavior = Nature + Nurture

For more on genotype and environment influences on a plant's phenotype, see this Wikipedia page (optional).

Genotype (G) has a much larger influence on phenotype (P) than does environment (E) when considering simply inherited characteristics that result in large, qualitative differences. Supersweet sweet corn is going to be sweet corn and not starchy field corn regardless of whether it is grown in Minnesota, California, or in a greenhouse on Mars. The exact amount of sucrose may differ a bit depending on environmental stresses, like how hot or cool the growing season is (hot seasons tend to result in slightly more sugar), but the genotype has a much larger impact on the sweet phenotype than the environment. It is quite common for large differences to be inherited through a single gene that has a large impact. This is called **simple inheritance**, **major gene inheritance**, or **qualitative inheritance**.

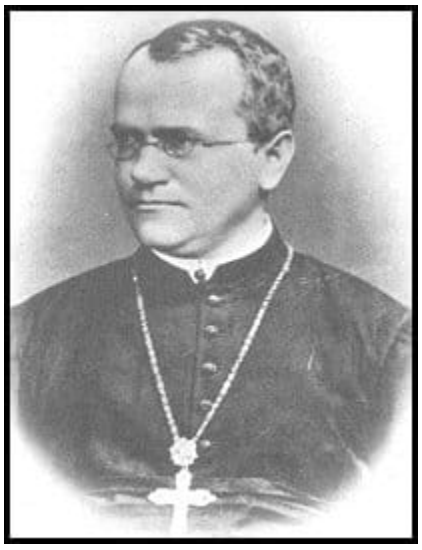
In contrast, environmental effects typically have a major impact on phenotype when considering inherited characteristics that are expressed as smaller, quantitative differences, such as those you might find when comparing common bean cultivated varieties (cultivars) for their seed yield, or spinach cultivars for the amount of chlorophyll in their leaves. The impact of the environment might even be larger than the effect of genotype. For example, the rank order of bean yield for three kidney bean cultivars grown in Minnesota might be Cultivar A > Cultivar B > Cultivar C, but if you grow them in Pennsylvania, it could be the reverse, due to a change in environment. It is common for small differences to be inherited through many genes each with a very small impact, where the cumulative effect of their acting together is noticeable. This is sometimes called **complex inheritance**, **minor gene inheritance**, or **quantitative inheritance**, because many genes each with small effect are involved.

Review question

1. Thinking back to the carrot questions above, will environment have a greater impact on root yield or root color?

Inheritance of a qualitative trait

Watch this video for an introduction to qualitative traits (11:29)



Gregor Mendel. Medical Heritage Library. CC BY-NC-SA 2.0

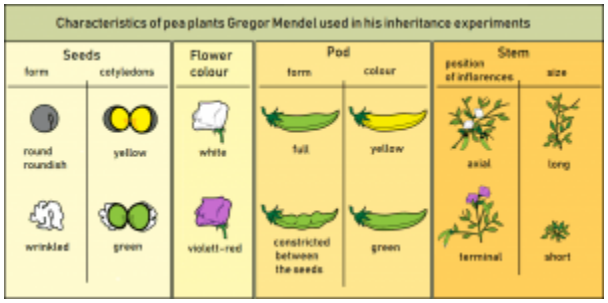
Gregor Johann Mendel, who lived from 1822 to 1884, was an Austrian monk and scientist who studied the simple inheritance of large, obvious differences among pea plants and developed the fundamental principles of modern genetics. He demonstrated that the large differences passed from parents to progeny are transmitted between generations through discrete units or packets of information that control the expression of specific characteristics, and that these discrete units are independently inherited. Take a look at this web page (optional) for background on Mendel, or browse here.

As noted above, Mendel chose pea, *Pisum sativum* L., as his model organism. Pea usually self-pollinates. It is one of those plants where the pollen is shed and the stigma is receptive even before the flower opens (recall that this is called **cleistogamy**). Egg and sperm come from the same plant and, following fertilization, form the embryo. The flower is conveniently large enough though that if you very carefully open up a flower bud a few days before the pollen sheds, you can remove the anthers and pollinate the

stigma with pollen from another plant, making it fairly easy to cross if you emasculate the flower and supply another source of pollen. If left to its own devices, however, the pea flower self-pollinates.

Mendel looked at a number of qualitative traits controlled by single genes, including:

Gene	Phenotype
Seed shape	smooth vs wrinkled
Seed color	green vs yellow
Flower color	purple vs white
Several other obvious pod and plant characteristics that can be seen by eye	



Characteristics of pea plants. LadyofHats. Public domain

Mendel crossed a parent plant grown from a smooth seed (P_1) to another parent (P_2) grown from a wrinkled seed. These parents were selected because they were true breeding, meaning that if they allowed to self pollinate they always produced the same type of seed. When P_1 was pollinated (crossed) with P_2, all of the seeds resulting from the cross (called F_1, short for first filial generation) were smooth-seeded.

Here's a summary of the experiment so far:

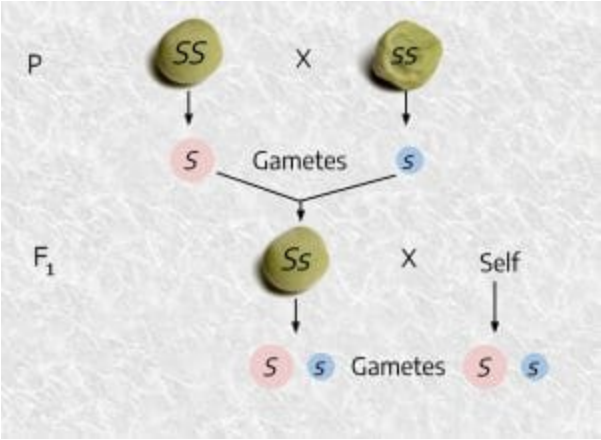
P_1 (smooth) X P_2 (wrinkled) → F_1 (all smooth)

Mendel then planted the F_1 seeds, let them naturally self-pollinate, and collected the seeds produced by these plants. He counted a total of 7324 F_2 (second filial generation) seeds and found that 5474 were smooth and 1850 wrinkled. This is roughly a ratio of 3 smooth : 1 wrinkled. This, and other similar results, led him to the development of a model where seed plumpness is controlled by one gene with two different versions (or alleles) of the genetic code for that gene. Furthermore, based on the results, when one of each allele was present in the F_1 progeny, the allele donated from the smooth seeded P_1 parent was dominant to the recessive allele donated from the wrinkled-seeded P_2 parent. **Dominant** here means that if two different alleles are present in an organism, but only one is expressed (like the smooth seed being expressed even though alleles for both smooth and wrinkled are present), the allele that is expressed is called the dominant allele, and the allele that is not expressed is called **recessive**. Recessive alleles are only expressed if no dominant alleles are present.

If we signify the dominant allele for smooth seeds as the upper case S and the recessive allele that codes for a wrinkled shape as lower case s, the three different possible genotypes are:

- SS diploids that are smooth (homozygous dominant).
- Ss diploids that are also smooth. Here, in the heterozygous genotype, you can tell which allele is dominant to the other. Both alleles are present (S and s), but only one is expressed — the S — so S must be dominant to s.
- ss diploids that are wrinkled (homozygous recessive).

Note that, by convention, the designation for the allele (like S or s) and the genotype (like Ss) is underlined.



F1 generation – Round/wrinkled pea crossing. Alejandro Porto. CC BY-SA 3.0

Above is a diagram showing the smooth (SS) and wrinkled (ss) parents crossing to form Ss (smooth) F_1 progeny. Recall that if an SS parent goes through meiosis, only an S type of gamete is formed. There cannot be any s gametes, because the parent only has the S allele. Likewise, only s gametes are possible when an ss parent undergoes meiosis and forms gametes. So Ss progeny is the only possible result from crossing an SS parent to an ss parent. The phenotype of all of these progeny will be smooth because S is dominant to s. Notice that, in this example, which is one of big, qualitative differences, there is no influence of the environment, so Phenotype = Genotype.

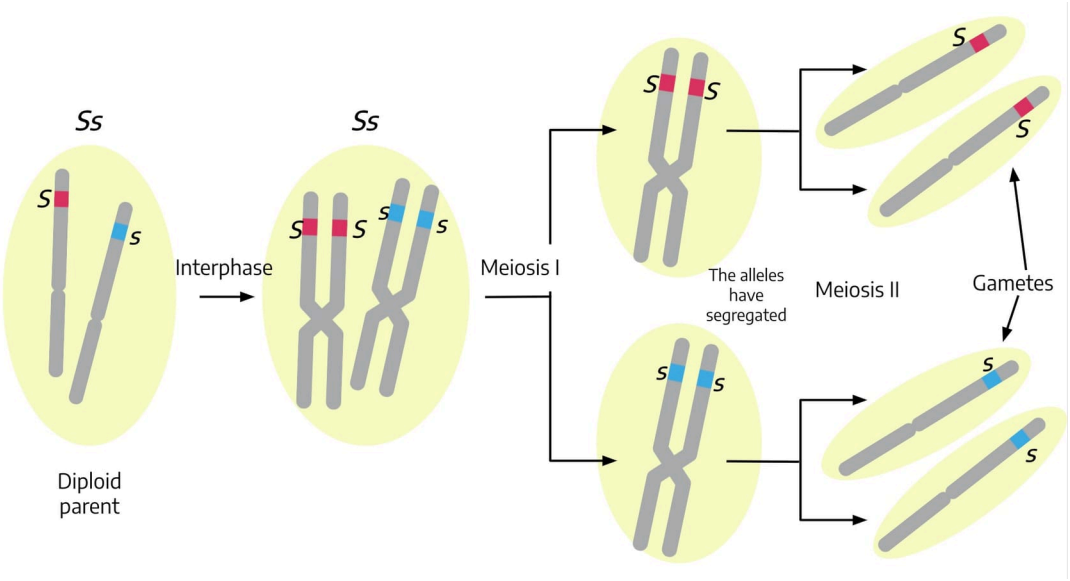
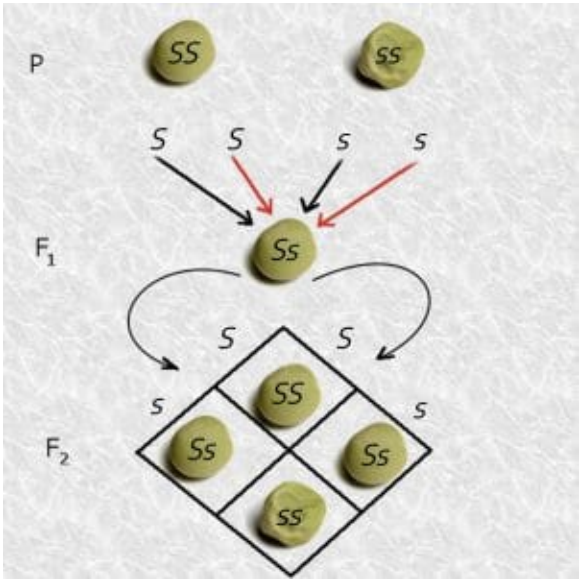


Image by Emily Tepe.

The next step in the experiment is to allow the smooth, Ss F_1 progeny to self-pollinate. The lower part of the above diagram shows that the F_1 plant will produce two types of gametes, S and s, in equal numbers. Think back to meiosis and gametogenesis. Just before a diploid cell with genotype Ss heads into meiosis, the homologous chromosomes (one carrying the S allele and the other carrying the s allele) replicate in interphase so that there are four sister chromatids, two with the S allele and two with the s allele. The illustration to the left shows how the S and s alleles segregate. The process of meiotic cell division will result in each of these sister chromatids winding up in a separate spore, so of the four male gametes formed during microgametogenesis, two are carrying S and two are carrying s. The one surviving gamete from megagametogenesis has an equal probability of being either S or s (recall that of the four spores, only one survives), so if you consider many egg cells, roughly half will be S and half will be s. Mendel's results, and his explanation, are thus consistent with what we know about meiosis.

You can use a simple tool called a Punnett Square to visualize the types of zygotes, and their expected frequency, formed from the male and female gametes resulting from self-pollination of an Ss individual, as shown below:



F2 Generation. Alejandro Porto. CC BY-SA 3.0

The male gametes, S and s are shown in the two columns across the top of the square, and the female gametes, also S and s, are listed down the left margin. Each cell shows the contribution of one male gamete and one female gamete.

In this example, self-pollinating (also called selfing) an Ss F_1 plant means that we list S and s as possible male gametes and also as possible female gametes, since both sperm and egg are from the same F_1 plant. The potential zygotes are shown in the four cells inside the square.

If you count up the results of from the Punnett square, you find that the genotypic ratios of the F_2 progeny are:

1 SS : 2 Ss : 1 ss

and the phenotypic ratios are:

3 S- (Smooth) : 1 ss (Wrinkled)

which is precisely the ratio that Mendel found between smooth and wrinkled seeds in his F_2 pea generation. Recall that the difference between the genotypic and phenotypic ratios occurs because S is dominant to s so you can't tell the phenotypic difference between SS and Ss genotypes.

Mendel's First Law — the law of segregation — states that during gamete formation each member of the allelic pair separates from the other member to form the genetic constitution of the gamete. That is, in the F_1, the Ss diploid produces S and s gametes, not Ss gametes. Mendel's work paved the way for figuring out this process.

Review question

1. Using the Punnett square diagram above, explain why the expected frequencies for the three possible genotypes should indeed be **1 SS : 2 Ss : 1 ss**.

Simultaneous inheritance of two qualitative traits

Watch this video for an introduction to independent assortment (12:01)

Here is a slightly more complex situation, but one that can still be understood through your knowledge of meiosis. We'll simultaneously consider seed shape (or plumpness) and another characteristic, seed color, that Mendel studied. Like seed shape, seed color is controlled by one gene with two alleles where:

- YY diploids are yellow
- Yy diploids are also yellow
- yy diploids are green

You can tell from the heterozygote Yy that the Y allele for yellow color is dominant to the recessive y allele for green.

Note that the gene for seed shape is on a different chromosome than the gene for seed color. Mendel didn't know this, as the concept of chromosomes had not yet been proposed. Because they are on separate chromosomes, seed color and seed shape will assort independently.

Let's start by crossing a plant that grew from a smooth, yellow seed known to have the genotype SSYY to a plant that grew from a wrinkled green seed with genotype ssyy.

SSYY X ssyy → ?

The only type of gamete that can be produced by the SSYY parent is SY, and the only type that can be produced from the ssyy parent is sy. The F_1 progeny can only be the double heterozygote SsYy, which has smooth, yellow seeds.

SSYY X ssyy → SsYy

Next, allow the SsYy F_1 progeny to self pollinate. Below is a diagram of key stages of meiosis for a cell with genotype SsYy. Note that the seed shape gene is on one type of chromosome (straight) and the seed color on another (squiggled).

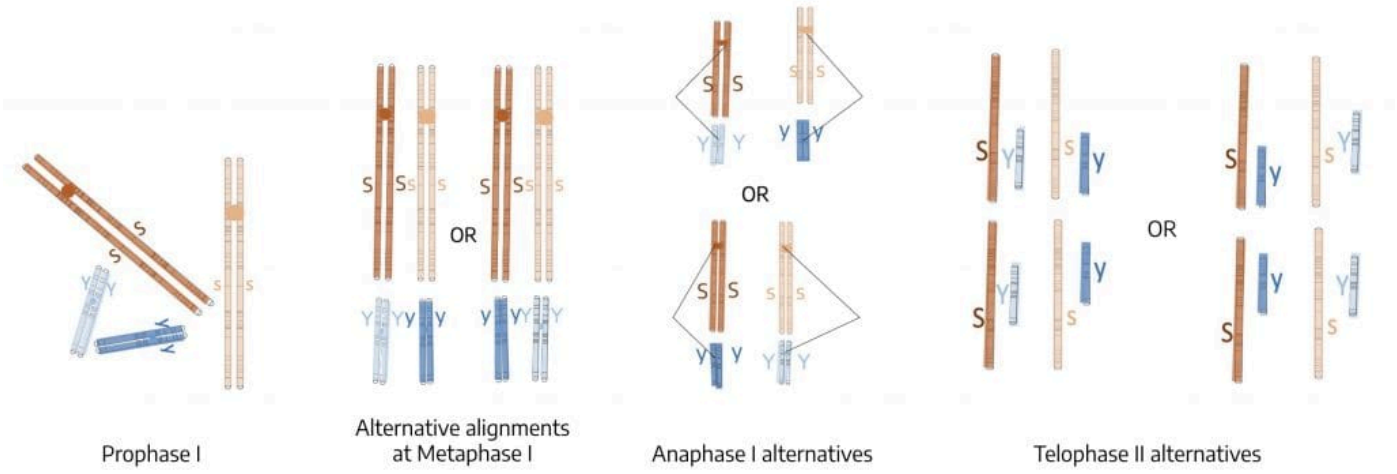
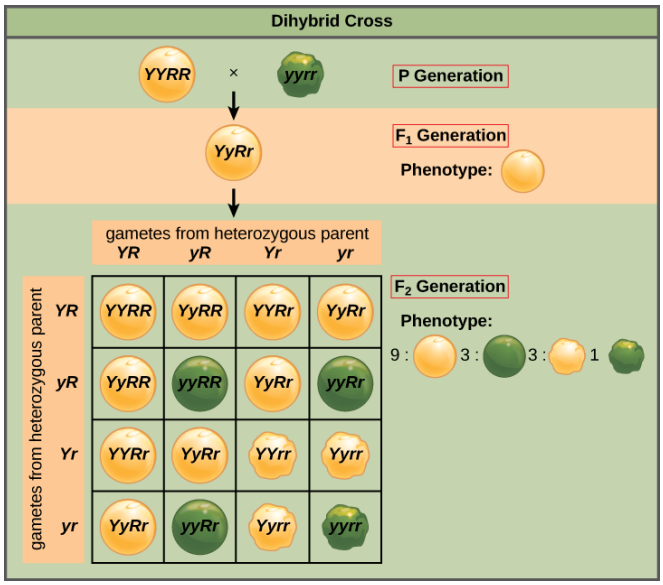


Image by Matthew Clark.

- At Prophase I the chromosomes are replicated and show sister chromatids.
- At Metaphase I we see that the homologs have synapsed and lined up on the metaphase plate. There are two ways that the recessive and dominant alleles can line up on a metaphase plate. The left side of Metaphase I shows that both dominant gene homologs are on the same side; the alternative alignment on the right side shows that the dominant homolog for one gene could just as likely line up with the recessive homolog for the other gene.
- The way they line up at Metaphase I determines how they separate at Anaphase I, so the diagram of Anaphase I shows two alternatives for how the homologs migrate to the poles. This has an impact on the types of spores produced in Telophase II.
- In the Telophase II frame above, the left side shows that. based on one of the Anaphase I alternatives, the result can be for the dominant S and the dominant Y to be together in one type of spore and both recessive genes together in other spores. Equally likely, as shown on the right, the result can b eone dominant gene with one recessive gene.



Yellow/green/wrinkled/round pea Punnett Square. OpenStax. CC BY 4.0

Meiosis and gamete formation in the SsYy F_1 thus results in an equal likelihood of four types of gametes: SY, sY, Sy and sy. If we create another Punnett Square to model self pollination of the SsYy F_1 and put these four gametes both across the top and down the margin (since we are allowing the plant to self pollinate, and the frequency and genotype of the gametes will be the same whether egg or sperm), we get the results shown.

Looking at the diagrams of the seeds in each cell, you can count the number of times each of the four possible phenotypes appears. The phenotypic ratios are:

9 S-Y- (smooth yellow) : 3 S-yy (smooth green) : 3 ssY- (wrinkled yellow) : 1 ssyy (wrinkled green)

The dash "-" in the genotype, like S-, means that the allele represented by the "-" could be either the dominant or the recessive allele because, regardless of which allele is there, the phenotype remains the same. So S- means both SS and Ss genotypes.

Don't memorize these ratios, but understand how they were obtained using the Punnett Square. When Mendel conducted this experiment and counted the seeds of each phenotype he obtained, he found:

315 smooth yellow, 108 smooth green, 101 wrinkled yellow, and 32 wrinkled green

which is pretty close to a 9:3:3:1 ratio.

This result for two genes on different chromosomes led to Mendel's Second Law — the Law of Independent Assortment. During gamete formation, the segregation of the alleles of one allelic pair is independent of the segregation of the alleles of another allelic pair (illustrated above with the alternative alignments at Metaphase I). That is, when gametes form from an SsYy F_1, and receive either S or s (as stated in the first law of segregation), whether Y goes with S to make up a SY gamete or whether y goes with S to make up a Sy gamete is completely by chance. Remember the mechanics behind this, from learning how homologs separate through independent assortment in Anaphase I of meiosis.

Mendel's initial insights on segregation and independent assortment are the foundation of genetics. He uncovered the core principles that were only later confirmed by our understanding of chromosomes, genes, alleles, and cell division. For another optional look at Mendel's laws, and another take on this material, see Phil McClean's (a Prof at NDSU) web site on Mendelian Genetics.

Review question

1. Cover up the Punnett Square above, and without peeking, fill in the cells on your own and derive the genotype and phenotype ratios from selfing the SsYy hybrid.

2. What are the differences between the law of segregation and the law of independent assortment?

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6.4: Linkage and Inheritance of Small Differences

Learning objectives

- Know the meaning of linkage and the impact of crossing over on linked loci.
- Recognize the difference between qualitative and quantitative inheritance.
- Understand how heritability is a measure of the genetic influence over a quantitative trait, relative to other non-genetic influences.

Review

The previous section included examples of simple inheritance, where large, obvious, discrete differences among plants are controlled by one gene and where one of the alleles is completely dominant over the other. Based on the inheritance patterns of round vs. wrinkled pea seeds described in that lesson, Mendel developed the Law of Segregation.

Often called Mendel's First Law, the Law of Segregation in modern terms states that, during gamete formation, the two alleles for the gene of interest (recall that in diploid cells there are two homologs for each type of chromosome, so there are potentially two versions or alleles of each gene) separate from each other during meiosis and are passed individually to the next generation through the egg and sperm. This is apparent in the mechanics of meiosis, where the homologs separate and migrate to opposite poles in Anaphase I and, following the separation of sister chromatids in Anaphase II, are packaged into separate gametes. In the self-pollination of a Smooth x Wrinkled F_1 pea example, the Ss diploid produces S and s gametes, not Ss gametes. The S and s are *segregated* into separate gametes.

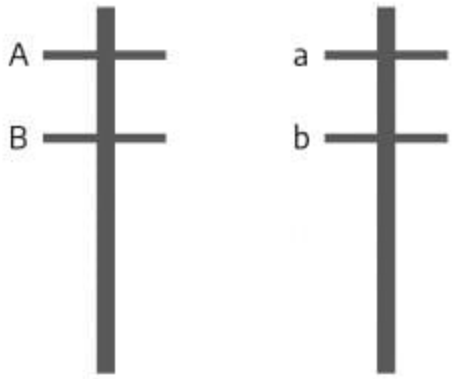
The previous lesson also tracked the joint inheritance of two genes on separate chromosomes that affect different traits (Smooth vs Wrinkled seeds and Yellow vs Green seeds), which leads to Mendel's Second Law — the Law of Independent Assortment. In modern terms, this law roughly states that, during gamete formation, the allocation of the alleles of a gene on one chromosome is independent of the allocation of the alleles of a different gene on a different (non-homologous) chromosome. So when gametes form from an SsYy F_1, and the gametes receive either S or s (as stated in the First Law of Segregation), then whether Y goes with S to make up a SY gamete, or whether y goes with S to make up a Sy gamete, is completely by chance. This is also seen in the diagram of meiosis and how the chromosomes divide at Anaphase I. Homologs separate at Anaphase I, and in the case of two different pairs of homologs, the way in which the first pair of homologs splits doesn't influence how the second pair of homologs splits. What Mendel discovered by examining segregation ratios (the ratios of each genotype resulting from a particular cross) can thus also be explained through the mechanics of meiosis. Mendel's thinking was revolutionary at the time, and a great example of thinking carefully about the outcomes of an experiment and developing a model of the process that explains the observed data.

Linkage

Watch this video for an explanation of linkage (7:47)

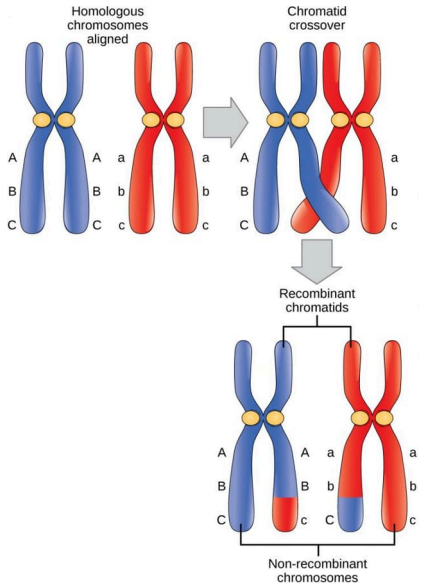
What if those two genes are positioned closely on the same chromosome rather than on separate chromosomes, as in the pea shape/pea color example? This situation is called linkage.

Imagine a case in which the hypothetical gene "A" (with alleles "A" and "a") and gene "B" (with alleles "B" and "b") occur at loci near each other on the same chromosome. Imagine further that one of the chromosomes has the dominant "A" and the dominant "B" allele while its homolog has both recessive "a" and "b" alleles. This situation is illustrated below.



Alleles that cannot independently assort. Image by Emily Tepe.

When these chromosomes go through meiosis the alleles at the two loci cannot independently assort because they are on the same chromosome — they are physically connected. As a result, the gametes will be either AB or ab. There will be no Ab or aB gametes, as you would normally expect from independent assortment, because the A allele is physically attached to the B allele, and the a allele attached to the b allele — they are on the same chromosome. The only way to get Ab or aB gametes together is through a physical breakage in the chromosomes between the two genes and the exchange of arms between homologs; recall that this is called **crossing over**.



Homolgs in prophase 1 crossing over. OpenStax. CC BY 4.0

The illustration shows homologs in Prophase I following synapsis (pairing) and where sister chromatids crossed over, with the cross-over event occurring between the loci for the two genes. The chromatids cross over and will exchange arms. When they separate at Anaphase I, the homolog that migrates to the left side will have one sister chromatid with the alleles AB and one with aB. The homolog that migrates to the right will have one chromatid that is Ab and another that is ab.

The frequency of crossing over is one way to describe the distance between the two genes on the chromosome. If crossing over is very infrequent — in this example, if there are very few Ab and aB gametes — the two genes must be very close to each other. This situation is called a **tight linkage**. If crossing over is quite frequent, approaching 50%, the two genes must be very far apart. If it appears that AB, ab, Ab, and aB gametes have equal frequency, this indicates that the genes are located on different chromosomes or are on the same chromosome, but separated so much that the frequency of crossing over is 50%, which has the same result as if they were on separate chromosomes.

The Wikipedia site on linkage provides a bit of additional information.

Review questions

1. Why can two linked genes NOT independently assort?
2. In the example above, will tight linkage result in many or few Ab gametes?
3. Would you expect the frequency of aB gametes to be roughly the same or quite different from the frequency of Ab gametes?

Quantitative traits — inheritance of small differences

Watch this video for an introduction to quantitative traits (8:28)

Recall that inheritance does not always involve large, qualitative differences. Inheritance of small differences that require more meticulous measurement and are reported in quantitative terms such as seed yield in kg/ha, number of chloroplasts per mesophyll cell, and grape sucrose content are very important in horticulture. Indeed, these small differences, when accumulated, can be more important than the large qualitative differences in horticultural food crops. Quantitative traits result in higher yield, earlier maturity, and greater cold tolerance, all of which, with patient intercrossing and persistent selection over many years, leads to continuous crop improvement.

In contrast to qualitative traits, the inheritance of quantitative traits may be influenced substantially by the environment. Recall the equation

Phenotype = Genotype + Environment

For quantitative traits, the Genotype component, or the influence of each of these quantitative genes, is quite small, and the influence of the Environment can be large relative to the contribution of Genotype.

You can visualize the difference between quantitative and qualitative inheritance by measuring a large set of plants of the same species (we'll call it a **population** of plants) for a particular characteristic (we'll use flower number per plant as an example). Using that data set containing flower numbers for a large number of plants, you can

- count the number of plants in the population that have one flower,
- count the number of plants with two flowers,
- count the number of plants with three flowers, and so on,

then calculate the frequency of each of these flower number classes in the population by dividing the number of plants with one flower by the total number of plants in the population, and so on for each of your flower number classes.

Next, you can make a graph plotting the flower number on the X axis against the frequency of plants with that flower number on the Y axis, giving a figure called a **frequency distribution**.

As an example, below are two databases containing hypothetical flower number data taken on 60 plants in two different populations. The first table is a hypothetical database illustrating what the population structure might look like if flower number was controlled by quantitative inheritance, and the second illustrates what the population might look like if flower number was controlled by qualitative inheritance. Both tables have three columns; the first shows the number of flowers, ranging from 1 to 15 per plant; the second shows the number of plants in the sample of 60 with the corresponding number of flowers; and the third shows the frequency of plants in the sample with the corresponding number of flowers per plant. In the quantitative database on the left, in the row corresponding to plants with four flowers, read across to see that there were two of these plants, and that their frequency was 2/60 = 0.0333, rounded to 0.03. This is called a frequency distribution table because it shows the frequency of plants with a particular class of a characteristic, in this case flower number per plant.

Notice that the frequencies in the quantitative table are spread out over a wide range of flower numbers, with a peak around seven flowers per plant. In the qualitative table, in contrast, the frequencies are clustered around two discrete flower numbers, with one large peak at about five flowers and a smaller peak at 13.

Quantitative example				Qualitative example		
# Flowers	# Plants	Frequency		# Flowers	# Plants	Frequency
1	0	0		1	0	0
2	0	0		2	0	0
3	1	.02		3	0	0
4	2	.03		4	3	.05
5	5	.08		5	30	.50
6	7	.12		6	9	.15
7	16	.27		7	3	.05
8	15	.25		8	0	0
9	6	.10		9	0	0
10	4	.07		10	0	0
11	2	.03		11	1	.02
12	2	.03		12	1	.02
13	0	0		13	12	.20
14	0	0		14	1	.02
15	0	0		15	0	0
Total	60	1.0		Total	60	1.0

These data are easier to understand in a graph, with the flower number on the X axis and the frequencies on the Y axis:

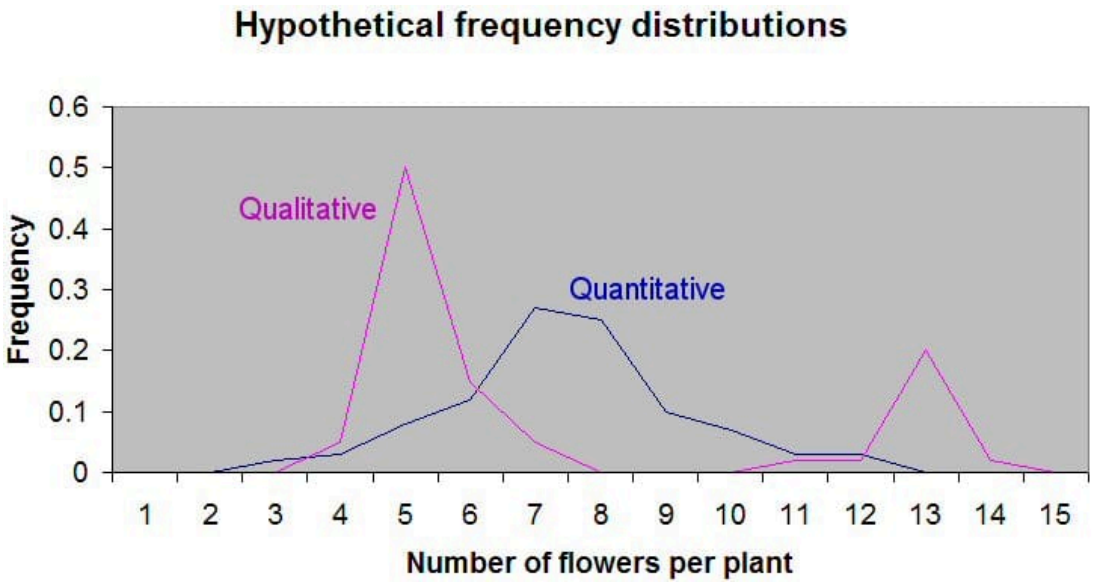


Image credit: Tom Michaels

Notice that the magenta line illustrating the qualitative inheritance distribution has two peaks at 5 and 13 flowers per plant, and that the dispersion around those peaks is quite narrow. Most values are either 5 or 13. In contrast, the blue line illustrating quantitative inheritance has a peak in the 7–8 flower per plant region, and there is a great deal of dispersion. There are many different values of flowers per plant, although the most frequent is in the 7–8 range.

The dispersion around the peaks is in part due to the influence of the environment. For qualitative traits (magenta line), this influence is small. For quantitative traits (blue line), it is larger. Also notice that if you added up the frequencies under the two

magenta curves, you would find that the curve with the peak at five flowers has three times the frequency of plants as the curve peaking at 13 plants. This 3:1 ratio is indicative of a single qualitative gene where the dominant allele is associated with, on average, five flowers per plant.

Review questions

1. Would you expect that a frequency distribution with two sharp peaks represents a qualitative or quantitative trait?
2. Would you expect that a frequency distribution which looks like a mound with one high point represents a qualitative or quantitative trait?
3. Would you expect that a frequency distribution with four sharp peaks represents a qualitative or quantitative trait? (hint: 9:3:3:1)

Heritability

Watch this video for an introduction to heritability (8:44)

Inheritance of quantitative traits is often associated with the term heritability. If a parent and its offspring have very similar values for a quantitative trait, the trait is considered to be highly heritable. Highly heritable traits tend to be under strong genetic control with little influence from the environment. In contrast, if the offspring values don't seem to have any relationship to that of the parent, the trait is considered to have low heritability. Low heritability usually results when the influence of the environment is quite high relative to the impact of the genotype on the trait being studied. If you are trying to improve a plant characteristic through breeding, you'll have much greater gain from selection if the trait has high heritability rather than low heritability. If a plant characteristic has high heritability, dramatic changes to the population from natural selection will also be more rapid (require fewer generations) than for a characteristic that has low heritability. See the graph below.

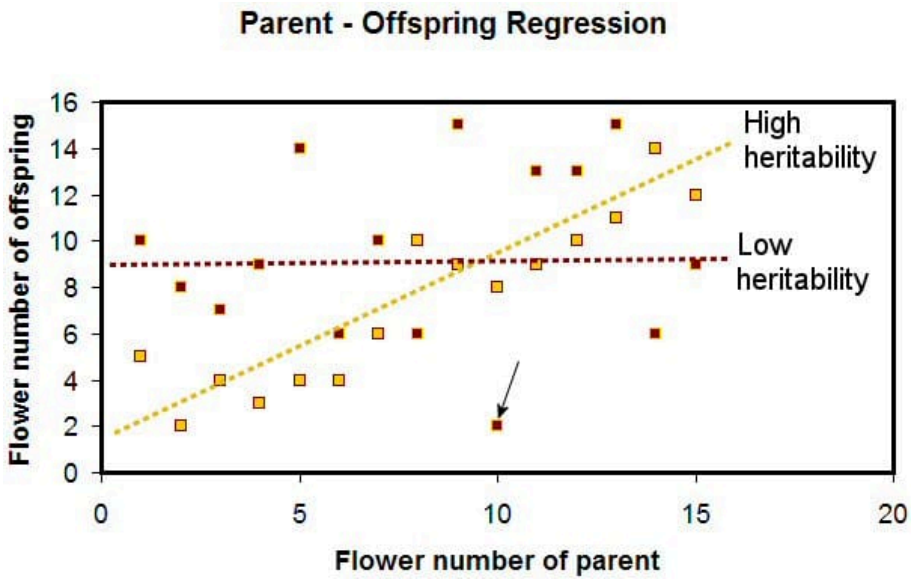


Image credit: Tom Michaels

The X axis represents the number of flowers on the parent plant, while the Y axis represents the average number of flowers on the offspring of those parents. A dot represents each parent-offspring data pair. For example, the maroon dot with the black arrow pointing to it represents a data point for a parent with 10 flowers whose offspring had, on average, two flowers (read the 2 off the Y axis).

The gold dots represent cases where the trait has high heritability. Note that you can draw a line with a positive slope through the gold dots, with the dots being relatively close to the line. This indicates high heritability, and means that the offspring's performance can be predicted based on the performance of the parent. If the parent has a high flower number, the offspring will as well. Plant breeders can make selections with the expectation that if they save seeds from superior plants, the offspring growing from those plants will exhibit the same superiority.

The maroon dots, in contrast, represent the situation of low or zero heritability, and have no line of good fit. Some parents with high flower numbers had offspring with low flower numbers and others with high flower numbers had offspring with high numbers. You can't predict the offspring flower numbers based on the parent flower numbers. This represents a nightmare for breeders. Some offspring of superior plants will be good as the parents, others will be better, and others will be wildly inferior.

Review questions

1. Would a breeder anticipate making greater gain from selection for a trait that has high heritability or low heritability?
2. If a characteristic is very heavily influenced by the environment and exhibits very little control by genotype, will the heritability be close to 0 (very low heritability) or close to 1 (very high heritability)?

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7: CELLULAR RESPIRATION AND FERMENTATION

Learning Objectives

- Understand how the process of cellular respiration converts glucose into usable energy, carbon dioxide, and water
- Explain why some organisms do fermentation instead of cellular respiration, even though this produces less usable energy
- Identify stages in cellular respiration where ATP is used and where it is produced
- Calculate net ATP produced from a single glucose molecule
- Make predictions about the rate of fermentation under different conditions

Cells convert glucose into usable energy (ATP) through cellular respiration, which includes glycolysis, the Krebs cycle, and oxidative phosphorylation. In low oxygen, some organisms use fermentation, producing less ATP. ATP powers cell functions, and experiments show how factors like temperature affect fermentation. Both autotrophs and heterotrophs rely on these processes to release energy.

7.1: Introduction

7.2: Cellular Respiration

7.3: Concept Mapping - Connecting Ideas Visually

Contributors and Attributions

- Maria Morrow (College of the Redwoods)

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7.1: Introduction

Part 1: Carbohydrates in Food

When you eat food, you are acquiring nutrients that you need to maintain homeostasis--to keep your internal conditions regulated to the specific parameters required for your survival and function. From these foods, you might get vitamins that your body cannot synthesize itself, amino acids needed to build proteins, and, in anything that is **food** in the scientific sense, carbohydrates that you can break down to use as energy.

Carbohydrates can be simple sugars--monosaccharides like glucose--to complex starches, often made of long chains of those same monosaccharides bonded together to form a much larger molecule called a polysaccharide. Some of these polysaccharides have bonds that our bodies have enzymes to break down, such as Amylose. Amylose is a starch composed of glucose **monomers** attached together by a glycosidic bond, forming a relatively straight line. In your mouth, you produce an enzyme called amylase that breaks the glycosidic bond, eventually turning the long chain of amylose into many molecules of glucose. Amylase functions best at pH 6.7-7.0 [connect to maintenance of homeostasis]. Other polysaccharides are bonded together in ways that we do not have enzymes for, like cellulose, the primary component of plant cell walls. This is why plants contain “dietary fiber,” which passes right through your system and “keeps you regular.”

Part 2: Converting Carbohydrates into Usable Energy

A molecule of glucose stores about 3,000 kJ of **chemical energy**. Chemical energy is the potential energy stored in the bonds that hold atoms within a molecule together. Everytime you break one of these bonds, that energy is released. Molecules of glucose are relatively stable, so this energy is safely stored inside the molecule. Because of this, we can transport glucose, dissolved in our blood, to areas in our body where it is needed or to our liver, where it can be stored for later in the form of glycogen. Plants can do the same through phloem cells, transporting glucose to areas of the plant where it can be stored long term as starch, such as the roots.

Because the glucose molecule is stable, the energy is trapped inside it. To access this energy, the glucose molecule must be broken apart. You can make this happen by applying large amounts of energy, such as heat from a fire--this is what happens when you burn wood or paper. These materials are plant-based, composed primarily of plant cell walls containing large amounts of cellulose. As we saw above, this cellulose is composed of long chains of glucose molecules. The wood itself doesn’t spontaneously catch fire, but when you apply enough energy, such as by igniting a small portion of it with a lighter or a match, you can cause some of those molecules to break apart. This releases energy in the form of light and heat, which can then provide the energy to break more molecules apart. This process is called combustion.

What was required to make this reaction happen? Carbohydrates, oxygen, and an initial energy input. A similar process happens inside most eukaryotic organisms. However, to avoid catching on fire, we break down the glucose molecule piece by piece, releasing small amounts of energy at a time, and using that energy to build molecules of something called **ATP** (adenosine triphosphate).

Unlike glucose, ATP is an unstable molecule. It has three negatively charged phosphate groups, all attached end-to-end. The negative charges on these phosphate groups repel each other, much like the two negative sides of different magnets. As the number of negative charges increases, the repulsion increases exponentially. Because of this, the third phosphate group holds a large amount of energy in its bond to the second. This phosphate group can be “donated” to a reaction (called phosphorylation), breaking the bond and releasing the stored chemical energy to power the reaction. The ATP loses its third phosphate group and becomes ADP (adenosine diphosphate), a relatively low-energy molecule. Our cells use ATP to power most of the work done in our bodies.

Key Point

While heterotrophic organisms like animals and fungi must consume other organisms to obtain carbohydrates, plants and other autotrophs synthesize their own carbohydrates. However, just like heterotrophs, **autotrophic organisms still need to do cellular respiration to access the energy stored in those carbohydrates.**

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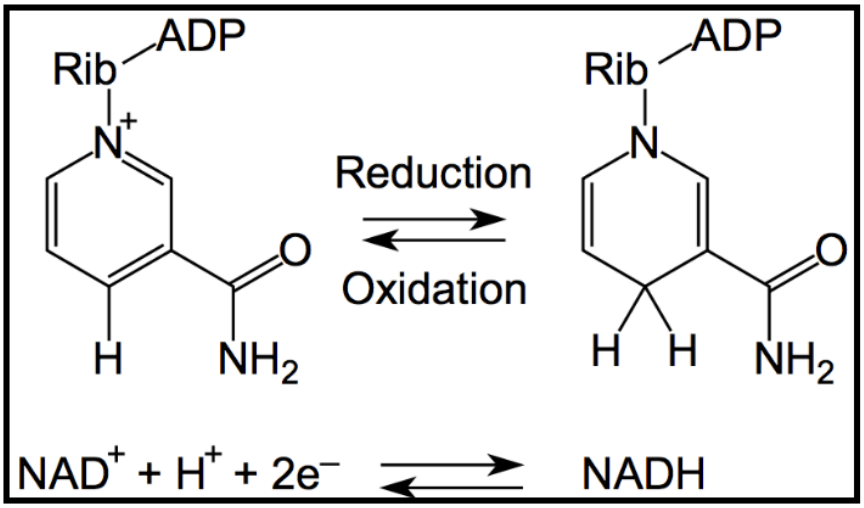
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7.2: Cellular Respiration

Step 1: Glycolysis

When glucose is transported into the cytoplasm of cells, it is broken down into two molecules of **pyruvate**. 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.

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 NAD+ are reduced to form NADH. When a molecule is reduced, electrons have been added to it. Electrons have a negative charge, so this is termed "reduction". 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. Because NADH carries two high energy electrons, it is often referred to as an **electron carrier**.



NAD+ can carry electrons (be reduced) by adding H+ ions

Figure 7.2.1: NAD+ to NADH reaction

Table 7.2.1: Summary Table of Reactants and Products of Glycolysis

Reactants (What went in?)	Products (What came out?)
1 Glucose	
2 NAD+	
2 ADP (net)	

Alternate Pathways: Fermentation

At this point, cells make a check: Is there oxygen present or not? If not, some organisms can go through a process called **fermentation**. In fermentation, glycolysis is the only part of glucose breakdown that a cell can do. Thus, only two net ATP can be gained from each glucose molecule. To continue doing fermentation, the cell must regenerate the NAD+ needed to do glycolysis.

There are two primary pathways to regenerate NAD+. In your body, cells can regenerate NAD+ by producing lactate and H^+. This is called **lactic acid fermentation**, though lactic acid is never actually produced, so it is a bit of a misnomer. Some bacteria, like *Lactobacillus*, are also capable of doing this type of fermentation.

Making Yogurt With Lactic Acid Fermentation

Put some milk into a flask and add a spoonful of yogurt. Mix thoroughly, cover, and place in a warm environment. Over the next 24 hours, the sugars in the milk will be fermented into lactate and H+ ions. This thickens the milk and adds acidity, making yogurt.

> Why did you add the spoonful of yogurt to start it? What did this add to the milk that would allow fermentation to occur?
>
> Why did you need to put it into a warm environment?
>
> Do you think the type of milk you use affects the time it takes to get yogurt? Explain your answer.

Another pathway to regenerate NAD+ is to produce CO_2 and ethanol (alcohol). Certain yeasts, like Saccharomyces cerevisea, perform this type of **alcohol fermentation** when they do not have access to oxygen.

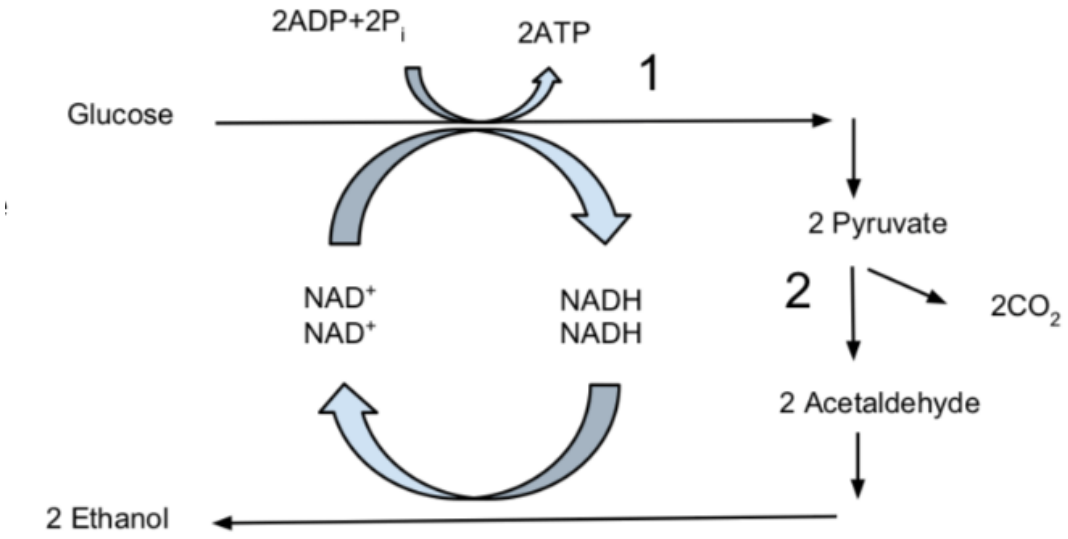


Figure 7.2.2: Alcohol fermentation, David Carmack [CC BY-SA 3.0]

Experimental Design: Rates of Alcoholic Fermentation

For this experiment, you will be attempting to answer the following question:

> "What factors influence the rate of fermentation by yeast?"

You will have the choice between one of two **independent variables**. The independent variable is the variable you are asking questions about. It should be the only thing that you establish as different between your treatment groups:

1. Type of juice used
2. Temperature of fermentation chamber

> Why would it be important to only have one independent variable?

For the **dependent variable**, you will measure the circumference of a balloon that has been placed over your fermentation flask. The dependent variable is the one that you measure to determine the influence of the independent variable on your different treatments.

> Why would the circumference of the balloon be a good indicator for the rate of fermentation? What will the balloon be collecting?

Choose an independent variable and make a prediction on how it will influence the dependent variable. This is called your **hypothesis**.

To measure the effects of the independent variable on the rate of fermentation, you'll need to establish **treatment groups** and controls. Your treatment groups should have some modification to the independent variable (such as different temperatures or different types of juice). Choose three different variations of your independent variable and record them below:

T1:

T2:

T3:

Controls are established to account for any additional variables within the experiment, as well as to give you information on whether your experiment actually worked. A **positive control** should always work (give expected results). In this experiment, fermentation should definitely occur in the positive control for this experiment. If fermentation does not occur in the positive control, you know something about your experiment is off and you could be getting false negatives. Think of a positive control you could use for your experiment and record it below:

Positive control (C+):

A **negative control** is just the opposite. In a negative control, you want to see no change from initial conditions. If there is a change in the dependent variable in the negative control, this gives you a baseline of variability that you can expect in the absence of changes to the independent variable. For example, in this experiment, a negative control should have no fermentation occurring and thus, no inflation of the balloon. However, gases can expand in higher temperatures, so a negative control placed in a warmer environment would have expansion of the balloon. This gives us some baseline data for how temperature will affect the gases in the balloon without the influence of fermentation. Think of a negative control you could use for your experiment and record it below (you may need more than one):

Negative control(s) (C-):

Now that you have designed the experiment, it is time to run it and collect data on the dependent variable. Enter your results into the table below:

Table 7.2.2: Change in Balloon Circumference During Fermentation

Treatment Group	Initial Circumference (cm)	Final Circumference (cm)	Change in Circumference (cm)

Table 7.2.3: Change in Balloon Circumference for Controls During Fermentation

Control	Initial Circumference (cm)	Final Circumference (cm)	Change in Circumference (cm)
C+			
C-			

Once you have collected your data, you need to interpret it and draw conclusions about your hypothesis.

Does the data support your hypothesis or not? Explain your answer.

Were there any variables that could have influenced your experiment that you did not control for? If so, how could you adjust this experiment to account for these on a future trial?

Consult as a class about your findings. Did everyone perform the experiment the same? Did they get the same results?

Compare the results of the class for the two different independent variables. Which had a stronger influence on rate of fermentation: the type of juice or the temperature? Attempt an explanation for these findings.

Connecting back to cellular respiration, how much ATP is produced from one molecule of glucose if a cell only goes through glycolysis?

Why do organisms ferment instead of going through the process of cellular respiration?

We used the balloon to collect gases produced during fermentation. However, the balloon was necessary for another reason (hint: it relates to the previous question). Why else did we cover the flask with the balloon?

Step 2: The Link Reaction

If oxygen is present, cellular respiration can continue (more on this in the next section). 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 $\mathrm{CO_2}$. The electrons from this broken bond are captured by another molecule of NAD+, reducing it to NADH.

Step 3: The Citric Acid (Krebs) Cycle

The acetyl-CoA enters a cycle which, much like glycolysis, involves the action of many different enzymes to release energy and transport it in energy-carrying molecules: ATP, NADH, and another electron carrier, $\mathrm{FADH_2}$. This cycle takes place within the matrix of the mitochondrion.

In the space below, draw a mitochondrion in a cell. Show where **glycolysis**, the **link reaction**, and **citric acid cycle** happen. It may help you to include the compounds involved in each stage, such as glucose, NAD+, $\mathrm{CO_2}$, and others.

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 $\mathrm{H^+}$ 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 $\mathrm{FADH_2}$ drop off their electrons at a protein complex within the **inner mitochondrial membrane.** This effectively "turns on" this protein complex, which pumps a $\mathrm{H^+}$ 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 $\mathrm{H^+}$ from the matrix into the intermembrane space. This is appropriately named the electron transport chain.

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 $\mathrm{H^+}$ from the matrix, forming a water molecule ($\mathrm{H_2O}$). 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.

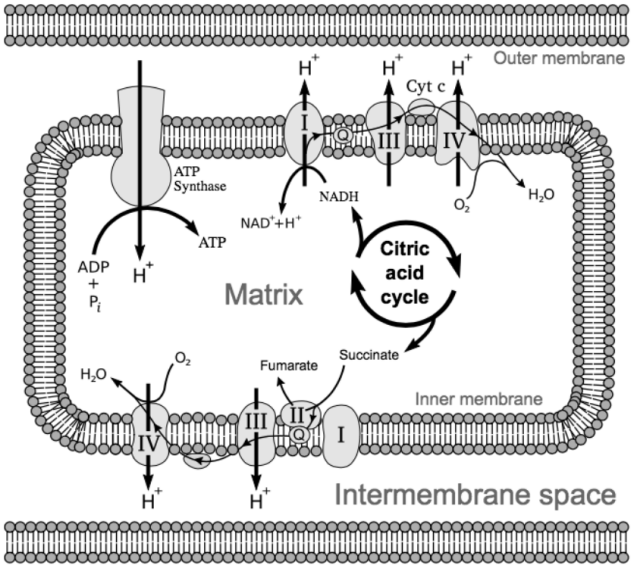


Figure 7.2.3: Mitochondrion and Electron Transport

The diagram above shows the interaction between the citric acid cycle and the electron transport chain inside the mitochondrion. There are two functioning electron transport chains and a single ATP synthase that uses the H^+ gradient established by those H^+ pumps to make 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

Experiment: Understanding the Relationship Between Cellular Respiration and Photosynthesis

1. Put 50 mL of tap water into a flask (Flask A) and add a pH indicator, such as phenol red. Record the initial color of the solution in the table below.
2. Get out a stopwatch and have a partner ready to time you. When they say go, use a straw to blow into the water + indicator. As soon as it changes color, your partner should stop the stopwatch and you should stop blowing through the straw. Record the time below.
3. Repeat step 1 to set up another flask (Flask B).
4. This time, before you blow into the straw, do 30 seconds of intense exercise, such as running around outside, jumping jacks, burpees, or something else fun. As soon as you are done, have your partner time you as you blow through the straw into the new flask. Stop as soon as the color changes and record the time below.
5. Put a sprig of Elodea (or other aquatic plant) into Flask B, cork both flasks so no gases can get in or out, and set them both under a light source.
6. Observe these flasks over the course of the lab and make note of any color changes.

Table 7.2.4: pH Changes Measured by Indicator Color

	Initial Color	Time to Change	Changes Under Light Source?
Flask A			
Flask B			

Why did the color of the indicator change when you blew into the liquid? What caused the change?

Did the pH of the solution go up or down?

Was there any difference in timing of color change between your two trials? If so, what might explain this difference?

Explain what you observed after you added the plant to Flask B.

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7.3: Concept Mapping - Connecting Ideas Visually

Either individually or as a group, create a concept map on a separate piece of paper or whiteboard that relates the processes of photosynthesis and cellular respiration. The words in the word bank below should go into bubbles. Arrange these bubbles in a way that helps communicate relationships between the words, then connect the bubbles with lines that have a verb or action phrase attached to them. It might help to start by organizing the words into related groups. You can use words more than once.

> For example, you could group CO_2 and **ATP** together, then draw a line connecting them to **RuBisCO** and **Calvin Cycle**. The verb for the connecting line could be “used in”. You could then draw a line from those two that said “produces”. What would that line connect to?
>
> **Word Bank:** Put these terms in bubbles
>
> O_2
>
> H_2O
>
> CO_2
>
> H^+
>
> ATP
>
> Glucose
>
> Photon
>
> Electrons
>
> Chloroplast
>
> Stroma
>
> Thylakoid membrane
>
> Mitochondrion
>
> Matrix
>
> Inner mitochondrial membrane
>
> Cytoplasm
>
> High energy electron carriers
>
> NADH
>
> NADPH
>
> $FADH_2$
>
> Glycolysis
>
> Krebs cycle
>
> Electron transport chain
>
> Chemiosmosis

RuBisCO

Calvin cycle

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8: PHOTOSYNTHESIS AND PLANT PIGMENTS

- Understand that colors we see are determined by reflected light and relate this to the absorption spectrum of pigments
- See how photosynthesis converts electromagnetic energy into chemical energy
- Know the stages where products and reactants of photosynthesis are produced or used, respectively
- Relate the process of photosynthesis to the structure of a leaf
- Use thin layer chromatography (TLC) to determine which pigments are present in plant tissues
- Determine the Rf values of pigments on a TLC strip
- Determine the relative polarity of a pigment based on the polarity of the TLC solvent
- Identify anatomical structures in leaves involved in photosynthesis and explain their function in this process

Photosynthesis lets plants turn sunlight into food! Using pigments like chlorophyll, they absorb light and convert it into energy. This happens in two stages: the light stage (makes ATP and NADPH) and the Calvin cycle (uses those to build glucose). Different plants use special tricks like C4 and CAM pathways to save water or work better in heat. Plus, plants also breathe—just like us—using oxygen to make energy at night!

8.1: Introduction

8.2: Pigments

8.2.1: Pigments and Evolutionary Adaptations

8.3: Discovery of Photosynthesis

8.4: Photosynthesis

8.5: Light Stage

8.6: Enzymatic Stage

8.7: C_4 Pathway

8.8: C4 and CAM Photosynthesis

8.9: True Respiration

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- Thumbnail: Diagram of a chloroplast

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8.1: Introduction

To understand photosynthesis, we must first understand a bit about light. Light is a form of **electromagnetic energy**, meaning it travels as a wave and does not require a medium to move through. Light, unlike sound, can travel to us from the sun through the vacuum of space. Once it gets to Earth, there are particles for it to either reflect off of, be absorbed by, or pass through. Depending on the length of the light wave--think about stretching or compressing a slinky--and whether it is reflected or not, our eyes will either interpret it as different colors, or we will not be able to see it at all. In fact, our eyes only pick up a tiny fraction of the light spectrum.

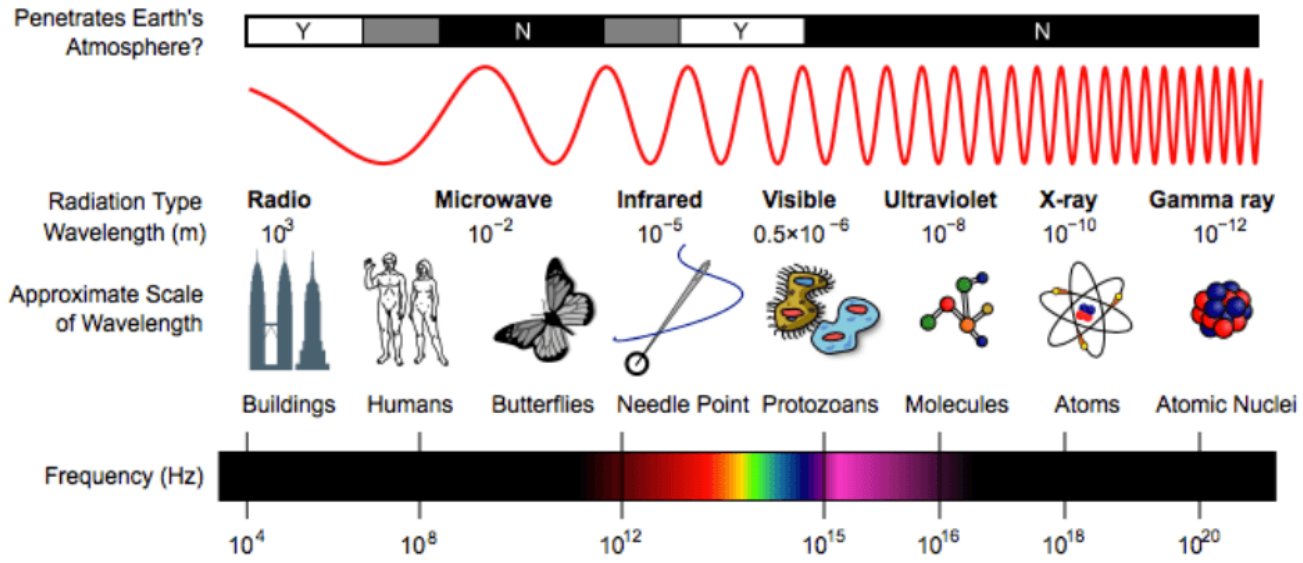


Figure 8.1.1: The Electromagnetic Spectrum, Inductive load by NASA via Wikimedia Commons [CC BY-SA 3.0]

When we look at objects, we may see them as being a certain color. This is because that object reflects that particular wavelength of light back at us. Objects that are white reflect the entire spectrum back at us. Objects that are truly black absorb all of the light, reflecting nothing back. Objects that are a particular color, such as green, absorb all of the other wavelengths of visible light except green, reflecting that green out to our eyes. **Pigments** are molecules that reflect specific colors.

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8.2: PIGMENTS

The molecule **chlorophyll a** has a specific shape. This shape causes wavelengths of light that we see as a dark bluish green to be reflected back. Change the shape of that molecule by adding only two atoms, making it **chlorophyll b**, and the light that is reflected back is now less blue and more yellow.

What does this have to do with photosynthesis? Organisms that perform photosynthesis do so by absorbing light and converting it into usable energy. This absorbed light is not reflected back. This means that the color of the pigment(s) that the organism has will determine the wavelengths of light that the organism can use. For example, plants have two types of chlorophyll molecules, chlorophyll a & b. Each of these reflects green light, meaning that green light cannot be used for photosynthesis. To help capture a bit more of the spectrum, plants have accessory pigments called carotenoids that reflect yellow, orange, and red light, absorbing a portion of the green part of the spectrum.

Chlorophylls tend to mask most other pigments in plants, so to see these other pigments, we need to separate them. You will use a process called **thin layer chromatography** to extract pigments from leaves, then dissolve them in a solvent.

Thin Layer Chromatography (TLC)

> Note
>
> Below is a list of suggested materials. Spinach is suggested for the leaves, as it is easy to acquire and rich in pigment. However, consider comparing the pigments in different types of leaves for a more interesting experiment.

Materials needed:

- Mortar and pestle
- Sand or similar material
- Soft leaves (e.g. spinach)
- Extraction solvent: 3 parts propanone to 2 parts ethoxyethane (diethyl ether)
- Capillary tubes
- Test tubes and corks
- TLC paper strips (cut to size of test tube--about 1 cm less in length)
- Chromatography solvent: 5 parts cyclohexane, 3 parts propanone, and 2 parts ethoxyethane
- Pencil
- Forceps

Procedure for Thin Layer Chromatography

1. **Extracting the pigments**.
   a. Prepare your TLC strip by drawing a line across the paper in pencil 2 cm from the bottom of the strip and set aside. **Important note**: Handle the strip as little as possible so oils from your hands do not interfere with the process.
   b. Under a hood or in a well-ventilated room, put some of the leaves into the mortar with a little bit of sand (to help break the tissue apart) and some extraction solvent.
   c. Grind the leaves with the pestle until they have turned to mush. You may need to add more extraction solvent as it soaks into the leaf tissue.
2. **Thin layer chromatography**.
   a. Pull the mush to one side of the mortar. Place the end of a fine capillary tube into the liquid, then transfer the liquid in the tube to a point in the center of your line.
   b. Repeat this process, drawing more liquid from the mortar, until you have a small, concentrated dot of pigment. For best results, keep the dot as concentrated in one place as possible.
   c. Under a hood, add 1 cm of chromatography solvent to your test tube and place this in a test tube rack (label your tube if multiple people are using the same rack).
   d. Add your strip to the tube with the line you drew in pencil sitting about 1 cm above the level of the solvent, then cork the

tube.

3. **Calculating Rf values and determining polarity**.
    a. Check on your TLC strip regularly and have a pencil with you. When the solvent has traveled up the TLC strip about 1 cm from the top of the strip, remove the strip from the test tube and draw a line in pencil at the edge of the solvent front.
    b. Allow the strip to dry, then measure the distance from the original line you drew (where the pigment started) to the solvent front.
    c. Next, measure the distance from where the pigment started to the farthest point that each pigment traveled.
    d. Calculate the Rf value of each pigment: divide the distance the pigment traveled by the distance the solvent traveled.

Both the chromatography solvent and the extraction solent you used are **nonpolar** compounds, meaning they lack residual charges. Nonpolar compounds dissolve well in nonpolar solutions, while polar compounds do not. Pigments that are more nonpolar will dissolve better in this solvent, traveling farther up the strip. More **polar** pigments that have residual charges (like water) will not interact much with the solvent, staying closer to the bottom of the strip. High Rf values from TLC using a nonpolar solvent means the pigment is more nonpolar. Lower Rf values mean the pigment is more polar.

Draw or tape your TLC strip and label as many pigments as you can (see the next page for more information on pigments). Record the Rf values of each pigment next to its label.

Which pigment is more polar, chlorophyll a or chlorophyll b? How can you tell?

How many pigments were present in your leaf sample?

Which pigments were the most nonpolar (least polar, highest Rf values)?

If there were polar pigments in the leaves and you used a nonpolar solvent to extract the pigments from the leaf, would they dissolve and be present in the solution you used to run your TLC experiment? How might this impact your results?

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8.2.1: Pigments and Evolutionary Adaptations

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8.2.1: Pigments and Evolutionary Adaptations

Cyanobacteria were potentially the first organisms to do oxygenic photosynthesis -- the variety of photosynthesis that produces oxygen as a waste product. To do this, cyanobacteria use the pigment chlorophyll a. This is the only pigment directly involved in photosynthesis, but other pigments called accessory pigments can absorb wavelengths of light, then transfer this energy to chlorophyll a. Cyanobacteria have accessory pigments called **phycobilins** that allow them to absorb more of the blue and red portions of the spectrum of light. The pigment **phycocyanin**, a blue phycobilin, resulted in the cyanobacteria's more common name: blue-green algae.

> Which part of the spectrum of light do you think phycocyanin absorbs?

The red algae were the first lineage of organisms to have true chloroplasts, derived from the endosymbiosis of a cyanobacterium, and so they have the same pigments: chlorophyll a and phycobilins. In particular, the red algae derive most of their coloring from a red phycobilin called **phycoerythrin**. This pigment reflects red, meaning it absorbs the blue portion of the spectrum.

Red algae are almost entirely marine and have been found deep in the water column. The record for algal depth was set by a coralline red alga found 268 m (about 880 feet) below the surface. Why is this so impressive? As light travels through water molecules, much of it is reflected back or refracted off course. High-energy blue light is more likely to penetrate deeper into the water column, so it is essential that the algae are able to capture it. Because both chlorophyll a and phycocyanin would reflect much of this blue light instead of absorbing it, red algae make use of phycoerythrin to capture it, making them appear red.

Green algae are more likely to live in shallow marine waters, freshwater, or even terrestrially. This group of organisms has lost the phycobilins present in its red algal ancestors and has adapted chlorophyll b and carotenoids, instead. **Carotenoids** can help mitigate damage caused by solar radiation, as well as absorb some of the green parts of the spectrum. These pigments are reds, oranges, and yellows..

As you saw in your TLC strip, chlorophyll b appears more yellow while chlorophyll a appears more blue. What portion of the spectrum is chlorophyll b absorbing that chlorophyll a is not?

> What color were the carotenoids on your TLC strip?
>
> Where might you see carotenoids in your daily life?
>
> Brown algae have chlorophyll a and chlorophyll c, as well as the carotenoid **fucoxanthin**, which gives them their golden brown color. Compare the available specimens of cyanobacteria, red algae, green algae, and brown algae. What do the colors of these organisms tell you about where they live?
>
> Which pigment do all of these organisms have?

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8.3: Discovery 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 willow tree experiment. He started with a willow tree of 2.27 kg. Over 5 years, it grew to 67.7 kg. However, the weight of the soil only decreased by 57 grams. Van Helmont came to the conclusion that plants must take most of their weight from water. He did not know about gases.

Joseph Priestley ran a series of experiments in 1772 (Figure 8.3.1). 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.

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 8.3.2) using a crystal prism. He found that *Spirogyra* algae produce oxygen mostly in the blue and red parts of the spectrum. This was a huge find. It tells that the key photosynthetic pigment should accept blue and red rays, and thus reflect green rays. Blue-green **chlorophyll** best fits this description.

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 (Figure 8.3.3). However, the reverse is not exactly true, and light is able to intensify

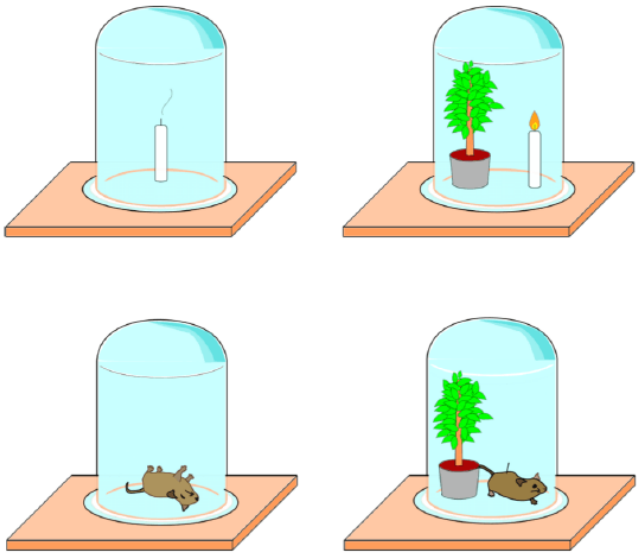


Figure 8.3.1 Experiments of J. Priestley (1772).

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**. The first is a **light stage**. This stage relates to the intensity of the light. The second stage is the **enzymatic** (light-independent) stage which relates more with the temperature. Light reactions depend on the amount of light and water; they produce oxygen and energy in the form of ATP. Enzymatic reactions depend on carbon dioxide and water; they take energy from the light reactions and produce carbohydrates. Sometimes, enzymatic stage is called "dark" but it is not correct because in darkness, plant will run out of light-stage ATP almost immediately. Only some C_4-related processes (see below) could run at night.

Since water molecules are spent on light stage to make oxygen and at the same time are accumulating (see below), one of the

best “equations” describing photosynthesis as a whole is

$$CO_2 + H_2O + light \rightarrow carbohydrates + H_2O + O_2 \tag{8.3.1}$$

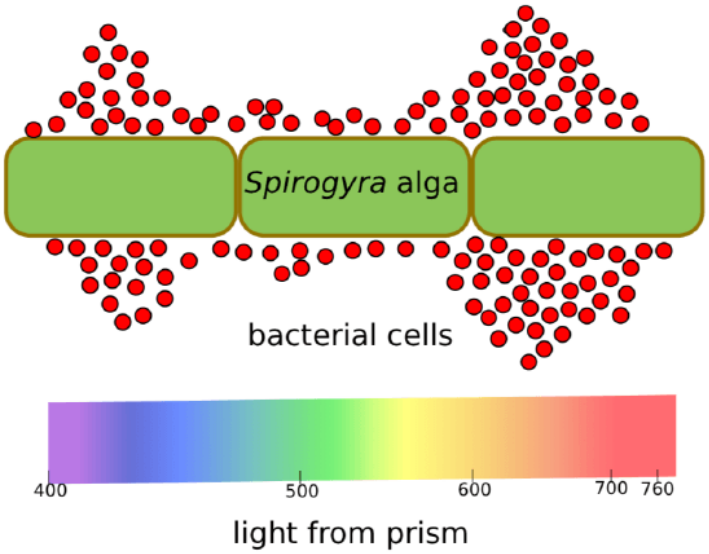


Figure 8.3.2 Experiment of Th. Engelmann (1881).

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8.4: Photosynthesis

Photosynthesis is a process used to harness the energy from sunlight to ultimately bond carbon atoms from carbon dioxide into molecules of glucose. This occurs in two major phases--the light dependent phase and the light independent phase--and requires chlorophyll a. Both phases take place inside of the chloroplasts of eukaryotic photosynthesizers or across folded membranes within prokaryotes. For simplicity's sake, we will focus on the eukaryotes and describe these processes in relation to chloroplast anatomy (sorry, bacteria, back seat again).

Anatomy of a Chloroplast

Chloroplasts are surrounded by at least two membranes. The two membranes were derived from the original cyanobacterium that was engulfed but not digested (Keeling, 2004). Inside of the inner membrane, the chloroplast has a jelly-like matrix, much like the cytosol of the cell, called the **stroma**. The stroma surrounds a series of folded membrane-bound structures, **thylakoids**, that resemble pancakes and are stacked (again, much like pancakes) into columns called **grana** (granum, singular). The thylakoids appear dark green, as the **thylakoid membrane** is full of chlorophyll molecules. Enclosed inside each thylakoid is a region called the **thylakoid space**.

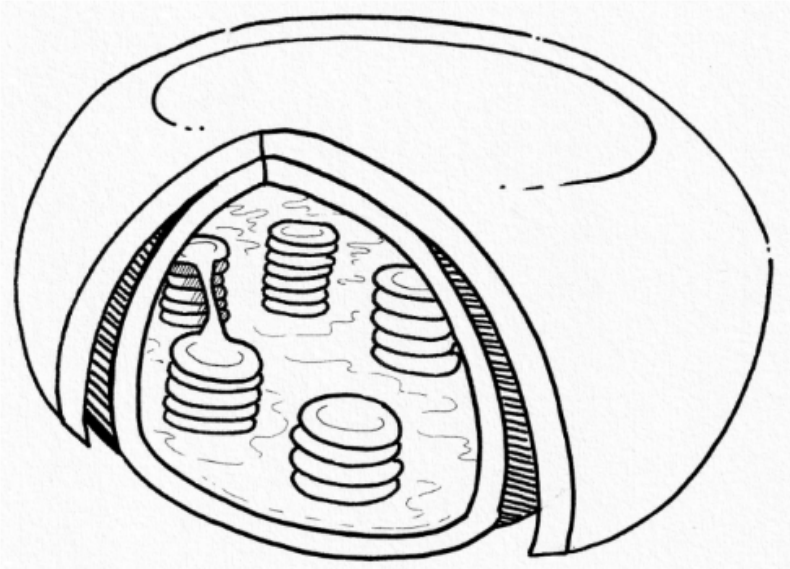


Figure 8.4.1: Diagram of a chloroplast

Label the bolded structures in the diagram of the chloroplast. Indicate the origin of each membrane of the chloroplast.

Light-dependent Phase: The electron Transport Chain

This phase is called the light-dependent phase because to begin this process, a particle of light, called a **photon**, of the correct wavelength must be absorbed by a molecule of chlorophyll a, embedded in a complex called photosystem II (**PSII**).

The energy from the photon causes an electron to be knocked off of the chlorophyll molecule and this electron is shuttled to an adjacent protein complex. More on this in a second.

The chlorophyll molecule needs to replace the electron it lost so that it is ready to respond to the next photon. A water molecule is split at the base of PSII, releasing two electrons and producing oxygen and 2 protons (H^+) into the thylakoid space. Make note of each time H+ is added to the thylakoid space, as this creates a buildup of positive charges, which repel each other.

Back to that first electron. The protein complex it is shuttled to is a proton pump. When the electron enters the protein complex, it effectively switches on the proton pump, causing H^+ to be pumped from the stroma and into the thylakoid space.

The electron then jumps to another proton pump, causing another H+ to be pumped from the stroma into the thylakoid space.

This electron has depleted much of its energy, so it must enter another photosystem (**PSI**) to be reenergized by another photon.

The re-energized electron is then transported to an enzyme called **NADP+ reductase**, which reduces (adds electrons to) a molecule of NADP+ to create high-energy **NADPH**. This requires two electrons, but this process involves a continuous flow of electrons, so another one arrives shortly after the first.

This is the end of the **electron transport chain**. However, there is another component to this phase. Inside the thylakoid membrane, H^+ are building up, creating a storage of energy across the thylakoid membrane as they repel against each other. Even though they are tiny (a single proton), they cannot pass freely through the membrane due to the positive charge.

Instead, an enzyme called ATP synthase allows the H^+ passage to the other side. The flow of H^+ through the enzyme causes it to spin, much like a turbine, converting the stored energy into kinetic energy (movement).

ATP synthase converts this kinetic energy into chemical energy by using it to add phosphate groups onto molecules of ADP. This creates unstable, high energy **ATP** molecules that can be used to power other cellular processes.

Apply it: Work with your labmates to design a model that illustrates the light-dependent phase of photosynthesis. Consider the materials available in lab (including, potentially, other students), as well as whether your model will have moving parts. What is the best way to communicate this process?

> Below is an example of a model of the electron transport chain in photosynthesis. Can you talk your way through what is happening? Try explaining this process to a partner.

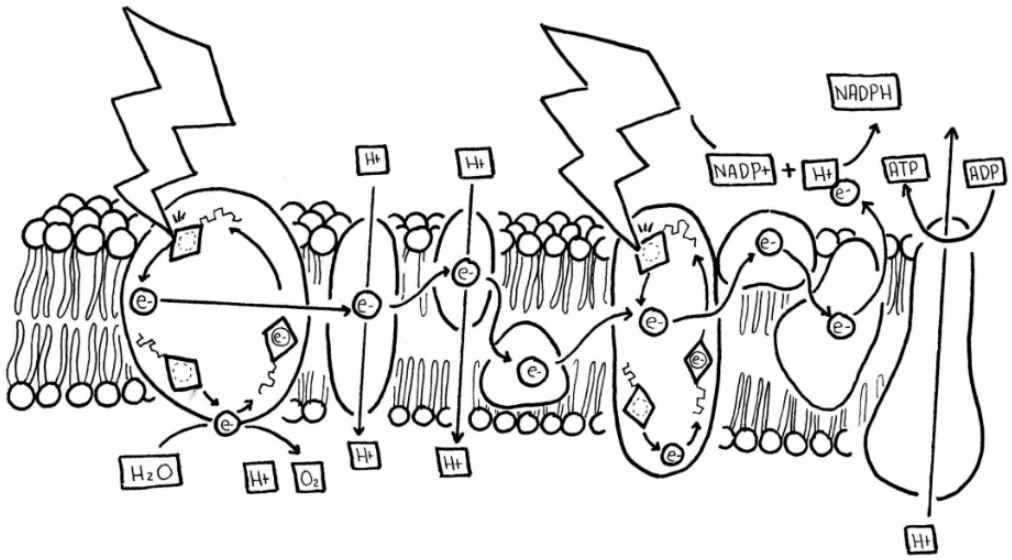


Figure 8.4.1: Diagram of photosynthesis Electron transport chain

Light-independent Phase: The Calvin Cycle

The light-independent phase takes place in the stroma of the chloroplast. During this phase, called the **Calvin Cycle**, the chemical energy stored in the NADPH and ATP produced during the light-dependent phase is used to build molecules of glucose. This happens in three major stages.

1. **Carbon Fixation**: Carbon dioxide (CO_2) enters the plant through the stoma, diffuses into the cells, then into the chloroplast. An enzyme called **RuBisCO** (a much easier way to say Ribulose-1, 5-bisphosphate carboxylase/oxygenase) bonds CO_2 to a 5-carbon molecule called RuBP. This breaks into two 3-carbon molecules of 3-PGA.
2. **Reduction**: NADPH donate electrons and ATP donates a phosphate group to convert each 3-PGA into G3P, two of which are required to make glucose. For every six G3P made, only one goes on to make glucose, the rest must be recycled.
3. **Regeneration**: To keep the cycle going, RuBP must be regenerated. Using energy and phosphate donated by more ATP, five

G3P are recycled to make three more RuBP.

This process can happen during day or night, but it requires a steady input of ATP, NADPH and CO_2.

The reactants above are required to complete this process. What are the products of the light independent phase?

For each of the products and reactants in the chemical reaction for photosynthesis written below, identify where it was either produced or consumed.

Table 8.4.1: Summary Table for Photosynthesis

Phase	Where does it take place?	Reactants	Products
Light dependent			
Light independent			

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8.5: Light Stage

The light stage participants include photosystems (“chlorophyll”), light, water, ATPase, protons, and a hydrogen carrier ($NADP^+$).

The basic idea of light stage is that *the cell needs ATP* to assemble (later) carbon dioxide into sugar (Figure 8.5.2). To make ATP, the cell needs electrical current: **proton pump**. To make this current, the cell needs the difference of electric charge (difference of potentials) between **thylakoid** (vesicle or membrane pocket) and **matrix** (stroma) compartments of the chloroplast (Figure 2.3.1). To make this difference, the cell needs to segregate ions: positively charged go from outside and stay inside, negatively charged go from inside to outside. To segregate, the cell needs the energy booster—sun rays caught by the **chlorophyll** molecules embedded in the thylakoid membrane. The chlorophyll molecule is non-polar (similarly to membrane lipids) and contains magnesium (Mg). It is easy to excite the chlorophyll molecule with light; excited chlorophyll may release the electron if the energy of light is high enough.

To make carbo*hydrates* from carbon dioxide (CO_2 apparently has no hydrogen), the cell needs hydrogen atoms (H) from hydrogen carrier, NADP+ which at the end of light stage, becomes NADPH.

The main event of the light stage is that chlorophyll reacts with light, yielding electron (e^-) and becoming oxygenated, positively charged molecule. Then electron, proton and $NADP^+$ react to yield NADPH which will participate in enzymatic reactions later on. The positively

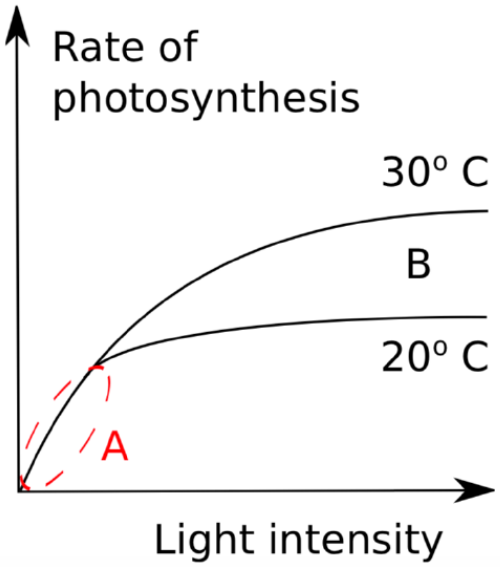


Figure 8.5.1 *Explanation of experiment of F. Blackman (1905). A—low light, little tempera- ture effect; B—high light, significant temperature effect.*

charged chlorophyll is extremely active chemically, therefore it splits water molecules (“photolysis of water”) into protons (which accumulate inside thylakoid), oxygen (O_2) and electron. The electron returns to chlorophyll. When increasing gradient reaches the threshold, the **proton pump** starts to work as protons (H^+) pass along the gradient. The energy of passing protons allows for the ATP synthesis from ADP and P_i (inorganic phosphate). On the other side of membrane, these protons make water with hydroxide ions.

In the previous paragraph, “chlorophyll” is actually two photosystems: photosystem II (P680) and photosystem I (P700). Photosystem II (contains chlorophyll and carotenes) is more important. It splits water, makes proton the gradient and then ATP, and forwards electrons to photosystem I. Photosystem I contains only chlorophylls and makes NADPH.

Ultimately, the light stage starts from light, water, $NADP^+$, ADP and results in an accumulation of energy (ATP) and hydrogen (NADPH) with a release of oxygen which is a kind of exhaust gas (Figure 2.3.1).

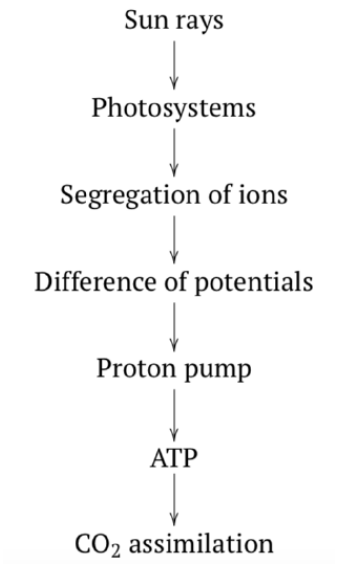


Figure 8.5.2 The logical chain of light stage reactions (hydrogen carrier not shown).

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8.6: Enzymatic Stage

The enzymatic stage has many participants. These include carbon dioxide, hydrogen carrier with hydrogen (NADPH), ATP, ribulose biphosphate (RuBP, or C_5), and Rubisco along with some other enzymes. Everything occurs in the matrix (stroma) of the chloroplast.

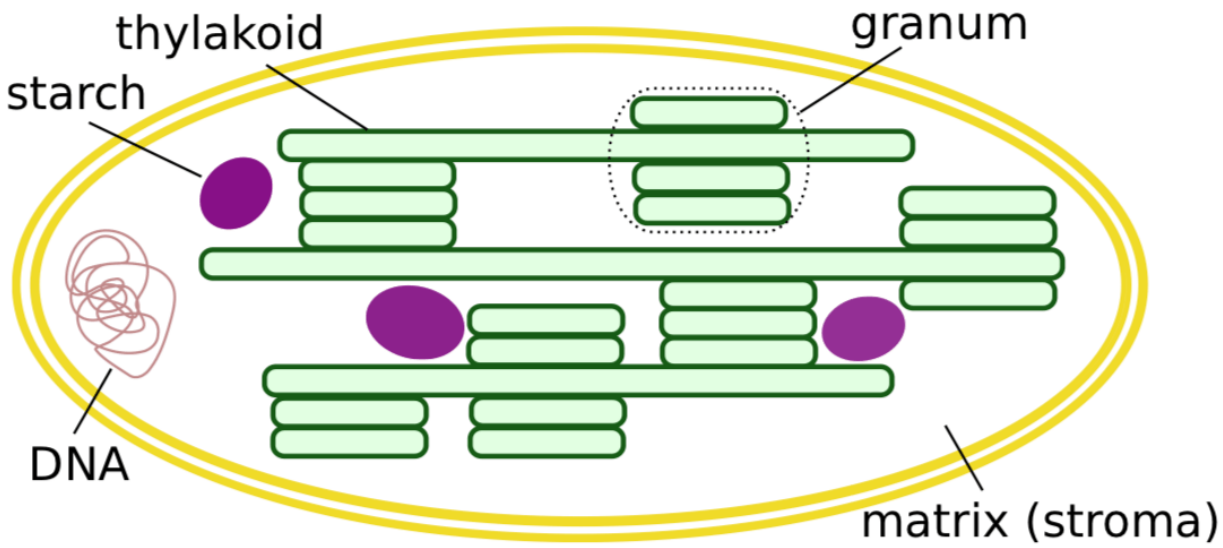


Figure 8.6.1 Chloroplast.

The main event of the enzymatic stage is CO_2 assimilation with C_5 into short-living C_6 molecules. Assimilation requires Rubisco as an enzyme. Next, this temporary C_6 breaks into two C_3 molecules (PGA). Then, PGA will participate in the complex set of reactions which spend NADPH and ATP as sources of hydrogen and energy, respectively; and yields (through the intermediate stage of PGAL) one molecule of glucose ($C_6H_{12}O_6$) for every six assimilated molecules of CO_2. $NADP^+$, ADP and P_i will go back to the light stage. This set of chemical reactions returns RuBP which will start the new cycle of assimilation. Consequently, all reactions described in this paragraph are part of the cycle which has the name “Calvin cycle” or “C_3 cycle” (because the C_3 PGA molecules here are most important).

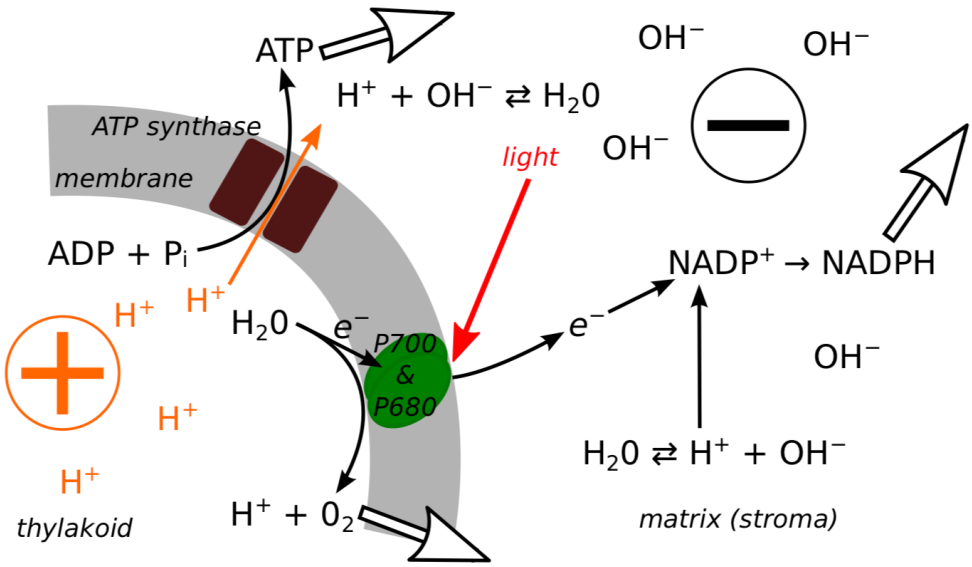


Figure 8.6.2 Scheme of the enzymatic stage of photosynthesis. Numbers in green show how carbon is assimilated without changing the amount of RuBP.

In all, enzymatic stage starts with CO_2, NADPH, ATP and C_5 (RuBP). It ends with glucose ($C_6H_{12}O_6$), NADP+, ADP, P_i and the same C_5. With an addition of nitrogen and phosphorous, glucose will give all other organic molecules (Figure 8.6.3).

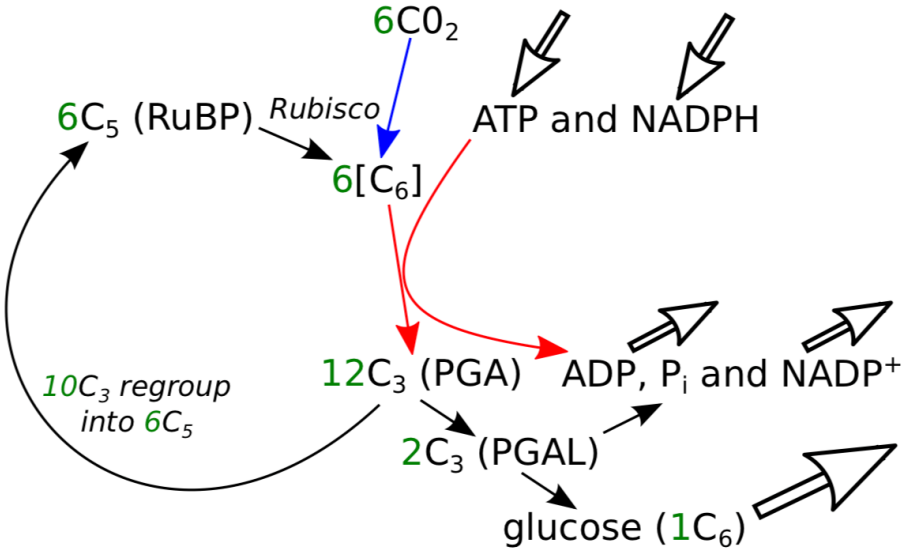


Figure 8.6.3 *Scheme of the enzymatic stage of photosynthesis. Numbers in green show how carbon is assimilated without changing the amount of RuBP.*

To summarize, the logic of photosynthesis (Figure 8.6.4) is based on a simple idea: *make sugar from carbon dioxide*. Imagine if we have letters “s”, “g”, “u”, and “a” and need to build the word “sugar”. Obviously, we will need two things: the letter “r” and the energy to put these letters in the right order. The same story occurs in photosynthesis: it will need hydrogen (H) which is the “absent letter” from CO_2 because sugars must contain H, O and C. NADP$^+$/NADPH is used as hydrogen supplier, and energy is ATP which is created via proton pump, and the proton pump starts because light helps to concentrate protons in the reservoir.

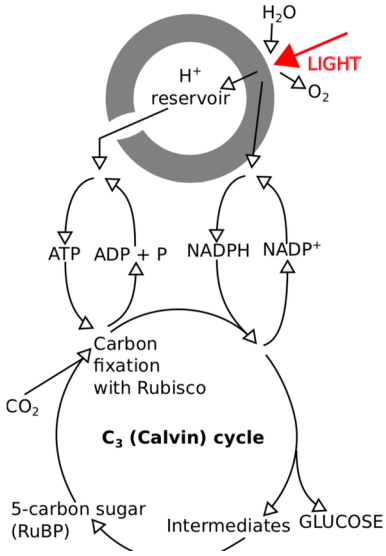


Figure 8.6.4 Summary of the photosynthesis. (Based on the idea from Arms & Camp, 1986).

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8.7: C_4 Pathway

Rubisco is the enzyme of extreme importance since it starts the assimilation of carbon dioxide. Unfortunately, Rubisco is "two-faced" since it also catalyzes photorespiration (Figure 8.7.1). **Photorespiration** means that plants take oxygen instead of carbon dioxide. Rubisco catalyzes photorespiration if there is a high concentration of oxygen (which usually is a result of intense light stage). Rubisco oxygenates C_5 (RuBP) which turns into PGA and PGAL, becoming glycolate. This glycolate is returned to the Calvin cycle when the cell uses peroxisomes and mitochondria, and spends ATP. The process of photorespiration wastes C_5 and ATP which could be more useful to the plant in other ways.

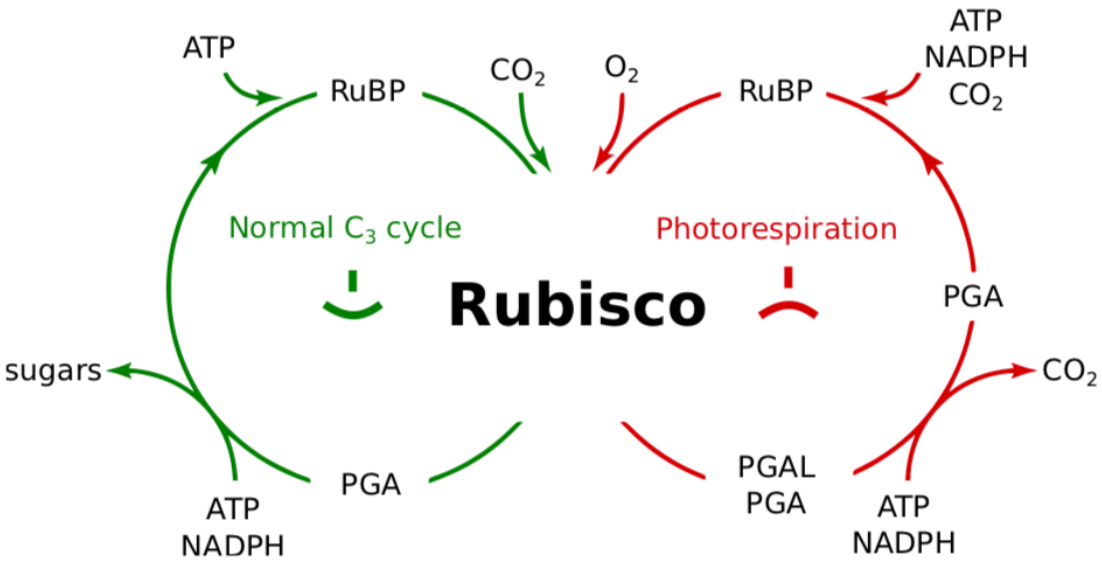


Figure 8.7.1 Rubisco is two-faced enzyme.

If concentration of CO_2 is high enough, assimilation will overcome photorespiration. Consequently, to minimize the amount of photorespiration and save their C_5 and ATP, plants employ **Le Chatelier's principle** ("**Equilibrium Law**") and increase concentration of carbon dioxide. They do this by temporarily bonding carbon dioxide with PEP (C_3) using carboxylase enzyme; this results in C_4 molecules, different organic acids (like malate, malic acid) with four carbons in the skeleton. When plant needs it, that C_4 splits into pyruvate (C_3) plus carbon dioxide, and the release of that carbon dioxide will increase its concentration. On the final step, pyruvate plus ATP react to restore PEP; recovery of PEP does cost ATP. This entire process is called the "**C_4 pathway**" (Figure 8.7.2).

Plants that use the C_4 pathway waste ATP in their effort to recover PEP, but they still outperform photorespiring C_3-plants when there is an *intensive light and/or high temperature and consequently, high concentration of oxygen*. This is why in the tropical climate, C_4-crops are preferable.

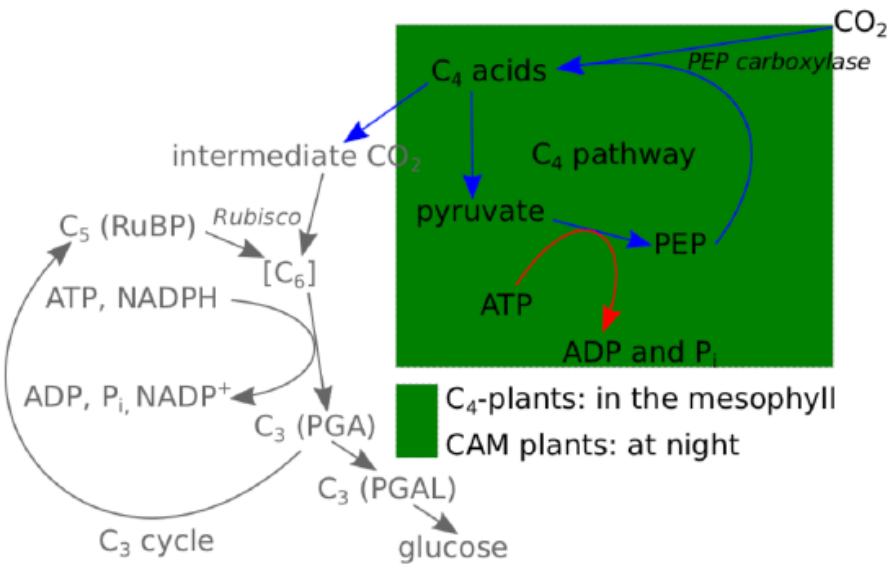


Figure 8.7.2 *C_4 pathway (in blue).*

Two groups of plants use the C_4 pathway. Many desert or dryland plants are CAM-plants which drive the C_4 pathway at night. They make a *temporal separation* between the accumulation of carbon dioxide and photosynthesis. CAM-plants make up seven percent of plant diversity, and have 17,000 different species (for example, pineapple (*Ananas*), cacti, Cactaceae; jade plant, *Crassula* and their relatives).

"Classic" C_4 plants drive C_4 pathway in leaf mesophyll cells whereas their C_3 is located in so-called **bundle sheath cells**. This is a *spatial*, rather than temporal separation. These C_4-plants make up three percent of plant biodiversity and have more than 7,000 different species (for example, corn, *Zea*; sorghum, *Sorghum* and their relatives). In all, both variants of C_4 pathway relate with concentration of carbon dioxide, spatial or temporal (Figure 8.7.3). Both are called "carbon-concentrated mechanisms", or CCM.

There are plants which able to drive both C_3 and C_4 pathways (like authograph tree, *Clusia*), and plants having both "classic" C_4 and CAM variants (like *Portulacaria*).

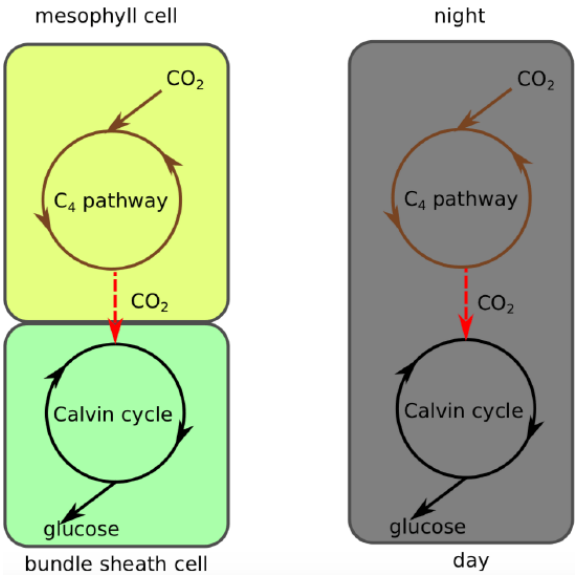


Figure 8.7.3 C_4 plants (left) and CAM plants (right).

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8.8: C4 and CAM Photosynthesis

The enzyme RuBisCO needs a high CO_2 environment to function efficiently. If the ratio of oxygen to CO_2 gets too high, RuBisCO will bind oxygen instead and waste energy in the process. This is called **photorespiration** and accounts for a large amount of yield loss for crops in hot areas. Why does photorespiration happen?

If it is too hot or dry, plants often close their stomata to prevent water loss. This prevents CO_2 from entering the leaf, as well as prevents O_2 from exiting. Oxygen builds up inside the leaf and photorespiration happens instead of the Calvin cycle. Though this wastes energy for the plant, preventing water loss is often a larger priority. However, some plants have evolved special ways of performing photosynthesis that prevent or limit photorespiration.

C4 Photosynthesis is for Plants Adapted to Hot Environments

In most photosynthesis, the first product of the Calvin cycle is a 3 carbon compound, so this type of photosynthesis is called C3. For plants adapted to particularly hot environments, the first compound formed has 4 carbon atoms, hence **C4 photosynthesis**. In these plants, RuBisCO is restricted to the bundle sheath cells of the leaf. Carbon dioxide is converted into an acid and transported into the bundle sheath cells where it will be converted back into CO_2. This keeps the concentration high where RuBisCO is active, preventing photorespiration.

CAM Photosynthesis is for Plants Adapted to Dry Environments

CAM plants are often found in desert environments. It is too hot and/or dry to keep stomata open during the day, so they only open them at night. However, there is no light at night to do photosynthesis. To solve this, CAM plants have evolved to take in CO_2 at night and store it in the central vacuole in the form of an acid. This is where CAM gets its name: Crassulacean Acid Metabolism. During the day, the acid is converted back into CO_2, and the Calvin cycle can take place alongside the electron transport chain.

In both of these types of photosynthesis, compounds must be formed, transported, and broken back apart again. Each of these tasks costs energy to perform, but it outweighs the energy lost by photorespiration.

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8.9: True Respiration

The common misconception about plants is that their only energy-related metabolic process is photosynthesis:

$$CO_2 + H_2O + \text{energy} \longrightarrow \text{carbohydrates} + O_2$$

However, as most eukaryotes, plants have mitochondria in cells and use *aerobic* (oxygen-related) respiration to obtain energy:

$$\textbf{carbohydrates} + \mathbf{O_2} \longrightarrow \mathbf{CO_2} + \mathbf{H_2O} + \textbf{energy}$$

Typically, plants spend much less oxygen in respiration than they make in photosynthesis. However, at nights plants do exactly the same as animals, and make only carbon dioxide!

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9: TISSUES AND ORGANS - HOW THE PLANT IS BUILT

Learning Objectives

- Identify the major types of plant tissues and their functions.
- Describe how tissues are organized into plant organs such as roots, stems, and leaves.
- Compare the anatomical differences between monocots and dicots.
- Explain how plants grow through primary and secondary growth.
- Recognize structural adaptations of plant organs to different environmental conditions.

Plants are built from tissues and organs that help them grow, survive, and thrive. Tissues like epidermis protect, parenchyma stores and photosynthesizes, and vascular tissues (xylem and phloem) move water and food. Organs include roots (anchor and absorb), stems (support and transport), and leaves (photosynthesize). Each part has special structures and adaptations to help plants live in different environments.

9.1: Tissues

9.2: Organs and Organ Systems

9.3: The Leaf

9.3.1: Inside Leaves

9.4: The Stem

9.4.1: Inside Stems

9.5: The Root

9.5.1: Inside Roots

9.6: Atlas- Roots, Steams, and Leaves

9.6.1: Roots

9.6.1.1: Primary Growth

9.6.1.1.1: Root Long Section (Zea mays)

9.6.1.1.2: Monocot Roots

9.6.1.1.3: Eudicot Root Cross Section (Ranunculus)

9.6.1.2: Secondary Growth

9.6.1.3: Root Systems

9.6.2: Stems

9.6.2.1: Primary Growth

9.6.2.2: Secondary Growth

9.6.2.3: Woody Shoot Structures

9.6.2.4: Modified Shoots

9.6.3: Leaves

9.6.3.1: Leaf Parts and Arrangement

9.6.3.2: Monocot Leaves

9.6.3.3: Eudicot Leaves

9.6.3.3.1: Adaptations to Water Availability

9.6.3.4: Modified Leaves

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9.1: Tissues

From now on, we will frequently use multiple names of plants$_2$ group, they are summarized on Figure 9.1.1, and in more details—on Figure 6.1.1.

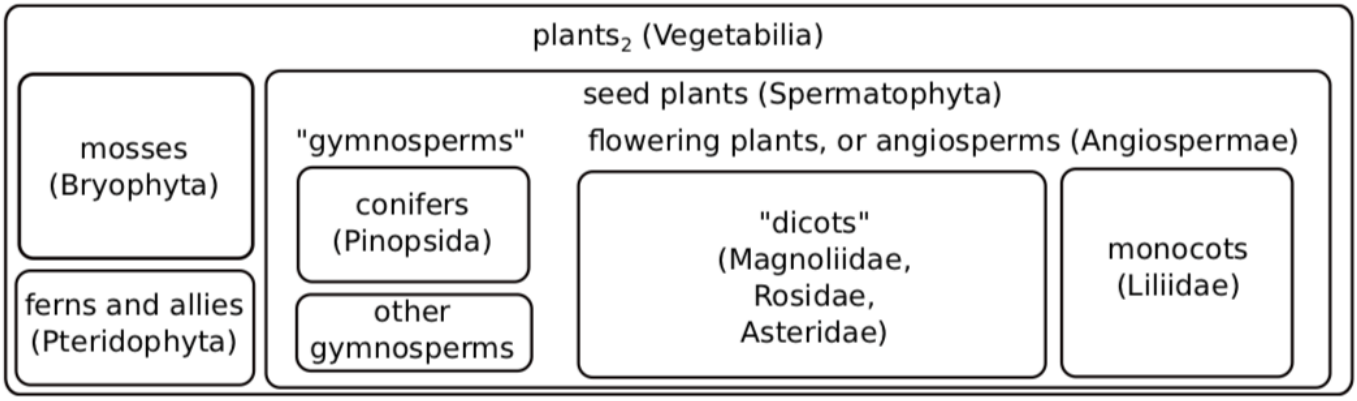


Figure 9.1.1 Plants$_2$ classification: overview.

Epidermis and Parenchyma

Why did plants go on land? In order to escape competition with other plants for resources like the sun and nutrients, but also to obtain much more sunlight that was otherwise seriously reduced underwater. The move to land also helped plants escape predators. Lastly, plants benefited from this change because they escaped from the **temperature-gases conflict**: warmer temperatures are good for organisms but significantly decrease the amount of gases diluted in water.

Although this action solved several problems, it also raised new issues that needed to be dealt with. The most important was the risk of drying out. To combat this, plants developed their first **tissue**: epidermis (complex surface tissue) covered with a cuticle (plastic-like isolation layer) which served a purpose similar to a plastic bag. For the really small (millimeters) plant it is enough because, in accordance to surface / volume law (i.e., when body size grows, body surface grows slower then body volume (and weight)), they have high relative surface, and diffusion can serve for gas exchange. However, bigger plants also need to exchange gases, and they developed stomata which served as a regulated pore system. The remaining cells became second tissue: parenchyma (tissue or cell type of spherical, roughly connected living cells) or ground tissue (same as parenchyma (see) but only applied for tissue), or **main tissue**).

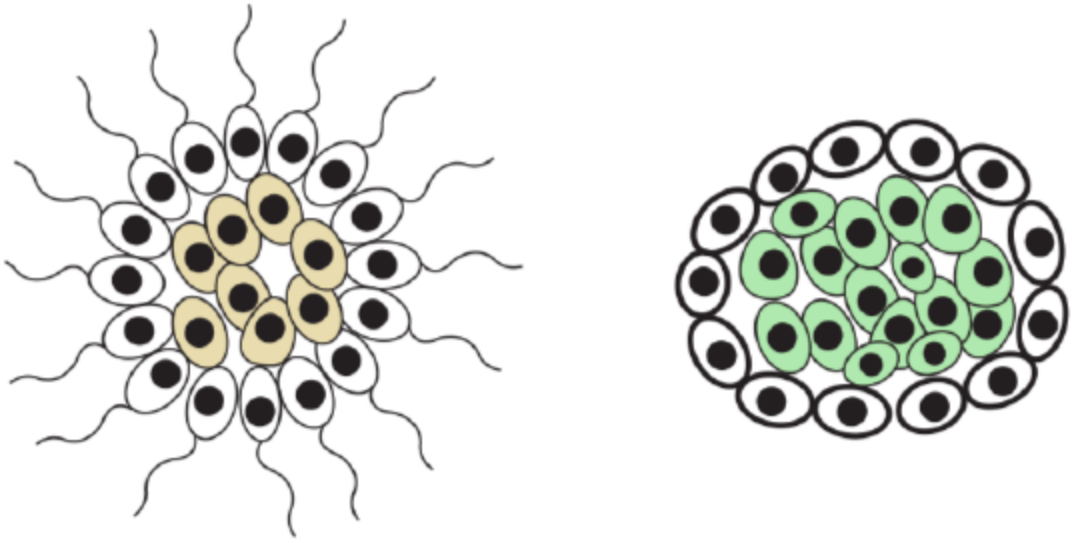


Figure 9.1.2 Phagocytella (proto-animal) with kinoblast and phagocytoblast vs. proto-plant with epidermis and ground tissue.

Another response (Figure 9.1.3) for drying was a development of *poikilohydricity* (see below), the ability to hibernate in (almost) dried condition. As hibernation is generally dangerous since it requires "system restart", that evolutionary route did not become the main. Tissue is a union of cells which have common origin, function and similar morphology. Tissues belong to organs: organ is a union of different tissues which have common function(s) and origin. Plants have simple and complex tissues. The simple tissues (tissues with uniform cells) are composed of the same type of cells; complex tissues (tissues with more than one type of cells) are composed of more than one type of cell, these are unique to plants.

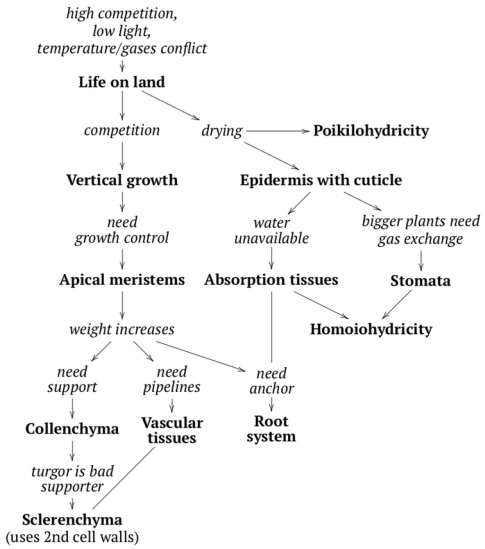


Figure 7.14.

Parenchyma (Figure 9.1.4) 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*. 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). Contrary to parenchyma (which is a simple tissue), **epidermis** is a complex tissue composed of epidermal and stomata cells. Its main functions are *transpiration, gas exchange and defense*.

As it seen here, plants acquired tissues in a way radically different from animals (Figure 9.1.2): while plants regulate gas and water exchange in response to terrestrial environment, animals actively hunt for food (using kinoblast tissues) and then digest it (with pagocytoblast tissue).

Supportive Tissues: Building Skyscrapers

When more and more plants began to move from the water to the land, competition once again became a problem (Figure 9.1.3). To solve this, plants followed “Manhattan solution”: they grew vertically in order to be able to escape competition for the sunlight and therefore must develop **supportive tissues**.

Collenchyma (Figure 9.1.4) is living supportive tissue that has elongated cells and a thick primary cell wall. Its main function is the mechanical support of young stems and leaves via turgor.

Sclerenchyma (Figure 9.1.4) is a dead supportive tissue that consists of long fibers or short, crystal-like cells. Each cell has a 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.

Three times in their evolution plants found the new application for lignin or similar polymers: at first, similar chemicals covered the spore wall which was an adaptation to the spore distribution with wind. Then similar chemicals were used to make cuticle, “epidermal plastic bag” to prevent transpiration outside of stomata. Finally, with acquiring of sclerenchyma, plants found how to use dead cells with completely lignified cell walls.

By the way, stomata likely had a similar fate, they historically appeared on sporangia to help them dry faster and release spores effectively. Regulation of transpiration is their second function.

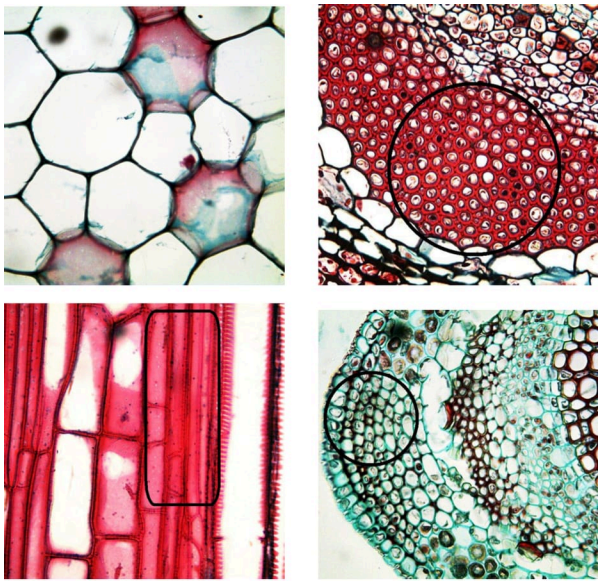


Figure 9.1.4 Left to right, top to bottom: parenchyma, sclerenchyma (cross- and longitudi- nal sections) and collenchyma. First three photos from the stem of Helianthus, fourth from Medicago stem. Magnification ×400.

Cell types and tissues

“Parenchyma” and “sclerenchyma” terms are freShoot systemquently used in two ways: first, to name tissues (or even classes of tissues) which occur in multiple places of the plant body, and second, to name the cell types which are components of tissues. Therefore, it is possible to say “parenchyma of stem”, “parenchyma of stem pith”, “parenchyma of xylem” and even “leaf mesophyll is a parenchyma”.

Meristems: the Construction Sites

Plant growth requires centers of development which are meristemssites of cell division. Apical meristems are centers of plant development located on the very ends of roots (RAMroot apical meristem) and stems (SAMstem apical meristem). They produce intermediate meristems (like procambiumintermediate meristem developing into cortex, pith and procambium)

which form all primary tissuestissues originated from RAM or SAM (optionally through intermediate meristems). The lateral meristemcambium, meristem appearing sideways or **cambium** originates from the procambium which in turn originates from apical meristems. It usually arises between two vascular tissues and its main functions are thickening and producing secondary vascular tissuessecondary phloem and secondary xylem (Figure 9.1.5).

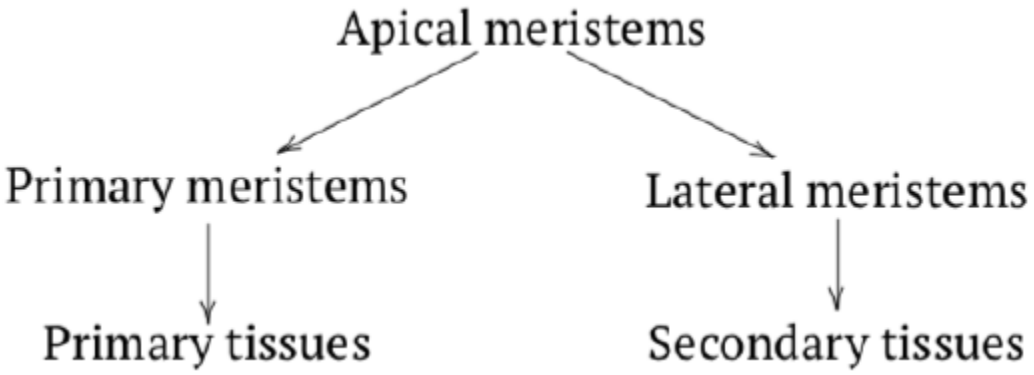


Figure 9.1.5 Meristems and tissues.

Other meristems include: **intercalary** which elongate stems from the “middle”, **marginal** which are located on margins which are responsible for leaf development and **repair** meristems arising around wounds, they also control vegetative reproduction.

Vascular Tissues

Bigger plants escaped from competition and performed effective metabolism. However, with all the growth the plants went through, their size became too big for slow symplastic plasmodesmata connections. Another, filter paper-like apoplastic transport was also not powerful enough. The solution was to develop **vascular tissues**, xylem and phloem (Figure 9.1.6, Figure 5.5.1).

The main functions of xylem are the transportation of water and mechanical support. The **xylem** tissue transporting water may be found either in a vascular bundle or a vascular cylinder. The three types of xylem cells are **tracheary elements** (these include **tracheids**

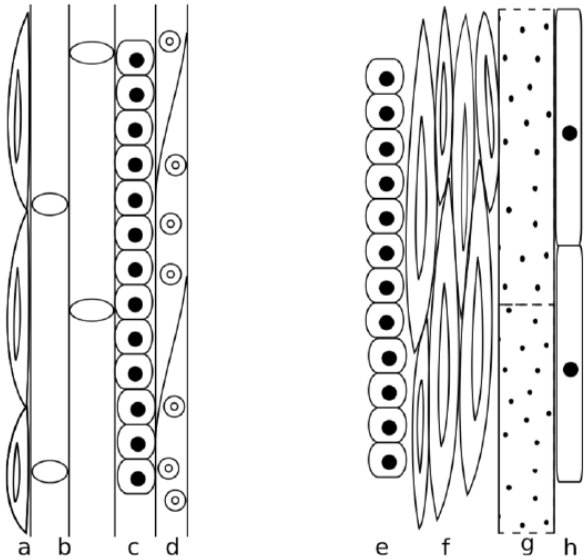


Figure 9.1.5 Cells of xylem (left, a–d) and phloem (right, e–h): a fibers, b vessels with open perforations, c parenchyma, d tracheids with pits, e parenchyma, f fibers, g sieve tubes, h companion cells.

and **vessel member**), **fibers**, and **parenchyma**. Xylem elements, except for the parenchyma, are rich in lignin and are main components of wood. Tracheids are closed on both ends and connected with **pits** whereas vessel members are more or less open

and connects via **perforations**. Tracheids, vessel members and fibers are dead cells. Xylem parenchyma, on the other hand, is alive.

Pits of tracheids consist of a pit membrane and the torus in a center, there are *no openings*. The presence of tracheids and/or vessel elements has evolutionary significance. Vessels (made of vessel members) are more effective; consequently, more "primitive" plants have more tracheids whereas more "advanced" have more vessel members. As an example, gymnosperms have only tracheids while most flowering plants have tracheids and vessel members. Individual development also mimics this evolutionary trend. Younger flowering plants have more tracheids whereas mature plants have more vessel members. Primary xylem mostly has tracheids and vessels with scalariform perforations whereas secondary xylem (which originates from cambium) consists mostly of vessels with open perforations. The common name for secondary xylem is **wood**.

It is a mistake to think that tracheids are better than vessels. In fact, the main problem is frequently not too slow but too fast water transport. Tracheids have an advanced connection system (called torus) which has the ability to close pore if the water pressure is too high and therefore more controllable. Leaking would be less dangerous in tracheids. And in water-poor environments (like taiga in winter), plants with tracheids will have the advantage. Contrary, having vessels is like to have race car for ordinary life; only flowering plants "learned" how to use them effectively.

Dead cells are useful but hard to control. However, if xylem transport needs to be decreased, there is a way. Xylem parenchyma cells will make tyloses"stoppers" for tracheary elements made by parenchyma cells ("stoppers") which will grow into dead tracheary elements and stop water if needed. Many broadleaved trees use tyloses to lower xylem transport before the winter.

The **phloem** tissue transporting sugars generally occurs adjacent, or right next to, the xylem, with the xylem facing the inner part of the plant and the phloem facing the outer part of the plant. The main functions of the phloem are the transportation of sugars and mechanical support. The four types of phloem cells are: **sieve tube cells** , **companion cells**, **fibers** (the only dead cells in phloem), and **parenchyma**. Sieve tube cells of flowering plants have cytoplasm flowing through perforations (sieve plates) between cells but do not contain nuclei. Companion cells will make proteins for them. However, in gymnosperms and more "primitive" plants there are no companion cells at all, so sieve tube cells do contain nuclei. This is comparable to red blood cells in vertebrates: while mammals have them anucleate, erythrocytes of other vertebrates contain nucleus. The secondary phloem generally has more fibers than the primary phloem.

This small table summarizes differences between xylem and phloem:

	Xylem	**Phloem**
Contains mostly	Dead cells	Living cells
Transports	Water	Sugar
Direction	Up	Down
Biomass	Big	Small

Periderm

*Peridermperidermsecondary dermal tissue is a secondary dermal tissue which arises inside the stem ground tissue, closer to the surface. Like the other dermal tissue (epidermis), it is a complex tissue. It includes three layers (starting from surface): phellemexternal layer of periderm, cork (**cork**), phellogencork cambium, lateral meristem making periderm (**cork cambium**) and phelloderminternal layer of periderm (Figure 9.1.7). Phellem consists of large dead cells with secondary walls saturated with suberin, and is the main, thickest component of periderm. Phellogen is a lateral meristem, like cambium; it often arises fragmentarily (and also temporarily) and does not cover the whole stem under-surface. But when phellem starts to grow, all peripheral tissues (like epidermis) will be separated from water transport and eventually die. Phellogen makes phellem towards the surface, and phelloderm towards the next layer (phloem). Phelloderm is a minute tissue, and does not play significant role in the periderm.

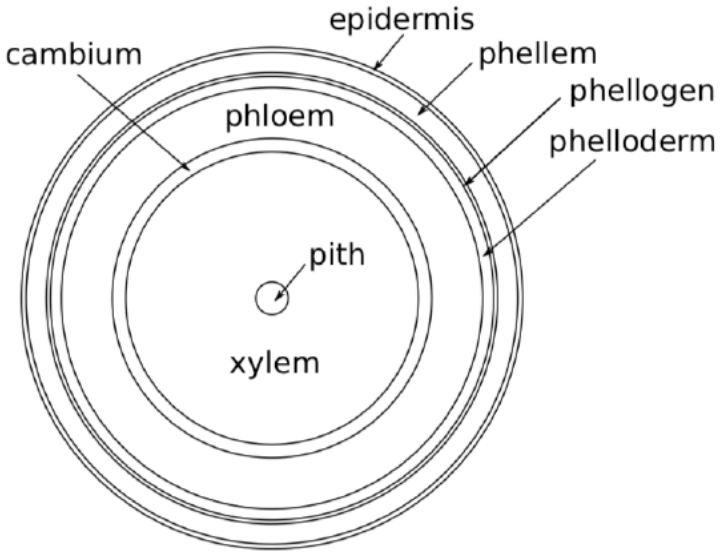


Figure 9.1.7 Principal location of stem tissues (simplified).

In older plants, phellogen arises deeper, sometimes inside phloem and separates outer layers of phloem from vascular cylinder. All this mixture of tissues (phellogen, phellem, phelloderm, epidermis and upper layers of phloem) considered as a **bark**.

Absorption Tissues

Poikilohydric plants that do not save water plants do not save water and they can survive even complete desiccation because their cells will hibernate. An example of a poikilohydric plants would be mosses. **Homoiohydric** plants that save water plants (which are majority of plants$_2$), however, do save water. They try to support the water content and do not survive complete desiccation. An example of a homoiohydric plant would be any "typical" plant, saying, corn. Somehow similar traits are comparable in poikilothermic animals, such as reptiles, and homoiothermic animals, such as birds and mammals, except in reference to body heat rather than water conservation.

Absorption tissues are always simple, primary tissues. Most important of them is **rhizodermis**(rhizoderm), or **root hairs**, which originates from protoderm (proto-epidermis), but its lifespan is much shorter than of epidermis. There are other absorption tissues, for example, **velamen**, which originates from the root cortex and consists of large, empty, easy to get wet dead cells.

Other Tissues

Secretory tissues spread across the plant body, concentrating in leaves and young stems. These tissues may secrete latex, volatile oils, mucus and other chemicals. Its functions can be attraction or dis-attraction, communication or defense, and many others.

In addition to tissues, plant body may contain **idioblasts**, cells which are quite dissimilar from surrounding cells. Idioblasts used for accumulation of unusual (and possibly dangerous) compounds like **myrosinase**, protein splitting glucosinolates into sugars and toxic isothiocyanate (**mustard oil**). We use mustard oil as a spice but for the plant, it works like a binary chemical weapon against insect herbivores: when myrosinase-containing idioblasts are damaged, mustard oil kills damaging insects. Among plants, the whole order Brassicales from rosids is capable to produce myrosinase, examples are different cabbages (*Brassica* spp.), papaya (*Carica*), horseradish tree (*Moringa*) and many others.

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9.2: Organs and Organ Systems

Vegetabilia (Figure 6.1.1) have three different types of body construction (Figure 9.2.1). The most primitive plants have thallus body, more advanced is the shoot (unipolar) plant body, and most land plants have the bipolar plant body. The thallusflat, non-differentiated body plant body is flat, similar to leaf but do not differentiated into particular organs. Most gametophytes (except true mosses) have this type, and also few sporophytes (which mostly are reduced water plants). **Shoot (unipolar) plant body** consists only of branching shoots, roots are absent. This is typical to all Bryophyta sporophytes, mosses (Bryopsida) gametophytes, and also to sporophytes of Psilotopsida (whisk ferns). Finally, **bipolar plant body** present has both shoots and roots (Figure 5.3.1). Most bipolar plants have shoots consist of stems and leaves, but this is not an absolute requirement since young plant stems are normally green and can do photosynthesis.

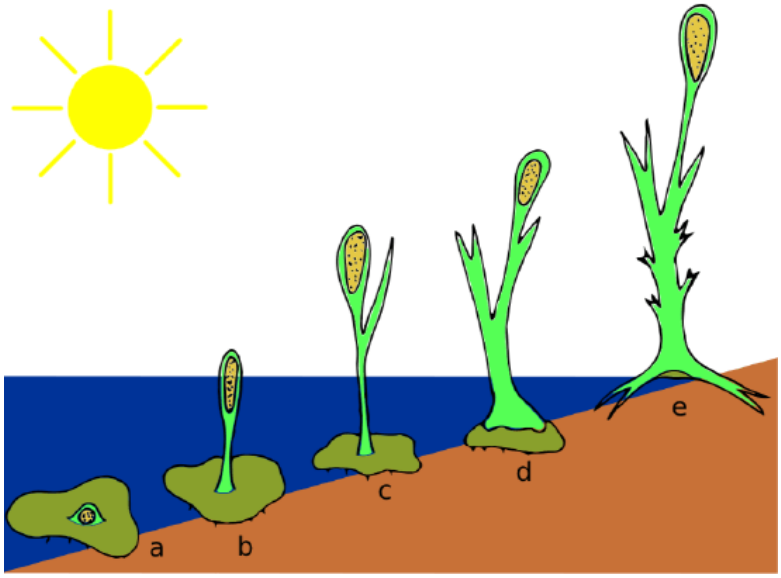


Figure 9.2.1 Evolution of plants$_2$ body types: a–e thallus gametophytes, a thallus sporophyte, b–d shoot sporophyte, e bipolar sporophyte.

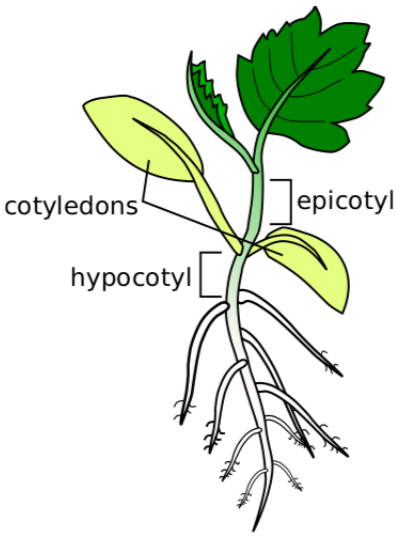


Figure 9.2.2 Young seedling with epicotyl and hypocotyl.

Typical organs of bipolar plant are stems (axial aerial organs with continuous growth), leaves (flat lateral organ with restricted growth), roots (axial soil organ modified for absorption) and **floral units (FU)** which are elements of the generative system (fructifications) such as a pine cone or any flower.

Buds, fruits, seeds and specific to seedlings hypocotyl and epicotyl are **non-organs** for different reasons: **buds** are just young shoos, **fruit** is the ripe flower, **hypocotyl** is a part of stem between first leaves of the seedling (cotyledons) and root (i.e., stem/root transition place), epicotylfirst internode of the stem is first internode of stem (Figure 9.2.2), and finally, **seed** is a chimeric structure with three genotypes so it is impossible to call it “organ”.

Root, stem, leaf and FU are *four basic plant organs* (Figure 9.2.3) which in bipolar plant could be grouped in root and shoot system; the latter is frequently split into *generative shoot system* (bearing FU), and *vegetative shoot system* (without FU).

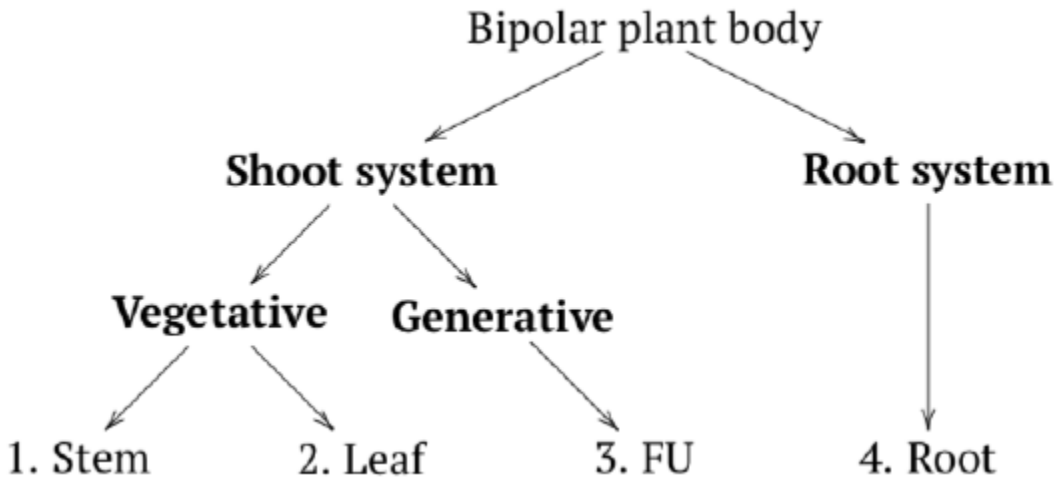


Figure 9.2.3 Bipolar plant: **organ systems** and four organs.

Vegetative shoot system usually consists of main and secondary shoots; shoots contain terminal buds, axillary (lateral) buds, stem (nodes and internodes) and leaves. We will start from leaves.

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9.3: THE LEAF

The first and ultimate goal of every plant is photosythesis. If a plant is multicellular, it usually develops relatively large, flat structures which goal is to catch sun rays. Terrestrial plants are no exception; most probably, they started to build their body with organs similar to present day leaves.

A leaf is *lateral photosynthetic organ of shoot with restricted growth*. Its functions are photosynthesis, respiration, transpiration, and synthesis

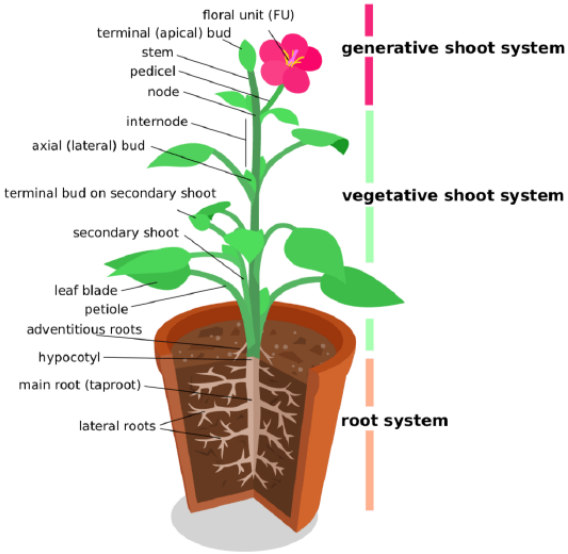


Figure 9.3.1 Systems of organs and organs of bipolar plant.

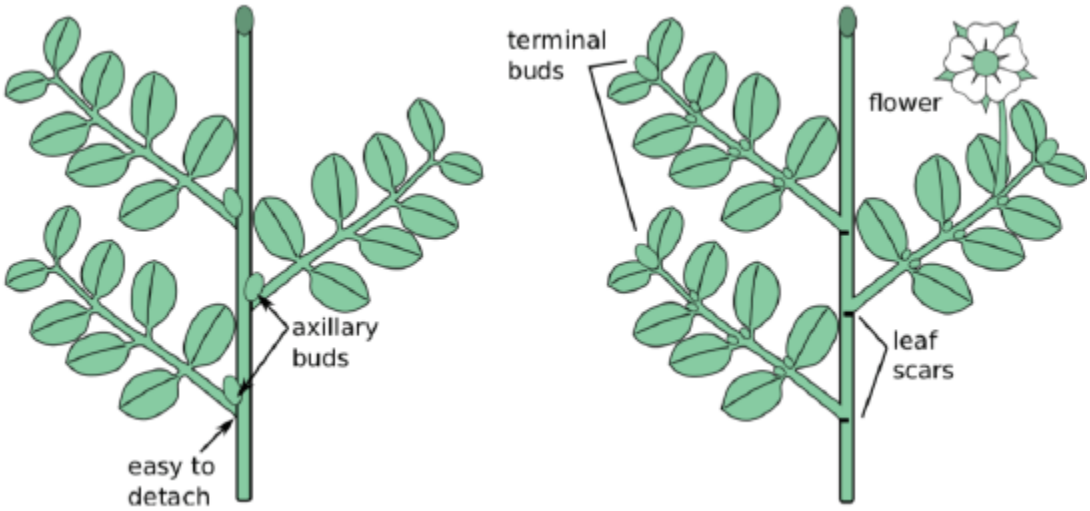


Figure 9.3.2 How to distinguish compound leaves (left) from branches (right).

of secondary chemicals. Features of a leaf (i.e., characters help to distinguish it) include having a bud in the axil, not growing by apex, not producing new leaves or shoots, and having *hierarchal morphology* (see below).

Morphology of the Leaf

Morphology means external, well visible structural features whereas **anatomy** needs tools like a scalpel and/or microscope to

study needs tools like a microscope and/or scalpel. Leaves are very important in plant morphology. The ability to describe the leaf is a must even for novices in botany.

In all, *plants are fractal organisms*, like Sierpinski triange (Figure 9.3.3). All fractals are self-similar (Figure 9.3.4), and plants are no exception. Self-similarity, or "Russian doll effect" means that almost every part of plant may be a part of the bigger complex, this bigger one—the part of even bigger system, and so on. This is what we see in leaves as *levels of hierarchy*. *Simple leavessimple leafleaf with one level of hierarchy have just one level of hierarchy whereas compound leaves have two or more levels of hierarchy. *Compound leavescompound leavesleaves with two or more level of hierarchy are sometimes mixed with branches but there are many other characteristics which allow to distinguish them (Figure 9.3.2).



Figure 9.3.3 One of simple fractals: Sierpinski triangle.

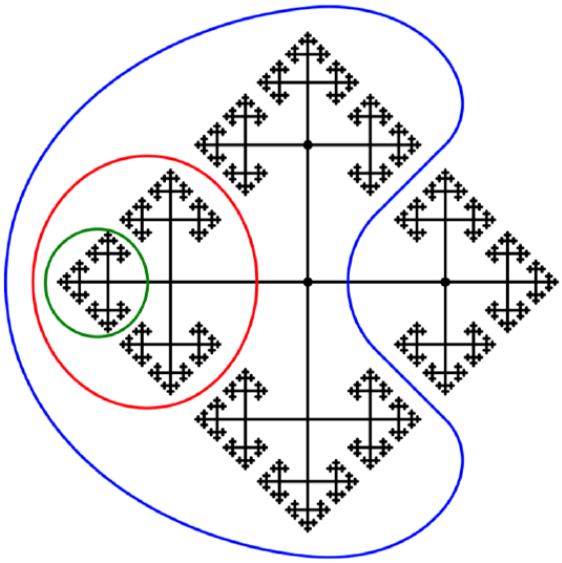


Figure 9.3.4 The example of self-similarity.

To describe leaves, one should always note the level of hierarchy like "on the first level of hierarchy, the shape is ..., on the second level of hierarchy, the shape is ..." As it was mentioned above, leaf hierarchy is similar to Russian dolls: every smaller doll has a bigger doll (next hierarchy level) outside. For example, if the leaf is compound (consists of multiple leaflets), the overall shape of it could be, saying, round (circular) but the shape of individual leaflet of the very same leaf could be ovate (Figure 9.3.5). As a result, the description will say that on first level of hierarchy the leaf is ovate, and on the third level—circular.

There are three types of leaf characters: general, terminal, and repetitive. **General characters** are applicable only to the leaf as a whole are only applicable to the whole leaf. **Terminal characters** are applicable only to the leaf terminals (leaflets) are only applicable to the terminal leaflets. Terminals are the end parts of leaves, they do not split in smaller terminals; clover leaf, for example, has 3 terminals. Lastly, repetitive characters repeat on each level of leaf hierarchy. General and terminal characters do not depend on hierarchy. **Repetitive characters** are applicable to the leaf parts on each level of hierarchy may be different on each step of hierarchy.

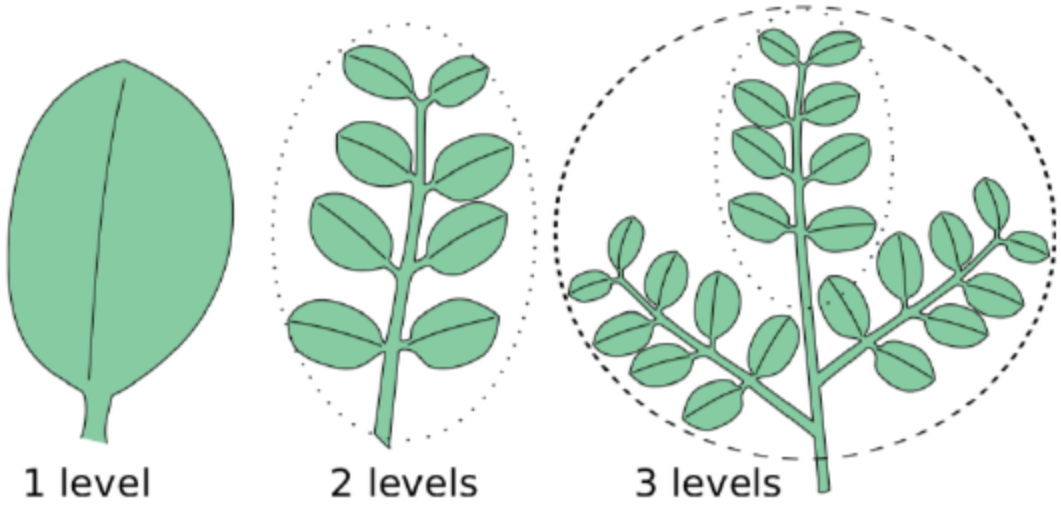


Figure 9.3.5 Leaves with one, two and three levels of hierarchy. Please note that the last leaf is ovate on the first and second level but circular on the third level of hierarchy.

General characters of leaf include **stipules** and other structures located near leaf base (Figure 9.3.6): **sheath** (typical for grasses and other liliids) and **ocrea** (typical for buckwheat family, Polygonaceae).

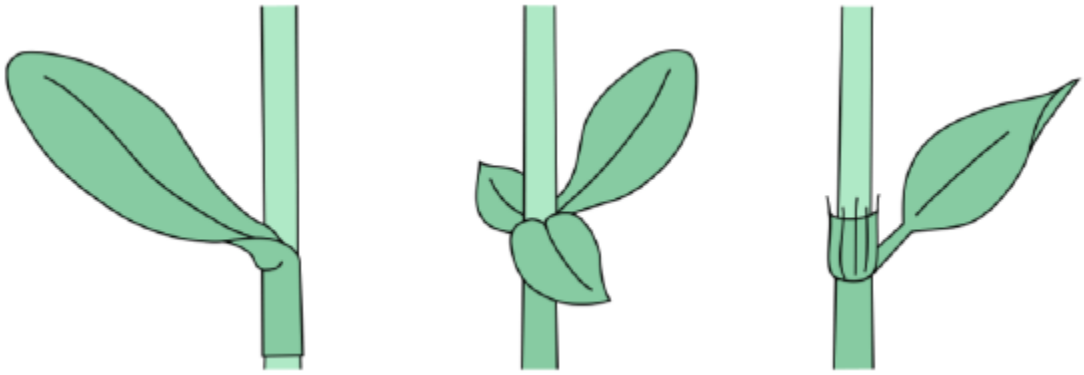


Figure 9.3.6 From left to right: sheath, stipules and ocrea.

Repetitive characters are the shape of the leaf (Figure 9.3.7), leaf dissection, and whether the blade is stalked (has petiole) or not.

Terminal characters are applicable only to terminal leaflets of leaves. These characters (Figure 9.3.9) are the shape of the leaf blade base, the leaf tip, the type of margin, the surface, and the venation. The base of the leaf blade could be **rounded**, **truncate** (straight), **cuneate**, and **cordate**. The leaf apex could be **rounded**, **mucronate**, **acute**, **obtuse**, and **acuminate**. Leaf margin variants are **entire** (smooth) and **toothed**: **dentate**, **serrate**, **double serrate** and **crenate**.

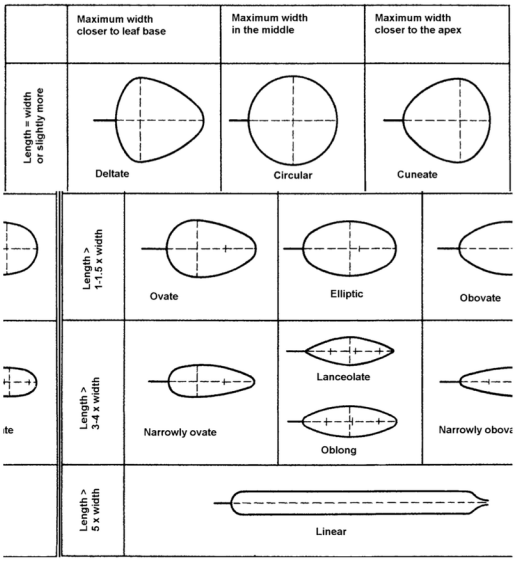


Figure 9.3.7 Leaf shapes.

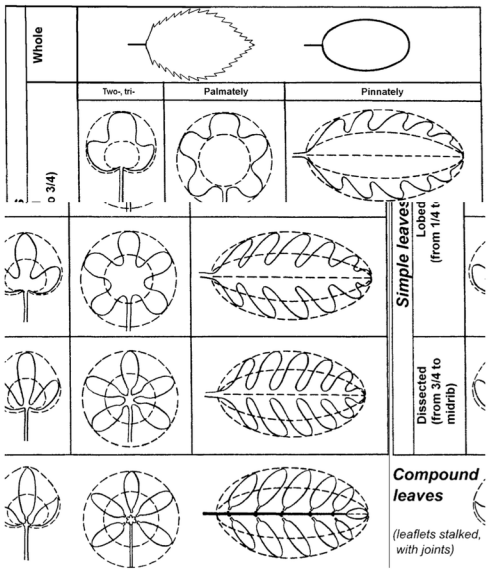


Figure 9.3.8 Leaf dissection.

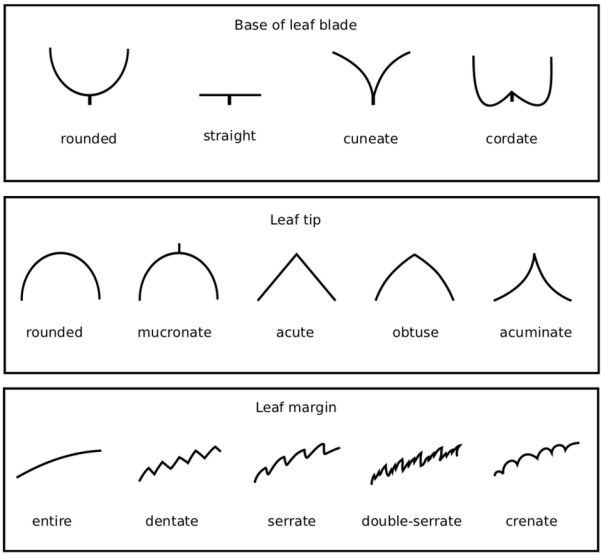


Figure 9.3.9 Terminal leaf characters.

Leaf veins are vascular bundles coming to the leaf from stem. Frequently, there is a **main vein** and **lateral veins** (veins of second order). There are multiple classifications of leaf venation; and example is shown on the Figure 9.3.10.

Note that in **dichotomous** venation, each vein divides into two similar parts which is known as dichotomous branching. The example of dichotomous venation is the leaf of maidenhair tree, ginkgo (*Ginkgo biloba*). Another frequently segregated type of venation is **parallellodromous**, but in essence, this is acrodromous venation in linear leaves (for example, leaves of grasses) where most of veins are almost parallel.

To characterize the whole leaf, one might use the following plan:

Lateral \ Main	No	One	Several
No	Apodromous	Hyphodromous	Acrodromous
Several	Dichotomous	Pterodromous	Actinodromous

Figure 9.3.10 The simple classification of leaf venation.

1. General characters (leaf as a whole):

    (a) stipules (present / absent, deciduous / not, how many, size, shape);

    (b) base (sheath / no sheath, ocrea / no ocrea)

2. First level of hierarchy: repetitive characters:

(a) symmetry (symmetrical / asymmetrical);

(b)shape;

(c) dissection;

(d) petiole (presence and length)

3. Second level of hierarchy

4. Third level of hierarchy, and so on

5. Terminal characters (leaflets):

(a) base of leaf blade (rounded, truncate, cuneate, cordate);

(b) apex (rounded, mucronate, acute, obtuse, acuminate);

(c) margin (whole, dentate, serrate, double serrate, crenate);

(d) surfaces (color, hairs etc.);

(e) venation (apo-, hypho-, acro-, ptero-, actinodromous)

Heterophyllyh 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. A leaf mosaics refers to the distribution of leaves in a single plane perpendicular to light rays, this provides the least amount of shading for each leaf.

Leaves have seasonal lives; they arise from the SAM through **leaf primordia**, and grow via marginal meristems. The old leaves separate from the plant with an **abscission zone**.

The famous poet and writer Johann Wolfgang Goethe is also considered a founder of plant morphology. He is invented an idea of a “primordial plant” which he called “Urpflanze” where all organs were **modifications** of several primordial ones. In accordance to Goethe’s ideas, plant morphology considers that many visible plant parts are just modifications of basic plant organs.

Modifications of the leaf include **spines** or **scales** for defense, tendrilsorgan modifications using for climbing for support, **traps**, “sticky tapes”, or **urns** for interactions (in that case, catching insects), **plantlets** for expansion, and **succulent** leaves for storage. Plantlets are little mini plants that grow on the main plant and then fall off and grow into new plants; the most known example is *Kalanchoë* (“mother of thousands”) which frequently uses plantlets to reproduce. Plants that have insect traps of various kinds are called carnivorous plants (in fact, they are still photoautotrophs and use insect bodied only as fertilizer). Several types of these are the cobra lily (*Darlingtonia*), various pitcher plants (*Nepenthes*, *Cephalotus*, *Sarracenia*), the butterwort (*Utricularia*), the sundew (*Drosera*), and the best known, the Venus flytrap (*Dionaea*).

Anatomy of the Leaf

Anatomically, leaves consist of epidermis with stomata, **mesophyll** (kind of parenchyma) and vascular bundles, or veins (Figure 9.3.12). The mesophyll, in turn, has palisade and spongy variants. Palisade mesophyll is located in the upper layer and serves to decrease the intensity of sunlight for the spongy mesophyll, and also catches slanted sun rays. The **palisade mesophyll** consists of long, thin, tightly arranged cells with chloroplasts mostly along the sides. The **spongy mesophyll** are roughly packed, they are rounded and have multiple chloroplasts (Figure 9.3.11).

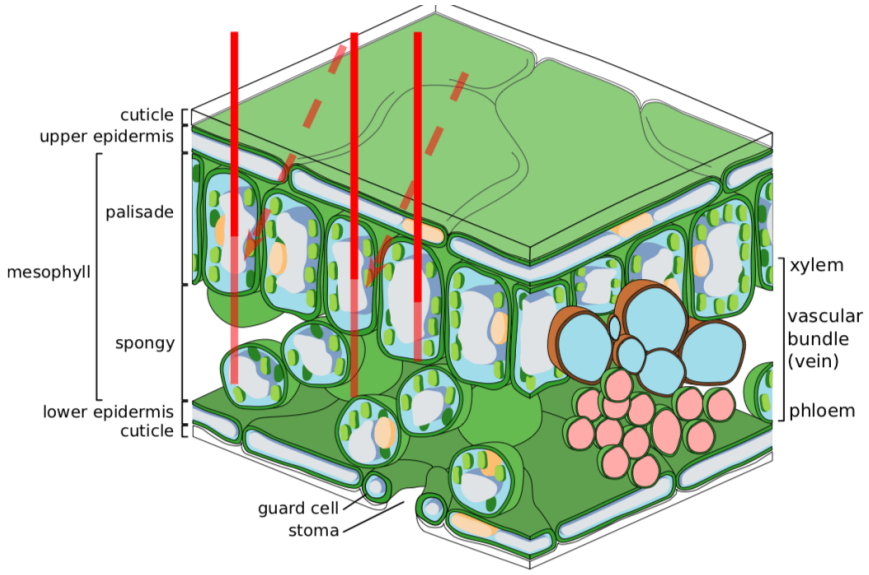


Figure 9.3.11 Leaf anatomy.

When a typical stem vascular bundle (which has xylem under phloem) enters the leaf, xylem usually faces upwards, whereas phloem faces downwards. Bundles of C_4-plants have additional bundle sheath cells in their vascular bundles.

The epidermis includes typical epidermal cells, stomata surrounded with guard cells (also optionally with subsidiary cells), and trichomes. Almost all epidermal cells are covered with waterproof cuticle, rich of lignin and waxes.

The stomata assists in gas exchange, cooling and water transpiration. There are two guard cells paired together on each side of the stoma. These guard cells are kidney beans shaped and have a thicker cell wall in the middle. The thicker cell wall on the inside makes use of the so-called “bacon effect” (when bacon slice curved on the

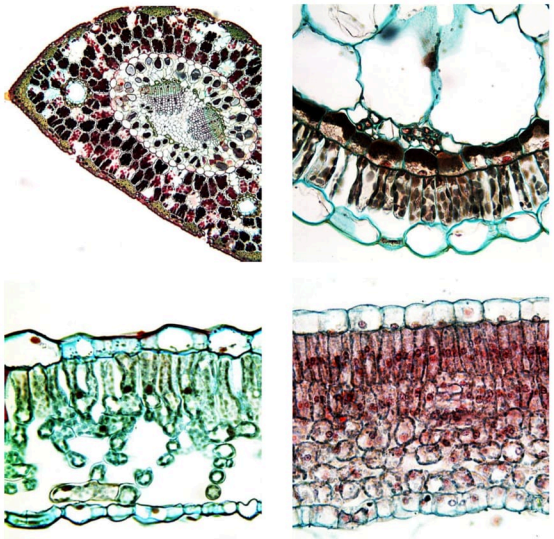


Figure 9.3.12 Left to right, top to bottom: leaf of sclerophyte Pinus, leaf of salt-avoiding (succulent-like) halophyte Salsola (epidermis is at the bottom), shade leaf of Sambucus, leaf of Syringa with guards cells (bottom left). Magnifications ×100 (first) and ×400 (others).

frying pan) because thinner part of the cell wall is more flexible and therefore bends easier. The same curving effect might be seen in blowing air balloon with the piece of scotch on one side. The opening of the stoma starts from K^+ accumulation, then osmosis inflates guard cells, and finally the uneven cell wall facilitates the opening of stoma. The stoma closes when the potassium ions exit the cell and water amount decreases in its vacuoles (Fig [STOMA]).

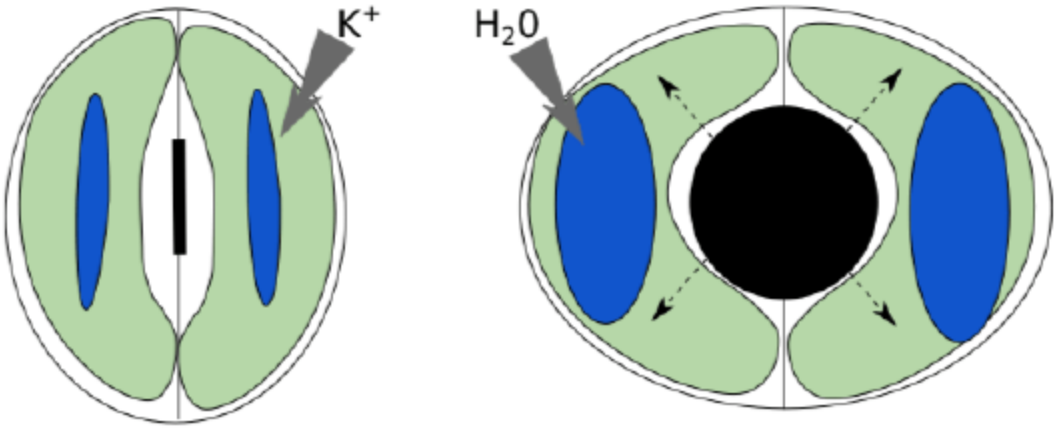


Figure 9.3.13 Closed and opened stoma. Cell walls are white, cytoplasm green, vacuoles blue.

In most cases, the lower epidermis contains more stomata than the upper epidermis because the bottom of the leaf is cooler and transpiration there is safer. A similar logic is applicable to trichomes (hairs): they are also more frequent on the lower side of the leaf.

Ecological Forms of Plants

When plants adapt to the particular environment conditions, leaves usually respond first. Conversely, one can estimate the ecology of plant simply looking on its leaves.

In regards to water, there are four main types of plants: xerophytes, mesophytes, hygrophytes, and hydrophytes. **Xerophytes** are adapted to the scarce water (Figure 9.3.12), they could be **sclerophytes** (usually with prickly and/or rich of sclerenchyma leaves) and **succulents** (with water-accumulating stems or leaves). **Mesophytes** are typical plants which adapt to regular water. **Hygrophytes** live in constantly wet environment, their leaves adapted to high transpiration and sometimes even to guttation (excretion of water drops). **Hydrophytes** grow in water, their leaves are frequently highly dissected to access more gases dissolved in water, and their leaf petioles and stems have air canals to supply underwater organs with gases.

In regards to light, plants could be sciophytes or heliophytes. **Sciophytes** prefer the shade to sunlight, their leaves contain mostly spongy mesophyll. **Heliophytes** prefer the full sun and therefore have leaves filled with palisade mesophyll. The intermediate group are “partial shade” plants.

Halophytes, nitrate halophytes, oxylophytes, and calciphytes are ecological groups adapted to the over-presence of particular chemicals. **Halophyte** plants are frequent, they accumulate (and look similarly to succulents), excrete or avoid (which looks like sclerophyte) sodium chloride (NaCl). They grow in salty places: sea shores, salt deserts and solonets prairies. **Nitrate halophyte** plants grow on soils rich in $NaNO_3$. **Oxylophytes** grow in acidic soils, whereas calciphytesplants adapted to over-presence of $CaCO_3$ grow in basic, chalk soils rich in $CaCO_3$.

Leaves will also reflect adaptations to the substrate, ecological forms named **psammophytes** (grow on sand), **petrophytes** (grow on rocks), and **rheophytes** (grow in fast springs). The latter plants frequently have serious simplifications in their body plan, their leaves and stems are often reduced to form a thallus-like body.

Parasitic plants could be classified in mycoparasites, hemiparasites, and phytoparasites. **Mycoparasitic** plants feed on soil fungi, **phytoparasitic** plants are either plant root parasites or plant stem parasites lacking chlorophyll and photosynthesis. **Hemiparasitic** plants are those which still have chloroplasts but take the significant part of water and even organic compounds from the host plant (like mistletoe, *Viscum*).

9.3.1: Inside Leaves

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9.3.1: Inside Leaves

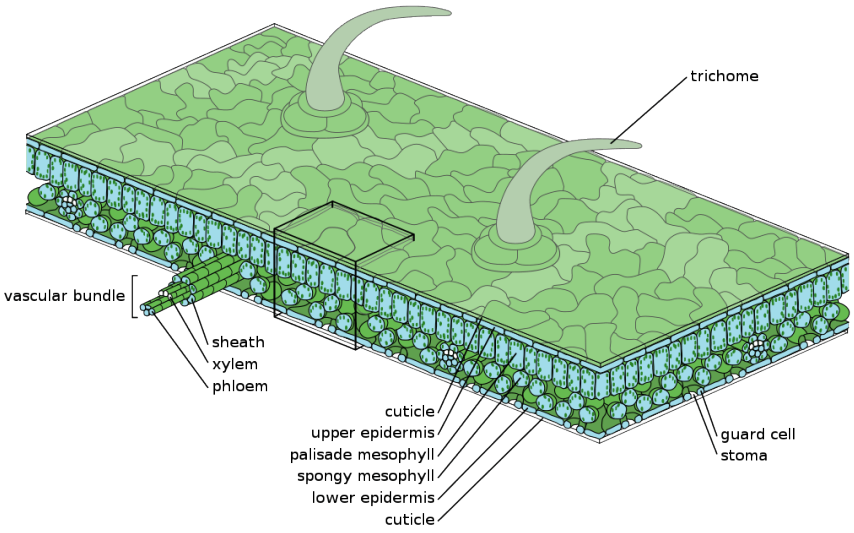
Learning objectives

- Recognize the internal cellular structure of leaves.
- Describe how the structure facilitates photosynthesis.
- Describe how the structure facilitates gas exchange.
- Explain why leaves in autumn turn from green to yellow, orange, and red.

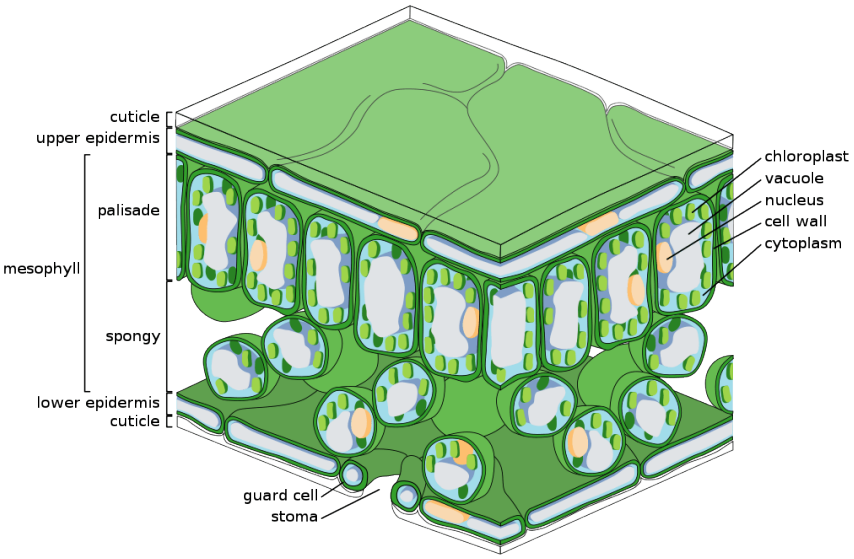
Leaf anatomy

Learning leaf anatomy is a bit like taking a sandwich apart and seeing what's inside. We'll start with the upper surface and progress down through the leaf. Here are the layers you will find:

- Upper epidermis with cuticle. The cuticle is a protective waxy coating of cutin on epidermis cells, restricting water loss and preventing disease.
- Palisade mesophyll — densely packed, columnar-shaped, elongated cells full of chloroplasts. Chloroplasts are structures inside plant cells that contain chlorophyll and are the site of light capture during photosynthesis. These are analogous to cortex parenchyma cells in the stem, but in the leaf they are specialized for light energy capture.
- Spongy mesophyll — loosely packed cells with large air spaces between them. The air spaces allow movement and exchange of gases, specifically oxygen, carbon dioxide, and water vapor. Spongy mesophyll cells also contain chloroplasts.
- Vascular bundle — xylem, phloem, and bundle sheath cells along with nearby parenchyma and either sclerenchyma or collenchyma fibers for support.
- Lower epidermis with guard cells that regulate the size of the stomata, the gaps in the epidermis that allow gas exchange between the atmosphere and internal parts of the leaf.



Leaf structure. Zephyris. CC BY-SA 3.0.



Leaf tissue structure. Zephyris. CC BY-SA 3.0.

In the graphic above, you can see the spongy and palisade mesophyll in detail. During the growing season, these cells are packed with chloroplasts containing the pigment chlorophyll. Chlorophyll absorbs red and blue wavelengths of light to power photosynthesis, and reflects green light back to our eyes, making leaves appear green to use in spring and summer.

Watch this video about colors we see in leaves:

Review this article, Why Leaves Change Color.

Chromoplasts (not to be confused with chloroplasts) are cellular organelles that contain types and colors of pigments other than the chlorophyll found in chloroplasts. In late summer and fall, the mesophyll cell chloroplasts produce chlorophyll at a slower rate than earlier in the year. As the existing chlorophyll reaches the end of its functional lifespan and eventually degenerates, the amount of chlorophyll declines over time. Because chlorophyll replacement doesn't make up for chlorophyll loss, the green color fades from the leaves. Meanwhile, the non-green pigments in the chromoplasts hold their own or increase in quantity, including the yellow and orange from the carotenoid pigments and the red from the anthocyanin pigments.

Carotenoid pigments are present in the leaf all growing season, but during the warm part of the season they're hidden by the high concentration of green-colored chlorophyll. When the cool autumn weather comes, the days shorten and the chlorophyll concentration in the chloroplasts declines. The carotenoids in the chromoplasts don't degenerate as quickly as the chlorophyll does, so we get a beautiful display of oranges and yellows in the leaves once the green is gone. These orange and yellow colors can be counted on every year because the carotenoids are produced and present all year long.

In contrast to the carotenoid pigments, the amount of red color in leaves from the anthocyanins differs from autumn to autumn. Anthocyanins are produced primarily in the autumn in response to bright light and excess plant sugars in leaf cells. Warm, sunny days encourage sugar production in leaf mesophyll, and cool nights hinder the transport of these sugars out of the cells, so the sugars stay in leaves. The high sugar then stimulates anthocyanin production. Warm, bright days + cool nights = red leaves. In years with overcast days and warmer nights, there is less sugar production in the leaves and the sugars translocate (move out) from the leaf mesophyll cells to other locations in the tree, so there is less anthocyanin pigment produced and less red color in the leaves. You might see this happening on individual trees: on the sunlit, southwest side of the tree you might find leaves with more red than on the shaded, northeast side. This effect of weather on anthocyanin is particularly noticeable in trees such as sugar maples.

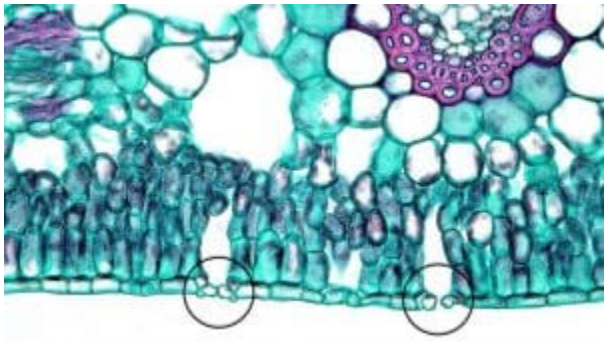
Some other woody plants, like sumac, seem to be bright red in later September and early October regardless of the weather conditions. Other trees, like birch and oak, will be yellow or tan even with warm bright days and cool nights.

Here is a cross section of a pear leaf showing the same cells illustrated in the graphic shown earlier.



Micrograph cross section of leaf. Berkshire Community College Bioscience Image Library. Public domain

The palisade mesophyll is highly adapted for capturing light energy. As noted earlier, the cells are packed tightly together, filled with chloroplasts, and make up the cell layer just under the protective epidermis on the top surface of the leaf oriented toward the sun. The spongy mesophyll cells below the palisade layer are less densely packed together, so the region is laced with air channels. This makes the spongy mesophyll highly adapted for gas movement and air exchange around the cells.



The circles show the guard cells around the stomata on the lower surface of the leaf. bccoer. CC0.

Guard cells surround a gap in the epidermis. This gap is called a stoma or stomate (plural = stomata), and is the portal through which gas exchanges between the interior and exterior of the leaf. Gases in the intercellular spaces between spongy mesophyll cells are free to move out of the stomata into the atmosphere, and atmospheric gasses are free to move in. As we will see later when we address photosynthesis, healthy plants must have the ability to move oxygen (a waste product of photosynthesis) out of the leaf, and carbon dioxide (a raw material for building sugars) into the leaf. Water vapor must also be able to move out of the leaf as part of the transpiration process.

The vascular bundle (the xylem and phloem in the graphic above) is highly adapted for transport of fluids. Water and dissolved minerals move up the xylem from the roots and into the leaf. Sugars produced in the leaf during photosynthesis move out of the leaf through the phloem and are translocated to other parts of the plant. The thick-walled bundle sheath cells that surround the xylem and phloem provide mechanical support, and contribute to some types of photosynthesis. Wikipedia has a good illustration showing the tissues associated with the vascular bundles. Take a look.

Review questions

1. Which layer of cells in the leaf are most highly adapted to intercept light? Describe three ways in which these cells are specialized for this purpose. Hint: two have to do with position or orientation in the leaf, and one with the plastids they contain.

2. Which leaf cell layers are key to gas exchange?
3. What happens to the green pigments in leaves when the weather turns cold in the fall? Why do some leaves turn yellow, orange, and red, instead of turning brown?

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9.4: THE STEM

The **stem** is an *axial organ of shoot*. It has functions of support, transportation, photosynthesis, and storage. Stem has radial structure, no root hairs and grows continuously.

Morphology of the Stem

Stem morphology is simple. Its components are **nodes** (places where leaves are/were attached) and **internodes**, long or short (in the last case, plant sometimes appears to be stemless, rosette-like).Stems are different by the type of phyllotaxis. The **phyllotaxis** refers to the arrangement of leaves. If there is one leaf per node, it is a **spiral** (**alternate**) arrangement. Two leaves per node means **opposite** arrangement: two leaves per node arrangement. Opposite leaves can be all in the same plane or each pair can rotate at 90°. If there are more than two leaves per node, it is a **whorled** arrangement, and each whorl can also rotate. Each type of spiral phyllotaxis has its own angle of divergence. Multiple types of spiral leaf arrangement mostly follow the **Fibonacci sequence**:

$$\frac{1}{2}, \frac{1}{3}, \frac{2}{5}, \frac{3}{8}, \frac{5}{13}, \frac{8}{21}, \ldots \tag{9.4.1}$$

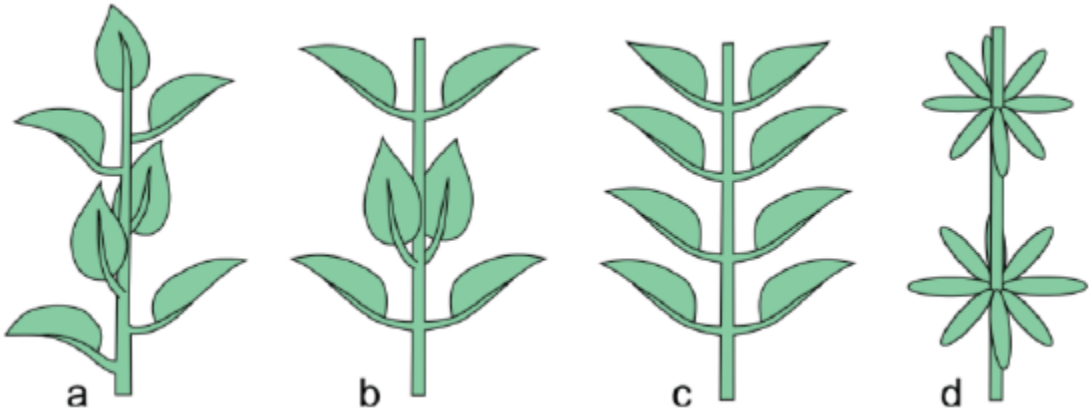


Figure 9.4.1 Types of phyllotaxis (leaf arrangement): a spiral (alternate), b and c opposite, d whorled.

This sequence of numbers made with simple rule: in the every following fraction, the numerator and denominator are sums of two previous numerators and denominators, respectively. The sequence looks fairly theoretical but amazingly, it is fully applicable to plant science, namely to different types of spiral phyllotaxis (Figure 9.4.2).

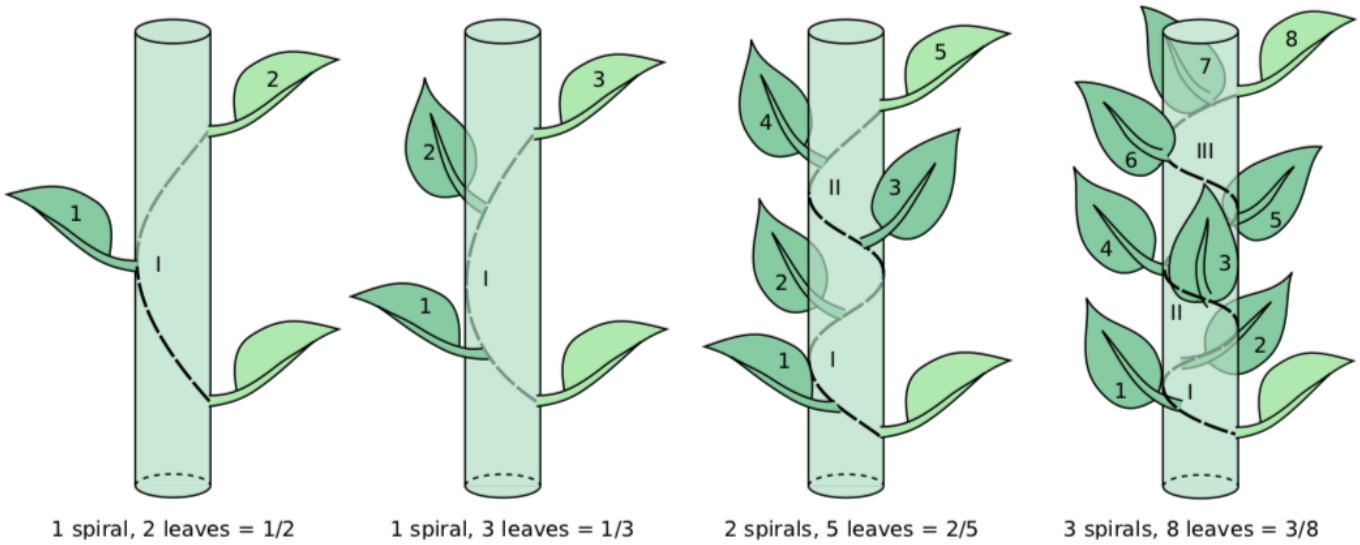


Figure 9.4.2 Four first Fibonacci types of spiral phyllotaxis: $\frac{1}{2}$, $\frac{1}{3}$, $\frac{2}{5}$, and $\frac{3}{8}$.

To determine formula of spiral phyllotaxis, one needs to start with arbitrary leaf (or leaf scar) and then find the next (upper) one which is *directed the same way*, lays on the same virtual line. Then, the imaginary spiral should be drawn trough basements from the started leaf to the corresponding upper leaf. This spiral should go through all intermediary leaves, there might be one, two or more intermediary leaves. Also, the spiral will go at least one time around the stem. (Instead of the imaginary spiral, it is sensible to use a thin thread). One needs to count all leaves in the spiral except the first, and also count number of rotations. The number of leaves counted will be the denominator of the formula, and the number of rotations is the numerator. This is how Fibonacci numbers appear in plant morphology.

These phyllotaxis formulas are relatively stable and sometimes even taxon-specific. For example, grasses (Gramineae) have $\frac{1}{2}$ phyllotaxis, sedges (*Carex*) $\frac{1}{3}$, many Rosaceae (like apple, *Malus* or cherry, *Prunus*) have $\frac{2}{5}$, willows frequently have $\frac{3}{8}$, *et cetera*. It is still not absolutely clear why the spiral phyllotaxis is under such a theoretical mathematical rule. The most feasible hypothesis emphasizes mathematical problem of circle packing and the competition between leaf primordia around SAM.

Anatomy of the Primary Stem

Plant evolution resulted first in the **primary stems** with no lateral meristems and secondary tissues. Only long after plants “learned” how to thicken their stems.

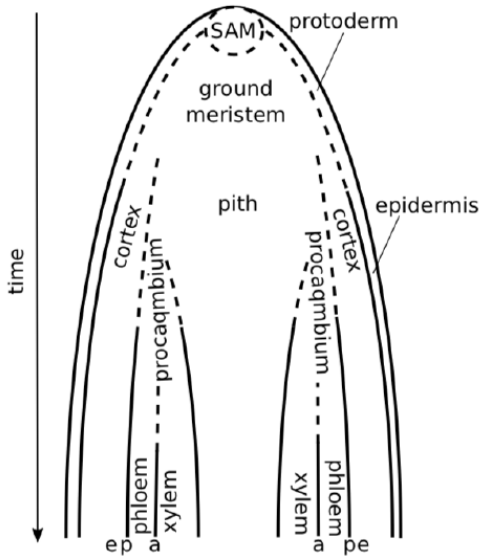


Figure 9.4.2 Developmental origin of stem tissues (simplified). Letters e, p, a show respectively where **e**ndoderm, **p**ericycle and v**a**scular c**a**mbium might appear.

Development of stem starts from stem apical meristem (SAM) on the top of plant. The SAM produces three **primary meristems**: procambium, protoderm, and ground meristem. **Protoderm** cells differentiate into epidermal cells. The **ground meristem** differentiates into the cortexexternal layer of primary stem or root and pithcentral layer of primary stem or root. The **procambium** raises between the **cortex** and the **pith**. It forms **vascular bundles** or **vascular cylinder**.(Figure 9.4.2).

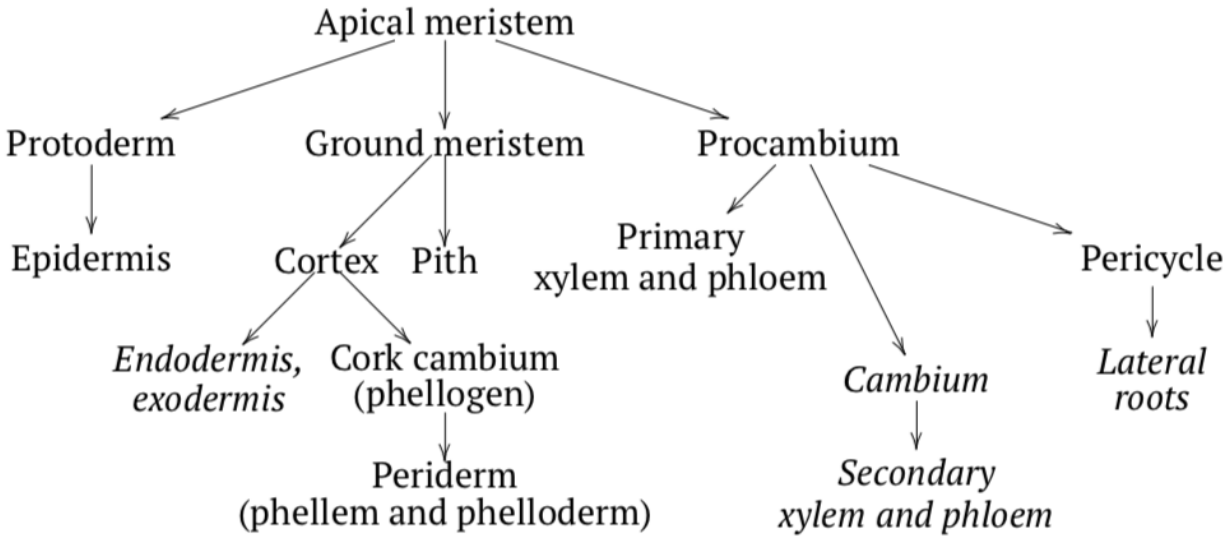


Figure 9.4.3 Developmental origin of stem tissues (detailed). Root tissues have similar ways of development.

The outer layers of the procambium form the *primary phloem*. The inner layers become the *primary xylem*. The middle layer can be entirely spent or will make cambium for the secondary thickening. At times, the layers of the outside of the procambium can form a **pericycle**. Sometimes the innermost layer of the cortex can form an **endodermis** (endoderm) (Figure 9.4.3), and outermost layer makes the exodermis (exoderm). All these layers are some kind of the “border control” between functionally different layers of stem. Another frequent variant is the development of collenchyma in the cortex adjacent to epidermis.

Vascular bundles connect leaves and stems. In many plants, they form a ring on the cross-section of the stem. Parenchyma (ground tissue) between vascular bundles typically belongs to both cortex and pith. Another variant is a *vascular cylinder*, structure which fully encircles the stem. Liliid (monocot) stems generally have dispersed vascular bundles. These three variants are **steles**, overall configurations of the primary vascular system of the plant stem (Figure 5.5.1). The most frequent kinds of steles are **eustele** (vascular bundles in a ring), **solenostele** (vascular cylinder) and **ataktostele** (dispersed vascular bundles).

All these types were probably originated from **protostele**, configuration where central xylem is surrounded with phloem and no pith is present (Figure 5.5.2). While the protostele was typical for many prehistoric plants, now only some lycophytes (*Huperzia*) have protostele in stems.

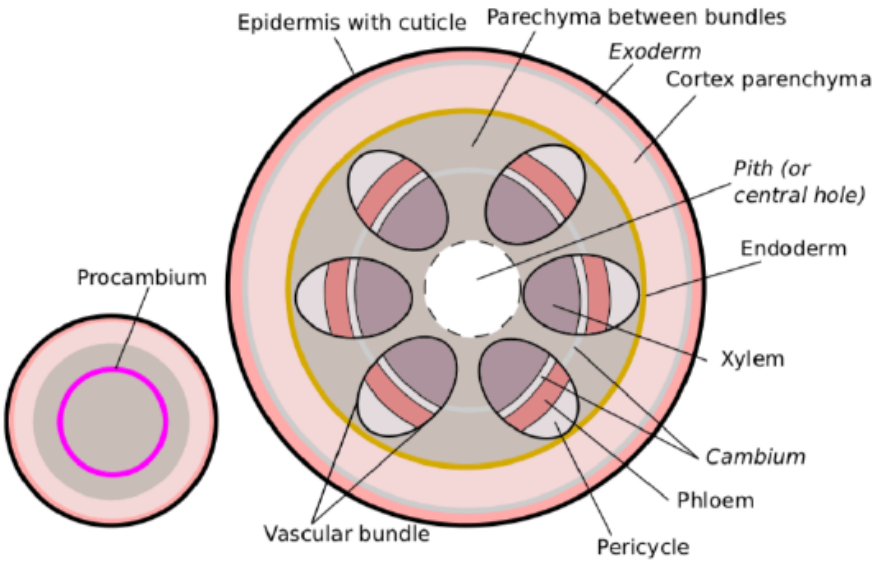


Figure 9.4.3 Anatomy of the primary stem (right). Slanted font is used for “optional” tissues. Small image on the left is the young stem consisted of epidermis, cortex, procambium and pith.

Saying that, it is important to note that roots of most plants have vascular tissues arranged similarly to protostele.

9.4.1: Inside Stems

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9.4.1: Inside Stems

Learning objectives

- Discuss how stems grow by elongation and by increasing their girth or diameter.
- Identify the tissues that are initially produced by apical meristems and the cells into which they eventually mature.
- Distinguish monocot and dicot stems based on the arrangement of the vascular bundles.
- Describe the functions of some of the specialized cells in the stem.

Introduction to stems



Notice this image of a palm tree because it will come up again later. Think about where and how it is growing. Travel Aficionado – CC BY-NC 2.0

Herbaceous plants are plants whose above-ground plant parts die back to the soil surface at the end of the growing season. Herbaceous plant shoots grow in length and diameter in the same way that roots do: the apical meristem at the tip of the stem produces new cells and then those new cells enlarge in length and volume in the region of elongation just behind the meristem. Stems of herbaceous plants typically do not thicken very much and rely instead on branching to grow laterally (although there are exceptions like sunflower and tomato whose stems do thicken noticeably). Branching of the shoot is initiated at nodes where there are axillary buds containing axillary meristems that grow into branches.

Continued growth of the stem in diameter, like you find in a tree where the trunk and branches increase in diameter each year, requires an active lateral meristem called the cambium. Cambium is a meristem in the vascular tissue positioned between the xylem and phloem that continues to produce new xylem cells toward the interior of the stem and new phloem cells toward the exterior. Production of xylem and phloem from cambium cells is called secondary growth and is typical of woody perennial plants. We will explore plants with secondary growth in a different lesson.

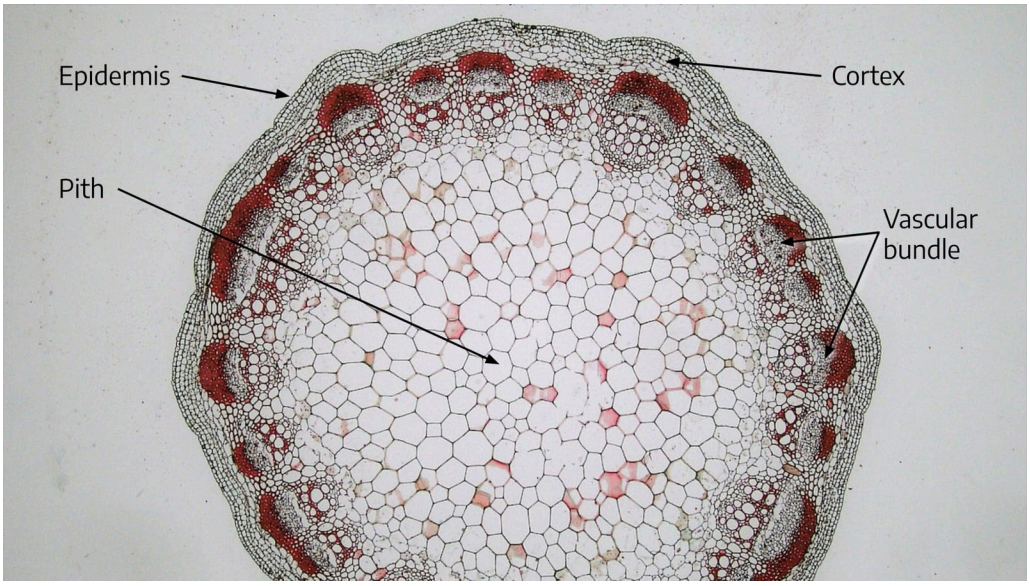
Some herbaceous plants are annuals, like beans and pansies, where the whole plant dies over the winter. These plants complete their life cycle from seed to flower to seed in one year. Other herbaceous plants, like Kentucky bluegrass and chrysanthemums, are herbaceous perennials where only the above-ground growth dies over winter (unless it is a really nasty winter). The root, or in some cases underground stem tissue, stores nutrients for the next season's growth. In spring when soil and air temperatures are sufficiently warm, new shoots emerge from nodes on compact stem tissues often called crowns. The cells in the crown tissue survive the harsh winter temperatures because they accumulate sugars and other compounds that act as antifreeze compounds. They are located very close to the soil surface, or even protected a bit by the soil. This position on or in the soil, plus snow cover, results in much warmer temperatures around the crown than the air temperature above the snow. In fact, the air temperature can

be -20°F above the snow and only a few degrees below freezing (32°F) around the crown.

Dicotyledonous stems

Watch this video for a detailed description of dicot stems (2:19).

This micrograph of a herbaceous dicot stem shows four basic parts (in order from outside to inside): epidermis, cortex, vascular bundle, and pith. Notice how the vascular bundles of dicots are arranged in a ring around the circumference of the plant stem with the cortex to the outside and pith to the inside.



Dicot stem. Berkshire Community College Bioscience Image Library. Public domain

Epidermis – This tough covering is a single layer of living cells. These cells are closely packed and function to protect the internal parts of the plant. The walls are thickened and covered with a thin waxy waterproof layer called the cuticle that reduces water loss from the plant. Stomata with guard cells are found in the epidermis, and these function to allow gasses into and out of the stem, similar to their function in leaves. In some stems either unicellular or multicellular hair-like outgrowths, called trichomes, appear from the epidermis. Below is an image of trichomes on a tomato stem, inflorescence, and leaf.

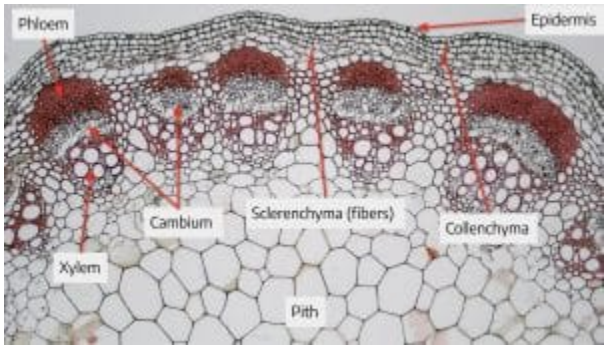


Tomato stems, leaves, and inflorescences have abundant trichomes. Quinn Dombrowski – CC BY-SA

Cortex – Also known as the ground meristem, the cortex is found just inside the epidermis and extends toward the interior of the stem. It is made up of three types of cells: parenchyma, collenchyma, and sclerenchyma.

Vascular bundles – This region contains sclerenchyma fibers that strengthen the stem and provide protection for the vascular bundle. In dicots, the vascular bundles form a distinct ring. A mature vascular bundle consists of three main tissues – xylem, phloem, and cambium. The phloem is always located toward the outside of the bundle and the xylem always toward the center. The cambium separates the xylem and phloem, and, in those plants where secondary growth takes place, the cambium produces new xylem and phloem cells: xylem toward the center, phloem toward the outside.

The **pith** occupies the central part of the stem and is composed of thin-walled parenchyma cells often with larger intercellular spaces than you would find in the cortex.



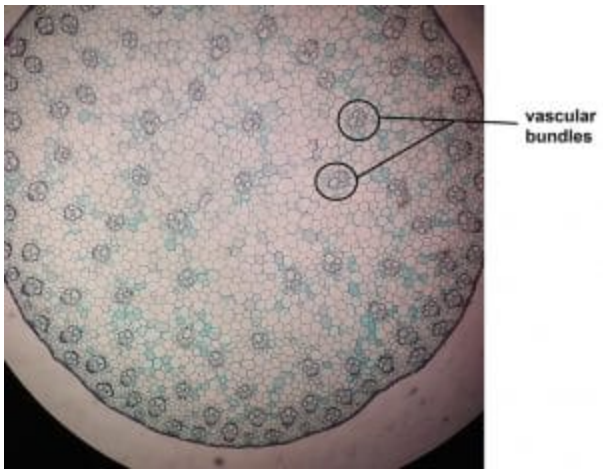
Cross section of a young sunflower (Helianthus) stem, magnified 100x. Berkshire Community College Bioscience Image Library. Public domain

In this cross section of a dicot stem note the collenchyma cells in the cortex just under the epidermis. Sunflower stems are quite tough, and this toughness is in part due to the layer of collenchyma cells positioned to give the stem mechanical stability. Toward the outside of each vascular bundle are fibers of sclerenchyma that also contribute to the sunflower stem's toughness. Then, moving from the outside to the inside, you will find phloem, a layer of cambium, and then xylem. The pith is in the center.

Now you might recall that just above we said that herbaceous annuals like sunflower don't have cambium to increase the girth of the stem, so what's with the cambium in this picture of a sunflower stem? Well, you will see a layer of cambium between the xylem and phloem of dicot stems, and it is active for a while and produces a modest amount of xylem and phloem which contributes to the sunflower's larger diameter stem. However, this cambium tissue is not continuously active as in woody stems, and the plant does not survive through the winter.

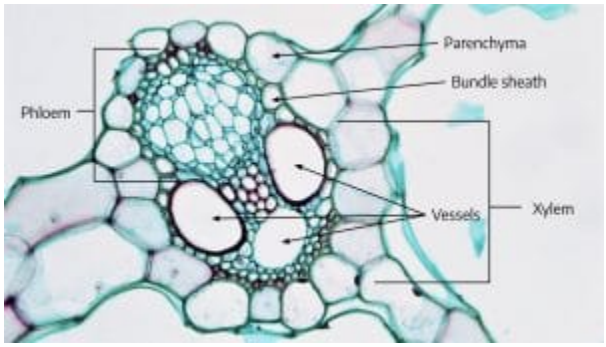
Monocotyledonous stems

The tissues making up monocot stems are essentially the same as what we saw in dicots with the main difference apparent in the placement of the vascular bundles. In monocots, vascular bundles are scattered throughout the stem instead of being oriented in a ring. Since there is no ring of vascular bundles, there is no "inside" pith and "outside" cortex. All the ground tissue is considered to be cortex.



Monocot corn stem cross section showing vascular bundles. Melissa Ha. CC BY-NC 2.0

In monocot vascular bundles the phloem is always oriented toward the outside of the plant and the xylem toward the inside. There is no cambium and no secondary growth. Around the outside of the vascular bundle is a layer of parenchyma cells called the bundle sheath. This layer of cells is very important in photosynthesis. For now we will consider it a protective covering and supportive sheath around the vascular bundle.



Monocot stem showing vascular bundles. Berkshire Community College Bioscience Image Library. Public domain.

One final note

So why the palm tree? Because it is an exception.

A palm tree is a monocot, but unlike other monocots whose stems are quite thin (like grasses, for instance), their primary stems do increase in girth from year to year even though they do not have secondary cambium. Palms have a special layer of meristematic cells, called the primary thickening meristem, oriented toward the outside of the stem that each year can initiate new vascular bundles and new parenchyma cells. Each year the stem expands in girth as a result of the palm's production of new parenchyma and vascular bundles. You don't need to memorize this – it is just an example of an interesting exception to the rule.



Ringless palm tree trunk. readerwalker – CC BY-NC-SA 2.0

Review questions

After completing this section, you should be able to answer these questions:

1. Herbaceous perennials die back to the ground in the spring. Where do they get the energy to grow the next spring, and from what tissue do new shoots emerge?
2. Dicots typically have a pith while monocots do not. Why?
3. Could you distinguish between a monocot and dicot stem based on the arrangement of the vascular bundles?

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9.5: THE ROOT

Root is a latest evolutionary innovation in the vegetative plant anatomy. Many “primitive” plants (all mosses and even some ferns like *Psilotum*) do not have roots; some flowering water plants like the> rootless duckweed (*Wolffia*) or the coontail (*Ceratophyllum*) have also reduced their roots. However, large homoiohydric plants need the constant supply of water and minerals, and this evolutionary challenge was responded with appearance of the root system.

The **Root** in *an axial organ of plant with geotropic growth*. One of root functions is to supply anchorage of the plant body in soil or on various surfaces. Other functions include water and mineral absorption and transport, food storage, and communication with other plants.

Morphology of the Root

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”).

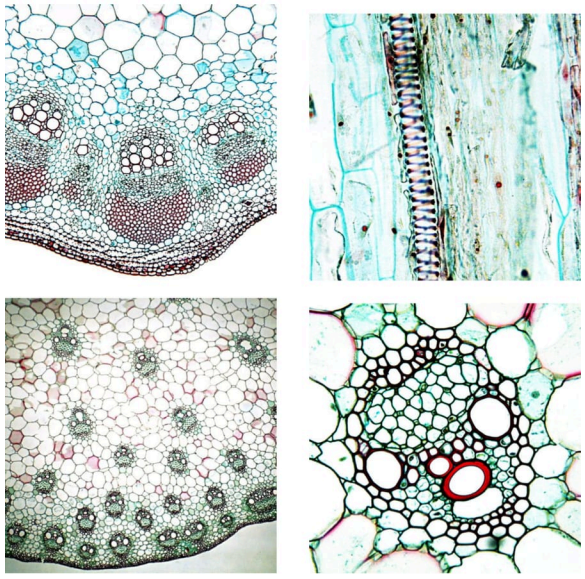


Figure 9.5.1 Left to right, top to bottom: eustele (stem segment), xylem vessel (longitudinal section) and ataktostele (stem segment and vascular bundle). First photo is from the stem ofHelianthus, second from Trifolium, last two from the stem of Zea. Magnifications ×100 (first and third) and ×400 (second and fourth).

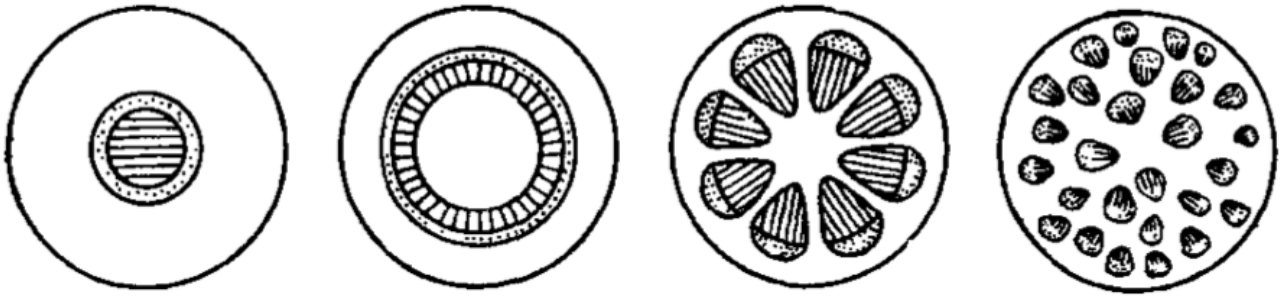


Figure 9.5.2 Steles (left to right): protostele, solenostele, eustele, ataktostele. Xylem is lined, phloem is dotted.

Along with having different systems, there are different types of roots: **primary root** originated from the root of the seedling, **secondary (lateral) roots** originate from the primary roots, and **adventitious roots** originate on stems (sometimes also on leaves), the example are prop roots of screw pine (*Pandanus*).

Roots employ many different modifications which help to protect, interact and storage. For example, roots of parasitic plants are modified into **haustoria** which sink themselves into the vascular tissue of a host plant and live off of the host plant's water and nutrients.

Roots of mangroves (plants growing in ocean coastal swamps) are frequently modified into *supportive aerial roots* ("legs"). Since these swamp plants need oxygen to allow cell respiration in underground parts, there are **pneumatophores**, specialized roots which grow upward (!) and passively catch the air via multiple pores. Plants which grow on sand (psammophytes, see above) 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.

Some orchid roots are green and photosynthetic (Figure $9.5.3$)! However, as a rule, root is the heterotrophic organ, because root cells have no access to the light.



Figure $9.5.3$ Photosynthetic roots of leafless orchid Chiloschista segawai.

Root nodules present on the roots of nitrogen-fixing plants, they contain bacteria capable to deoxidize athmospheric 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.

Anatomy of the Root

On the *longitudinal section* of young growing root, there are different horizontal layers, zones: root cap covering *division zone*, *elongation zone*, *absorption zone*, and *maturation zone* (Figure $9.5.4$). The **root cap** protects the root apical meristem (RAM), which is a group of small regularly shaped cells. A small, centrally located part of the RAM is the **quiescent center** where initial cells divide and produce all other cells of root. Root cap is responsible for the geotropic growth, if the root tip comes into contact with a barrier, root cap will feel it and will grow on a different direction to go around it.

The **elongation zone** is where the cells start to elongate, giving it length. The **absorption zone** where the rhizodermis tissue (root hairs) develops and where water and nutrients are absorbed and brought into the plant. Within the **maturation zone**, root hairs degrade, many cells start to acquire secondary walls and lateral roots develop (Figure $9.5.4$).

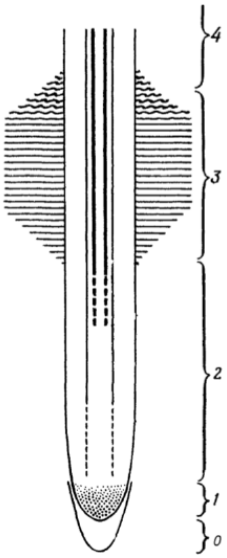


Figure 9.5.4 Root zones: 0 root cap, 1 division zone, 2 elongation zone, 3 absorption zone, 4 maturation zone.

On the *cross-section* of the root made within absorption zone, the first tissue is the rhizodermis, which is also known as the root epidermis, then cortex, which segregates external *exodermis* and internal *endodermis* one-cellular layers, and vascular cylinder (Figure 9.5.5). Typically, roots have no pith. In some cases (for example, in orchids), cortex may give multi-layered *velamen* (see above), another absorption tissue.

Vascular cylinder is located in the center of the root, it contains the pericycle which is made of mostly parenchyma and bordering endodermis. Pericycle cells may be used for storage, they contribute to the vascular cambium, and initiate the development of lateral roots. Consequently, lateral roots are developing endogenously and break tissues located outside, like aliens in the famous movie. Root phloem is arranged in

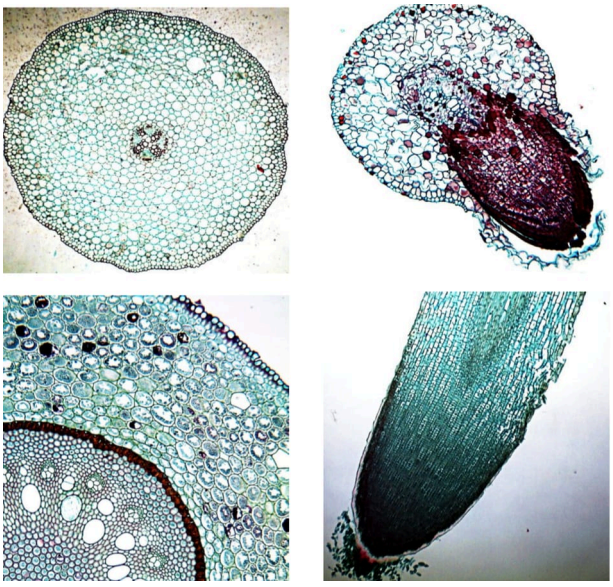


Figure 9.5.5 Left to right, top to bottom: Ranunculus root with 4-rayed xylem, Salix root with the lateral root developing, Smilax root with visible Casparian stripes in the endodermis; Zearoot longitudinal section with root cap, division and elongation zones. Magnifications ×100 (second) and ×40 (others).

several strands whereas xylem typically has a radial, sometimes star-shaped structure with few rays (Figure 9.5.6). In the last case, phloem strands are located between rays of xylem.

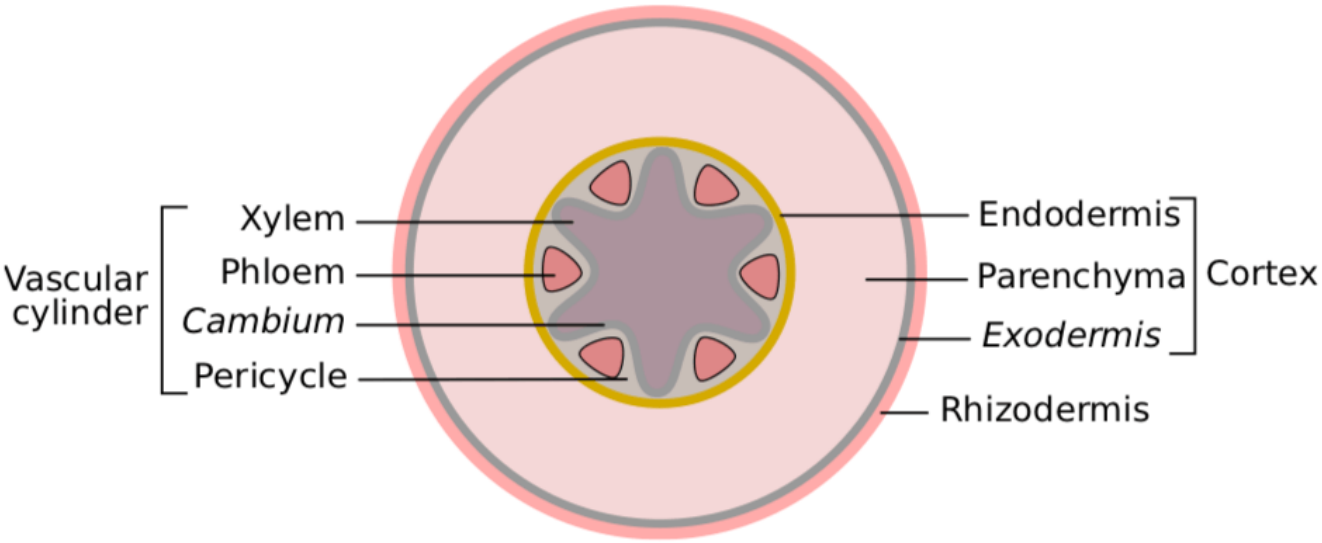


Figure 9.5.6 Anatomy of root: cross-section through the maturation zone.

Root tissues develop in the way similar to stem, RAM gave rise to ground meristem, procambium, and the protoderm, which in turn make all primary tissues mentioned above. Later, pericycle develops into lateral roots or the vascular cambium which in turn produces into the secondary xylem and phloem. The secondary root is similar to secondary stem (see below).

Water and Sugar Transportation in Plants

Plants need water to supply photosynthesis (the oxygen is from water!), to cool down via transpiration, and to utilize diluted microelements. Dead velamen (paper-like), rhizoids (hair-like), and living rhizodermis (rhizoderm) are responsible for water uptake.

In rhizodermis, root hairs increase the surface area where the plant has to absorb the nutrients and water. To take water, hair cells increase concentration of organic chemicals (the process which needs ATP) and then use osmosis. There are two ways that water transport may go: apoplastic or symplastic. *Apoplastic* transport moves water through the cell walls of cortex: from the rhizodermis to the endodermis. Endodermis cell walls bear **Casparian strips** (rich of hydrophobic suberin and lignin) which prevent the water from passing through the cell wall and force *symplastic* transport (Figure 9.5.7) through cytoplasms and plasmodesmata. Symplastic transport there is directed to the center of root only and requires ATP to be spend.

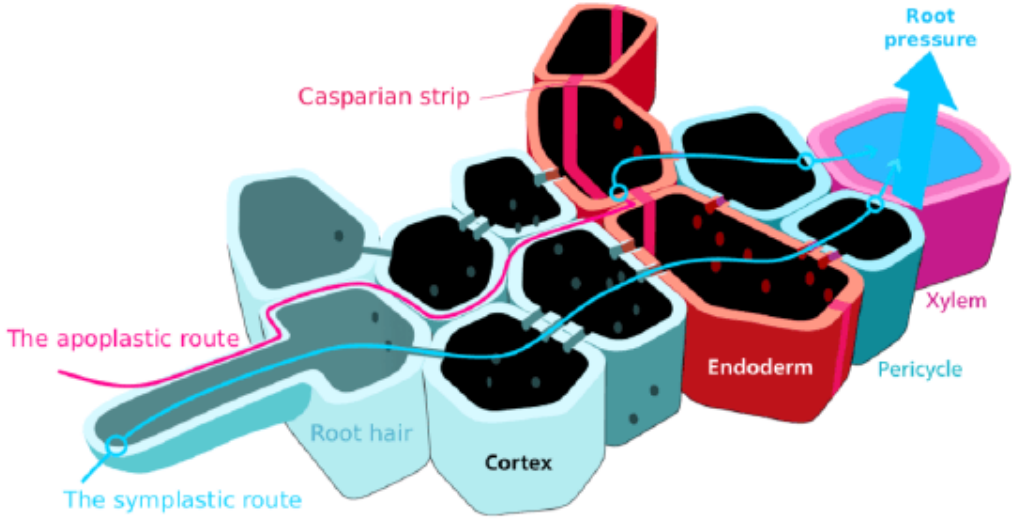


Figure 9.5.5 Symplastic and apoplastic transport in root.

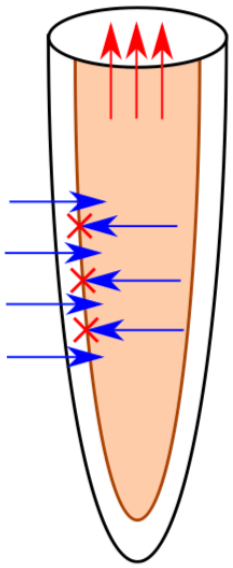


Figure 9.5.5 The origin of root pressure: water comes into vascular cylinder but cannot go back because of endoderm (brown line). The only possible way is to go up.

By pumping water inside vascular cylinder and not letting it back, endodermis cells create the root pressurepressure force made solely by roots (Figure 9.5.8). It is easy to observe on tall herbaceous plants cut near the ground: drops of water will immediately appear on the cutting. Inside tracheary elements of xylem, water moves with the root pressure, capillary force and the sucking pressure of transpiration. The latter means that water column does not want to break and if water disappears from the top (stomata on leaves), it will move water inside plant. The main direction of water movement is from roots to leaves, i.e. upwards.

Products of photosynthesis (sugars) are moving inside living cells of phloem; these cells (sieve tubes) use only symplastic transport to distribute glucose and other organic compounds among all organs of plants. In fact, phloem transports these components in all directions: to the flowers (usually upwards), and at the same time to the roots (usually downwards).

9.5.1: Inside Roots

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9.5.1: Inside Roots

Learning objectives

- Explain how roots elongate and increase in diameter via primary and secondary meristems.
- Identify the tissues in the root that originate from the root meristems and the cells into which they eventually mature.
- Distinguish between monocot and dicot roots.
- List the functions of the cells in plant roots.

Please read the OpenStax pages summarizing root biology. This resource reinforces several of the topics addressed below, so you may read it either before or after you complete this chapter. You don't need to memorize the information there; use it to reinforce the content below.



Roots. Leonard J Matthews – CC BY-ND 2.0

Root review

The functions of roots include:

- Anchoring the plant in the soil (and stabilizing the soil).
- Supporting the upright growth of the plant.
- Providing a site for the symbiotic relationship of the plant with particular beneficial fungi and bacteria.
- Absorbing water and dissolved minerals from the soil.
- Storing nutrients like starch for subsequent use by the plant (tap roots and tuberous roots are examples of geophytes that store nutrients in roots).

Angiosperm (flowering) plants are often classified by whether they rely on a primary root system an adventitious root system. A plant doesn't necessarily have only primary or just adventitious roots. One of these systems, however, will be dominant. Whether a root is considered primary or adventitious depends on whether the root traces back to the radicle (embryonic root) or arises from (normally underground) stem tissue.

Tap root (or primary root) system

Tap or primary roots arise as a continuation of the embryonic radicle tissue and persist into maturity. Secondary roots (also called

lateral roots) arise from the primary root, and tertiary roots arise from the secondary. This primary –> secondary –> tertiary root formation is the usual rooting system for dicots. Next time you see a dandelion or other weed that doesn't look like a grass, yank it up and look at the root system. The main root you see (assuming that it didn't break off when you pulled it up) is probably a tap root. The photo on the right, above, demonstrates this point. It shows a young taproot system with many secondary roots branching off the primary root.



This *Desmanthus spp.* plant has a strong central taproot with many lateral or secondary roots. Btcpg – CC BY-SA 4.0

Adventitious or fibrous root system

In plants of this type, the primary root, which originates from the radicle, weakens prior to maturity and new, vigorous, adventitious roots arise from stem tissue. Adventitious roots may grow from nodes or might arise from the internodes. They originate from parenchyma cells in the cortex of the stem. Dig up a clump of turfgrass and look at the roots. Turfgrass has a fibrous root system, as does corn.



Adventitious corn roots. NY State IPM Program at Cornell University. CC BY 2.0.

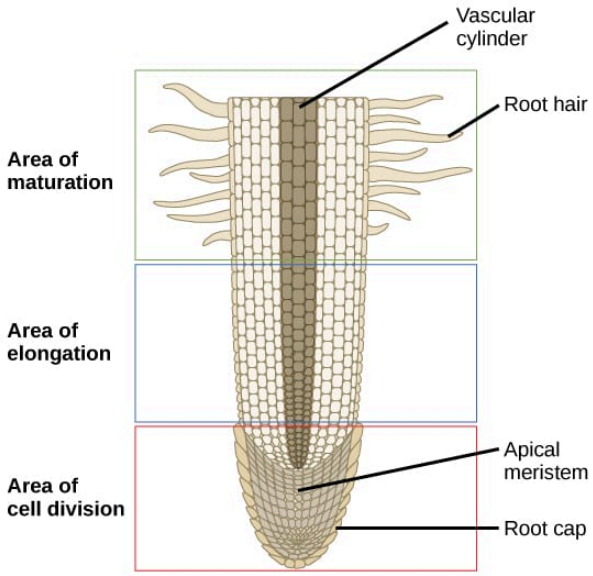
As noted above, although adventitious roots originate from the stem they don't have to emerge from a node. While it's not apparent in the photo, the adventitious corn roots you see above do trace back to a node. In contrast, in the photo of a tomato stem, below, we see emergence of adventitious roots from both node and internodal regions of the stem.



Tomato stem with adventitious roots. Mark. CC BY 2.0

Internal root structure

Watch this video to take a closer look at root structure (6:21):



Root with areas labeled. CNX OpenStax. CC BY 4.0 International

Root cap

Shaped like a thimble, this structure covers the tip of the root and provides protection as the root grows into the soil. These parenchyma cells are produced by the root's meristem which is just behind the root cap. The outer cells of the root cap are continuously worn away through contact with the soil, and new cells are added to the inner portion.

In addition to protecting the interior of the root, the cap secretes a mucilage which stabilizes the water content of the surrounding soil, ensuring longer-lasting nutrition to the root system and making for easier root probing. Finally, the root cap contains statocytes, specialized cells that help the plant sense gravity and grow accordingly. These cells are full of starchy organelles which settle at the lowest part of the cell and encourage growth in that direction. If the root cap, with these statocytes, is removed, a plant may grow in random directions because it has lost the ability for gravitropism (growth in response to gravity).

Root meristem

The cells here divide rapidly via mitosis to form new cells. New cells are laid down toward the root cap to replace those worn away during root growth, and also laid down away from the root cap. These new cells laid away from the root cap elongate and then mature into more specialized root tissues.

Region or zone of elongation

In this region, the cells produced by the root meristem undergo rapid elongation — they expand in length and volume. Root growth is the result of two processes: new cell production by the root meristem, and subsequent elongation of those new cells. This growth pushes the root further into the soil and also expands the diameter of the root. Within the region of elongation just behind the meristem you will find the following undifferentiated tissues:

- Protoderm — new cells laid down toward the exterior of the root which will mature to become the root dermal tissue (primarily epidermis cells).
- Procambium — new cells in the central part of the root which will mature to become the vascular tissue (xylem, phloem, and vascular cambium), labeled in the illustration above this section as the vascular cylinder.
- Ground meristem — the new cells lying between the protoderm and procambium that will mature to become the cortex tissue (primarily parenchyma cells).

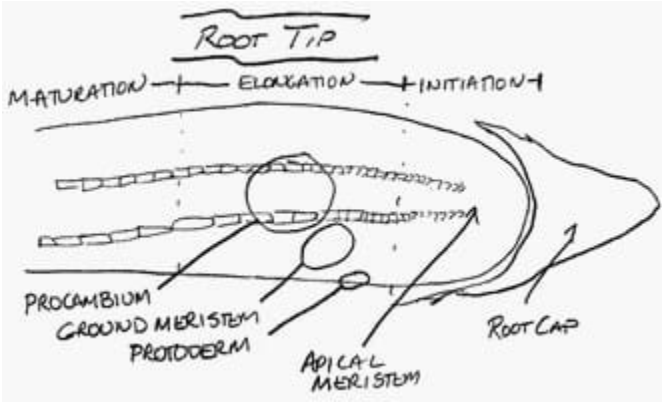
Region of differentiation (also called the region of maturation)

Here the root becomes thicker, and secondary or lateral roots are initiated. In this region the protoderm, procambium, and ground meristem cells undergo differentiation into the specialized cells associated with the dermal, vascular, and cortex tissues, as noted above.

Root-hairs begin to form in the region of differentiation; these are fine outgrowths of epidermis cell walls and membranes, and increase the area of absorption of the root.



Here is a magnified image of a root, and a drawing to point out the various components. Jen Dixon – CC BY-NC-SA 2.0



Root tip. Image credit: Tom Michaels

Review questions

1. What two processes result in root growth?
2. Protoderm will differentiate or mature into what type of tissue? How about procambium? And ground meristem?

3. Do adventitious roots arise from stem tissue or from the primary root? Are they always found emerging from nodes or from internodes, or does it depend on the type of plant?

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9.6: ATLAS- ROOTS, STEAMS, AND LEAVES

9.6.1: Roots

9.6.1.1: Primary Growth

9.6.1.1.1: Root Long Section (Zea mays)

9.6.1.1.2: Monocot Roots

9.6.1.1.3: Eudicot Root Cross Section (Ranunculus)

9.6.1.2: Secondary Growth

9.6.1.3: Root Systems

9.6.2: Stems

9.6.2.1: Primary Growth

9.6.2.2: Secondary Growth

9.6.2.3: Woody Shoot Structures

9.6.2.4: Modified Shoots

9.6.3: Leaves

9.6.3.1: Leaf Parts and Arrangement

9.6.3.2: Monocot Leaves

9.6.3.3: Eudicot Leaves

9.6.3.3.1: Adaptations to Water Availability

9.6.3.4: Modified Leaves

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9.6.1: ROOTS

The root system of a plant serves two primary functions: water absorption and anchorage. Roots with a higher surface area will be better adapted to absorbing water because they have more area to interact with the soil environment. Increased interaction with the soil environment can also contribute to increased anchorage, but there are always trade-offs. If roots become too fine, they will be easily broken and lose the anchorage function. Additionally, finer roots can also **lose** more water if the soil environment becomes dry. Alternatively, roots with more volume are able to store more water, starches, or other materials belowground. The balancing of these trade-offs with localized environments has resulted in a great diversity of root types and morphologies.

9.6.1.1: Primary Growth

9.6.1.1.1: Root Long Section (Zea mays)

9.6.1.1.2: Monocot Roots

9.6.1.1.3: Eudicot Root Cross Section (Ranunculus)

9.6.1.2: Secondary Growth

9.6.1.3: Root Systems

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- 11: Roots by Maria Morrow is licensed CC BY-NC 4.0.

9.6.1.1: PRIMARY GROWTH

All plant roots begin in primary growth, which is a lengthening of plant organs. Primary growth involves the root apical meristem, primary meristems, and primary tissues.



Figure 9.6.1.1.1: These wheatgrass seeds have recently sprouted, producing fresh root and shoot growth. This would be an excellent place to look for roots in primary growth. Note that, even though it is a tangled mess, the individual roots are not branching very much. Instead, they are growing like long, thin threads. At the tip of each of these threads, you would find a root apical meristem. Photo by Maria Morrow, CC BY-NC.

YouTube Video

This interactive element is not available in this format. Visit the link or scan the QR code to access it online.

View this YouTube Video online

Video 9.6.1.1.1: This video by Ben Montgomery provides a walkthrough of the internal structures and organization of plant roots, including lateral root formation. Sourced from YouTube.

- Primary Growth

9.6.1.1.1: Root Long Section (Zea mays)

9.6.1.1.2: Monocot Roots

9.6.1.1.3: Eudicot Root Cross Section (Ranunculus)

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- 11.1: Primary Growth by Maria Morrow is licensed CC BY-NC 4.0.

9.6.1.1.1: Root Long Section (Zea mays)

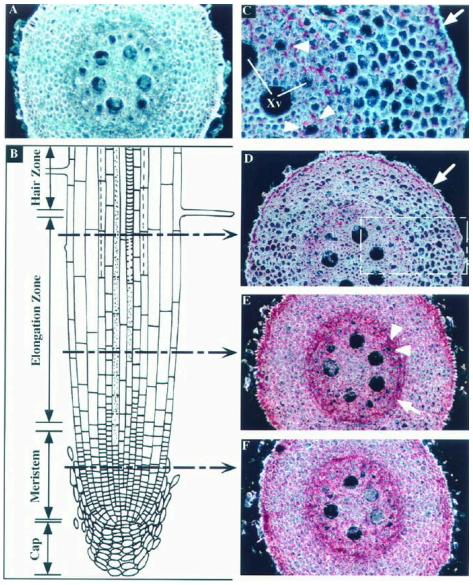


Figure 9.6.1.1.1.1: This figure is from a study exploring the expression of a particular mRNA in corn roots (shown as red in the images, but not important to understanding the anatomy). In B, we see a diagram of a longitudinal section through a growing root tip. The region labeled "Meristem" is the Zone of Division, covered by the root cap. The Elongation Zone is were cells get larger, and the region labeled "Hair Zone" is the Zone of Maturation, where cells are clearly differentiated and can start to specialize. D, E, and F show cross sections of the root in these zones. The large gaps in the cross sections are vessel elements, located within the vascular cylinder. Image retrieved from the open-access paper High Expression of the Tonoplast Aquaporin *ZmTIP1*in Epidermal and Conducting Tissues of Maize, Barrieu et al. 1998, published in Plant Physiology.

Figure 9.6.1.1.1.2: A diagram of a growing root tip. The tip of the root is covered by a cap of cells (C). Most of the root is covered by small projections (root hairs). The region of the root with hairs is labeled E. Between the area covered with hairs and the area covered by the cap, the root is labeled D. A=Root hair, B=Root cap, C=Zone of Division, D=Zone of Elongation, E=Zone of Maturation. Image from the public domain with labels added by Maria Morrow.

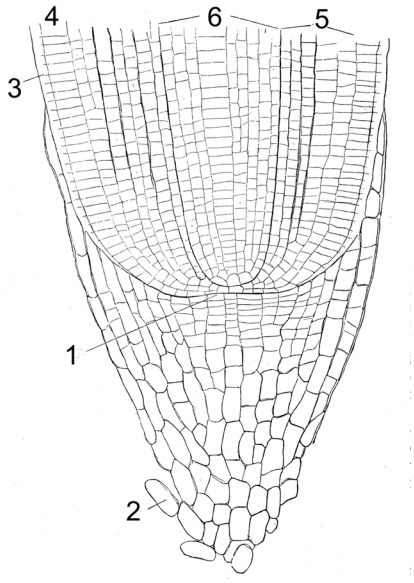


Figure 9.6.1.1.1.3: Anatomy of the root tip, zone of division. The first image is a *Zea mays* root tip. The second image is an illustrated diagram to show the tissues, labeled as follows: 1=Root apical meristem (RAM), 2=Root cap cell, 3=Rhizodermis (epidermis of the root), 4=Protoderm, 5=Ground Meristem, 6=Procambium. Photo by Maria Morrow, CC BY-NC. Illustration from de:Benutzer:Griensteidl, Public domain, via Wikimedia Commons.

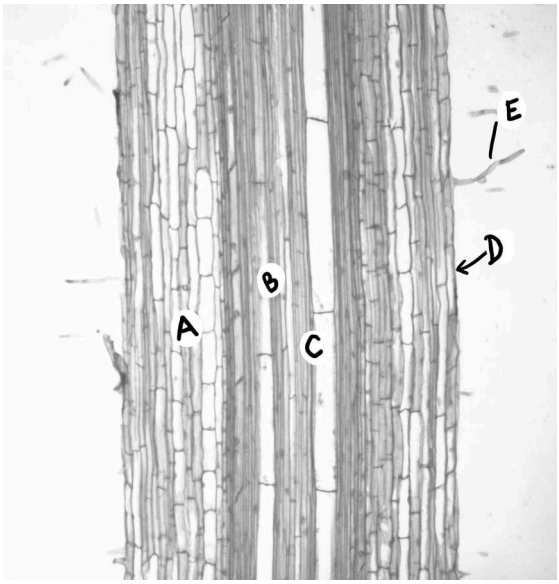


Figure 9.6.1.1.1.4: A longitudinal section through the zone of elongation. A=Cortex, B=Pith (or where the pith would be, this section may be slightly off center, capturing more of the vascular tissue), C=A vessel element in the vascular tissue, D=Epidermis, E=Root hair. Image by Maria Morrow, CC BY-NC.

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9.6.1.1.2: Monocot Roots

Zea mays

Zea mays (corn) is often used as a model organism for monocot anatomy.

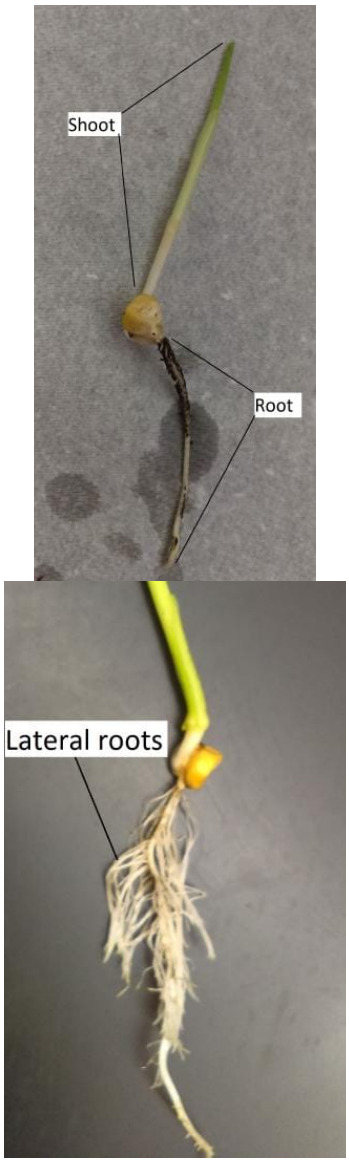


Figure 9.6.1.1.2.1: The images above show a corn seedling in two different stages of development. The first image is of the corn seedling at an earlier stage. It has produced a shoot (with one cotyledon) and a long root (radicle). In the second image, you can see that it has gotten larger by comparing the size of the seed coat from the corn kernel (caryopsis). The radicle has developed into a root system with many lateral roots branching off to the sides. Photos by Melissa Ha, CC BY-NC .

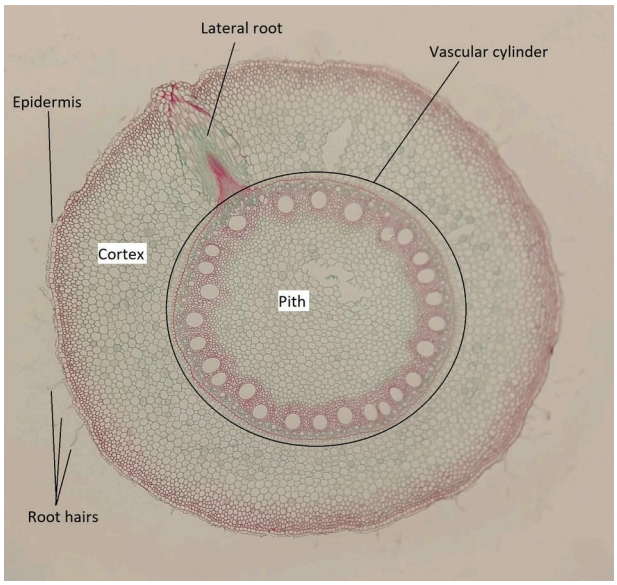


Figure 9.6.1.1.2.2: Corn root cross section. The major regions of the root are labeled in the cross section above. The epidermis is the outermost layer of cells and includes elongated cells called root hairs. The cortex is the region of cells between the epidermis and the vascular tissue. The pith is the region of cells contained within the cylinder of vascular tissue. A lateral root is emerging from the vascular cylinder. Photo by Maria Morrow, CC BY-NC.

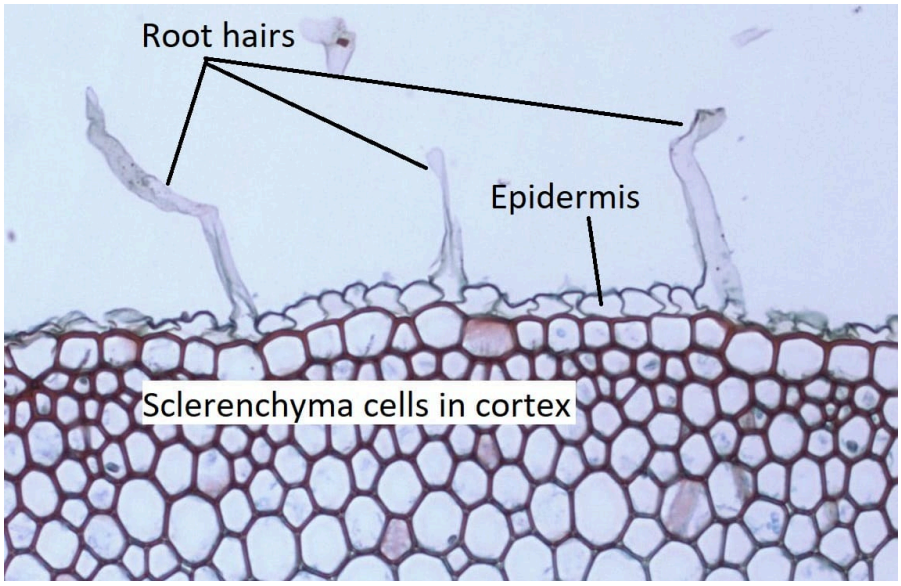


Figure 9.6.1.1.2.3: Corn root cross section, close up of epidermis and root hairs. The epidermis is the outermost layer of cells, produced by the protoderm. These are parenchyma cells. The epidermis includes long, thin cells that project outward called root hairs. Root hairs are specialized for absorbing water and will only be found in young, growing root tips. The cells below the epidermis are part of the cortex. Many of these have become sclerenchyma cells with thick secondary walls. Compare the cell walls found in the epidermis to those found in the cortex. Photo by Maria Morrow, CC BY-NC.

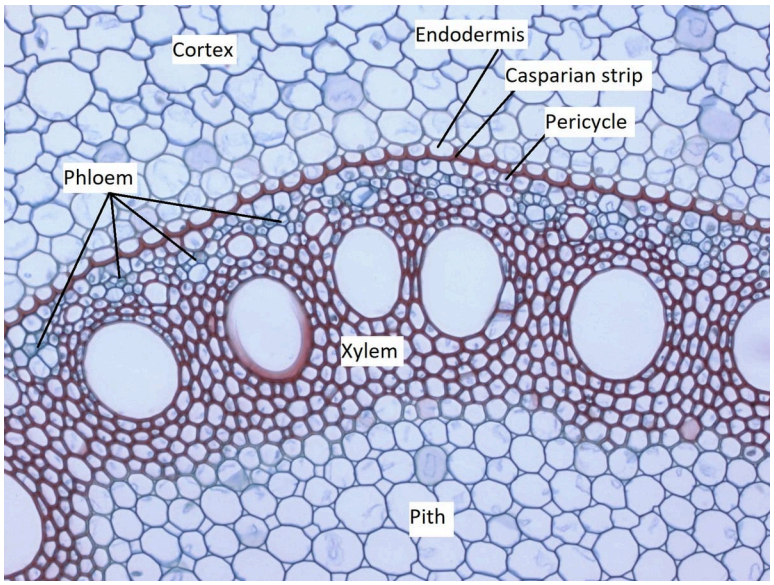


Figure 9.6.1.1.2.4: Corn root cross section, close up of part of the vascular cylinder. A band of cells travels across the center of the image, making a slight arc. This is a segment of the vascular tissue, which is arranged in a cylinder within the root. The vascular cylinder is within a suberized layer of cells that forms the border of the cortex, called the endodermis. The suberin wax layer coating the endodermal cells is the Casparian strip. Just inside the endodermis (below it, in this image orientation) is a layer of cells called the pericycle. This is where lateral roots are produced. The phloem tissue is composed of pockets of cells with thinner walls (stained blue). The rest of the cells in the vascular cylinder have thick secondary walls (stained red) and are part of the xylem tissue. When the cells begin to have thin, blue-stained walls again (in this image), you've reached the pith. Photo by Maria Morrow, CC BY-NC.

Smilax

The organization of tissues in a Smilax root is similar to that in a corn root.

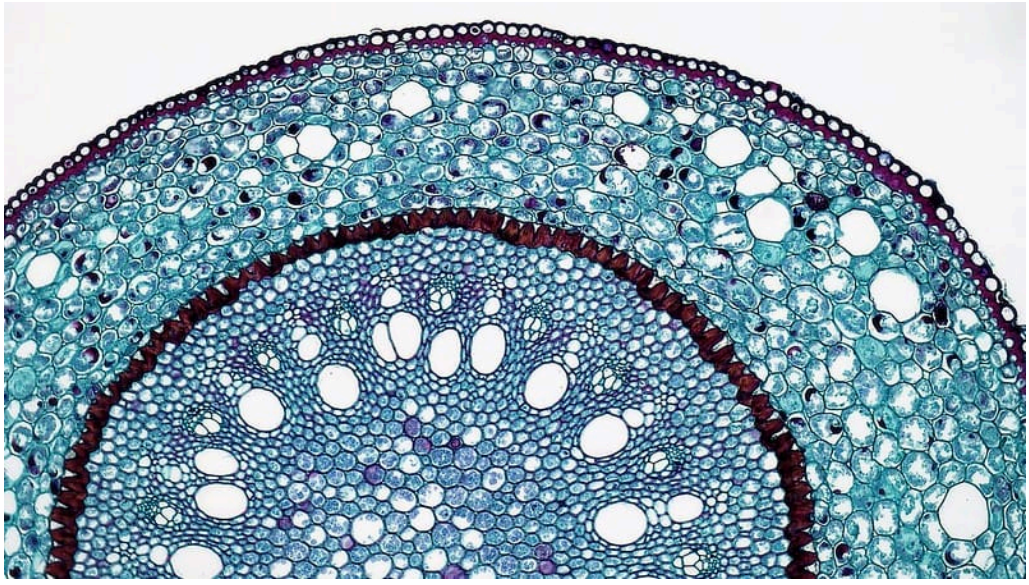


Figure 9.6.1.1.2.5: A cross section through a Smilax root. Compare this cross section to the corn root above. The staining is slightly different, so you cannot rely on color, alone. Image is in the Public Domain, sourced from Berkshire Community College Bioscience Image Library.

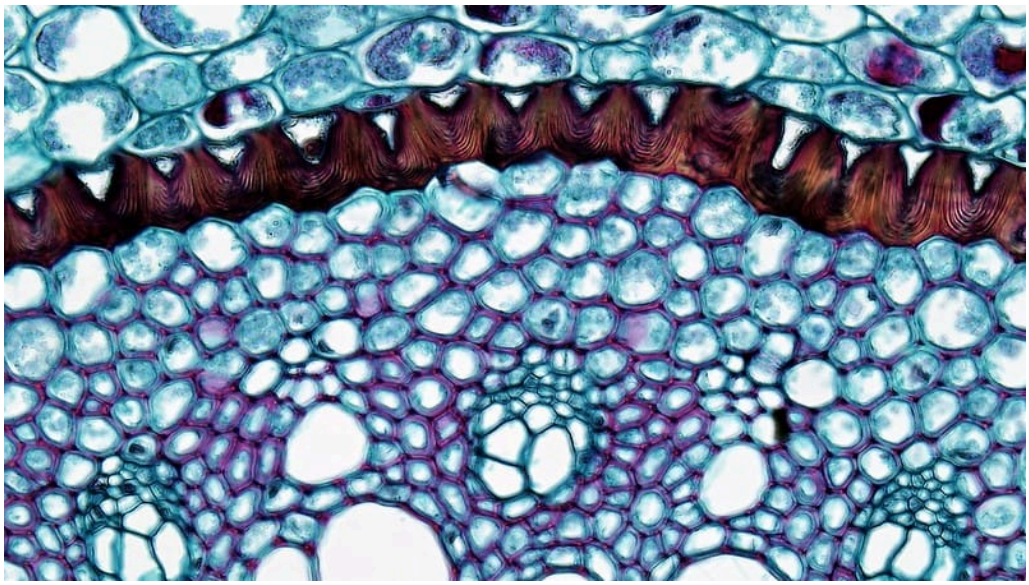


Figure 9.6.1.1.2.6: A close up on the multilayered Casparian strip of the Smilax root. The layers of Casparian strip look a bit like fingerprints or growth rings in wood, forming tightly packed layers surrounding each cell. Compare the thickness of this Casparian strip to the corn root. What would cause the difference in thickness? Image is in the Public Domain, sourced from Berkshire Community College Bioscience Image Library.

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9.6.1.1.3: Eudicot Root Cross Section (Ranunculus)

Ranunculus

Figure 9.6.1.1.3.1: A cross section of a young *Ranunculus* root. The epidermis and cortex are in a similar arrangement as in monocots. However, the vascular cylinder has no internal pith region. Instead, it is composed entirely of vascular tissue with xylem at the center in a Y-shape and phloem filling the regions between the arms of the Y. Photo by Melissa Ha, CC BY-NC with labels added.

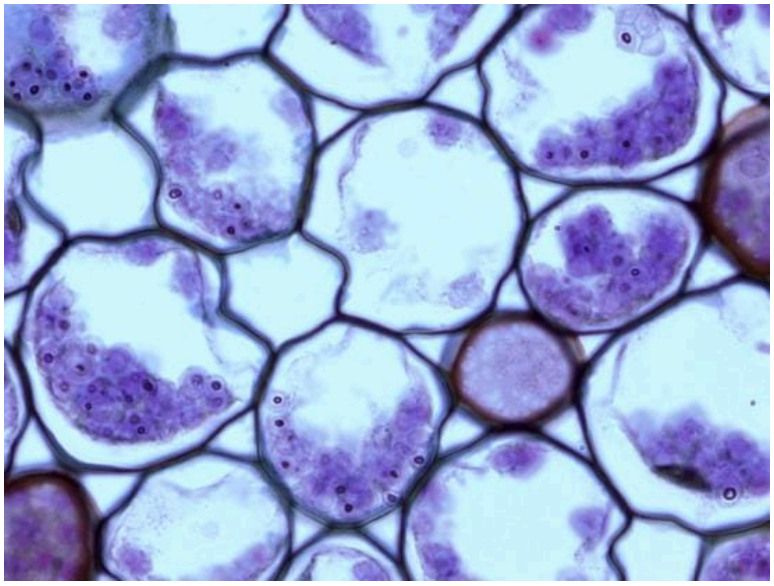


Figure 9.6.1.1.3.2: A close up on the cortex cells of the *Ranunculus* root. These cortex cells are also called storage cells because they contain many amyloplasts (stained purple) that store starch. Defined areas that do not contain amyloplasts are likely intercellular spaces (areas between cells). Photo by Maria Morrow, CC BY-NC.

Young Root

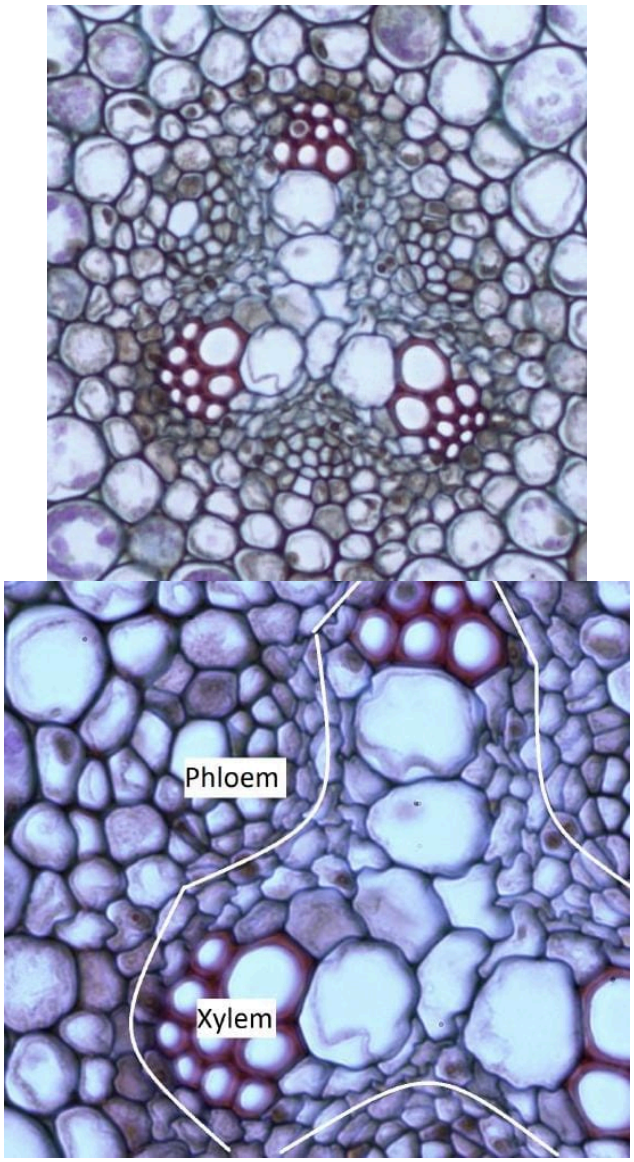


Figure 9.6.1.1.3.3: A close up on the vascular cylinder of the young *Ranunculus* root. At this stage, the vascular tissue does not have a well-defined boundary from the cortex (see the image on the left). Some of the xylem cells are stained red. These cells have developed their secondary walls and reached functional maturity. The others have only primary walls and are still developing. In the image on the right, the Y-shape of the xylem has been indicated by white lines. Those white lines represent the location of the procambium, which produces xylem to the inside and phloem to the outisde. One of the three pockets of phloem tissue is labeled. Photos by Maria Morrow, CC BY-NC.

Mature Root

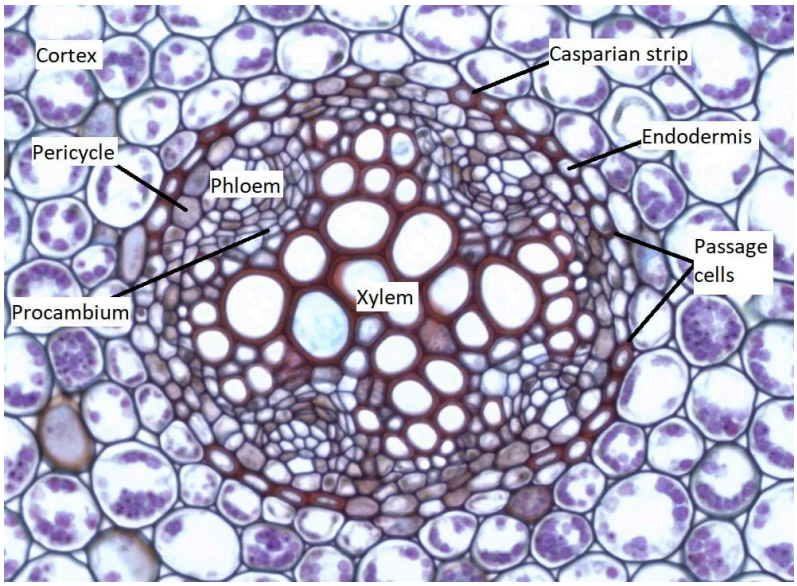


Figure 9.6.1.1.3.4: A close up on the vascular cylinder of a mature *Ranunculus* root. The vascular cylinder is now clearly defined by the boundary of the endodermis (the innermost layer of the cortex), which is beginning to be covered by Casparian strip (which stains red, making the covered cells look like they have a secondary wall, but they do not). There are regions of the endodermis that appear to have no Casparian strip or only have it between adjacent cells. These groups of cells, called passage cells, are located at the tips of the four xylem arms (which are in an X-shape, now). Eventually, all of the cells in the endodermis will be coated. Photo by Maria Morrow, CC BY-NC.

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9.6.1.2: Secondary Growth

In secondary growth, primary tissues and residual meristematic tissues produce secondary meristems, which then produce secondary tissues. Whereas primary tissues allow for vertical growth, secondary tissues allow for lateral growth: they allow stems and roots to become wider by producing **wood**. In addition to growing wider, secondary growth exchanges the living epidermis for a thick layer of dead, waterproofed cells called cork. The cork and a few other layers of tissue comprise something called the periderm, or perhaps more familiarly called **bark**.

This type of growth first evolved in gymnosperms. It is also present in many angiosperms. As a general rule, monocots do not undergo secondary growth (though some, like bamboo, have an analogous process).

Gymnosperms

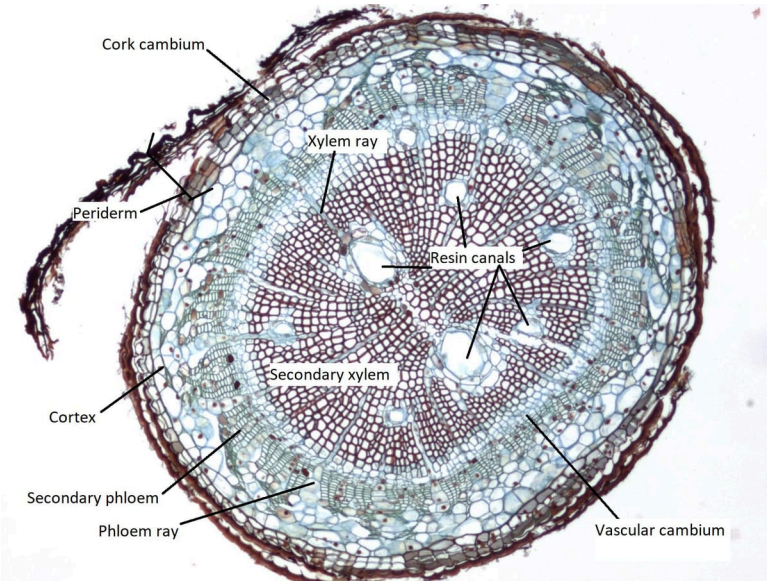


Figure 9.6.1.2.1: A cross section of a pine root in the early stages of primary growth. The first layer of periderm is forming, causing the epidermis to slough off. The periderm is currently the outermost layer, compose of a few layers of suberized cork cells, the cork cambium, and large cells called the phelloderm. The cortex is just inside the phelloderm and is getting smaller as the root grows. Ranks of cells just inside the cortex are secondary phloem cells (stained a blue-green color) which are being produced by the vascular cambium (a ring of cells stained light blue between the xylem and phloem). Just within the vascular cambium, making up the center of the root, is the secondary xylem (stained red, due to the secondary wall). There are large holes in the secondary xylem where resin canals are traveling through. Strings of parenchyma cells traverse laterally through the vascular tissue. These are called xylem rays and phloem rays, depending on their location within the vascular tissue. Image from Berkshire Community College Bioscience Image Library, CC0, via Wikimedia Commons.

Angiosperms

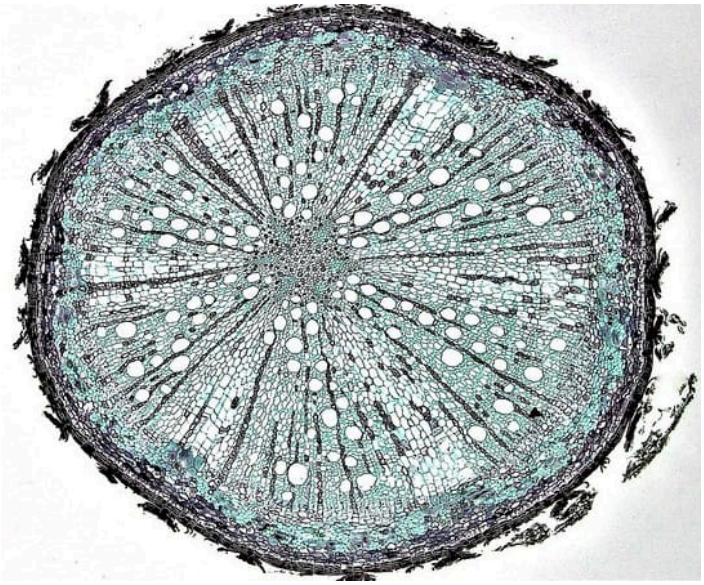


Figure 9.6.1.2.2: Older *Quercus* root, 40x. "In young roots, the vascular cylinder is surrounded by two rings of cells, the pericycle and endodermis, and above these layers the cortex and epidermis. In older roots underling activity of the cork cambium replaces the epidermal and cortical tissues with a protective zone of cork rich periderm. The outermost layer of periderm consists of layers of cork cells, the phellem, which produce the waterproofing substance suberin. Cork cells are dead at maturity. Deep to the phellem is a layer of living cork cambium or phellogen and just beneath that layers of cork parenchyma or phelloderm. Many cells in the periderm contain dark staining tannins. The vascular cylinder consists of an outer narrow ring of phloem,and deep to this, the vascular cambium. The vascular cambium remains active, producing annual growth of secondary phloem towards the outside of the root and secondary xylem towards center of the root. Because of greater production of xylem, the bulk of the vascular cylinder is dominated by radially arranged rays of secondary xylem interspaced with medullary rays of parenchyma cells. Annual growth rings of spring and summer wood is difficult to distinguish in roots. Both the pericycle and endodermis, which wrap vascular cylinder in younger roots, are lost due to seasonal growth of the vascular cylinder. The center of the root is made up of primary xylem." Caption text and image from Berkshire Community College Bioscience Image Library, CC0, via Wikimedia Commons.

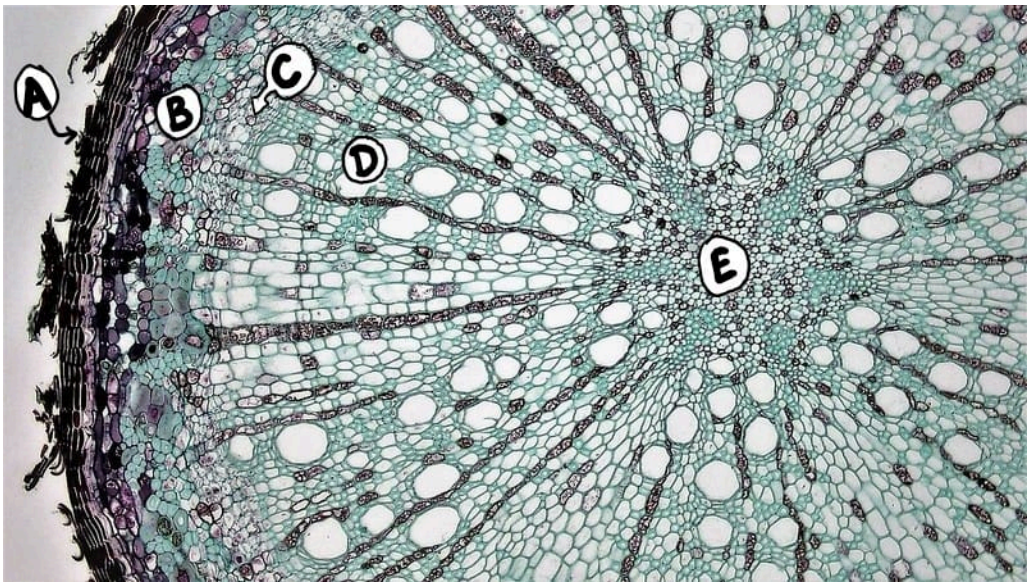


Figure 9.6.1.2.3: A labeled cross section through an older *Quercus* root, 100x. A=Periderms, B=Secondary Phloem, C=Vascular Cambium, D=Secondary Xylem, E=Primary xylem. Image from Berkshire Community College Bioscience Image Library, CC0, via Wikimedia Commons. Labels added by Maria Morrow.

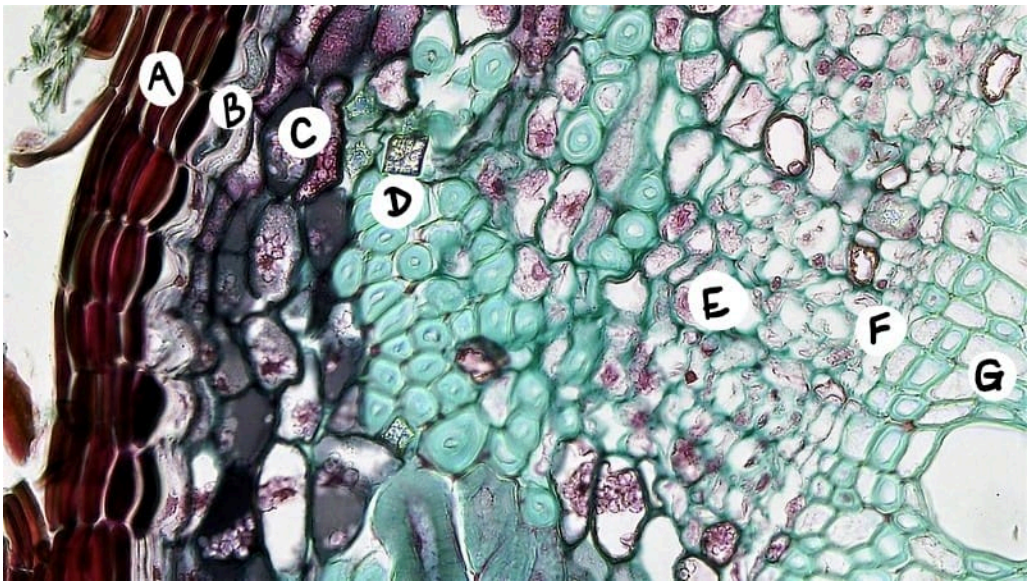


Figure 9.6.1.2.4: A labeled cross section through the outer tissues of an older *Quercus* root, 400x. A=Cork cells, B=Cork cambium, C=Phelloderm (A, B, and C=Periderm), D=Secondary phloem fibers, E=Secondary phloem, F=Vascular cambium, G=Secondary xylem. Image from Berkshire Community College Bioscience Image Library, CC0, via Wikimedia Commons. Labels added by Maria Morrow.

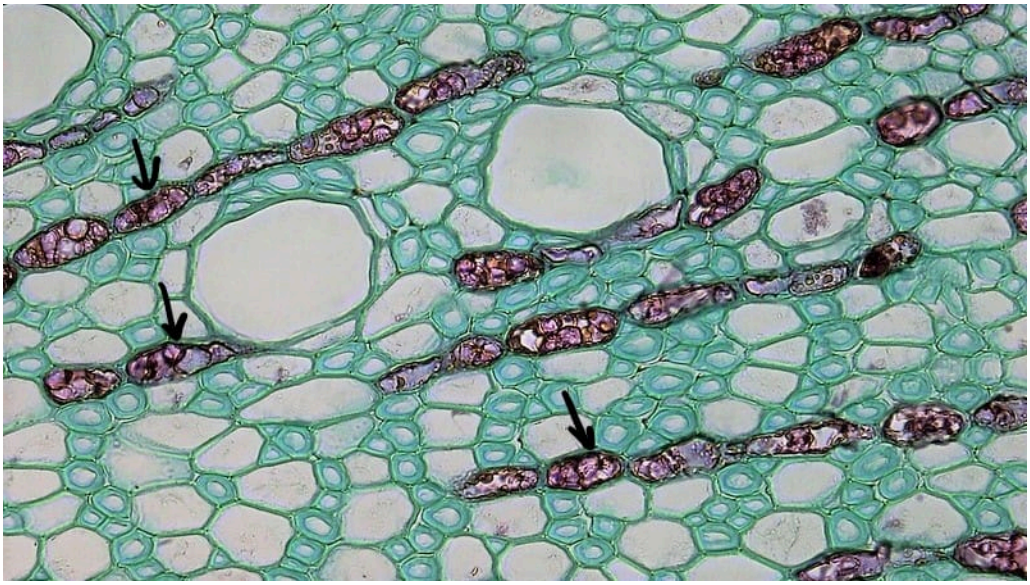


Figure 9.6.1.2.5: A cross section through the secondary xylem of an older *Quercus* root, 400x. The rows of darker cells (indicated by arrows) are parenchyma cells that traverse the secondary xylem and phloem. In the xylem, they are called xylem rays. In the phloem, they are called phloem rays. Image from Berkshire Community College Bioscience Image Library, CC0, via Wikimedia Commons. Labels added by Maria Morrow.

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9.6.1.3: Root Systems

Taproots

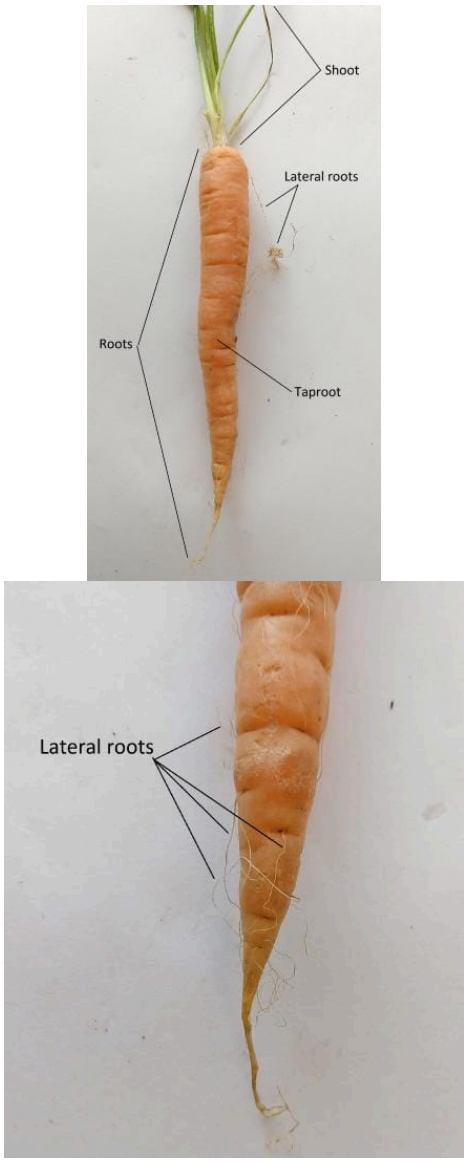


Figure 9.6.1.3.1: The carrot vegetable we eat is the taproot of a carrot plant. The large, central root (what we call a carrot) is a taproot and has many much smaller lateral roots that emerge from the sides. These are not root hairs, which would appear more like a microscopic fuzz at the ends of these lateral roots. Photos by Maria Morrow, CC-BY 4.0.



Figure 9.6.1.3.2: Some plants invest far more in their below ground tissues than their above ground ones. In this image, an enormous taproot of the small, prostrate plant *Abronia latifolia* (the yellow sand verbena) has been explosed as the dune sand has blown away from this area over time. How does investment in this taproot structure benefit this plant, considering the shifting, sandy environment? Photo by Maria Morrow, CC-BY 4.0.

Netted Roots

Figure 9.6.1.3.3: The netted root system of *Zea mays*. There are many roots of approximately the same diameter that then branch off into smaller roots. There is, distinctly, no one larger root. This is a netted root system. Photo by Maria Morrow, CC-BY 4.0.

Contractile Roots



Figure 9.6.1.3.4: The base of a dandelion rosette, showing a contractile root. The central root shown, where the leaves of the rosette meet at the base, looks like a compressed slinky. This is a contractile root, which can respond to seasonal changes in water availability to keep the dandelion plant at ground level. As water swells the soil, it can rise up. In response, this contractile root can swell with water, extending and allowing the plant to stay at the surface. In the case of a drought, the root can contract as the soil level drops. Photo by Melissa Ha, CC-BY 4.0.

Adventitious Roots



Figure 9.6.1.3.5: Adventitious roots of a kalanchoe plant. Many house plants reproduce themselves easily, lending to their cultivation and sale. The kalanchoe is extending a branch outward and producing new roots from its stem tissue. Notice the seven projections traveling down from the branch. These are adventitious roots, because they are produced by the stem. If this branch were cut off, it could be established as a new plant, due to the presence of these roots. Photo by Melissa Ha, CC-BY 4.0.

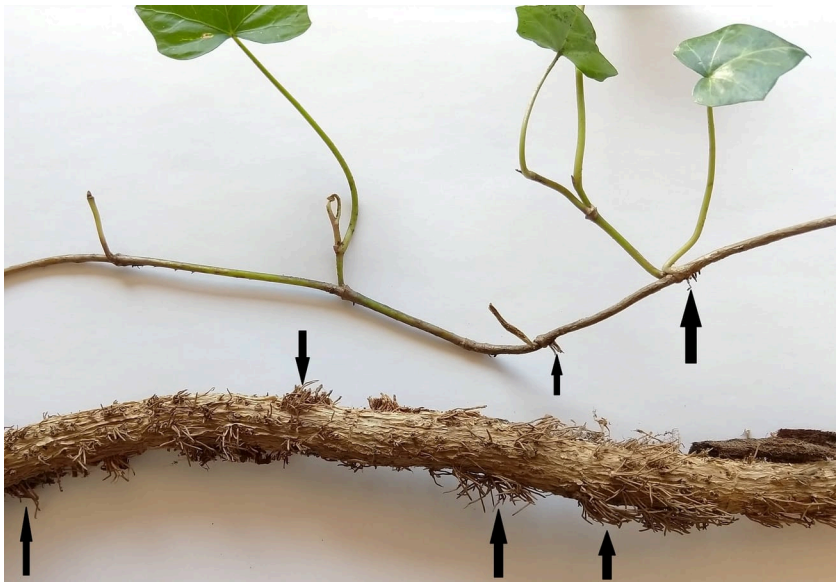


Figure 9.6.1.3.6: Vining plants frequently produce adventitious roots. This image shows two English ivy stems, a younger one on the top and a much older one on the bottom. The young stem has small clusters of adventitious roots emerging from the stem at nodes opposite to the leaves. Two of these are indicated by black arrows. On the older stem, adventitious roots emerge along the entire length, making it look hairy. There are a few particularly dense clusters, indicated by arrows. Photo by Maria Morrow, CC-BY 4.0.

Prop Roots.

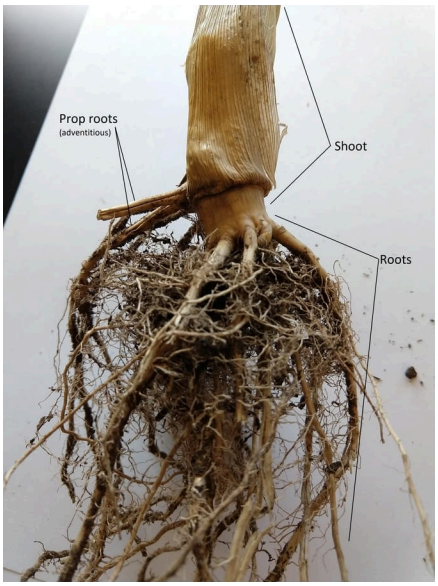


Figure 9.6.1.3.7: Zea mays also has prop roots that emerge from the stem. Above the netted root system, there is a short collar, then sheathing leaves emerge, indicating the transition to shoot tissue. At the base of these leaves, several prop roots are emerging. These prop roots, whose function is to give the plant extra stability from above ground, are also adventitious roots. Photo by Maria Morrow, CC-BY 4.0.

Pneumatophores



Figure 9.6.1.3.8: Mangroves grow in the intertidal zone where they spend much of the day inundated by water. Roots need to take in oxygen for cellular respiration. On strategy to gain access to oxygen is the development of aerial roots called pneumatophores (lung-bearers). The many pointed structures emerging from the soil under these *Avicennia* trees in Mumbai are pneumatophores. Photo by Dr. Raju Kasambe, CC BY-SA 4.0, via Wikimedia Commons.

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9.6.2: STEMS

The shoot of a plant is responsible for two major functions: photosynthesis and reproduction. In most plants, the leaves carry out **photosynthesis**, while the stems provide stability to elevate those leaves above potential competition. In annual plants, whose entire life cycle from germinate to death is completed in a single year, the epidermis on the stem is often photosynthetic, as well. All stems undergo primary growth. In gymnosperms and many angiosperms, stems will transition into secondary growth to form woody tissues.

9.6.2.1: Primary Growth

9.6.2.2: Secondary Growth

9.6.2.3: Woody Shoot Structures

9.6.2.4: Modified Shoots

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9.6.2.1: Primary Growth

Tissues in the shoot are derived from the shoot apical meristem (SAM). Just like in the root, the SAM produces three primary meristems, which produce the primary tissues:

- Protoderm → Epidermis
- Ground meristem → Cortex and pith (simply ground tissue in monocots)
- Procambium → Primary xylem and primary phloem

These primary tissues will then either differentiate into specialized cells or, as is the case in many eudicots, become meristematic and produce secondary tissues.

Coleus Stem Tip

Though it looks a bit alien, this is a section through a growing tip of a plant. In the center, where the alien's head might be, is a region of small, densely packed cells. This is the SAM of the apical bud. On either side of the SAM, like two upraised arms, are the leaf primordia. These are the early stages of developing leaves. Through the center of these leaf primordia is a darker region of small cells. This is the procambium, which will develop into the vascular tissue. Lining the outer edge of the SAM and the youngest portions of the leaf primordia is the protoderm. As the protoderm matures into the epidermis, it produces hair-like projections called trichomes. Between the protoderm and the procambium is the ground meristem.

On either side of the growing tip are two other darkened lumps of densely packed cells. These bud primordia will develop into axillary buds, producing either branches or flowers. Each bud primordium has its own SAM.

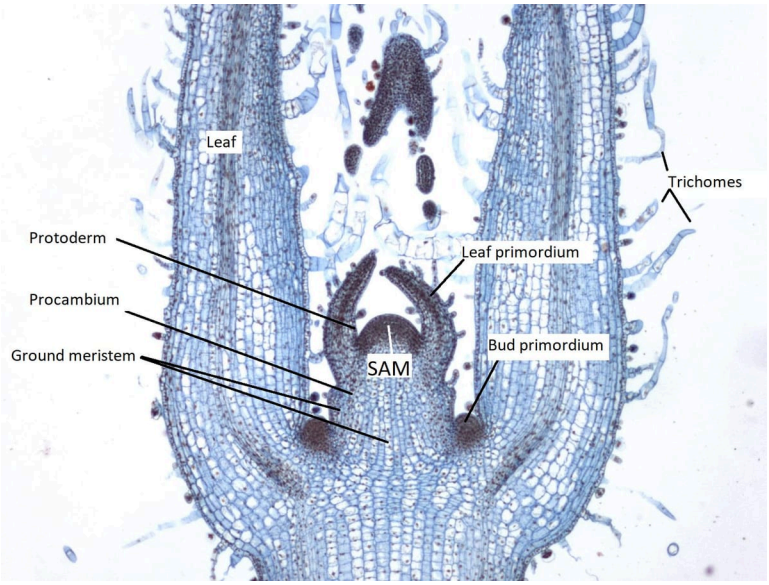


Figure 9.6.2.1.1: A partial view of a Coleus shoot tip long section. If we anthropomorphize it a bit and think of it as a humanoid with horns, it might be easier to conceptualize where the different parts are. The two "arms", held straight up into the air, are the leaves. Each leaf has many multicellular trichomes along its epidermis and a central strand of vascular tissue. Where the shoulders would be, there are two dark regions. These are bud primordia that will develop into axillary buds. They are dark in color because they are regions of intense cell division as they are rapidly growing. The "horns" are leaf primordia that will develop into leaves, much like the "arms". Between the two horns, at the top of the "head", is the shoot apical meristem (labeled SAM). All of the cells in the shoot are derived from this region. The protoderm runs along the exterior, near the SAM and leaf primordia. The procambium forms the vascular tissue and can be found in the center of the leaf primordia. The ground meristem forms the cortex and pith and can be found in the regions between the protoderm and procambium. Photo by Maria Morrow, CC BY-NC.

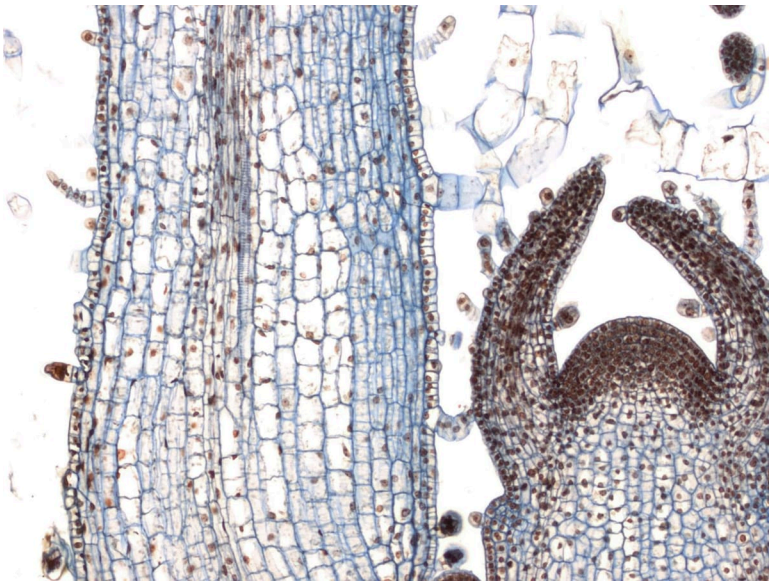


Figure 9.6.2.1.2: A closer view of the Coleus shoot tip long section. Can you locate the SAM and primary meristems? Look for regions of densely packed cells, as these are all meristematic tissues, actively dividing to produce more cells. Photo by Maria Morrow, CC BY-NC.

Monocots

Figure 9.6.2.1.3: A cross section of a *Zea mays* stem. The organization of tissues differs from the *Zea mays* root. Most notably, the vascular tissue is arranged in bundles, rather than a central cylinder. These bundles are densely packed toward the outside of the stem, then occur less frequently toward the inside. Because there is no distinct delineation of the tissues produced by the ground meristem, it is now called ground tissue (as opposed to cortex and/or pith). Photo by Maria Morrow, CC BY-NC.

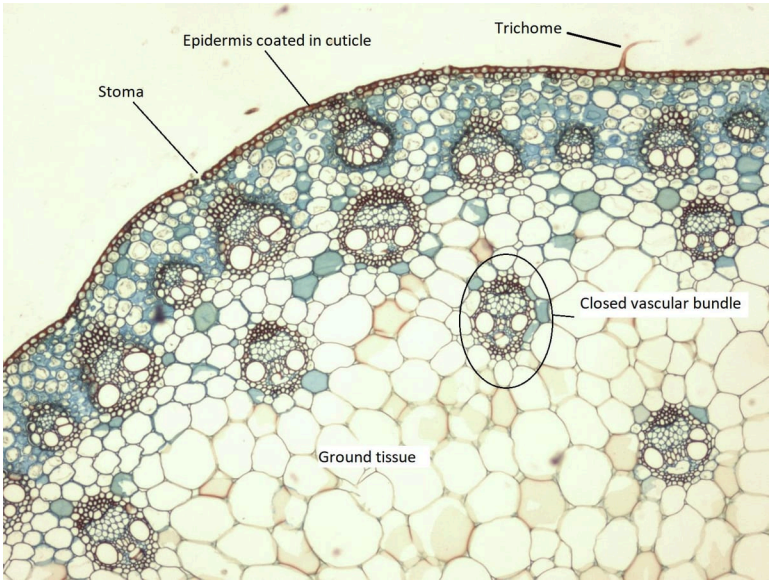


Figure 9.6.2.1.4: A closer view of a portion of the *Zea mays* stem. The epidermis is the outermost layer, coated in a thick cuticle that stains red. There are gaps in the epidermis where stomata are located, as well as a hair emerging (a trichome). The vascular bundles are situated within the ground tissue. Photo by Maria Morrow, CC BY-NC.

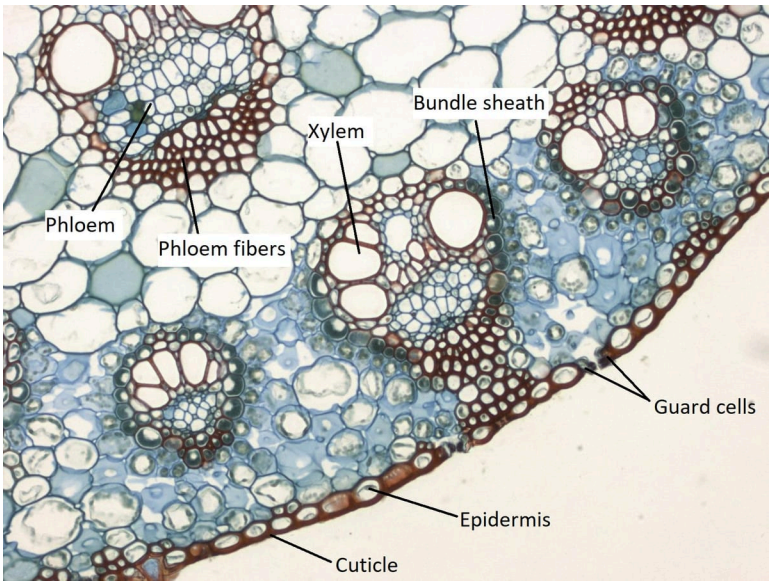


Figure 9.6.2.1.5: A cross section of a *Zea mays* stem highlighting the vascular bundles. In the epidermis, the cuticle and guard cells are easier to distinguish in this image. Vascular bundles are arranged close to the epidermis with the xylem (stained red) toward the interior of the stem and the phloem (stained blue) toward the exterior. Each bundle is surrounded by a layer of cells called the bundle sheath. Photo by Maria Morrow, CC BY-NC.

Eudicots

Helianthus

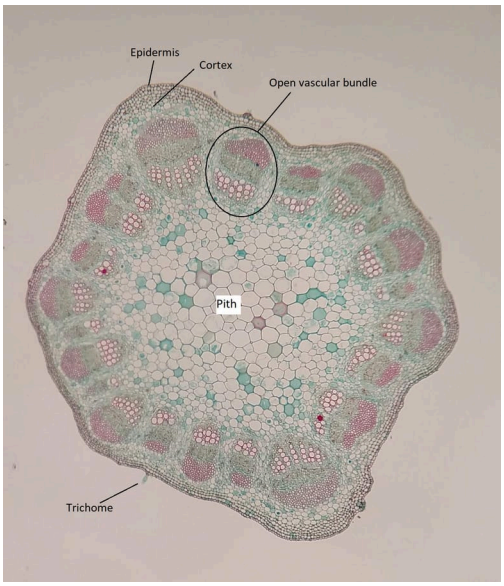


Figure 9.6.2.1.6: A cross section of a *Helianthus* stem. The outermost layer of cells is the epidermis. There is at least one trichome visible. Inside the epidermis is the cortex, which is composed largely of collenchyma in this plant. A ring of vascular bundles separates the cortex from the pith. Regions between the bundles are called pith rays. These vascular bundles are considered "open" because they have procambium tissue. Photo by Maria Morrow, CC BY-NC.

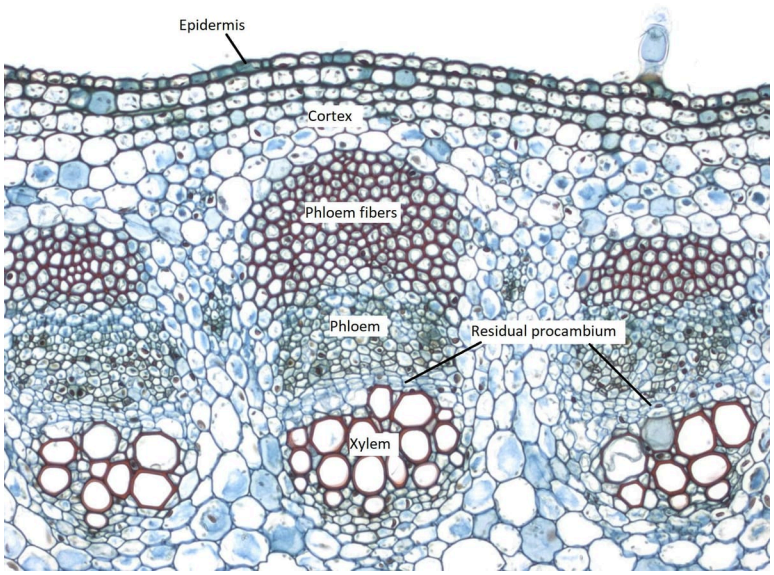


Figure 9.6.2.1.7: A closer view of a young *Helianthus* stem. The outermost layer of cells (in this image, the topmost) is the epidermis. There is a blue, light-bulb shaped structure emerging from the epidermis in the upper left. This is a trichome. Beneath the epidermis, three layers of densely packed collenchyma cells and several layers of parenchyma make up the cortex. Three large vascular bundles are shown. There is a large cluster of phloem fibers at the top of each bundle, stained red due to the secondary walls. Below that is the phloem, which is separated from the xylem (large, open cells that are stained red) by the residiual procambium (densely packed, light blue cells). Photo by Maria Morrow, CC BY-NC.

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9.6.2.2: Secondary Growth

Gymnosperms

Full Stem Cross Sections, *Pinus*

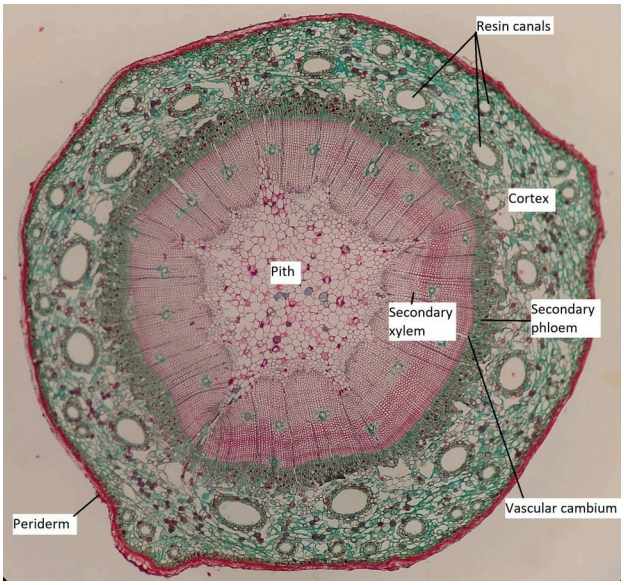


Figure 9.6.2.2.1: A cross section of a pine stem that is approximately one year old. The epidermis may still be present just outside the layer of periderm that has formed, but will soon slough off. Large (and small) resin canals are present in the cortex region. Just inside the cortex, a layer of more densely packed cells is the secondary phloem. This is separated from the secondary xylem by a thin layer of meristematic tissue: the vascular cambium. The secondary xylem, stained pink, has small blue-stained resin canals traversing it. Some of the cells in the xylem look darker than others. Within this layer of secondary xylem, at the center of the stem, are the large parenchyma cells of the pith. Photo by Maria Morrow, CC-BY 4.0.

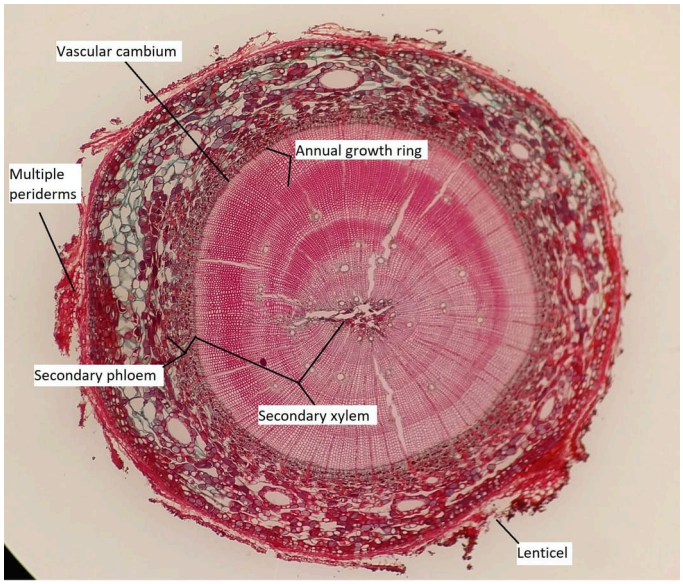


Figure 9.6.2.2.2: A cross section of a pine stem that is 4 years old. The epidermis is gone and several layers of periderm (outer bark) have formed around the outside of the stem. Tears in the periderm form lenticels. Inside the periderm is cortex with embedded resin canals. The secondary phloem is a thin ring of tissue surrounding the secondary xylem. Within the secondary xylem, several growth rings can be distinguished, with regions of more densely packed cells formed in the dry and/or cold season abutting larger cells formed in the following growing season. Photo by Maria Morrow, CC-BY 4.0.

Vascular Tissue

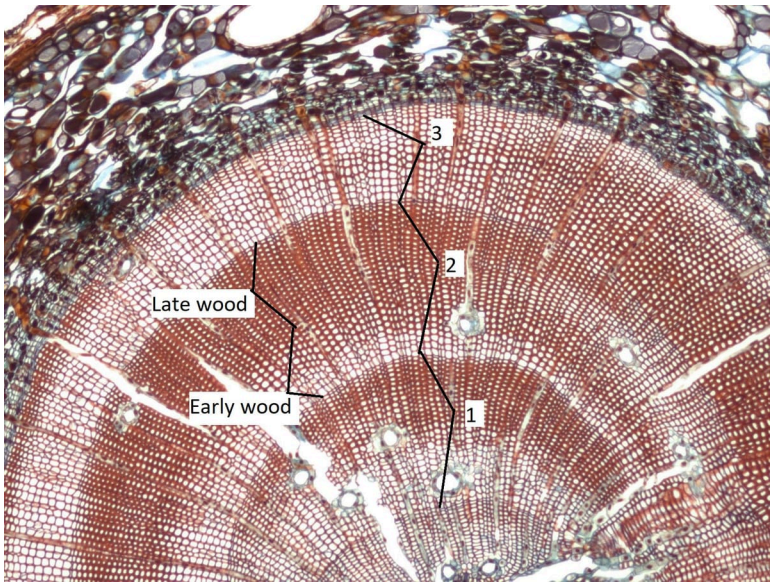


Figure 9.6.2.2.3: A close up on the annual growth rings formed in a pine stem. Within the secondary xylem, regions of more densely packed cells formed in the dry and/or cold season are called late wood. These alternate with rings of larger cells formed in the following growing season, called early wood. An annual growth ring is composed of the early wood and late wood formed in a single year. This stem has at least 3 annual growth rings. Photo by Maria Morrow, CC-BY 4.0.

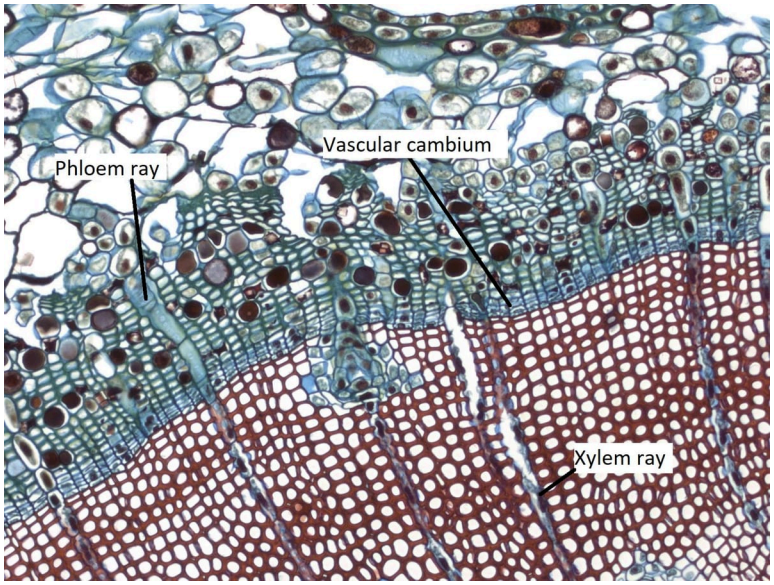


Figure 9.6.2.2.4: A magnified view of the vascular tissue and, specifically, the vascular cambium. The top of the image is composed of cortex cells. Quite abruptly, the cells become smaller and more tightly packed, appearing in columns. This is the secondary phloem tissue. The vascular cambium is below the phloem cells and appears as a line of flattened, light blue-stained cells. Just below the vascular cambium, the secondary xylem is composed of tracheids with red-stained secondary walls. Lines of parenchyma traverse the phloem (phloem rays) and xylem (xylem rays). Photo by Maria Morrow, CC-BY 4.0.

Periderm



Figure 9.6.2.2.5: A magnified view of the periderm (outer bark). The top of the image is composed of cork cells, which are empty and squished together. They are also coated in suberin. The cork cambium can be distinguished as one to two lines of small cells, all with visible nuclei. Just below the cork cambium, large cells that are filled with stained contents make up the phelloderm. These three layers comprise one periderm layer. Image from the Public Domain, sourced from Berkshire Community College Bioscience Image Library with labels added by Maria Morrow.

Wood



Figure 9.6.2.2.6: A driftwood stump found at the beach, with annual growth rings indicated by black arrows. This tree may have died from a fungal infection (*Leptographium wageneri*) that stained the wood. A black stain is present in the most densely packed cells of the late wood, making annual growth rings visible. At least 11 years of growth can be seen, potentially more. Photo by Maria Morrow, CC-BY 4.0.



Figure 9.6.2.2.7: The difference between sapwood and heartwood can sometimes be seen distinctly in where moss and algae grow on cut logs. These two logs both have algal growth (and moss, in the second image) in the sapwood region. Yet, it cuts off abruptly as it reaches the heartwood. What might cause this? Photos by Maria Morrow, CC-BY 4.0.

Angiosperms

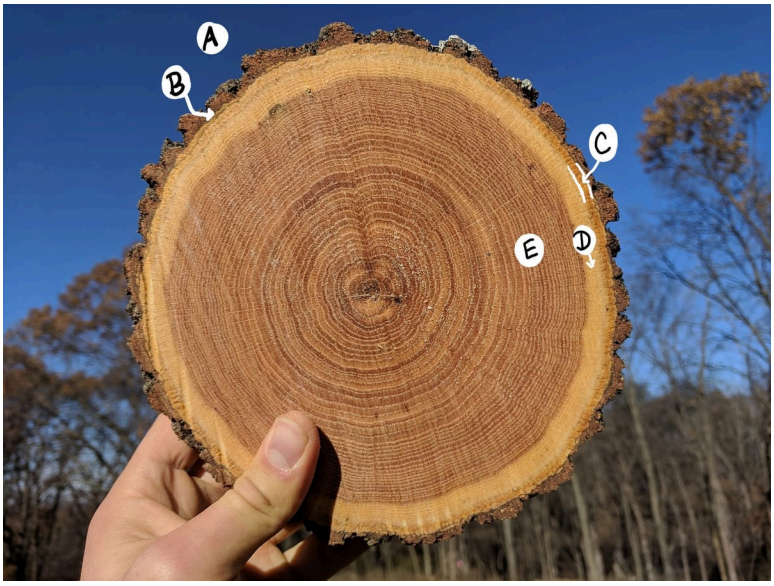


Figure 9.6.2.2.8: A section through an oak tree (*Quercus*). The outer bark is darker and jagged (A). Just under the outer bark is a thin layer of inner bark (C). B indicates the transitional zone between inner and outer bark. D and E are the wood, but D is still active in water conduction (sapwood). The vascular cambium would be located between C and D. A=Periderms (outer bark), C=Secondary phloem (inner bark), D=Sapwood (active xylem), E=Heartwood (inactive xylem). D+E=wood. Photo by Rbreidbrown, CC BY-SA 4.0, via Wikimedia Commons with labels added by Maria Morrow.

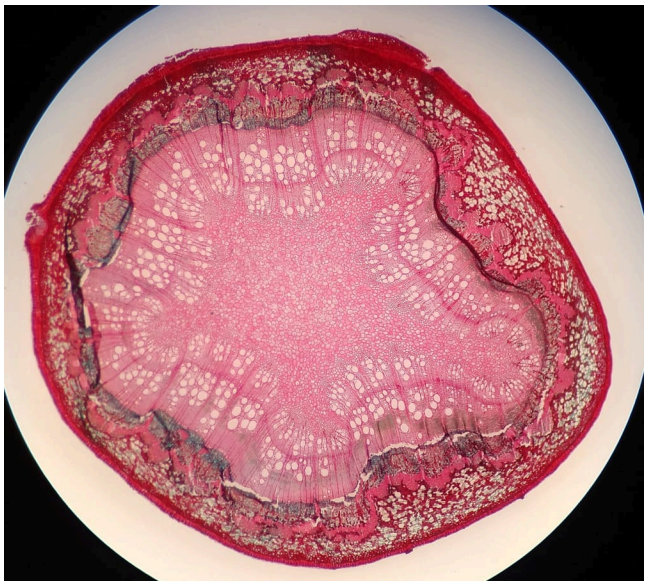


Figure 9.6.2.2.9: The arrangement of tissues in an angiosperm in secondary growth is similar to a gymnosperm. One way to determine whether you are looking at an angiosperm or gymnosperm cross section is to look for the presence of large, open cells in the xylem (vessel elements). Gymnosperms (excepting the gnetophytes) only have tracheids, whereas angiosperms have both tracheids and vessel elements. Can you tell how old this stem was by looking at the secondary xylem? Photo by Maria Morrow, CC-BY 4.0.

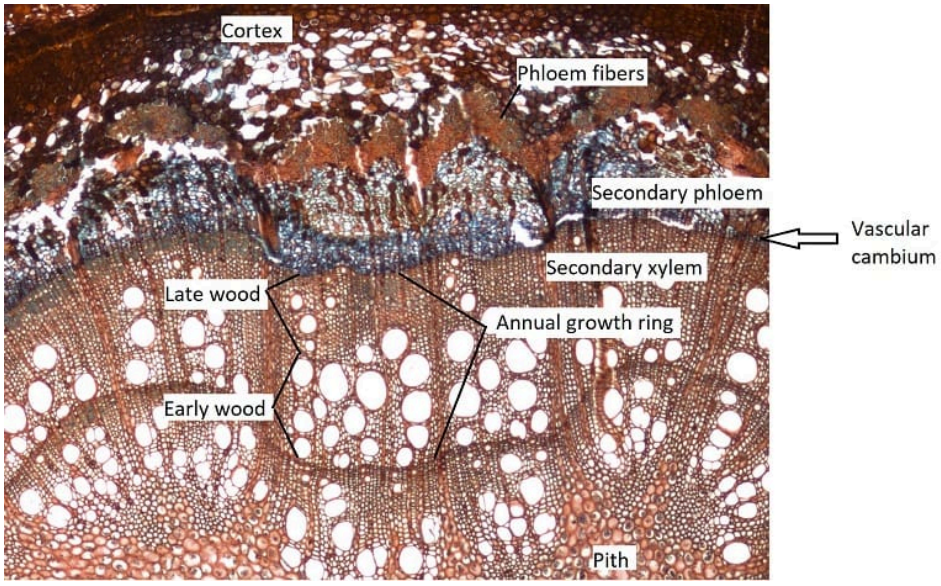


Figure 9.6.2.2.10: A cross section of the vascular tissue in a two year old oak stem. The cortex is separated from the secondary xylem by large bundles of phloem fibers. Below the phloem fibers are the conducting cells of the secondary phloem. The vascular cambium, indicated by the white arrow, separates the phloem from the xylem. In the xylem, there are two growth rings. A small bit of the pith can be distinguished at the bottom. Photo by Maria Morrow, CC-BY 4.0.

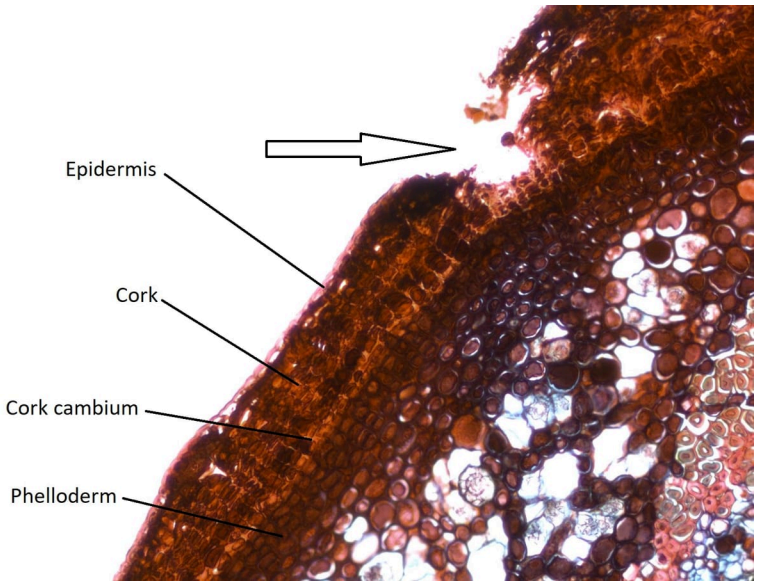


Figure 9.6.2.2.11: A lenticel in the periderm of an oak. The white arrow indicates a tear in the periderm, called a lenticel, that allows for gas exchange after the epidermis is lost. A thin layer of epidermis, coated in cuticle (stained pink), can be seen hugging the edge of the periderm. This will soon slough off. A lighter strip within the periderm cells (all stained an orange-brown) is the cork cambium. Image from the Public Domain, sourced from Berkshire Community College Bioscience Image Library with labels added by Maria Morrow.

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9.6.2.3: Woody Shoot Structures

Figure 9.6.2.3.1: A woody shoot and labeled scars. The most prominent scar on this shoot is the v-shaped leaf scar, which is lined with circular vascular bundle scars. Above the leaf scar, in the crotch of the v it forms, is a round axillary bud scar. Covering the bark are many small, circular scars. These are lenticels. Photo by Maria Morrow, CC BY-NC.



Figure 9.6.2.3.2: A piece of birch bark. The lenticels in birch bark form as long tears, as opposed to the circular ones in Figure 9.6.2.3.1. Photo by Maria Morrow, CC BY-NC.

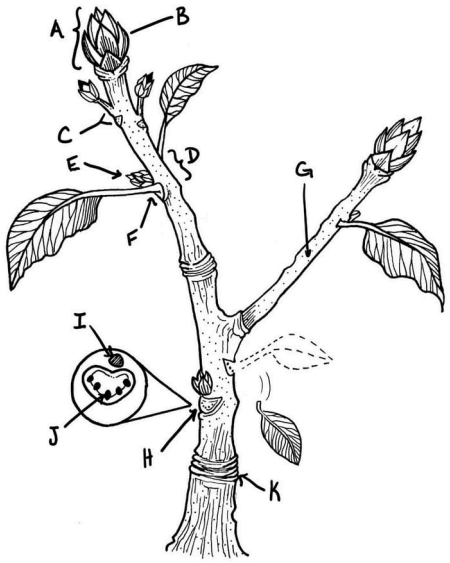


Figure 9.6.2.3.3: Diagram of a woody shoot (angiosperm). A=Terminal (or apical) bud, B=Terminal bud scale, C=Node, D=Internode, E=Axillary bud (in the leaf axil), F=Leaf, G=Lenticel, H=Leaf scar, I=Axillary bud scar, J=Vascular bundle scar (within the leaf scar), K=Terminal bud scale scars. The region between sets of terminal bud scale scars on a branch represents one year of growth. Diagram by Nikki Harris, CC BY-NC with labels added by Maria Morrow.

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9.6.2.4: Modified Shoots

Horizontal Stems

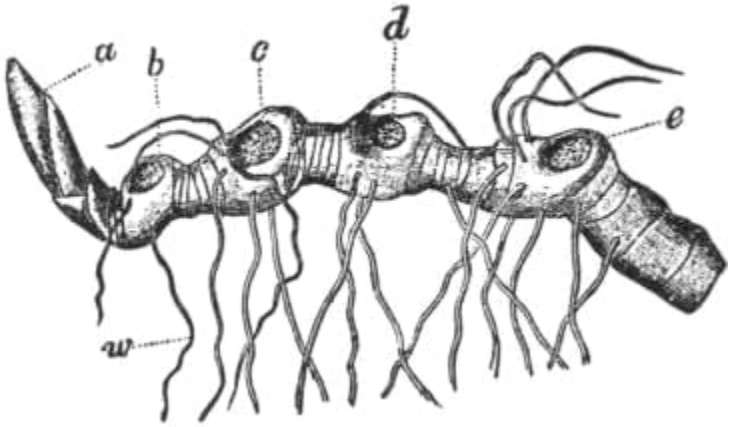


Figure 9.6.2.4.1: Rhizome of *Polygonatum multiflorum*. a=Bud of next year's aerial shoot; b=Scar of this year's, and c, d, e=scars of three preceding years' aerial shoots; w=adventitious roots. Diagram by AnonymousUnknown author, Public domain, via Wikimedia Commons.



Figure 9.6.2.4.2: Rhizome of *Alpinia purpurea.* Adventitious roots emerge from stem tissue that travels horizontally underground. Rhizomes can be distinguished from roots by the presence of nodes. Note the layers created by the sheathing, papery leaves of the rhizome. Below the stem, root like structures sprout out horizontally, but there are distinct sections or nodes to these structures (roots). Photos by Filo gèn', CC BY-SA 4.0, via Wikimedia Commons.

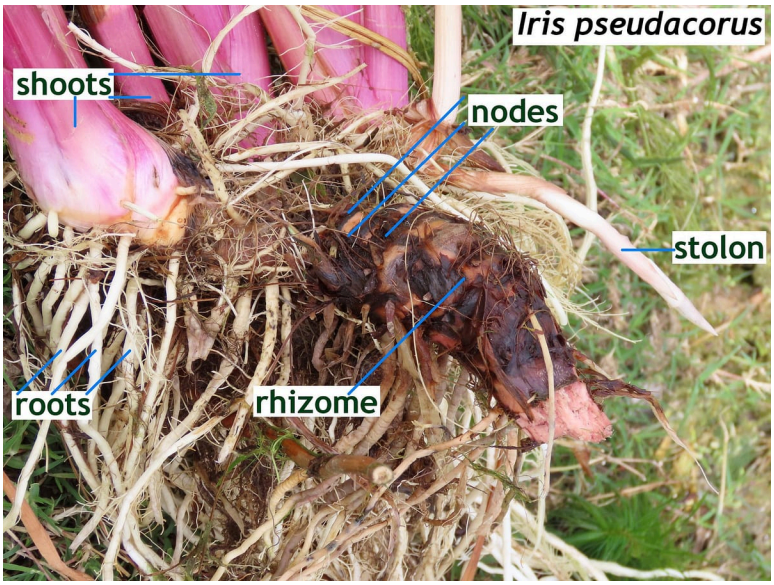


Figure 9.6.2.4.3: There is a lot going where these *Iris* shoots meet the roots. The shoots are emerging upward in the left hand corner, showing a pinkish hue from anthocyanin pigments. True roots emerge from the base of these shoots, pointing in the opposite direction and pigment-free. A large rhizome travels horizontally from the cluster of shoots and three nodes are indicated. A stolon (a horizontal above ground stem) emerges above the rhizome. Image by JonRichfield, CC BY-SA 4.0, via Wikimedia Commons.



Figure 9.6.2.4.4: Examples of horizontal stems. Ginger rhizomes are thick and belowground (top), and stolons of this spider plant are aboveground with long internodes (bottom). Top image by Sengai Podhuvan (CC-BY-SA), and bottom image by Eptalon (CC-BY-SA).

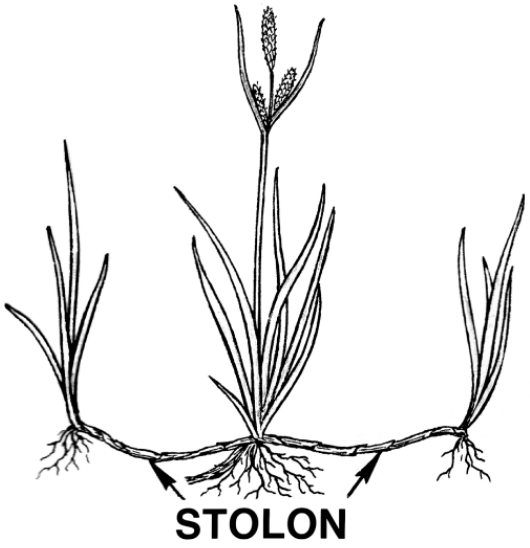


Figure 9.6.2.4.5: A stolon is an above ground horizontal stem. Some plants, such as strawberries (right) or the spider plant in Figure 9.6.2.4.4, use stolons to asexually reproduce clonal plants. Drawing on left by Pearson Scott Foresman, Public domain, via Wikimedia Commons. Photo on right by Amy Change, CC-BY-SA.

Storage Stems





Figure 9.6.2.4.6: Potato tubers are expanded, belowground stems modified for starch storage. Each "eye" on a potato is a node where a new shoot could emerge. First image by pxhere (public domain). Second image by Robin Corps and uploaded to flickr.com on January 23, 2006, licensed under the Creative Commons Attribution-Share Alike 2.0 Generic license.

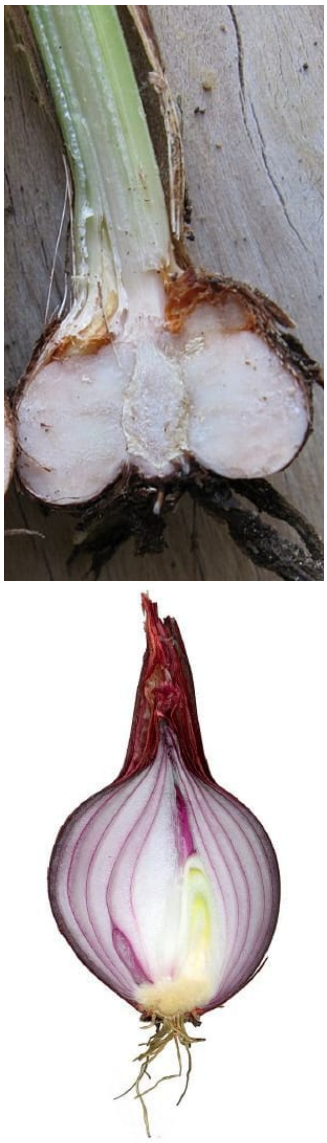


Figure 9.6.2.4.7: Both corms (left) and bulbs (right) are similar looking modifications for storage. The *Crocosmia* corm has a thick, expanded stem stores starch, and the leaves that surround it are non-photosynthetic and papery. The onion bulb has a relatively small stem surrounded by thick, fleshy leaves. Corm image by JonRichfield (CC-BY-SA), and onion image by Amada44 (CC-BY-SA).

Sharp Armaments



Figure 9.6.2.4.8: Thorns (first) and prickles (second). 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. First image by Rasbak (CC-BY-SA), and second image by Ingrid Taylar (CC-BY).

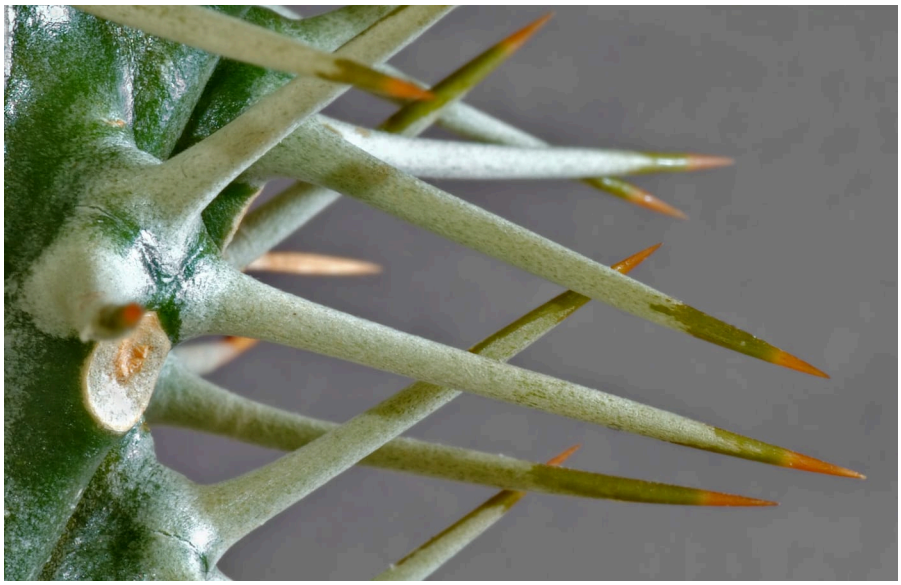


Figure 9.6.2.4.9: Cactus spines are not stems, but modified leaves. These spines have a thick cuticle and stomata can be seen as darker green areas within the pale white cuticle. Photo by André Karwath aka Aka, CC BY-SA 2.5, via Wikimedia Commons.

Climbing



Figure 9.6.2.4.10: The tendrils of the wild cucumber plant arise from stems. Other plants, such as *Lathyrus*, make tendrils from leaf tissue. Image by erwin66as (public domain)

Photosynthesis



Figure 9.6.2.4.11: Cladophylls in *Asparagus* (left) and actual leaves of young asparagus marked by black arrows (right). Left image by DenesFeri (CC-BY-SA), and right image by Sam Saunders (CC-BY-SA).



Figure 9.6.2.4.12: 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 9.6.2.4.13: Phylloclades in Christmas cactus. Image by Mokkie (CC-BY-SA).

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9.6.3: LEAVES

Leaves are specialized organs for performing photosynthesis. A leaf is often a relatively large, flat surface used to optimize sunlight capture. However, surfaces are areas that water can evaporate from, so a large amount of surface area exposed to sunlight results in increased transpiration. The anatomy of a leaf has everything to do with achieving the balance between photosynthesis and transpiration 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.

9.6.3.1: Leaf Parts and Arrangement

9.6.3.2: Monocot Leaves

9.6.3.3: Eudicot Leaves

9.6.3.3.1: Adaptations to Water Availability

9.6.3.4: Modified Leaves

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9.6.3.1: Leaf Parts and Arrangement

In angiosperm anatomy, a leaf can be identified by where it emerges from the node. In a node, a leaf emerges below the axillary bud.

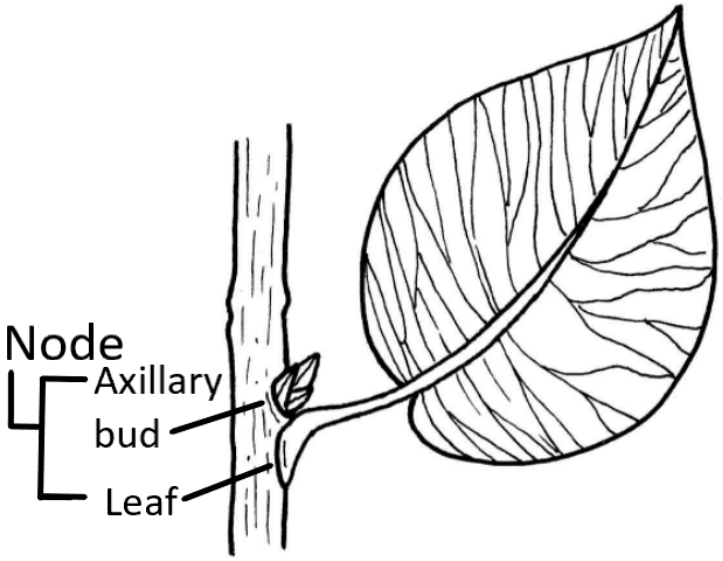


Figure 9.6.3.1.1: A diagram of a node. Each node is comprised of a leaf (on the bottom) and an axillary bud (on the top, located in the axil where the petiole meets the stem). Diagram by Nikki Harris, CC-BY 4.0 with labels added.

Leaf Parts

Leaves are generally composed of a few main parts: the **blade** and the **petiole**.

Figure 9.6.3.1.2: A leaf is usually composed of a blade and a petiole. The blade is most frequently the flat, photosynthetic part. The petiole is a stem that attaches the leaf blade to the main stem of the plant. As plants have radiated, diversified, and adapted to different environments, you'll see that there are many variations on this theme. The photo on the left is a palmate leaf, the diagram on the right is a pinnate leaf. Photo by Maria Morrow, CC-BY 4.0. Diagram on the right from Chapter 3.4.2, Botany, by Algiers, Ha, and Morrow.

The Leaf Blade and Vascular Arrangement

The leaf blade is (usually) the flat, photosynthetic part of the blade. In eudicots, the leaf will have a central midvein (also called the midrib), with smaller veins branching off from there. This type of vein organization is called **netted venation**. The edge of the blade is the **margin**.

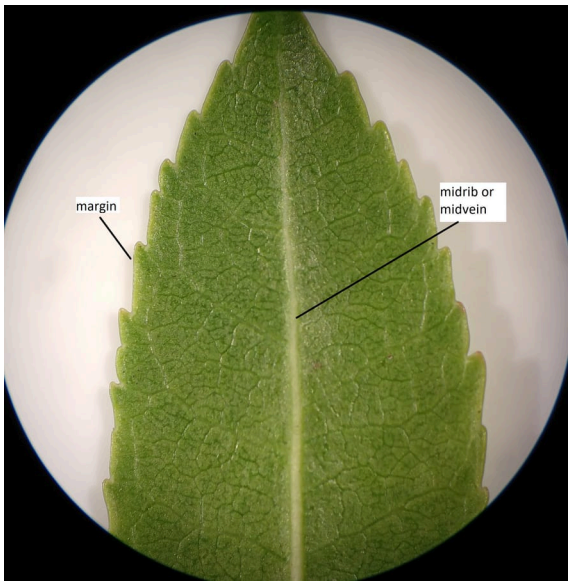


Figure 9.6.3.1.3: The adaxial (left) and abaxial (right) surfaces of a eudicot leaf blade. The margin is the edge of the leaf and its morphology can be useful for identification. This leaf margin could be described as serrate, much like a serrated knife. In the center of the leaf, a large central vein stands out. This is the midrib or midvein. Many smaller diameter veins branch out from the midvein. Photos by Maria Morrow, CC-BY 4.0.

In monocots, the veins may be all approximately the same size or there may be a larger midvein, but the veins run parallel to each other. This is called **parallel venation**.



Figure 9.6.3.1.4: A plantain (*Plantago* sp.) leaf. This monocot has several large veins that run parallel to each other, lacking any true midvein. Photo by Maria Morrow, CC-BY 4.0.

The Petiole

Most leaves have a stem that attaches the blade of the leaf to the rest of the plant. This is the petiole. However, in some plants, the leaves do not have a petiole and the blade is directly attached to the plant stem. These leaves are **sessile** (lacking a petiole).



Figure 9.6.3.1.5: The first image shows a branch of a tree with petiolate leaves. Each leaf blade is attached to the main branch by a short stem (petiole). In the second image, the leaf blades are attached directly to the main stem (sessile). Photos by Maria Morrow, CC-BY 4.0.

Stipules

Some plants will have paired appendages found at the base of the leaf. These are called **stipules**. Stipules can look leaf-like or take on other forms (e.g. spines or tendrils).

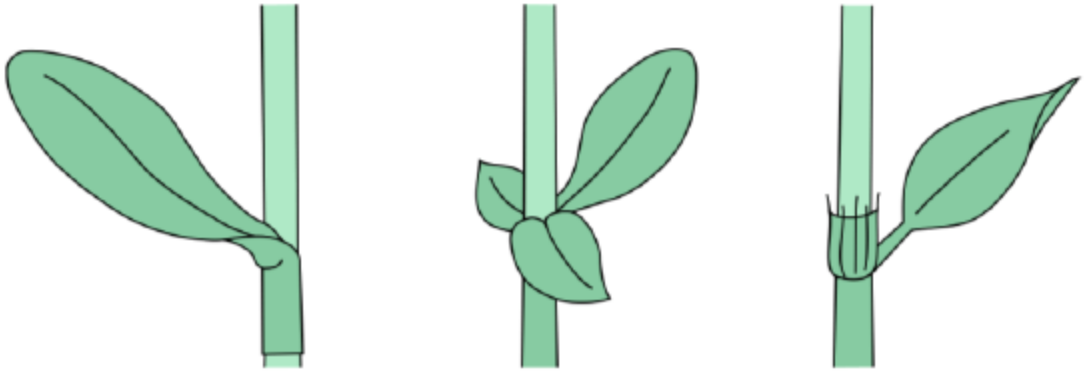


Figure 9.6.3.1.6: From left to right: sheath, stipules and ocrea. Diagram from Chapter 3.4.2, Botany, by Algiers, Ha, and Morrow.



Figure 9.6.3.1.7: Stipules of *Hibiscus*. Each leaf on this plant has two long, flat, green projections at the base. These are the stipules, adapted for photosynthesis (flat and green). Image by Nadiatalent, CC BY-SA 3.0, via Wikimedia Commons.





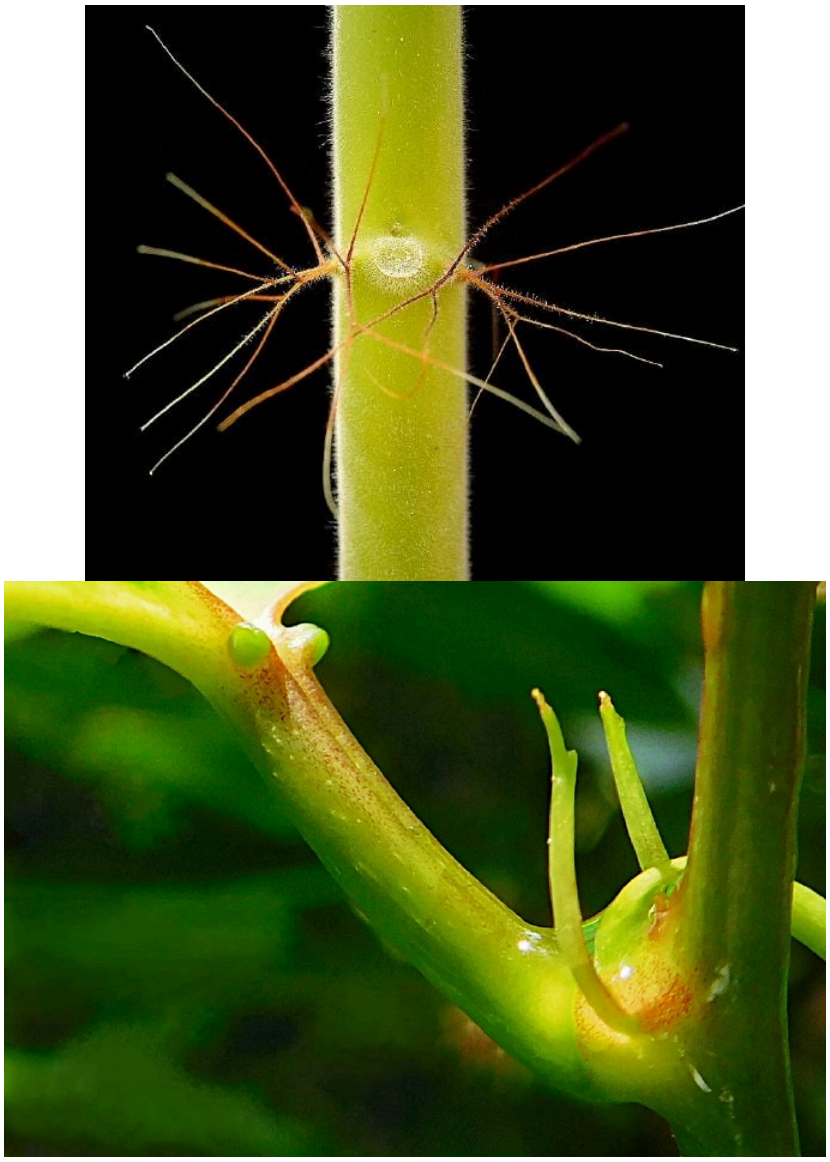


Figure 9.6.3.1.8: A variety of stipule morphologies. First image: Ton Rulkens from Mozambique, CC BY-SA, via Wikimedia Commons. Second image: Christian Fischer, CC BY-SA, via Wikimedia Commons. Third image: Frank Vincentz, CC BY-SA, via Wikimedia Commons. Fourth image: Filo gèn', CC BY-SA, via Wikimedia Commons.

Compound Leaves

A **compound leaf** looks like a branch with leaves emerging from it. However, these leaves are not accompanied by axillary buds (i.e. they do not emerge from a node). This branch is in fact a compound leaf composed of **leaflets**. Though there are no buds at the base of the leaflets, there will be a bud at the base of the compound leaf's petiole.

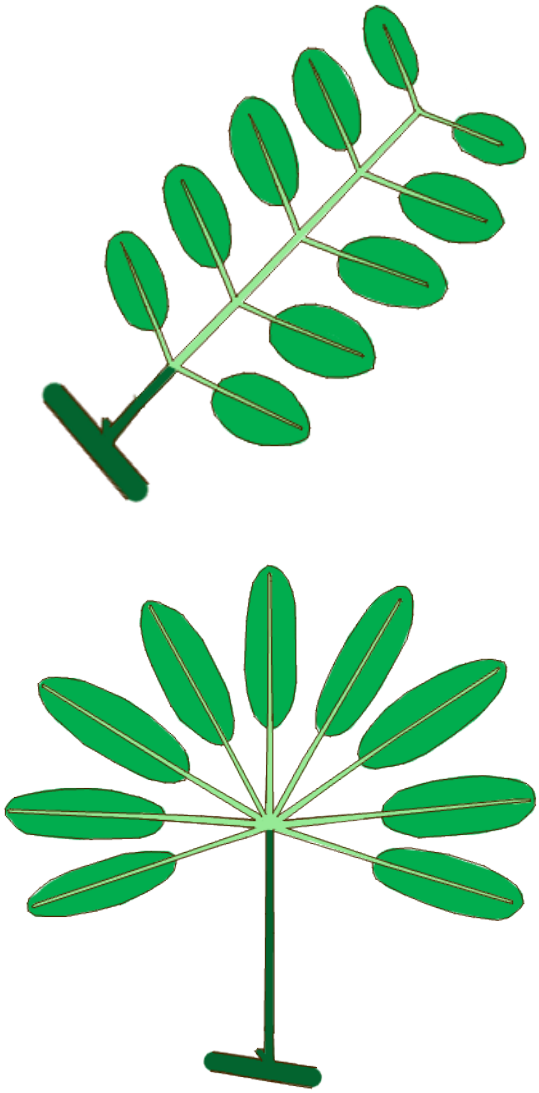


Figure 9.6.3.1.9: Compound leaves. The leaf on the left is pinnately compound, petiolules attach to a central rachis. The leaf on the right is palmately compound, petiolules all meet at the tip of the petiole and radiate outward. Diagrams by Michael G. Simpson. Redrawn and color: User:RoRo, Public domain, via Wikimedia Commons.

A compound leaf can be **palmate** or **pinnate**. In a pinnate compound leaf, the leaflets are attached to a central stem called a **rachis**. The leaflets can be sessile or may be attached to the rachis by **petiolules**. Compound leaves can be even more complex by being compounded multiple times.

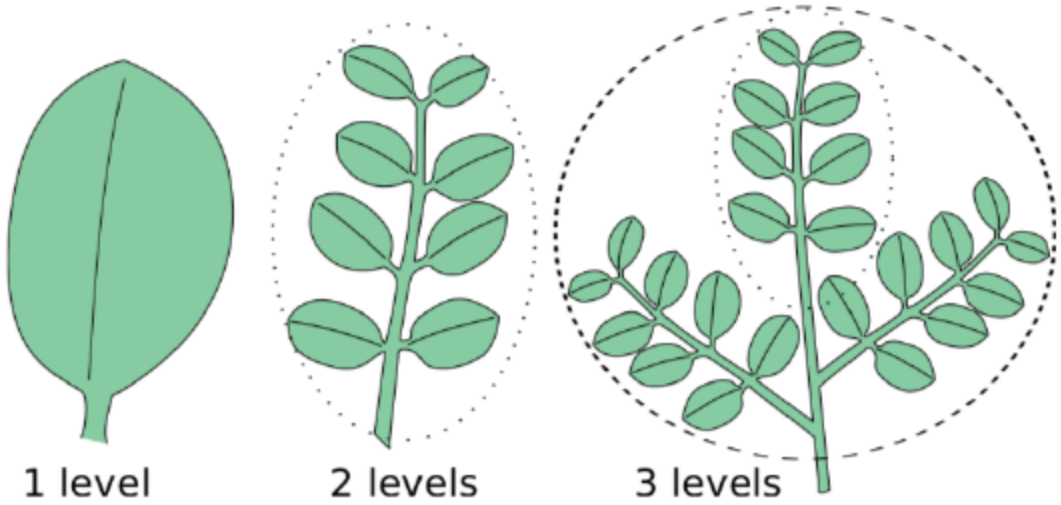


Figure 9.6.3.1.10: Leaves with one, two and three levels of hierarchy. Please note that the last leaf is ovate on the first and second level but circular on the third level of hierarchy. Diagram from Chapter 3.4.2, Botany, by Algiers, Ha, and Morrow.

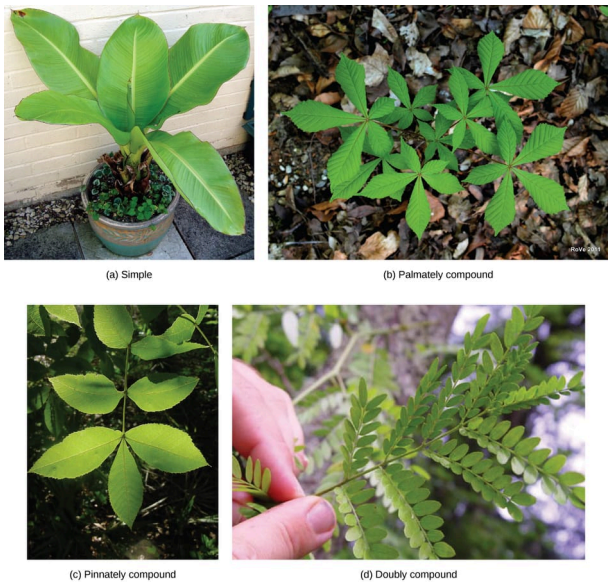


Figure 9.6.3.1.11: Leaves may be simple or compound. In simple leaves, the lamina is continuous. The (a) banana plant (Musa sp.) has simple leaves. In compound leaves, the lamina is separated into leaflets. Compound leaves may be palmate or pinnate. In (b) palmately compound leaves, such as those of the horse chestnut (Aesculus hippocastanum), the leaflets branch from the petiole. In (c) pinnately compound leaves, the leaflets branch from the midrib, 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).

Leaf Arrangement

In angiosperms, leaf arrangement is determined by how many leaves emerge per node.

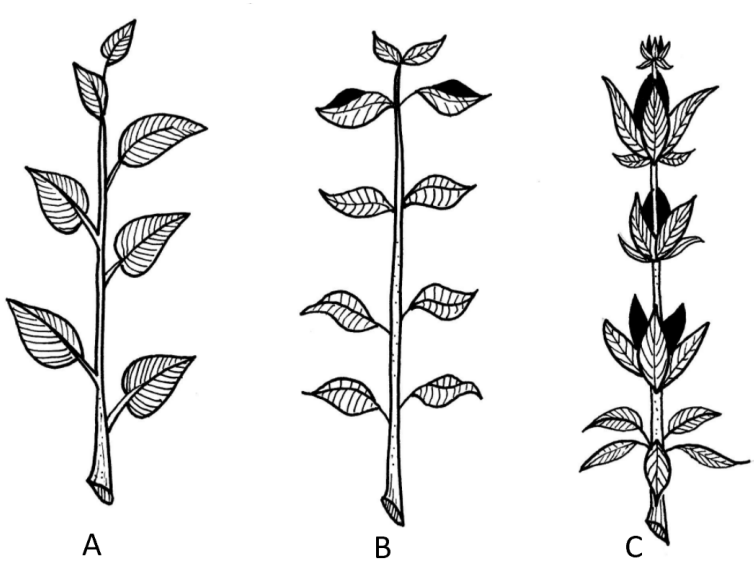


Figure 9.6.3.1.12: Types of leaf arrangement. In shoot A (far left), the leaves emerge one at a time. Shoot A has alternate leaf arrangement. In shoot B (middle), two leaves emerge per node, directly across from each other. Shoot B has opposite leaf arrangement. In shoot C, five leaves emerge at each node. Three or more leaves from a node is a whorled leaf arrangement. Diagram by Nikki Harris, CC-BY 4.0 with labels added.

Alternate Leaf Arrangement

In **alternate leaf arrangement**, one leaf emerges per node, giving the appearance of alternating leaves.



Figure 9.6.3.1.13: This salal (*Gaultheria shallon*) branch has alternate leaf arrangement. The leaves emerge with one per node. In this plant, a small bend occurs in the stem at each node, giving it a zig-zag shape. Photo by Maria Morrow, CC-BY 4.0.

Opposite Leaf Arrangement

In **opposite leaf arrangement**, two leaves emerge per node. Think of this as how your arms are opposite each other on your torso.



Figure 9.6.3.1.14: Both of the plants shown in the images above have opposite leaves, with two leaves emerging at each node opposite from each other on the stem. Photos by Maria Morrow, CC-BY 4.0.

Whorled Leaf Arrangement

In **whorled leaf arrangement**, three or more leaves emerge per node. I try to remember this as "around the whorled (world)", because the leaves often encircle the stem.



Figure 9.6.3.1.15: This member of the lily family has whorled leaves. There are between 5 and 8 leaves emerging at each node, making the plant look as if it were a tiered cake. Photo by Maria Morrow, CC-BY 4.0.

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9.6.3.2: Monocot Leaves

Macroscopic Features

Monocot leaves tend to have parallel venation, as opposed to the branching patterns seen in eudicots.



Figure 9.6.3.2.1: These two monocot leaves both have parallel venation. It is more obvious in the leaf on the right. However, if you look closely at the leaf on the left, 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-NC.

Microscopic Features

The model organism for monocots in botany is usually corn (*Zea mays*). Below, you'll see examples of corn leaf cross sections to demonstrate monocot leaf anatomy. Note that there are approximately the same number of stomata on either side of the leaf, that the vascular bundles are all facing you in cross section (because they run parallel to each other), and that the mesophyll is not divided into two distinct types. Note: There are exceptions. Many monocots will have a more specialized mesophyll arrangement.



Figure 9.6.3.2.2: A cross section of a corn (*Zea mays*) leaf. See the caption in Fig. 13.2.3 for a detailed description of the features present. Photo by Maria Morrow, CC BY-NC.

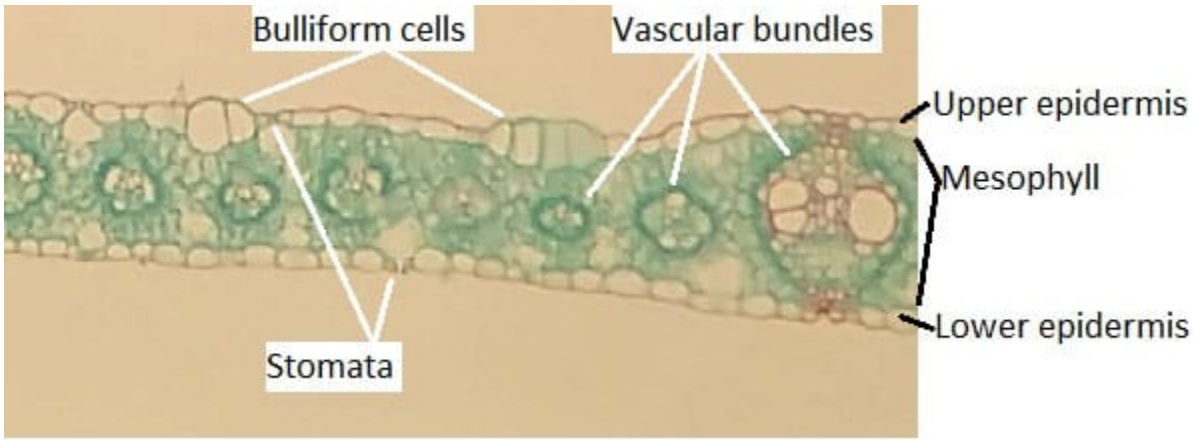


Figure 9.6.3.2.3: A cross section of a section of a corn leaf, labeled. The upper epidermis is composed of parenchyma cells that appear empty. There are two clusters of enlarged cells within the upper epidermis. These are bulliform cells and are not present in the lower epidermis. Stomata occur in approximately even numbers in both the upper and lower epidermis. Eight vascular bundles can be seen, the one on the far right is much larger than the others. In the larger vascular bundle, it is easier to distinguish the large, open vessel elements (stained red). Within the vascular bundle, the xylem tissue is closer to the upper epidermis and the phloem tissue is closer to the lower. Each vascular bundle is surrounded by larger cells with darkly-stained contents. These make up the bundle sheath. The tissue around the vascular bundles is the mesophyll. Photo by Maria Morrow, CC BY-NC.

Bulliform Cells

The bulliform cells present in the upper epidermis are not common to all monocots. This is an adaptation you can find in many grasses that are adapted to hot or dry environments. To avoid water loss, the bulliform cells can contract, causing the leaf to roll up and reduce surface area.

In the image below, you can see a leaf from the beach grass *Ammophila* rolled in on itself. Can you find the bulliform cells?

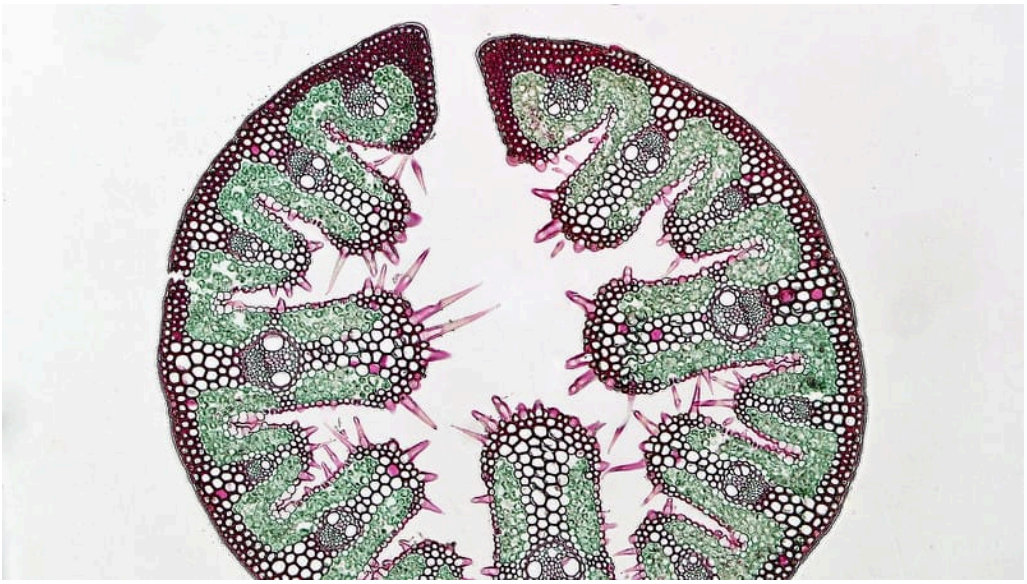


Figure 9.6.3.2.4: This European beach grass (*Ammophila arenaria*) leaf has rolled up due to shrinking of the bulliform cells. The upper epidermis is now highly invaginated and located on the inside of the rolled leaf. Image from the Public Domain, sourced from Berkshire Community College Bioscience Image Library.



Figure 9.6.3.2.5: This is a close up of the same European beach grass (*Ammophila arenaria*) leaf as above. The lower epidermis has a thick hypodermis (stained red). A thick cuticle can be seen coating the epidermis. On the right side of the image, there is a fold in the upper epidermis (which has many trichomes). At the folding point, several slightly larger cells can be seen. This is a region of bulliform cells, which allowed the leaf to fold and roll inward. Image from the Public Domain, sourced Berkshire Community College Bioscience Image Library.

Vascular Bundles

In the vascular bundle, the xylem will be on the top (adaxial side) and the phloem will be on the bottom (abaxial side). If you think about the way a leaf emerges from the plant, this matches the way the xylem and phloem are oriented in the stem, with the xylem toward the center of the stem and the phloem closer to the outside/epidermis.

The vascular bundle is often surrounded by inflated parenchyma cells that form a structure called a **bundle sheath**. In C4 plants, like corn, this is where the Calvin Cycle would take place.

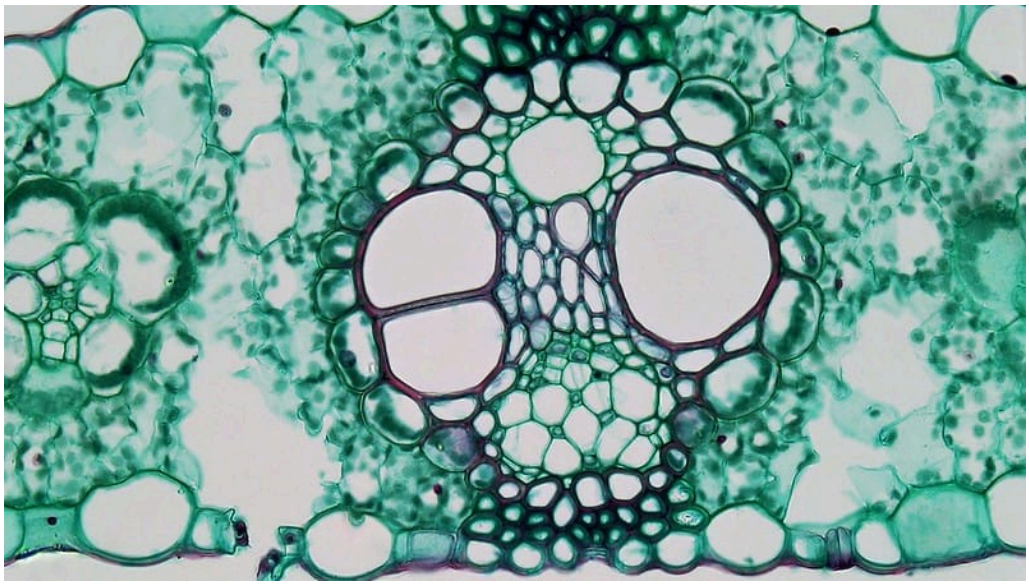


Figure 9.6.3.2.6: A vascular bundle of a corn (*Zea mays*) leaf. There are two vascular bundles in this image. The one on the left is difficult to distinguish and most of what you see are the enlarged bundle sheath cells. The larger vascular bundle on the right has less prominent bundle sheath cells, 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. Image from the Public Domain, sourced from Berkshire Community College Bioscience Image Library.

Below is an image of a vascular bundle in another monocot, Yucca. This vascular bundle has large groups of sclerenchyma cells within it, a smaller group above the xylem and a much larger group below the phloem. How might you distinguish the sclerenchyma cells from the parenchyma cells? Consider the thickness of the cell wall(s) and how each cell type reacts to stains.

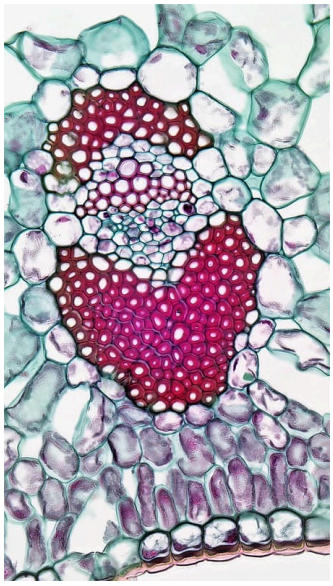


Figure 9.6.3.2.7: A vascular bundle from a Yucca plant (a monocot). The large groups of thick-walled, red-stained cells are sclerenchyma. These provide rigid support in the region of the vascular bundle. Image from the Public Domain, sourced from Berkshire Community College Bioscience Image Library.

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9.6.3.3: EUDICOT LEAVES

Macroscopic Features

Eudicot leaves tend to have netted venation, with a larger central vein (the midrib or midvein) that branches off into a network of smaller veins. In the image below, you can see this branching pattern in a skeletal leaf.



Figure 9.6.3.3.1: 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-NC.

Microscopic Features

Eudicot leaves can usually be distinguished by netted venation at the macroscopic level, but they also differ at the microscopic level. Note the difference in organization between the tissues in the leaf below and the leaves shown in the monocot section.

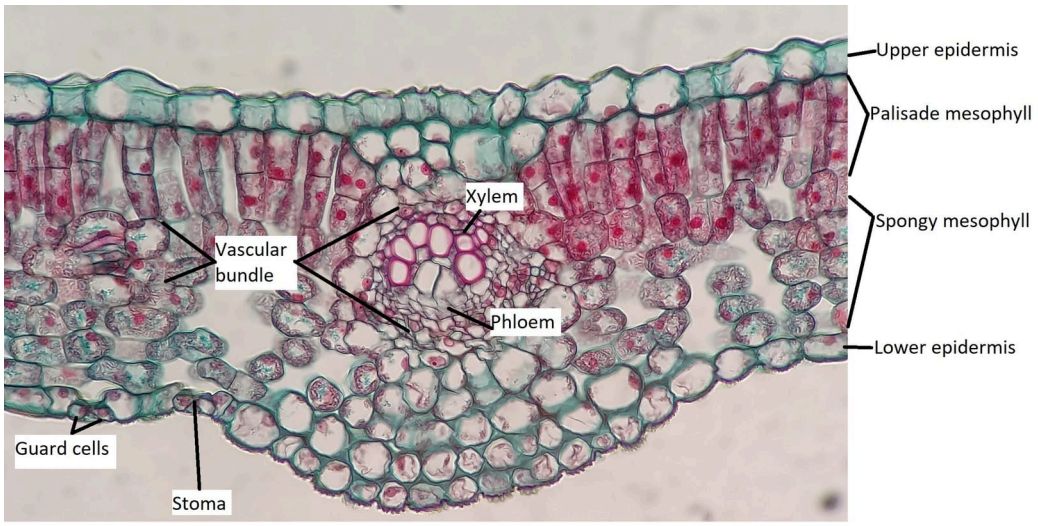


Figure 9.6.3.3.2: A cross section through a eudicot leaf. The upper epidermis is a single layer of parenchyma cells. There are no stomata present in the upper epidermis of this leaf. Below the epidermis, cells (appearing pink due to staining of the nuclei and chloroplasts) are arranged in columns, forming 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. Photo by Maria Morrow, CC BY-NC.

Cuticle

You will often see a waxy cuticle coating the surface of most plant tissues. In leaves, the location and thickness of the cuticle can give you clues about the environment that the plant has adapted to.

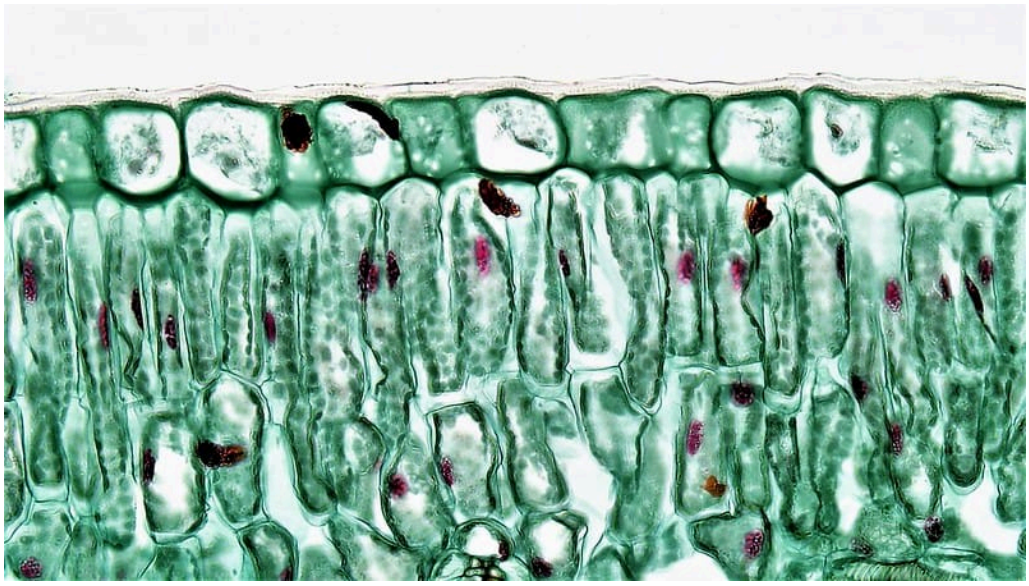


Figure 9.6.3.3.3: A cross section through the upper epidermis and palisade mesophyll. On top of the upper epidermis of this leaf, a transparent layer of cuticle is visible, sealing the top of the leaf. This waxy layer protects the leaf and forms a barrier to the movement of water. Image is in the Public Domain, sourced from Berkshire Community College Bioscience Image Library.

Vascular Bundles

Seeing vascular bundles of eudicots in cross sections can be confusing. The organization of tissues in the much larger midrib vascular bundle is often spread out into a semicircle, still with xylem on the top and phloem on the bottom, but they can be

difficult to distinguish. In addition to this, the smaller veins are not oriented in the same direction, as they are in monocots.

In the image below, 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. Often with these oblique sections, you can distinguish the xylem cells by their strange secondary wall thickenings -- they look a bit like coiled springs.

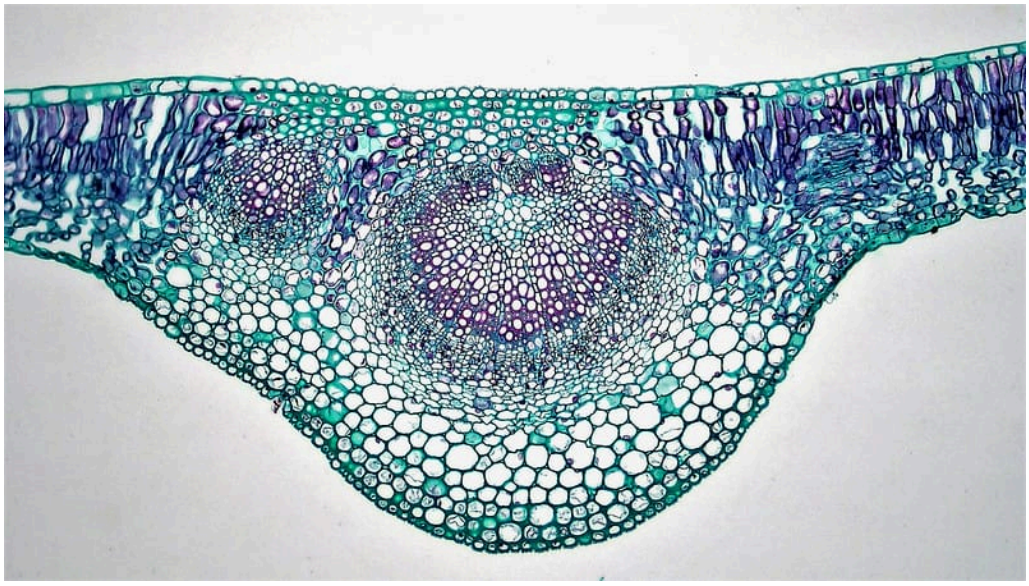


Figure 9.6.3.3.4: A cross section through the midvein of a eudicot leaf. The xylem tissue within the large vascular bundle is arranged in an arcing semi-circle, with phloem tissue in an arc traveling just below it. There are layers of collenchyma cells under the epidermis both above and below the midvein. What would be the function of these collenchyma cells? Image is in the Public Domain, sourced from Berkshire Community College Bioscience Image Library.

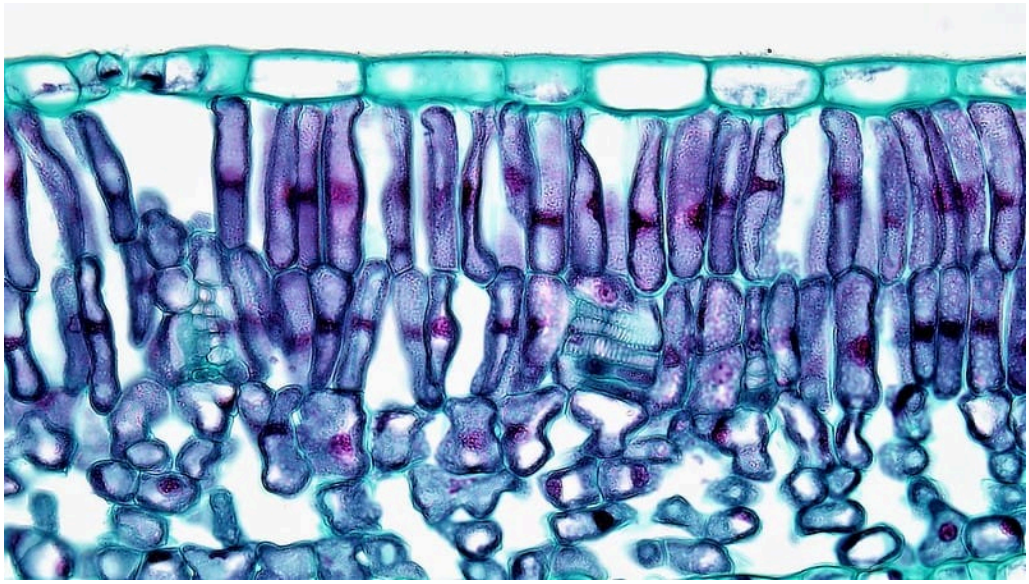


Figure 9.6.3.3.5: Just to the right of the center of this image, you can see the coiled spring appearance of the xylem vessel elements that have been caught in an oblique section. Image is in the Public Domain, sourced from Berkshire Community College Bioscience Image Library.

9.6.3.3.1: Adaptations to Water Availability

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9.6.3.3.1: Adaptations to Water Availability

The morphology and anatomy of a leaf can allow you to predict the conditions that the plant is adapted to. In particular, what is the water availability in that plant's environment?

Mesophytic Leaves

A leaf in "normal" conditions is called **mesophytic** (meso- means middle), meaning it is not particularly adapted for either high or low water conditions.

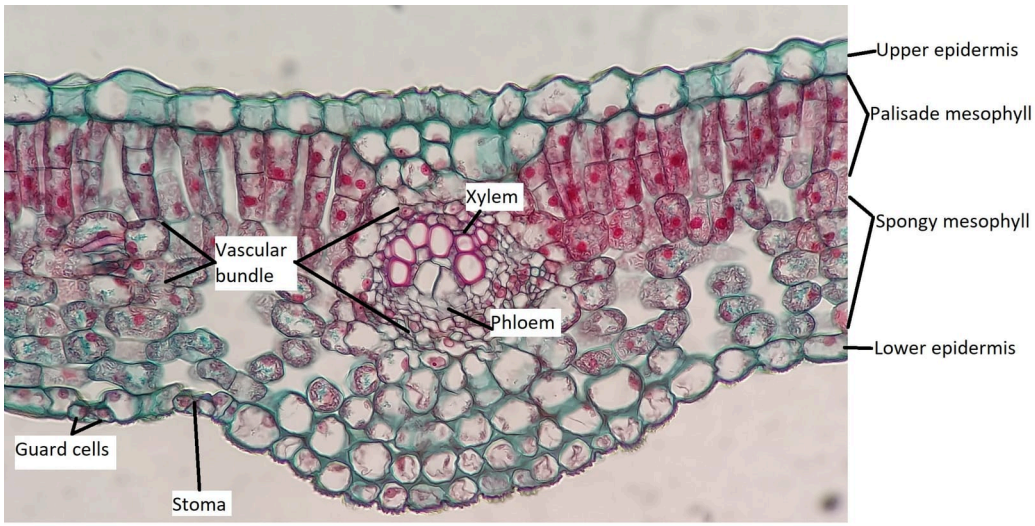


Figure 9.6.3.3.1.1: A cross section through a mesophytic leaf. The arrangement of tissues in a mesophytic leaf is as described in Fig. 13.3.2. As you look at adaptations to water availability, the arrangement of tissues in the leaf above will serve as the "standard" condition for leaves. Photo by Maria Morrow, CC BY-NC.

Hydrophytic Leaves

Hydrophytes (literally "water plants") are adapted to living in aquatic conditions.



Figure 9.6.3.3.1.2: A cross section through a dichotyledonous hydrophyte, *Nymphaea* (a water lily). The organization of tissues in this leaf is described in depth in Fig. 13.3.1.4. The important point here is to note the similarities between this eudicot leaf and the monocot leaf shown in Fig. 13.3.1.3. The similarities in tissue arrangement are due to convergent evolution to an aquatic lifestyle, as opposed to relatedness. Photo by Maria Morrow, CC BY-NC.

Below is an image of another hydrophytic leaf. This one is from a monocot, Potamogeton. Note the similarity to the Nymphaea leaf and the distinct differentiation between regions of mesophyll. A good example of convergent evolution to similar environmental pressures!



Figure 9.6.3.3.1.3: A cross section through a hydrophytic monocot leaf (Potamogeton). Note the similarity in internal anatomy to the hydrophytic eudicot Nymphaea shown in Fig. 13.3.1.2. Image is in the Public Domain, sourced from Berkshire Community College Bioscience Image Library.

Tissue Organization

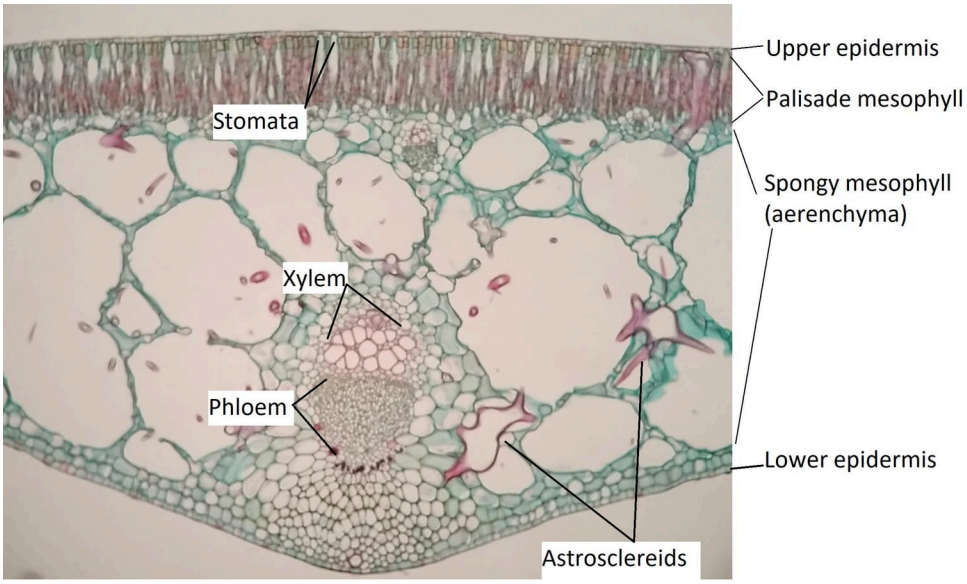


Figure 9.6.3.3.1.4: A cross section through a dichotyledonous hydrophyte, *Nymphaea* (a water lily). The upper epidermis is a thin layer of parenchyma with many stomata. Below each stoma, there is a chamber of air located within the palisade mesophyll (this makes them easier to find). Under the palisade mesophyll is a much larger region of spongy mesophyll than we would find in a mesophytic plant 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 caught in strange views during the sectioning process. Photo by Maria Morrow, CC BY-NC.

Location of Stomata

Because *Nymphaea* is aquatic and sits on top of the water, the stomata are located only in the upper epidermis. You can locate them in the cross section by finding the gaps (stomatal pits) in the palisade mesophyll. Why wouldn't there be stomata in the lower epidermis?

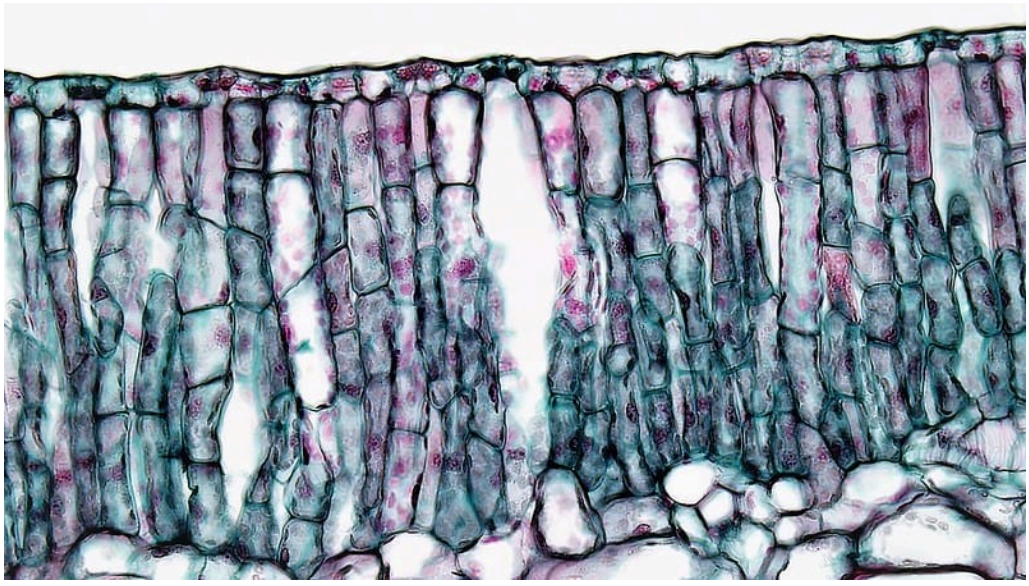


Figure 9.6.3.3.1.5: A close up of the stomata and stomatal chambers in *Nymphaea*. In the center of the image, there is an elongated empty space within the palisade mesophyll. At the top of this space, there are two guard cells flanking a closed stoma. At least three other stoma are present in the upper epidermis captured in this image, though the stomatal chambers haven't been captured as clearly in this section. Can you find them? Image is in the Public Domain, sourced from Berkshire Community College Bioscience Image Library.

Other Features

If you see strange branching structures within your Nymphaea leaf cross section, you may be looking at an **astrosclereid** (astro- meaning star). This is a branching sclerenchyma cell with a thick secondary wall. What function might these cells have?

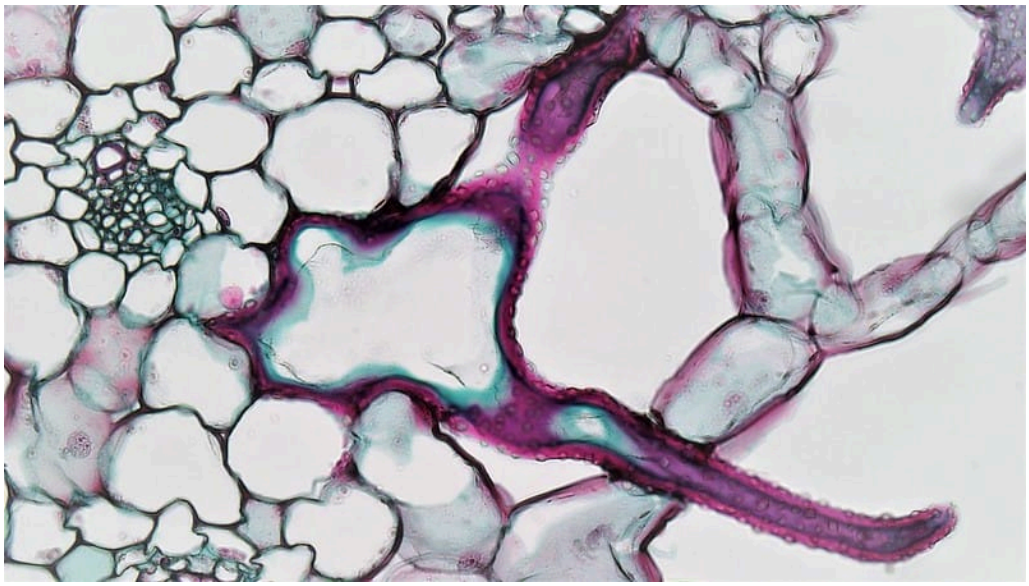


Figure 9.6.3.3.1.6: A close up of an astrosclereid found in a *Nymphaea* leaf, caught in partial section. These sclerenchyma cells are covered in pits and have long, sharp arms. Some span the entire width of the leaf. Image is in the Public Domain, sourced from Berkshire Community College Bioscience Image Library.

Xerophytic Leaves

Xerophytes (literally "dry plants") are adapted to living in dry conditions with low water availability.



Figure 9.6.3.3.1.7: A cross section through a xerophytic leaf (*Nerium*). At first glance, the organization looks similar to a mesophytic leaf. However, there are several adaptations that allow this plant to lose less water (see Figure 9.6.3.3.1.8). Photo by Maria Morrow, CC BY-NC.

Tissue Organization

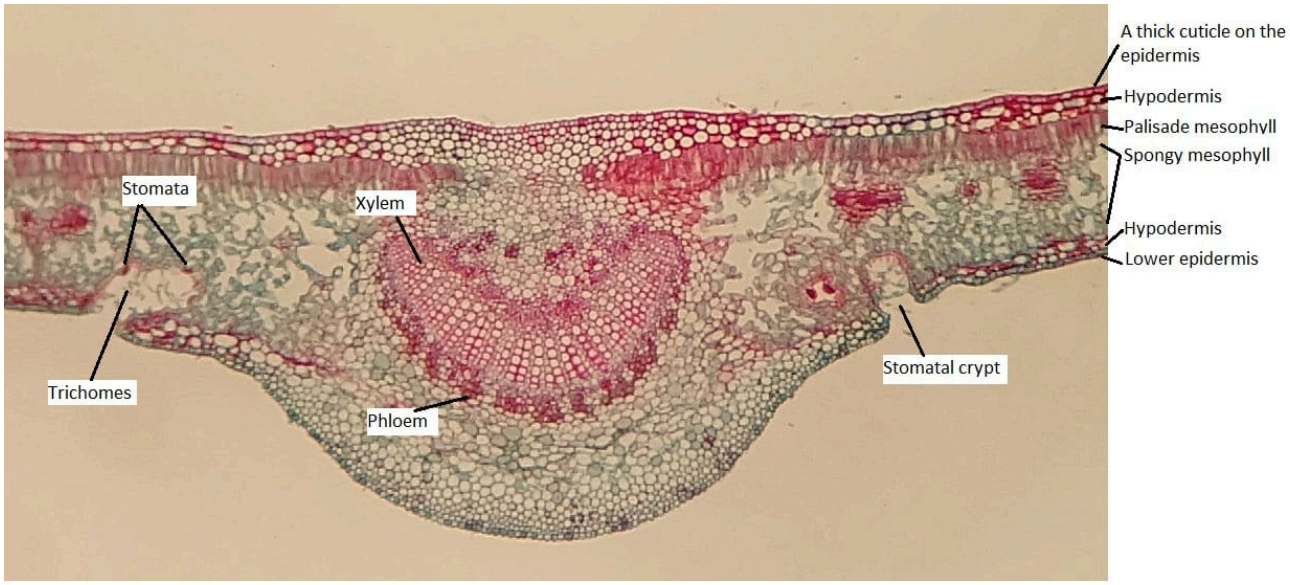


Figure 9.6.3.3.1.8: Tissue organization through a xerophytic leaf (*Nerium*). On the right side of the image, the layers of tissue are labeled from the upper surface of the leaf to the lower. The upper epidermis of the leaf is sealed by a thick, waxy cuticle. There are no stomata present in the upper 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 (see Figure 9.6.3.3.1.9). Stomata are located within these, surrounded by trichomes. Photo by Maria Morrow, CC BY-NC.

Cuticle Thickness

The image below shows the cuticle of the *Nerium* leaf. Notice how thick it is on the upper (adaxial) surface of the leaf and how it changes in thickness as it transitions to the lower (abaxial) surface.

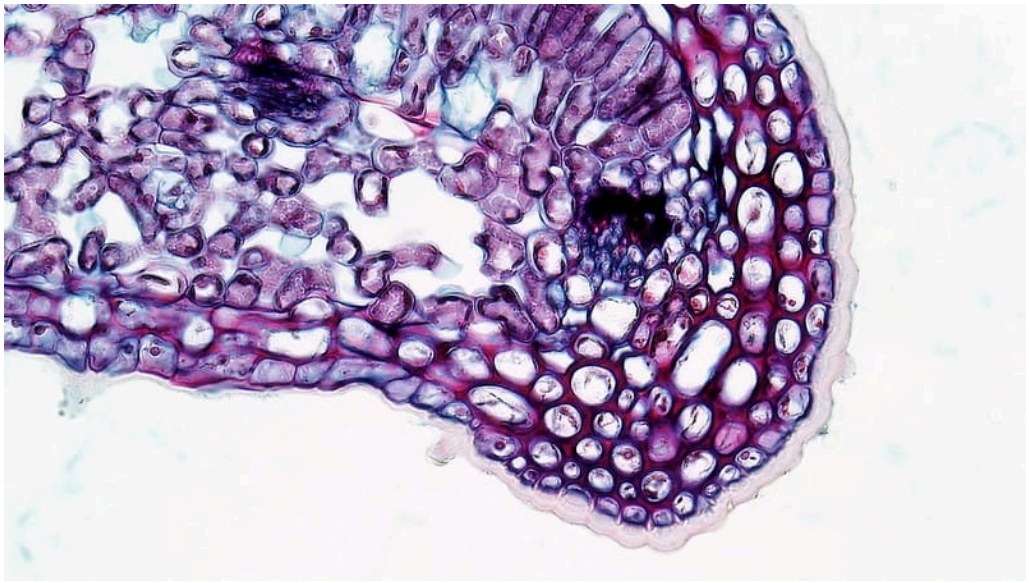


Figure 9.6.3.3.1.9: The margin of a xerophytic leaf. There is a thick cuticle on the upper epidermis (it looks like a transparent skin). The cuticle gets thinner as it transitions to the lower epidermis. Image is in the Public Domain, sourced from Berkshire Community College Bioscience Image Library.

Location of Stomata

In xerophytic leaves, stomata tend to be located on the lower (abaxial) surface. This side of the leaf is usually cooler, as the upper (adaxial) surface is facing the sun. In extremely dry conditions, stomata might be further protected from the desiccating outer air by being located in **stomatal crypts**.

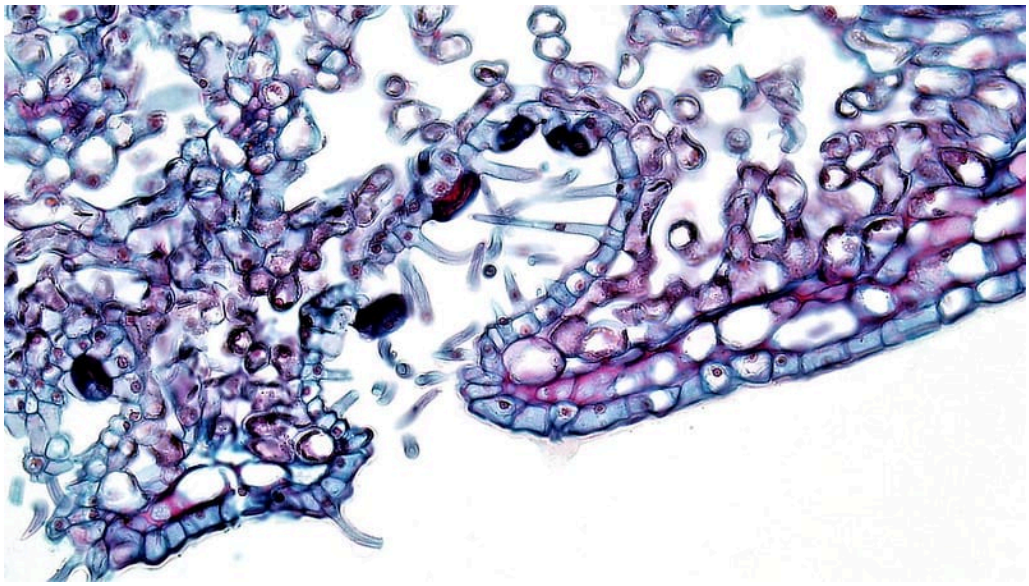


Figure 9.6.3.3.1.10: A stomatal crypt in the lower epidermis of a *Nerium* leaf. The epidermis folds inward, creating a small cave-like structure called a crypt. The stomata are located on the epidermis inside the crypt, surrounded by trichomes. Image is in the Public Domain, sourced from Berkshire Community College Bioscience Image Library.

Gymnosperms: The Original Xerophytes

Though pines are not angiosperms, they have xerophytic leaves (needles). Note the features this pine needle has in common with the *Nerium* leaf.

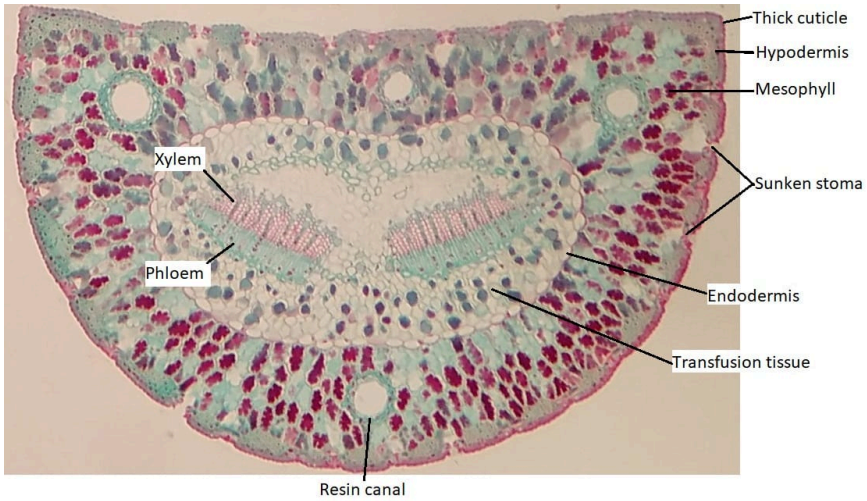


Figure 9.6.3.3.1.11: A cross section through a pine needle. Much like the *Nerium* leaf, this leaf is coated in a thick cuticle and there is a hypodermis below the epidermis (because this leaf is so round, there is not really a distinct 'upper' and 'lower'). There are no stomatal crypts, but the stomata are sunken, located in the hypodermis (see Figure 9.6.3.3.1.12). 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. Photo by Maria Morrow, CC BY-NC.

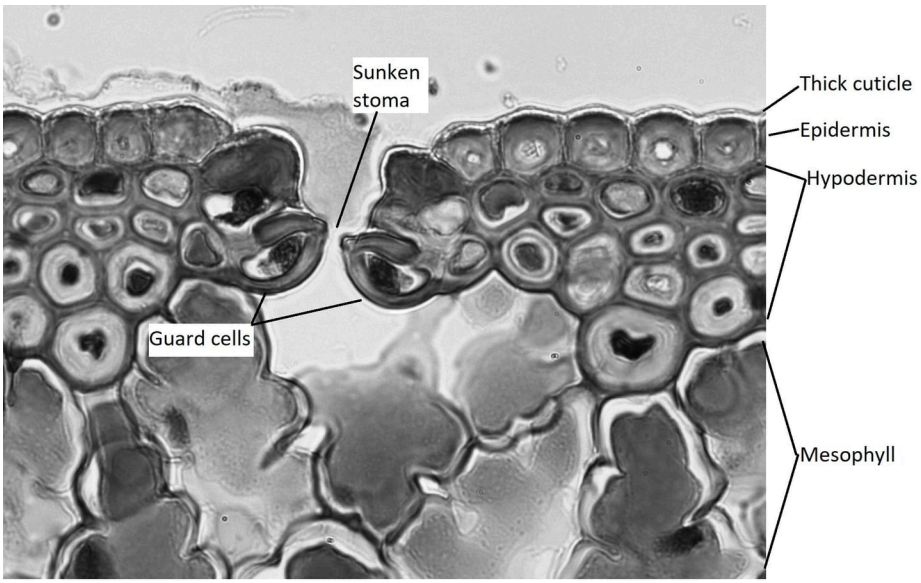


Figure 9.6.3.3.1.12: A closer view of a sunken stoma and the outermost layers of the pine needle. The thick cuticle is visible as a transparent layer coating the small epidermal cells. Each of the epidermal cells has a thick cell wall. The hypodermis is composed of 3-4 layers of small, tightly packed cells that also have thick walls (sclerenchyma). The guard cells of the stoma are located about 3 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. Photo by Maria Morrow, CC BY-NC.

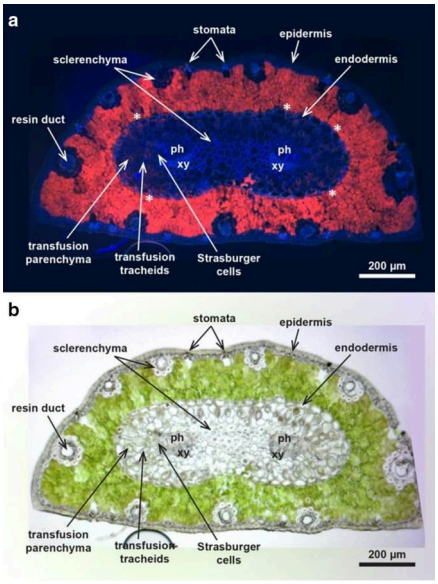


Figure 9.6.3.3.1.13: Two pine needle cross sections. In a) the mesophyll cells glow red (autofluoresce), in b) the mesophyll cells are green due to chlorophyll. Photosynthesis takes place in the mesophyll cells. "Scots pine needle cross-section photographed using a light microscope with UV excitation at 365 nm resulting in tissue autofluorescence (**a**), the same section photographed in the bright field (**b**). *x* xylem, *ph* phloem, asterisks indicate the radial thickening of the endodermal cells resembling the Casparian strip." Image and quoted caption text from the open-access paper Tissue-specific element profiles in Scots pine (*Pinus sylvestris* L.) needles. Pongrac, P., Baltrenaite, E., Vavpetič, P. *et al.* Tissue-specific element profiles in Scots pine (*Pinus sylvestris* L.) needles. *Trees* **33,** 91–101 (2019).

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9.6.3.4: Modified Leaves

The structure and function of a leaf can be modified over the course of evolution as a plant adapts to a particular environment. Some leaves may be converted to storage structures below ground (as with a bulb) or into plant defense structures (as with a spine). When function of the leaf blade is no longer primarily photosynthesis, some other plant part is usually modified to take its place. A **phyllode** is a petiole that has become flat and photosynthetic, looking much like a leaf blade.

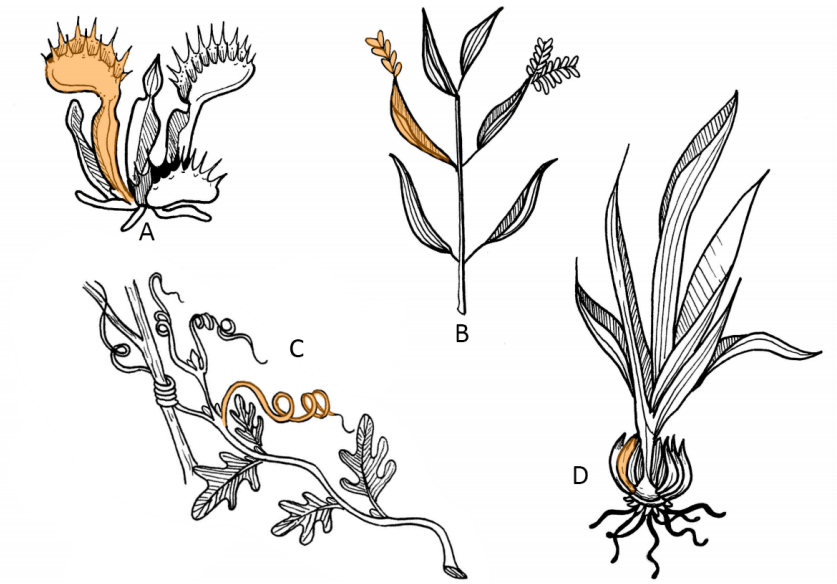


Figure 9.6.3.4.1: A diagram of leaf modifications. In each plant (A-D), one leaf has been shaded with orange. In A, the blade has been modified for a trap, the petiole is flattened into a phyllode. In B, the blade is a compound leaf and the petiole is flattened into a phyllode. In C, some of the leaves are 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 4.0 with labels and color added by Maria Morrow.

Bulb



Figure 9.6.3.4.2: The onion bulb has a relatively small stem (tan tissue just above the roots) surrounded by thick, fleshy leaves. Image by JonRichfield (CC-BY-SA).

Succulent

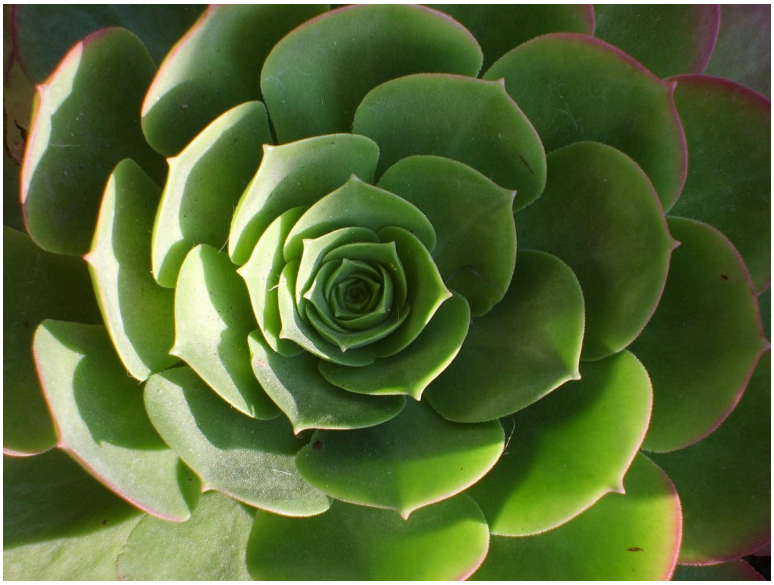
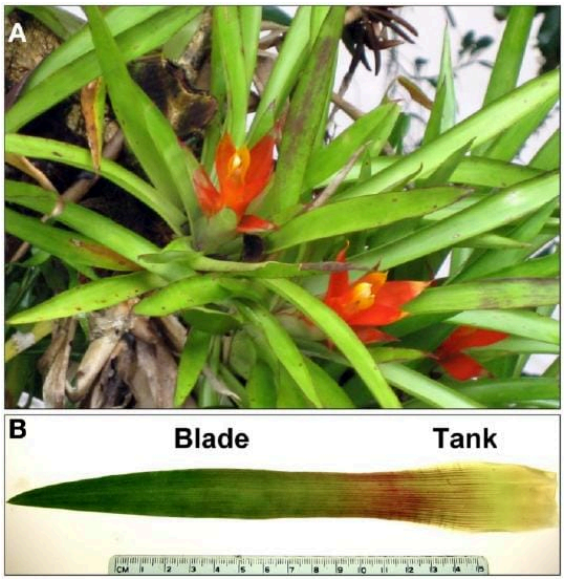


Figure 9.6.3.4.3: Succulent leaves are thickened for water storage. This water-storing tissue is called hydrenchyma (see Figure 9.6.3.4.4, bottom). Photo by Simon Burchell, CC BY-SA 4.0, via Wikimedia Commons.



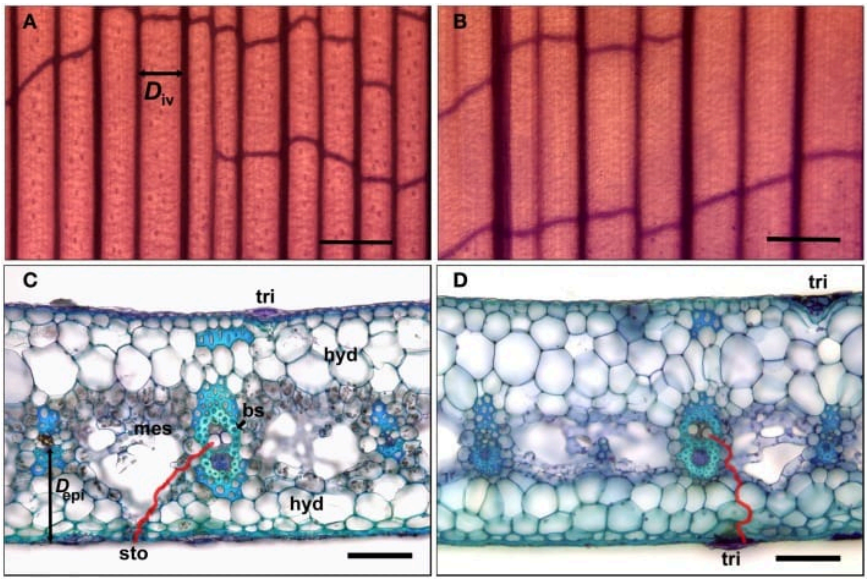


Figure 9.6.3.4.4: Top: "(A) Plants of *Guzmania lingulata* in the field at La Selva biological Station, Costa Rica, and (B) a single leaf of *G. lingulata* labeled with the two leaf regions examined." Bottom: "Sections of leaves of *G. lingulata* used to measure anatomical traits. Leaf clearings of the leaf blade (A) and tank region (B) used to determine interveinal distance (Div; black arrow); scale bars in (A) and (B) = 500 μm. Cross-sections of the leaf blade (C) and tank region (D); red lines indicate pathways for water between vein and abaxial surface (red line in (C) used to calculate Dmes; black arrow indicates distance between vein and epidermis Depi); scale bars in (C) and (D) = 50 μm. Abbreviations: bundle sheath cells (bs), hydrenchyma (hyd), mesophyll (mes), stomate (sto), and trichome (tri)." Figures and caption text from Leaf Hydraulic Conductance for a Tank Bromeliad: Axial and Radial Pathways for Moving and Conserving Water, North et al. 2013. Creative Commons Attribution 3.0 Unported.

Tendril



Figure 9.6.3.4.5: Many plants in the bean family (Fabaceae) produce leaf tendrils where all or part of the leaf forms a tendril. The first image is an illustration of a plant with compound leaves, some of the leaflets forming tendrils. The second image is of *Vicia villosa* with the terminal leaflets forming three tendrils. First image from Elsie Garrett Rice, Public domain, via Wikimedia Commons. Second image from Harry Rose from South West Rocks, Australia, CC BY 2.0, via Wikimedia Commons.



Figure 9.6.3.4.6: "Leaf tendrils: In weak-stemmed plants, leaf or a part of leaf gets modified into tendrils i.e., a green coiled threadlike structure which helps in climbing around the support. Gloriosa or Glory Lily has leaf tip modified into tendrils." Image and caption text by Krishna satya 333, CC BY-SA 4.0, via Wikimedia Commons.

Spine

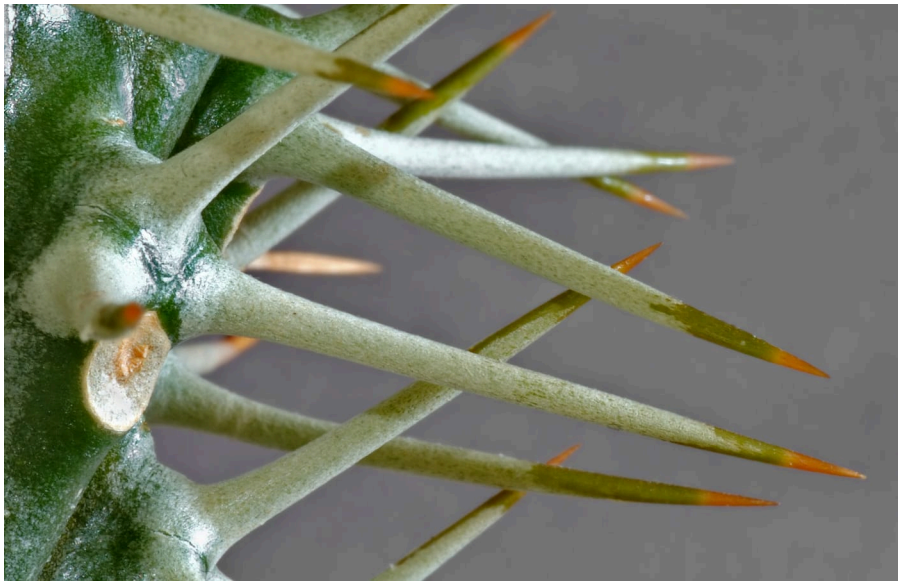


Figure 9.6.3.4.7: Cactus spines are not stems, but modified leaves. These spines have a thick cuticle and stomata can be seen as darker green areas within the pale white cuticle. Photo by André Karwath aka Aka, CC BY-SA 2.5, via Wikimedia Commons.



Figure 9.6.3.4.8: Ocotillo leaf petioles form into spines. Note the axillary buds present in the axil of each spine. Photographed by and copyright of (c) David Corby (User:Miskatonic, uploader) 2006. This file is licensed under the Creative Commons Attribution-Share Alike 3.0 Unported license.



Figure 9.6.3.4.9: Stipular spines of an *Acacia* sp. The paired sharp armaments subtend the leaves on this woody shrub. Dr Mary Gillham Archive Project, CC BY 2.0, via Wikimedia Commons.

Traps



Figure 9.6.3.4.10: 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 4.0. Last two photos credit a: modification of work by Peter Shanks; credit b: modification of work by Tim Mansfield, adapted from Botany by Algiers, Ha, and Morrow.

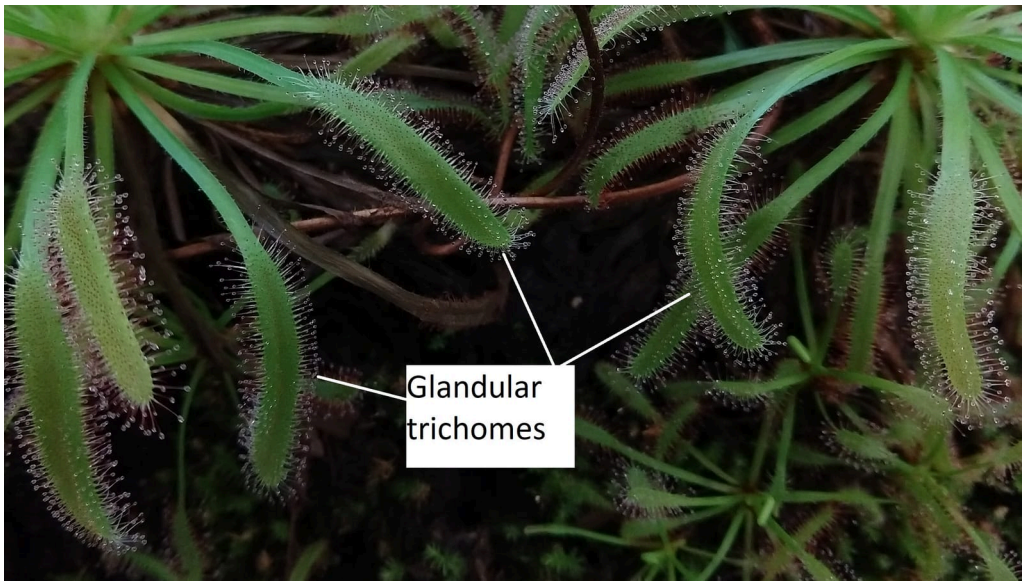


Figure 9.6.3.4.11: The ends of sundew (*Drosera* sp.) leaves are covered with glandular trichomes. Each trichome has a blob of sticky fluid at the tip. Insects are attracted to the fluid, becoming trapped in it, and the plant can slowly digest their bodies for the mineral nutrients that are lacking in their environment. Photo by Maria Morrow, CC-BY 4.0.

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10: HOW PLANTS GROW, PART 1

Learning objectives

- Identify the unique features that distinguish shoots, leaves, and roots.
- Describe ways in which stolons and rhizomes are modified stems.
- Identify the types and parts of the major shoots, leaves, and roots.

The organization of the plant is not unlike that of our own bodies. At the simplest level, cells are organized into tissues; these form organs that make up the plant body. At each level of this organization are specializations for the specific functions that occur during the plant's life cycle. In this chapter, you'll explore the structures and functions of leaves, shoots, and roots.

10.1: Vascular Plant Form

10.2: Leaves

10.3: Shoots

10.4: Roots

10.5: Terms

10.6: Vascular plant anatomy- primary growth

10.7: Secondary Growth

10.7.1: Introduction

10.7.2: Secondary Tissues in the Root

10.7.3: Flowcharts of Development

10.7.4: Secondary Tissues in the Shoot

10.7.5: Dendrochronology

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10.1: Vascular Plant Form

One of the striking features of plants is their diversity in form. This is nicely demonstrated with a visit to a greenhouse but can also be seen by looking at outdoor plants, both in native habitats and in gardens. At the same time, all seed plants are fundamentally the same in form and follow a pattern depicted in the Figure 1 and described as being 'modular' and 'recursive' . What accounts for the apparent diversity in plant form when they are basically put together the same way? There are six key areas of variation that influence the above-ground form of flowering plants and these are listed below and are main sections of this chapter. While the bulk of the chapter deals with flowering plants the form of non-flowering seed plants and vascular plants without seeds is also discussed.

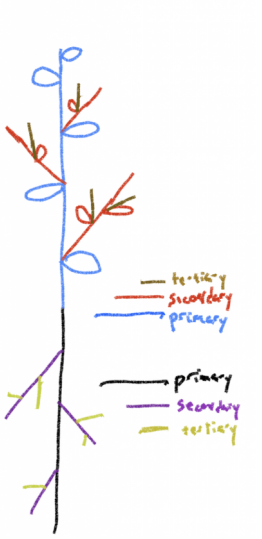


Figure 1 The modular and recursive nature of plant form

TOPICS

- Flowering plants
  - Factors affecting above ground form
    - Internode length
    - Branching frequency
    - Variation in the size, shape and orientation of leaves
    - Direction of growth of stems and branches
    - Presence or lack of secondary growth
    - Loss of parts (leaves and branches)
  - Below-ground form
- Form of non-flowering seed plants
- Form of vascular plants without seeds

Factors affecting flowering plant form I: Internode length

Do dandelions have stems (Figure 2a)? They must, because they have leaves and leaves are always attached to stems, but dandelion stems certainly are not very evident because they are so very short. You could say that dandelions are 'vertically challenged' and as a result, their leaves are very closely clustered, forming what is known as a rosette. Rosettes are a common plant life form and result from the fact that the distance between individual leaves is extremely short, making it appear that there is no stem. While the leaves of dandelion typically run horizontally, parallel to the ground, some plants, like Amaryllis (Figure 2b) also have very short stems but with leaves that are oriented more vertically. Dandelions live for a number of years and

never produce a recognizable stem, although they do produce branches that are flowering stalks. Other plants, including both agricultural crops (e.g., carrots, beets, cabbage, turnip) and common weeds (e.g., mullen, burdock, 'wild' carrot, garlic mustard) are biennials. They form a rosette in their first growth season (Figure 3) and in their second year of growth they 'bolt' as the stem produces much longer internodes to produces a more 'normal-looking' , elongate stem, upon which are born flowers (Figure 4) . A small number of plants, including the one used to make tequila, are a rosette for multiple years, maybe 7-10, before the stem 'bolts.'



Figure 3 Mullen, a common weed, showing its rosette form after one year of growth



Figure 4 Mullen, showing its form after a second year of growth—the stem has bolted an the internode length (the distance between leaves) if much greater than in the first year of growth

What determines internode length?

Recall that leaves and stem material are produced in the embryonic region called the apical meristem at the very tip of stems. In this region new cells are produced by mitosis and the cells are organized as new stem material and as leaf primordia, outgrowths from the stem that grow and produce the structures that we know of as leaves. In dandelions and other rosette plants, the distance between leaves is very short. As mentioned above, internode length may vary with age, or more specifically vary with environmental factors that coordinate with age, in which case plant form may drastically change with age (see images of mullen, above). Internodes produced in the first season of growth are very short, those in the second season of growth, after the plant has been exposed to a cold period, are a great deal longer.



Figure 5 Many root crops, including turnip are biennials harvested at the end of the summer after planting. If allowed to overwinter they will bolt, producing flowers and seeds but reducing the amount and quality of the root material.

What are the consequences of producing rosettes as opposed to stems with leaves more widely spaced (Figure 5, 6)? One factor is microclimate, rosette leaves, if they are close to the ground, may be in a very different environment that leaves that are elevated. A second factor is self-shading of leaves, although this is influenced by several other factors including the size of the leaves and their distribution. Additionally, plants with short stems and clustered leaves are also more likely to be shaded from above because the stem is not carrying leaves upwards and potentially above the neighboring plants. At the same time, growing upward exposes the plant to a number of problems that are not present if it stays low to the ground. One is mechanical. Growing upward requires stems to be able to resist the combined effects of gravity and wind. Another problem is that an elevated shoot apical meristem becomes more apparent and vulnerable, at least to some herbivores. How significant this is depends on the herbivore—something big, and especially something big with a big nose (think deer!) might have a hard time nipping the tip of a dandelion, but have no difficulty nipping the tip of a tomato plant. However, this is not an issue for smaller herbivores like Japanese beetles. The loss of the terminal apical meristem is particularly damaging because it eliminates the source of growth, although growth may continue by the activation/stimulation of lateral buds.



Figure 6 Impact of internode distance. The top image of a Diffenbachia stem shows the widely spaced-out leaf scars about 3 cm apart. The bottom image of cabbage shows a very distinctive rosette form.

Factors affecting flowering plant form II: Branching frequency

Note the images of Diffenbachia and cabbage. Like dandelion, they have no branches. 'Typical' plants with modular growth and a dendritic form have branches and the branches have branches. This repetitive pattern is one of the familiar aspects of plant form that makes them so appealing as an artistic model. However, some plants, like dandelion, have no branches, there is just one axis to the plant, and this gives them, and other plants, a distinct look.

Recall that branches result from the fact that as the shoot apical meristem elongates and produces embryonic leaves it also produces a potential branch, called a branch primordium or bud primordium in the 'axil' of each leaf, placed just above where the leaf attaches to the stem. A branch primordium is a replica of the shoot apex, an embryonic shoot capable of elongating and producing a shoot with leaves upon it. All that needs to happen to produce a branch is that the branch primordium be stimulated to start growing. Branch upon branch upon branch can be produced as each shoot in turn produces leaves that have branch shoots appear from their base. This does not happen in dandelion and in many other plants, both rosette and non-rosette. In such plants, growth occurs solely from the original shoot, although many of them will form branches if the original shoot apical meristem is removed. In dandelion, although branch primordia are produced, they are only activated to grow after being transformed into flower primodia (technically inflorescence primordia). Thus, when activated, they produce not a branch but a leafless dandelion 'flower' (technically it is an inflorescence, a cluster of flowers, not a single flower). This type of growth pattern is also seen in Aloe and a number of other rosette plants.

Frequently one may see a cluster of dandelion plants together, which might appear like a group of branches. However, these are usually formed when the stem of a dandelion is broken off (usually as the result of someone trying to pull it up). The root that remains is stimulated to form new (adventitious) shoots. Often what happens is that multiple shoots are produced by a single root, forming in a cluster of stems. Each of them originated separately from the root tissue, so what you see is not a cluster of branches but instead a cluster of adventitious shoots.

Often branches don't look like branches

In grasses, the branches often aren 't recognized as such. They appear at the base of the plant when branch (bud) primordia of the lowest leaves (more details on grass leaves are given below) are stimulated to grow in one of three ways (Figure 7): (1) extending vertically, producing a leafy stem called a tiller (on non-grasses this sometimes called a' sucker 'or a' pup') that is basically the same in structure and function as the original stem; (2) extending horizontally and above-ground, producing only rudimentary leaves with very reduced blades and elongate sheaths. These horizontal stems (branches) are called stolons; (3) extending horizontally but below ground, again producing only rudimentary leaves. These horizontal underground stems (branches) are called rhizomes. Stolons and rhizomes are sometimes considered a means of reproduction; they can also be thought of as providing mobility. Eventually both produce vertical, photosynthetic stems that originate from the bud primordia associated with the rudimentary leaves. A number of plants (e.g., goldenrods, asters) that appear to exist as vertical stems are actually a group of vertical branches all connected to a below-ground stem (rhizome).

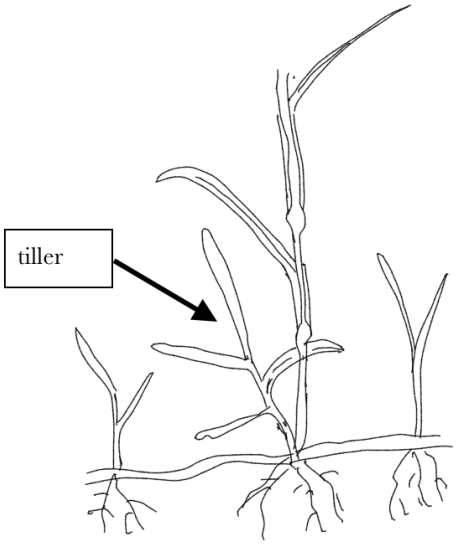


Figure 7 Grass plants commonly produce branches that are called tillers and generally originate from the branch primordia produced along with the earliest leaves. Grasses also produce horizontal running branches that are called stolons if they are above-ground and rhizomes if they are below-ground

Factors affecting flowering plant form III: Variation in the size, shape and orientation of leaves



Figure 8 Banana plant. The vertical structure is not a stem but instead a cylindrical group of leaf sheaths oriented vertically.

In contrast to dandelions, which look like they don 't have a stem when they actually do, grasses (and a number of other plants, including bananas) possess something that looks like a stem but actually isn' t. The 'trunk' of a banana plant is actually a cluster of leaf bases tightly wound (Figure 8) around each other and called a 'pseudostem' because it has the appearance of a stem. Bananas and grasses are monocots, a group that includes orchids and a number of other flowering plants. One feature commonly found in monocots, and specifically in banana and grasses, is a leaf with two main parts (Figure 9) . One part is called the blade; this is typically flattened and extends outward from the plant and is often roughly horizontal to the ground. This is the part that most people recognize as a leaf. If you follow the blade back to the rest of the plant, it abruptly narrows (a great deal in banana, less so in grasses) to a section of the leaf that is vertically oriented and cylindric. This part of the leaf is called the sheath. Early in the growth of both grasses and bananas the structure that looks like a stem is actually just multiple leaf sheaths extending upward from a very short stem, like a dandelion stem.

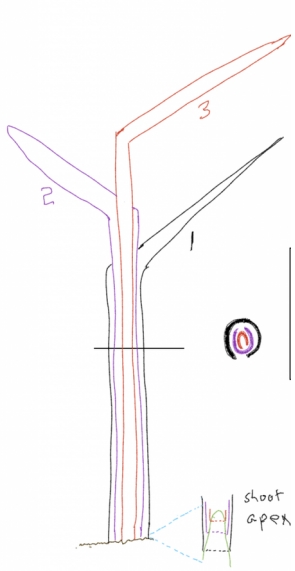


Figure 9 Longitudinal view of a grass pseudostem, showing three grass leaves elongating from a very short stem, shown in expanded view in the bottom right. Each leaf has a vertically oriented sheath and a more horizontal blade. Newer leaves occur inside of older ones.

While dandelion leaves are generally horizontally displayed, in grasses the bases of the leaves (i.e., the sheaths) are vertical. The more recently produced leaf sheaths are located inside of older ones and they collectively form a structure that seems like a stem. In grasses and bananas, the stem eventually elongates, the result of very large increase internode length of the youngest leaves. If one were to measure the internode length for a grass for the first 10 leaves it might be (in mm and starting with the first leaf produced): 1, 1, 1, 1, 1, 10, 50, 100, 150, 200. After producing six leaves the stem is 6 mm in height, after producing four more leaves it is 506 mm in height. The stem 'telescopes' upward inside of the sheaths, and often exposes the uppermost nodes, the actual point attachment of leaves to the stem. When the stem of a grass or a banana elongates, it signals the end of the life of that stem and its associated leaves. An inflorescence is produced at the end of the stem, with flowers that develop into fruits. Nutrients are mobilized from the leaves to the developing seeds and fruits. As noted above, many grasses and bananas branch from the base and this may perpetuate the organism even if the original shoot flowers, senesces and dies.

Dandelion, grass and banana leaves just scratch the surface of variation in leaf form. Palm leaves may be up to 25 m in length and duckweed leaves are about 3 mm. Most leaves are flat but some are thick (succulent) and may be round and bead like (Figure 11). Leaves can be lobed and toothed in a variety of ways. Many leaves are dissected into parts sometimes in ways that it isn't obvious whether one is looking at a leaf or a leaflet.



Figure 10 Duckweed, one of the smallest flowering plants, with leaves less than 3 mm. It floats on the surface of ponds and streams.



Figure 11 Coconut palm has leaves that typically are several meters long; some palms have leaves over 20 m long.



Figure 12 An example of leaf variation: string of pearl leaves are almost spherical



Figure 13 The leaves of tamarix are small and scale-like, forming what looks to be a photosynthetic stem. A similar form is found in junipers.

Factors affecting flowering plant form IV: The direction of growth of stems and branches: vertical, horizontal or something in between

Although most familiar plants have a main stem and branches that grow upwards, this is not always the case. Branches may be hidden below ground because they do not grow vertically but instead extend horizontally below the ground. As a result, multiple stems rising from the ground may not be separate plants but actually be branches that extend vertically from a main stem that is running horizontally below ground. While most familiar plants have stems that grow upwards, the exact angles vary and some run horizontally, producing what is known a 'prostrate' growth form seen in partridge berry and strawberry below (Figure 14-15)



Figure 14 Partridge berry



Figure 15 Strawberry plants

Some plants (pin oak) have branches that extend roughly 90 degrees from a vertically oriented stem, i.e., they extend horizontally. Other plants have branches that run more vertically, perhaps at an angle of 45 degrees from the main stem.

It is also quite common that orientation changes, generally in a controlled manner. In the example of grasses or banana described above the original stem is vertical but 1st order branches may run horizontally (if they are rhizomes or stolons) and third order branches (i.e., branches off of the stolon/rhizome) again run vertically. Thus plants vary in the way that the original stem and its branches are oriented, both within a plant and between different species.

Factors affecting flowering plant form V: whether or not the stems and branches exhibit secondary (generally woody) growth

Secondary growth allows plants to become wider and taller. While most people associate woodiness with trees, two other plant forms are woody: 'Shrubs' have no rigid definition but are tree-like but show limited growth in height but abundant branching (Figure 16). Most vines (lianas) are woody and have an interesting cellular nature that lacks sclerenchyma fibers and consists almost entirely of water conducting cells with relatively thin secondary walls. This is possible because they utilize the structure of other plants to provide support. Consequently vine wood has a low density and rigidity when compared to tree wood.



Figure 16 Sagebrush, a common shrub of the western US.

Factors affecting flowering plant form VI: shedding of plant parts

A final factor that impacts the 'look' of plants is the shedding of plant parts. Most plants discard pieces as they grow. Generally, the discarded parts are leaves but branches may also be shed (Figure17-18). Moreover, the loss of parts may be synchronous, as it is with most deciduous trees, but other plants may shed parts continuously. Plant structure is dynamic and parts are not solely being added, they are generally also being removed. These changes are often not noticed, except by gardeners/landscapers, because the changes are relatively slow, the new growth looks just like the old growth and the pieces shed are matched by pieces added. For most plants both the growth and the shedding are usually sporadic, occurring in spurts with inactivity between them.



Figure 17 Note that in most forests branches are not present close to the ground. There had been branches but they have been shed.



Figure 18 This is what is known as a 'wolf tree' one that initially grew in an open area and did not shed its lower branches.

Below-ground form

Root systems also have a variety of forms but, obviously, it is harder to see the form of root systems. One distinction that is often cited is the distinction between a taproot system, where the embryonic root (the one formed in the seed) persists and becomes the main trunk of the root system that connects with the stem. Note that a carrot is perhaps not the best example of this, even though it is often used, because in carrot the root is performing a carbohydrate storage function, something that does not have to be the case for plants with taproots. In contrast to taproots, many plants have a root system that forms from adventitious roots that are produced off of stem/rhizome/stolon and do not have a dominant, primary root. Fibrous root systems may only have a few levels of branching whereas taproots typically have more, especially as they age. The primary function of roots is to acquire water and the pattern of water distribution is significant to root system form, specifically lateral spread vs. vertical spread. Alfalfa roots are known to penetrate 15 meters down in order to obtain water. On the other hand, most cactus roots spread extensively but do not penetrate deep in the soil. Cactus also commonly produce roots quickly after a rain and then rapidly loose them (i.e., they senesce and die) as the soil dries.



Figure 19 Until one looks closely at the leaves, ginkgo trees appear like typical angiosperm trees. ◈They are widely planted, often in urban areas where they do well but they do not reproduce in the wild.

Form of seed plants without flowers

There are four groups of seed plants that lack flowers. Representatives of most of these groups are present in the 'Organisms to Know' section and are highly in red.

The ginkgophyte group only has a single species, ginkgo , which in form is typical of a deciduous (angiosperm) tree (Figure 19) except that the leaves are unusual, being fan shaped with bifurcating parallel veins. Ginkgo also has 'spur shoots' ('short shoots'), branches with a very short internode distance and consequently leaves clustered very close together. Spur shoots make identification of ginkgo easy during the winter months.

A second group are the conifers, including pines, hemlock, redwoods and juniper . Conifer leaves are usually present on the plant for more than a year (i.e., they are evergreen). Many conifers have needle like leaves although some have small, scale-like leaves that overlap each other, producing what are essentially photosynthetic twigs which are shed as a unit after senescence. Most conifers have tree-like forms (Figure 20) with a fairly rigid branching pattern that produces the characteristic 'Christmas tree' shape. There are a few conifers that are shrubs, primarily in the yew-family and some in the cedar family.



Figure 20 These are Blue Spruce showing a typical conifer form. Conifers do particularly well in montane habitats and also at high latitudes (the boreal zone)

A third group of non-flowering seed plants are the cycads, most of whom have a distinct form, generally with an unbranched, short stem axis and relatively long pinnately compound leaves (Figure 21). These stem and leaf features are found in two other groups with which cycads may be confused: tree ferns (see below) and palms (a group of flowering plants). Distinguishing between the three groups is easy if reproductive structures are present: palms produce flowers and seeds; cycads have no flowers but produce seeds in a type of cone; and tree ferns produce no seeds but have clusters of spores visible on the leaves).



Figure 21 Cycads showing their typical elongate pinnately compound leaf. Sometimes the trunk can grow to a meter or two. There is limited secondary growth and branching is rare

The fourth group of seed plants lacking flowers, the Gnetum group, has only three genera, each with a very distinctive forms *Welwitchia* (there is only one species and it lives in southern Africa) is by far the most bizarre of the group (Figure 22). It produces only two leaves which grow from the base and grow long and strap-like, often shredding longitudinally so it appears that there are more than two leaves. The apical meristem dies after these two leaves are produced and hence there is no stem. Reproductive structures are produced by the 'crown' at the base of the leaves and plants are either male or female.



Figure 22 Welwtichia mirabilis As if the specific epithet (mirabilis) weren't enough, the discover of this plant is quoted as saying “[I] could do nothing but kneel down and gaze at it, half in fear lest a touch should prove it a figment of the imagination.”

A second genus in the Gnetophyta groups is *Ephedra* (roughly 70 species) are highly branched shrubs with photosynthetic stems and small leaves that are soon shed (Figure 23).



Figure 23 Ephedra is a leaf-less, many branched shrub that grows primarily in arid regions. As can be seen the stems are green and photosynthetic.

The final Gnetophyte genus is *Gnetum* (roughly 40 species) which has species that look the most 'normal' (i.e., like many flowering plants) of the group, with 'normal' leaves (determinate structures with a petiole and a flattened blade) occurring on forms that could be described as small trees, shrubs or vines.



Figure 24 Horsetail— three stems showing the small, yellow scale-like leaves.

Form of vascular plants without seeds

We will consider three groups of plants that possess vascular tissue but do not produce seeds. Again, note that representatives of these groups are described in the 'organisms to know' section.

The least diverse and easiest to identify are the horsetails (*Equisetum*). There are less than 20 species and all look similar and have a distinctive form (Figure 24-25). They have below-ground rhizomes that produce erect ribbed and 'jointed' stems with whorls of minute, scale-like leaves occurring at the joints. Some species vary from forms with and without whorls of branches, while other species are strictly unbranched or strictly branched. Although relatives in the Paleozoic era, 300 million years ago, had tree-like forms with secondary growth and stems up to 30 m high, all living species show no secondary growth.



Figure 25 A branched form of horsetail emerging from a rhizome.

Most members of the clubmossgroup have a typical plant 'stem with leaves' structure. The stems and roots are vascularized and the leaves have a single vascular trace (vein). Probably because of this, leaves are small and often appressed to the stem, giving the plants a 'moss' look, although the plants and leaves are bigger than almost all mosses. Although representatives of the group used to possess secondary growth and tree-like forms, all forms present now are small, usually less than 20 cm tall, and non-woody (Figure 26-27). Most species have stolons or rhizomes from which vertical branches appear. These may or may not branch. One genus in the group (*Isoetes,* the quillworts) has a very different form. It is aquatic, unbranched plant with very short internodes, forming rosettes with awl-shaped leaves that may be 10 cm or more in length (Figure28).



Figure 26 A common forest clubmoss in northeastern forests. The yellow cylindrical structure (the 'club') is where it produces spores.



Figure 27 The clubmoss species shown above is sometimes called 'ground cedar' because its small, scale-like leaves are appressed to the stem, comparable to many cedars, trees in the conifer group.

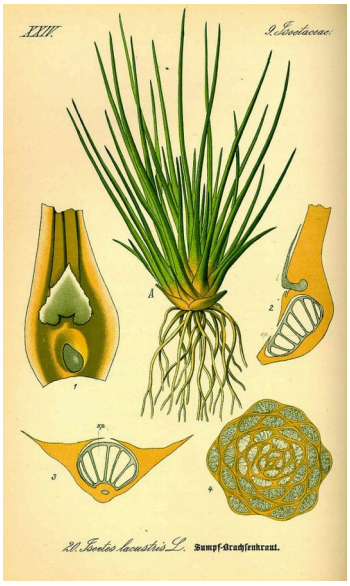


Figure 28 A quillwort, an aquatic genus in the clubmoss group with a very different structure.

The fern group is by far the largest group of vascular plants without seeds and it is the group with the most diversity in form, although the majority of ferns seen in north temperate habits are generally uniform in structure with an underground, woody (i.e. showing secondary growth) rhizome from which leaves arise (see sensitive fern, wood fern). Thus, when you see a fern you are generally seeing a group of leaves (fronds) that originate in a below-ground woody rhizome. Some species have rhizomes that are short and vertical and produce a circular cluster of leaves resulting in an urn-shaped display (Figure 29. Other species have rhizomes that run strictly horizontally and producing a more uniform 'patch' of ferns (Figure 30) the leaves can be more or less dense depending upon the pattern of leaf production along the rhizome.



Figure 29 A cinnamon fern, showing an urn-shaped cluster of leaves



Figure 30 Hay-scented ferns typically have leaves thet are not clustered.

In the tropics there are some ferns that are tree-like with an above ground stem vertically oriented stem that may be 2 m in height and superficially resemble palms and cycads. There also are aquatic ferns that are small and float on the surface of water (Figure 31), comparable to growth of duckweed, which is a flowering plant. A final example of the diversity in fern form is *Marsilea,* a fern that resembles four-leaf clovers (Figure 32) and has a very interesting pattern of sex.



Figure 31 An aquatic fern, Azolla, which floats on the water surface and has leaves about 1 mm in size that sometimes house nitrogen fixing cyanobacteria.

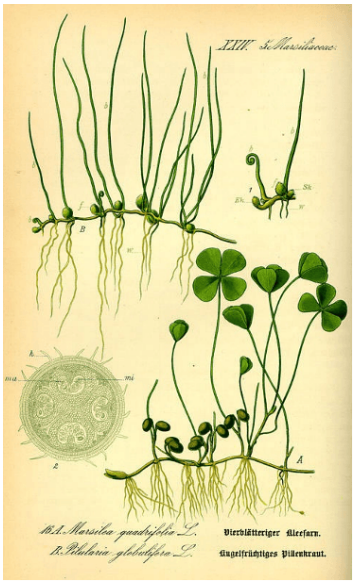


Figure 32 Two ferns that commonly grown in aquatic habitats, sometimes with leaves floating on the surface.

Further reading

- An excellent description of fern form

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10.2: Leaves

Learning objectives

- Identify the parts of the angiosperm leaf.
- Describe some of the ways in which leaf parts differ from plant to plant.
- Recognize the basic patterns of leaf shape and orientation of the veins in the leaves.

Leaves

Leaves are shoot structures that attach to stems and branches at nodes. Leaves are made up of cells that usually contain a high concentration of chloroplasts (cell organelles unique to plants) and are specialized sites for photosynthesis. We will explore photosynthesis in greater detail later; for now, remember that photosynthesis is the process of capturing light energy and converting it into chemical energy that can be stored in plants (like starch and sugar). In some plants, leaves may be modified for nutrient storage (as with onions, where the bulb is made up of fleshy leaves), or for support (as with peas, where some leaves are modified into tendrils that wrap around a trellis).

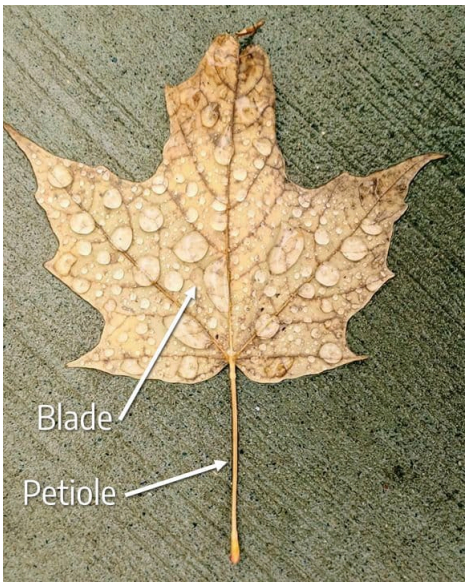


Photo by yooperann, CC BY-NC-ND 2.0.

Leaves are also the surface where water that has moved from the soil into the roots and up through the plant finally evaporates back into the atmosphere in a process called **transpiration**.

Angiosperms, which are flowering plants whose seeds develop inside an ovary, tend to have flattened leaves. Many perennial angiosperms (flowering plants that can grow for many years) have leaves that senesce, or die, at the end of each growing season and are replaced at the beginning of the next growing season. Gymnosperms, plants whose seeds are produced without the protection of an ovary, tend to have needle-like leaves. Perennial gymnosperms tend to hang on to their leaves for a number of years. This saves energy, since the plant doesn't need to grow a whole set of new leaves every year. The needle-like form helps retain moisture in harsh, dry climates, including those that are very cold and dry.

Leaf parts and venation

Angiosperm leaves typically have a blade or lamina, a flattened part with high chloroplast concentration. They may also have a petiole, the stalk that attaches the blade to the stem at a node. Stipules, small leaf-like bracts at the point of attachment of the petiole to the stem, may also be present. Some leaves have no petiole at all, and are termed sessile.

In contrast to the blade-petiole structure, grasses have a sheath-type structure in which the blade attaches to an envelope of leaf tissue that wraps around the shoot of the plant and then attaches to a lower node on the stem.

Leaf blades also have characteristic patterns of venation. In grasses, the veins lie parallel to each other and to the long edges of the leaf. We call this parallel venation, and it is typical of monocots. Most other angiosperms have a strong major midrib with veins branching from the midrib, smaller veins branching from those, and so on to form a netted venation throughout the leaf. This type of venation is typical of dicots.

Leaves may also have a palmate venation where several veins radiate from the point where the petiole attaches to the blade. Ginkgo tree leaves have palmate venation. The veins fork, then travel a bit, then fork again, travel, fork, and so on until the veins reach the margin (edge) of the leaf. Sugar maple leaves have a classic palmate venation with five lobes.



Photo by Matt Lavin, CC BY-SA 2.0.



Left: Corn leaves have parallel veins. Center: A leaf with netted veins. Right: Ginkgo tree leaves have palmate veins. L to R photo credits: Image by Hans Braxmeier, CC0; Thangaraj Kumaravel, a CC BY 2.0; Nate Hofer, CC BY-NC-SA 2.0.

Watch this video on leaf veins:

Leaf segmentation

Simple leaves

Simple leaves have uninterrupted leaf margins. The leaf may have lobes like the oak leaf, but the blade has one continuous margin. The venation differs in the two examples below. The oak leaf is pinnate, with a major vein heading down the midrib of the leaf. The maple leaf is palmate, with major veins that radiate from the point of attachment to the petiole.



Oak leaves have pinnate venation (L), while maple leaves have palmate venation (R). Photo credits L-R: Dendroica cerulea, CC BY-NC-SA 2.0; Richard Skiba, CC BY-NC-SA 2.0.

Compound leaves

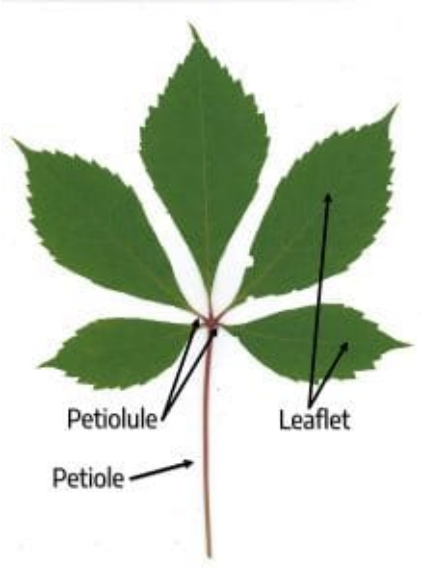
The sumac leaf is a good example of how a compound leaf has a blade that is completely interrupted and segmented into separate leaflets. What you see in the picture — the entire thing — is one leaf. The leaf is divided or segmented into leaflets.



Tree of heaven, (Ailanthus altissima) has pinnately compound leaves. Photo by Dr. Leslie J. Mehrhoff, CC BY 3.0.

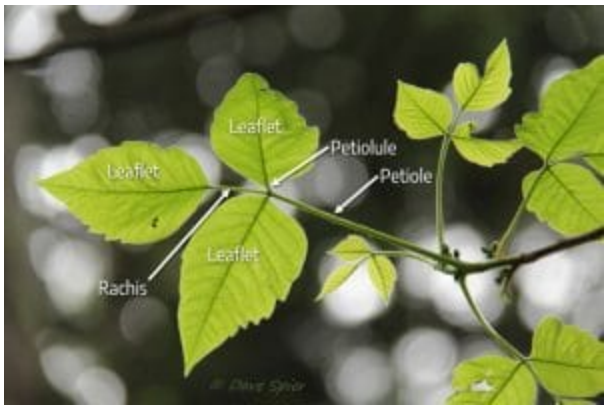
The petiole extends from the point of attachment at the node to the first leaflet. The central axis from that point on — from the first leaflet to the tip of the leaf — is called the rachis.

Virginia creeper is an example of a palmately compound leaf. The stalk that connects the leaflet to the top of the petiole is called the petiolule. In this case there is no rachis; all leaflets are attached directly to the top of the petiole.



Virginia creeper (Parthenocissus quinquefolia) has palmately compound leaves. Photo by Gavatron, CC BY-NC-SA 2.0.

Below is a compound leaf with three leaflets, called a **trifoliate** leaf. Soybean, clover, and dry bean all have trifoliate leaves. In contrast to the palmately compound leaf above, there is a rachis to which the central leaflet is attached.



Poison ivy (Toxicodendron radicans) has trifoliate leaves. Photo by DaveSpier, CC BY-NC-SA 2.0.

To tell whether a leaf is simple or compound, ook for attachment to a node. If the point of attachment doesn't appear to be a node, it is likely a leaflet attached to the rachis of a compound leaf.

Watch this video on compound leaves:

Additional optional reading

For more information about leaves, explore this Wikipedia page, starting about halfway down at the heading "Morphology (large-scale features)" and continuing through "Veins."

Review questions

- What advantage do angiosperm leaves have because they are flattened?
- What advantage do gymnosperm leaves have because they are needle-like?
- What is the difference between a simple leaf and a compound leaf?
- Is a petiolule found in a compound or simple leaf? To what structure does it attach?
- What is the difference between a leaf with palmate venation and a palmately compound leaf?
- Draw and label a picture of a leaf with these parts: rachis, petiole, petiolule, and leaflet.

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10.3: Shoots

Learning objectives

- Identify unique external features of shoots that distinguish them from roots.
- Locate the regions of origin for stems, branches, leaves, and inflorescences.
- Locate the regions of origin for stolons and rhizomes.
- Describe ways in which stolons and rhizomes are anomalies.



Small tomato plant in a pot. Photo by Daniel Morrison, CC BY 2.0

Shoots: Not only what's above the soil

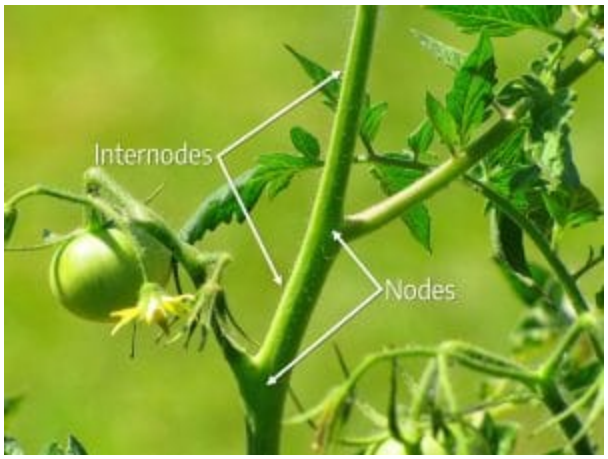
While it's generally true that the shoot of a plant is the part above the soil, there are exceptions; these will be explored below.

A shoot is made up of a central axis called the **stem**, and components that grow from specific places on that stem. The stem can be tall and thick in diameter, like in a sunflower, or quite compact and compressed, like in an onion, where the stem may never get above the soil surface. The stem can be rigid like a corn stalk or floppy like a watermelon vine. In each case, the stem is the central axis to which the other shoot components attach. The stem doesn't need to be upright; it can grow horizontally.

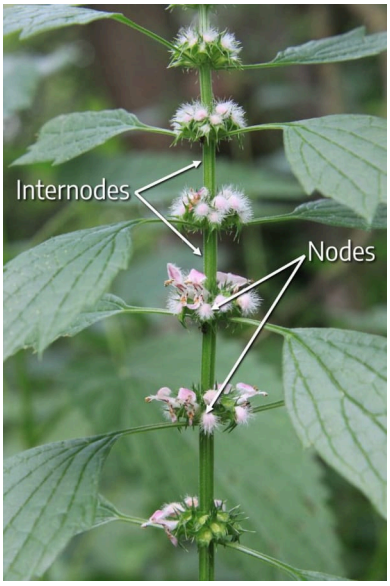
Watch this video to see examples and parts of shoots:

Nodes and internodes

The distinguishing external feature of a stem, and of the branches that arise from the stem, is its repeated node – internode – node – internode construction. A node is the place of origin on the stem for branches, leaves, and inflorescences. Sometimes the node is slightly swollen and obvious, other times not; it depends on the type of plant. Located at the nodes are buds (a colloquial term; later we'll call them meristems) made up of cells that, given the correct biochemical signal, will rapidly divide and grow into branches, leaves, or inflorescences. More than one bud can grow from a node, so a node can support several structures.



This tomato plant has clearly distinguishable nodes and internodes. Photo by Greyerbaby, CC0.



It's easy to see the nodes and internodes on motherword (*Leonurus cardiaca*). Photo by Emilian Robert Vicol, CC0.

In another chapter we will see how the plant stem has internal bundles of "pipes" that make up the vascular system through which water, nutrients, sugars, and other plant metabolites flow. At the nodes, some of these pipes diverge from the main bundle to provide nutrients, water, sugars, and other metabolites to the branches, leaves, and inflorescences that form at the node.

Between nodes are stretches of stem called **internodes**. One architectural function of the internode is to spatially orient the leaves, branches, and inflorescences. Long internodes, for example, will spread the leaves out along a stem so that they aren't shading each other as much as if the internodes were short. Nodes also help with leaf orientation.

The location of nodes determines whether the leaves are located, which is called leaf arrangement, and leaf arrangement is a characteristic of a particular type of plant.

- **Alternate** — the leaves are attached at nodes on alternate sides as they go up the stem.
- **Opposite** — the leaves grow directly opposite each other on the stem.
- **Whorled** — the leaves are oriented in a whorled formation in which their point of attachment appears to spiral up the stem.



Photos by (L to R) jlevinger, CC BY-NC-SA 2.0; John Tann, CC BY 2.0; Frank Vincentz, CC BY-SA 3.0.

Nodes are important because they are where leaves, branches, and inflorescences originate; the internodes are important because their length has a profound impact on plant architecture.



Goldenrod inflorescence. polyphemus_polly. CC BY-NC 2.0

With inflorescences, it can be difficult to tell where the stem stops and the inflorescence begins. One difference is that the stem has nodes and internodes, while the inflorescence does not.

What about vines?

Watch this video showing shoots, nodes, and internodes on vines.

What about grasses?

Take a look at this video to see node/internode structure on grasses. (Note: You can ignore the mention of a Wednesday class. This video is also used in an in-person class.)

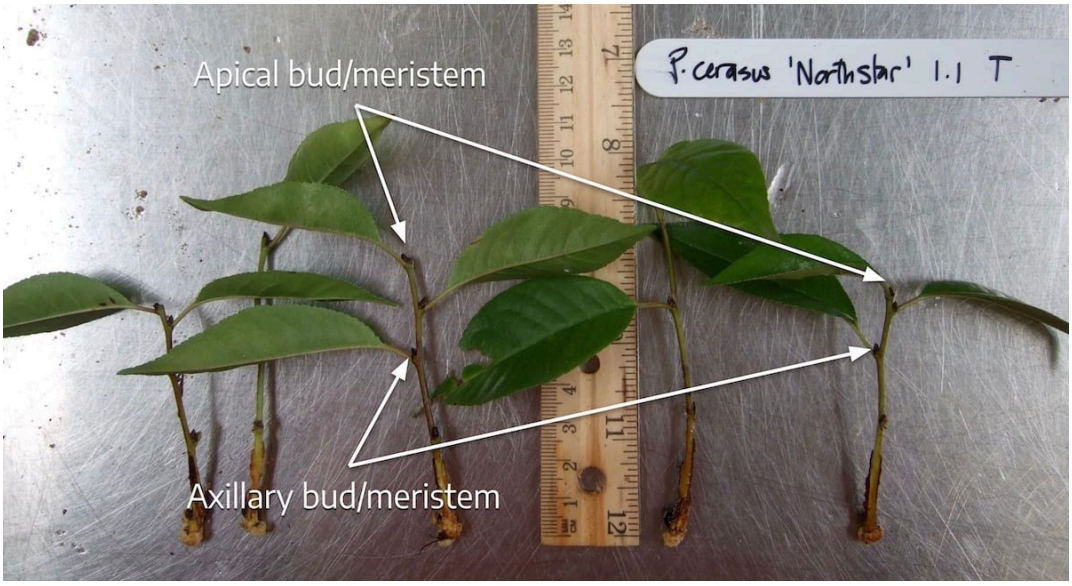
What about trees?

In this video, you'll see nodes and internodes on trees.

More about meristems

Watch this video to take a closer look at meristems.

The tip of the stem is called the apex, and the bud at the tip is called the apical bud, or apical meristem. In the image below, a bud has formed at the apex of the stem. This bud contains a meristem that will “break” or become active next spring and result in early season stem growth.



These cuttings of ‘Northstar’ cherry were collected from the tips of the twigs, and are called terminal cuttings. Photo by Emily Tepe.

The crotch formed between the leaf petiole (the stalk that attaches the leaf blade to the shoot stem) and the stem or branch is called the leaf axil, and the buds in that crotch are called axillary buds or axillary meristems. You can see two sets of axillary meristems in the image. If pruned above the axillary buds, the plant will grow from these nodes. Removing the apical meristem is one way to encourage branching. If you’ve ever grown basil, you know that snipping or pinching leaves off right above a node encourages more leaves to grow from that node. This function also gives plants a way to respond to feeding damage or injury by having dormant buds that can grow when prompted.

Review questions

- Looking a photo of a plant, can you identify the stem, nodes, and internodes?
- Can you recognize different types of leaf arrangements on different plants you see?
- Buds at the nodes can develop into one or more of three different structures. What are these three structures?
- What type of buds are found in the crotch between the leaf petiole and the stem?

Stolons and rhizomes

Stolons



Strawberry plants send out stolons which form new plants at the ends. Photo by Emily Tepe.

Some types of plants produce branches from nodes on the stem that are very close to, or right at, the soil surface. These branches, which have long internodes and lie on the surface of the soil, are called stolons. Not all plants produce stolons, but strawberry is a common example of a plant that does. The “runners” that extend out from the mature strawberry plant are in fact stolons. Stolons have the same typical repeating node/internode structure of a stem, but unlike other branches of the plant, at the nodes of the stolon, adventitious roots can form. Adventitious roots are roots that emerge from the stem rather than from roots. Even though they emerge from the stem above ground, they still act like roots. They anchor the stolon to the ground and absorb water and nutrients for the plant’s use. Leaves, and even branches, can also form from the stolon nodes.

One of the main purposes of stolons is to propagate a plant. The mature strawberry plant sends out a stolon and a new plantlet forms at the stolon node. Once the plantlet is rootedm you can cut the stolon internode between the plantlet and the main stem and transplant the plantlet. For instance, you can start a new patch of strawberry plants by cutting off these plantlets and planting them in a bed.



Potato plants produce underground stolons which swell to form the tubers we eat. oliva732000. CC BY-SA 2.0

Potato is another plant that produces stolons; in this case the stolons are often below ground rather than above the soil. Potato tubers (the part that we eat) are formed from swellings of these stolons. When we grow potatoes we mechanically hill soil up around the potato stem during the growing season to cover the developing tubers, preventing them from turning green and bitter from exposure to sunlight.

Rhizomes

Rhizomes are another type of stem tissue originating from a node. In this case it is typically a node that is below the surface of the soil. A rhizome also grows horizontally and has nodes and internodes, but unlike stolons, it is underground. The ginger in the produce section of the grocery story is misnamed ginger “root,” but is actually a rhizome, and you can tell that this is stem tissue because it has nodes and internodes. The nodes are the faint, slightly raised rings around the circumference of the rhizome. If you see nodes and internodes on a plant part, the tissue is stem tissue and not root tissue, even if it is underground.



Green shoots emerging from an iris rhizome. Science and Plants for Schools. CC BY-NC-SA 2.0

Rhizomes and stolons are the exceptions to the general notion that shoot tissue is above the soil surface. They are branches, complete with nodes and internodes, but are underground (rhizomes) or near the soil surface (stolons). They are stem tissue.

Turfgrass provides an example of rhizomes, stolons, and another structure typically associated with plants in the grass family called **tillers**. Here is an optional reading about those structures in turfgrass.

This video describes and shows an example of rhizomes.

Review questions

- What is the term for a horizontally growing stem that is near to or on the soil surface, and that can form adventitious roots at its nodes?
- What is the term for an underground, horizontally growing stem?
- What is one of the main purposes of stolons?
- What type of tissue are rhizomes, stolons, and tubers? Stem tissue or root tissue?

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10.4: Roots

Learning objectives

- Locate and identify characteristics of the primary root, lateral or secondary roots, and root hairs.
- Distinguish two major types of root systems and how they develop.

Roots

The general perception is that roots are the parts of the plant that are found in the soil. While this is typically true, there are exceptions, just as there are with the notion that all shoots are above ground. To recognize roots, we'll look at more than whether or not they are in the soil.



Types of plant roots. Gordon Johnson from Pixabay. Pixabay license

Unlike stems and branches, roots don't have a node/internode pattern of construction. There are no nodes, no internodes, no leaves, and no branching from regular spots, as you find with stems and branches. Roots do have structures but, in contrast to stems and branches, these structures emerge irregularly from the root according to where they are needed, and to some extent according to inherited tendencies, rather than emerging at specific zones the way leaves, branches, and inflorescences emerge from nodes on the stem.

Watch this video for a short intro to roots.

Purposes of roots

Anchorage

Roots keep the plant moored to the soil in a particular place. This "anchorage" not only facilitates other functions for the plant, but provides a benefit for the soil. An extensive root system helps hold the soil in place so that it is less likely to be eroded by wind or rain. Where there are roots the soil tends to be retained. No roots, and the soil easily gets washed or blown away. On the flip side, if conditions are poor the plant can't pull up roots and move somewhere else where prospects for growth are better.

Support

The roots, particularly the tap root that we examine below, provides the foundation for upright growth.

Absorption

Roots are the structure of the plant that absorb water and soluble nutrients..

Symbiotic interaction with other organisms

Roots of plants from the taxonomic family Fabaceae — which are commonly called legumes, and include plants like peas, beans, clover, and locust trees — can form a symbiotic relationship with Rhizobia bacteria. This results in nitrogen fixation, which allows for the conversion of nitrogen from the atmosphere into nitrogen compounds that the plant can use to produce proteins and other building-block molecules. For nitrogen fixation to occur, rhizobia require a plant host; they cannot independently fix nitrogen. These bacteria fix nitrogen after becoming established inside root nodules of plants in the Fabaceae family.

Roots also develop associations with Mycorrhizal fungi. In contrast to the Rhizobia bacteria, which only symbiotically interact with a narrow range of plants, Mycorrhizae (mycorrhizae is the plural of mycorrhiza) are fungi that grow in association with roots of a wide range of plants — perhaps most plants. The mycorrhizae help acquire phosphorus from the soil and make it available to the plants' roots. Mycorrhiza may also enhance water uptake.

Watch this video about symbiotic relationships between roots and soil organisms.

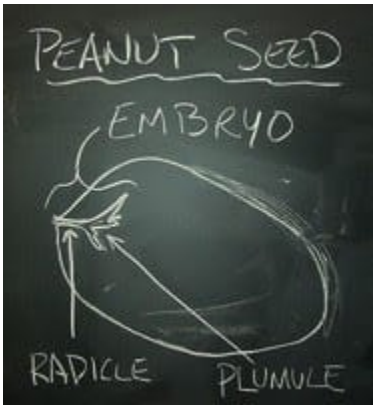
Nutrient storage

Roots of some plants can swell and store high-energy compounds like starch and sugar. Examples include carrots, beets, sweet potato — but not white potato. Roots also store some protein and other nutrients, but the focus is typically on high-energy carbohydrates.

Review questions

- What external features clearly differentiate roots from stems?
- What purposes do roots serve beyond absorption of water and nutrients?
- What are two examples of living organisms that symbiotically interact with roots? How do they differ in terms of the plants they infect and the benefits they provide?

Root systems

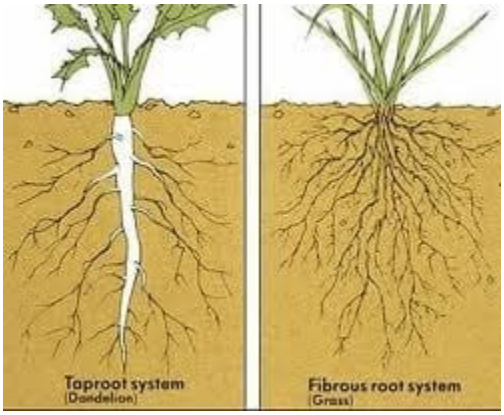


Peanut seed embryo. Image credit: Tom Michaels

A plant's root originates in the embryo formed within the seed. The section of the embryo that is root tissue is called the radicle (note the spelling). At the tip or apex of the radicle is a region of rapid cell division and growth called an **apical meristem** (you

may recall that shoots have an apical meristem too). As a result of the apical meristem's rapid cell division, the radicle grows down into the soil. The root that forms from the embryonic radicle is called the primary root. This sketch of half of a peanut seed shows the radicle that is part of the embryo inside the seed. The plumule is the embryonic shoot.

Shortly after germination and establishment of the seedling, plants generally develop one of two types of root systems: tap root or fibrous root.



"File:Tap and fibrous root.jpg" by Cassandra gonzales is licensed under CC BY-SA 4.0

Watch this video to see the differences between tap roots and fibrous roots.

Tap root systems

The tap root is persistent, meaning that it is retained throughout the life of the plant; it is also defined as a strong primary root that grows downward into the soil. This tap or primary root is the central axis off of which lateral or secondary roots branch in irregular patterns in response to the availability of high-quality soil — soil with adequate moisture, nutrients, and favorable soil structure (proper particle aggregation and pore space that fosters gas exchange and moisture retention).



Dandelion is an example of a plant that has a tap root. See the taproot and many small secondary roots. Science and Plants for Schools, CC BY-NC-SA 2.0

Lateral or secondary roots typically grow relatively parallel to the soil surface, while the primary or tap root grows perpendicular to the soil surface. Tertiary roots branch off of secondary roots, again in response to nutrient and moisture availability.

A tap root system provides strong leverage and anchorage in the soil. If firmly connected to an upright stem, the tap root can resist uprooting by wind whipping at the shoot and herbivores yanking on the leaves and branches. Both the pigweed and the

velvetleaf pictured here are tall, upright plants. The strong taproot helps provide the underground leverage to hold those plants upright.

Fibrous root systems

Fibrous root systems begin the same as tap root systems...with a radicle growing from the seed. However, after a period of early growth, the radicle or primary root stops growing (or slows its growth) and roots begin to form from the stem tissue that is underground, but just above the primary root. These roots emerging from stem tissue are **adventitious** roots — indicating that the roots emerge from the main stem.



Red and white onions. Alice Henneman. CC BY 2.0

In beans there are two types of adventitious roots. The roots that emerge from the region just above where the main stem stops and the root begins are called basal roots (basal because they are at the base of the main stem). The roots that emerge above these basal roots are called hypocotyl roots. As we'll see in a later chapter, the portion of the stem just above the root-shoot transition zone is called the **hypocotyl**. Adventitious roots that contribute to the fibrous root system stay close to the soil surface. Fibrous root systems are excellent at holding soil in place because they are thin, extensive, and weblike. This is why various types of grasses, which have fibrous root systems, are planted in areas that are subject to erosion from flowing water following rains. The fibrous root systems of the grasses, once established, hang on to the soil particles like a web of very thin, interlaced fingers.

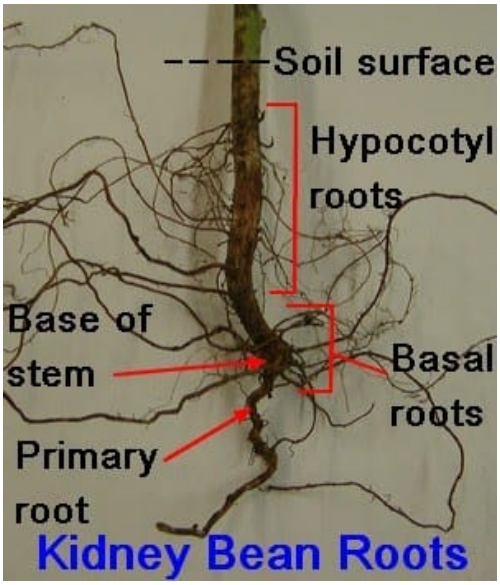
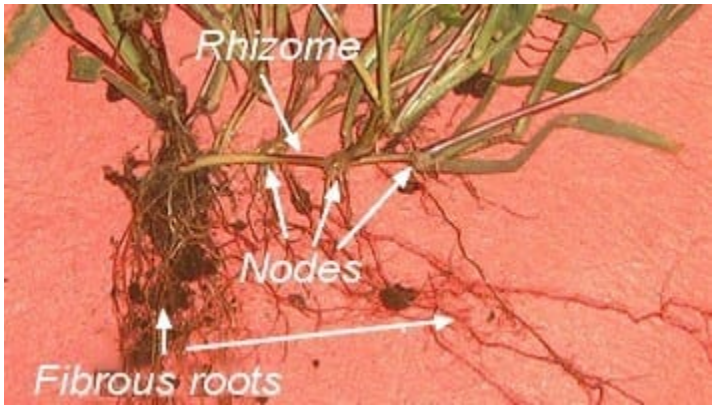


Photo credit: Tom Michals.

The kidney bean root system pictured above has been growing for a few weeks. You can identify the soil line on the stem by where the stem coloration transitions from green to cream or buff color. The root doesn't start immediately after the stem enters the soil. Instead, the stem continues underground for about an inch. Notice the point where the width of the stem drastically reduces; this is where the primary root tissue starts. Again, the primary root traces directly back to the radicle, which is part of the embryo

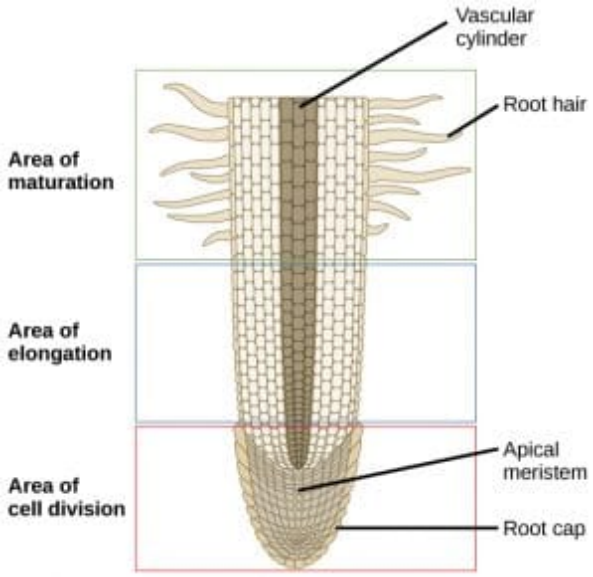
in the seed. Just above where the root starts are the basal roots, and above these are the hypocotyl roots. As noted above, basal and hypocotyl roots are adventitious roots, as they emerge from the stem.



Rhizome of Echinopogon ovatus. The roots emerging from nodes indicate the rhizome is stem tissue.

In this picture of *Echinopogon ovatus*, known as hedgehog grass in its native Australia, you can see the rhizome or underground stem that is typical of spreading grasses. Note the nodes on the rhizome, which indicate that it is shoot tissue, not root tissue. Also note that the roots emerging from these nodes. The roots are adventitious because they emerge from shoot tissue rather than from the primary root (which disintegrates early in the growth of grasses). Shoot tissue often also emerges from these nodes.

Both tap root systems and fibrous root systems rely on root hairs to gather moisture and nutrients. Root hairs are extensions of the outer layer of cells (called the **epidermis**) of young roots. Root hairs live for only a few weeks, deteriorate, and are then replaced by fresh root hairs.



Areas of a root. CNX OpenStax, CC BY 4.0 International

Corn (below) provides another example of adventitious roots. In this case, the roots are formed from shoot tissue above the soil and then angle down toward the soil. These are the “brace” or "prop" roots of corn. Sometimes they reach the ground, and other times they hang in the air. The roots that reach the soil branch extensively and are important for moisture and nutrient absorption. Below is a photo of the adventitious brace roots of *Prunella vulgaris*.



Adventitious prop roots on corn plant. Krish Dulal, CC BY-SA 3.0



“Self-heal (Prunella vulgaris) showing stolons and adventitious roots” by Science and Plants for Schools, CC BY-NC-SA 2.0

Review questions

- What is the difference between a tap root system and a fibrous root system?
- From what cells on young roots do root hairs form?
- What is the radicle? Does it persist in all mature plants?

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10.5: Terms

These are the important terms from this chapter to be sure to know. You might also find these in later chapters.

Adventitious	Tissue arising from an organ other than expected.
Adventitious roots	Roots that emerge from the stem rather than roots.
Alternate leaves	Leaves are attached on alternate sides as they go up the stem.
Apex	Tip of the stem.
Apical bud	Bud located on the tip of the stem.
Apical meristem	Group of more or less continually dividing cells located at the tip of a shoot or root.
Axil	Upper angle between a lateral structure and the stem to which it is attached.
Axillary bud	Bud borne in the axil of a stem.
Axillary meristem	Group of more or less continually dividing cells located at the axils of a stem.
Basal root	Root that emerges from the region just above where the main stem stops and the root begins.
Bract	Leaf attached to the terminal node, which is part of the inflorescence rather than the stem. It may also be found at the base of each pedicel.
Branch	Vegetative growth coming from a node on the main stem.
Bud	Immature vegetative or floral shoot or both, often covered by scales; also called a meristem.
Chlorophyll	Green photosynthetic pigment found in plants, algae, and cyanobacteria that captures light for photosynthesis.
Compound leaf	Leaf with a blade margin that is completely interrupted and segmented into separate leaflets.
Fibrous root	Root system where the radicle grows and then rapidly slows or completely halts in growth. Once this happens, roots will emerge above the radicle and from the stem tissue located below the soil.
Hypocotyl roots	Roots that emerge above the basal roots.
Internode	Stem regions between nodes in plants.

Lamina	Another name for a leaf blade.
Lateral or secondary roots	Roots that extend horizontally from the primary root and serve to anchor the plant securely into the soil. This branching of roots also contributes to water uptake, and facilitates the extraction of nutrients required for the growth and development of the plant.
Leaf	A usually green, flattened, lateral structure attached to a stem and functioning as a principal organ of photosynthesis and transpiration in most plants.
Leaf axil	Upper angle between a leaf petiole and the stem to which it is attached.
Leaf blade	Broad portion of a leaf; does not include the petiole.
Leaf margin	Edge of the leaf blade.
Leaf primordia	Young leaves, recently formed by the shoot apical meristem, located at the tip of a shoot.
Leaf scar	Mark indicating the former place of attachment of petiole or leaf base.
Leaf sheath	Structure where the blade attaches to an envelope of leaf tissue that wraps around the shoot of the plant and attaches to a lower node on the stem.
Leaflet	Small leaf-like structure that is found on compound leaves. Multiple leaflets make up a single compound leaf.
Lenticel	Small opening in the cork of woody stems that allows for gas exchange.
Meristem	Group of continuously dividing cells; also called a bud.
Midrib	Main vein, generally in the center of the leaf, from which secondary veins emerge.
Node	Stem region of a plant where one or more leaves attach; location of lateral buds.
Opposite leaves	Leaves that grow directly opposite each other on the stem.
Palmate venation	Where several veins radiate from the point where the petiole attaches to the blade. The veins fork, travel a bit, fork again, travel, fork, and so on until they reach the margin of the leaf.
Palmately compound leaf	Compound leaf where the petiolules of the leaflets connect directly to the petiole (no rachis).
Parallel venation	Distribution or arrangement of a system of veins in a leaf blade in a non-intersecting network. The veins are parallel to each other and the long edge of the leaf.
Petiole	Stalk by which most leaves are attached to a stem; part of the leaf structure, not the stem.

Petiolule	Stalk that connects the leaflet to the top of the petiole.
Pinnate venation	Type of webbed venation where there is a strong midrib and the secondary veins fan out opposite one other.
Pinnately compound leaf	Compound leaf where the leaflets are arranged opposite one another on the rachis.
Primary meristem	Apical meristems on the shoot and root apices in plants that produce plant primary tissues.
Primary root	Root that forms from the embryonic radicle.
Prop root	Adventitious root that arises from the stem, penetrates the soil, and helps support the stem, as in corn.
Radicle	Embryonic root that breaks through the seed coat during germination and develops into the seedling's root system.
Rhizome	Horizontal stem growing just below the soil surface.
Root	Organ that anchors the plant into the soil, takes up water and nutrients, and stores food.
Root hair	Thin, hairlike outgrowth of an epidermal cell of a plant root that absorbs water and minerals from the soil. Root hairs live for only a few weeks, deteriorate, and are then replaced by fresh root hairs.
Sessile	When a leaf lacks a petiole; called a sessile leaf.
Shoot	Made up of a central axis (stem) with a repeating pattern of nodes and internodes.
Simple leaf	Leaf with an uninterrupted blade margin.
Stem	Supporting and conducting organ usually developed initially from the epicotyl and growing upward, and consisting of nodes and internodes.
Stipule	Usually a pair of appendages located at the base of a leaf but may be fused into a ring around the stem; variable in size, shape, and texture; serves for protection or to attract pollinators.
Stolon	Stem with long internodes that grows along the surface of the ground.
Storage root	Root that is modified for storage of nutrients, such as carrots and beets.
Tap root	Main root of a plant, usually stouter than the lateral roots and growing straight downward from the stem.
Terminal bud	Bud located at the apex of a stem.

Trifoliate leaf	Compound leaf with three leaflets that attach to a rachis.
Tuber	Swollen, underground, modified stems that store food.
Venation	Pattern of veins on a leaf.
Whorled leaves	Leaves oriented in a whorled formation in which their point of attachment appears to spiral up the stem.

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10.6: Vascular plant anatomy- primary growth

Learning Objectives

- Define primary growth and explain its origin from root and shoot apical meristems.
- Describe the basic anatomy of flowering plants as it relates to primary growth.
- Identify key tissues and structures formed during primary growth in roots and shoots.
- Explain how developmental changes occur as a plant ages and grows away from the apical meristem.

As described in Chapter 6 the three organs of vascular plants (roots, stems and leaves) have the same basic structure: a boundary of dermal tissue enclosing ground tissue that has one too many strands of vascular tissue running through it. The three organs differ in the distribution of vascular tissue: in roots it occurs as a single central strand; in stems, the vascular tissue occurs as multiple bundles imbedded in ground tissue; and in leaves the vascular tissue often occurs as a reticulate network of veins or as parallel strands of vascular tissue. In both cases there is ground tissue filling the space between vascular strands and dermal tissue. This basic anatomy is easily seen in asparagus if one trims the base and looks at the cut end, the dermal tissue is the tougher outside, the vascular bundles are seen as small circles scattered in the outer portion of the stem, and ground tissue makes up the rest. Roots and shoots show two polarities, a radial polarity, meaning that tissues and cells differ as one moves outward from the center (along a radius), and a proximate/distal polarity, meaning that cells at the tips of organs, where they are produced, differ from cells away from the tip, cells which are older. Leaves have a tip to base polarity and often have a top/bottom polarity.



Figure 1 Germinating sunflower seeds. The tip of the shoot is between the two leaves (cotyledons). The junction between the root and stem is at the soil surface. Note that the root of the seedling in the foreground is (atypically) running horizontally. and showing numerous root hairs

In this chapter, we describe in more detail the plant anatomy of flowering plants resulting from primary growth (growth derived from root or shoot apical meristems), and consider the developmental changes and consequently the patterns shown with age (distance from the apex).

TOPICS

- Root development
- Mature root anatomy
- Shoot development

- Mature shoot anatomy
- Leaf development
- Leaf anatomy

Root Development

If a root is sectioned along the long axis (i.e., a longitudinal section) its developmental pattern is readily apparent. Near the tip is the meristem, recognized by the small size of cells and by mitotic activity , often evidenced by the appearance of chromosomes. Moving back from the tip (proximally, towards the plant body) one encounters older and more mature cells, recognizable because they are larger, no longer dividing , and possess features that distinguish different cell types, e.g., secondary cell walls of tracheids and vessel tube members. Because there is no more cell division or expansion after one moves a short distance from the root apex , the diameter of the root showing only primary growth is generally constant along its length , except for the terminal few millimeters. (Roots exhibiting secondary growth do increase in diameter and are discussed in the next chapter). Cells that are produced by the root apical meristem expand the most in a distal/proximal direction (up/down, assuming the root is vertical) and produce cells that are elongate in this direction. There is much less expansion radially, hence roots primarily grow longer, not wider and this growth occurs near the root tip. Even more significant than the expansion of individual cells is the fact that most cell divisions in the meristematic zone divide cells in cross-section, so most of the additional cells that the meristem produces are in the longitudinal (distal/proximal) plane. This is similar to how a unicellular filament divides to extend itself, with cell divisions that are perpendicular to the long axis of the filament. Cell divisions in the root apical meristem adds cells in the distal direction and only to a limited extent do roots add cells radially. M ost roots are roughly 20 to 100 cells wide (a ssuming only primary growth) but roots are often millions or trillions of cells long.

Assuming a cell division that adds to the number of cells in the distal/proximal plane, a second key consideration following cell division is whether the cell that remains meristematic (and does not grow) is distal (towards the tip) or proximal (towards the rest of the plant). In the vast majority of cell divisions of root meristematic cells, the cell that remains meristematic is distal, and the expansion of the other cell pushes the meristematic region into the soil. However, in a small portion of cells it is the proximal cell that remains meristematic and the distal cell matures and becomes part of the protective root cap, located at the extreme distal end of the root. The cells of this root cap are continually sloughed off as the root extends through the soil, and the root cap ensures that meristematic cells themselves are not sloughed off.

Developmental changes in primary root growth

Proceeding proximally from the root tip one encounters the following regions which transition gradually and overlap:

- zone of cell division, the embryonic region, often less than one millimeter
- zone of cell expansion, generally only a few millimeters in extent, a region where cells are elongating, and to a much lesser extent, getting bigger in diameter;.
- zone of cell maturation, a region where cells develop characteristic features. This zone extends from less than a cm to several cm in length. In the youngest part of this zone root hairs are produced but they soon senesce and are lost from the plant

Significant aspects of cell maturation zone include (in order from the tip as one moves proximally):

- conducting elements of the phloem become functional
- the waterproof compound suberin is deposited as a **casparian strip**
- conducting elements of the xylem become functional
- root hair appearance and disappearance. Root hairs are extensions off of dermal cells. They are produced after these cells have stopped elongating but are present for only a short time before senescing. Hence, root hairs are only present in a relatively small section of the root.

The significance of the casparian strip

These hydrophobic deposits initially occur as a band that blocks water movement through the wall from the outside to the inside. Eventually the entire endodermal cell wall is coated. The casparian strip forces water and any minerals dissolved in water to enter the cytosol at some point in their journey between the soil and the xylem tissue. Before the casparian strip is deposited, i.e., in the youngest part of the root, water can move from the soil to the center of the root through the ' **apoplast** ' , a term that describes the collective space of cell walls and any water filled spaces between cells, which typically includes at least 10% of

the tissue volume. Because the endodermal cells are tightly bound to each other, once the casparian strip is deposited water is forced to move through the **symplast** in order to cross the endodermis and get to the interior of the root. The symplast is a term that describes the collective volume of the cytosols of all cells, collective because all cells are interconnected by plasmodesmata, membrane bordered cytoplasmic threads that run between cells.

The casparian strip of the endodermis, once deposited:

1. allows the plant to regulate what minerals do and do not enter the xylem tissue, the conduit to the top of the plant
2. allows the plant to, under certain conditions, concentrate solute concentrations in the root xylem because the apoplast solution inside the endodermis and connected to the xylem tissue is separated by a two membranes (one providing entry into the symplast, one providing exit from the symplast) from the apoplast solution outside the endodermis that is continuous with the soil
3. **decreases** the ease with which water can move from the soil to the root xylem.

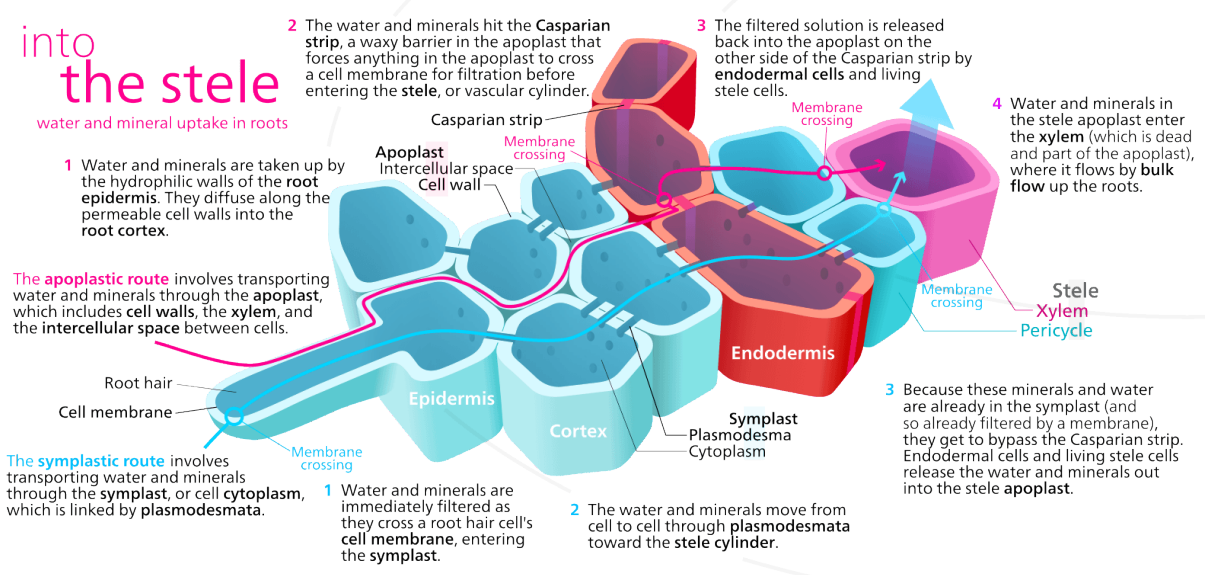


Figure 2 Diagram of a root showing root hair, epidermis, cortex, endodermis and stele (central core of vascular tissue). Traced in blue is a symplastic route for water to move from the soil to the stele. Traced in red is an apoplastic route except for where the casparian strip of the endodermis forces water to enter the symplast.

Role of root hairs

Root hairs appear when of the epidermal cells produce a thin outgrowth, called a root hair, that extends perpendicularly from the root into the soil. The root hair is thin (~ 10 um) but may extend several mm into the soil. As discussed earlier , although root hairs greatly increas e the area available for water and nutrient absorption , their more significant effect might be in increasing the volume of soil within certain distance to the root. Considering root hairs, w ater/nutrients may :

- enter the cytosol of the root hair and then proceed inwards through the symplast
- enter the cell wall of the root hair and move through the apoplast to the interior of the roo t (note that once the casparian strip is deposited in the endodermal cell walls, this root is blocked
- move through the soil to the root proper, by-passing the root hair

For moist soils water may move most quickly through the soil rather than using the routes involving the root hairs and it is possible that root hairs may be most significant in nutrient absorption rather than water absorption

Mature root anatomy

A typical root cross section shows dermal tissue on the outside, surrounding a region of ground tissue (the cortex) which surrounds the endodermis, recognizable because the suberized layer of the cell wall picks up stain. Just inside the endodermis is the pericycle, a ring of parenchyma cells which can be stimulated to form root apical meristems that grow out of the root to form lateral roots. Inside the pericycle is the vascular tissue which is arranged differently in different roots. Some roots have a central

pith of parenchyma cells while most roots have a central, solid core of vascular tissue.

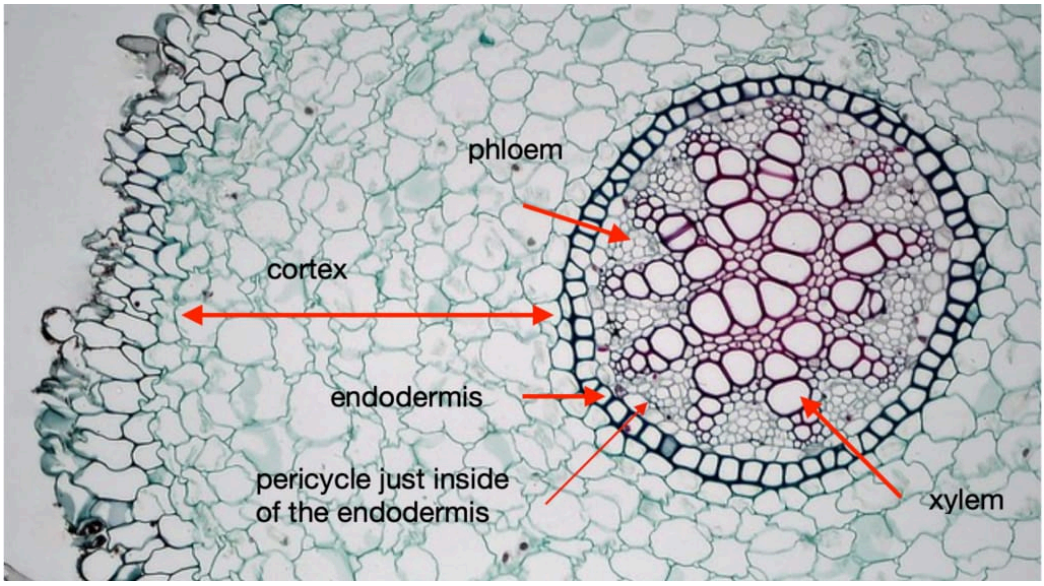


Figure 3 Cross section of a mature root.

Shoot Development

The basic pattern of development for shoots is the same as that for roots: a terminal region of cell division above a region of cell growth above a region of cell maturation. But shoot growth is more complicated than root growth in several ways, one is the fact that shoot apical meristem not only extends the stem but it also produces embryonic leaves (leaf primordia) and branch shoots (bud primordia) positioned just above the leaves. The presence of these structures divides the stem into nodes, the places where leaves connect with the stem, and internodes, the spaces between nodes. Both of leaf and bud primordia develop vascular tissue that needs to be connected with the vascular tissue of the main stem. If one were to follow the vascular tissue in a leaf or a branch back to the main stem, one would observe one or more bundles of vascular tissue extending from the leaf/branch to the stem. This accounts for the presence of 'vascular bundles' in the stems of flowering plants: fundamentally they represent the traces of vascular tissue running to the leaves and branches. At the nodes one can see vascular traces diverging from the stem to enter leaf and branch primordia. Ferns, horsetails, clubmosses and a number of fossil plant groups have different patterns of vascular tissue distribution within the stem (described as 'stelar structure') and, because vascular tissue is often represented in fossils, its distribution has been useful in classifying fossilized vascular plants.

Leaf primordia are produced in a characteristic pattern that depends upon the species of plants. The most easily described pattern is one where leaves are produced in pairs on opposite sides of the stem. S equentially, leaves are produced in pair s occur ring with a 90 ^{o} rotation from the previous pair of leaves, i.e., if you were viewing a stem from the top and the first pair of leaves were north and south the next set of leaves would be east and west. The next set of leaves produced would be back to the original north-south orientation. Most plants have a more complicated **phyllotaxy** , i.e., arrangement of leaves, that can be described by counting the number of new leaves and the number of rotations around the stem before you end up with a leaf directly under another leaf.

While the elongation of roots, brought about the expansion of newly produced cells, is generally consistent in time and space, occurring soon after cells are produced and very close to the root apical meristem, elongation of stems is not as consistent. Elongation of shoots results from extension of the internodes. In some plants, internode growth occurs close to the shoot tip, resulting in a stem with leaves that separate from each near the tip of the shoot and at a pace consistent with the production of new leaf primordia. In other plants internodal growth is delayed or absent, producing very short stems with multiple leaves very close together (rosettes). Such a structure may be permanent or may be temporary until a particular cue is received and the stem 'bolts' , rapidly elongating by increasing the space between leaves, e.g., in spinach. Some monocots (see below), in particular grasses, have meristematic zones at the nodes of stems and at the base of the blade of the grass leaf. This meristems are activated if the stem or leaf above them is damaged (usually from grazing).

In contrast to roots, there is no maturation of cells on the distal side of the shoot apical meristem, i.e., there is no 'shoot cap' (cf. the root cap) derived from the apical meristem. Generally, the shoot apical meristem is not being pushed through the soil so

the function that the root cap provides is not generally required. However, the shoot apical meristem is covered by young leaves which grow very close to the tip of the shoot and are able to cover it. Some stems, called rhizomes, do grow through the soil and they are protected by modified leaves called cataphylls that protect the shoot apical meristem and form a pointed structure that can more easily be pushed by growth through the soil. Similar modified leaves, called bud scales, cover the shoot apical meristem of woody plants during the extended periods when they are not growing. While roots often are actively growing much of the year and certainly all of the growing season, shoot growth for plants in seasonal habitats is often much less extensive. Many plants, especially trees, exhibit growth (extension of stems) for only a short period, often less than 30 days. Often cell division occurs much earlier than cell growth, often as much as eight months earlier.

Mature shoot anatomy

Traditionally, flowering plants were separated into two groups, monocots and dicots, based on a number of features, one of which was stem anatomy. While the monocot group is still considered to be a valid phylogenetic entity, most workers consider 'dicots' to be an artificial grouping, and have separated dicots into 'eudicots' and several other groups. The vast majority of the former dicot group are eudicots and in the discussion below we will use the term dicots.

Dicot stems have vascular bundles arranged in a ring close to the margin of the stem. The tissues running from the outside to the inside are: epidermis, cortex, vascular bundles (in a ring), with variable amounts of ground tissue in between the bundles), pith.

Monocot stems differ from dicot stems in having vascular bundles scattered throughout the stem.

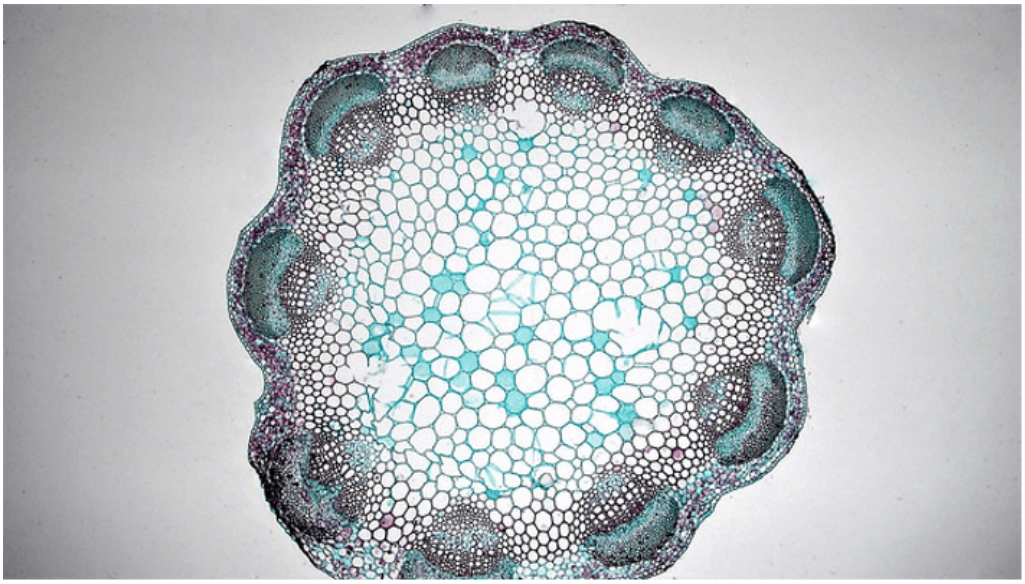


Figure 4 Clover (Trifolium), a dicot, stem, showing vascular bundles arranged in a ring with a large central pith. Vascular bundles have sclerenchyma cells to the outside and phloem and xylem tissues as one moves inward.

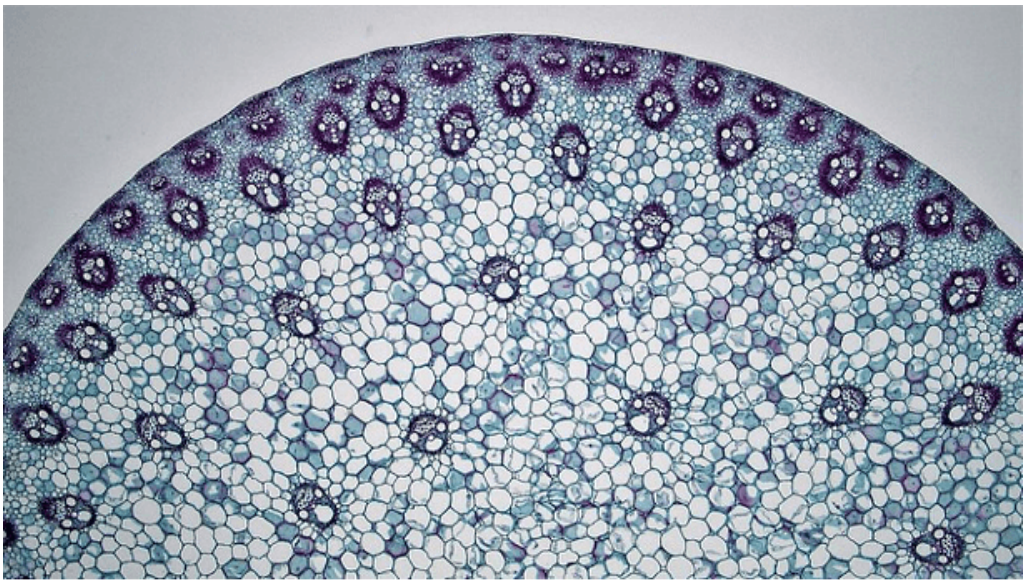


Figure 5 Zea (corn, a monocot), stem cross section showing numerous vascular bundles embedded in ground tissue.

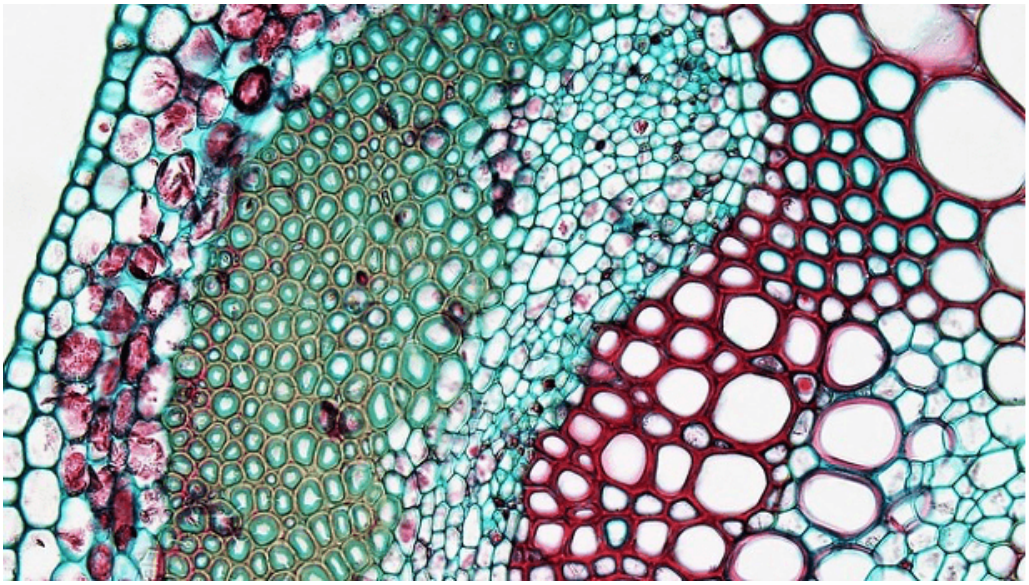


Figure 6 Outer section of dicot stem showing as vascular bundle. Moving from the outside: dermal tissue, cortex, sclerenchyma (stained greenwith thick walls), phloem tissue (stained blue), xylem tissue (stained red with thick cell walls)

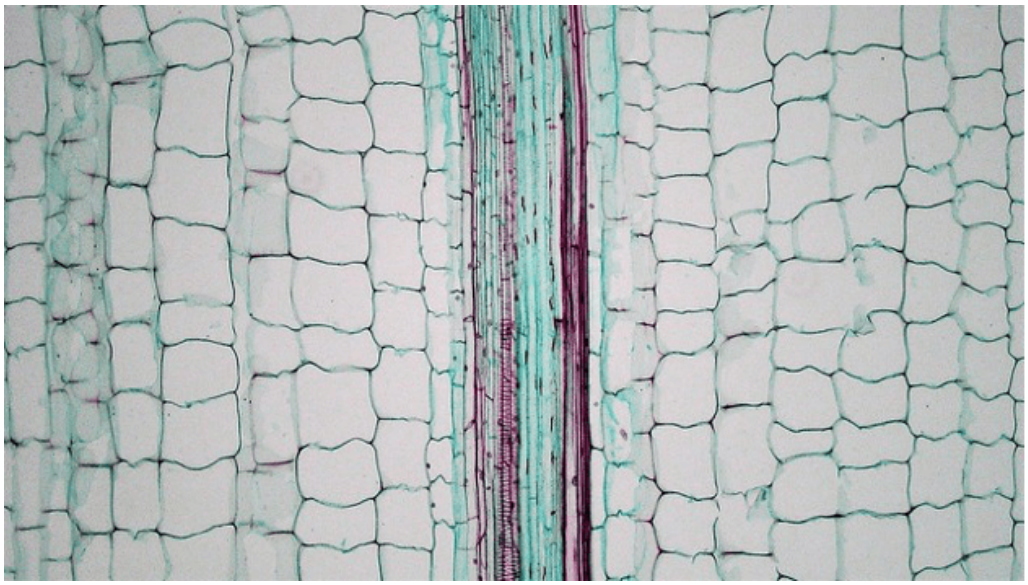


Figure 7 longitudinal section of stem showing vascular bundle with red stained cells. This in enlarged below.

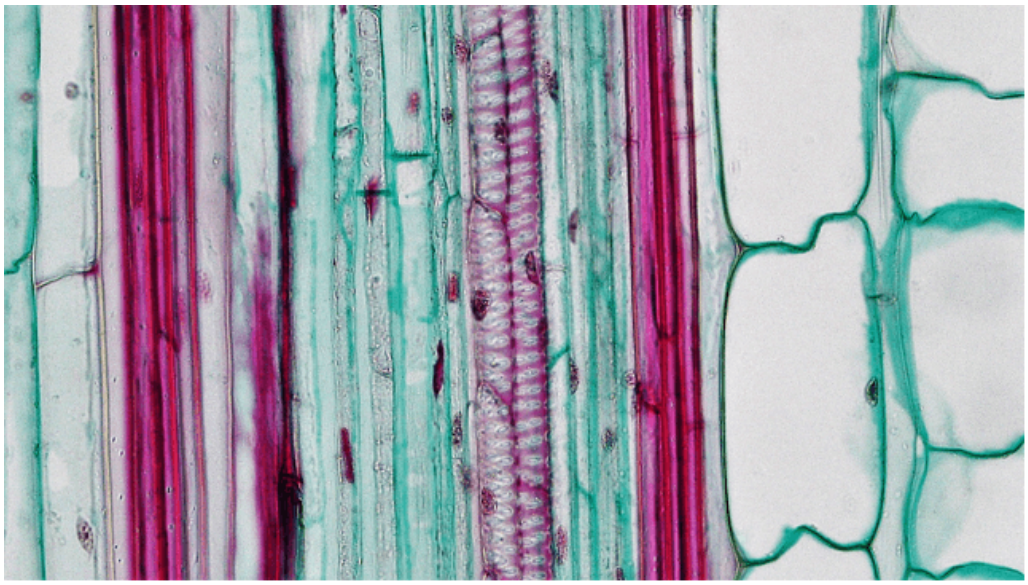


Figure 8 Longitudinal section showing vessels Note that typically the secondary cell wall of vessel tube members is not laid down continuously and often occurs as rings, or spirals. Also stained red a sclerenchyma fibers whose secondary walls are laid down continuously.

Leaf development

Unlike roots and shoots, leaves are determinate structures whose developmental pattern is comparable to humans and frogs. They start as an embryo called a leaf primordium whose cells both divide and subsequently grow for a defined period of time to produce a three-dimensional form that is often substantially more complex than the cylindrical structure of roots and stems. Moreover, the diversity in leaf form found in vascular plants, especially for flowering plants, far exceeds that found in roots or stems. After cellular division and growth cease, the leaf remains in an 'adult' form for a (generally) defined period of time before it undergoes its final developmental process of senescence that ultimately results in the leaf's separation from the plant (abscission). Leaf senescence and abscission will be discussed later but it is important to emphasize here that these developmental processes are highly significant to the life of the plant.

Intercalary meristems are present in some leaves, in particular grass leaves, and allow a leaf whose tip (distal portion) has been grazed to resume growth and replace lost photosynthetic area. The ability to grow in this manner has been particularly important to the success of grasses.

Leaf structure

Many leaves show a polarity between the upper surface and the lower, with the lower epidermis having stomata while the upper surface does not. Additionally, the ground tissue of the upper part of the leaf is layered with cells that are oriented parallel to ea ch other (this region is called the palisade mesophyll) while the mesophyll cells of the lower part of the leaf (called the spongy mesophyll) has cells that are not oriented in a consistent way relative to each other and have much larger air spaces between individual cells. Many monocot leaves have veins that run parallel to each other and this means that if you cross section the leaf you are likely to see cross sections of all the vascular bundles. In most dicot leaves the veins run at various angles and a cross section through the leaf is unlikely to show cross sections through any other bundle except the main central vein.



Figure 9 Lilac leaf showing upper and lower epidermis, the central vein in cross section with red stained vascular tissue, a palisade layer that is general two rows of cells and a spongy mesophyll layer.

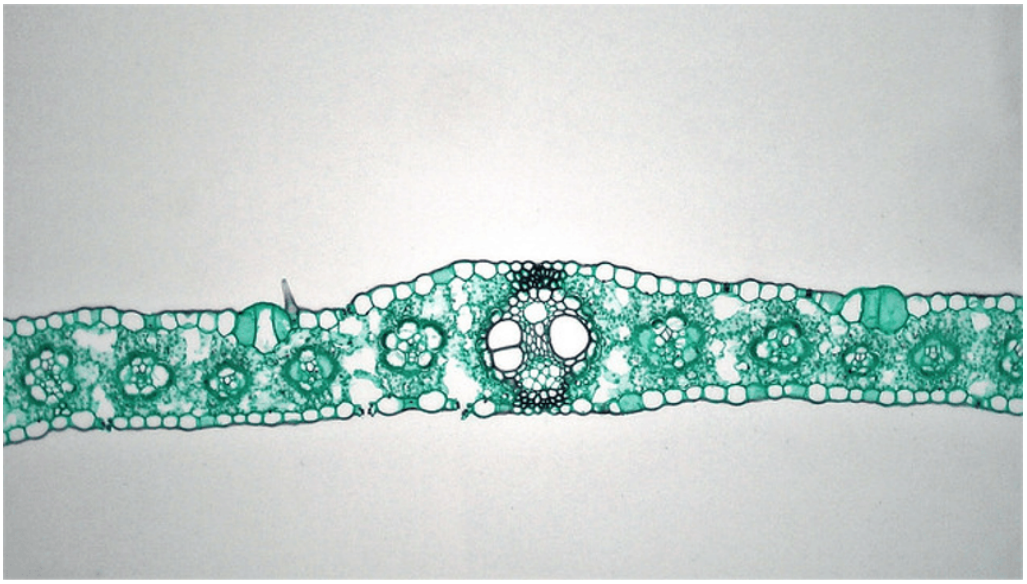


Figure 10 Cross section of corn leaf showing multiple vascular bundles and a mesophyll that is not split into palisade and spongy components.

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10.7: SECONDARY GROWTH

Learning Objectives

- Learn the sequence of development of meristems and tissues in secondary growth
- Understand the tradeoffs (costs and benefits) of secondary growth
- Identify anatomical features of woody stems
- Determine the age of a tree based on annual growth rings

10.7.1: Introduction

10.7.2: Secondary Tissues in the Root

10.7.3: Flowcharts of Development

10.7.4: Secondary Tissues in the Shoot

10.7.5: Dendrochronology

Contributors and Attributions

- Maria Morrow (College of the Redwoods)
- Thumbnail: Tilia stem cross section.

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10.7.1: Introduction

The two questions you answered above are essential to understanding the evolution of **secondary growth**. In secondary growth, primary tissues and residual meristematic tissues produce secondary meristems, which then produce secondary tissues. Whereas primary tissues allow for vertical growth, secondary tissues allow for lateral growth: they allow stems and roots to become wider. How might this impact the ability of a plant to grow taller?

In addition to growing wider, secondary growth exchanges the living epidermis for a thick layer of dead, waterproofed cells called cork. The cork and a few other layers of tissue comprise something called the periderm, or perhaps more familiarly called **bark**. Consider the tradeoffs between having a living exterior with guard cells vs. a thick layer of waterproofed dead cells. How might this impact the ability of the plant to interact with the outer environment? How might this impact the ability of the outer environment to interact with the interior of the plant?

Variations on this type of growth appear in a few places, but the evolution of gymnosperms (conifers and their relatives) is when the more typical secondary growth appears in evolutionary history. As you will see in later labs, the gymnosperms evolved during a period in Earth's history when inland seas were drying out and plants were migrating further from the water. This group of plants is specialized for growing tall (think Coast redwoods) or living in harsh, low-water environments. As a general rule, monocots do not undergo secondary growth, so this lab will only address eudicots.

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10.7.2: Secondary Tissues in the Root

In roots, the formation of both secondary meristems involves the pericycle. The pericycle and some **residual procambium** join together to form the **vascular cambium**, a secondary meristem that produces vascular tissue. The other secondary meristem, the **cork cambium**, is initially formed solely from the pericycle.

Each of these secondary meristems divides in two directions to form a different secondary tissue to the inside and outside of the meristematic layer, respective to the center of the plant.

The vascular cambium produces **secondary xylem** to the inside of the root and **secondary phloem** to the outside.

The cork cambium produces **phelloderm**, a storage tissue, to the inside of the root and **cork**, a protective layer of dead, suberized cells, toward the outside. These three layers -- phelloderm, cork cambium, and cork -- are referred to as a **periderm**. As the first periderm layer is formed, it separates the epidermis, cortex, and endodermis from the conductive tissues of the root. The epidermis and cortex cells die and are shed as secondary growth proceeds.

> The pine root below has one layer of periderm fully formed. Can you label the tissues and meristems described above? What are the large holes in the root?

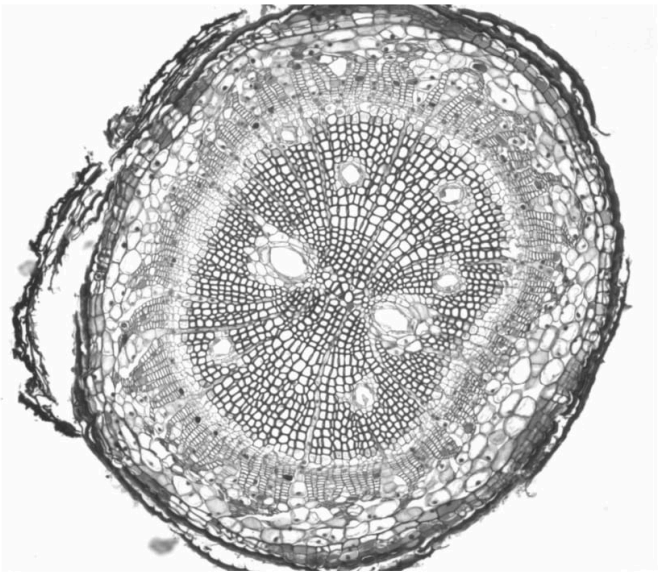


Figure 10.7.2.1: Pine Root Cross Section

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10.7.3: Flowcharts of Development

Below are two flowcharts. The upper represents the pathway of development in the shoot, while the lower represents the development of the root. Both of these include secondary growth. Fill in the missing pieces of each flowchart.

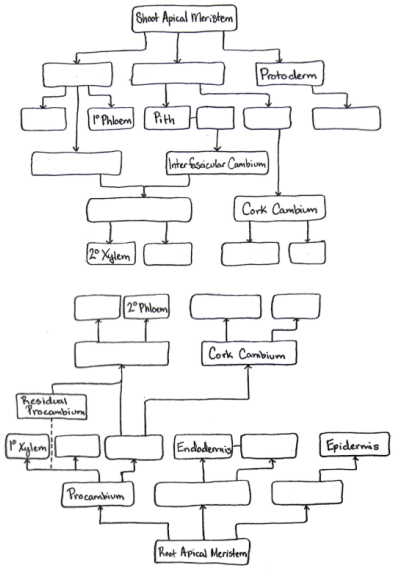


Figure 10.7.3.1: Flowchart of shoot development

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10.7.4: Secondary Tissues in the Shoot

Secondary Vascular Tissue

Though the secondary tissues are all the same, the sequence of secondary meristem development in shoots is a bit different than in roots. Shoots have no pericycle, so the secondary meristems must be formed from different tissues. In shoots, the vascular cambium is formed from residual procambium within the vascular bundles (**fascicular cambium**) joined by tissue in the pith rays (**interfascicular cambium**).

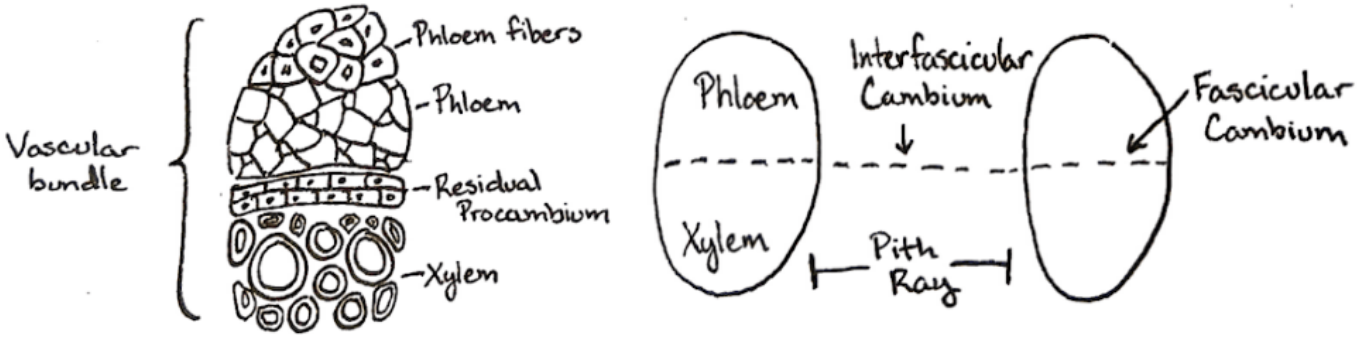


Figure 10.7.4.1: The vascular bundle of a eudicot stem

This layer of cells will divide to produce secondary xylem toward the inside of the stem and secondary phloem toward the outside. The conducting cells in the secondary xylem are dead at maturity. As the stem matures, these dead cells become separated from the living cells and the plant would be unable to direct the transport of materials into and out of the center of the plant. To solve this, plants have pathways of living cells that traverse the xylem and phloem called rays. **Xylem rays** radiate outward from the center of the stem until they reach the vascular cambium. At this point, they become **phloem rays**. Some of these will balloon out into large deltas of cells in the phloem tissue, while others will remain narrow strips of cells.

The secondary phloem becomes densely packed with layers **secondary phloem fibers** that provide structural support for the stem to grow tall.

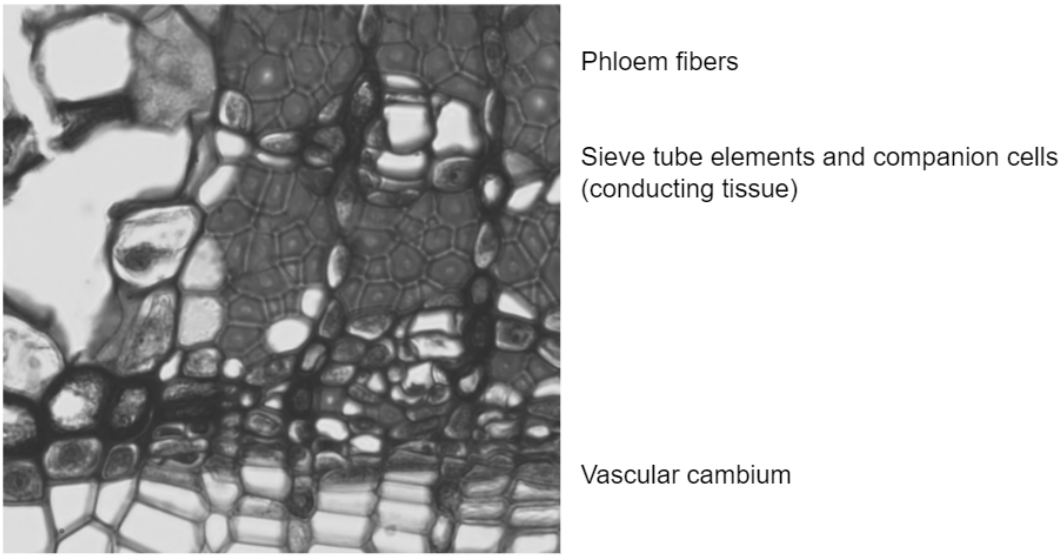


Figure 10.7.4.2: Close up of vascular cambium

Vessel elements in secondary xylem

In the secondary xylem, different diameter conducting cells form in wet and dry conditions. Larger diameter cells form in the wet season when water is plentiful. As the seasons transition to drier whether or approach freezing conditions, cells are smaller. Because most climates have a wet and dry season each year, you can track years of growth by the formation of these **annual growth rings** in the secondary xylem.

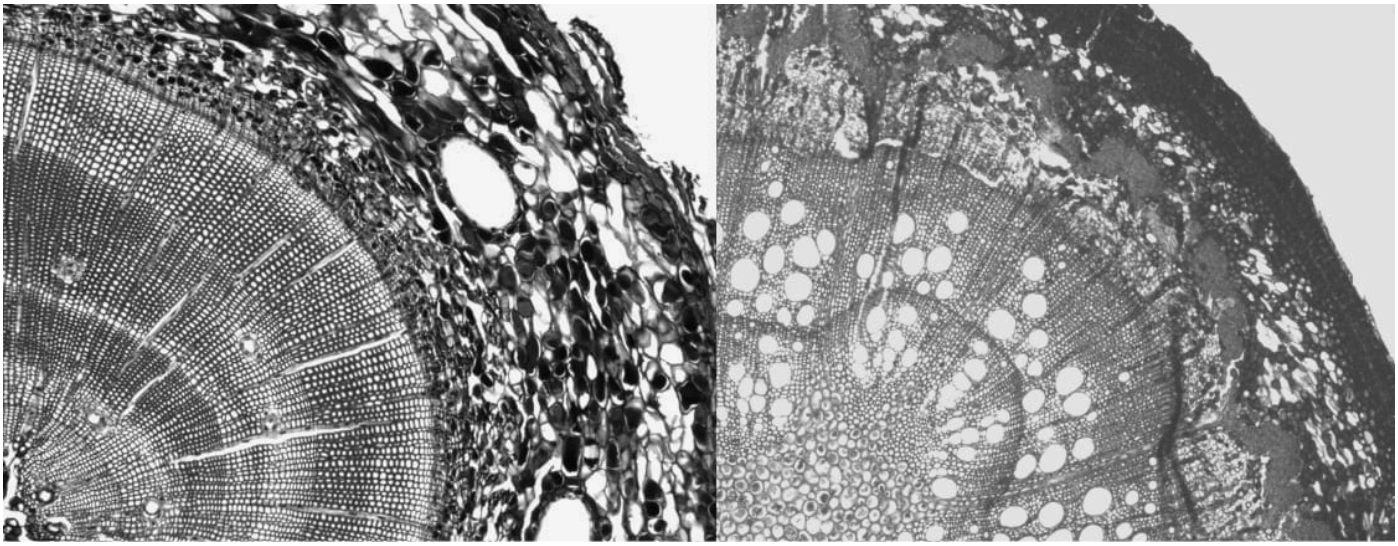


Figure 10.7.4.3: Tilia stem cross section

> On the left is a pine stem, on the right is an oak. In the pine stem, the cells are a more similar diameter because they are all tracheids. On the right, The largest diameter cells are vessel elements. How old are each of these stems?

Resin canals

In answer to the previous question about the roots, those giant holes in the pine stem (as in the roots) are resin canals. These canals transport a sticky substance called resin. Much like the latex produced in some flowering plants, resin acts as a defense compound and a wound sealant.

> Resin canals are also present in some groups of angiosperms, particularly tropical trees. Why might these structures occur more commonly in tropical plants?

The cork cambium is formed directly from the cortex. Layers of periderm are continually formed and shed until the cortex runs out. At this point, secondary phloem de-differentiates and forms the new layers of cork cambium.

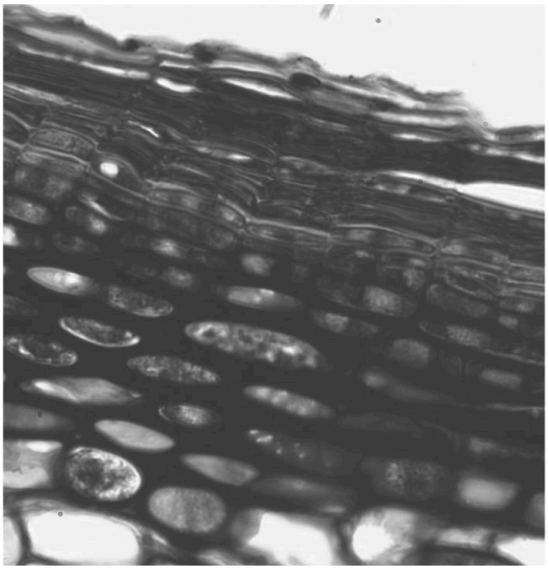


Figure 10.7.4.4: Periderm

Because the periderm is suberized and dead, it cannot have living guard cells to regulate pores and control gas exchange with the environment. Because the cells on the inside are still alive and respiring, gas exchange is still necessary. This is accomplished through tears in the periderm called **lenticels** (shown below).

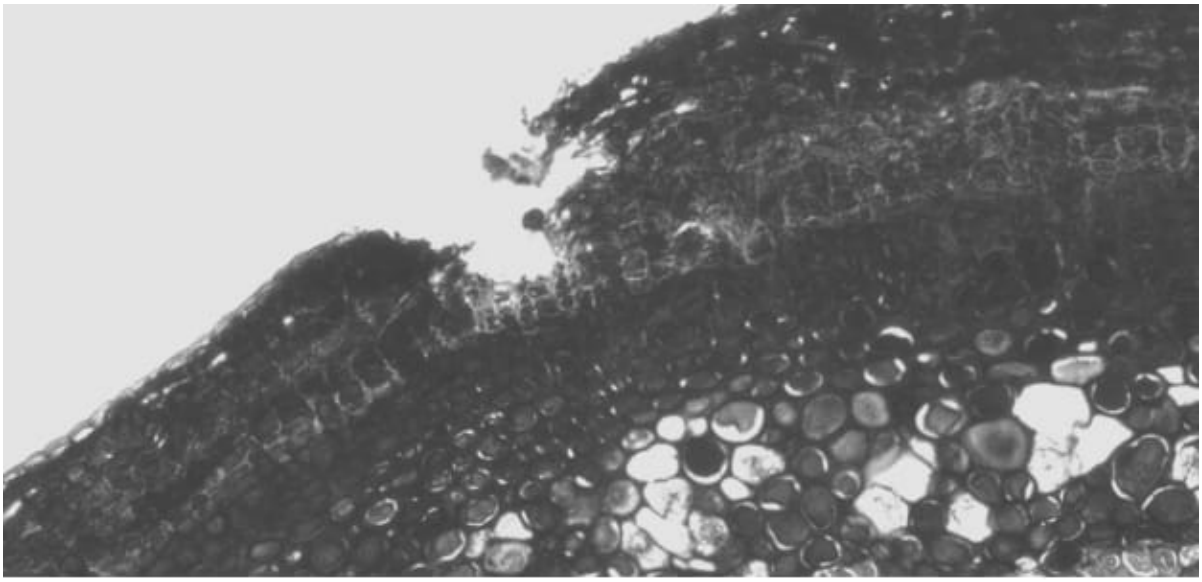


Figure 10.7.4.5: Lenticel

In a mature woody stem, the layers of periderm are referred to as the **outer bark** and the secondary phloem is the **inner bark**. The secondary xylem is called **wood**. Secondary xylem that is still actively involved in conducting water is called **sapwood**, while inactive xylem is called **heartwood**. The cross section below is too young to have these last two features.

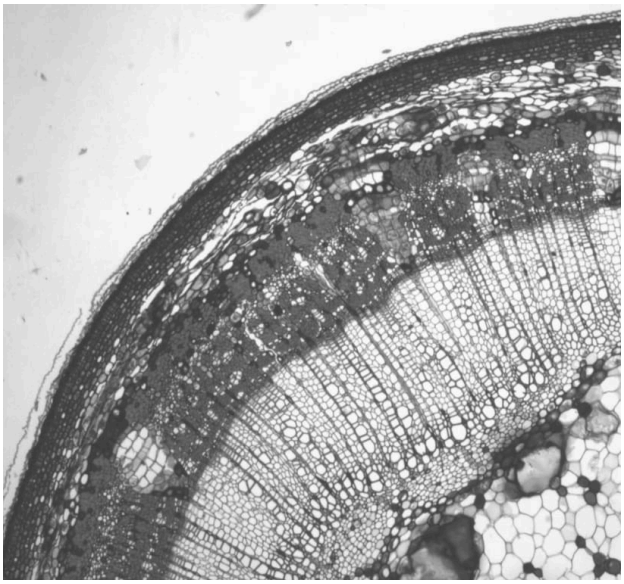


Figure 10.7.4.6: Cross section of a woody stem

In the stem cross section above, label the following: **pith, secondary xylem, xylem ray, vascular cambium, secondary phloem, phloem ray, cortex, phelloderm, cork cambium, cork,** and **epidermis**. Next, indicate where the oldest and youngest xylem cells are located.

Note: the newest cells will be located closest to the meristem that produced them!

Where is the vascular cambium?

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10.7.5: Dendrochronology

Dendrochronology is a process used to determine the order and timing (chronology) of events using information in tree rings (dendro- refers to trees). These rings form in response to environmental conditions, storing information on climate and historic occurrence of fires in an area. Essentially, you bore a hole into a living tree and extract a thin section column of the wood. This becomes your reference specimen, as you date each annual ring, tracing back from the present date. Your reference specimen can then be used to determine the timing of events in dead trees, potentially tracing back thousands of years.

Imagine that the sample below is from your reference specimen. The example core shows features you might see in a tree core and how to interpret them.

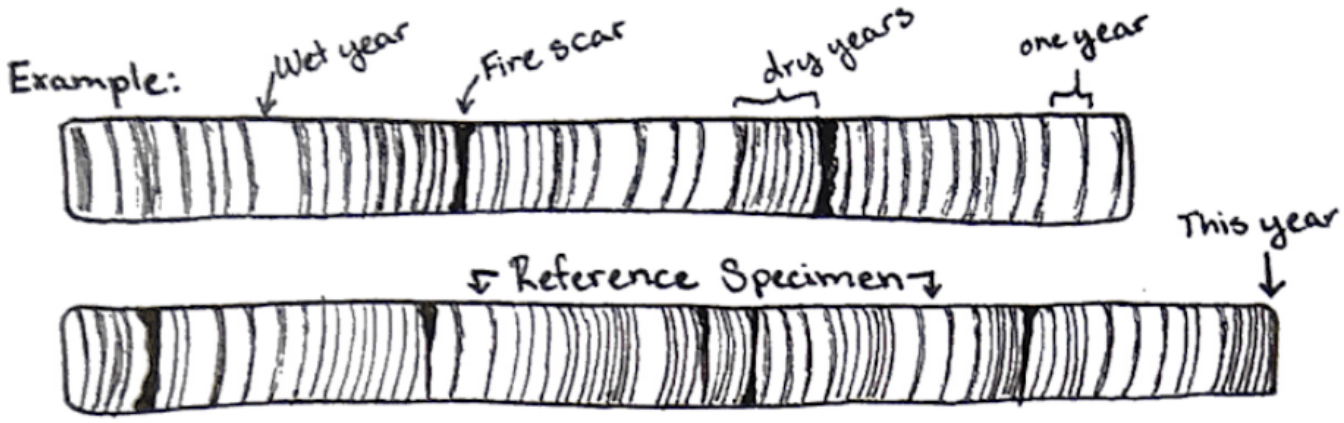


Figure 10.7.5.1: Tree core example and reference specimen

How old is this tree? At which dates did rainy years occur? Which periods represent droughts? When did fires occur? Make notes on the annual rings with the date and notable events.

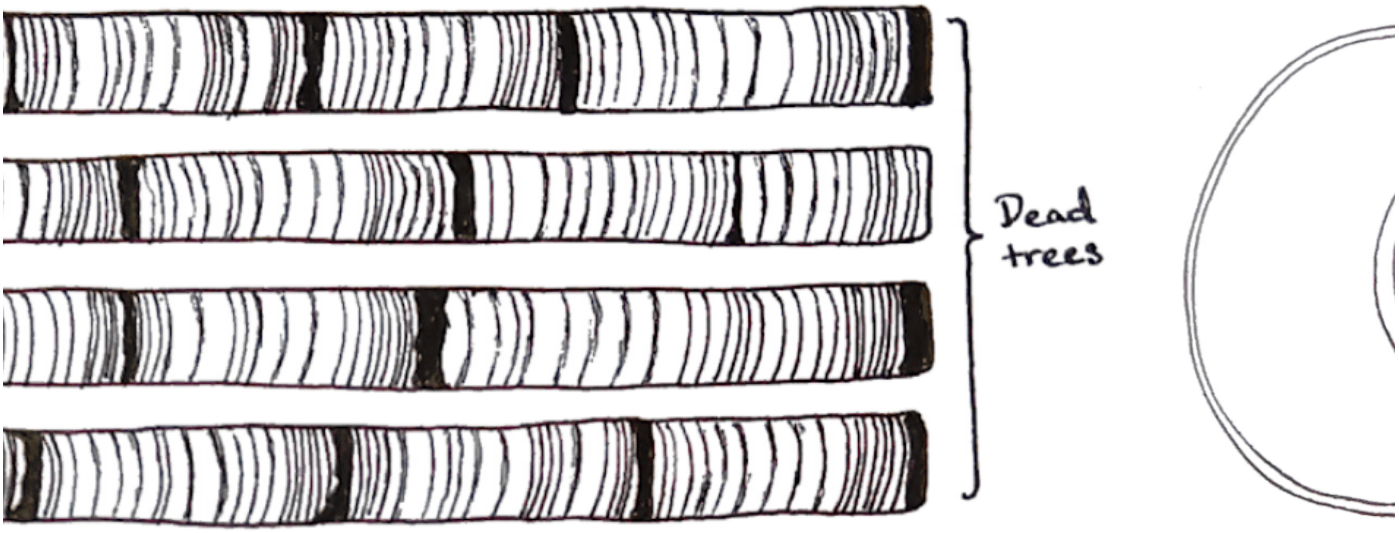


Figure 10.7.5.2: Dead tree cores

Using your reference specimen, date the events in the following dead trees of unknown age from the same forest. It will be easiest to do this by cutting out each core and aligning it next to the reference. There is no text on the bottom of this page on the opposite side, so cut away!

Based on the dendrochronology you just performed, what did you determine about the history of this forest and climate in this region? Be as specific as possible in your answer.

What is the oldest date that you calculated on the tree core present?

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11: HOW PLANTS GROW, PART 2

Learning objectives

- Recognize the general patterns of plant growth and the diversity of flowers found in angiosperms.
- Distinguish the two types of growth patterns found in angiosperms — determinate and indeterminate.
- Compare the diversity and types of compound inflorescences.

In this chapter we explore the two main types of plant growth, determinant and indeterminate, and the vast diversity in form and number of inflorescences. As you learn the vocabulary, think about why each plant has these growth forms. A species with more flowers and seeds, for example, may be a better fit in its environment than a plant with a small number of flowers, but larger and more robust seeds.

11.1: Growth Patterns and Inflorescences

11.2: Atlas- Inflorescence Types

11.3: Plant Hormones

11.4: Terms

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11.1: Growth Patterns and Inflorescences

Learning objectives

- Recognize the general patterns of plant growth and the diversity of flowers found in angiosperms.
- Recognize the two types of growth patterns found in angiosperms — indeterminate and determinate.
- Identify the names of parts of simple and compound inflorescences.
- Recognize the diversity of arrangements of these parts.

Vegetative and reproductive growth patterns

Annual plants are produced from seed in the spring and die at the end of the growing season. These plants typically have a vegetative phase early in their lifespan, followed by a reproductive phase.

During the vegetative phase, stem growth takes place through the addition of new cells — including new nodes and internodes — by the apical meristem (the growing point or bud at the tip of the stem) and through elongation of those new cells. Leaves and branches then emerge at the nodes.

Eventually, and typically at very specific and predictable times, hormonal signals within the plant that are triggered by external agents such as night length or sustained temperatures stimulate the formation of reproductive buds or meristems at nodes. These reproductive meristems give rise to inflorescences. The appearance of these inflorescences signals the transition of the plant from vegetative to reproductive stages.



Determinate or indeterminate? Pumpkin vine by Krista76, CC BY-NC-SA 2.0

Determinate growth

Watch this video on determinate and indeterminate growth patterns (0:52)

In some plants, the apical meristem itself transforms into a reproductive meristem and produces an inflorescence at the end of the stem, called a **terminal inflorescence**. This determinate growth is beneficial in ornamental plants because it places flowers at the ends of the stems and branches, where they are clearly displayed and showy. Next time you walk past a bed of flowering plants, look at where the flowers are held on the plant. In most cases, they will be at the tip of the stems and branches and positioned on the outer periphery of the plant.



Grasses are determinate. Leonora (Ellie) Enking, CC BY-SA 2.0

Determinate plants are also popular in agriculture because the plant produces all or most of its flowers at about the same time. The fruits ripen synchronously and can be harvested during a narrow window of time rather than ripening at various times during the season, which would stretch harvest out over many weeks. Corn is an obvious example, with the tassel at the top of the plant being a terminal male inflorescence and the corn ear a terminal female inflorescence. This type of growth pattern is called **determinate** because once the apical meristem of the plant transforms into a reproductive meristem, the number of nodes on that stem has been determined and will not increase. The stem may increase a bit in length through the elongation of the cells in the internodes, but no additional nodes will be formed.

Indeterminate growth

In other plants, the apical meristem remains a vegetative meristem that is capable of forming new nodes and internodes throughout the season. Once the hormonal signals are right, reproductive axillary meristems at the nodes below the apical meristem produce inflorescences. Even though the reproductive phase has begun, the plant can still grow new nodes and internodes from the apical meristems on stem and branches. As the season progresses and as new nodes are formed by the apical meristem, these nodes also mature to support the formation of more reproductive meristems and the growth of inflorescences.



Many tomato plants are indeterminate. square foot hydroponics, CC BY-NC-ND 2.0

This type of growth is called indeterminate since the number of nodes on the stem and branches is not determined, and more can be added throughout the year. For ornamental plants, indeterminate growth can mean highly desirable season-long flowering by an individual plant. For food plants, it means that fruits ripen at different times and so are available for a longer period of time through the year (many tomato cultivars are indeterminate). This may not be favored in large agricultural operations where the

preference is for the efficiency of one simultaneous and large harvest, but it is great for gardeners who like small amounts of their produce to ripen throughout the season.

Watch this video to see examples of determinate and indeterminate plants (2:48)

Watch this video about how determinate and indeterminate growth patterns impact edible plants (1:07)

Inflorescences

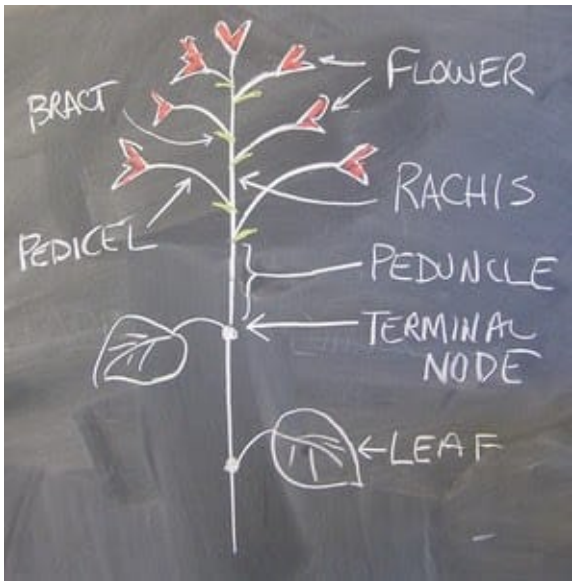
The inflorescence is the flowering structure of the plant. Some inflorescences are very simple and support only one flower. These are called **solitary** or **sole flower** inflorescences, and the stalk attaching the flower to the node from which it grew is called the peduncle.



Salvia farinacea (Blue Sage). guzhengman. CC BY-NC-SA 2.0

Other inflorescences can support multiple flowers and display complex branching patterns.

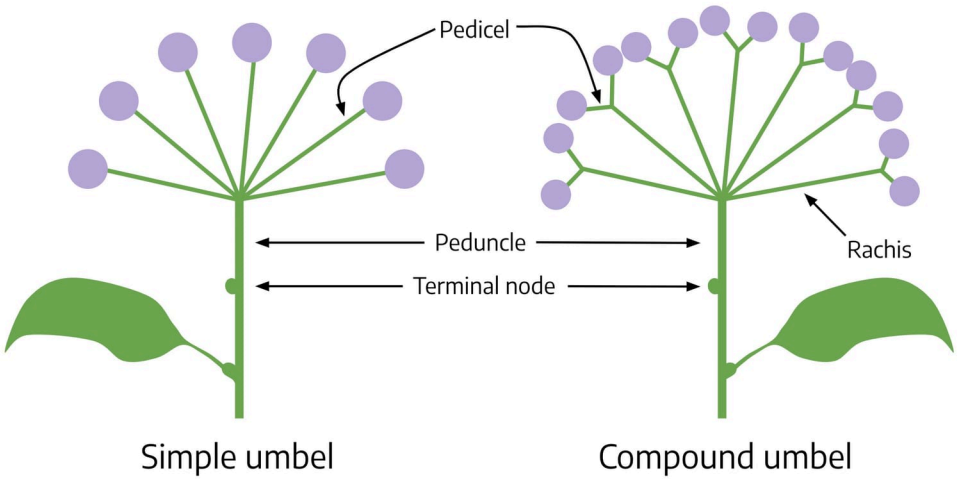
The drawing to the right depicts a hypothetical inflorescence that supports multiple flowers. Toward the bottom are the last two nodes of the stem. The next-to-last node supports a leaf, and the terminal node supports an inflorescence and a leaf. Since that leaf is associated with the inflorescence, rather than emerging from a stem node, botanists call it a “bract,” even though it may look like a smaller version of the plant’s other leaves. Since the terminal node transforms to be reproductive, this plant must have determinate growth.



Inflorescence with labels. Image credit: Tom Michaels

The stem-like part of the inflorescence between the point where it emerges from the terminal node of the stem and the point where the branches of the inflorescence begin is called the **peduncle**. The central axis of the inflorescence, starting at the point where the first inflorescence branch is attached, is called the rachis. The rachis may subdivide one or more times, and these subdivisions are considered part of the rachis. Finally, there is a short stalk connecting the flower to the rachis; this is called the pedicel.

This type of inflorescence, with peduncle, pedicel, and single-flower structure, is called a simple inflorescence. An inflorescence with a group of flowers is called a compound inflorescence. A type of compound inflorescence with multiple flowers originating from a common point is an umbel. The illustration below shows a simple umbel compared to a compound umbel. On the left, in the simple umbel, the pedicels radiate out from a central point at the end of the peduncle and attach to a single flower. On the right, in the compound umbel, rachi radiate out from the end of the peduncle, and an umbel is attached to the end of the rachis.



Simple and compound umbels. Illustration by Emily Tepe.

Inflorescences can be amazingly complex structures. This site about inflorescences will help you recognize some of the possible arrangements and perhaps start looking for this complexity when you are out among plants.

Watch this video about flower structures (3:15)

Watch this video on flower structures that are a little harder to figure out (1:49)

Review questions

- Explain the difference between determinate and indeterminate growth.
- Draw a simple inflorescence and label the peduncle, pedicel, and flower(s).
- Describe the differences between a bract and a leaf.

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11.2: Atlas- Inflorescence Types

Spathe & Spadix



Figure 11.2.1: In the image on the left, the spathe is shown wrapped around and enclosing the spadix (not visible). The spathe on a Calla lily looks like one large, funnel-shaped, white petal. In the image on the right, the top of the spadix is shown. This part of the spadix is covered with the male florets, making pollen. Photos by Maria Morrow, CC BY-NC.

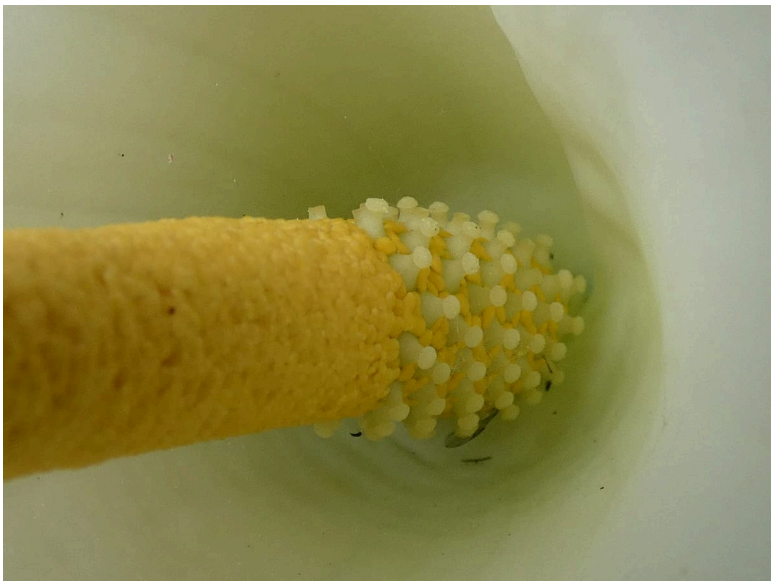


Figure 11.2.2: This is the base of the Calla lily spadix. It is covered with female florets. The gynoecium is shaped like a bowling pin, each with a large knob-like stigma at the top. Photo by Maria Morrow, CC BY-NC.

Head (also called a composite or capitulum)



Figure 11.2.3: A dandelion head inflorescence. Each "petal" is actually composed of five fused petals of a single floret. The tube-like structures emerging upward are the styles, each with two curled stigma lobes. Because this inflorescence has no disc flowers, it is called a ligulate head. Photo by Maria Morrow, CC BY-NC.



Figure 11.2.4: This oxeye daisy has a head inflorescence with two types of florets. In the center, there are yellow disc florets. These have five short petals and radial symmetry. Lining the outside of the inflorescence are white ray florets. These have several petals fused together in one long strap-like, bilaterally symmetrical corolla. The image on the right shows the bracts lining the outside of the inflorescence, called phyllaries. People commonly mistake these as sepals when considering this inflorescence as a single flower. Photos by Maria Morrow, CC BY-NC.



Figure 11.2.5: Clovers are quite beautiful, particularly up close. The fuzzy ball it produces is composed of many bilaterally symmetrical florets, typical of the flower morphology found in the legume family. These florets all attach to the same receptacle. Can you locate the calyx and corolla of each floret? Photo by Maria Morrow, CC BY-NC.

Spike



Figure 11.2.6: This *Plantago* inflorescence is a wind-pollinated spike. The florets have no showy perianth. The prominent structures seen here are the large anthers, located at the end of long, thin filaments. These florets are sessile, attached directly to the peduncle with no pedicels. Photos by Maria Morrow, CC BY-NC.

Raceme

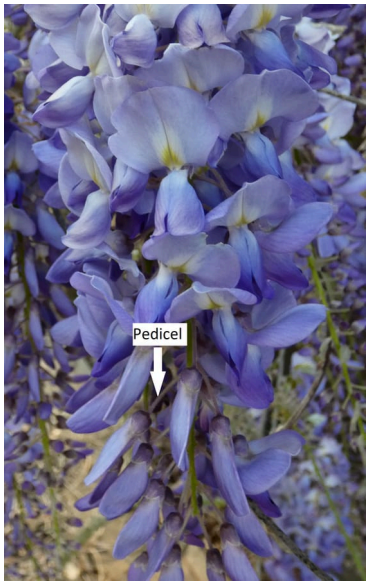


Figure 11.2.7: This Wisteria inflorescence is a pendant raceme. The florets are each attached to the peduncle by a short stem called a pedicel. One of these is indicated in the image with a white arrow. Wisteria is also in the legume family. Can you see the similarity between these florets and the ones in the clover inflorescence in Figure 11.2.5? Photo by Maria Morrow, CC BY-NC.

Catkin





Figure 11.2.8: Willows produce catkins. In the first image, there are several female catkins. There is no showy perianth or androecium, just a large gynoecium for each floret, giving the appearance of a spiky stick. In the second image, there is an androecium instead of a gynoecium. The yellow anthers are held out on thin filaments, making these male catkins look like yellow, fuzzy caterpillars. Photos by Maria Morrow, CC BY-NC.

Umbel

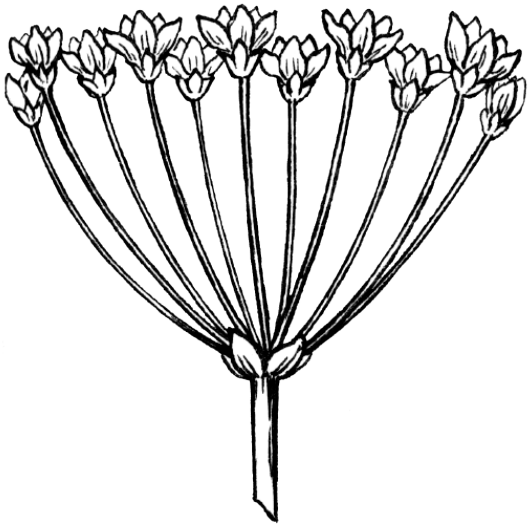




Figure 11.2.9: In an umbel, the pedicels all emerge from the top of the peduncle. The *Allium cernuum* inflorescence on the right is a drooping umbel. Drawing by Pearson Scott Foresman, Public domain, via Wikimedia Commons. Photo on the right by Steve Ganley, CC-BY-NC.



Figure 11.2.10: A compound umbel is when each pedicel then forms its own umbel. Drawing by H.M. Dixon, Public domain, via Wikimedia Commons. Photo of *Aegopodium podagraria* by Сергей, CC-BY-NC.

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11.3: Plant Hormones

Learning objectives

- Understand the role of the five major hormone groups in plant growth and development.
- Recognize that cells, tissues, and organs have unique competency to respond to specific hormones.
- Connect specific hormones to plant responses and how they are used in plant propagation.

How plants respond to hormones

The five major groups of plant hormones — auxins, cytokinins, gibberellins, ethylene, and abscisic — acid are distinguished by their chemical structures and the response they evoke within the plant (see Table 4.1). For any cell to respond to a hormone it must be competent to perceive the chemical. Some cells simply lack the ability to "see" the hormone and do not respond to its presence. Competency to perceive a hormone depends on a cell's physiology when the hormone is present. If the hormone is perceived, its unique chemical structure causes a chain reaction or signal transduction that involves changes in gene expression and cell morphology. These cellular responses to hormones can lead to changes we see in the plant, such as movement towards light, a transition from vegetative growth to flowering, or the closing of leaf stomata due to drought stress.

The perception of the hormone occurs in cells and throughout a tissue or organ, depending on where the hormone is located, the concentration of the hormone, and the developmental state and physiological condition of the cell. Many cells within a tissue can respond in a coordinated manner, resulting in changes in the whole plant. Hormones are often made in one cell and translocated to other cells where they are perceived, and the response may occur far away from the site of hormone synthesis. Responses to hormones are studied through exogenous application of the chemical to a plant tissue — the hormone is applied to the outside (exo) of the plant and observations are made on how the plant responds. For hormones that are a gas, like ethylene, this means the hormone can be translocated from one plant to another plant. The plants are essentially talking to one another, using a wide variety of molecules.

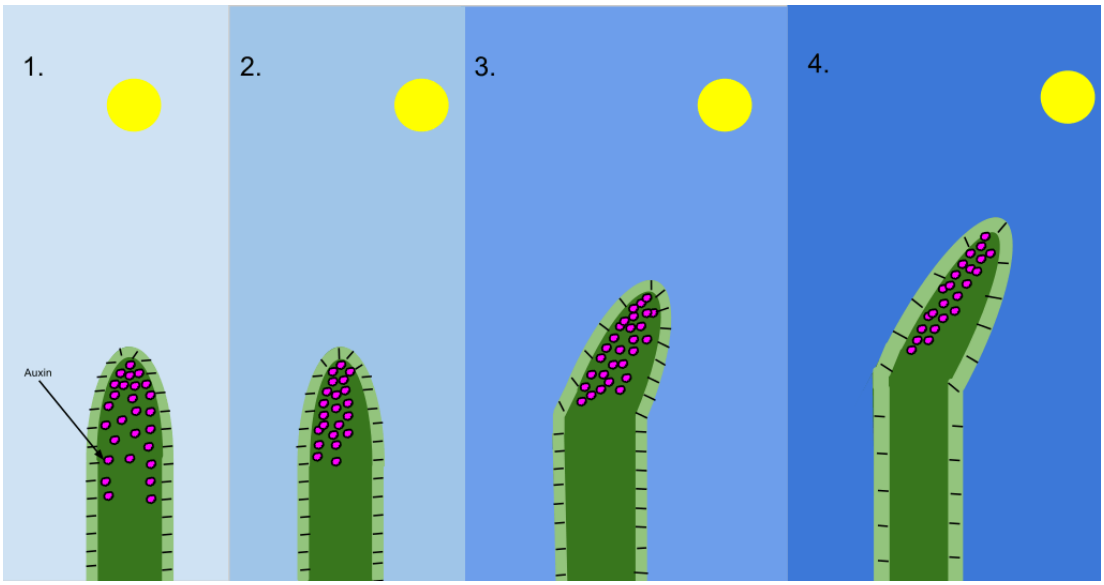
Experiments in which hormones are exogenously applied to a plant reveal how plants respond to hormones; much of our knowledge about the role hormones play in plant growth is from this type of experiment. Whenever a hormone is exogenously applied, however, it is also interacting with all of the hormones present in the plant. These are **endogenous** hormones (**endo** means internal), and the cell responds according to the sum of all hormones in its presence. This can complicate the interpretation of responses to exogenous hormone applications.

The hormones used in plant propagation can be naturally occurring and found in many plants, or can be synthetic or synthesized to mimic the structure and response of a naturally occurring hormone. Synthetic hormones are often used instead of naturally occurring versions because they are less expensive to obtain, may cause greater or longer lasting responses, and can be less susceptible to degradation in the plant and during storage. Because exogenous application of hormones play a role in manipulating or disrupting plant growth, they are used extensively as herbicides (weed killers) and can be targeted to certain types of plants based on how certain species respond to the different structure.

Plant responses to hormones and their application in plant propagation

Auxin

Auxins are a group of related molecules that are involved in almost every aspect of the plant's life cycle. Auxins stimulate growth through cell elongation, which is integral to the plant's responses to environmental changes. Auxins are responsible for two types of growth responses: **phototropism**, the bending or growth of a shoot toward light, and **gravitropism**, a change in growth occurring after a change in gravitational force. The diagram below shows indoleacetic acid (IAA, illustrated with pink dots), a naturally occurring auxin, moving from the sunny to the shady side of a shoot tip. The differential accumulation of auxin on the shady side of the shoot causes those cells to increase growth and bends the shoot tip toward the light. Auxin's stimulation of cell growth is also important in healing wounds and forming calluses after pruning.



1. This is a normal plant that has the sun positioned almost directly over the plant. During this time, the auxin (pink dots) that lies within the plant is evenly distributed. 2. The sun is now positioned at an angle to the plant. The repositioning of the sun causes the auxin to move the other side of the plant, and becomes more concentrated. This overload of auxin next to these cells causes them to start to grow or elongate. 3. This results in the the plant to look like it is growing toward the sun. 4. If the sun moves to the other side of the plant, the auxin would again move to the other side of the plant and become concentrated on the side of the plant that is farthest away from the sun. 5. The same growth or elongation of the cells on this side of plant would continue to grow towards the sun. Image by MacKhayman. CC BY-SA 3.0.

The ability of auxin to regulate growth can be turned against weeds (plants out of place). The synthetic auxin 2,4-dichlorophenoxyacetic acid, or 2,4-D, is a common herbicide that interrupts normal growth regulation when applied to the plant, causing leaf drop and death. Because dicotyledonous (dicot) plants have a higher competency to respond to 2,4-D, 2,4-D can be used as a selective herbicide to kill dicot weeds in lawns and corn fields, which are resistant, monocotyledonous (monocot) grasses. The grass is unharmed due to its lower competency to respond, while the dicot plants are killed.

In general, auxins are produced in the young leaves of a plant and translocated downward to older tissues. This downward translocation controls apical dominance, where growth of axillary buds is suppressed. Removal (pinching) of the shoot tip where auxin is being produced, as shown in the three photos of mint below, releases the axillary buds from apical dominance and they begin to grow. This is a common horticultural practice, increasing branching and flower production. Pinching is often used in seedling plants such as basil or zinnias to get globe forms in a pot instead of tall, single-stemmed plants.



One of the most important uses of auxin in plant propagation is to stimulate the growth of adventitious roots — roots that emerge from anywhere on the plant other than from the roots — on shoot cuttings. The photo below shows cuttings from two different *Acer ginnala* (Amur maple) plants that have different competencies to form adventitious roots. Both cuttings were treated with auxin, but only the competent plant forms adventitious roots (on the left). The cutting from a plant that lacks competency to respond to auxin did not form roots (right) and will eventually die.

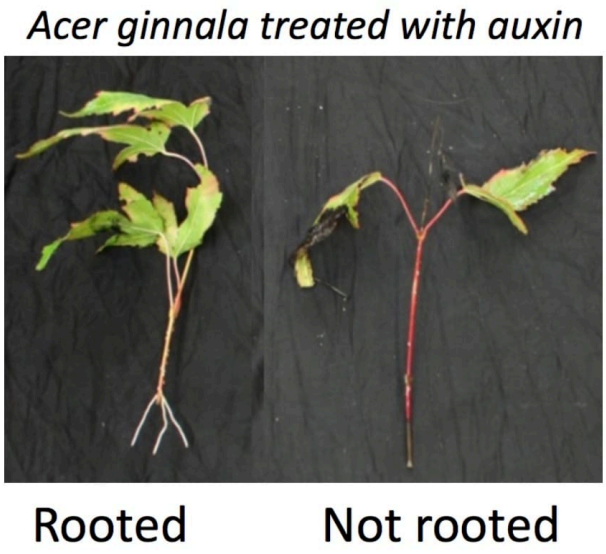


Image by Matthew Clark

This form of asexual (clonal) propagation is used by both horticultural professionals and hobbyists. The competency for rooting cuttings can be species specific or seasonal. Collecting stems from a plant to use for cuttings can be more successful in the growing season, as with the Amur maples shown above. With plants such as grapes, however, cuttings are made and rooted during the winter when the vines are not actively growing. The video below demonstrates how shoot cuttings are taken from Amur maples, treated with auxin, and incubated in a high-humidity environment for several weeks to form adventitious roots. Exogenous application of auxin is not required for adventitious rooting of all plants. Some plants can form many adventitious roots without exogenous applications, because the endogenous auxin that occurs naturally in the shoot is sufficient for root formation.

Cytokinins

Like auxins, cytokinins are a group of related molecules that regulate growth and development. However, the plant's response to cytokinin is very different from the responses to auxin. Cytokinin comes from the word cytokinesis, which means cell division. You will learn about cytokinesis, specifically mitosis, in Chapter 13.

Cytokinins promote cell division, where one cell splits and two new daughter cells are formed. Cytokinins are important regulators of plant growth and development.

Cytokinins have an interesting interaction with auxin in plants. In the 1950s, Skoog and Miller were researching the growth of *N. tabacum* stems in tissue culture. They discovered that they could use specific ratios of an auxin (IAA) and a cytokinin (kinetin) to direct the growth of the stem tissue in culture. A high ratio of cytokinin relative to auxin led to shoot formation, a higher level of auxin led to root formation, and equal levels of each produced callus growth, which is undifferentiated plant cell growth. Skoog and Miller's transformational discovery formed the basis of the "MS" plant medium that remains popular for plant propagation using tissue culture.

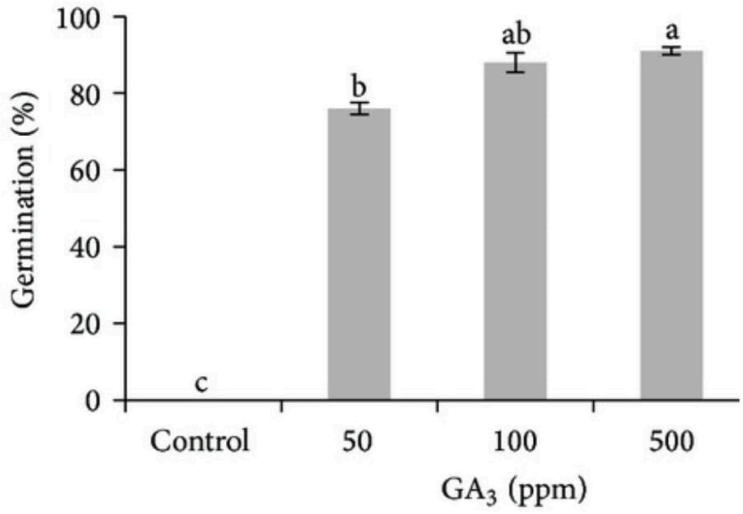
Watch this video to learn more about the propagation of plants in synthetic media with exogenous hormones in tissue culture.

Gibberellins

Gibberellins, or gibberellic acid (GA), are a group of over 100 molecules that are primary regulators of stem elongation and seed germination. They were discovered during research on the cause of the "foolish seedling" disease of rice. The disease, characterized by tall plants with little grain, is caused by an infection with *Gibberella fujikora*, a parasitic fungus that produces GA in the rice shoots, causing increased stem elongation.

In Chapter 9.2, on seed physiology, you will learn that some seeds are dormant and do not germinate even when the proper environment is provided. Seed dormancy, which has several causes and evolutionary advantages, always has the common feature of preventing seed germination until the time, season, or seed physiology is correct. Planting a dormant seed or a dead seed gives the same result: no germination. For plant propagators, dormancy can be confusing, raising the question "are my seeds dead or

are they dormant?" Either condition prevents germination and plant propagation. Treating seeds with GA is a common method to break dormancy and facilitate germination. GA treatment of *Gentiana lutea* (bitter root) seeds, for example, increases germination from 0% (no germination) to over 80% when treated with 100 parts per million (ppm) GA (see the graph of germination on the left). If a propagator of *G. lutea* had not known about seed dormancy, they may have assumed their bitter root seeds were dead. For most plants, GA is the endogenous hormone that triggers seed germination.



Abscisic acid

While GA facilitates seed germination, abscisic acid (ABA) inhibits it. Abscisic acid is a single molecule that regulates germination and the response of a plant to reduced water availability during drought stress. ABA levels increase as water becomes less available to the plant, evoking several responses, including the closing of stomates. Closing stomata slows transpiration (also called evapotranspiration), the movement of water in the plant from the root to stem to leaf and out through the stomata into the atmosphere. You'll read more about stomata and the movement of water in Chapter 11, Plants and water.

Reducing water content is one of the final steps in seed maturation and is important for seed longevity by reducing metabolism to a minimum, which is the quiescent nature of mature seeds. Increasing endogenous ABA levels in seeds prepares them to survive lower water content, is important to seed maturation, and prevents precocious germination (vivipary). Seeds with low levels of ABA during seed development may prematurely germinate. Low ABA levels may result from a genetic mutation or environmental causes. Vivipary in some fruits is not uncommon and may occur during storage of fruit in the grocery store.

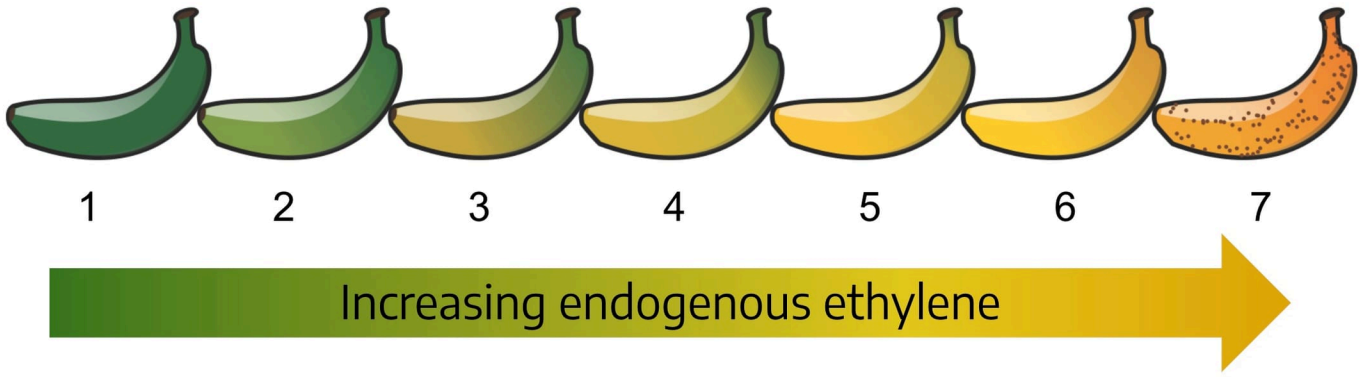


Apple in vivipary. Image by Matthew Clark.

Ethylene

Ethylene is well known as the gaseous, ripening hormone. It also regulates seedling growth and the formation of root hairs, and can lead to epinasty — the bending of branches downwards.

Many plants are sensitive to the effect ethylene has on fruit ripening. The iconic examples are tomato and banana. These fruits are climacteric — they continue to ripen after harvest. The perception of ethylene by the cells that make up the fruit triggers the ripening process and the production of more ethylene. As the concentration of ethylene increases, so does the speed of the ripening. Picking immature or green fruit enables shipment over long distances, because the fruit is firmer and less likely to be damaged in transit. The green fruit can then be treated with ethylene from an ethylene generator (right) to accelerate ripening.



Seven ripening stages of banana.

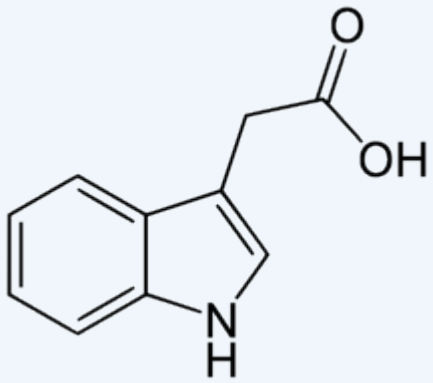
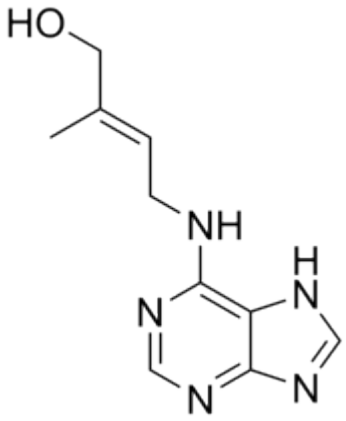
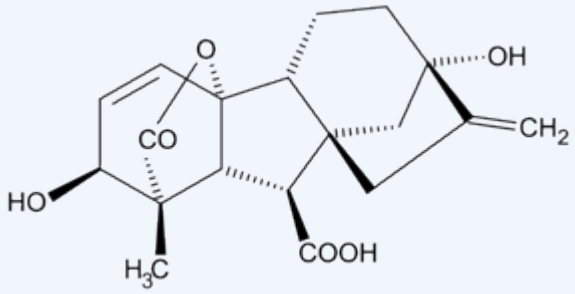
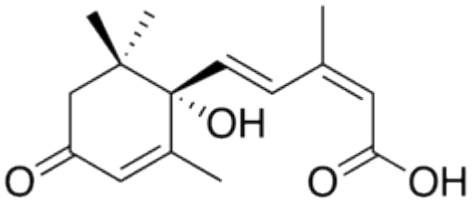
For other fruit crops, the introduction or production of ethylene is to be avoided to prevent over-ripening and spoilage. To prevent the generation of ethylene during fruit storage, ethylene is scrubbed from the air using an air filter system. Reducing the ethylene concentration means slower ripening and less spoilage.

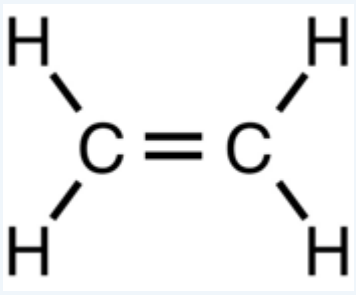
The process of senescence is also triggered by ethylene production and is important in the cut flower industry. Keeping cut flowers away from gases with ethylene-like activity helps keep floral arrangements looking fresh. Reducing ethylene action prolongs the vase life of many cut flowers as well as the storage of fruits.

Review

The five major groups of plant hormones control many aspects of plant growth and development and have important applications in plant propagation. However, many other molecules are also key to the plant's response to its environment. These highly diverse signal molecules modulate the plant's physiology through complex interactions. A cell's response to the many different hormones is a sum of its genetic makeup, its physiology, and the environment.

Table 4.1

Hormone	Structure	Synthesized versions	General responses	Application
Auxin (indoleacetic acid; IAA)		Indole butyric acid (IBA); Naphthalene acetic acid (NAA), 2,4-Dichlorophenoxyacetic acid (2,4-D)	Adventitious rooting, tropisms, apical dominance	Adventitious rooting of shoot cuttings
Cytokinin (zeatin)		Benzyladenine (BA, BAP or benzylaminopurine), Thidiazuron (TDZ), kinetin	Cell division	Shoot formation in plant cultures
Gibberellin (GA3 shown)		Over 100 types, named by GAnumber (for example GA3)	Promotes seed germination and stem elongation	Germination of dormant seeds
Abscisic acid		None, although it can be synthesized	Seed dormancy, response to water stress, leaf drop	Genetic manipulation for drought resistance

Ethylene		Natural gas, propane and their byproducts from burning	Fruit ripening, epinasty, root hair formation	Promote or prevent fruit ripening

Review questions

- Describe the general response the plant has to each of the five major plant hormones and the factors that affect the response of a plant.
- Explain the difference between endogenous and exogenous plant hormones.
- Describe an application for each of the plant hormones in plant propagation specifically or horticulture in general.

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11.4: Terms

These are the important terms from this chapter to be sure to know. You might also find these in later chapters.

Abscisic acid	A hormone that regulates seed maturation and responses to changes in water availability.
Adventitious root	A root that emerges from anywhere on the plant other than from the roots.
Angiosperms	A group of flowering plants whose seeds develop inside an ovary.
Annual plant	A plant that is produced from seed in the spring and dies at the end of the growing season.
Apical dominance	Where a shoot suppresses growth of floral or vegetative axillary buds below the growing point.
Auxins	A group of related hormones that regulate many aspects of plant growth and development and are key to stimulating adventitious rooting.
Competency	The ability to respond to a signal, such as a plant hormone.
Compound inflorescence	An inflorescence with a group of flowers and includes a rachis.
Cytokinins	A group of related molecules that regulate cell division and are key to stimulating adventitious shoot formation.
Determinate	When the stem of a plant terminates in a flowering stalk and new stem growth continues from subterminal lateral buds.
Endogenous hormone	A hormone that occurs within the plant.
Ethylene	A gas that regulates fruit ripening and plant senescence.
Exogenous hormone	The application of a hormone to a plant.
Floret	A single flower in a compound inflorescence.
Flower	A reproductive structure in a flowering plant.
Gibberellins	A group of related molecules that regulate seed dormancy.
Gymnosperms	A group of plants whose seeds are produced without the protection of an ovary.
Indeterminate	When the apical meristem remains a vegetative meristem capable of forming new nodes and internodes throughout the season. Once the hormonal signals are right, reproductive axillary meristems at the nodes below the apical meristem produce inflorescences.
Inflorescence	The complete flower structure of a plant; includes the flower, pedicle, rachis, and peduncle.
Natural hormone	A hormone made by a plant.
Pedicel	The short stalk that holds up the flower.
Peduncle	The large, central stalk that attaches the rachi to the stem of the plant.
Perception	The ability of a plant cell or tissue to detect a hormone that depends on a cell's physiology at the time the hormone is present.
Perennial	A plant that lives for more than two growing seasons (more than two years); perennials may be woody or herbaceous (the latter with underground perenniating structures).
Plant hormone	A signal molecule that regulates growth, development, and responses to environmental and other signals, also known as a plant growth regulator or phytohormone.

Rachis	The stalk of a flower that is situated between the peduncle and the pedicel on a compound leaf. Also the name for the central axis on a compound leaf where the leaflets are attached.
Reproductive meristem	The apical meristem that transforms into the reproductive tissues (the inflorescence) of the plant.
Response	The action taken by the plant after perception of a signal.
Senescence	A regulated process that results in cell death and is associated with leaf fall and death of the plant.
Signal transduction	The process in which the perception of a signal, such as a hormone, is moved within a cell, cell to cell, or throughout a tissue.
Simple inflorescence	A type of inflorescence with a peduncle, rachis, pedicel, and single flower structure.
Synthetic hormone	A hormone made by people; can mimic the response of a naturally occurring hormone.
Tropism	A growth or turning response to an environmental or other signal such as phototropism (response to light) or gravitropism (response to gravity); can be controlled by auxin and other hormones.
Umbel	An inflorescence with multiple flowers originating from a common point.
Woody perennial	A plant that lives for more than a year, has hard rather than fleshy stems, and bears buds that survive above ground in winter. Trees, shrubs, many vines, and bamboo are examples of woody perennials.

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12: MERISTEMS AND FLOWERS

Learning objectives

- Understand the meristems of primary and secondary growth and the specialized tissues they produce.
- Understand flower morphology and how sexual reproduction via pollination occurs.

Plants have meristematic cells that are not differentiated, but that are destined to divide and produce other cells that may also divide, elongate, and differentiate into specialized cells and tissues. This process is called **growth**. A highly specialized structure produced after the transition from a vegetative meristem to a reproductive meristem is called a **flower**. Floral organs are arranged in concentric circles or whorls and are the site of sexual reproduction.

12.1: Meristem Morphology

12.2: Flower Morphology

12.3: Atlas- Flower Morphology

12.4: Terms

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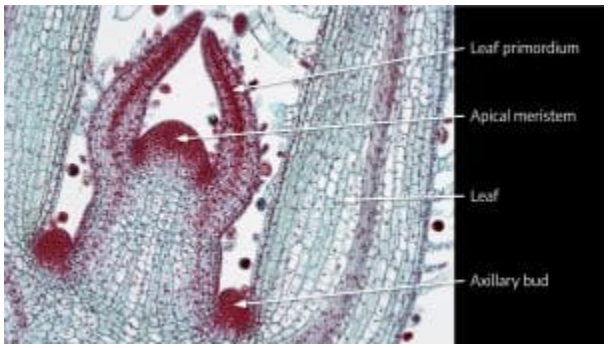
12.1: Meristem Morphology

Learning objectives

- Differentiate between primary growth from apical meristems and secondary growth from lateral meristems.
- Describe two types of lateral meristems and the types of tissues that are derived from these meristems.

Primary growth from meristems

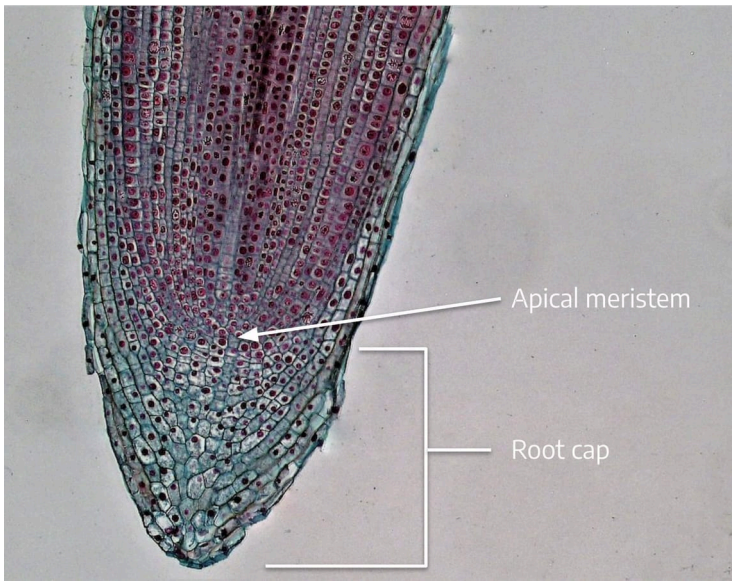
You'll recall that the apical meristem is the site of cell division and new cell production at the tips of the plant stems and roots. The cells that make up the meristem are undergoing mitotic cell division to produce more cells. These new cells result in growth and development of plant tissues. (If you haven't previously studied mitosis, you'll have the opportunity to do so during this class.) For now it is sufficient to know that **mitosis** is the process of cell division where one plant cell divides into two identical cells.



Microscope view of coleus shoot tip with labels. BlueRidgeKitties, CC BY-NC-SA 2.0

Above is a micrograph of a coleus shoot tip. You can see the dome of the apical meristem at the very tip of the shoot surrounded by leaf primordia (rudimentary leaves). On the far left and far right are the cells of two growing leaves. You can see a trace of vascular tissue on the left leaf near the "L" of the leaf label. There is another red stained area called the axillary bud, which we've studied previously. The axillary bud is another very small shoot tip with a meristematic area. Axillary buds are found at a node and typically occur where a leaf petiole attaches to a stem. The axillary buds in this stage of growth are inactive, but in time may begin active cell division and develop into new branches off of the main stem.

The coleus micrograph is clearly stem tissue because you can see leaves and leaf primordia, so where are the nodes and internodes? The region where the leaves are attached, and where you find the axillary buds, is a node. Above this is the internode, and at the top where you find the leaf primordia is another node.



Apical meristem with root cap. Berkshire Community College, Public Domain.

The root meristem looks very different from the shoot apical meristem. Recall that, unlike branches that develop at nodes, lateral roots are formed adventitiously, as the result of meristematic activity in the pericycle cells of the root's vascular system in the zone of maturation. We don't see a node-internode structure like we saw with the coleus shoot tip.

When meristem cells divide, whether in the shoot or the root, one of the two resulting sister cells typically continues to be a meristem cell. The other sister cell divides a few more times and then differentiates into dermal, cortex, or vascular tissue in the stem or root. Meristem cells that remain meristematic are called initials because they continue to divide, producing new cells. The other sister cells that divide once or twice more and then differentiate are called derivative cells. The xylem and phloem tissues that result from differentiation of derivative cells are called primary xylem and primary phloem, where the word "primary" signals that the cells originated from cell divisions of the apical meristem.

To reiterate, young stems and roots have primary xylem and primary phloem that formed as a result of differentiation of derivative cells. Primary xylem and primary phloem cells trace back to an apical meristem.

Earlier you learned the arrangement of the vascular tissues in monocot and dicot stems and roots. Remember that mitotic cell divisions in the apical meristem result in lengthening of the root or shoot through production of new cells plus the elongation of those cells. With a few exceptions, this is the only type of growth — growth that is initiated by cell division in the apical meristem — you'll find in monocots. Dicots, however, have another type of growth — from a different type of meristem — that results in thickening of the stem.

Review questions

1. If shown a micrograph of an apical meristem, how would you determine whether it is from a root or a shoot?
2. What happens to the initial cell mentioned in the question above? Does it continue to divide?

Secondary growth (thickening): Introducing lateral meristems

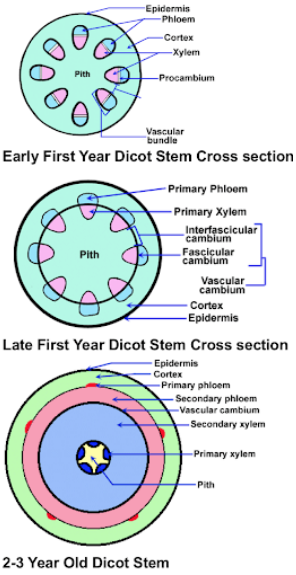
Watch this video for a closer look at apical and lateral meristems (2:26)

Unlike annual herbaceous plants that only survive for one growing season, and whose stem and root cells trace back to cell divisions of the apical meristems, woody plants and shrubs are perennial dicots that have the capacity for secondary growth and can survive from year to year.

Some annual herbaceous dicot plants, like tomatoes, can have secondary growth, but for now let's consider those the exceptions and focus on perennial dicot woody plants. Secondary growth is the result of activity by a special type of meristem called a

lateral meristem. As with apical meristems, lateral meristems are made up of cells that undergo mitotic cell division. Mitosis in lateral meristems results in lateral growth (thickening of the stem or root) and adds to the girth of a plant rather than its length. Remember that length is the outcome of cell division in the apical meristem plus elongation of those cells. Girth or thickening is the result of lateral meristems. We'll learn about two types of lateral meristems: vascular cambium, and cork cambium.

Vascular cambium



Images by Dr. Thomas L. Rost, emeritus professor at UC-Davis.

Let's start with the vascular cambium.

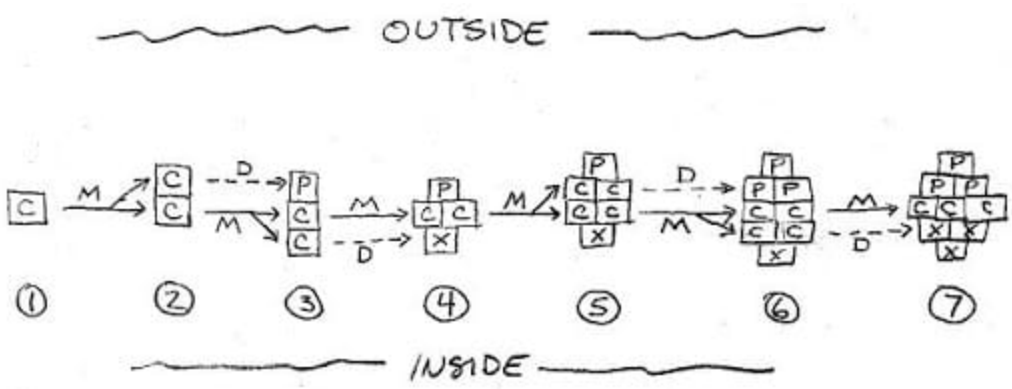
The three drawings on the right show a cross section of a stem for an imaginary woody dicot. The top drawing illustrates the stem early in the first year of growth, and shows the vascular cylinders arranged in a ring around the stem. The phloem is oriented to the outside, the xylem to the inside. A thin layer of parenchyma cells between the xylem and phloem has differentiated into the fascicular cambium (fascicular refers to bundles, in this case, cambium in the vascular bundles). The fascicular cambium is meristematic and can divide to produce new phloem toward the outside and new xylem to the inside. The new xylem and phloem produced by the cambium are called 2o (secondary) xylem and 2o phloem. Recall that the original xylem and phloem that differentiated from the apical meristem's derivative cells are called the 1o (primary) xylem and 1o phloem.

The middle drawing is of the same stem later in the year. The cortex (cortical) parenchyma cells that lay between the vascular cylinders directly in line with the fascicular cambium begin to differentiate into a type of cambium called interfascicular cambium (cambium between the bundles). This is symbolized by the line connecting the vascular cylinders. This cambium is also meristematic, and produces 2o xylem and 2o phloem.

The cross section on the bottom illustrates the stem in its second or third year of growth, when there is a noticeable buildup of 2o xylem and 2o phloem with remnants of 1o xylem and 1o phloem.

In summary, the vascular cambium is a lateral meristem formed by differentiation of parenchyma cells located between the primary xylem and phloem into fascicular cambium, followed by differentiation of cortical parenchyma between the vascular cylinders into interfascicular cambium. After a few years of secondary growth, fascicular and interfascicular cambium can no longer be distinguished, and it is all simply known as vascular cambium. This layer of cambium runs vertically (assuming that the stem is oriented vertically) and parallel to the surface of the woody stem.

The illustration below shows how the cambium divides to produce 2o xylem and 2o phloem, with the outside of the stem toward the top of the page. Frame #1 shows a single cambium cell (C). This cell divides mitotically (M) to form two cambium daughter cells (Frame #2). Frame #3 shows that the cambium cell on the top differentiates (D) into a phloem cell (P-toward the outside) and the other cambium cell divides mitotically (M).



Cell division and differentiation from cambium to xylem/phloem. Tom Michaels

This type of cell division, in which new cells are formed either to the outside or inside, and the cell wall that separates the two new cells is parallel to the outside of the stem, is called periclinal division. Periclinal division by the cambium makes new cells that add girth to the plant. The cells that are added subsequently differentiate into xylem and phloem depending on their location to the outside or inside of the cambium. The meristem needs to divide periclinally to add girth to the plant stem.

In Frame #4, pay particular attention to a different type of cell division, where the cambium cell has divided so that the wall between the two cells is perpendicular to the outside of the stem. This is called anticlinal division. The meristem occasionally needs to divide anticlinally because as the stem is growing in girth, the diameter of the ring of vascular cambium must expand to keep up, or it will split into pieces and no longer form a continuous ring around the stem. Frame #4 also shows that the cambium cell to the inside has differentiated into xylem (X). In Frame #5, the two cambial cells that formed from anticlinal division now each divide periclinally.

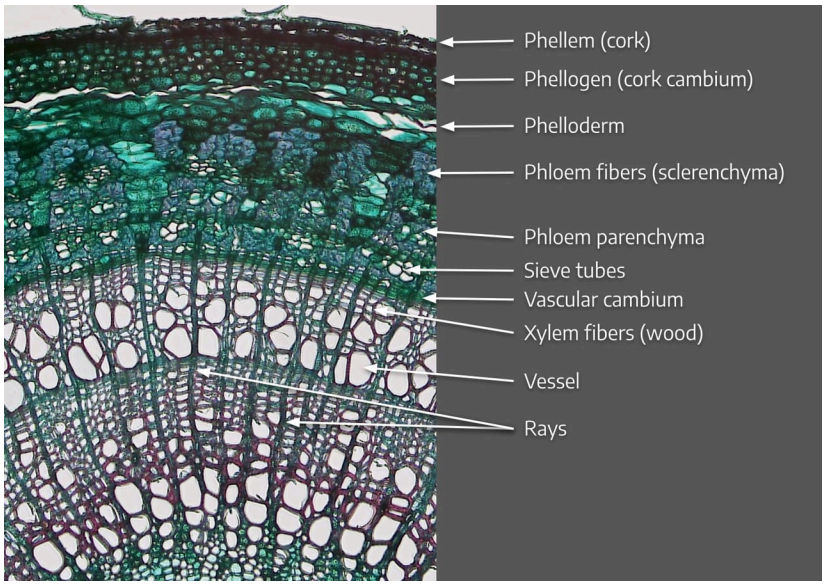
Watch this video for a demonstration of periclinal and anticlinal division (3:50)

Review questions

1. How might you recognize a plant that has secondary growth?
2. In a perennial woody dicot, how do the discrete vascular bundles found in the new seedling stem become continuous rings of xylem and phloem in the three-year-old woody stem?
3. Explain what is happening in Frames #6 and #7 in the drawing above. Note that there are two important changes: differentiation and anticlinal division.

Cork cambium

Let's look at the second type of lateral meristem, cork cambium. Cork (called "phellem" in this image) provides a protective covering around the expanding trunk of the woody plant.



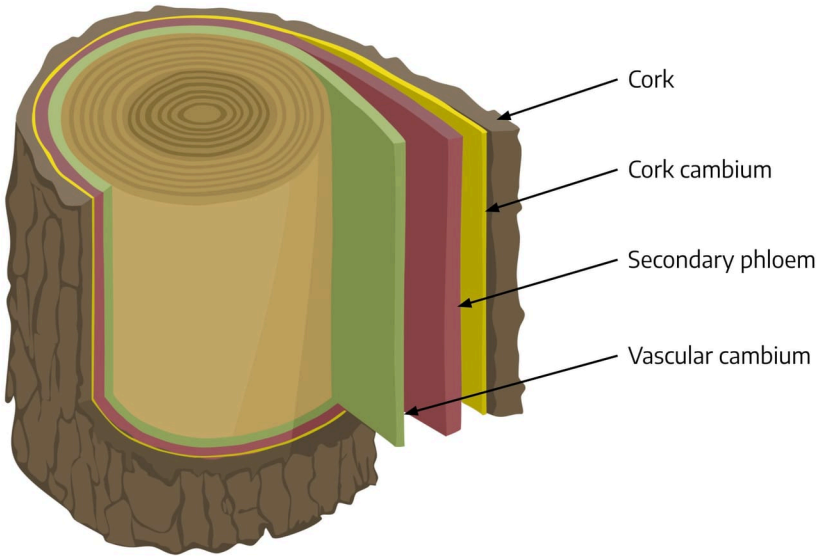
Public domain image labeled by Emily Tepe.

Cork develops in plants with secondary growth after the initiation of secondary xylem and phloem and the expansion of the stem and root's girth. Cortex parenchyma cells next to the epidermis of the young stem differentiate into the cork cambium (also called phellogen), which is meristematic. The cork cambium lays down some new cells toward the inside called phelloderm, but lays down most of its new cells to the outside, and these derivatives of the cork cambium differentiate into the cork cells. The cork cells are lined with a waxy substance called suberin (we first saw this substance in conjunction with the Casparian strip around endodermis cells) that make the cells impermeable to water and gases. Breaks in the cork cells, called lenticels, allow gas and water exchange. You can see these lenticels in corks from wine bottles (wine corks are made from the thick cork of the Cork Oak, *Quercus suber*). Cork cells die when they mature. These cells replace the protective function provided by epidermis in young roots and stems. Cork cambium and its derivatives (phelloderm and cork) are called the periderm.

Botanically speaking, the word pb_glossary id="1215"]"bark"[/pb_glossary] refers to all of the tissues exterior of the vascular cambium. So bark includes:

- Primary and secondary phloem
- Phelloderm if present
- Cork cambium
- Cork

Look again at the list above and note that the phloem is part of the bark. This is often overlooked!



Cross section of trunk. Dpaczesniak. CC BY-SA 4.0.

This illustration summarizes the layers introduced above, but omits the phelloderm. If you were to add a label for the phelloderm, where would it be? In mature trunks the phelloderm is quite a thin layer in the bark though, particularly relative to the cork layer, so that is probably why it is absent in this illustration.

If you peel bark from a living tree, you are exposing the surface of the vascular cambium of the tree, and on the inside of the bark will be the phloem. Peeling off bark will kill the plant because you are removing phloem, which disrupts the ability of the plant to move sugars through the trunk of the tree, exposes the tree to moisture loss and predator invasion, and kills the vascular cambium through desiccation. Killing the vascular cambium halts production of new xylem which will subsequently interfere with water transpiration up the stem. This is what happens when rodents girdle the trunks of young fruit trees (left) just below the snow line as they feed on the tender tissues over winter.



Photo of a girdled trunk. Emily Hoover

A tree's annual rings are found in the secondary xylem. In the spring, the newly produced xylem cells have thin walls and are large in diameter so they can accommodate the abundance of soil moisture that is typical of April and May.



Trunk cross section showing sapwood and heartwood. MPF, CC BY-SA

As the growing season progresses and soil moisture levels are depleted, the cell walls of newly produced xylem are thicker and the diameter of the xylem cells diminishes. In the next spring, the newly produced xylem cells are once again thin-walled and large. The distinct contrast between the small-celled late summer wood from the previous year and the large-celled spring wood from the following year is noticeable, and this line of demarcation between late summer and spring xylem is called the **annual ring**. In the image to the right you can see the darker xylem, called heartwood, and the lighter xylem, called sapwood. Heartwood is older xylem that is clogged with resins that darken the cells and limit their ability to transport water. Sapwood is younger, resin-free, and still functioning to conduct water up the trunk.

There isn't nearly as much phloem as xylem in a woody plant. Phloem isn't produced as rapidly as xylem, and is crushed between the vascular and cork cambium layers, so we don't see annual rings in phloem.

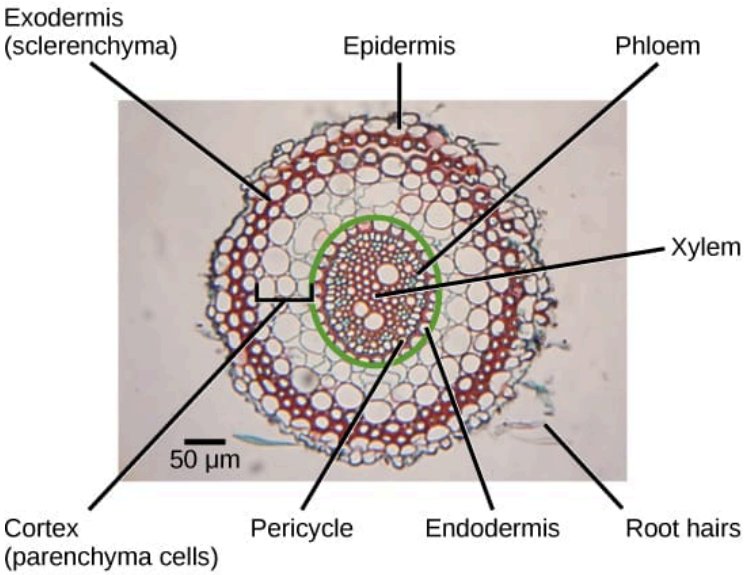
Watch this video for a look at what makes up bark (2:38)

Review questions

1. Describe the origin of annual rings. If a woody dicot is growing in a tropical climate where the weather is the same day in and day out, will you find annual rings in the wood?
2. What is the most exterior cell layer in an herbaceous stem called? What is the most exterior layer of cells in a five-year-old woody perennial plant stem called.
3. If some kids in your neighborhood get hold of a little hatchet and chop off thin slices of bark all the way around the base of one of your trees, what will happen to the tree? Why?

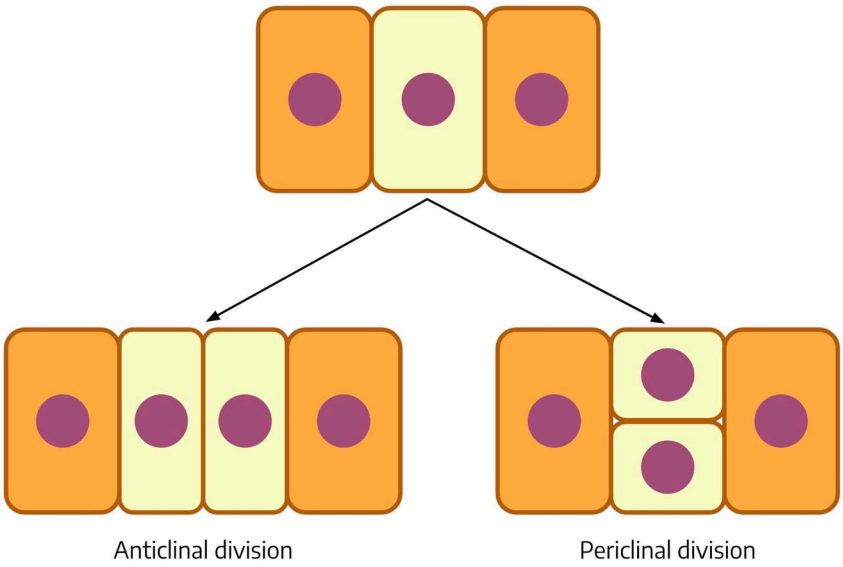
What about roots?

Roots of woody perennial dicots also have vascular and cork cambium. The vascular cambium arises from parenchyma cells lying between the xylem and phloem in roots, just as in stems. The illustration below shows the initiation of the vascular cambium in a young root. It looks like a trace of white between the primary xylem in the middle and the primary phloem in each of the four lobes of the vascular cylinder. With age, the cambium encircles the root and produces (secondary) xylem to the inside, and (secondary) phloem to outside, again just as in stems. Older roots with secondary growth also have a periderm similar to that found in the stem that replaces the function of the epidermis. If you've ever tried to dig in the soil surrounding a mature tree, you know that roots are as tough and woody as the branches above ground.



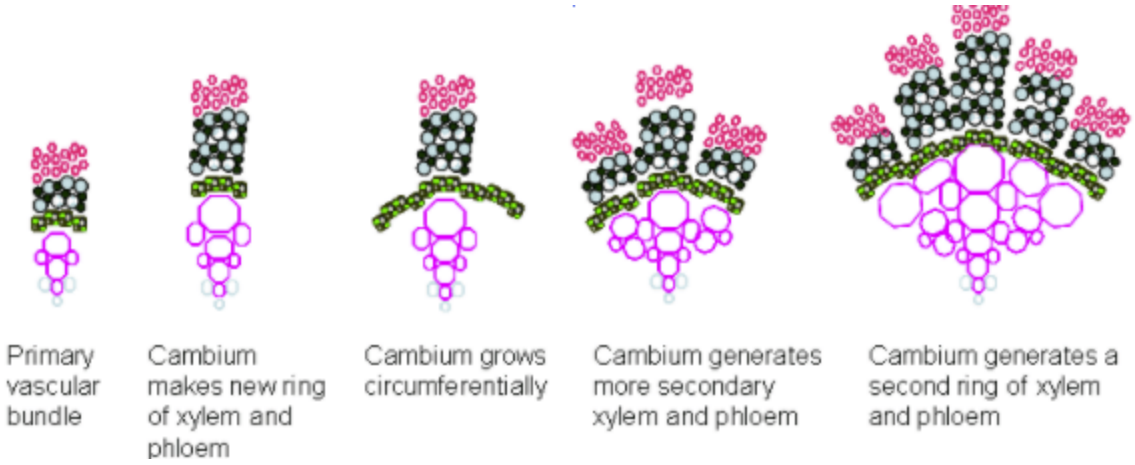
Root cross section with cell types. CNX OpenStax, CC BY 4.0

Here is a diagram to help you visualize lateral meristems including cell division.



Anticlinal and periclinal division.

The next diagram shows a vascular bundle as it grows by dividing both periclinally and anticlinally.



Ross Koning at Eastern Connecticut State University has a helpful site regarding secondary plant growth (optional reading) with descriptions and images that explain secondary growth in the stem vascular column, in the stem dermal tissues, and in the roots. L. Rost from U.C.-Davis has this nice explanation of secondary growth in roots (more optional reading).

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12.2: Flower Morphology

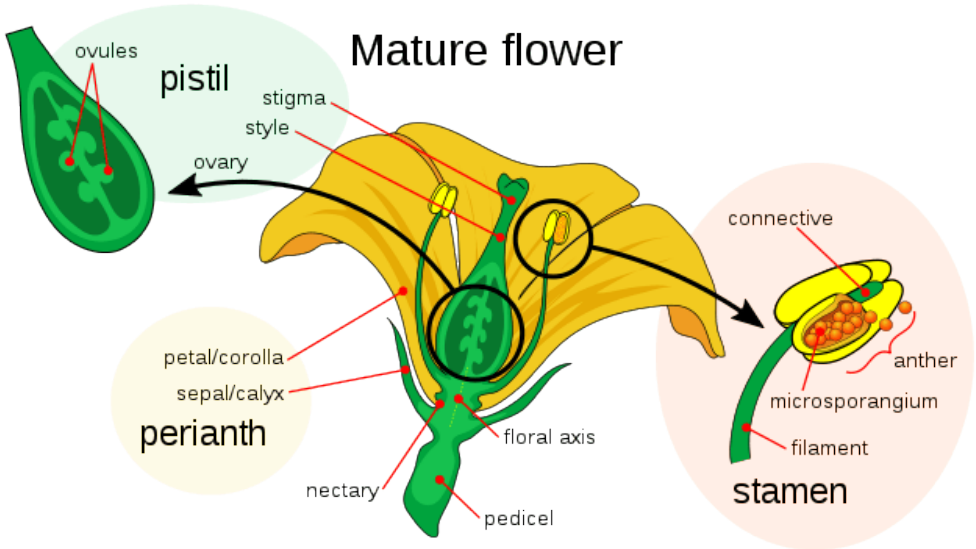
Learning objectives

- Identify the parts of a flower.
- Describe how the whorls of floral parts are related to leaves emerging from nodes on a stem.
- Describe ways in which flower structure affects pollination.

General introduction to flower parts

The angiosperm flower is built upon a structural foundation consisting of a compressed stem with four nodes and three internodes. For a visual image of these compressed nodes, imagine pushing down on a telescoping radio antenna so that the antenna sections slide down into each other. At the very top of the fully compressed antenna you'll still see the tips of each of the sections of the antenna, and this resembles the highly compressed nodes and internodes of a stem. The region of the stem containing these four compressed nodes is called the receptacle.

We have seen other examples of compressed stems with very short internodes, including the basal plate of the onion. In each of these cases we find leaves attached to these tightly compressed nodes. In the onion, the leaves are modified for water and nutrient storage as bulb scales. In the dandelion, the leaves are unmodified, but are arranged in a low-growing rosette. The flower is another example of a very compact stem with four nodes and three internodes. The leaves on this stem are highly modified to serve a reproductive function. They are so highly modified that, except for the structures at the fourth node, the parts don't resemble leaves at all.



Main parts of a mature flower. LadyofHats, Public Domain

Complete the flower parts tutorial (strongly recommended) from the science department of John Burroughs School in St. Louis; it will introduce you to, or help you review, the parts of a flower using a graphic like the one shown here.

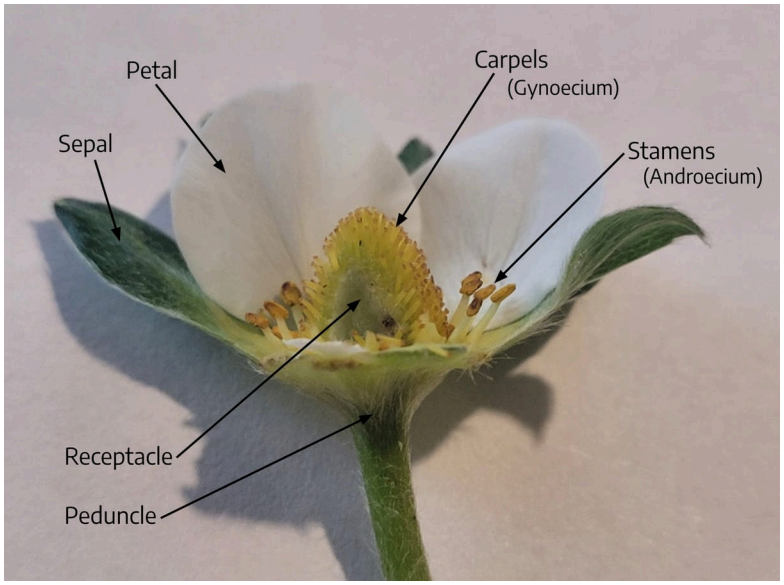
In #8 in the tutorial the author calls the structure the carpel and notes that pistil is an archaic term. You can use either **carpel** or **pistil** in this course, but we'll usually say **carpel**. **Pistil** is sometimes still for the structure if it is composed of two or more fused carpels.

After completing the tutorial you know that the flower is actually a shortened branch containing a stem with four very compact nodes. This short stem is called the **receptacle**. From the nodes on the receptacle emerge four different kinds of modified leaves that collectively have these names:

- Calyx: the fourth node, at the base of the receptacle, individually called sepals; these are the parts that still bear some resemblance to leaves
- Corolla: the third node, individually called petals
- Androecium (Greek derivation meaning “men’s house”): the second node
- Gynoecium (Greek derivation meaning “women’s house”): the first node at the tip of the receptacle

For clarity, instead of using a number to refer to a particular receptacle node, we’ll use the name of the modified leaves attached to that node. For instance, we’ll call the fourth node where the calyx is attached the “calyx node,” the third node where the corolla is attached the “corolla node,” and so on.

We’ve noted that the calyx, corolla, androecium, and gynoecium are modified leaves. This may be surprising because, in particular, the androecium and gynoecium are highly specialized for sexual reproduction.



Strawberry flower. Image by Andrew Petran and Emily Tepe.

The nodes where these modified leaves are attached are often called whorls since usually two or more of these modified leaves are attached radially around the node. Monocots generally have three modified leaves attached at each node, while dicots usually have four or five attached at each node. One interesting feature of the strawberry flower shown above is the enlarged gynoecium node of the receptacle that is covered by carpels. The receptacle will become the red culinary “fruit,” while the actual botanical fruits will be the achenes (you’ve considered them seeds, but they are a type of fruit) embedded into the outer surface of the receptacle.

Watch the next two videos to learn more about flower parts and about the specialized florets of an Asteraceae flower.

Watch this video on flower structure.

Watch this video to explore the structures of an Asteraceae flower.

Review questions

1. What is the receptacle?
2. Draw a flower and label the parts, including the nodes.
3. What is the relationship between a whorl and a node? In what way is this relationship connected to the concept that a flower’s corolla is made up of modified leaves?

Calyx

The fourth whorl at the base of the receptacle is the **calyx whorl**. The calyx is made up of modified leaves called **sepals**. In some

species the sepals look like miniature leaves; they are green and photosynthetic. In other species, like the lily, they are showy and almost indistinguishable from the petals. When sepals and petals are showy and indistinguishable, they are called tepals.

The saffron flower, below, is the source of the rare spice gathered from the long, red-orange stamens that you can barely see inside the opening flower. Notice that there are apparently no sepals. That is because the three sepals and three petals of this monocot plant look the same; they are therefore tepals.

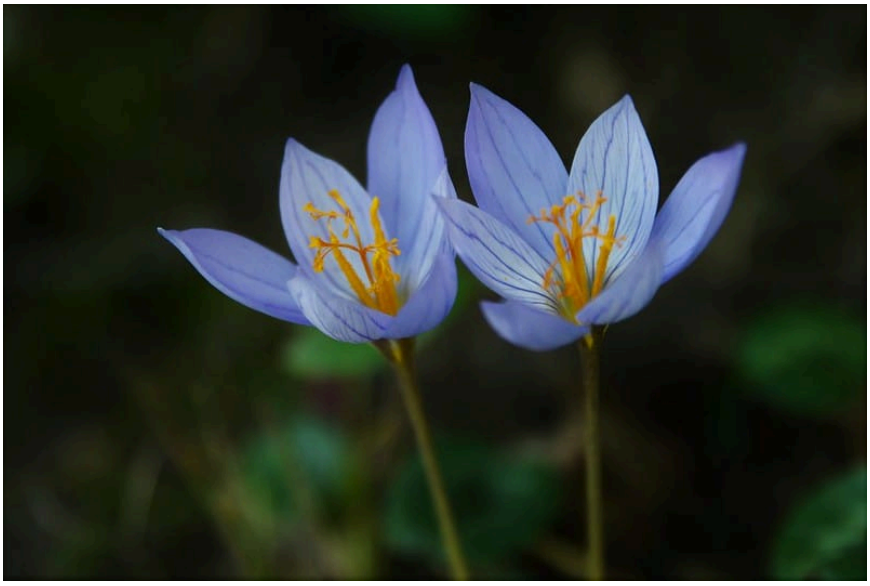


Photo of a saffron flower. Faruk Nafiz Ertürk, CC BY-SA 2.0

It may interest you to know that saffron is a geophyte that grows from a corm. We introduced geophytes in a previous lecture as plants that develop underground organs that allow the plant to survive during periods of hostile environmental conditions.

Watch this video on tepals.

Corolla

The next whorl toward the tip the receptacle bears the **corolla**. The corolla is composed of highly modified leaves called **petals**. Petals attract pollinators through their bright colors and showy patterns. Petals may also exude nectar near their site of attachment to the receptacle to reward insects who visit the flowers and, when doing so, spread pollen from flower to flower. Color patterns on the petals may simulate a “bulls eye” or landing strip that provides the insect with a visual guide pointing to the location of the nectar, as in the violet, below.



Photo of a violet. Inga Munsinger Cotton, CC BY 2.0

The calyx and corolla are collectively named the perianth. Some flowers lack a perianth. Corn is an example; it is wind pollinated and has no need for a showy perianth to attract insect pollinators.

Review question

1. Sepals and petals are modifications of what other plant structure?

Androecium



Rose of Sharon flower Tim Green CC BY 2.0



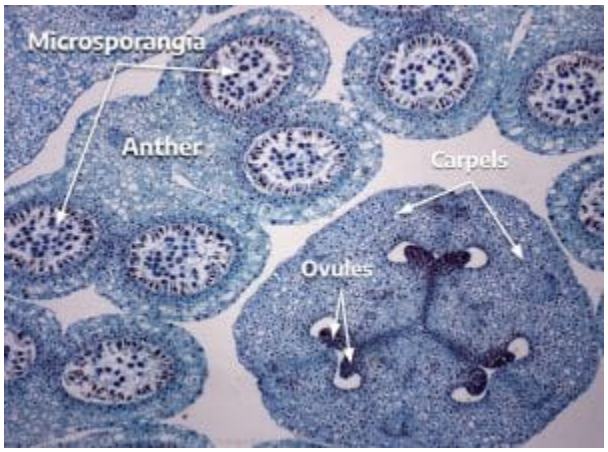
Tomato androecium. pxfuel.com Public domain.

The third whorl as we move towards the tip of the receptacle is the **androecium whorl**. The androecium is composed of modified leaves called **stamens**. Stamens are found in many different arrangements. The picture of the Rose of Sharon flower, in the top photo above, shows an androecium composed of an abundance of stamens in an open arrangement. In contrast, the 10 stamens in the tomato androecium (bottom photo above) are fused into a cone that surrounds the gynoecium. The tomato's cone of stamens is a structure through which the tomato encourages self-pollination. It is difficult for pollen from another plant to get to the stigma of the carpel before pollen from the flower's own stamen.

Stamens have two distinct components:

Filament (a long stalk)

- The filament has an architectural function, in that it lifts the anther to a position where it can effectively release pollen grains into/onto the pollinator.
- It also has a physiological (or some might say plumbing) function, in that it connects the anther to the plant's vascular system so that it can receive water and nutrients.



Cross section of a developing flower. Marc Perkins. CC BY-NC 2.0

Anther (usually four sacs containing pollen grains).

- Inside the pollen sacs are microsporangia and microspore mother cells where a special type of cell division called **meiosis** takes place (to be covered later). Meiosis in the microsporangia leads to formation of the male gametes (sperm) that will be packaged in a pollen grain.

The image above shows a cross section through a developing flower, showing components of the androecium and gynoecium.

Gynoecium

The whorl at the tip of the receptacle supports the **gynoecium**. The gynoecium is composed of carpels. Several carpels may be fused into a compound carpel (which may also be called a pistil). The Berberis (Oregon Grape) flower on the right has a fused carpel; the photo clearly shows the locule (inner chamber) with the ovules.

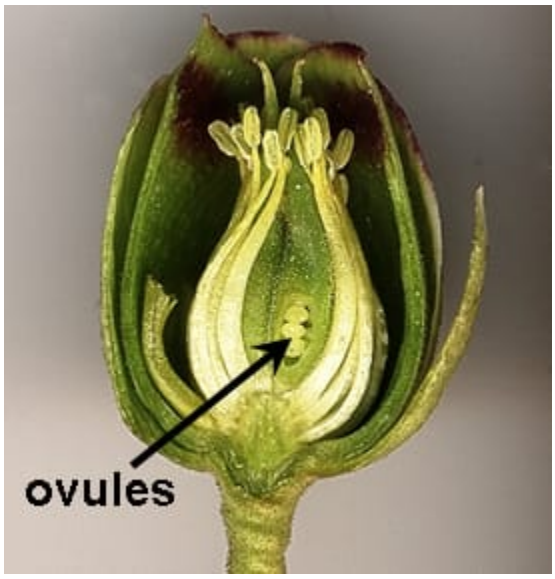


Photo of Berberis (Oregon Grape) Simon Garbutt CC BY-SA 3.0

As you saw in the tutorial, the carpel consists of three parts:

Stigma

A tip on the end of the structure called the stigma.

Style

The stalk that elevates the stigma.

Ovary

The swollen base, which includes:

- A chamber called a locule
- Inside the locule, one or more ovules
- Inside the ovules, an embryo sac — the megasporangia and megaspore mother cells, which when fertilized by pollen the ovule become a seed
- Meiosis of megaspore mother cells in the embryo sac leads to the formation of the female gametes (eggs)



Drawing of a hypogynous (a), a perigynous (b) and an epigynous flower (c). Gustav Hegi. Public domain

When you begin to compare structural differences among flowers, you will find that the position of the calyx and corolla relative to the ovary differs between some species. A more complete description of that relative alignment can be seen in the picture above, and is described here:

Epigynous flowers

Other flower parts are attached ABOVE the ovary.

This is called an **inferior ovary** because the gynoecium node isn't positioned right at the tip of the receptacle, but rather is sunken down into the receptacle below where the androecium, calyx, and corolla are attached. This means that the ovary is surrounded by other tissues, primarily receptacle tissue. This will have an impact on whether any accessory plant tissues make up the fruit. More on that later.

Perigynous flowers

The ovary is surrounded by the fused bases of flower parts (calyx, corolla, androecium) that surround the ovary.

Hypogynous flowers

Other flower parts are attached BELOW the ovary. This is called a superior ovary because the ovary sits above the point of attachment of the top whorl.

A flower that has all four of the parts described above — Calyx, Corolla, Androecium, and Gynoecium — is called a "complete" flower. Flowers missing one or more parts are described as "incomplete." We noted earlier that corn produces a flower without perianth. Such a flower could be described as "incomplete."

Review questions

1. Sperm are produced from microspores contained in what plant part? To which whorl is this part attached?
2. Eggs are produced from megaspores contained in what plant part? To which whorl is this part attached?
3. Which type of ovary is shown in the tutorial graphic at the beginning of this lecture from which you learned the parts of the flower?
4. In what way does the filament of the stamen have an architectural function? How might this make a difference to the plant's reproduction?

Pollination patterns

A flower with both androecium and gynoecium — that is both male and female parts — is called perfect or bisexual or hermaphroditic. Perfect flowers may be capable of self-pollination. Pollen produced within the flower may fall on a stigma in the same flower, and the sperm that it carries may fertilize the egg in the ovule. Sometimes, the timing of events during the stages of flower maturation encourage self-pollination. For instance, in some species the anther matures and pollen is shed, and the stigma is receptive, before the flower even opens. This is called cleistogamy, and is common in self-pollinating agricultural crops. Self pollination is encouraged because it is difficult for pollen from another flower to get to the stigma within a closed flower before pollen from the flower's own anther gets there first. Flowers that are fully open when mature are chasmogamous and facilitate pollination from other flowers.

On the other hand, the development timing of male and female organs in a different species might encourage outcrossing by releasing pollen when the stigma in the same flower is not receptive, or vice versa. This relative timing is called Protandry when the pollen is shed before the stigma is receptive, and Protogyny when the stigma is receptive prior to pollen shed.



Male and female watermelon flowers. Pollinator. CC BY-SA 3.0

There are also genetic mechanisms called self-incompatibility, through which the stigma and style recognize pollen produced by the same plant and stop fertilization, thereby avoiding self pollination and promoting mixing genetic material (DNA) from diverse individuals.

Some plants produce imperfect male and imperfect female flowers on the same plant. The flowers containing only androecium are called staminate (male) flowers while the flowers with only gynoecium are called pistillate (female) flowers. Squash and melons, such as the watermelon shown above, are examples of plants with imperfect flowers. Corn and cucumber are others. Notice the enlarged receptacle and inferior ovary at the base of the pistillate flower of the watermelon. These flowers, because they are missing one of the four parts, could also be described as incomplete.

For the ultimate avoidance of self pollination, some plants have only staminate or only pistillate flowers. A single-sex plant like this is called dioecious (plants with both sexes, whether perfect or imperfect flowers, are called monoecious). Hops, asparagus, and hemp are examples of dioecious crop plants.

Review questions

1. Which floral characteristics or patterns of timing favor self-pollination?
2. Which floral characteristics favor cross-pollination?
3. When you eat asparagus, is the plant part you are eating more likely to be male or female? Why?

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12.3: Atlas- Flower Morphology

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.

Floral Symmetry

Flowers that have multiple lines of symmetry (like a starfish) are **radially symmetrical**, also called actinomorphic. Flowers with only a single line of symmetry (like you) are **bilaterally symmetrical**, also called zygomorphic.

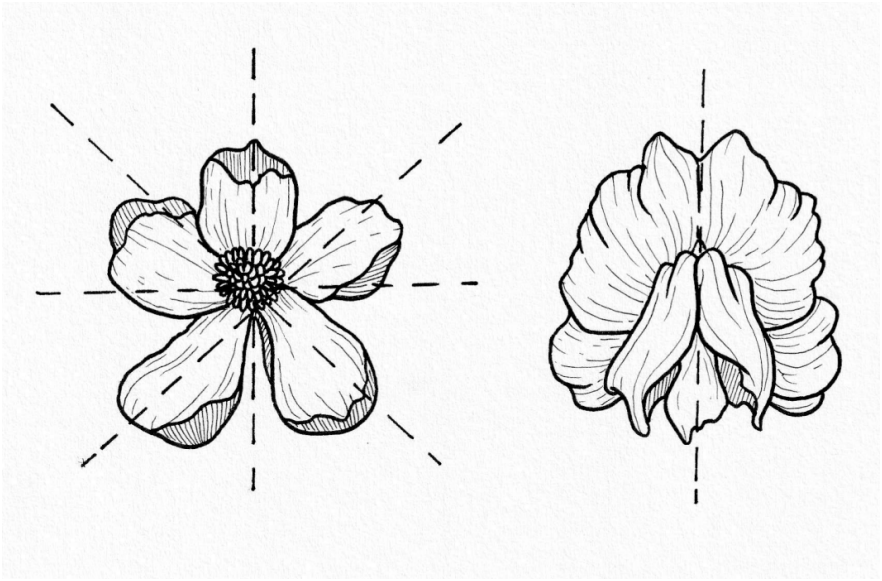


Figure 12.3.1: On the left is a picture of a radially symmetrical flower. It has five petals that all radiate out from a central point, like a star. We can draw many lines of symmetry through this flower, where if we folded the flower along that line, the two sides would line up with each other. (Note: 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.

Radial Symmetry (Actinomorphic)



Figure 12.3.2: These are two duplicate images of the same flower. This *Trillium* flower has three lines of symmetry: one that travels from the tip of each petal down between the remaining two petals. The lines are drawn in on the picture on the right so you can compare. Photos by Maria Morrow, CC BY-NC.



Figure 12.3.3: Just as with the set of images above, these are two duplicate images of the same flower and the image on the right has lines of symmetry drawn in. This salmonberry flower has five lines of symmetry, though only three have been drawn in. Can you find the other two? Photos by Maria Morrow, CC BY-NC.

Bilateral Symmetry (Zygomorphic)



Figure 12.3.4: Again we have two duplicate images, but this one includes several florets. This cluster of bleeding hearts has two florets that each have a line of symmetry added in the image on the right. On each heart-shaped floret, the line travels from top to bottom, dividing it into two equal halves. There are no other lines of symmetry we could draw. Photos by Maria Morrow, CC BY-NC.



Figure 12.3.5: Again we have two duplicate images with the image on the right showing a line of symmetry drawn in. This violet has one larger petal on the bottom with two smaller petals winging out to either side. We can draw one line of symmetry through the center of the larger, lower petal and between the 4 smaller petals (as shown on the right). Due to the presence of the single, larger petal, there are no other lines of symmetry we could draw. Photos by Maria Morrow, CC BY-NC.

Whorls

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**. If one of those missing whorls is either the androecium (pollen-producing) or gynoecium (seed-producing), the flower is also **imperfect**.



Figure 12.3.6: 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 12.3.7: 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.

Ovary Position

We can use the location of the ovary to further distinguish between flowers. 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), 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.

Superior Ovary (Hypogynous Flowers)



Figure 12.3.8: 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. Image by Gustav Hegi (1876–1932), Gustav Dunzinger, Public domain, via Wikimedia Commons.

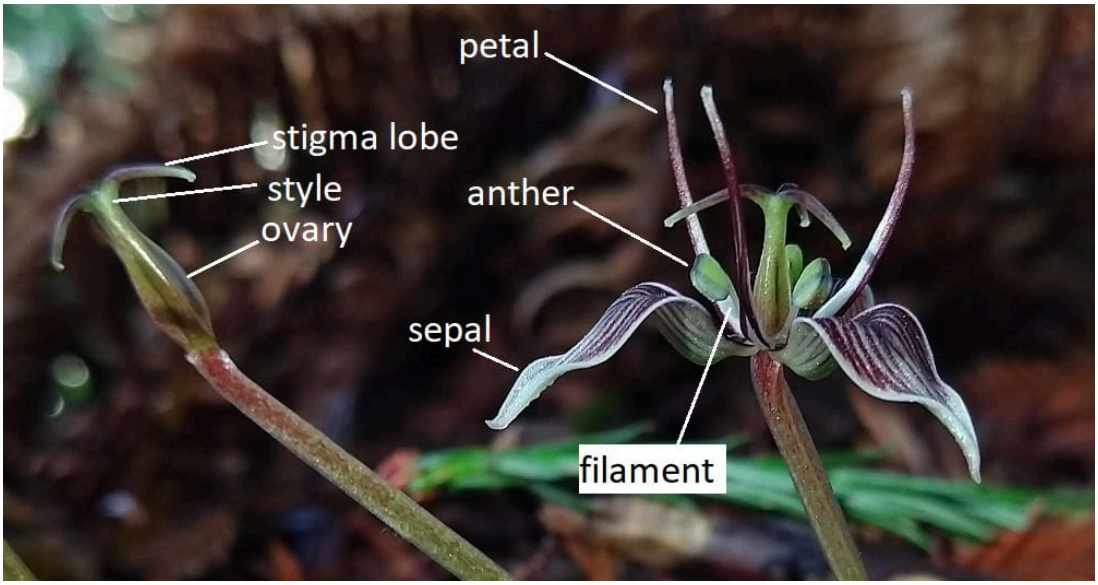


Figure 12.3.9: In the image above, we see two flowers (actually two florets of an underground umbel!) of a fetid adderstongue, *Scoliopus bigelovii*. The one on the left has shed all whorls except the gynoecium. This allows you to see what the gynoecium looks like and where it is positioned in the one 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.

Inferior Ovary (Epigynous Flowers)

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).



Figure 12.3.10: A drawing of an epiogynous flower. The calyx, corolla, and androecium fuse together above the gynoecium. The ovary sits below these other whorls, an inferior ovary. Image by Gustav Hegi (1876–1932), Gustav Dunzinger, Public domain, via Wikimedia Commons.

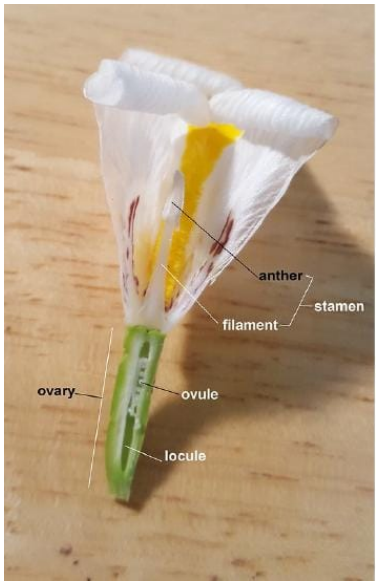


Figure 12.3.11: In this flower, the floral whorls are situated above the ovary, which is the elongated, green tube that contains the ovules. Photo by Melissa Ha, CC BY-NC.

Semi-inferior Ovary (Perigynous Flowers)

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 12.3.12: A drawing of 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. Image by Gustav Hegi (1876–1932), Gustav Dunzinger, Public domain, via Wikimedia Commons.

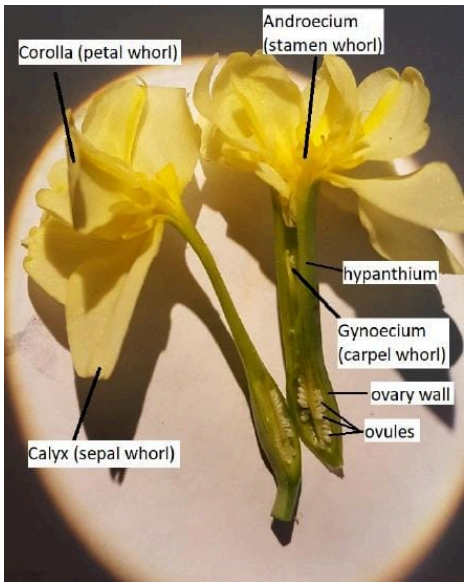


Figure 12.3.13: In this flower, the floral whorls join together where the petals and sepals seem to end. They then form a long, tubular hypanthium that looks much like an inferior ovary from the exterior. However, you can see the actually ovary (filled with ovules) is located only at the base of this structure. Photo by Melissa Ha, CC BY-NC.

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12.4: Terms

These are the important terms from this chapter to be sure to know. You might also find these in later chapters.

Androecium	One of the whorls of a flower and is all of the male reproductive parts; stamens.
Annual rings	Demarcation between small-celled later summer and large-celled spring secondary xylem.
Anther	Pollen-bearing component of the stamen.
Anticlinal division	Type of cell division in which the new cells have divided so that the wall of the cells is perpendicular to the outside of the stem.
Axillary bud	Bud borne in the axil of a stem.
Bark	All tissues exterior of the vascular cambium, including the primary and secondary phloem, phelloderm (if present), cork cambium, and cork.
Bisexual	A flower that has both the androecium and gynoecium; also called hermaphroditic or perfect flower.
Calyx	One of the whorls of a flower; located at the base of the receptacle, and contains all the sepals.
Carpel	Composed of three parts: stigma, style, and ovary.
Cell division	Process in mitosis where one plant cell divides into two identical cells.
Chasmogamy	When the anther matures after the flower opens and pollen is shed before the stigma becomes receptive; common in non self-pollinating crops.
Cleistogamy	When the anther matures, pollen is shed, and the stigma is receptive before the flower opens; common in self-pollinating crops.
Complete flower	Where all four whorls are present: calyx, corolla, androecium, and gynoecium.
Cork	Outer protective tissue of bark; also called phellem.
Cork cambium	Lateral meristem responsible for secondary growth that replaces the epidermis in roots and stems; also called phellogen.
Cork cells	Cells located in the cork; lined with suberin and dead at maturity.
Corolla	One of the whorls of a flower consisting of all the petals.
Cortex	Also known as the ground meristem; found just inside the epidermis, extends toward the interior of the stem and root, and is made up of three types of cells: parenchyma, collenchyma, and sclerenchyma.
Derivative (cells)	Other sister cells that, after the initial meristematic initial cells are created, divide once or twice more and then differentiate.
Dermal	Outside of the plant; provides protection for the plant cells they surround.
Dioecious	When an entire plant has only male or only female flowers; means “two houses.”
Epigynous	When the perianth and androecium are positioned above the ovary; also called an inferior ovary.
Fascicular cambium	Cambium within the vascular bundle.
Filament	Stalk that holds up the anther so that pollen grains can be effectively released.
Gynoecium	One of the whorls of the flower and is all of the female reproductive parts; carpels.
Heartwood	Older, darker xylem in the stem that is clogged with resins that limit the transport of water.
Hermaphroditic	A flower that has both the andreocium and gynoecium; also called a perfect flower or bisexual.
Hypogynous	When the perianth and androecium are attached below the ovary; also called a superior ovary.

Imperfect flower	Flower that has only the androecium OR only the gynoecium present.
Incomplete flower	Flower missing one or more of the four whorls.
Inferior ovary	When the perianth and androecium is positioned above the ovary; also called an epigynous flower.
Initials (cells)	Meristem cells that remain meristematic because they continue to initiate new cells.
Interfascicular cambium	Cambium between the vascular bundles.
Lateral meristem	Specialized meristems made up of cells that undergo mitotic cell division.
Lenticels	Breaks in the cork cells that allow gas and water exchange.
Locule	Chamber in the ovary.
Monoecious	When an entire plant has both male and female parts (can be perfect or imperfect); means “one house.”
Ovary	Part of the carpel; contains ovules which develop into seeds.
Ovary wall	Provides protection to the ovules; also called the pericarp.
Ovule	Part of the ovary that contains an embryo sac; surrounded by the nucellus, which develops into a seed after fertilization.
Peduncle	Large, central stalk that attaches the rachi to the stem of the plant.
Perfect flower	A flower that has both the andreocium and gynoecium; also called hermaphroditic or bisexual.
Perianth	Both the calyx and corolla.
Periclinal division	Type of cell division where the new cells are formed either to the outside or inside and the cell wall that separates the two new cells is parallel to the outside of the stem.
Periderm	Consists of the cork cambium, phelloderm, and cork.
Perigynous	When the ovary is surrounded by the fused bases of the perianth and androecium.
Petals	Modified leaves that make-up the corolla; showy, and attract pollinators.
Phellem	Another name for cork.
Phelloderm	New cells that are laid down toward the inside of the stem or root by the cork cambium.
Phellogen	Another name for cork cambium.
Pistil	Term used when several carpels are fused together.
Pistillate flower	An imperfect flower that contains only the gynoecium.
Primary (cells)	Cells that originate from cell divisions of the apical meristem.
Primary growth	Growth that results from activity by an apical meristem; causes the elongation of the cells in the apical meristem region, which leads to increasing plant length.
Primary phloem	Phloem tissue that results from differentiation of derivative cells (procambium).
Primary xylem	Xylem tissue that results from differentiation of derivative cells (procambium).
Protandry	When the pollen is shed before the stigma is receptive.
Protogyny	When the stigma is receptive prior to the pollen shedding.
Receptacle	Base of the flower where the floral parts are attached.
Sapwood	Younger, lighter xylem in the stem that is resin-free and transports water up the trunk.

Secondary growth	Growth that results from activity by a lateral meristem; causes thickening of the stem or root rather than elongation.
Secondary phloem	New phloem formed on the outside and produced by the fascicular cambium.
Secondary xylem	New xylem formed on the inside and produced by the fascicular cambium.
Self-incompatibility	When there are genetic mechanisms that inhibit self-pollination of a flower.
Self-pollination	When the pollen from the plant pollinates the stigma of the same plant.
Sepals	Outermost whorl of the flower that protects the flower and photosynthesizes.
Stamen	Modified leaf; collectively makes up the androecium. A stamen is made-up of the anther and filament.
Staminate flower	An imperfect flower that contains only the androecium.
Stigma	Receptive apex of the carpel of a flower, on which pollen is deposited at pollination.
Style	Part of the carpel that elevates the stigma to a position for reception of pollen; conduit for pollen tube growth.
Suberin	Waxy substance present in the cell walls of corky tissues; impermeable to water and gases.
Superior ovary	When the perianth and androecium are attached below the ovary; also called a hypogynous flower.
Tepal	When the sepals and petals are showy and indistinguishable.
Vascular cambium	Lateral meristem producing vascular tissues.
Vascular tissue	System containing vessels that carry or circulate fluids and dissolved minerals in the plant; composed of xylem, phloem, and bundle sheath cells.
Whorl	Node on the receptacle where the four types of modified leaves are attached (four whorls of a flower).

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13: THE ORIGIN OF FLOWERING

Learning Objectives

- Explain the evolutionary innovations that distinguish flowering plants (angiosperms) from other seed plants.
- Describe the structure and function of flowers, fruits, and their reproductive components.
- Understand the diversity and classification of inflorescences and pollination strategies.
- Identify the major types of fruits and their modes of seed dispersal.
- Recognize key characteristics of important angiosperm families such as Fabaceae, Asteraceae, and Poaceae.

This chapter explores the fascinating evolution of flowering plants, or angiosperms, often referred to as “Spermatophyta 2.0” — an upgraded version of seed plants. Unlike gymnosperms, angiosperms have several unique features such as enclosed ovules, double fertilization, and highly efficient reproductive strategies. These innovations allowed them to outcompete other plant groups, especially in the understory where gymnosperms struggled due to their slower life cycles.

13.1: Spermatophyta 2.0

13.2: The Flower and the Fruit

13.3: Three plant families you wanted to know but were too afraid to ask

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13.1: Spermatophyta 2.0

Flowering plants (angiosperms, Angiospermae) are sometimes referred to as “Spermatophyta 2.0.”, or “upgraded gymnosperms”. In fact, there is no single character which unequivocally differs flowering plants from other seed plants. Only several characteristics combined together will distinguish angiosperms. Flowering plants have their ovules inside an additional cover: **pistil** which corresponds with megasporophyll (sporangium-bearing leaf); later, the pistil develops into the *fruit*. These plants have an almost complete reduction of gametophytes: three or even two cell of the pollen (male gametophyte) and seven (sometimes even four) cells in **embryo sac** (female gametophyte), there are no archegonia or antheridia. Like gnetophytes, they have double fertilization. The sperms (spermatia) come through the pollen tube (like in conifers and gnetophytes). One sperm fertilizes the egg cell, and the other sperm fertilizes the biggest cell of embryo sac (Figure $13.1.1$).

While the first fertilization results in a “normal” diploid zygote which grows into embryo, the second fertilization ignites the process of feeding tissue development. This feeding tissue is **endosperm**$_2$, frequently triploid ($3n$) since it *originates from the sperm and cell with two nuclei* and sperm, or diploid ($2n$), if the biggest cell of embryo sac (**central cell**) had one nucleus only.

Double fertilization may be explained in several ways:

1. the second fertilization results in second, “altruistic” embryo which sacrifices itself to feed the sibling;

2. second fertilization is only a signal which initiates the development of endosperm and it does not really matter which genotype it has;

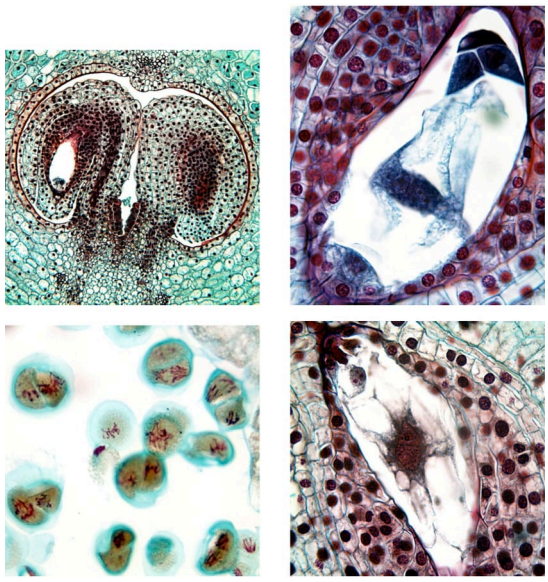


Figure $13.1.1$ Left to right, top to bottom: Lilium (Liliidae) ovules, female gametophyte (em- bryo sac), meiosis II in pollen sacs and double fertilization (egg cell on top is fusing with first sperm, second sperm nucleus in the center is fusing with the nucleus of the central cell). Magnifications ×100 (first) and ×400 (others).

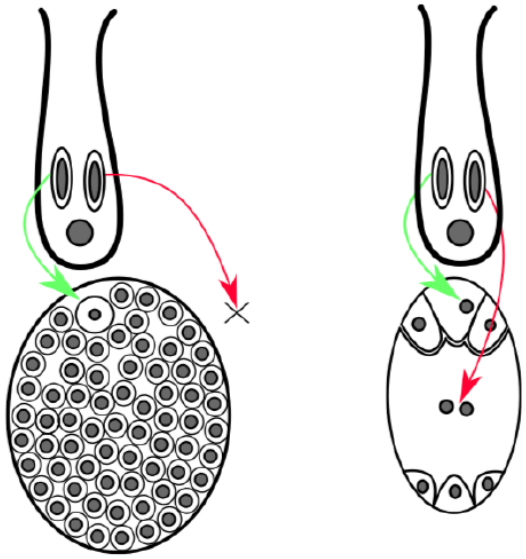


Figure 13.1.2 Single fertilization (left) and double fertilization (right). Egg fertilization is in green color. Note that in double fertilization second sperm fertilizes (red arrow) cell sister to egg (central cell in angiosperms), originated from the same megaspore.

3. to make a functional nutrition tissue, angiosperms need a polyploid genome whereas its origin is not so important.

Second hypothesis explains well how angiosperms saved time and resources. Third hypothesis is indirectly supported by the fact that in animals, namely two families of scale insects, there is a similar process (zygote descendant joins sister cell of the egg) which resulted in special polyploid bacteriome, tissue rich of symbiotic bacteria.

One way or another, flowering plants abandoned pre-fertilization development of the nutrition tissue, and changed endosperm$_1$ to endosperm$_2$ (Figure 13.1.2).

In the Mesozoic era, gymnosperms were the dominating plants of the tree story. However, in the uderstorey, herbaceous spore plants did not surrender to seed plants and were still dominating. Amazingly, there were almost no herbaceous gymnosperms! The explanation is that gymnosperms, being quite advanced in general, had a slow and ineffective life cycle.

While ferns and mosses have one “gunshot” in their life cycles (this is fertilization, because dissemination of spores is mainly random), seed plants have *two*: first, they want to *pollinate* the target plant, and second, they still need to *fertilize* egg cell. Naturally, keeping these two

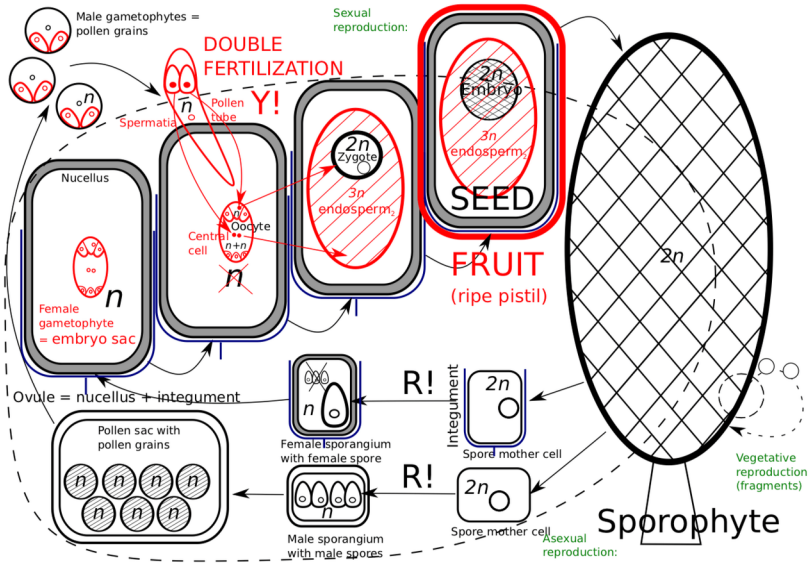


Figure 13.1.1 Life cycle of angiosperms. Innovations (comparing with the the ancestral seed plant life cycle) are in red.

"gunshots" is more complicated then keeping one.

Second shot ancestrally uses water, but higher seed plants managed to get rid of it with pollen tube. First shot used wind which is a natural pollination agent. However, more sophisticated pollination (like insect pollination) was hard to achieve, partly because it requires edible parts like nectar or excess pollen.

If gymnosperms were to increase the speed of life cycle, make more sexual structures, grow rapidly, improve vegetative reproduction, make better pollination and seed dispersal, they could win the competition with ferns in the understory. This is exactly what happened with flowering plant ancestors. Flowering plants grow fast and restore missing (eaten) parts with high speed, they **parcellate** (clone from body parts) easily, they have small and numerous floral units (flowers) which are frequently bisexual but protected from self-pollination and adapted to insect pollination, they guard ovules with pistil wall, their pollen tube grows in hours (not days and weeks), they use fruits to distribute seeds.

Since gymnosperm fertilization occurs *after* gametophyte development, there is frequently a waste of resources: if fertilization does not occur, then all nutrition tissue (endosperm$_1$) will be lost; such empty seeds are unfortunately not rare among gymnosperms. Fertilization of angiosperms involves the *signaling event*: when second sperm fertilizes central cell, it "rings a bell" saying that the first fertilization is now completed. Endosperm (endosperm$_2$ in that case) will start to develop only after the fertilization, and resources will not be wasted. This agile life cycle is the main achievement of angiosperms.

There is a growing evidence that these ancestors were *paleoherbs*, herbaceous plants (and maybe, even water plants like one of the most primitive angiosperms, fossil *Archaefructus*, or basal extant *Ceratophyllum*). Right after they won a competition with herbaceous spore plants, they started to conquer the tree storey again, and now, angiosperms dominate the Earth. There are more than 250,000 species of them which is more than any other group of living beings except insects. There are about 300 families and around 40 different orders. The only places that angiosperms do not grow are the open ocean and the central Antarctic.

The life cycle of angiosperm (Figure $13.1.3$) begins much like that of other seed plants; however, when it reaches the point of fertilization, it changes. The male gametophytes, pollen grains, produce pollen tubes which rapidly grow to the ovule and deeper, to the embryo sac. The embryo sac typically has seven cells and eight nuclei (two nuclei in the central cell). The first sperm fertilizes the egg and produces the zygote whereas the second sperm fertilizes the central cell and produces the mother cell of the endosperm$_2$:

1. 1st sperm cell (1st spermatium, n) + egg cell (n) $\rightarrow$ zygote ($2n$)
2. 2nd sperm cell (2nd spermatium, n) + central cell ($2n$ or sometimes n) $\rightarrow$ mother cell of endosperm$_2$ ($3n$ or sometimes $2n$)

(At the time of fertilization, central cell could be haploid, with one nucleus, or diploid, with two nuclei; this is because it runs mitosis without cytokinesis at the end. Consequently, nucleus of the second sperm fuses with either one or two nuclei and endosperm$_2$ is either diploid or (more often) haploid.)

At the end of life cycle, the flowering plant develops the fruit (Figure 8.2.1). Each part of the fruit is of different origin: fruit skin and wall are from mother plant pistil, seed coat is from mother plan ovule, endosperm$_2$ is a result of second fertilization, and embryo is a daughter plant resulting from the first fertilization.

What is interesting, the embryo of angiosperms is still parasitic: it lives on endosperm which originates from (fertilized, ignited) cell of female gametophyte—in essence, still similar to mosses.

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13.2: The Flower and the Fruit

The Flower

A flowercompact generative shoot with sterile, male and female zones, specifically in that order, **other flower terms see in the separate glossary in the text** (Figure 13.2.3) is a compact generative shoot that is comprised of three zones: sterile (*perianth*), male (*androecium*), and female (*gynoecium*) (Figure 13.2.2). Perianth is typically split into green part (*calyx*, consists of *sepals*) and color part (*corolla*, consists of *petals*). Sometimes perianth consists of similar parts which are neither sepals nor petals: *tepals*. This might be seen in the tulip (*Tulipa*) flower where tepals change their color from green (like in calyx) to red, white or yellow (like in corolla).

The general characters that a flower has are 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. The position of the gynoecium refers to whether the ovary is superior or inferior (Figure 13.2.6). *Inferior ovary* (cucumber, *Cucumis*, apple *Malus* or banana *Musa*) will develop into a fruit where stalk and remnants of perianth are on the opposite ends, whereas *superior ovary* will make fruit where stalk is placed together with perianth (like in tomatoes, *Solanum*). More terms are described in the following separate small glossary:

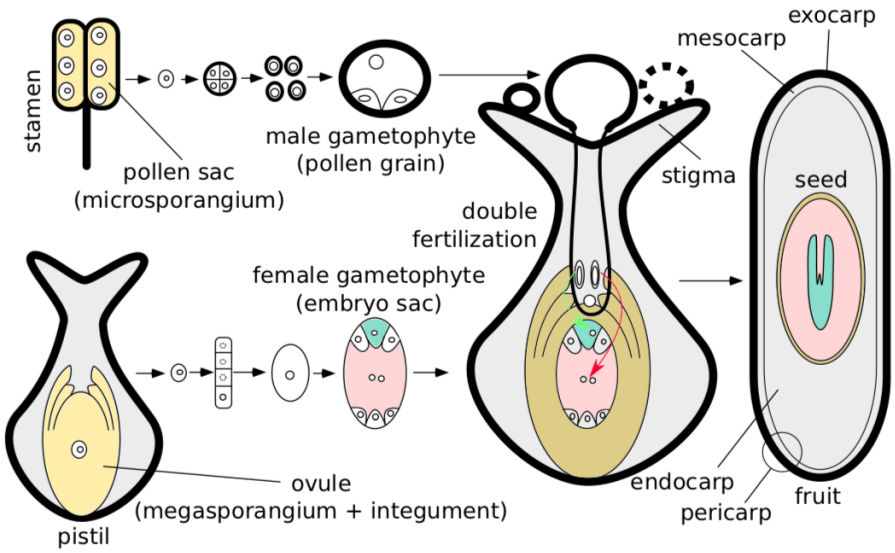


Figure 13.2.1 The origin of fruit. Note correspondences between different parts (shown with color).

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 13.2.2)

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



Figure 13.2.2 Zones in hellebore (Helleborus) flower: sterile perianth, male androecium and in the center, female gynoecium (inside, three ovules are well visible).

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.

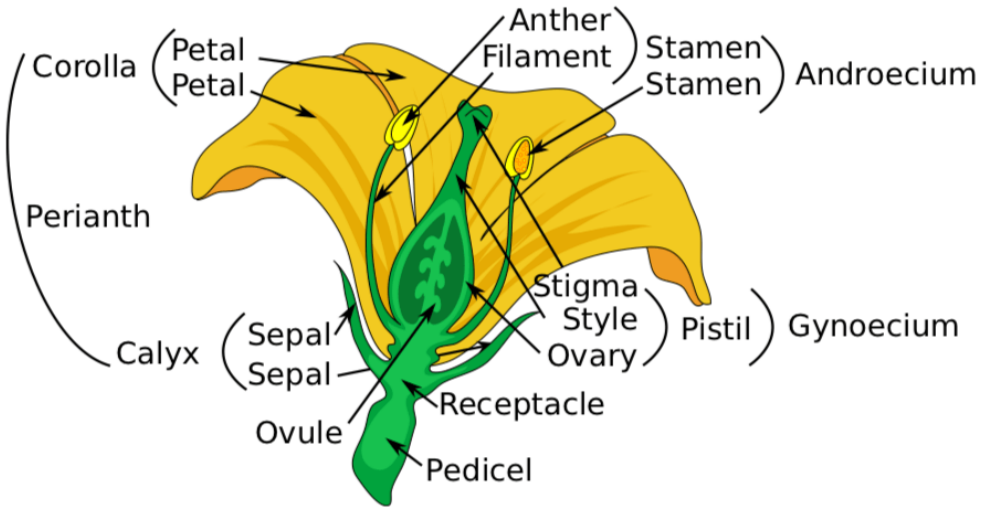


Figure 13.2.3 *Most important parts of the flower.*

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, **formula**: ∗
>
> **ZYGOMORPHIC FLOWER** A flower having only one plane of symmetry, **formula**: ↑
>
> **PERFECT FLOWER** A flower having both sexes
>
> **MALE / FEMALE FLOWER** A flower having one sex, **formula**: ♂ / ♀ (Figure 13.2.5)

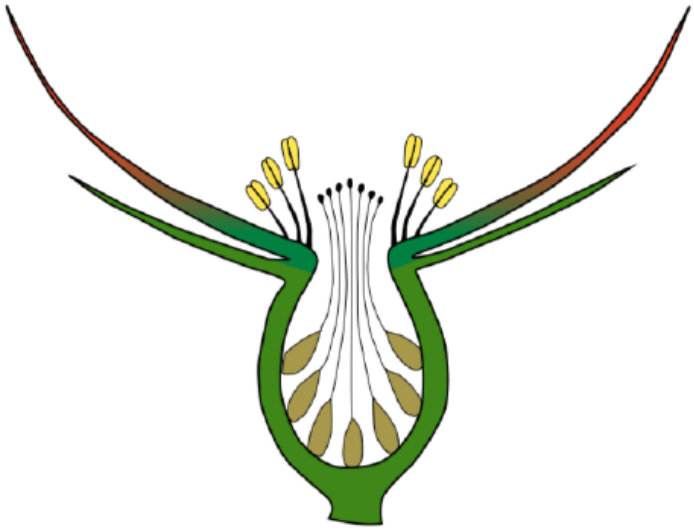


Figure 13.2.4 Flower with hypanthium (cup-shaped receptacle).

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**: $G_{\underline{...}}$

INFERIOR OVARY most of the flower is attached on the top of ovary, **formula**: $G_{\overline{...}}$

(Inferior ovary only corresponds with monomeric or syncarpous flowers.)

WHORL flower parts attached to one node

Flower formula and diagram

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:

$*K_4C_4A_{2+4}G_{\underline{(2)}}$: flower actinomorphic, with four sepals, four petals and six stamens in two whorls, ovary superior, with two fused carpels



Figure 13.2.5 Diagram of male (left) and diagram and scheme of female (central and right) flowers of sedges (Carex). Note the perigynium (external cover of pistil).

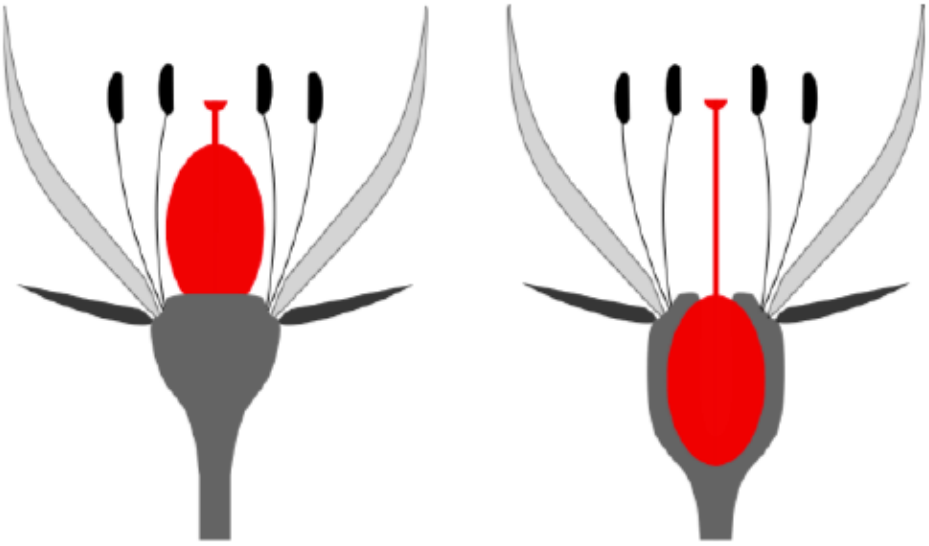


Figure 13.2.6 Position of ovary: superior (left, hypogynous flower) and inferior (right, epigynous flower).

$\uparrow K_{(5)}[C_{(1,2,2)}A_{2,2}]\underline{G_{(2\times2)}}$: 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; "∨" = "*or*"

BRACKETS "[]" and "()" show fusion

COMMA "," shows inequality of flower parts in one whorl

MULTIPLICATION "×" shows splitting

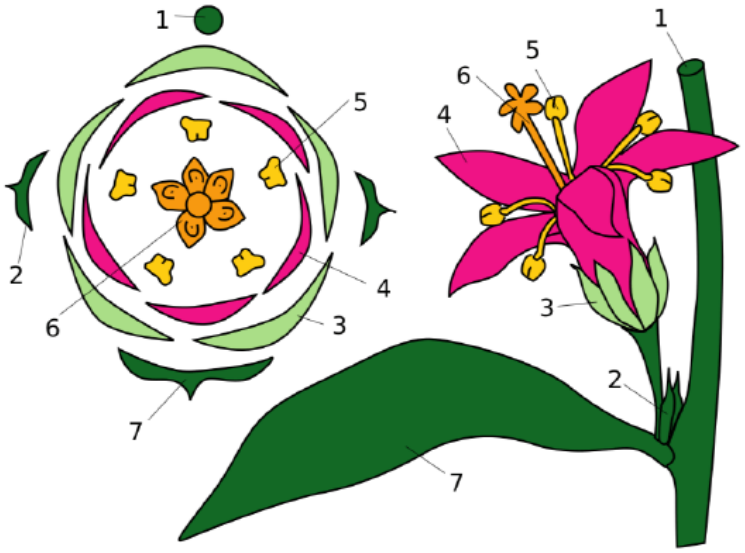


Figure 13.2.7 How to draw a diagram (graphical explanation): compare numbers on plant and on diagram.

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 13.2.7); formula of the flower shown there is $*K_5C_5A_5\underline{G_{(5)}}$.

ABC model

All parts of flower have a specific genetic developmental origin explained in the *ABC model* (Figure 13.2.8). There are three classes of genes with expression which overlaps as concentric rings, and these genes determine which cells develop into particular organ of the flower. If there are A and C genes expressed, cells will make sepals and pistils. In areas where A and B are active, petals will form; areas where B and C are active are the sites where stamens will appear. A will make a sepal, C will "create" a carpel:

- A alone $\rightarrow$ calyx
- A + B $\rightarrow$ corolla
- C + B $\rightarrow$ androecium
- C alone $\rightarrow$ gynoecium

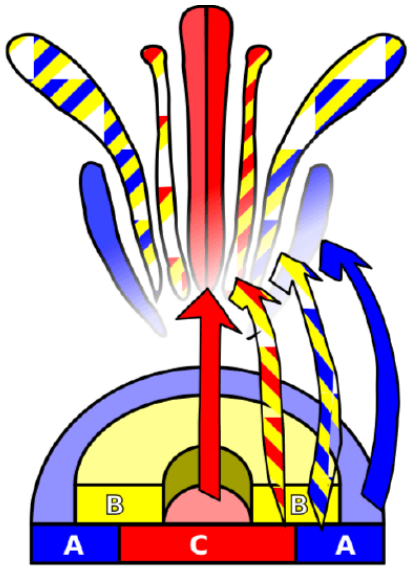


Figure 13.2.8 ABC model of flower development.

Origin of flower

An example of a primitive magnoliid flower would be *Archaefructus* which is a fossil water plant from the lower Cretaceous time period in China. Its fructifications (flower units, FU) were very primitive and did not yet form a compacted flower, instead, there were multiple free carpels, and paired stamens (Figure 13.2.9).

Another ancestral flowering plant is *Amborella*,a small forest shrub of New Caledonia (Figure 13.2.10), which is an island in the Pacific Ocean.

Amborella has irregular flowers, a stylar canal, unusual 5-celled embryo sacs that have one central cell, and only four other cells (egg cell and its “sisters”). A stylar canal is a canal that leads to the ovary that the pollen tubes pass through so these plants are not completely “angiospermic”, this represents one of the stages of the origin of pistil (Figure 13.2.11).

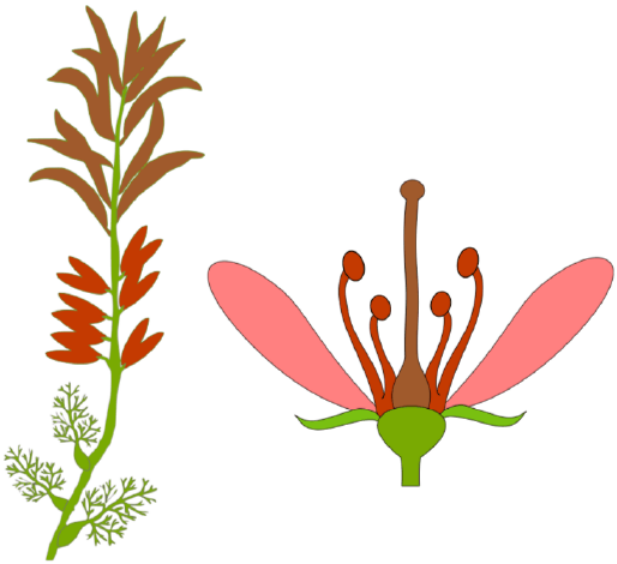


Figure 13.2.9 Comparison of Archaefructus flower (left) and typical flower (note colors). (Modified from various sources.)

The Inflorescence

Inflorescence is an isolated generative shoot (shoot bearing FU). Together, inflorescences make **generative shoot system**. Its diverse structure is of not lesser importance than the structure of vegetative shoot system.

The vast diversity of inflorescences can be split into four groups, or "models" (Figure 13.2.12). Sole flower is sometimes considered as a "Model 0".

Two models are most widespread. Model I inflorescences are based on the racemebasic monopodially branched inflorescence (Model I) (*monopodially branched* generative shoot). They are simple or double and mostly monopodial (Figure 13.2.14).

Model II inflorescences (Figure 13.2.13) bear or consist of closed (s*ympodially branched*) units. The most complete but more rare variant is **thyrsus**, whereas reduced variants (*monochasia* and *dichasia*) are more frequent.



Figure 13.2.10 Amborella trichopoda, sister group to all other flowering plants. White ruler equal to 1 mm.



Figure 13.2.11 Amborella pistil, longitudinal section: stylar canal is green, embryo sac red.

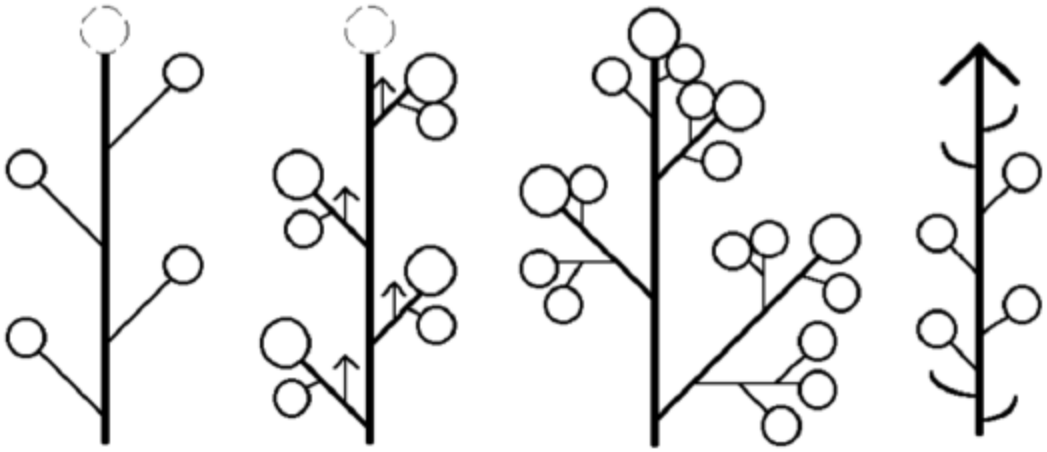


Figure 13.2.12 Four kinds of inflorescences (left to right): Model I (raceme-based), Model II (thyrsoid) , Model III (panicle) and Model IV (intercalate).

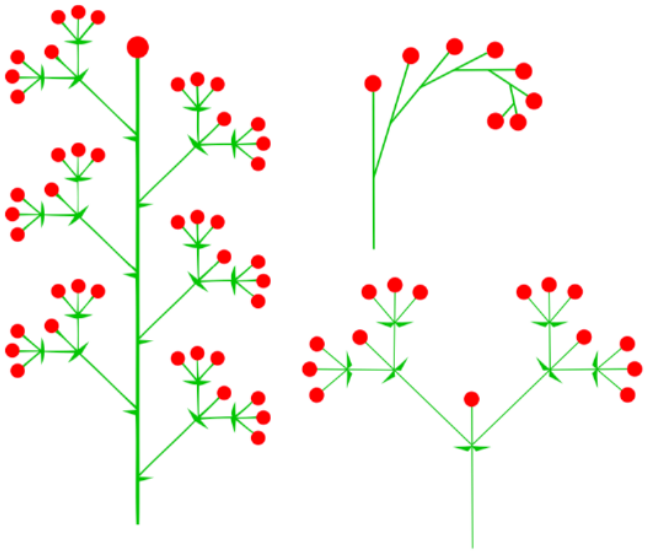


Figure 13.2.13 Model II inflorescences (from top to bottom): thyrsus, dichasium and monochasium (cincinnus).

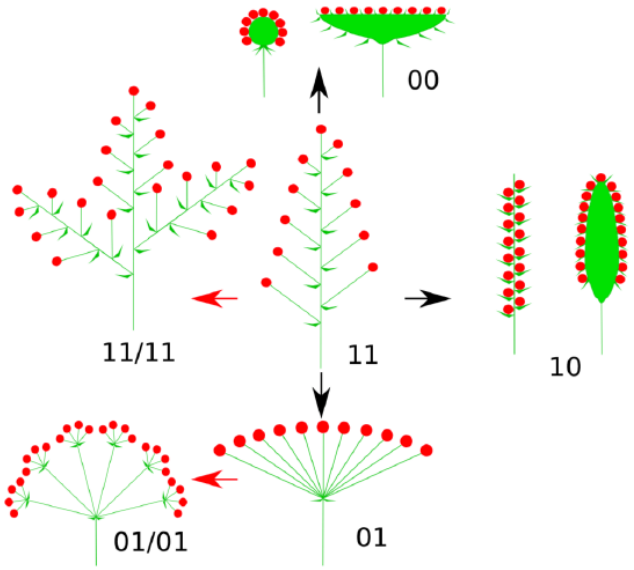


Figure 13.2.14 Different Model I inflorescences and their evolutionary connections. Digits represent the simple encoding system: first position is main axis, second position are secondary axes (flower pedicels), 1 means developed, 0 reduced. Double inflorescences have four digit positions, for the first and second orders of branching. Some names: 11 raceme, 11/11 double raceme, 10 spike and spadix, 01 umbel, 01/01 compound umbel, 00 head.

Pollination

Pollination could be of two types: self- and cross-pollination. **Cross-pollination** can happen in both abiotic and biotic ways. Abiotic would be represented by gravity, wind, or water; biotic would be performed by agents like insects, birds, bats, or in some cases tree mammals like possums. Wind-pollination is seen as being wasteful and unintelligent due to the fact that the plant needs to produce so much more pollen without any precise targeting.

Adaptation to the particular pollination agent results in different pollination syndromes. 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).

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**.

If pollination needs to be avoided, apomixis will prevent it. **Apomixis** requires reproductive organs, but there is no fertilization. One type of apomixis is **apospory** when an embryo develops from the maternal diploid tissue when an embryo develops from the maternal diploid tissue, but does not go through the meiosis stage. In this process, asexual reproduction will have become vegetative. Another type of apomixis would be **apogamy** (parthenogenesis) when embryo develops from an unfertilized gamete after diploidization has occurred. Here, vegetative reproduction evolved from sexual reproduction.

The Fruit

A *fruit* is defined as *ripened ovary, flower, or whole inflorescence*. The origins of the fruit coat and the **pericarp** (Figure 13.2.15) which is comprised of the *exocarp*, *mesocarp*, and *endocarp*, are mostly from the wall of the pistil.

Fruits can be simple, multiple, or compound. *Simple fruitssimple fruitfruit originated mostly from one pistil come from a single pistil (like cherry, *Prunus*). *Multiple fruitsmultiple fruitfruit originated from many pistils are formed from many pistils of the same flower (strawberry, *Fragaria*). A compound fruitfruit originated from the whole inflorescence: infrutescence (infructescense) would be a pineapple (*Ananas*) or fig (*Ficus*) which comes from multiple flowers (inflorescence).

Fruits can be dry or fleshy. An example of *dry fruit* is a nut like peanut (*Arachis*) or walnut (*Juglans*). Examples of *fleshy fruits* include apples (*Malus*) or oranges (*Citrus*).

Fruits also delegate dispersal function to their different parts. *Dehiscent fruitsdehiscentfruits which open (like canola, *Brassica*)

open and delegate dispersal to individual seeds.

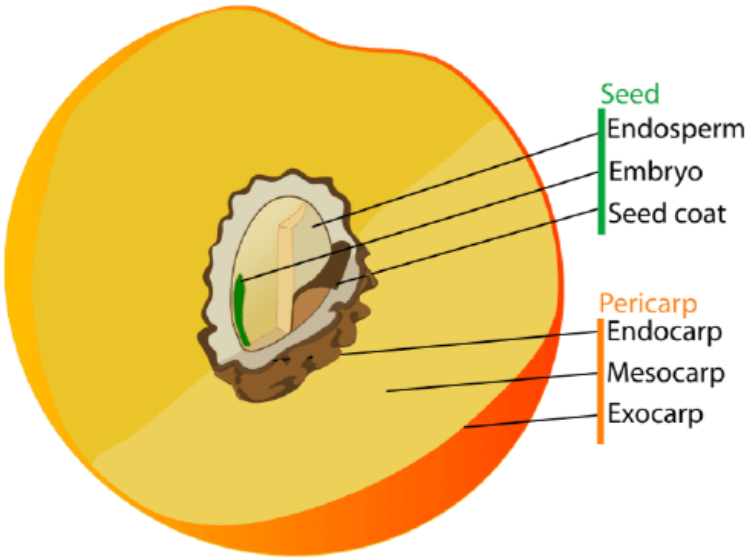


Figure 13.2.15 Scheme of drupe (e.g., peach) with three levels of pericarp. Note that pit is essentially endocarp + seed.

Indehiscent fruits (like papaya, *Carica*) will not open and will be dispersal units (**diaspores**) themselves.

Schizocarp fruits (like in spurge, *Euphorbia* or maple, *Acer*) are in between: they do not open but break into several parts, and each of them contains one seed inside. For example, maple fruit consists of two “wings”, each of them contains the part of fruit and one seed.

In addition, simple fruits could be monomerous (1-seeded) like nut or achene (sunflower, *Helianthus*), or bear multiple seeds (like follicle in tulip, *Tulipa*).

All these different variants have their own names partly described in the following table:

Type	Consistency	Opening	Example(s)
Simple	Fleshy	Indehiscent	Drupe, Berry, Hesperidium, Pome
Simple	Dry	Dehiscent	Capsule, Legume (pod), Silique (Figure 8.3.1)
Simple	Dry	Schizocarpic	Regma, Samara, Shizocarp
Simple	Dry	Indehiscent	Caryopsis (grain), Nut (incl. acorn), Achene
Multiple	Fleshy	Indehiscent	Multiple drupe
Multiple	Dry	Dehiscent	Follicle
Multiple	Dry	Indehiscent	Multiple nut
Compound	Fleshy	Indehiscent	Compound berry
Compound	Dry	Indehiscent	Compound nut

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13.3: Three plant families you wanted to know but were too afraid to ask

Angiosperms is a giant (quarter of million species) class with four subclasses (Figure 13.3.1):

- **Magnoliidae** being the most primitive with flowers of numerous free parts (like water lily, *Nymphaea*, fossil *Archaefructus* and *Amborella*);
- **Liliidae** or **monocots** are grasses, palms, true lilies and many others with trimerous flowers;
- **Rosidae** with pentamerous or tetramerous flowers and free petals;
- **Asteridae** most advanced, bear flowers with fused petals and reduced number of carpels.

Rosids and asterids each comprise about 1/3 of angiosperm diversity.

Among the numerous taxonomic groups described by scientists in the last 300 years, families of flowering plants hold the distinct place. They were established in collaborative efforts of French botanists, namely Michel Adanson and Antoine

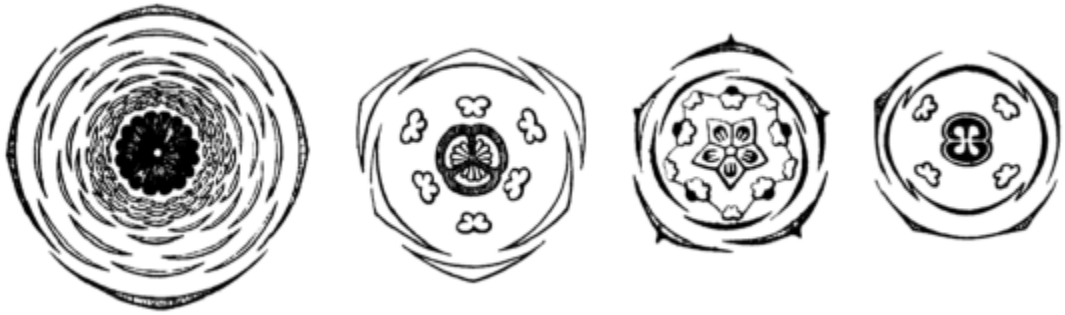


Figure 8.2.7 for graphical explanation of the flower diagram.

Jussieu. Adanson based his research on methods which are now frequently called “bioinformatics” and therefore was long ahead of his time. Jussieu proved Adanson’s ideas by establishing the living garden where plants were arranged by these families. At first, families were not accepted by “fathers of botany” like Carolus Linnaeus. But with time, more and more facts were accumulated which support the ideas enclosed in the families differentiation. The most amazing was almost absolute support of plant families concepts with new molecular methods. Many groups which looked stable (like orders of birds and mammals) appeared less robust than plant families. This is why plant families are so important.

Practically, families provide a great help in knowing plants. For example, the flora of whole North America has 20,000 species of plants. It is almost impossible to remember them all. However, there are only 200 plant families in North America. Therefore, knowing the family saves lots of time and efforts in plant determination.

Several plant families are especially important since they play a big role in economics, form widespread types of vegetation, or are simply extremely rich in species. Three of these families will be characterized below. Characterization of family should follows the plan below:

1. Meta-information: name, position in classification, number of species, distribution
2. Ecological preferences
3. Morphology and anatomy of stem, leaf and root
4. Generative organs from inflorescence to fruit, including flower diagrams and formulas. Seed.
5. Representatives and their importance

Leguminosae, or Fabaceae—legume family

Belong to rosids (Rosidae). Up to 17,000 species, third largest angiosperm family after Compositae (aster family) and Orchidaceae (orchids). Widely distributed throughout the world, but preferably in tropics. Have root nodules with *nitrogen-fixing*

bacteria. Leaves alternate, pinnately compound (once or twice), with stipules.

Three subfamilies (Caesalpinioideae, Mimosoideae, Papilionoideae) often treated as separate families. Sepals 5, united. Petals 5, in Papilionoideae they are free, unequal and have special names: *banner*, *keel* and *wing* (Figure 13.3.2), in Mimosoideae they fuse and form tube. Stamens often 10 with 9 fused and one free stamen; in Mimosoideae, stamens are numerous. Singe pistil with single carpel. Flower formula of Mimosoideae is

$$*K_{(5)}C_{(5)}A_{5-\infty}G_{\underline{1}} \tag{13.3.1}$$

Papilionoid legumes have formula like

$$\uparrow K_{(5)}C_{1,2,2}A_{1,[4+5]}G_{\underline{1}} \tag{13.3.2}$$

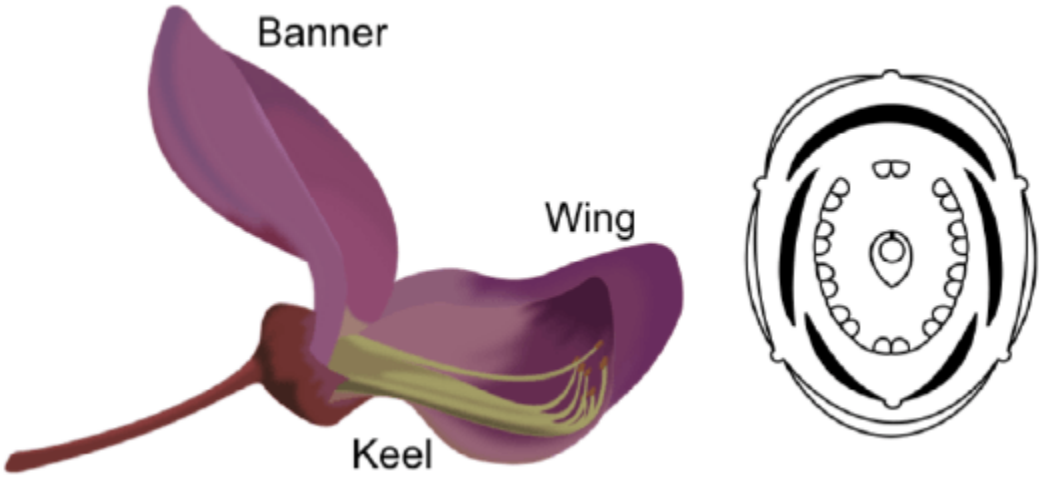


Figure 13.3.2 Leguminosae. Flowers of Papilionoideae subfamily.

Fruit is a legume (pod): dehiscent with one camera; this is different from silique of cabbage family (Cruciferae) which has two cameras (Figure 13.3.3). Mature seeds without endosperm.

Representatives of Leguminosae:

- Mimosoideae: stamens numerous, petals connected

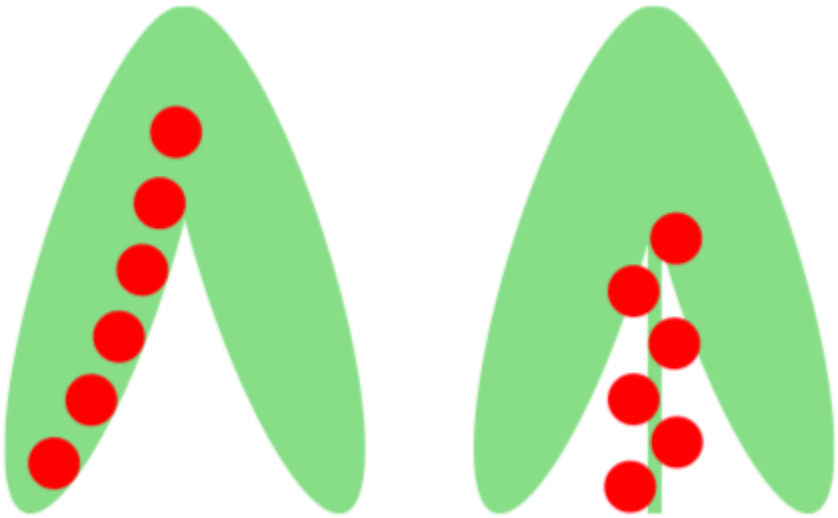


Figure 13.3.3 Opened pod (Leguminosae) versus silique (Cruciferae), seeds are red.

-*Acacia*—dominant tree of African and Australian savannas, often with phyllodes

-*Mimosa*—sensitive plant

- Papilionoideae: stamens 9+1, petals 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

Compositae, or Asteraceae—aster family

Belong to asterids (Asteridae). More than 20,000 species—second place in flowering plants. Cosmopolitan, but better represented in temperate and subtropical regions. Prefer open spaces. Herbs, rarely woody plants; store carbohydrates as inulin (not starch), sometimes have resin or laticifers (subfamily Cichorioideae). Leaves are alternate or opposite, without stipules, with pterodromous venation.

Flowers in involucrate heads which mimic one flower (Figure 13.3.4). Calyx reduced to hairs or bristles (pappus), petals fused in tube or ligula (with 5 or 3 teeth). Stamens 5, fused by anthers, pollen lifted up and distributed by outer sides of stigmas, this is *secondary pollen presentation* (Figure 13.3.5). Pistil has 2 carpels, ovary inferior. Fruit is achene, mature seed has almost no endosperm. Flower formula of the tubular (disk) flower is

$$*K_{\infty}C_{(5)}A_{(5)}\underline{G_{(2)}} \tag{13.3.3}$$

Ligulate (ray) flower typically has formula like

$$\uparrow K_{\infty}C_{(3\vee 5)}A_{(5)}\underline{G_{(2)}} \tag{13.3.4}$$



Figure 13.3.4 Compositae: head and one ligulate (ray) flower.

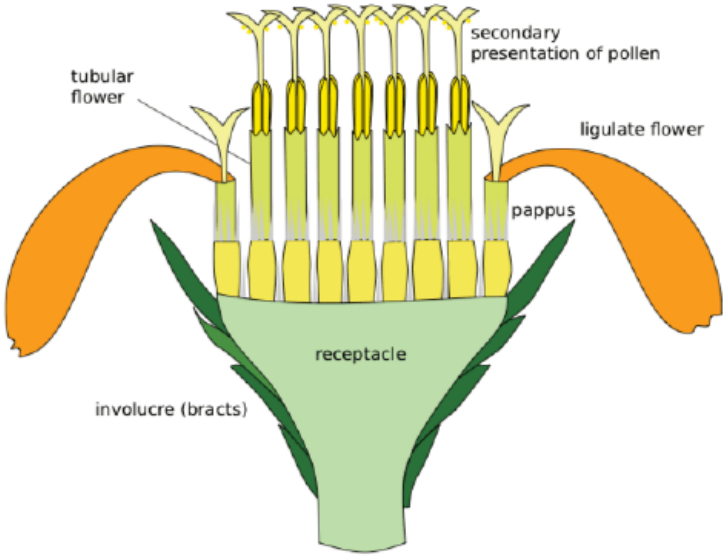


Figure 13.3.5 Features of Compositae: two types of flowers, secondary pollen presentation, pappus.

Fruit of aster family is one-seeded **achene** (it is a frequent mistake to call it “seed”). In achene, walls of inferior ovary are tightly fused with seed coat. Achenes frequently bear diverse dispersal structures: trichomes, teeth, hooks and others.

Oil plants, vegetables, ornamentals and medicinal plants distributed in multiple subfamilies, most important are three:

- 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

Gramineae, or Poaceae—grass family

Belong to liliids (Liliidae, monocots). Approximately 8,000 species distributed throughout the world, but most genera concentrate in tropics. Prefer dry, sunny places. 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). Stems of grasses are usually hollow and round. Leaves with sheaths.

Flowers reduced, wind-pollinated, usually bisexual, form complicated spikelets. Each spikelet bears two *glumes*; each flower has *lemma* and *palea* scales (Figure 13.3.6). Perianth is reduced to lodicules. Stamens from 6 to 1 (most often 3), with large anthers. Flower formula is

$$\uparrow P_{0-3}A_{0-3+2-3}\underline{G_{(2)}} \tag{13.3.5}$$

Fruit is a *caryopsis*; it includes flower scales. Seed contains embryo with *coleoptile*, *coleorhiza* and *scutellum* (Figure 7.5.7).

Most primitive grasses are bamboos (Bambusoideae subfamily). There are many other subfamilies. Two are especially economically important:

- Pooid (Pooideae) grasses usually are C_3 plants, wheat (*Triticum*), rice (*Oryza*), barley (*Hordeum*) and rye (*Secale*) belong to this group.
- Panicoid (Panicoideae) grasses are mostly C_4 plants like corn (*Zea*), sorghum (*Sorghum*) and sugarcane (*Saccharum*).

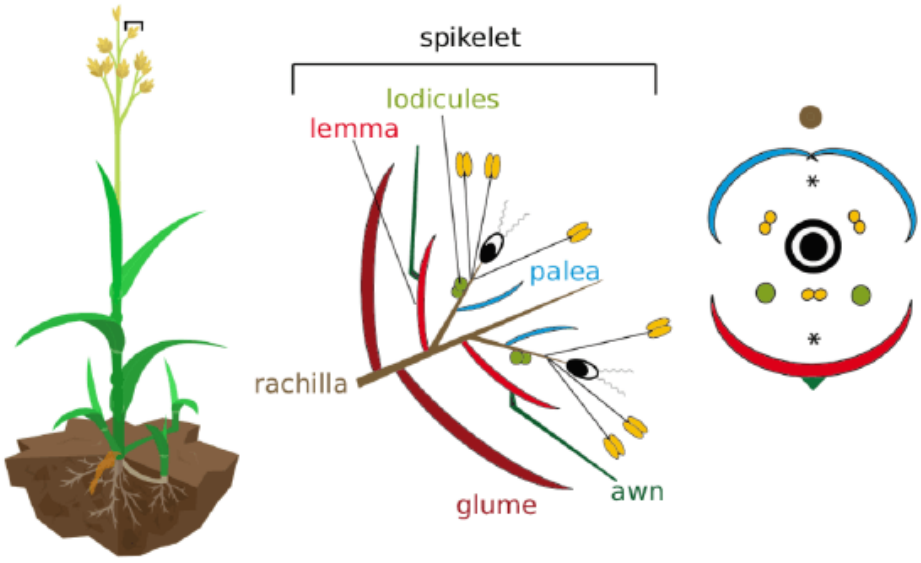


Figure 13.3.6 Gramineae: one plant, scheme of spikelet and flower diagram.

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14: THE ORIGIN OF TREES AND SEEDS

Learning Objectives

- Explain how secondary growth and branching enabled the evolution of tree-like plant forms.
- Describe the diversity of plant life forms and shoot modifications.
- Understand the evolutionary origin and structure of seeds in seed plants.
- Compare the major groups of gymnosperms and their reproductive adaptations.
- Differentiate between monocot and eudicot seed structure and germination patterns.

Competition over resources (primarily water and sun light) always drove plant evolution. The most logical way to escape competition was to enlarge the body. But if only primary tissues are available, this growth is strictly limited. Without secondary thickening, the trunk will easily break under the weight of growing crown, and the plant will die. This is easy to see in plants which still dare to develop the tree-like habit without secondary growth: tree ferns and palms. In addition, tree ferns have no bark which limits their distribution to the really wet places. On the other hand, thickening of stem will allow for branching, and branching allow for even bigger aboveground body. But then, new problems associated with both size and life cycle will pose another great challenge.

14.1: Secondary Stem

14.2: Branching Shoot

14.3: Life Forms

14.4: Modified Shoot

14.5: Origin of the Seed

14.6: Spermatophyta - Seed Plants

14.7: Introduction to Seed Germination

14.8: Atlas- Monocots vs. Eudicots

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14.1: Secondary Stem

In many seed plants, secondary growth begins in their first year within the stem and continues on for many more years. These plants are classified as *woody*. They develop *secondary tissues* like periderm and wood, and even *tertiary* structures like bark.

The first step in producing secondary phloem and xylem (other names are metaphloem and metaxylem) is to form the vascular cambium, which involves cell division inside the vascular bundles and the parenchyma that are between the bundles (Figure 14.1.1). The vascular cambium divides in two directions. The cells that are formed to the outside become the *secondary phloem*, and those formed to the inside are the *secondary xylem* (Figure 14.1.3). After several years, central pith disappears under the pressure of growing wood, and only traces of primary xylem (protoxymem) can be seen *under* the thick secondary xylem. Altogether, these tissues (pith + primary xylem + secondary xylem) are **wood** (Figure 14.1.2).

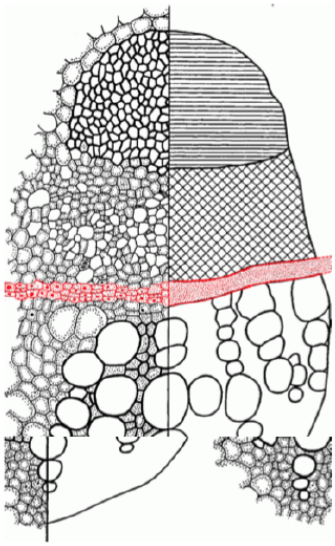


Figure 14.1.1 Vascular bundle on the stage of cambium (red) formation. Xylem is located downward, phloem upward. Note that cambium forms also between vascular bundles.

The secondary phloem forms outside of the vascular cambium, and traces of primary phloem (protophloem) are visible above it. It is rich in fibers, and unlike the wood, it does not form annual rings.

Most of cambium cells are **fusiform initials** forming axial vessel elements, while some cambium cells are ray initialscambium cells which make rays and they form **rays**: combinations of parenchyma cells and tracheids transporting water, minerals and sugars (because it is dark inside the stem and only respiration is possible) *horizontally*. Rays are visible best on the **tangential** section of the stem (when section plane is tangent to the stem surface); two other possible sections (**radial** and **transverse**) show axial components of the stem better. In the secondary phloem, rays are sometimes *dilated* (wedge-shaped).

The cambium usually does not work evenly all year round. In temperate climates, a *ring* forms for each growing season and makes it possible to determine the age by counting the growth rings. This is because at the end of season cambium makes much smaller (“darker”) tracheary elements. Trees growing in climates without well-expressed seasons will not make annual rings. To tell the age of a tree, researchers observe the number and thickness of annual rings that are formed. This is called *dendrochronology*.

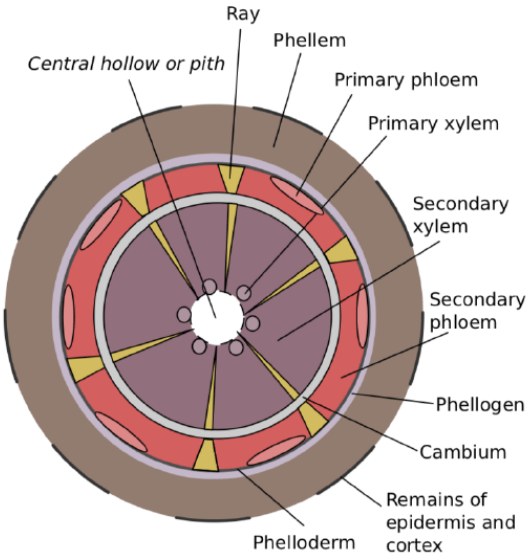


Figure 14.1.2 Anatomy of the secondary stem. Radial view.

Some trees (like oaks, *Quercus*) have large vessel elements are found primarily in the wood formed early in the season (early wood); this pattern is known as **ring porous**. 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.

Vesselless wood of conifers is of a simpler structure with relatively few cell types. There are simple rays and frequently *resin ducts*; resin is secreted by specialized cells.

In the tree trunk, the lighter wood near the periphery is called **sapwood** and has functioning xylem where most of the water and minerals are transported. Darker wood closer to the center is called **heartwood** and is a non-functional, darkly colored xylem (Figure 14.1.4). Tracheary elements are dead cells and to block them, plants uses tylosesvessel element “stoppers” which also help control winter functioning of vessels. A tylose forms when a cell wall of parenchyma grows through a pit or opening into the tracheary element; they look like bubbles.

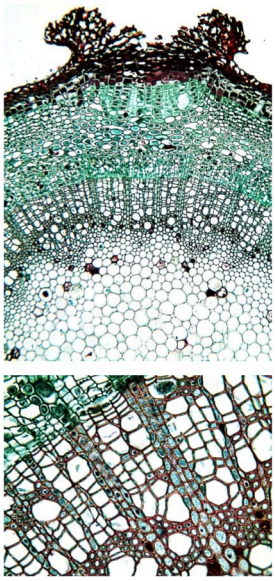


Figure 14.1.3 Top to bottom: Sambucus secondary stem in the beginning of growing, lenticel is on the top, Sambucus cambium (top left) and secondary vascular tissues. Magnifications×100 (first) and ×400 (second).

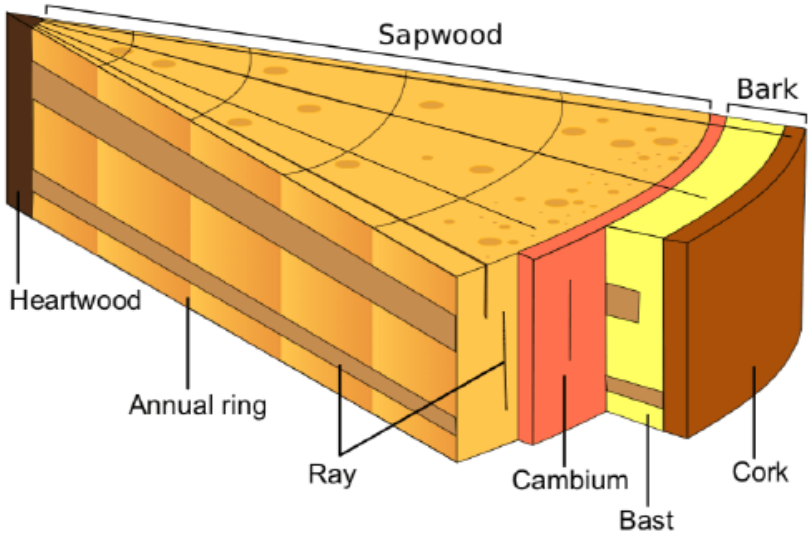


Figure 14.1.4 Piece of trunk. Radial and transverse views.

Most liliids (for example, palms) do not have lateral 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. Few other liliids (like dragon blood tree, *Dracaena*) have **anomalous secondary growth** which employs cambium but this cambium does not form the stable ring.

Constantly thickening stem requires constantly growing "new clothes", secondary dermal tissue, periderm. Periderm is a part of bark. *Bark is everything outside vascular cambium*. It is unique structure which is sometimes called "tertiary tissue" because it consists of primary and secondary tissues together:

- $\text{trunk} = \text{wood} + \text{vascular cambium}\ (\text{“cambium”}) + \text{bark}$
- $\text{wood} = \text{secondary xylem} + \text{primary xylem} + [\text{pith}]$[1]
- $\text{bark} = \text{bast}\ (\text{primary} + \text{secondary phloem}) + \text{periderm} + [\text{cortex}] + [\text{epidermis}]$
- $\text{periderm} = [\text{phelloderm}] + \text{cork cambium}\ (\text{phellogen}) + \text{cork}\ (\text{phellem})$

Each year, a new layer of phellogen (cork cambium) appears from the parenchyma cells of the secondary phloem which makes bark multi-layered and uneven. On the surface of a young stem, one may see **lenticels**, openings in phellem layer which supply the internals of the stem with oxygen; together with rays, lenticels work as ventilation shafts. To produce lenticels, some phellogen cells divide and grow much faster which will finally break the periderm open.

Apart from the lenticels, older or winter stems have **leaf scars** with **leaf traces** on their surface. The first are places where leaf petiole was attached, and the second are places where vascular bundles entered the leaf.

The secondary structure of root reminds the secondary structure of stem, and with time, these two organs become anatomically similar.

References

1. "Optional" tissues are given in brackets, synonyms in parentheses.

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14.2: Branching Shoot

Secondary stem allows for extensive branching. In seed plants, branching is based on the axial buds. These buds are located in axils of leaves and develop into secondary shoots. There are two main types of branching: monopodial and sympodial (Figure 7.3.1).

- **Monopodial branching** is when the buds do not degrade and all the shoots continue to grow.
- **Sympodial branching** is when the terminal buds do degrade (make FU and/or die out) and the lateral shoot closest to the terminal bud now becomes the terminal shoot and continues the vertical growth. This happens because the terminal SAM suppresses the downstream meristems by producing the auxin hormone (apical dominance). Apical dominance is a basis of multiple gardening trimming techniques.

Monopodial branching creates the conical (spruce-like) crown whereas sympodial branching will create crowns of many different shapes. Monopodial growth is considered to be more primitive. Some monopodial trees may even die if the terminal bud is damaged. Even more ancestral mode of branching is **dichotomous**, when every branch splits into two; this is frequent in lycopods and some other Pteridophyta.

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14.3: Life Forms

Thickening and branching change the appearance of plant. The most ancient classification employ both branching and thickening and divide plants into trees, shrubs and herbs. This approach was the first classification of *life forms*. Life forms tell not about evolution, but about how plant lives. We still use this classification. With some modifications, it plays a significant role in gardening:

- **Vines** Climbing woody and herbaceous plants
- **Trees** Woody plants with one long-lived trunk
- **Shrubs** Woody plants with multiple trunks
- **Herbs** Herbaceous plants, with no or little secondary xylem (wood). Sometimes, divided further into annuals (live one season), biennials (two seasons) and perennials.

This classification system has many downfalls. What is, for example, the raspberry? It has woody stems but each of them lives only two years, similar to biennial herbs. Or what is duckweed? These small, water-floating plants with ovate non-differentiated bodies are hard to call “herbs”.

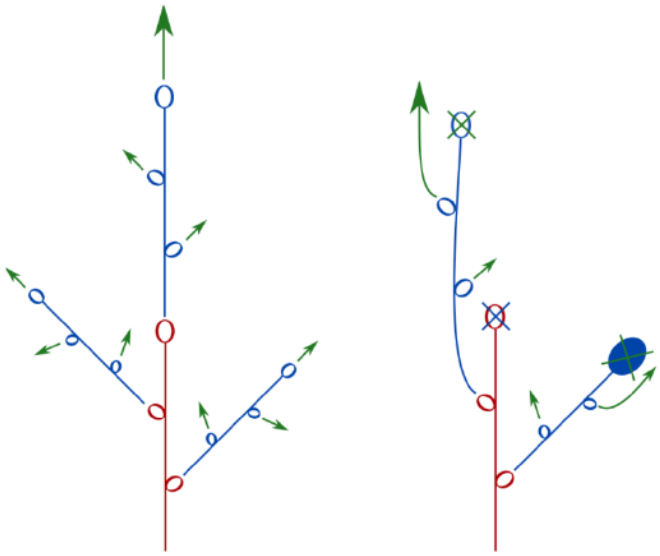


Figure 14.3.1 Monopodial (left) and sympodial branching. First, second and third years of growth are red, blue and green, respectively. Note that rightmost branch developed the FU (blue oval).

As one can see, the actual diversity of plant lifestyles is much wider than the classification above.

Architectural Models Approach

During the winter, it is easy to see that some tree crowns have similar principles of organization. In the winter-less climates, the diversity of these structures is even higher. On the base of branching (monopodial or sympodial), location of FU, and direction of growth (**plagiotropic**, horizontal or **orthotropic**, vertical), multiple *architectural models* were described for trees. Each model was named after a famous botanist such as Thomlinson, Corner, Attims, and others. In temperate regions, one of the most widespread models is Attims (irregular sympodial growth): birches (*Betula*) and alders (*Alnus*) grow in accordance with that model (Figure 14.3.2). In tropical regions, many plants (like palms and cycads) have single thick trunks crowned with large leaves, this is Corner model (Figure 7.4.1).

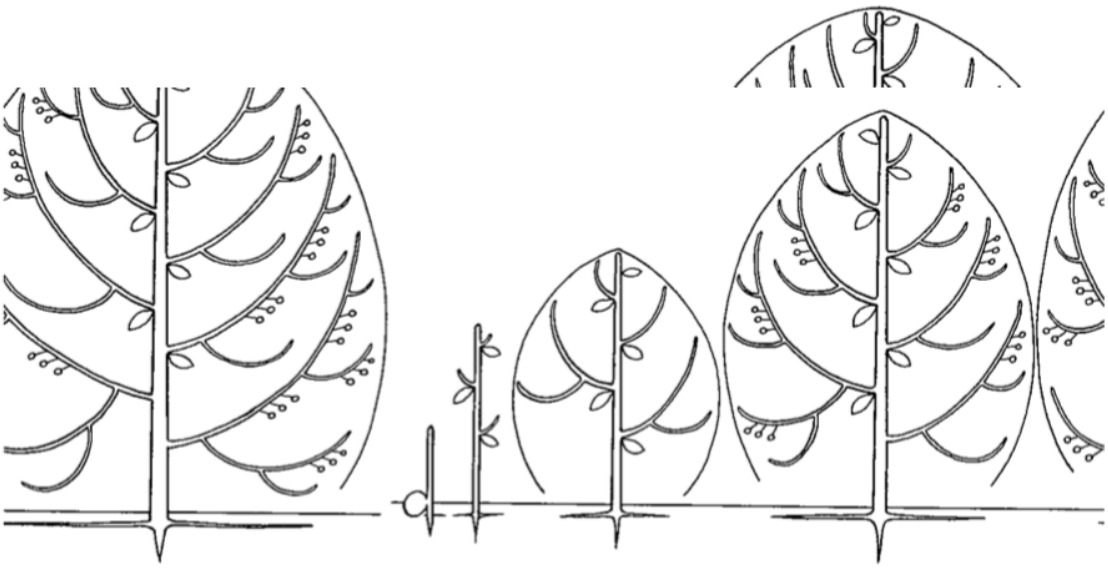


Figure 14.3.2 Attims architecture model of tree growth. (From Halle et al. (1978)).

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14.4: Modified Shoot

Like leaves and roots, shoots and stems also have modifications. Some examples are rhizomes, stolons, tubers, bulbs, corms, thorns, spines, cladophylls, and stem traps. **Rhizomes** (example: ginger, *Zingiber*) are underground stems that burrow into the ground just below the soil surface, and usually tend to 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.

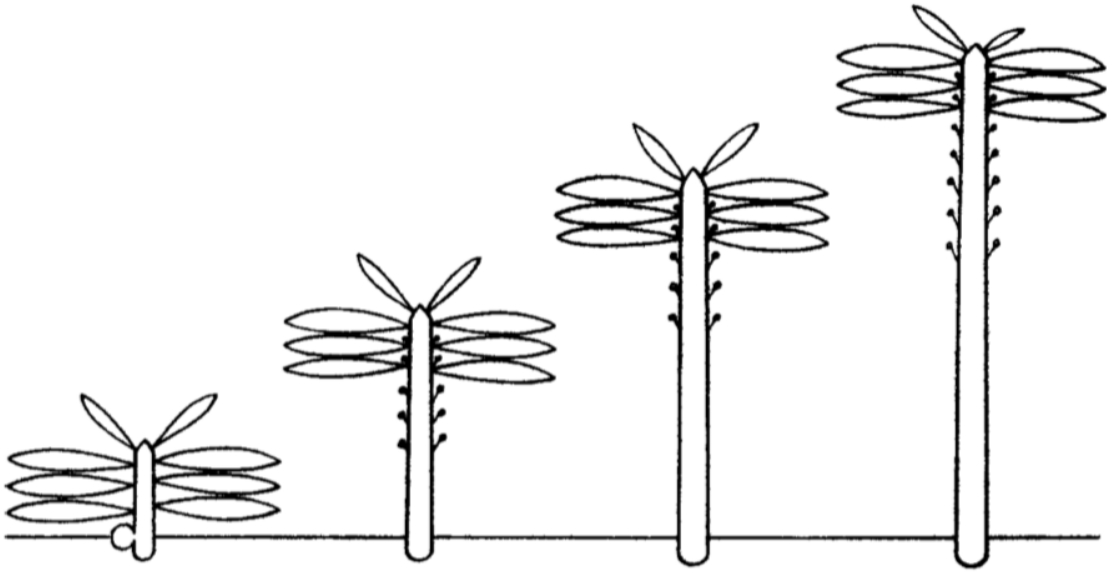


Figure 14.4.1 Corner architecture model of tree growth. (From Halle et al. (1978)).

Stolons (runners) are aboveground horizontal shoots, which sprout and produce a new plants (example: strawberry, *Fragaria*). **Tubers** (example: potatoes, *Solanum*) are enlarged portions of rhizomes. 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 shoot structures that are used for storage. A **corm** (example: crocus, *Crocus*) is a short, thick underground storage stem with thin scaly leaves. A **bulb** (example: onion, *Allium*) differs from a corm in the fact that it stores its nutrients in its fleshy leaves (Figure 14.4.2).

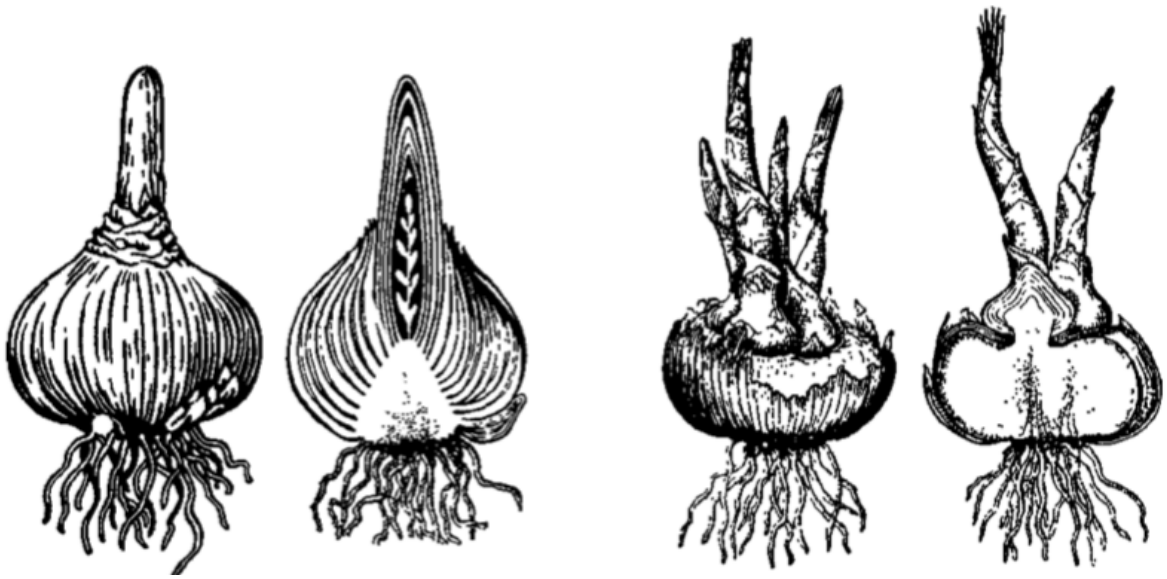


Figure 14.4.2 Bulbs (left) and corms. (Modified from various sources).

Thorns (example: hawthorn, *Crataegus*) are defensive shoots that help to protect the plant from predators. **Spines** are not

modified stems, but rather modified, reduced leaves or stipules, or bud scales (example: almost all cacti, Cactaceae family). **Prickles** (example: rose, *Rosa*) are modified surface tissues of stem.

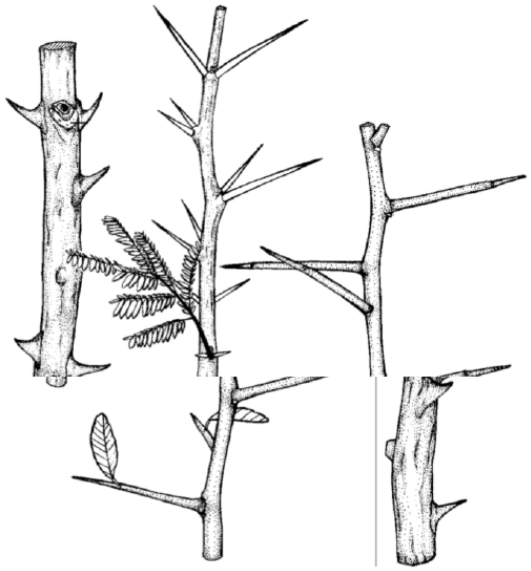


Figure 14.4.3 Prickles, spines (from stipules) and thorns (from Charles-Dominique et al., 2016).

Cladophylls (examples: Christmas cactus, *Schlumbergera*; ribbon plant, *Homalocladium*) are leaf-like, flattened shoots. **Phyllodes** are actually leaf modifications (example: Australian acacias, *Acacia*) they visually similar to cladophylls but originated from flattened leaf petioles. Shoot **insect traps** are used by some carnivorous plants, such as bladderwort (*Utricularia*). The following table emphasizes the diversity of organ modifications:

	Leaf	Stem	shoot
Absorption	Absorption leaves (bromeliads)	Rhizoids	*Default*
Defense	Spines, scales	Thorns, prickles	Spines
Expansion	Plantlets	Rhizomes, stolons, runners	Adventive buds
Interactions	Traps, sticky epidermis, urns, colored leaves	Traps, insect nests	Haustoria, mycorrhizae, root nodules, nematode traps, insect nests
Photosynthesis	*Default*, phyllodes	Cladophylls	Green roots (orchids)
Storage	Succulent leaves, pitchers	Bulbs, corms, tubers	Storage roots
Support	Tendrils, false stems, floats, suckers	*Default*, tendrils	Buttress, aerial and contractile roots, suckers

Please note that superficially similar structures (e.g., shoot and leaf tendrils) might have different origin.

Raunkiaer's Approach

Christen Raunkiaer used a different approach to classify life forms which is useful to characterize the whole *floras* (all plant species growing on some territory), especially temperate floras. He broke plants down into six categories: epiphytes, phanerophytes, chamaephytes, hemicryptophytes, cryptophytes and therophytes.

Epiphytes do not touch soil (they are aerial plants), *phanerophytes* have their winter buds exposed, *chamaephytes* "put" their winter buds under the snow, winter buds of *hemicryptophytes* on the soil surface, *cryptophytes* in the soil and/or under water, and *therophytes* do not have winter buds, they go through winter as seeds or vegetative fragments (Figure 14.4.4). Typically, northern floras have more plants of last categories whereas first categories will dominate southern floras. Note that Raunkiaer "bud exposure" is not far from the hardiness in the dynamic approach explained below.

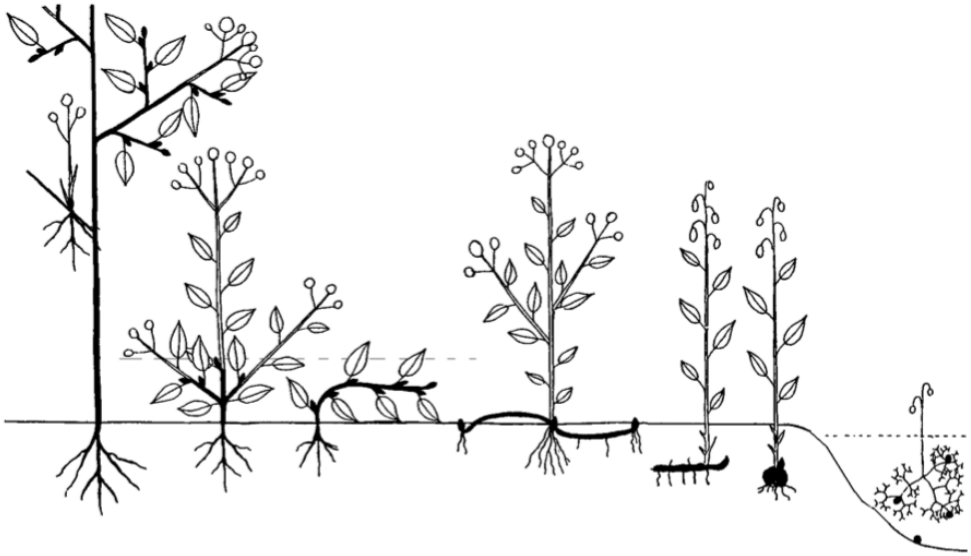


Figure 14.4.4 Life forms in accordance to Raunkiaer. From left to right: epiphyte (on branch), phanerophyte, chamaephyte, hemicryptophyte, two cryptophytes (with rhizome and with bulb), and therophyte. Dashed line on the left is the projected snow level. (From Raunkiaer (1907), modified).

Dynamic Approach

There are many life forms classifications. This is because life forms represent numerous *secondary patterns* in plan diversity, along with the main pattern which taxonomy wants to describe.

Dynamic life forms classification uses the fact that in nature, there are no strict borders between different life forms. If we supply the pole to some shrubs, they may start to climb and therefore become vines. In colder regions, trees frequently lose their trunks due to low temperatures and form multiple short-living trunks: they become shrubs. Conversely, in tropics, many plants which are herbs in temperate regions, will have time to develop secondary tissues and may even become tree-like.

Dynamic approach uses three categories: hardiness, woodiness, and slenderness (Figure 14.4.5). *Hardiness* is a sensitivity of their exposed parts to all negative influences (cold, heat, pests etc.) This is reflected in the level of plant exposure, plants which are hardy will expose themselves much better. *Woodiness* is the ability to make dead tissues, both primary and secondary (reflected in the percentage of cells with secondary walls). High woodiness means that plants will be able to support themselves without problems. *Slenderness* is an ability to grow in length (reflected in the proportion of linear, longer than wide, stems). Low slenderness results in rosette-like plants. Combining these three categories in different proportions, one may receive all possible life forms of plants.

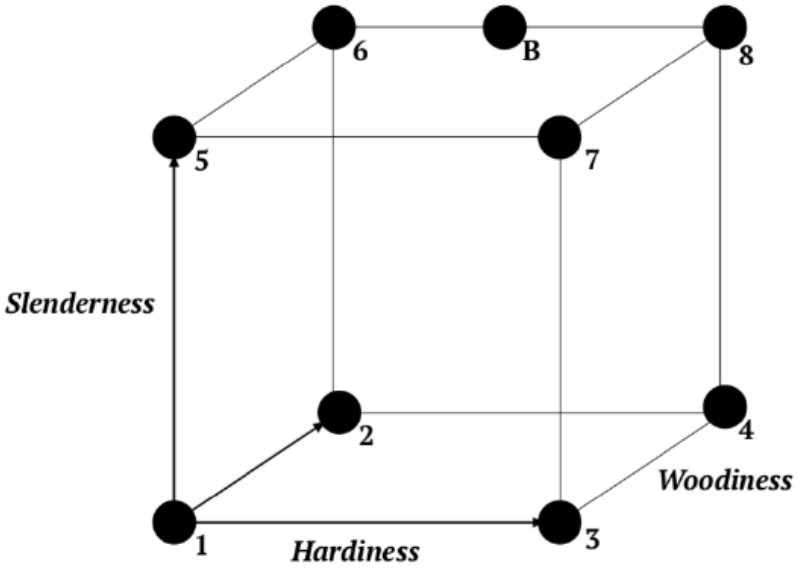


Figure 14.4.5 Dynamic life forms: 3D morphospace.

These three categories could be used as variables of the 3D morphospace. Every numbered corner in the morphospace diagram (Figure 14.4.5) represents one extreme life form:

1. Reduced floating annuals like duckweed (*Lemna*). Please note that zero hardiness is impossible; duckweed hardiness is just low.
2. Short annual herbs like marigold (*Tagetes*); they accumulate wood if warm season is long enough.
3. Bulb perennials like autumn crocus (*Colchicum*).
4. Australian “grass trees” (*Xanthorrhea*) with almost no stem but long life.
5. Herbaceous vines like hops (*Humulus*).
6. Monocarpic tree-like plants like mezcal agave (*Agave*).
7. Perennial ground-cover herbaceous plants like wild ginger (*Asarum*).
8. Trees like redwood (*Sequoia*).

What is even more important, all possible positions on the “surface” and inside this cube also represent life forms. For example, the dot marked with “B” are slender, woody but only partly hardy plants. The partial hardiness means that vertical axes will frequently die, and then new slender woody axes develop from scratch. Woody wines and creeping bushes will correspond well with this description. As you see, this morphospace not only classifies existing plants but also could predict possible life forms.

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14.5: Origin of the Seed

When plants developed the secondary growth, the almost unlimited perspectives opened for enlarging their body. However, these giants faced a new problem.

Big animals like elephants, lions, and whales tend to produce minimal number of offspring but increase the child care to ensure survival. This is called ***K*-strategy**, this is opposite to ***r*-strategy** usually smaller creatures which employs big numbers of offspring, and most of them will not survive (Figure 14.5.1).

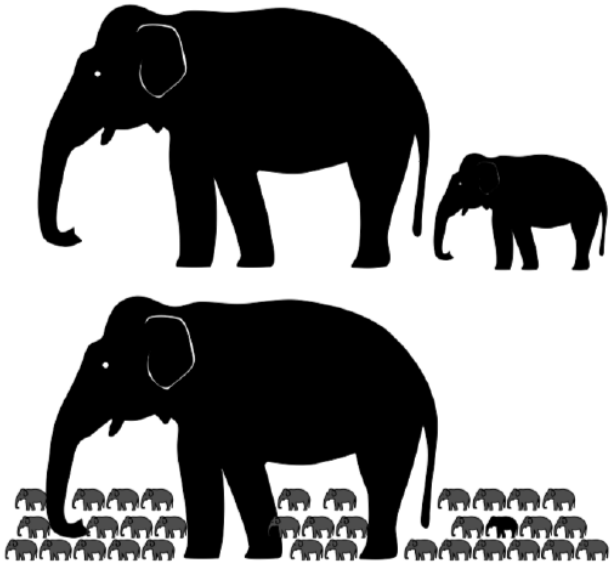


Figure 14.5.1 K-strategic elephant and r-strategic (like codfish) elephant. The second does not exist. Why?

Analogously, bigger plants would need to do the same as *K*-strategic animals: make few daughter plants but defend and supply them with all needs until they mature. However, big secondary thickening spore plants were not capable of family planning; they still made billions of spores and then left them to fend for themselves. Naturally, only few from these billions would survive to become fertilized.

Spore reproduction is cheap and efficient but as birth control is not available, 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 start to grow simultaneously and then suppress each other and even die from over-population. But if the environmental conditions are bad, then none of the gametophytes will survive so there would be no new saplings to replace the old trees.

It is similar to the so-called “dinosaur problem”. This situation arose when giant Mesozoic reptiles also lost the control for their offspring: their egg size was limited due to physical restrictions, therefore, young dinosaurs were so much smaller than adults; then the only possible strategy was to leave them alone (Figure 14.5.2). As a result, at the end of Mesozoic dinosaurs either decreased in size (became birds), or went extinct.

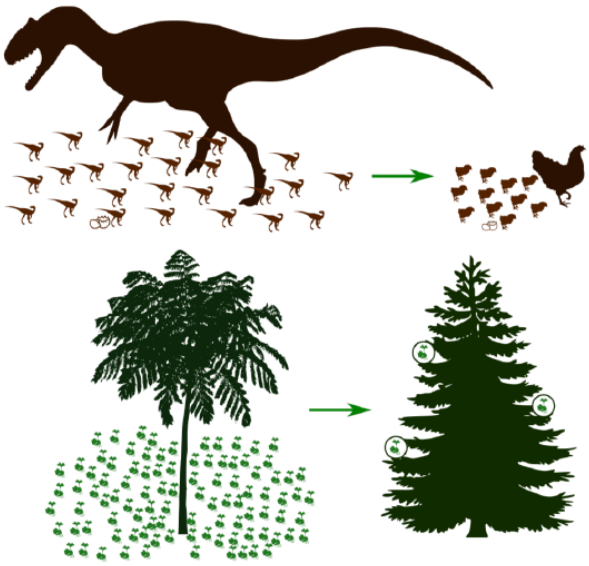


Figure 14.5.2 How dinosaurs and ferns solved the problem of conflicting strategies.

Plants, however, kept their size and survived. This is because they developed the seed (Figure 14.5.3). A *seed is the result of enforced control of the sporophyte over the gametophyte*. The idea of a seed is to hide most of the heterosporous life cycle *inside mother plant* (Figure 14.5.3). In seed plants, everything happens directly on the mother sporophyte: growing of gametophytes, syngamy, and growing of daughter sporophyte. Consequently, the female spore (megaspore) never leaves the sporangium. It germinates inside, waits for fertilization and then the zygote grows into and embryo, still inside the same sporangium.

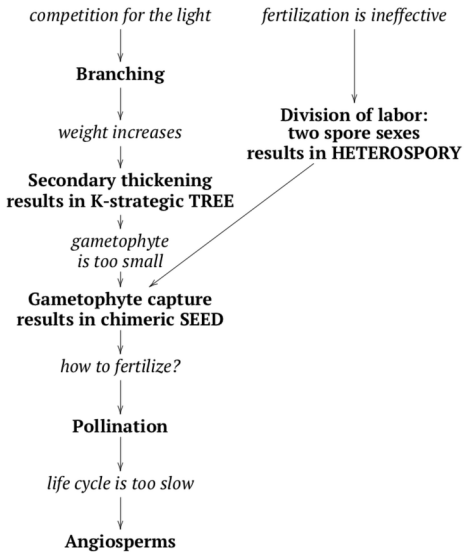


Figure 5.1.3.

What will finally leave the mother plant is the *whole female sporangium with gametophyte and embryo on it*. This is the seedchimeric structure with mother (seed coat), daughter (embryo) and endosperm genotypes. It can be defined as *chimeric structure with three genotypes*: seed coat (mother plant megasporangium, $2n$), endosperm (female gametophyte, n), and daughter sporophyte (embryo, $2n$).

It should be noted here that flowering plants have endosperm of different origin; it is called *endosperm*$_2$ and usually is triploid ($3n$) whereas female gametophyte endosperm is haploid (n) endosperm$_1$haploid nutrition tissue originated from female gametophyte. The other note is that apart from seed coat (which originates from integumentextra cover of megasporangium(s), megasporangium extra cover(s)), mother sporophyte also gives nucelluswall of megasporangium (wall of megasporangium) which sometimes is used as a feeding tissue for the embryo. This last tissue is called perispermnutrition tissue originated from nucellus (see).

One problem is still left. How will sperms reach female gametophyte and egg cell? The target is now 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* which are called **pollen grains**. Plants have no legs so they always need a third party in their sex, this is mostly wind or insects. A pollen grain is *not a spore*, mother sporophyte cares about male lineage too, and male spore grows into very small male gametophyte. It contains multiple haploid cells; some of which are sperms.

The lesser problem is: How would these sperms will swim to the egg cell? Some seed plants will excrete the drop of liquid from the top of the **ovule** (integument(s) + megasporangium), whereas the other, more advanced way is to grow a sperm delivery tool, the **pollen tube** (Figure 14.5.4) made from one of the pollen grain cells. Fertilization with pollen tube is often called **siphonogamy**.

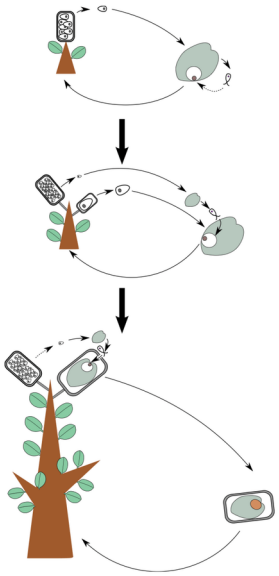


Figure 14.5.3 The origin of seed (see explanation in the text). Sporophyte is on the left, gametophytes and seed—on the right or/and on the top. First stage—isosporic life cycle, second stage—heterosporic life cycle, third stage—seed plant life cycle.

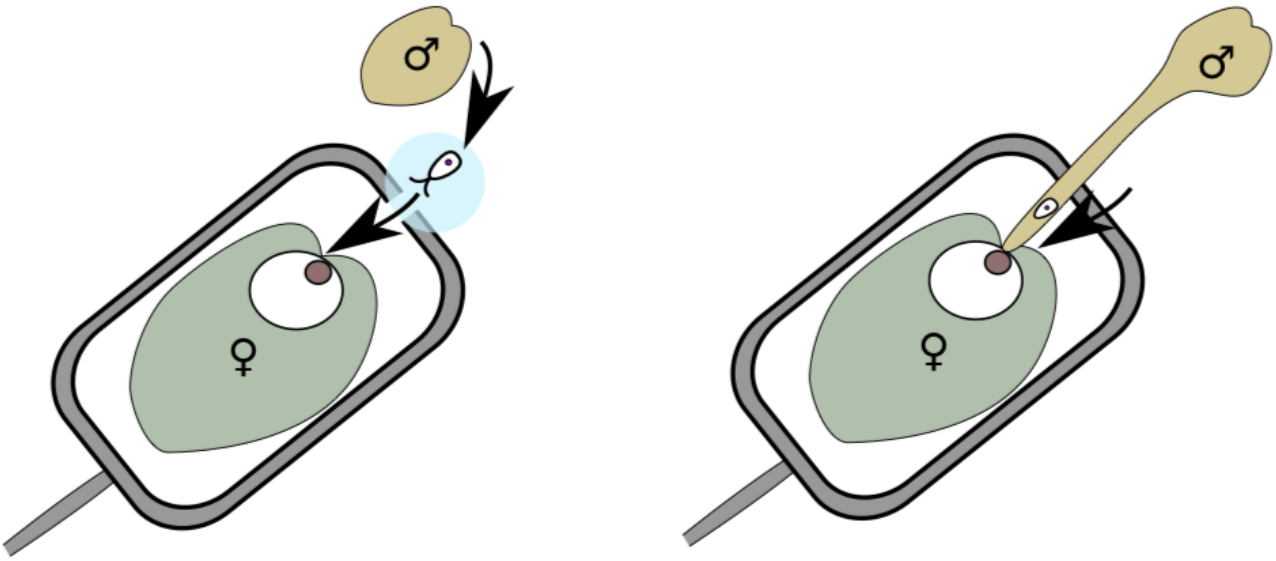


Figure 14.5.4 Open fertilization in seed plants (left) with the help of liquid extracted by mother plant; and fertilization with pollen tube (right), or siphonogamy, with the help of pollen tube growing from male gametophyte. Among extant seed plants, only cycads and ginkgo have the open fertilization.

Consequently, seed plants with the pollen tube do not have flagella even on male gametes; these cells are **spermatia**: aflagellate, non-motile male gametes. (Below, we will continue to call all male gametes “sperms”). Pollen tube also allows only two male gametes per gametophyte: in living world, male gametes are usually competing for fertilization—this selects the best genotypes; whereas in higher seed plants, competition is between pollen tubes. 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.

The cycle of a seed plant (Figure $14.5.4$) begins with a sporophyte ($2n$) and has both the female and male organs where some cells undergo meiosis. Inside the ovule (which is the megasporangium with extra covers), female gametophyte (n, future endosperm $_1$) produces the egg cells. Male gametophytes (pollen grains) ripen in the pollen sacseed plants: microsporangium which is the microsporangium. The pollen sac sends out the pollen grains which meet up with the ovule. The pollen grain then releases the sperms which fertilize the egg cell, and a zygote is formed. The zygote grows into embryo (which uses endosperm as a feeding tissue) and then into the sporophyte.

Several plant lineages met this “seed challenge”, there were seed lycophytes and also seed “horsetails”. However, seed ferns made it first and became ancestors of *seed plants*.

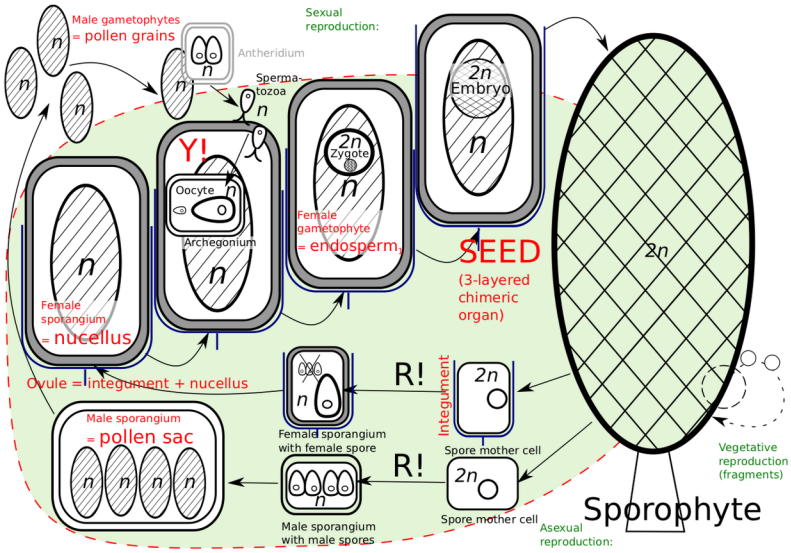


Figure $14.5.5$ Life cycle of seed plants. Innovations (comparing with the heterosporic life cycle) are in red.

Seed Structure and Germination

Seeds are diverse. For example, in an onion (*Allium*), a seed (Figure $14.5.6$) has endosperm, one cotyledonembryonic leaf (embryonic leaf), *radicle* (embryonic root), and the lateral embryonic bud (*plumula*).

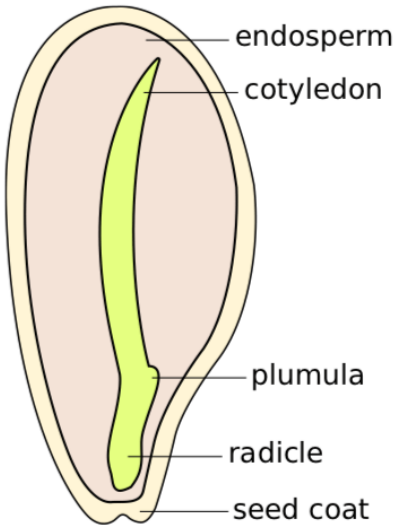


Figure 14.5.6 Monocot seed.

Beans (*Phaseolus*) and other Leguminosae are examples of seeds without endosperm—actually, it was there, but growing embryo usually eats it out completely. These seeds have two large cotyledons. Grass (Gramineae) seeds contain several specific organs, namely coleoptile, coleorhiza, and scutellum. The *scutellum* is an enlarged cotyledon, *coleoptile* is the bud cover, and *coleorhiza* covers the embryonic root, radicle (Figure 14.5.7). Onion and grasses are monocots with lateral embryonic bud. Other seed plants have a terminal embryonic bud and two or multiple cotyledons. Pine (*Pinus*) is an example of a plant that has multiple (five or more) cotyledons. Some plants like orchids (Orchidaceae) do not have developed embryo and even endosperm in seeds, their germination depends on a presence of symbiotic (mycorrhizal) fungus.

The first step in germination and starts with the uptake of water, also known as *imbition*. After imbition, enzymes are activated that start to break down starch into sugars consumed by embryo. The first indication that germination has begun is a swelling in the radicle. In onion and pea (*Pisum*), a structure that looks like a hook goes up through the soil and expose cotyledons and both hypocotyl and epicotyl (first internode). In beans, grasses, and palms, only epicotyl is exposed aboveground whereas cotyledons and hypocotyl remain underground.

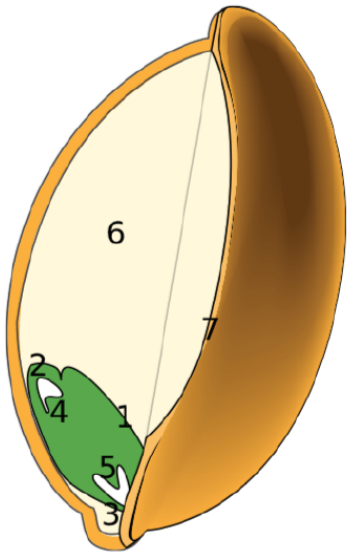


Figure 14.5.7 Grass seed. 1 scutellum (= cotyledon), 2 coleoptile (bud cover), 3 coleorhiza (radicle cover), 4 embryo bud (= plumula), 5 radicle (= embryo root), 6 endosperm, 7 seed coat.

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14.6: Spermatophyta - Seed Plants

Seed plants consist of approximately 1,000 species of non-angiosperms (gymnosperms) and about 250,000 species of angiosperms. They have a sporic life-cycle with sporophyte predominance, and seeds. The gametophyte is reduced to cells inside the ovule or pollen grain. Males have a minimum number of cells being three and females being four. The antheridia are absent and in flowering plants (Angiospermae) and Gnetopsida the archegonia are also reduced. The sporophyte will always start as an embryo located inside the nutrition tissue, endosperm$_1$ which is the female gametophyte or in endosperm$_2$ (see the next chapter). Spermatophyta have axillary buds (buds in leaf axils). Like ferns, they are megaphyllous and homoiohydric, and have a secondary thickening. Higher groups of seed plants lost flagellate spermatozoa and developed pollen tubes. The classes of Spermatophyta are Ginkgoopsida, Cycadopsida, Pinopsida, Gnetopsida, and Angiospermae.

Ginkgoopsida is just one species; ginkgo or maidenhair tree (*Ginkgo biloba*). This plant is long extinct in the wild but is grown on Chinese temple grounds as a decorative tree. Ginkgo is a large tree bearing distinctive triangle-shaped leaf with dichotomous venation. This plant is also dioecious (as an exception among plants, *Ginkgo* has sexual chromosomes like birds and mammals) and the pollen is transported by wind to female (ovulate) trees. The pollen grains of the ginkgo plants produce two multi-flagellate spermatozoa; the edible seed is fruit-like and becomes ripe after lying on the ground for a long time. Maidenhair tree has symbiotic cyanobacteria in cells. As ginkgo probably went through the population bottleneck, there are very few, almost no, phytophagous insects that can damage ginkgo leaves. The only fungus which is capable to eat them, *Bartheletia*, is also a living fossil.

Cycadopsida—cycads is a class with few genera and about 300 species that grow mostly in tropics. Only one species grows naturally in the United States, *Zamia pumila*, and can be found in Florida and Georgia. Cycads are palm-like plants with large, pinnate leaves. Their wood is rich of parenchyma since stem has anomalous secondary thickening. They are all dioecious and its cone is large and protected by prickles and woody plates. The ovules of these plants are attached to modified leaves (**megasporophylls**) that are gathered in upright cones. Like ginkgo, they have multi-flagellate spermatozoa, archegonia and large oocyte. Cycad seeds are distributed by animals. Life cycle is extremely slow.

Pinopsida—conifers are the most widely known and economically important among gymnosperms. Conifers consist of approximately 630 species. Most of them are temperate evergreen trees, but some are deciduous, such as larch (*Larix*). The stem has a large amount of xylem, a small cork, and minute pith. The ovules are attached to specialized leaves, **seed scales**, and are compacted in cones with **bract scales** (Figure 14.6.1). Some conifers, like junipers (*Juniperus*) and yews (*Taxus*), lack woody cones; these plants have fleshy scales. Seeds are distributed by wind and animals.

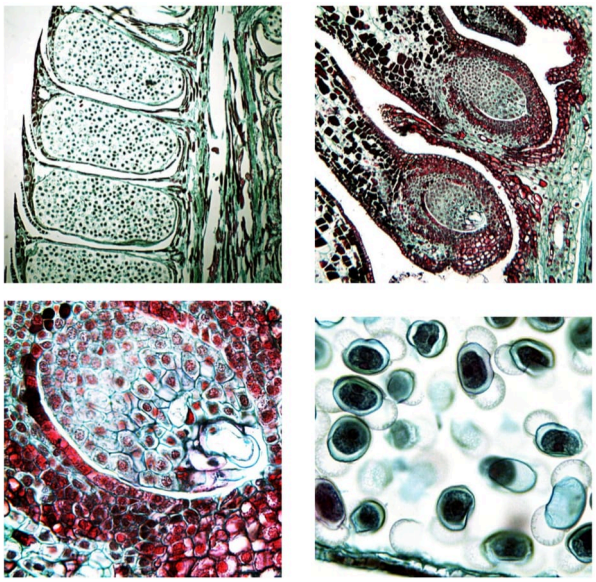


Figure 14.6.1 Left to right, top to bottom: Pinus (Pinopsida) microsporangia (pollen sacs), ovules sitting on seed scales, female gametophyte (endosperm1) and multicellular male ga- metophyte (pollen). Magnifications ×100 (first and second) and ×400 (third and fourth).

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. Among families of conifers, Pinaceae (pine family) have resin and needle-like leaves; *Pinus* have them in shortened shoots, **brachyblasts**, and their large cones have woody scales. Cupressaceae (cypress family) do not have resin, produce small cones that have a fused bract and seed scales, have dimorphic leaves, and some of their genera (like "living fossil" *Metasequoia* from China) are deciduous in an unusual way: they drop whole branches, not individual leaves.

Gnetopsida—gnetophytes are sometimes called chlamydosperms. They are a small class with only three genera that are not at all similar: *Ephedra*, *Welwitschia*, and *Gnetum*. While these plants morphologically remind of angiosperms, they are molecularly related more to other gymnosperms. *Ephedra* are horsetail-like desert leafless shrubs, *Gnetum* are tropical trees, and *Welwitschia* are plants which have a life form that is really hard to tell (Figure 14.6.2).



Figure 14.6.2 Gnetopsida "even man out" game: Gnetum, Welwitschia, Ephedra, and ... Coffee. Which is where?

Ephedra has archegonia, but in *Gnetum* and *Welwitschia* they are reduced. On the other hand, *Ephedra* and *Gnetum* have double fertilizationthe process when two brother male gametes fertilize two sister female cells: both male nuclei fuse with cells of the one female gametophyte (endosperm$_1$): with egg cell and another haploid cell, sister to the egg. Double fertilization in gnetophytes results in two competing embryos, and only one of them will survive in future seed.

Both *Gnetum* and *Welwitschia* have vessels (like angiosperms). *Gnetum* also has angiosperm-like opposite leaves with pterodromous venation, like, for example, coffee tree (however, this probably is a result of modification of dichotomous venation). Ovules of chlamydosperms are solitary and covered with an additional outer integument; the male gametes are spermatia moving inside pollen tube.

Welwitschia is probably most outstanding among gnetophytes. There is only one species that occurs 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 parallelodromous venation. The secondary thickening is anomalous, wood has vessels. Plant is insect-pollinated, and its winged seeds are dispersed by the wind. Fertilization is not double, but, along with pollen tubes, involves the most crazy structures: *prothallial tube*s which grow from female gametophyte and meet with pollen tubes to make zygote.

Life cycles determine the basic diversity of plants, they designate plant phyla. Let us compare three types of life cycles again (Figure 14.6.3) and again (Figure 14.6.4). What is visible on all these schemes, as well as on all similar schemes from above, is growing complexity of cycle, growing reduction of haploid stage, and growing self-similarity within the cycle.

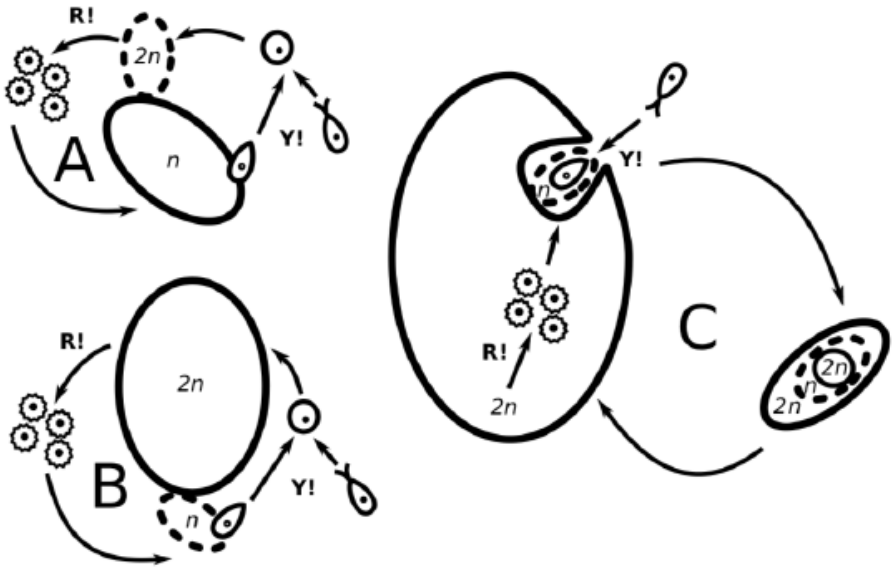


Figure 14.6.3 Life cycles of mosses (A), ferns (B) and seed plants (C): black and white scheme.

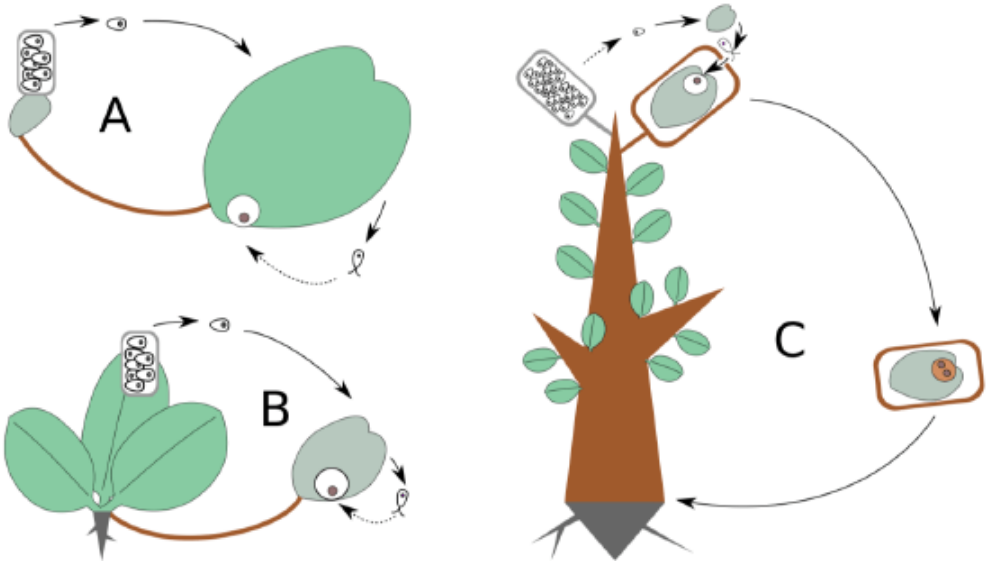


Figure 14.6.4 Life cycles of mosses (A), ferns (B) and seed plants (C): color scheme.

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14.7: Introduction to Seed Germination

Learning objectives

- Describe the differences between epigeal and hypogeal seedling emergence.
- Understand the terms that are used to describe different parts of the seedling as it emerges.

Seeds and their importance



"Germinating bean seed" by Jose Bañuelos, CC BY-NC 2.0

A **seed**, in botanical terms, is an embryonic plant enclosed inside its seed coat. Typically, the seed also has stored energy (proteins and carbohydrates) that are used by the seed during germination to establish itself when environmental conditions are favorable for growth. The stored energy is what makes seeds valuable for humans, too. Seeds are important in our daily lives because they feed us (food), feed livestock (aka, feed), and provide us with fuel and fiber for personal, home, and industrial purposes.

Seeds are by far the most common mode by which plants reproduce, and most people are familiar with their role in plant propagation and reproduction. The evolutionary advantage of reproduction by seed is the mixing of genetic material through meiotic recombination and the transfer of gametes (pollen) from one parent to another. This mixing of male and female parent genetics results in seeds, and thus seedlings, that are unique from one another and from the parents. The seeds may be dispersed locally or distributed far away through many mechanisms, such as wind, animals, insects, and water. Seedlings will germinate and grow, and those that are most fit in the environment will reproduce and pass on their genes to the next generation. This ability of plants to adapt to local environments and to pass on their genes is evolution in action, as new variations and even new species emerge and disappear from the landscape.

One advantage of seed production is that plants generally produce copious amounts of seed. Each seed may have slightly different germination requirements, a reflection of the diversity resulting from sexual recombination and an evolutionary strategy that allows seeds to germinate at different times. Seeds are able to remain dormant until the conditions are suitable for plant growth and survival, and have mechanisms that prevent germination before winter, during droughts, or in low-light environments. Some weedy species are excellent at interpreting these signals and may lie dormant for years in the soil "seed bank," only germinating when the seed has been exposed.

Seedling emergence

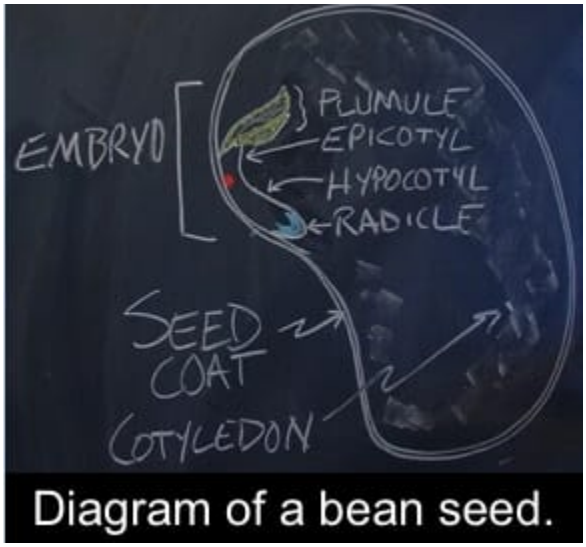


Image credit: Tom Michaels

Most seeds have a very slow metabolism when they are mature, which puts them in a state of quiescence: alive, but not growing and not physiologically active. At germination, the seed's metabolic pathways are activated, leading to embryo growth and emergence of a new seedling. Germination begins with activation by water uptake. We call this **imbibition**, and sometimes the seed or fruit requires special treatment for water to get into the seed and start this process. We often use the emergence of the radicle (the embryonic root) from the seed coat as a measure of successful germination. Water uptake alone is not an indication that the seed is alive and growing, despite the expansion of seed tissues.

Cell division is taking place in the epicotyl, and the hypocotyl and the shoot and root are beginning to break through the seed coat. The new plant is beginning to grow and emerge from the soil.

Two types of seedling emergence

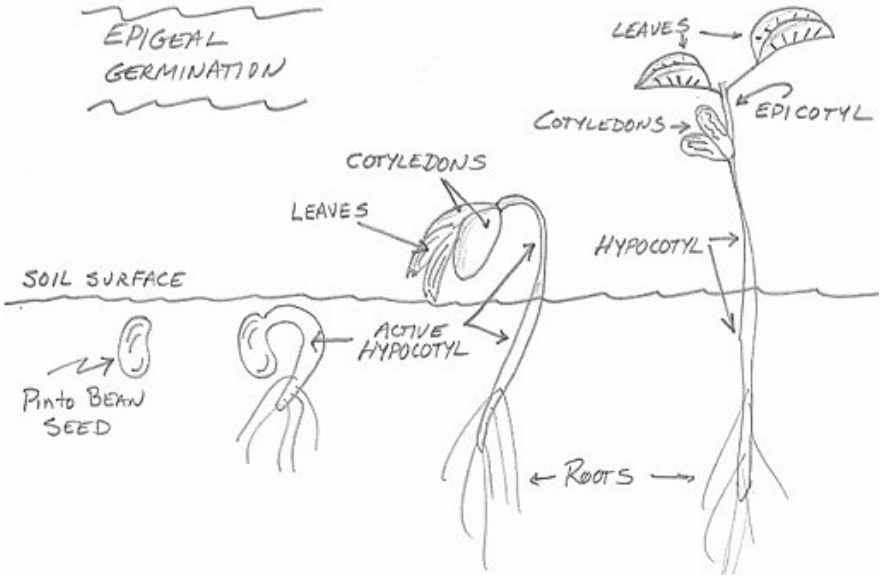
Epigeal and hypogeal

Epigeal and hypogeal are terms used to describe the position of the cotyledonary node during germination, indicating whether the node is above or below ground once the seedling has become established.

Epi means **above** while **Hypo** means **below**. The location of the cotyledonary node following seedling emergence is a characteristic used as a first step to differentiate plant species. The position of the cotyledon is affected by the rapidity of cell division in the hypocotyl region of the plant during germination and early seedling growth. The epicotyl is the embryonic shoot region above the attachment point of the cotyledons, and the hypocotyl the embryonic region below the cotyledon attachment point and extending down to where the root begins.

Epigeal

In this type of seedling emergence, cell division in the hypocotyl is initially more active and rapid than cell division in epicotyl. The actively dividing meristem in the hypocotyl causes cell growth and elongation that pushes some of the hypocotyl, as well as the cotyledonary node and epicotyl, above the soil surface. The cotyledonary node is above the ground — epigeal. The drawing shows four stages in the emergence of a pinto bean (*Phaseolus vulgaris* L.) which exhibits epigeal germination.

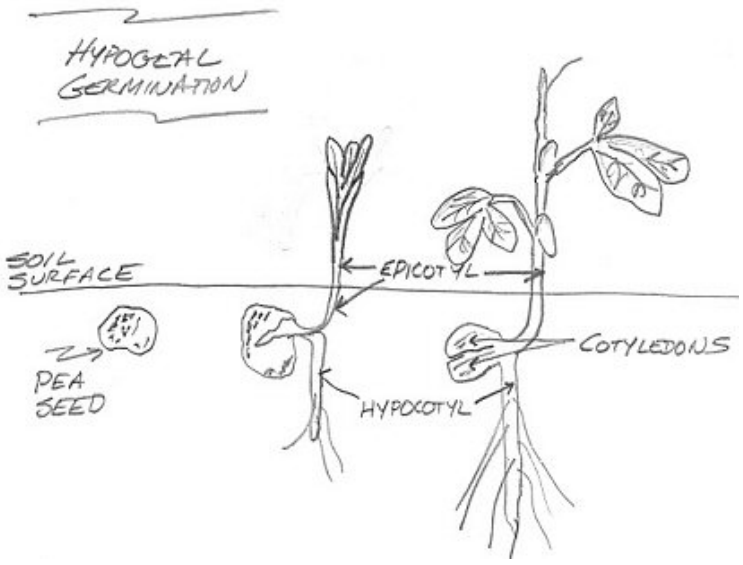


Epigeal germination. Image credit: Tom Michaels

This video shows germination of a bean seed over a 10-day time span.

Hypogeal

In this type of seedling emergence, the apical meristem at the tip of the epicotyl is more active than the hypocotyl. This cell division and elongation pushes the epicotyl above the soil while the cotyledons and all of the hypocotyl remain below the soil surface. The cotyledonary node is below the ground — it is hypogeal. The example above is a pea (*Pisum sativum* L.) which exhibits hypogeal germination.



Hypogeal germination. Image credit: Tom Michaels

This video shows hypogeal germination of pea, where the cotyledonary node stays below the soil, and this video shows epigeal germination of bean, where the cotyledonary node is pushed above the soil.

Review questions

- Does “epi” mean above or below? Above or below what?
- Diagram the seedling with the following: hypocotyl, cotyledons, epicotyl, and leaves.

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14.8: Atlas- Monocots vs. Eudicots

Monocots



Figure 14.8.1: Monocots like the grass shown on the left produce only one cotyledon (mono- for one, -cot for cotyledons). Eudicots (on right), also called dicots, get their name from having two cotyledons. Cotyledons are the first, fleshy leaves that enveloped the embryo as it grew. Image from Pengo, CC BY-SA 2.5, via Wikimedia Commons.

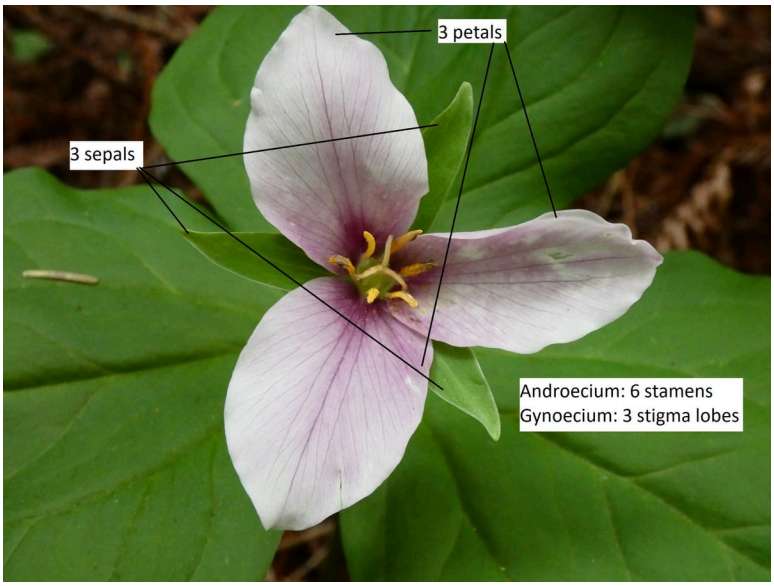


Figure 14.8.2: This Trillium is a monocot, which you can tell because it is 3-merous. There are three sepals, three petals, six stamens, and three stigma lobes visible in the gynoecium. Monocots have floral parts in sets of three (3-merous). Photo by Maria Morrow, CC-BY 4.0.

Eudicots



Figure 14.8.3: A eudicot seedling with two cotyledons. Photo by Maria Morrow, CC-BY 4.0.



Figure 14.8.4: 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.

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15: SEEDS

Learning objectives

- List three functions of a seed and identify its structures.
- Describe the process of seed germination.
- List the external factors required for seed germination.
- Understand dormancy and how the skilled plant propagator overcomes it.

Seeds are key to feeding the world's population as a nutrition and calorie source and for the propagation of most crops. In addition, being a fusion of paternal (pollen) and maternal (egg) genetic material, seeds create diversity; evolution acts on this diversity, and plant breeders take advantage of it to improve crops.

15.1: Seed Morphology

15.2: Seed Physiology

15.3: Terms

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15.1: Seed Morphology



Why a coconut? Because inside the coconut's fibrous husk is a seed (image: Coconut. Filo gèn. CC BY-SA 4.0).

Learning objectives

- List three functions of a seed and name the seed part that has that function.
- Identify the parts of the embryo and the structures they become.
- List the types of nutrients that are stored in seeds.
- Describe the differences between the tissues that provide protection for the seed.

Seeds and diversity

To review, the two fundamental ways of propagating plants and how they differ in their outcomes are sexual reproduction through seeds or spores, and asexual or vegetative reproduction through manipulation of various plant parts, including cuttings from leaves, roots, and stems, or grafting.

Asexual reproduction, also called vegetative propagation, normally results in progeny (offspring) that are an exact genetic copy of the parent plant that donates the vegetative parts used in propagation. All of the progeny propagated from the same plant contain the same genes as the parent plant, and the progeny are also identical to each other. Differences among progeny or between parent and progeny may arise as a result of mutation, but this is rare. More likely, any differences among plants that have been asexually propagated from the same parent occur because the growing environment differs from plant to plant in some important way (fertility, water, light). The way the plant looks and performs in a particular environment is called its phenotype. The collection of genes the plant contains is called its genotype. Vegetative propagation results in identical genotypes, but two plants with identical genotypes may have different phenotypes if they are grown in contrasting environments.

Sexual reproduction in weedy, native, or undomesticated plants typically results in seeds that are genetically different from either parent, and in progeny that are all genetically different from one another. Sexual reproduction in domesticated plants can also result in genetically diverse seed, but for those domesticated plants that are highly inbred, like peas, beans, and cereals other than corn (like barley, wheat, oats, and rice), sexual reproduction can also result in seeds that are genetically identical to the parent. For now, remember that sexual reproduction means that a seed is formed as a result of fusion of a sperm and egg cell, and that there is the potential for progeny to differ from the parent(s).

Sexual reproduction, and the genetically variable progeny that result, give a plant species a great deal of flexibility to adapt to new habitats and environmental conditions. Some progeny might be extremely well adapted to new niches and can thrive there, while some will not fit and will not survive and reproduce. To assist the species in spreading, the seeds of the plants that successfully reproduce often have strategies for dispersal away from the parent plant. This spread the species to diverse locations and new ecological niches, and also reduces the likelihood of too many plants of the same species competing with each other in a limited space for the same scarce resources.

Seed formation is normally assumed to be the result of sexual reproduction rather than vegetative propagation. In rare cases, however, an embryo can develop solely from maternal tissue with no fusion of egg and sperm. This is called apomixis. Apomixis is really a form of asexual reproduction disguised as sexual reproduction. The process results in a seed, but the embryo in the seed isn't the result of sex — the fusion of male and female gametes. All of the progeny are identical to the parent because the embryo is actually a clone (genetically identical offspring) of the plant on which the seed is produced. Kentucky bluegrass reproduces this way, as does dandelion. It is ironic that our lawns are often inhabited by two apomictic species ... the Kentucky bluegrass we struggle to grow, and the dandelions many homeowners go to great extremes to eradicate.

Basic seed morphology

Seeds have three main functions:

Propagation of the plant

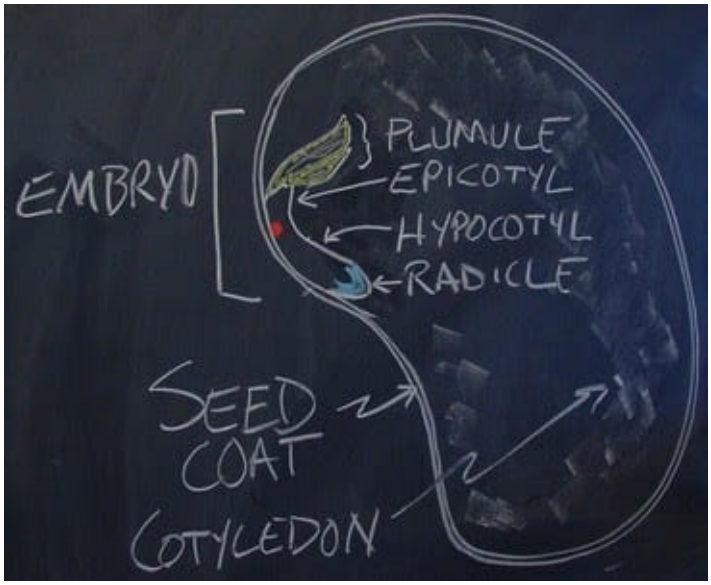
This is accomplished by the embryo, which is the nascent (new, young) plant resulting from the combination of genes from the male sperm, transmitted by the pollen, to the female egg, held in an ovule in the ovary. The embryo has an axis with one end differentiating into the shoot and the other into the root.

Nutrient storage

Two types of structures can store nutrients in the seed — the cotyledon and the endosperm. The nutrients fuel growth of the embryo.

Protection

The embryo and nutrient source need a tough covering for protection from the environment and predators, and this is typically, but not always, provided by a structure called the seed coat (sometimes called the testa).



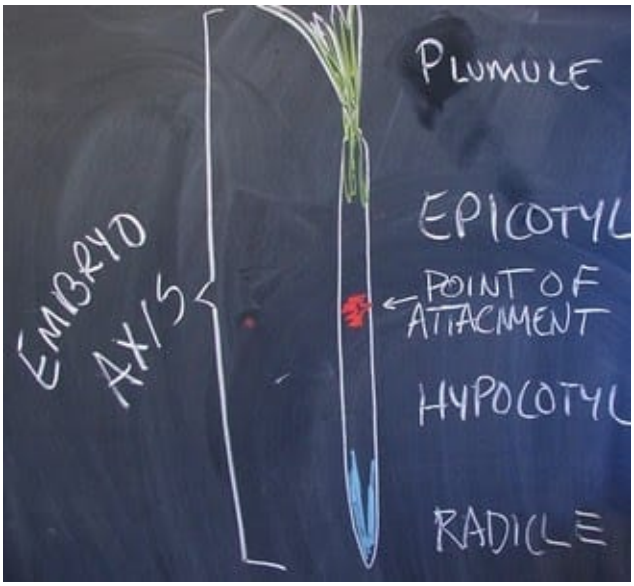
Cross section of kidney bean. Tom Michaels

The drawing above shows a simple cross section of a kidney bean seed (a dicot, but only showing one cotyledon), illustrating these three functions. The kidney-shaped part is the outline of the cotyledon, the main mass of the bean seed and the site of stored

nutrients. Sandwiched between the cotyledon halves is the embryo, which is the nascent plant. On the outside of the cotyledon is a thin layer that is the protective seed coat. The kidney bean seeds we see in the grocery store have a seed coat that typically has a light or dark maroon color. In peanuts, the different structures are easy to see when you pull the two cotyledons apart.

First function: Propagation of the plant by the embryo

In flowering plants the embryo is normally the result of fusion of egg and sperm. The egg is held within an ovule, which in turn is held within the ovary, which can hold several ovules, depending on the species. The egg is typically fertilized by sperm from pollen. The maturing ovule develops within the ovary of the maternal plant.



Embryo. Tom Michaels

A mature seed has an embryo with a linear arrangement of parts. This arrangement is called the embryo axis. The drawing above shows the embryo axis from the kidney bean, straightened out to show the individual structures.

- Embryo axis — the embryonic root and shoot
- Parts making up the shoot tissue of the embryo axis:
  - Plumule — the first true leaves of the plant that you can sometimes see already attached to the embryo. These leaves will emerge from the seed, rise above the soil surface, and start to collect energy from the sun.
  - Point of attachment — the spot shown in red in the diagram (it's not red on a real embryo) on the embryo axis where the cotyledon attaches. The cotyledon is attached to the embryo, and is actually part of the embryo. In the case of the bean, the cotyledon is a nutrient storage organ and the nutrients flow to the embryo through the point of attachment of the cotyledon to the embryo axis.
  - Epicotyl — the part of the embryo axis that is above (epi-) the point of attachment of the cotyledons
  - Hypocotyl — the part of the embryo axis that is shoot tissue below (hypo-) the point of attachment of the cotyledons, but above the radical. The hypocotyl is the part of the shoot between the attachment of the cotyledon and the start of the root (radicle).
- Part making up the root tissue of the embryo axis:
  - Radicle — the embryonic root tissue

At the tip of the epicotyl is the shoot apical meristem that will produce new nodes and internodes. If you're counting nodes on the embryonic axis, the first node on the stem starting from the point of transition of root to shoot is the point where the cotyledons attach. The cotyledons are actually embryonic leaves. The second node is where the plumule is attached.

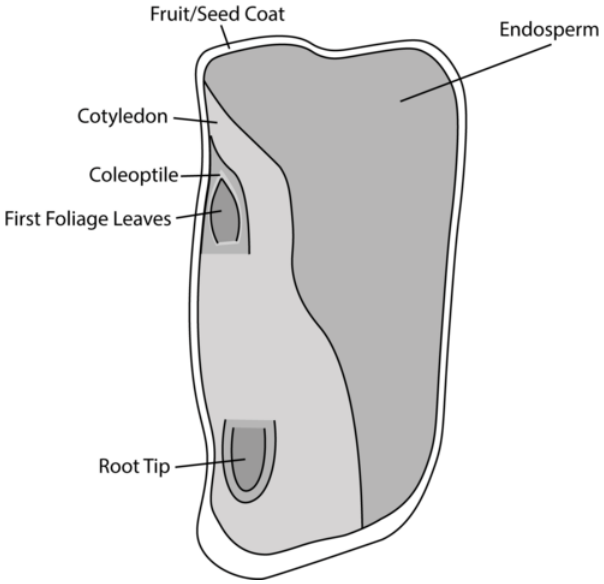
At the tip of the radicle is the root apical meristem that will produce the primary root.

Review questions

1. Differentiate among embryo axis, epicotyl, hypocotyl and cotyledon. Which are derived from the cell resulting from the fusion of egg and sperm?
2. Describe why apomixis results in a seed that is actually a form of asexual propagation.
3. Of the tissues making up the embryo axis (plumule, epicotyl, hypocotyl, radicle), which are shoot tissue and which are root tissue?

Double fertilization and the endosperm

In flowering plants (angiosperms), there is a phenomenon called “double fertilization.” The angiosperm pollen grain holds two sperm cells. One fertilizes the egg, and the resulting zygote grows to become the embryo. The other unites with two other maternal nuclei, called polar bodies, and these three nuclei together grow to become a tissue called endosperm (like the meat and milk of the coconut). This will be covered in more detail when we study meiosis and gametogenesis. For now, remember that in flowering plants there is a process called double fertilization that results in an embryo and an endosperm.



Cross section of corn seed. Sarah Greenwood. CC BY-SA 4.0

In grasses, like the corn in the illustration above, the endosperm is the major energy and nutrient storage tissue. This is different from the kidney bean, where the cotyledon is the storage organ. There is a cotyledon in the corn seed as well, but instead of storing energy and nutrients, it helps break down, absorb, and transfer the energy and nutrients stored in the endosperm to the embryo. Also in many monocots, there is a sheath covering the plumule and epicotyl that provides protection. This sheath is called the coleoptile. A similar sheath covers the radicle, and is called the coleorhiza. Coleoptile and coleorhiza are terms used specifically with plants in the grass family (Poaceae), and not in other families within monocots. Both function in providing protection to the emerging shoot and root. In the corn seed, the three functions of 1) propagation, 2) protection, and 3) nutrition are satisfied by the:

- Embryo (shown in this illustration extending from the shoot to the root) and that will propagate a new plant.
- Endosperm tissue that provides energy and nutrition for the embryo.
- Pericarp protecting everything inside. Remember that in corn, which produces a type of fruit called a caryopsis, the pericarp is fused right to the seed. The pericarp is the mature ovary wall of the female corn flower in the ear (labeled ‘seed coat’ in the illustration above).

This summary table contrasts corn and bean seed components:

	Cotyledon	Endosperm	Seed Coat	Pericarp
Corn – monocot	Energy absorption	Energy storage	Remnants (these tissues are absent or only fragments of tissue in the mature seed)	Protection (outermost layer of the corn kernel)

Bean – dicot	Energy storage	Remnants (these tissues are absent or only fragments of tissue in the mature seed)	Protection (outermost layer of the bean seed)	Protection (pod)

Second function: Storing energy and nutrients for embryo growth

Among flowering plants, energy and nutrients can be stored in the seed in the:

- Cotyledon
- Endosperm

What types of energy and nutrients are stored in these tissues? Think about the seeds you eat, and you can probably name many of these nutrients.

Carbohydrates

- Provide energy — complex molecules composed of carbon, hydrogen, oxygen.
- In plants, carbohydrates include starch and sugar.

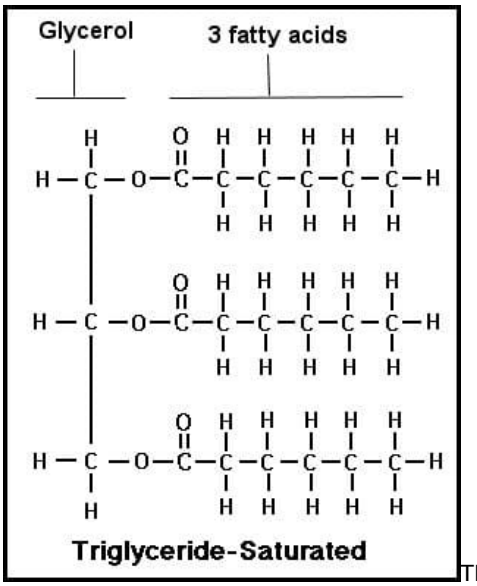
Protein

- Sources of amino acids for production of enzymes and other nitrogen-rich compounds.
  - Amino acids are the building blocks of proteins.
  - Protein is the solid material in tofu (pressed curds from coagulated soy milk). There are several different categories of protein in seeds based on the specific chemical structures of the molecules. Gluten is a type of protein found in wheat endosperm that confers elasticity to bread dough so that the stretchy dough traps the carbon dioxide given off by yeast in the bread-making process and forms a tender loaf full of air pockets.

Lipids

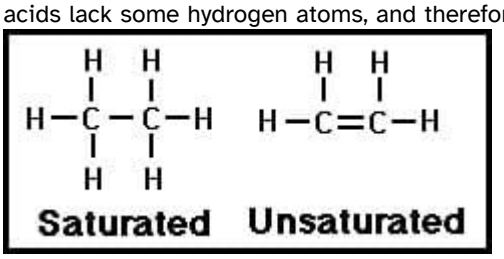
Plant oils, called triglycerides, are compact molecules for storing energy in a more compact way than in starch and sugar.

We are bombarded with a great deal of confusing nutritional information about lipids in our foods. When you encounter nutritional claims, keep this information in mind:

- 

The building blocks of a triglyceride are a Glycerol molecule plus 3 Fatty Acids. The illustration shows a triglyceride made up of glycerol linked to three saturated fatty acids.
- Fatty acids are long chains of carbon atoms with two hydrogen atoms attached to each carbon, except where there is a double bond between adjacent carbons on the chain. In the case of a double bond, each carbon involved in the double bond has only one attached hydrogen atom.

- Saturated fatty acids have no double bonds in the chain, and all carbon atoms in the interior of the chain have two attached hydrogen atoms — they are thus saturated with hydrogen atoms.
- Unsaturated fatty acids have one or more double bonds between one or more carbon atoms in the chain. These fatty acids lack some hydrogen atoms, and therefore the carbon atoms are not saturated with hydrogen — they are unsaturated.



- You have probably heard nutritional claims about saturated and unsaturated fats. The difference between the two is whether all the carbon atoms in the fatty acids are saturated with hydrogen atoms, or are missing hydrogen atoms as a result of double bonds in the carbon chain. Plant oils tend to be unsaturated, which results in them being liquid at room temperature — they have a low melting point. Animal fats tend to be saturated, which results in them being solid at room temperature — they have a higher melting point. If you are interested in more of the chemical nature of fatty acids, check out this link to The Fat Primer (optional reading).

Nutrient differences between monocots and dicots (legumes in particular)

Dicots

As noted above, seeds with two cotyledons tend to have cotyledons whose function is storage. Legumes (Fabaceae family) like beans, peas, soybeans, and lentils are dicots that tend to store large amounts of protein in their cotyledons. Some legumes have high protein, high lipid, and low carbohydrates (like soybean and peanut); these are called oilseeds because they have high lipid content and oil can be squeezed or otherwise extracted from them. Others have high protein, low lipid, and high carbohydrate (like pea and bean), and these are called pulse crops. Pulse crops are hugely important foods because they are edible protein sources. They are a key source of protein in vegetarian diets.

Monocots

Monocots have a cotyledon too, but as noted earlier the cotyledon is primarily used for absorption. In cereals the endosperm stores the nutrients, which tend to be primarily starch and sugar and low amounts of protein and oil.

As a rule, legume seeds are high protein (and in some cases like soybean and peanut high oil), while cereal grains like corn, wheat, oats, barley, and rice are high in starch.

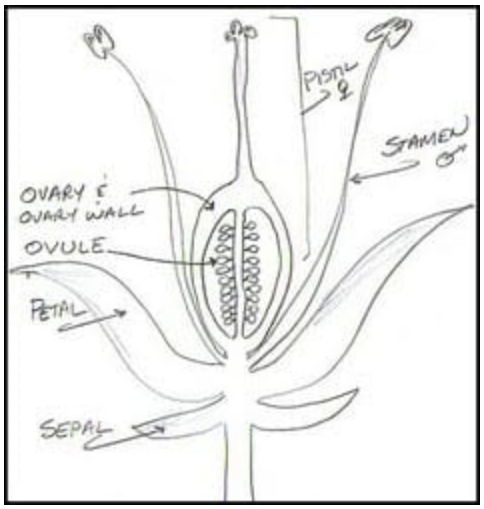
Review questions

1. What seed structure(s) contains carbohydrates?
2. What is the key characteristic of an unsaturated fatty acid?

Third function: Protecting the embryo and nutrients

Seeds have two layers of protection:

- The seed coat, which originates as ovule wall tissue.
- The pericarp, which originates as ovary wall tissue.



Cross section of a flower. Tom Michaels

The line drawing of a flower cross-section, right, shows sepals, petals, stamens (made up of a filament and anther), and carpel or pistil (made up of stigma, style, and ovary). Also identified are the ovary wall and the ovule wall. The ovary is at the base of the carpel and holds the ovules. The ovules are protected by the ovary and hold the egg. When the flower is fertilized, a pollen tube germinates from the pollen grain and grows into the stigma and down through the style. The sperm follows the pollen tube into the ovary. One sperm unites with the egg and the resulting zygote becomes the embryo. The other sperm unites with two polar nuclei to form the endosperm. This is the double fertilization noted earlier.

As the seed matures, the cells inside the ovule multiply and grow. The ovule wall, which is made up of maternal cells called integument tissue, matures to become the seed coat. An example of a seed coat is the red or tan “skin” on a peanut. The ovary wall (note the important difference between the words “ovule” and “ovary”) matures into the protective cover called the pericarp. Again using peanut as an example, the pericarp is the “shell” of the peanut. So peanuts-in-the-shell are an example of a pericarp (shell, ovary wall tissue) and a seed coat (skin, ovule wall tissue) protecting the cotyledons and embryo within the seed.

In contrast, when corn matures, the ovule wall smashes up against the ovary wall as the cells inside multiply and enlarge. The ovule wall cells disintegrate, so at maturity there are only remnants of the seed coat. The ovary wall matures into the pericarp of the corn seed, which is the hard exterior of the seed.

These words belong together:

- Ovule wall — Seed coat
- Ovary wall — Pericarp

You might be interested to know that you are probably wearing integument/seed coat tissue right now. The fine fibers attached to the outside of cotton seeds are made up of long chains of single cells of integument tissue and are extensions of the seed coat. These fibers are removed from cotton seeds, spun into a fiber, and woven into fabric.

Review question

1. When you eat green beans or snow peas as a (culinary) vegetable, are you eating pericarp, seed coat, or both?

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15.2: Seed Physiology

Learning objectives

- Describe the process of seed germination.
- List the external factors that are required for seed germination.
- Understand dormancy and the conditions needed for germination to occur.

Seed — a living plant in a quiescent state

In the ovary, within the ovule, after egg and sperm unite to form the zygote, the zygote cell repeatedly divides and develops into an embryo. The embryo differentiates into different structures — plumule, radicle, cotyledon(s), and the endosperm, seed coat, or pericarp develop. Once this development has occurred, the embryo's metabolism slows down to nearly zero and the maternal plant stops pumping energy into the seed. The nascent plant contained within the seed — really an embryo surrounded by nutritive tissue and a protective covering — is now independent of the mother plant. The seed, which is the next generation of plant, enters a quiescent phase.

Recall that the seed contains:

- An embryo, which is the new plant,
- A nutrient source (typically endosperm and/or cotyledon), and
- A protective covering (typically a seed coat and/or pericarp)

Why do plants produce seeds? Because seeds allow plants to:

- Propagate the next generation
- Generate genetically variable offspring that can be sorted through natural selection
- Survive harsh conditions
- Disperse into new environments



Red chile pepper. Nir Sinay. CC BY-NC-ND 2.0

The first of these reasons is obvious, to propagate. One parent plant generates many seeds, and through these seeds potentially bears many offspring. A kidney bean plant, for instance, might average 4 seeds per pod and have 20 pods hanging on the plant, so one plant yields 80 seeds. A nice ear of field corn will have 16 rows of kernels with 40 kernels per row, for a yield of 640 seeds. The tiny hot pepper in your garden has over 50 seeds, and 20 peppers on a plant would yield 1,000 seeds.

The second reason, genetically variable offspring, results from cross-pollination (mentioned above under Seed Morphology), which is particularly common in wild, undomesticated plants. When plants cross-pollinate, an egg is formed within the maternal plant. The genetic constitution of the developing embryo within the seed is 50% from the paternal plant, 50% from the maternal plant. The particular combination of genes in the developing seed is different from that in either parent plant, and from the other seeds on the same maternal parent. The seeds share some of the same genes, but the specific combination of genes is different. That difference results in genetic variability, which can be expressed as differences in plant height, flower color, leaf shape, fruit size, or other morphological or physiological characteristics. In nature, this variability is the raw material on which natural selection operates. In plant breeding, it is the resource that sustains our efforts to select improved plant varieties.

Due to their protective coating and quiescent metabolism, seeds can survive harsh conditions that will kill the parent plant such, as freezing cold, protracted drought, and even fires. Once conditions are again favorable for plant growth, the seeds can then germinate.

Seed dispersal

Watch this video for an explanation of seed dispersal in space and time (2:20)



Samaras are the flat-winged fruit produced by maple trees. Bob Larrick. CC BY-SA 2.0

Seeds disperse from the maternal parent plant “in space” through many wonderful and creative mechanisms for hitching rides on the wind, on animals, and sometimes *in* animals as they are eaten, pass through the gut, and are excreted.

You have probably seen fluffy cottonwood (poplar) seeds floating on the summer breeze, pulled burdock seeds off your sweater after bushwhacking through the woods in the fall, or washed bird guano full of mulberry seeds off your car’s windshield. These seeds all used strategies for dispersal in space. Vanderbilt University’s Bioimages (optional) includes photos of mechanisms that help spatially disperse seeds.

Seeds also disperse from the maternal parent plant “in time.” Some have dormancy mechanisms that delay germination until the next favorable growing season, which might be a year from now or even several years from now. Seeds are considered dormant if they are alive and don’t germinate even if provided with favorable conditions for germination. There are many dormancy mechanisms; we’ll address some of them later.

If you’ve ever dug up new sections of your yard for a garden, did you notice that, a few weeks after planting veggies or flowers in the spring, you saw a big flush of weeds? And if you pulled up all of those weeds and somehow prevented any new seeds from landing in the garden, you still got a big flush of weeds the next year? This is called the soil’s seed bank, and it’s due to dormant seeds that are resting in the soil. Every year a percentage of those seeds lose their dormancy and germinate, leaving you wondering in frustration whether the weeding will ever end. (It won’t.)

Review questions

1. What type of reproduction results in genetic diversity among seeds produced on the same plant?
2. Distinguish between mechanisms causing dispersion in time vs. dispersion in space.
3. What part(s) of the seed provide nutrition? Protection?

Germination

Germination is the reactivation of the seed's metabolism and the restoration of embryo growth. There are two main reasons why seeds don't germinate:

1. They could still be quiescent because favorable external conditions do not yet exist. In particular, the environment could be too dry or too cold, or the oxygen levels could be too low to support embryo growth.
2. They could be dormant — the characteristic that allows seeds to disperse in time.

External conditions

The external conditions required for germination to occur are:

- Water
- Oxygen
- Temperature
- Light (for some small or fine seeds, like lettuce)

Looking at these external conditions more closely:

Moist conditions allow the seed to imbibe water. Seeds are typically very dry — somewhere in the 8–15% relative humidity range — so they will readily take up moisture from damp soil. Water moves through the pericarp and seed coat into cells and leads to reactivation of the metabolic processes. The seed's nutritive reserves are metabolized for the embryonic cells to divide, enlarge, and differentiate.

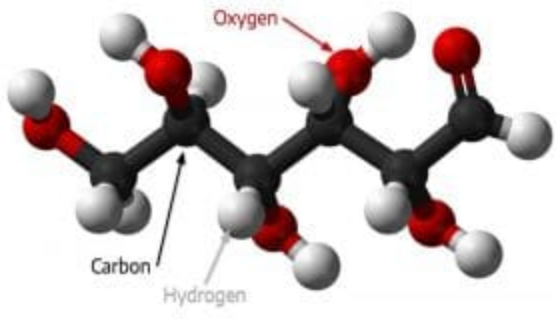
The breakdown of nutrient reserves to form energy for plant growth is called **respiration**, and it requires oxygen. The seed must have oxygen to respire. If you keep seeds in an oxygen-depleted atmosphere, they will not germinate. One all-too-common type of oxygen-depleted environment in which seeds are sometimes placed is waterlogged soil. If you over-water newly planted seeds, the water will keep oxygen from reaching the seeds, and although the seeds will imbibe water and swell as if everything is going well, they will not germinate, and will likely rot because there is not enough oxygen available to sustain respiration. Waterlogged soil also encourages growth of bacterial and fungal organisms that can infect and decompose the seed.

Depending on the species, seeds have various temperature requirements for germination. Some spring flowers will germinate when soil temperatures are quite cool, even below 50°F, while most of the seeds we plant in our gardens prefer temperatures in the 50–70°F range. Again, respiration is the reason. Molecules move around faster when they are warmer, and this movement encourages the chemical reactions required for respiration. If the seeds are cold and the molecules aren't moving around, the seeds won't germinate.

If light is required for seed germination, the species is said to be positively photoblastic. This characteristic allows the seed to remain dormant when buried deep underground, but to germinate when brought to the surface. As you might imagine, weeds that are successful in annually-tilled soils may be positively photoblastic. They remain dormant until tillage brings them to the soil surface.

A note about respiration

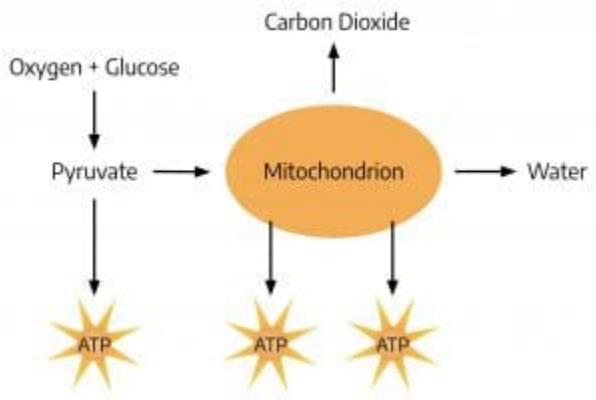
Respiration refers to the set of reactions that take place in the plant cell to convert chemical energy stored in molecules into a form of energy that can be readily used by the cell to power other chemical reactions. Respiration converts the starch stored in the endosperm or cotyledon into ATP (Adenosine triphosphate) (optional reading), which is used in the apical meristems and the radical of the embryo to fuel cell division and the production of new cells.



Glucose molecule. Public domain.

Starch is made up of a chain of glucose subunits. Glucose, shown in the three-dimensional model above, is a simple sugar that is made up of 6 carbon atoms, 6 oxygen atoms, and 12 hydrogen atoms. The shorthand formula for glucose is $C_6H_{12}O_6$. The shorthand formula for starch is $[C_6H_{12}O_6]n$, where the "n" indicates that there are "n" glucose molecules that, when linked together, make up a starch molecule.

When we put a quiescent, but not dormant, seed in the ground and it has access to appropriate moisture, warmth, and oxygen (and light if positively photoblastic), it begins to respire. Enzymes are secreted by the cotyledon and, depending on the species, by other specialized cells surrounding the cotyledon and endosperm, which break down the stored starch into its glucose subunits. It is important that the starch be broken down to glucose because glucose is a sugar that is physically small enough to pass through the semipermeable cell membrane; starch is too large to get through. Starch can't be moved from cell to cell, but glucose can. Starch can be stored in cotyledon or endosperm cells and be broken down to glucose, and that glucose then moves into the actively dividing meristem cells.



Cellular respiration. Emily Tepe

Once in the cell cytoplasm, the glucose is broken in half by a process called **glycolysis** to form a 3-carbon compound known as **pyruvate**. Pyruvate first reacts with a carrier molecule and then moves into the mitochondria — the powerhouse organelles in the cell — where it is further metabolized to yield high-energy molecules of ATP. The processes in the mitochondria require the presence of oxygen. The ATP moves out of the mitochondria and to the parts of the cells where chemical reactions are taking place that need energy.

Starch stored in the seed is a form of stored energy composed of glucose. Glucose is a transportable form of chemical energy that can move through cell membranes, so it helps surround the seed with chemical energy. Pyruvate is a compound formed from glucose that can move into the mitochondria and be broken down to yield ATP. ATP leaves the mitochondria and provides the cell with the energy needed for a wide range of chemical reactions.

The inputs for respiration are glucose and oxygen. Respiration converts the energy stored in the glucose into ATP that will power reactions throughout the cell. Carbon dioxide and water are the two waste products.

Seeds also store lipids and protein in the cotyledons. These too can be broken down during respiration. The lipids are first biochemically deconstructed into their components: glycerol and fatty acids. The glycerol molecule is made up of carbon, hydrogen, and oxygen — so it can also be converted to pyruvate and heads into the mitochondria for conversion to ATP. The fatty

acids take a different biochemical route, but still end up yielding ATP. Protein respiration is even more complicated, and yields nitrogen-containing building blocks of protein and cells called amino acids that are used in construction of other molecules in the cell. Stored protein in the seed is better at providing amino acid building blocks than it is in providing ATP to energize the cell. Protein can provide energy if necessary, but starch and lipid are more efficient energy storage molecules.

Storing seeds

Since germinating seeds require oxygen, moisture, and warmth, you can intentionally restrict germination by limiting one or more of these conditions. Why restrict germination? One reason is to store and save seeds for long periods of time. The most common method for storing seeds is to ensure that they remain dry. If you dry seeds in the sun on a low-humidity Minnesota day, you will get the seeds down to around 10% moisture, which is great for storage. (Don't bake them in the oven; too much heat will kill the embryo.) At a moisture level of 10% or lower you can put them into a glass jar with a tight lid and put them on a shelf for a few years of storage. To store them longer, you can put them in your freezer, which of course means that you have drastically reduced the heat in the seed, which will stall respiration even further and extend the life of the seed. In extreme situations, such as that maintained at the National Seed Storage Laboratory in Fort Collins, Colorado, seeds are dried and placed in oxygen-depleted conditions and stored in a freezer, or put in vials and suspended in the vapor over liquid nitrogen for storage at about -150°C.

For home storage of most garden seeds, get them dry, put them in a tightly lidded glass jar, and, to make them to last 5–10 years, put the jar in the freezer. To dry small amounts of seeds, you can use a home food dehydrator set on a very low temperature. Don't put your seeds in the refrigerator unless you have them very tightly sealed in an air-proof container, because refrigerators are damp. A refrigerator is a great place to store popcorn, because the humidity ensures that the kernels have enough moisture to pop strongly, but it's a poor environment for seed storage.

Dormancy

The second reason seeds resist germination is dormancy. Dormancy is when the seeds do not germinate, even though conditions for germination are favorable. Something about the seed prevents germination. Barriers to germination could include:

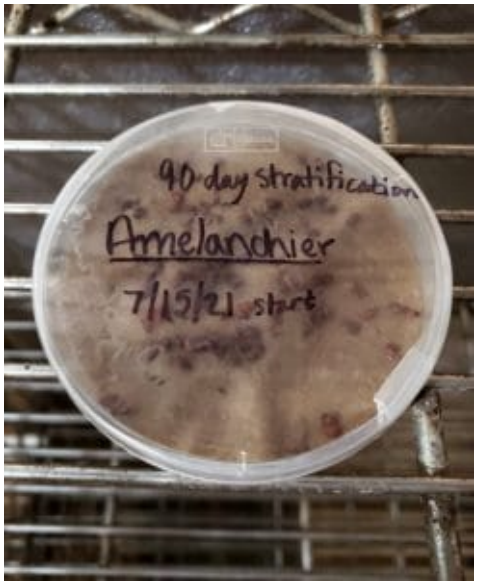
1. Barriers in the protective covering:
    - A seed coat, or pericarp, that is impermeable to water or oxygen.
    - Compounds that act as germination inhibitors that are embedded within the seed coat.
2. Barriers in the embryo:
    - Physiological immaturity of embryo — the embryo is initially immature and requires a period of cool temperatures or alternating warm and cool temperatures to fully mature.
    - Endodormancy in temperate plants — internal biochemical processes must be met in the seed before germination can begin. Endo-dormancy is the first stage of dormancy for many seeds from plants grown in temperate environments like Minnesota. Once the internal biochemical processes are met, the seed usually goes into eco-dormancy.
    - Ecodormancy — external factors are not optimal for germination. This is often due to temperatures being too cold, or to amounts of water not sufficient for germination.



Kentucky coffee tree seeds. Laura Irish

The ways in which horticulturists overcome seed dormancy depend on the type of dormancy. For seeds with impermeable seed

coat, such as the Kentucky coffeetree (*Gymnocladus dioicus*) seen above, a technique called scarification is used. Sandpaper is used to break through the seed coat until the white cotyledon is visible. Under warm, moist conditions, these seeds will germinate. To germinate a large amount of seed, there are other ways to break the seed coat, such as using acid to "etch" holes in the seed coat to allow for water imbibition.



Stratifying Amalanchier seeds. Laura Irish

In the case of endodormancy, we usually have to be patient. Seeds are placed in a cool (38–42°F) place under moist conditions. This process is called stratification. Depending on the plant species, stratification can take from 2 weeks to almost a year. It is as easy as putting seeds in a sealable plastic container or bag with moist media, and placing them into a refrigerator.

Dormancy is a great strategy for enhancing a plant's survival potential because germination is delayed until a later time when environmental conditions are more favorable. However, for horticulturists who prefer that a seed germinate as quickly as possible after being planted, dormancy is a nuisance. One of a horticulturist's important skills is to recognize dormancy, identify the dormancy mechanism, and take steps to overcome the inhibition so that plants can grow predictably from seed when planted.

Review questions:

1. What external factors are required for germination?
2. Outline the process through which the seed's embryo receives useful energy from the starch stored in the cotyledon or endosperm.
3. What are the factors required for successful long term seed storage? How do these compare to the factors required for germination?
4. What are the different types of dormancy?
5. If you knew a seed had ecodormancy, what would you do to encourage germination?

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15.3: Terms

These are the important terms from this chapter to be sure to know. You might also find these in later chapters.

Apomixis	A form of clonal reproduction where vegetative cells in the flower develop into zygotes to form seeds.
Carbohydrates	One of the three major types of nutrients found in seeds; provide energy in the form of starch and sugar.
Coleoptile	Protective sheath that covers in the plumule and epicotyl in the Poaceae family.
Coleorhiza	Protective sheath that covers the radicle in the Poaceae family.
Cotyledon	Food storage structure used in germination.
Dormant/ dormancy	Term used when seeds are alive and don't germinate when provided with favorable conditions for germination.
Double fertilization	Where one haploid male sperm cell fuses with the female haploid egg cell to form the diploid zygote, and the second haploid male sperm cell fuses with two egg cells to form a triploid endosperm.
Ecodormancy	When external factors, usually environmental, prevent a seed from germinating.
Embryo	Nascent (new, young) plant resulting from the combination of genes from the male sperm transmitted by the pollen to the female egg held in an ovule in the ovary.
Embryo axis	Embryonic root and shoot.
Endodormancy	When internal factors within the seed prevent germination.
Endosperm	Tissue that results from the second haploid male sperm cell fusing with two egg cells during fertilization.
Genotype	Genetic composition of an organism.
Lipids	Compact plant oils that store energy; also called triglycerides.
Pericarp	Ripened ovary wall; made-up of three parts: exocarp, mesocarp, and endocarp.
Phenotype	Physical appearance of an organism.
Plumule	First true leaves of the plant; emerge from the seed, rise above the soil surface, and start to collect energy from the sun.
Proteins	Sources of amino acids for production of enzymes and other nitrogen-rich compounds in the seed.
Quiescent	When a seed does not germinate until given proper conditions for germination (oxygen, water, temperature, and sometimes light).
Saturated fatty acids	Fatty acids that have no double bonds in the chain with all carbon atoms in the interior of the chain having two attached hydrogen atoms.
Scarification	Process used to break a physical seed dormancy (hard seed coat).
Seed coat	Outer layer of the seed.
Stratification	Process used to break a physiological dormancy, such as embryonic or endo/eco-dormancies.
Triglycerides	Another name for lipids.
Unsaturated fatty acids	Fatty acids that have one or more double bonds between one or more carbon atoms in the chain, lack some hydrogen atoms, and therefore the carbon atoms are not saturated with hydrogen.

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16: FRUIT

Learning objectives

- Define simple, aggregate, and multiple fruit.
- Explain the general characteristics of fleshy and dry fruits.
- Identify the difference between a true fruit and an accessory fruit based on structure and tissues.

Fruit are important for their culinary importance and provide calories, nutrition, and pleasure. They also are the location for the development of seeds — the most important means to propagate plants and the source of genetic variation.

16.1: Fruit Morphology

16.2: Atlas- Fruits

16.3: Terms

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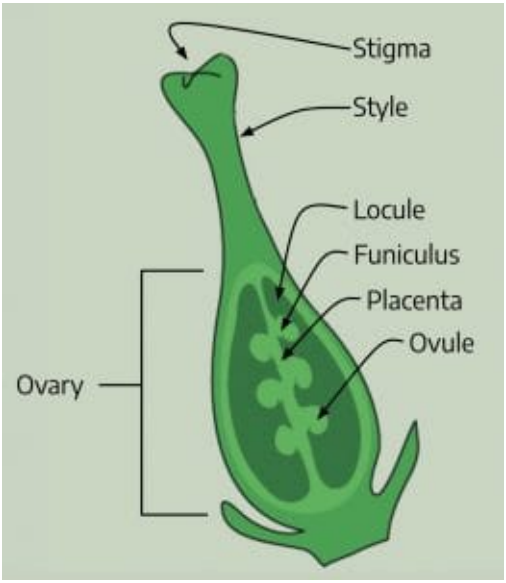
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16.1: Fruit Morphology

Learning objectives

- Define “fruit” from a botanical point of view.
- Describe the differences among simple, aggregate, and multiple fruits.
- Explain the general characteristics of fleshy and dry fruits.
- Identify the difference between a true fruit and an accessory fruit based on structure and tissues.

That’s a fruit? I thought it was a vegetable!

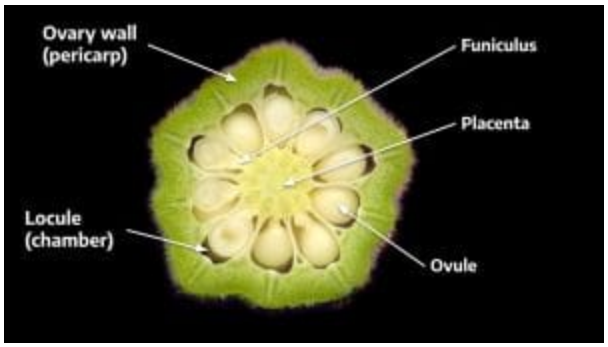


Carpel structure. OpenStax Biology. CC BY 4.0

The graphic to the right shows a cross section of the carpel. Recall that the carpel is the female reproductive structure that is attached to the top whorl of the flower — the gynoecium node. The carpel has three basic parts:

- The **stigma**, at the tip, and to which pollen grains adhere.
- The **style**, the channel of tissue through which the pollen tube grows.
- The **ovary**, at the base, and housing the ovules that contain the plant’s eggs.

The photo below shows a bit more detail about the carpel — in particular, the attachment of the ovules within the ovary via a stalk called the funiculus, emerging from the placenta. It also names the chamber in which the ovules hang: the **loculus** (or locule). Remember the locule, but you won’t need to remember funicule, funiculus, or placenta. If you do come across those names in the future, then recall that they relate to the attachment of the ovule within the ovary.

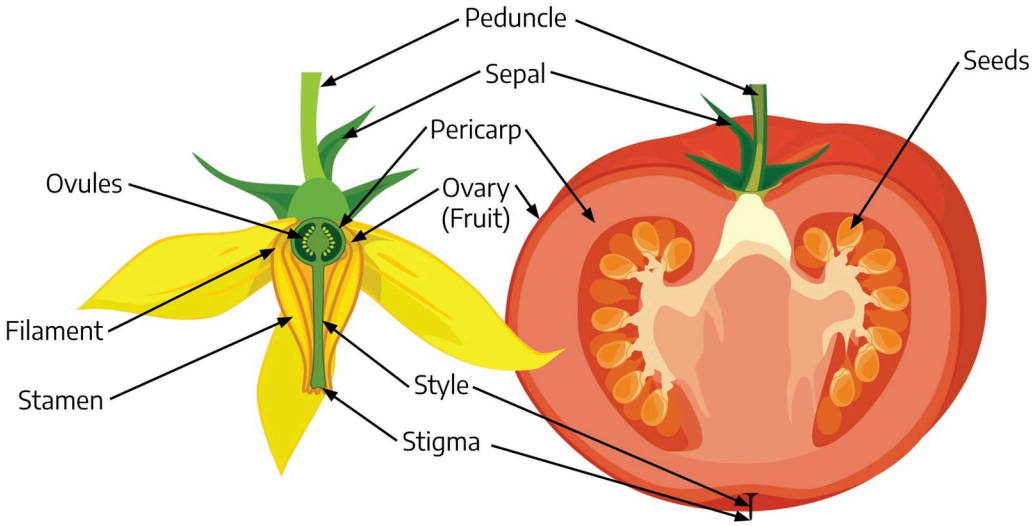


Carpel structure, cross section. Jmprouty. CC BY-SA 3.0

A fruit, in the botanical sense, is the ripened ovary together with the seeds within the ovary. People often think of a fruit from the culinary point of view, considering it to be the part of a plant that has seeds and when ripe is ready to eat, and think of vegetables as a savory food that is any edible part of a plant not associated with seeds (these include roots, stems and leaves). But some plant parts that, when we wear our chef's hat, we think of as vegetables, are really botanical fruits. That green pepper chopped up on your pizza is a botanical fruit, as is the tomato that's pureed to make the pizza sauce. A squash is another botanical fruit that we treat like a vegetable in the kitchen. Adding to the confusion is the legal decision that tomato fruits are vegetables (Nix v. Hedden 1893; The Washington Post). In Plant Propagation, we'll define fruits from the botanical standpoint: the ripened ovary of a flower, together with the seeds within that ovary.

Review the diagram below of the tomato flower and fruit to be sure you know exactly which parts of the flower develop into the fruit. In the flower, the ovary wall provides protection to the ovules that contain the egg — the female gametes. The egg cells within the ovules are fertilized by the sperm from the pollen, the ovules develop into the seeds, and the ovary matures into the fruit. For some species, fruits are brown, green, starchy, bitter, proteinaceous, dry, and durable. They may be inedible, unpalatable, or so small as to be terribly inconvenient as a food. The ovary wall doesn't always become a sweet and fleshy fruit like a peach. In kidney beans, for instance, it becomes a dry and brittle protective pod. Nevertheless, both the peach and the bean pod are botanical fruits.

The illustration shows a cross section of a tomato, with the fleshy ovary wall around the outside, locules (chambers) within the tomato, and seeds forming within the locules. The seeds are attached to the central placenta tissue by the funiculus.



Tomato flower and fruit. © Shutterstock, used with permission. Adapted and labeled by Emily Tepe.

Watch this videos to learn about flowers and fruits (2:45 min);

this video to learn about the structure of the ovary in the flower (3:40);

and this video on the structure of the mature tomato ovary or fruit (2:19).

Review activity

1. Draw a diagram of a flower showing which parts become the fruit.
2. Based solely on the botanical definition of a fruit, would the receptacle, petals, sepals or stamens be part of a true botanical fruit?
3. If you cut open a green pepper where is the locule?

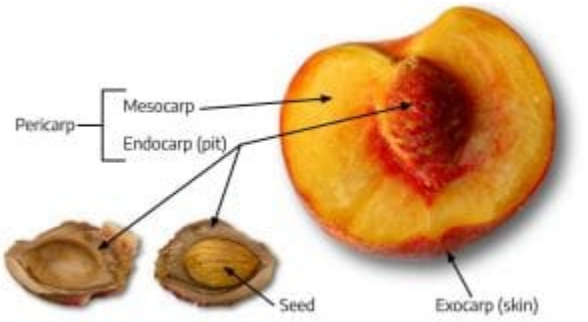
Parts of a fruit

The ripened ovary wall is called the **pericarp** — **peri** meaning around and **carp** referring to the carpel. Pericarp = around the carpel. The pericarp can be dry, as with bean pods, or fleshy like a peach, or sometimes both, as in an avocado, where the outer layer is leathery and the inner layer is fleshy.

The pericarp of a fleshy fruit typically has three layers, and each may have distinct characteristics. The photo of a peach below shows the layers making up the pericarp:

- Exocarp: the outer layer of the pericarp)also called the **epicarp**)
- Mesocarp: the middle layer (fleshy in this example)
- Endocarp: the inner layer (hardened with sclerenchyma cells in the coconut example below)

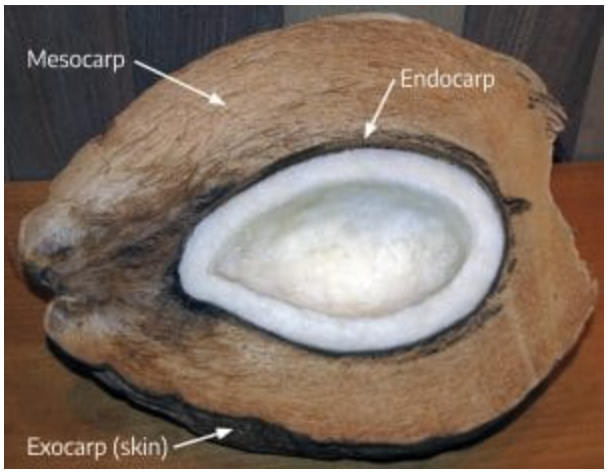
What type of cell makes up this hard shell of a walnut or peach?Sclerenchyma!



Peach with fruit parts. Liz West and An.ha. CC BY 2.0 and CC BY-SA 3.0

Depending upon the species, the exocarp may be tender, leathery, or hard. It may have oil glands (like in oranges and lemons) or hairs (like in kiwifruit). Similarly, mesocarps and endocarps may have various modifications that make them hard, soft, or leathery depending on the species. Remember that the pericarp is ripened ovary wall tissue and the exo-, meso- and endocarp are layers of that ripened ovary wall.

The coconut is a fruit. The photo below shows that the hard shell around the coconut that you see at the grocery store is actually the endocarp (the inside layer of the ovary wall). The fibrous mesocarp and the leathery exocarp have been removed from the coconut fruit by the time it reaches us. The fibrous mesocarp is used for other purposes like floor coverings in high-foot-traffic areas where a tough, durable fiber is needed.



Cross section of a coconut. James St. John. CC BY 2.0

A “nut” is a botanical name for a particular type of fruit. From a culinary perspective, there are many foods that we call nuts, but to a botanist a nut is a fruit with a particular structure.

You likely already knew that a peanut isn’t a nut; it’s a type of fruit called a legume, and is related to peas, beans, and locust trees. A cashew isn’t a nut either; it’s a type of fruit called a drupe. If you are interested in seeing other unusual fruits, visit the Fruits called Nuts page posted by W. P. Armstrong at Palomar College.

Review activity

1. Next time you’re grocery shopping, look around the produce section and try to figure out what parts of the fruits are the exo-, meso-, and endocarp. For instance, what are the parts that make up the banana? Where are those seeds?
2. Why are fruits important to plant propagation?

Types of fruits

Simple fruit

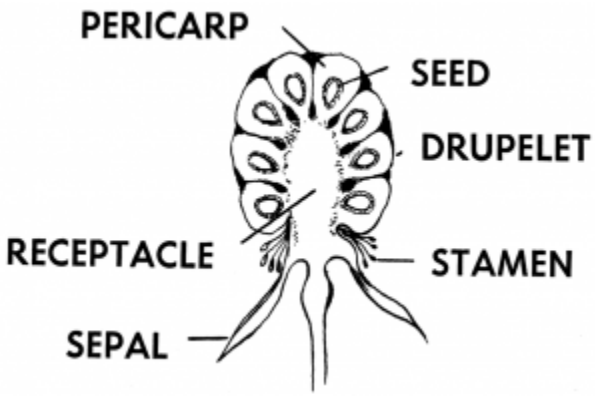
A simple fruit is formed from a flower with one carpel, or multiple carpels fused together so that it looks like just one carpel. The ovary wall surrounding the carpel or carpels ripens into an independent fruit (independent in the sense that it isn’t fused together with other ovaries). The photo below shows a grape, which is a simple fruit.



Cross section of a grape. Yelkrokoyade. GNU Free License 1.2

Aggregate fruit

In an aggregate fruit, the fruit is formed from the ripened ovaries present in one flower with numerous simple carpels. The ripened ovaries from that one flower coalesce into one larger unit, but you can still see evidence of the individual carpels. The raspberry, for instance, comes from one flower with many carpels. As the pericarps mature they mature together to form the thimble of the raspberry that we eat. You can still see the mosaic of individual ruby red carpels that fuse together to form the thimble. If you've ever harvested raspberries you know that the thimble pulls off a firm white structure, and that structure is the receptacle of the flower. Below is an illustration of the fruit structure.



Cross section of an aggregate fruit. Pearson Scott Foresman. Public Domain

Multiple fruit

A multiple fruit is formed from the ripened ovaries present in one flower with numerous simple carpels. The ripened ovaries from that one flower coalesce into one larger unit, but you can still see evidence of the individual carpels. In the photo of the pineapple, below, you can see individual flowers, some of which are still open and showing purple-pink petals. The pericarps of these individual flowers coalesce into one large multiple fruit.



Pineapple flowering. Peta Hopkins. CC BY-NC-ND 2.0

The distinction between aggregate fruit and multiple fruit has to do with the number of flowers involved in the fruit. An aggregate fruit is from one flower with many ovaries, and the multiple fruit is made up of multiple flowers.

Fruit types

Fruits are also categorized according to whether the pericarp at maturity is:

- Fleshy: accessory parts of the ovary develop into succulent tissues with a high moisture content.
- Dry: at maturity the fruit has a low moisture content. Dry fruit that opens and releases the seeds from the pericarp is called dehiscent and dry fruit that remains closed retaining the seed within the pericarp is called indehiscent.

A dry, dehiscent pericarp may split open along sutures in various ways, and these ways of splitting open are also characteristic of particular types of fruits.

Simple fruits

Simple fruits with fleshy pericarp (exocarp, mesocarp, endocarp):

Drupe

A stone fruit, derived from a single carpel and containing usually one or two seeds. The exocarp is a thin skin, the mesocarp may be fleshy, and the endocarp is hard (i.e., “stony”) as shown in the photo of the peach, below. Examples of drupes include peach, plum, cherry, apricot, and almond.



Apricot cross section. Fir0002/Flagstaffotos. CC BY-NC

Berry

A simple fruit formed from one flower with a superior ovary. The fruit has a fleshy pericarp, one carpel or multiple fused carpels,

and many seeds. A tomato (below) is a berry, a grape is a berry, blueberries and cranberries are berries...but a raspberry is not. (Remember that a raspberry is an aggregate fruit where the carpels do not fuse the way they do in multiple-carpel berries).



Cross section of a tomato. FoeNyx. CC BY-SA 3.0

Pepo

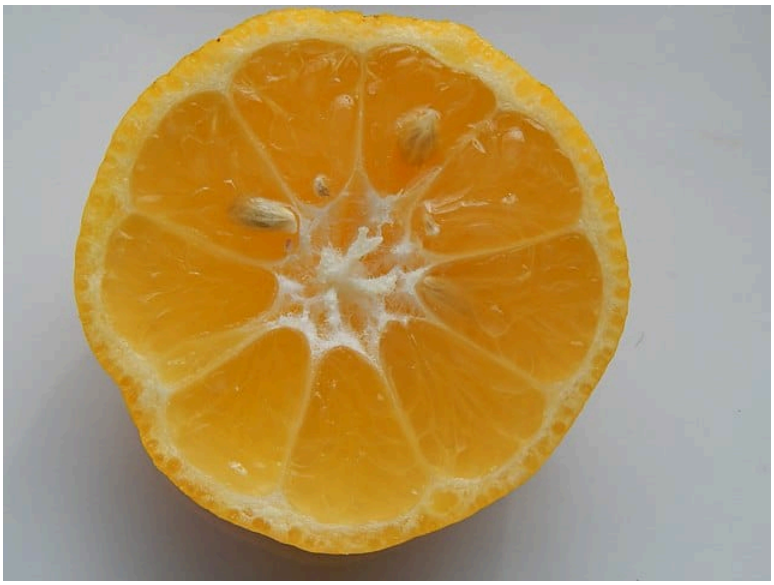
A simple fruit formed from one flower with an inferior ovary. The fruit has a fleshy mesocarp, a rigid or leathery exocarp, one carpel or multiple fused carpels, and many seeds. The photo of squash below shows the fusion of three carpels to form the fruit, each carpel having many seeds. The fleshy interior that we eat is the mesocarp. Other examples include zucchini, cucumber, summer squash, and winter squash such as acorn and butternut squash.



Cross section of squash. RoRo. CC0 1.0

Hesperidium

Like a berry, but with a leathery exocarp instead of a fleshy exocarp. Each section of the hesperidium represents one carpel in the flower, but in the mature fruit the exocarp and mesocarp form an uninterrupted cover. The interiors of the carpels are packed with fluid-filled vesicles that are actually specialized trichomes. The exocarp contains volatile oil glands in pits. The orange, below, is an example of a hesperidium. All citrus fruits are this type of fruit.



Citrus cross section. Forest and Kim Starr. CC BY 3.0 US

Simple fruits with dry pericarp, dehiscent

Legume

Dry fruit made up of a single, folded carpel, multi-seeded, dehiscent along two sutures. It is easy to see the funiculus in peas, When you open the pod to shell out the peas there is a small stalk attaching the pea seed to the pod; that's the funiculus. Beans are also legumes.



Pea pod. Inorikof. CC BY 2.0

Capsule

A dry, dehiscent fruit made up of several fused carpels. The photo below shows the exterior of the poppy capsules and a cross section showing the locules with seeds inside. The capsule may split open in several ways depending on the species. In a poppy, the cap pops off to eject the mature seeds.



Poppy capsule. Katharina N. Pixabay license

Simple fruits, dry pericarp, indehiscent

Caryopsis

A fruit from one carpel containing a single seed. The pericarp is fused to the seed. A corn kernel is a caryopsis. The outside of the corn kernel is the pericarp.



Maize kernel. Xochiquetzal Fonseca/CIMMYT. CC BY-NC-SA 2.0

Achene

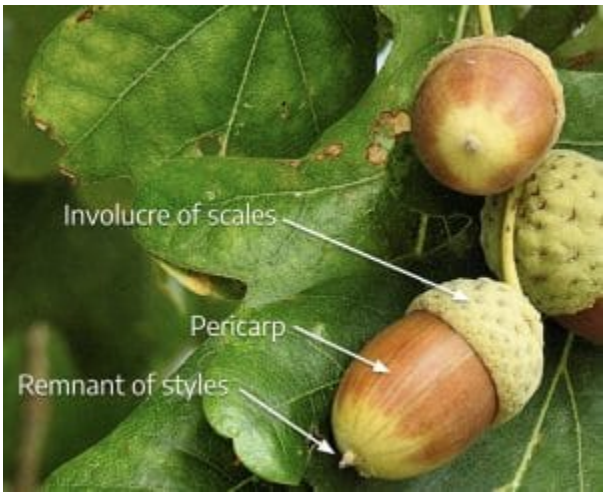
Like the caryopsis (one seed per ovary), but the seed can be threshed so that it is free of the pericarp. You can buy sunflower seeds "in the shell." The "shell" is the pericarp. We also discussed achenes earlier when looking at the actual fruits on a strawberry.



Sunflower seed. Benjamint444. CC BY-SA 3.0

Nut

A dry, indehiscent, one-seeded fruit with a hard exocarp. The ovaries that produce nuts have more than one carpel, but through abortion, only one seed matures. In the photo below, the pericarp of the acorn is partially encased in a tough covering called the involucre. True nuts will always have a hard exocarp and just one seed, while this is not always the case with culinary nuts. Peanuts, for instance, have a hard exocarp but multiple seeds. Horse chestnuts have a leathery exocarp and hard endocarp. True nuts have a hard exocarp.



Acorn. Piqsels. Public Domain

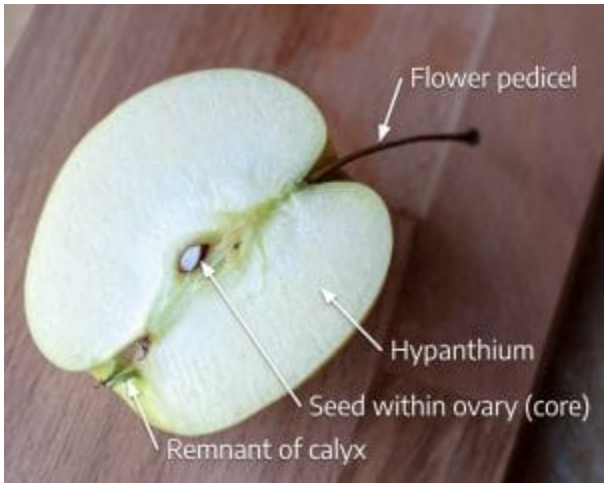
Review questions

1. What features distinguish simple, aggregate, and multiple fruits?
2. What is meant by dehiscent and indehiscent? How would you classify the corn caryopsis and the sunflower achene in this regard?

Accessory fruits

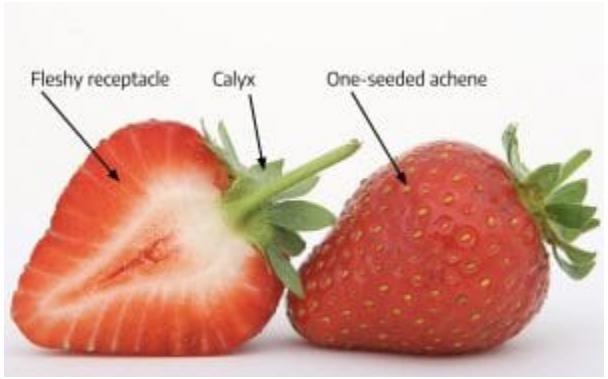
Earlier, we sawhow one or more of the other flower parts (androecium, corolla and calyx) can be attached below the ovary (hypogynous parts, superior ovary), above the ovary (epigynous parts, inferior ovary), or around the middle of the ovary (perigynous parts). In the case of epigynous and perigynous parts there are tissues surrounding the ovary to which the other flower parts attach and that can also adhere to the outside of the ovary and become part of the fruit. One example of a fruit from this type of flower where there is accessory tissue (hypanthium) adhering to the outside of the ovary wall is the pome, examples of which are the apple, pear, and quince. Another example is the strawberry, where together the receptacle tissue and ovary wall tissue form the strawberry fruit. Since it isn't part of the ovary wall, the receptacle tissue is considered an accessory tissue, so the strawberry,

instead of being a true fruit, is a type of fruit called an accessory fruit.



Apple. Piqsels. Public Domain

Apple is an example of a species where the culinary fruit part we eat is actually hypanthium tissue rather than ovary wall tissue. In an apple, the ovary is the papery core that encloses the seeds. Since the part we eat isn't the ripened ovary wall, the apple is called an accessory fruit, signifying that we are really enjoying hypanthium tissue (an accessory tissue), not ovary wall. The hypanthium is also the tissue that makes up the fleshy part of rosehips (fruit of roses) — logical, because apple and rose are in the same taxonomic family: Rosaceae. Plants in the same family have common flower (and therefore fruit) morphologies.



Strawberry. Robert Owen-Wahl. Public Domain

The situation can be very complex with plants like strawberry where the juicy part we eat is the swollen receptacle of the former flower and the actual botanical fruits are the brown specks sticking to the outside of the receptacle. The strawberry is an accessory fruit because the red fleshy part we eat is made up not of the ovary wall, but primarily of receptacle tissue. The strawberry is also an aggregate fruit formed from multiple ovaries present in one flower. The fruit is an achene that contains the single seed from a single ovary attached to the outside of the receptacle.

Review activity

1. Cut open an apple and identify where the hypanthium ends and the ovary wall begins.
2. Next time you are at the grocery store, identify which "fruits" are true fruits, accessory fruits, aggregate fruit, or multiple fruits.

You should know the types of categories, such as simple fruits, multiple, aggregate, dehiscent, indehiscent, and some examples, but you do not need to keep an exhaustive list in your mind. You should also know the definition of an accessory fruit and the relationship of these fruits to epigynous and perigynous flowers.

There are many more types of fruits. If you are interested in some optional reading you can discover more about fruit types. Or

do a Google search on “types of fruits” or on any of the specific fruit types mentioned above.

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16.2: Atlas- Fruits

Ovary Anatomy

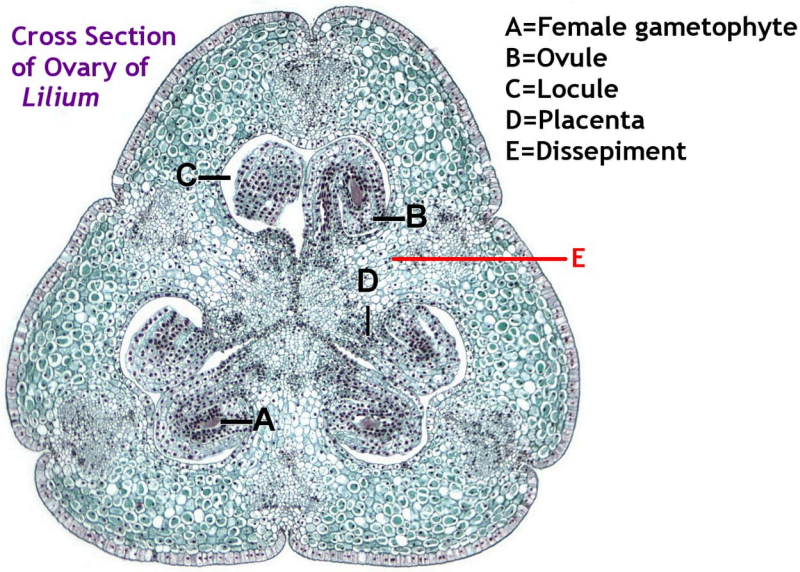


Figure 16.2.1: Cross section of *Lilium* ovary, showing A=Female gametophyte, B=Ovule, C=Locule, D=Placenta, E=Dissepiment. The label in red added to original contribution of File:Lilium ovary L.jpg provided by Jon Houseman and Matthew Ford. JonRichfield, CC BY-SA 4.0, via Wikimedia Commons.

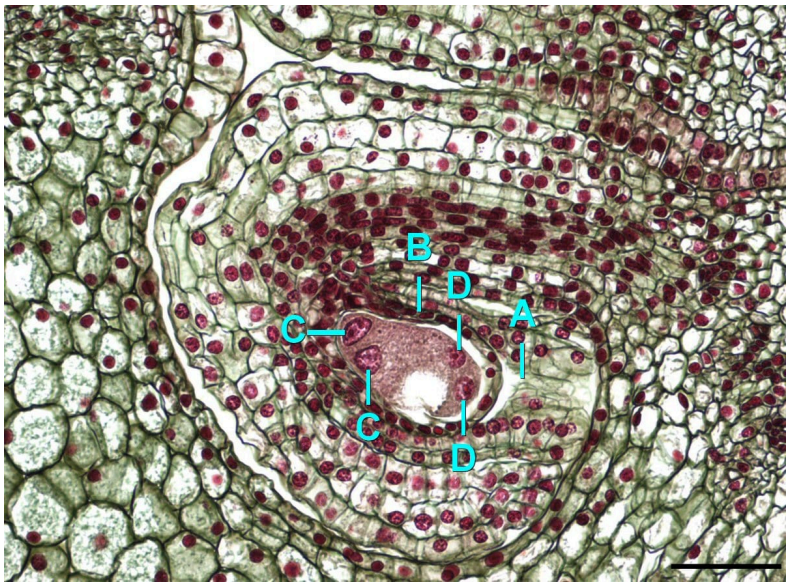


Figure 16.2.2: A *Lilium* ovary during the second stage of the four nucleate embryo. A-Micropyle, B-Integument, C-Antipodal cells, D-Synergid cells. Scale=0.1mm. Jon Houseman, CC BY-SA 4.0, via Wikimedia Commons.

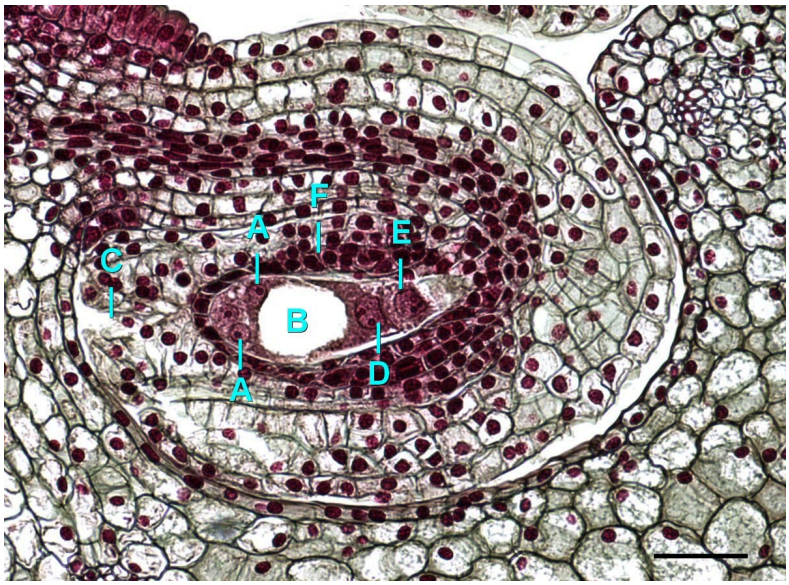


Figure 16.2.3: A *Lilium* ovary at the eight nucleate stage. A-Synergid cells, B-Vacuole, C-Micropyle, D-Polar nucleus, E-Antipodal cell, F-Integument. Scale=0.1mm. Jon Houseman, CC BY-SA 4.0, via Wikimedia Commons.

Transitioning from Flower to Fruit



Figure 16.2.4: 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.



Figure 16.2.5: Salal (*Gaultheria shallon*) is a shrub in the same family as blueberries and madrone trees. Each pendant, urn-shaped corolla will fall off, leaving the calyx behind. The inferior ovary will develop into a berry. In this image, younger flowers are being produced on the left side at the end of the inflorescence, while older flowers develop into fruits on the right side. Photo by Maria Morrow, CC-BY 4.0.

Fruit Anatomy

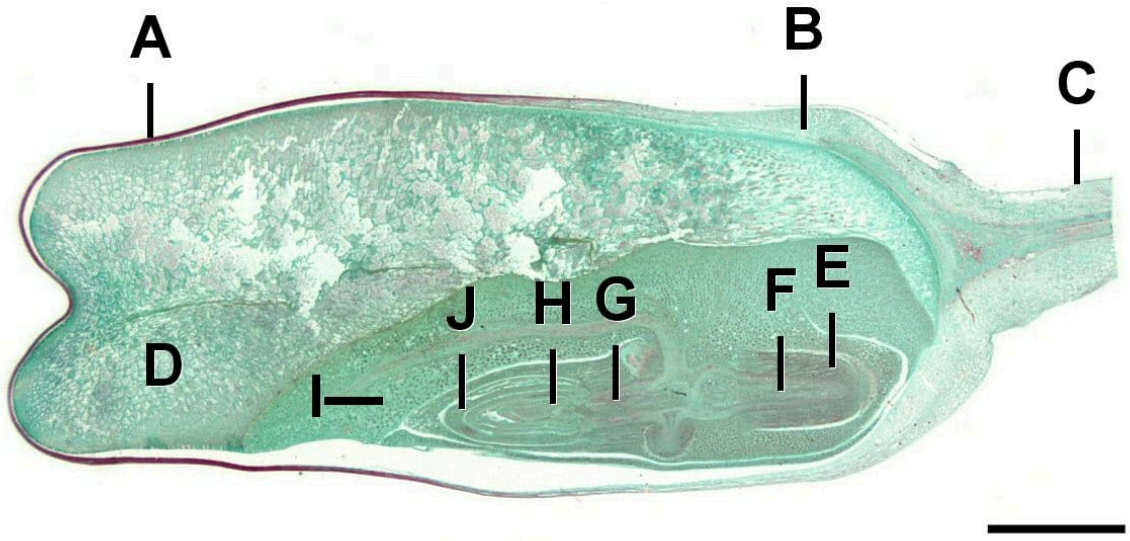


Figure 16.2.6: A *Zea mays* kernel. This fruit is a caryopsis, the seed coat is fused to the pericarp. Labels are as follows: A=Pericarp, B=Aleurone, C=Tip cap, D=Endosperm, E=Coleorhiza, F=Radicle, G=Hypocotyl, H=Plumule, I=Scutellum, J=Coleoptile. Scale=1.4mm. Jon Houseman, CC BY-SA 4.0, via Wikimedia Commons.

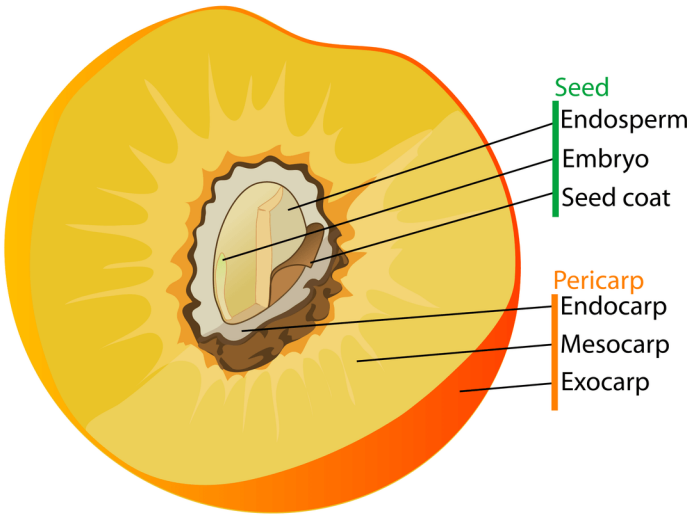


Figure 16.2.7: A diagram of a drupe. The pericarp of a fruit can be completely fused (as in Figure 16.2.7) or separated into distinct layers: the endocarp (innermost), mesocarp (middle), and exocarp (outermost). A drupe is a fruit type with a stony endocarp enclosing a single seed, a fleshy mesocarp, and a thin exocarp. Image by LadyofHats, Public domain, via Wikimedia Commons.

Some Common Fruit Types

Achene



Figure 16.2.8: These two images show the fruits produced from the head inflorescence of a dandelion. On the left, they are difficult to distinguish, forming a sphere around the receptacle. On the right, some of the fruits have been carried away on the wind, making the others easier to see. Each floret has produced an achene at the base (from an inferior ovary). Only the calyx remains, of the other floral whorls, and has formed into an umbrella-like structure for wind dispersal. Photos by Maria Morrow, CC-BY 4.0.

Berries

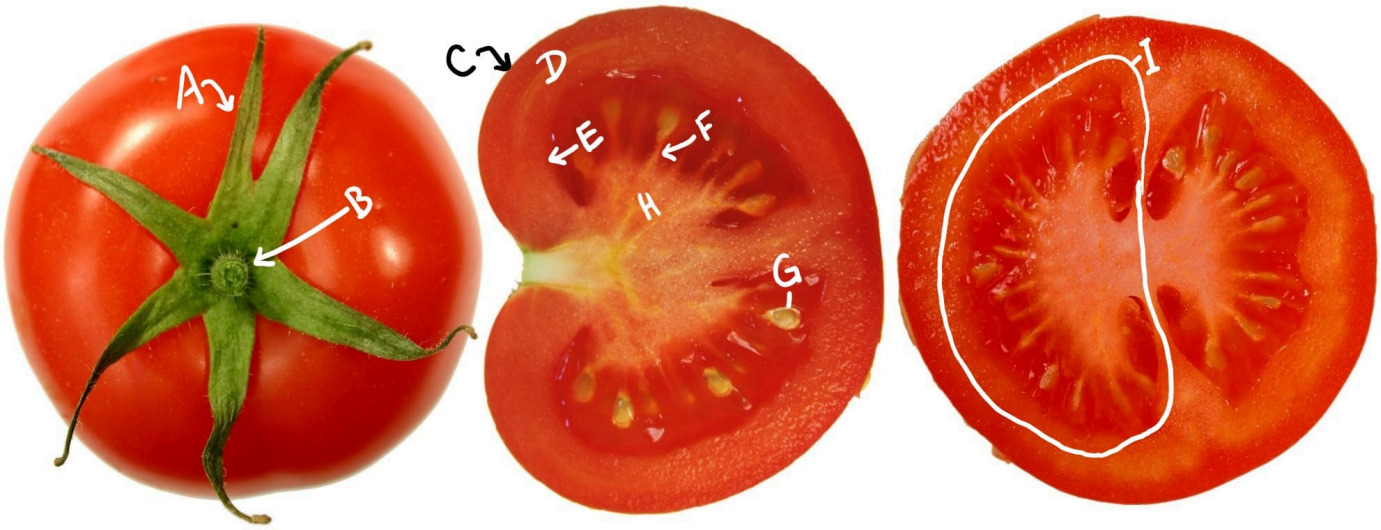


Figure 16.2.9: A tomato is a berry. The pericarp has distinct layers,but all are fleshy. The exocarp forms a thin skin around a fleshy mesocarp. There are many seeds. Labels are as follows: A=Calyx, B=Peduncle, C=Exocarp, D=Mesocarp, E=Endocarp, F=Funiculus, G=Seed, H=Placenta, I=Locule. Image of the tomatoes from © 2005 User:FoeNyx, CC BY-SA, via Wikimedia Commons with labels added by Maria Morrow.

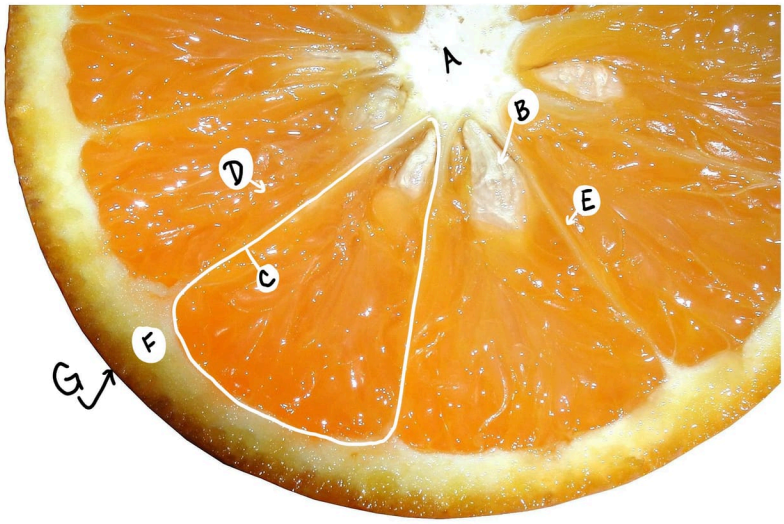


Figure 16.2.10: A hesperidium (citrus fruits) is a modified berry. The endocarp forms the skin around the segments, containing seeds and juice-filled trichomes. The exocarp forms an oily rind. A=Pith, B=Seed, C=Locule, D=Juice-filled trichomes, E=Endocarp, F=Mesocarp, G=Exocarp. Image of the orange slice from Paolo Neo, Public domain, via Wikimedia Commons with labels added by Maria Morrow.

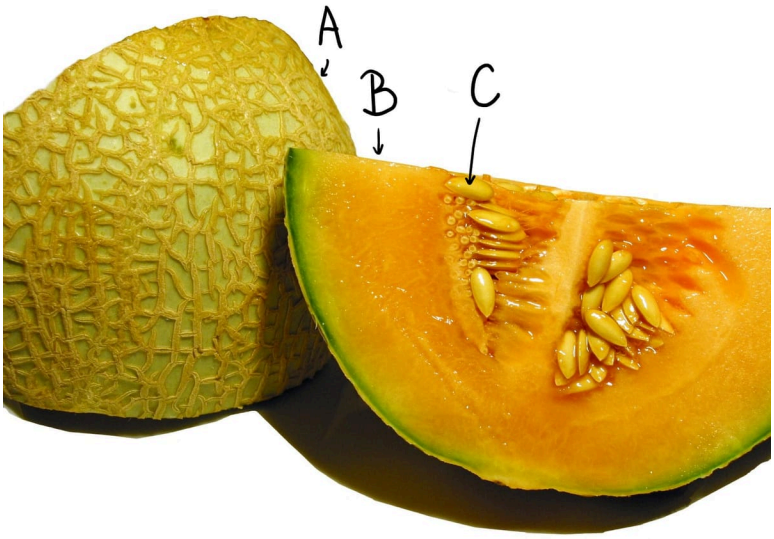


Figure 16.2.11: A pepo is another modified berry. The exocarp forms a (somewhat) tough rind (A). The mesocarp (B) is still fleshy. It contains many seeds (C). Image from User:Tomia, CC BY-SA, via Wikimedia Commons with labels added by Maria Morrow.

Accessory Fruits

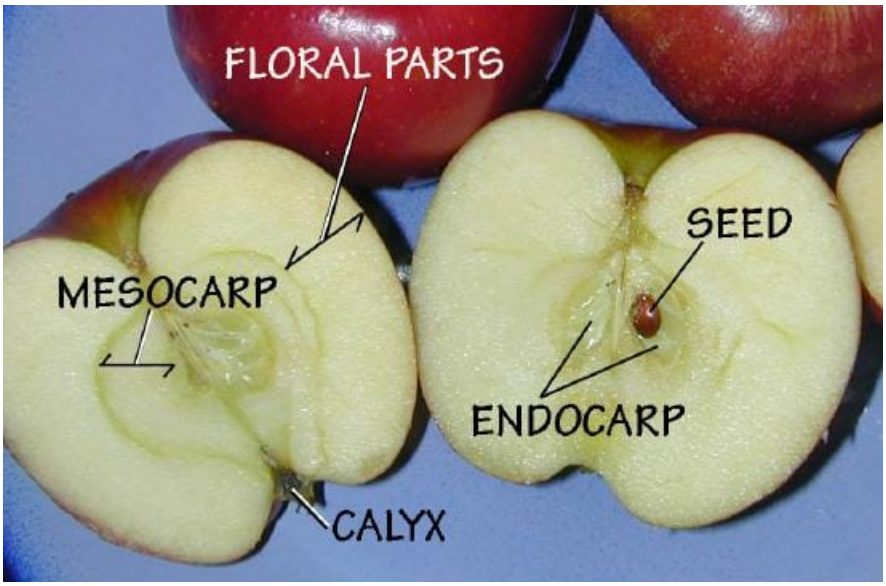


Figure 16.2.12: A pome is an accessory fruit made from a fleshy hypanthium. The papery core is the pericarp, which contains the seeds. Eric Guinther, CC BY-SA, via Wikimedia Commons.



Figure 16.2.13: 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. The calyx of the flower is the green, leafy part. If you look closely, you can see the styles attached to the achenes. Full strawberry photo author unknown, licensed under the Creative Commons Attribution-Share Alike 3.0 Unported license. Sliced strawberry photo by Paolo Neo, Public domain, via Wikimedia Commons.

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- 8.5: Fruits by Maria Morrow is licensed CC BY 4.0.

16.3: Terms

These are the important terms from this chapter to be sure to know. You might also find these in later chapters.

Accessory tissues	Tissue of the fruit that is from non-carpel origin, usually in epigynous and perigynous flowers — e.g., the flesh of an apple is hypanthium tissue and the ovary is the papery core that encloses the seed.
Aggregate fruit	Fruit formed from the ripened ovaries present in one flower with numerous simple carpels.
Dehiscent	Used to categorize fruits with seeds that separate from a dried pericarp.
Endocarp	Inner layer of the pericarp.
Exocarp	Outer layer of the pericarp.
Fruit (botanical sense)	Ripened ovary together with the seeds within the ovary.
Funiculus	Stalk that connects either an ovule or a seed to the placenta.
Indehiscent	Used to categorize fruits with seeds that are retained within the dried pericarp.
Mesocarp	Middle layer of the pericarp.
Multiple fruit	Fruit formed from the ripened ovaries from a cluster of flowers that are in close proximity in an inflorescence and that coalesce into one unit.
Pericarp	Ripened ovary wall; made up of three parts: exocarp, mesocarp, and endocarp.
Placenta	Part of an ovary where the funiculus attaches.
Seed	Ripened ovule containing a seed covering, food storage, and an embryo.
Simple fruit	Fruit formed from a flower with one carpel or multiple carpels fused together so that it looks like just one carpel.

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17: WATER AND LIGHT

Learning objectives

- Understand the meaning of photoautotroph and where in the plant the various photosynthetic reactions take place.
- Explain how the energy from light is converted into carbon-based chemical energy and building blocks in plants
- Map the movement of water from the roots to leaves and carbon-based building blocks from source to sink.

Plants are sessile and cannot move to locations that might be more suitable for growth and reproduction when environmental conditions become less than favorable. To maintain growth, plants monitor signals of light, temperature, humidity, wind, and soil water availability; these signals inform the plant on how to modify water movement and gas exchange, which also affect photosynthesis. These lessons review how these signals impact physiology and the role of photosynthesis in growth.

17.1: Plants and Water

17.2: Light and Photosynthesis

17.3: Terms

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17.1: Plants and Water

Learning objectives

- Summarize the mechanics of evapotranspiration.
- Describe how leaves adapt to lack of soil moisture.

Evapotranspiration

Most of the water molecules taken up by a plant's roots move up the stem into the leaves, out the stomata in the leaves, and then evaporate into the atmosphere. The stomata open to allow oxygen (as a waste product of photosynthesis) to escape the leaf, and carbon dioxide (donor of the carbon atoms that are the building blocks of the sugar molecules assembled during photosynthesis) to enter. When these stomata are open, water vapor exits. We often refer to stomata as associated with gas exchange in the leaves because of the movement of these three gasses: oxygen (out), carbon dioxide (in), and water vapor (out).

Evapotranspiration (often just called transpiration) refers to the movement of water in the plant from root to stem to leaf and out through the stomata to the atmosphere. This isn't just a dribble of water. An acre of corn will transpire about 3,000–4,000 gallons of water each day, and a large oak tree can transpire 40,000 gallons each year.

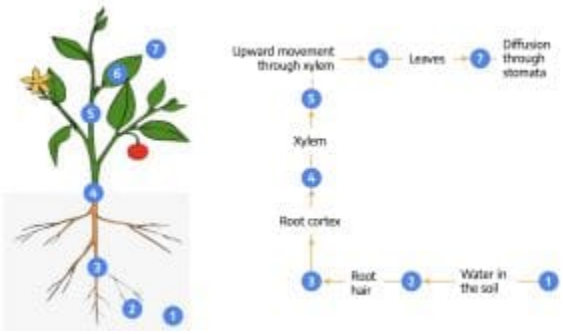


Diagram of evapotranspiration. Sheng-Yang He. CC BY-SA 4.0

As illustrated above, a stream of water is constantly moving up from the roots and out of the plant. Note the tissues and cells that are involved, and recall that water moves from the soil through the epidermis and cortex toward the xylem in the vascular bundle in one of two ways, symplastically or apoplastically. **Symplastic** means that water and minerals move interior to the cell membrane, or through cells, while **apoplastic** water moves around the cell membrane in the space outside the cell. Symplastic movement starts with water entering the epidermis cells through root hairs and then continuing from cell to cell through the cortex to the xylem in the vascular bundle. Entry of symplastic water into the root is regulated by the cell membrane of the root hair. Apoplastic movement of water occurs between the cells. This movement is unregulated until the water hits the cutin barrier formed by the Casparian Strip around the innermost layer of cortex cells in roots The Casparian strip blocks apoplastic water movement. The apoplastic water must then move symplastically into the cortex cells through the cell membrane, which controls the entry of water and minerals. From here, the water moves from cell to cell to the xylem, and then is pulled up the plant as described below.

The rate of evapotranspiration depends on environmental factors such as:

Light — Due to the occurrence of photosynthesis, plants transpire more rapidly in the light than in the dark. The guard cells, part of the stomata, are stimulated to swell, opening the stomata in the light of the day.

Temperature — As temperatures rise, water evaporates out of the leaves more readily. On hot summer days, leaves thus have a tendency to wilt due to lack of water in the soil and to the increased rate of transpiration.

Humidity — When the air around the leaf is drier, there is greater movement of water vapor out of the leaf than if the air around the leaf is saturated with water.

Wind — A breeze will clear water vapor away from the surface of the leaf, leaving the humidity on the leaf surface low and increasing the rate of transpiration.

Soil water availability — The water that is transpired must come from somewhere, and that somewhere is the soil. When the roots can't absorb enough water to keep up with the evapotranspiration demand, the leaves lose more water than they can replace. Water pressure inside the cells, called turgor pressure, is reduced because some water is pulled out of the cells to satisfy the demand from evaporation. This loss of turgor pressure relaxes the guard cells, causing the closure of the stomata, which shuts off a major avenue for gas exchange and the main channel for evaporation. This is a key strategy used by plants for managing stress from insufficient water. If the loss of turgor is severe, the plants will temporarily wilt. When the evapotranspiration demand is reduced through a change in environmental conditions, or when water supply increases, the cells again fill with water, turgor is reestablished, the stomata reopen, and the plant leaves recover from their temporary wilting. You have likely seen this happen when you have forgotten to water a house plant. So long as you water it soon enough, the plant regains turgor and survives the neglect.

Review questions

1. What is turgor pressure and how do leaves compensate when cells begin to lose turgor?
2. How can wind result in low turgor pressure?
3. What are three gasses that move through the leaf stomata? What is their involvement in plant function?

Mechanisms of water movement in plants

How does water move from the soil to root to stem to leaf and out to the atmosphere? This is a more complex question than it may first appear. Unlike animals, plants do not have a heart to pump water from roots to leaves. There is a push explanation and a pull explanation.



Guttation. Noah Elhardt. Public domain

Push explanation

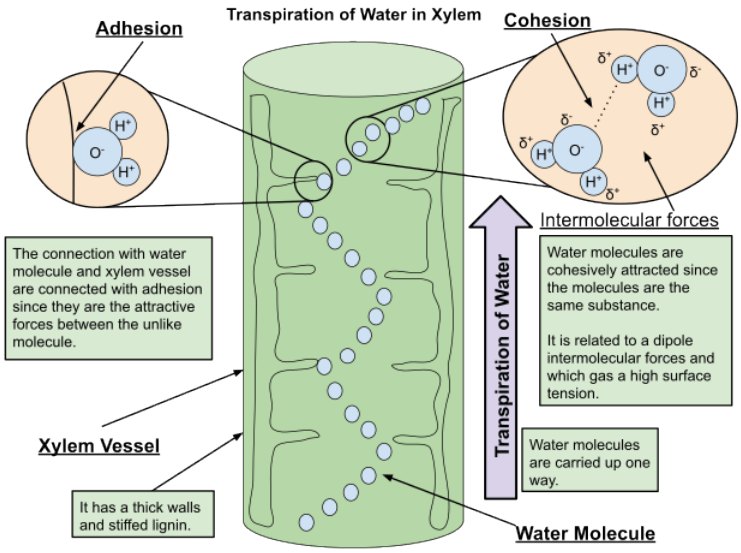
Water pressure (turgor) in the root cells during the night or during cloudy days can push water and dissolved materials up into the stem. This root pressure is the cause of guttation, the dew-like drops of water that are forced out of leaves. This same pressure is the force driving sap up the trunk of sugar maples in the spring. One problem with this mechanism is that, at most, root pressure can move water upwards only about 60 feet, and this only happens at night and when it is cloudy, and it only happens in some plants, but not in them all. So the push explanation has many limitations that make it unsatisfactory as a general theory for water movement up the xylem. How does water get to the top of a plant when it is sunny? And how does it make its way to the top of tall plants?

Pull explanation

Watch this video about transpiration (2:57)

The cohesion – adhesion – tension theory

Water is a polar molecule — like a magnet, it has positive (+) and negative (-) regions. When water molecules are near one other, the negative region of one molecule is attracted to the positive region of another. This attraction is called a hydrogen bond. This type of bond is weak compared to covalent bonds, where molecules share electrons, but when there are lots of hydrogen bonds holding these water molecules together, this type of chemical bonding is quite tenacious.



Cohesion/adhesion. FeltyRacketeer6. CC BY-SA 4.0

When water is held in a very small tube, such as an xylem vessel (above), the cohesion among water molecules due to the hydrogen bonds is very strong — strong enough to hold the column of water together very tightly over long distances, like from the root through the stem and into the leaf. Although an individual bond is weak, there are so many that a column has enormous tensile strength.

Water is also attracted to the walls of small tubes like xylem vessels. This force of adhesion between the water and walls of the xylem helps hold the water in the xylem against the downward force of gravity.

As a water molecule moves out of the leaf xylem into the air spaces among spongy mesophyll cells, out the stomate, and into the atmosphere through evaporation, it creates a void or empty space in the xylem, which is filled by the next water molecule in line. As this water molecule moves forward, it exerts tension (pulls) on the cohesive column of water that extends all the way back down to the root. As one water molecule leaves, the next takes its spot, and as it moves forward in line, it pulls upward the molecules behind it.

This force of cohesion-adhesion-tension is sufficient to pull water up to the top of the tallest tree, and is very effective while the sun is shining, when the stomata are open and transpiration is active.

The enormous flow of water through the plant isn't simply waste and the price the plant pays for having stomata open for oxygen and carbon dioxide exchange. Transpiration also:

- Provides water for photosynthesis (although not that much is needed — only about 1–2% of what is transpired).
- Moves minerals up from the roots for use in the leaf.
- Cools the plant through evaporation.

Review questions

1. What is guttation and what type of water movement mechanism is involved?
2. Identify the source of cohesion, adhesion, and tension in the theory of water movement that goes by that name.
3. Why could plants suffer nutrient deficiencies when they are grown in high humidity conditions or situations like greenhouses where there is no air movement?

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17.2: Light and Photosynthesis

Learning objectives

- Understand the meaning of photoautotroph in reference to plants.
- Explain how the energy from light is converted into carbon-based chemical energy and building blocks in plants.
- Identify where in the plant the various photosynthetic reactions take place.
- Explain how the carbon-based building blocks move to other parts of the plant and are used for energy, storage, and structures.

Photoautotrophs

Plants are autotrophs, meaning that they are self-nourishing (Greek autos = self and trophe = nutrition). Specifically, plants are photoautotrophs, because they use the energy from light to produce organic molecules with which they build their cells and store energy.

Organic molecules are compounds associated with living organisms that contain carbon atoms. It was once thought that organic molecules could only be synthesized in nature by living organisms through the intervention of a "life force." This hypothesis was disproved in 1828 when urea, a simple organic compound, was synthesized in a laboratory. Since that time, a major branch of chemistry, organic chemistry, has arisen to study and synthesize organic molecules. In contrast to organic compounds, inorganic compounds were historically defined as those lifeless minerals that are dug up from the ground.

Note that this chemical definition of **organic** (containing carbon atoms) has little or no relationship to the contemporary use of the word to describe a method of producing food. Organic food production, by regulation, relies strictly on inputs of organic molecules that come from life (like manure) and also on inorganic compounds like minerals, and eschews the use of organic molecules that have been synthesized by humans.

The organic molecules that a plant produces must be:

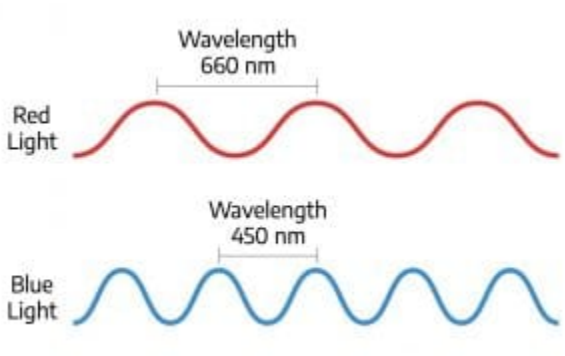
- Storable within the plant.
- Metabolized by the plant to yield energy for use in growth, maintenance, and producing other required organic molecules.
- Reasonably compact so that enough energy can be stored for growth.
- Transportable within the plant.
- Stable and non-toxic to the plant.

Since plants are photoautotrophs, they must have a mechanism for capturing energy from the sun or other sources of light and using that energy to produce organic molecules with the characteristics noted above. Photosynthesis is the process on which photoautotrophs rely to capture that light energy and to produce carbon-based organic molecules. The carbon used to make these molecules comes from the carbon dioxide (CO_2) in the atmosphere. Because photosynthesis removes carbon from the atmosphere and incorporates it into organic molecules which eventually become the plant's leaves, stems, roots, and fruits, photosynthesis is sometimes said to fix carbon. **Fix**, in this sense, means to secure or sequester rather than to repair.

If you follow the public discourse on climate change, you are aware that global warming is accelerated by the accumulation of greenhouse gasses in the atmosphere which trap and re-radiate sunlight and heat back to the earth. CO_2 is one of these greenhouse gasses. Removal of CO_2 from the atmosphere, for instance by planting trees that photosynthesize, fix carbon, and store the carbon-rich product as wood, is one method of carbon sequestration. An emerging and increasingly popular strategy for remediating greenhouse gas emissions is through the buying and selling of carbon credits, where industries that discharge CO_2 into the atmosphere purchase credits from organizations whose activities (such as tree planting) sequester carbon. Photosynthesis and sequestration of carbon by trees is one tool used to offset the industrial release of CO_2.

Review questions

1. In what sense does photosynthesis fix carbon?
2. Where does the carbon come from that is used by photosynthesis, and where does it go within the plant?

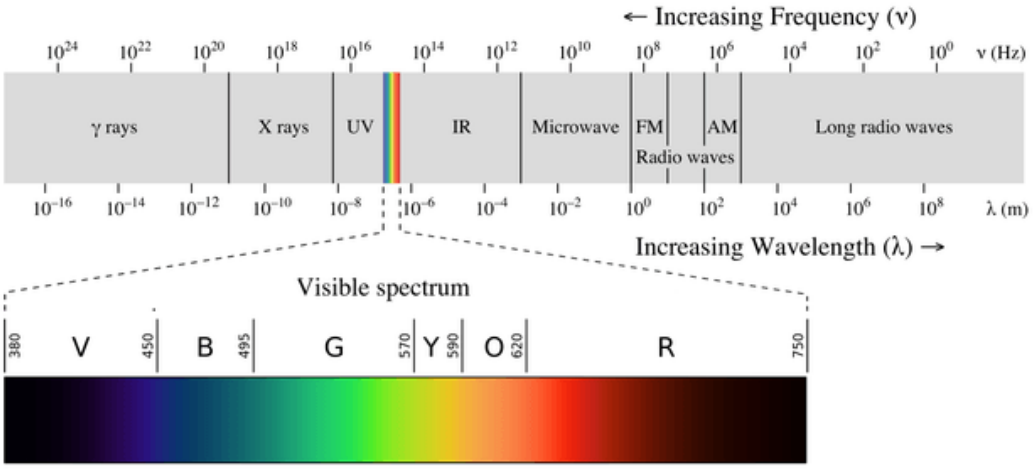


Red light/blue light wavelengths. Emily Tepe

Light reaction

Let's start with light, because that's where the plant gets the energy for photosynthesis. Here are some characteristics of light:

- Light travels in waves.
- The length of the wave is measured from one peak to the next and is called the **wavelength**, which differs for different colors of light.



Visible spectrum. Philip Ronan. CC BY-SA 3.0

- Within the visible wavelengths of light, the longest wavelengths are red light; outside the visible range of wavelengths, even longer wavelengths include infrared radiation, microwaves, and radio waves.
- Shorter visible wavelengths include blue and purple light, and beyond the visible range even shorter wavelengths include UV light, X-rays, and Gamma rays
- Light also has a particulate nature, and those particles are called photons.

The photons in light provide the energy that drives photosynthesis. This energy is used to incorporate carbon found in CO_2 from the atmosphere into organic molecules and, in particular, into simple sugars used by the plant. The chemical formula is the same for the two types of simple sugars produced by photosynthesis: glucose and fructose: $C_6H_{12}O_6$. The equation that summarizes photosynthesis is:

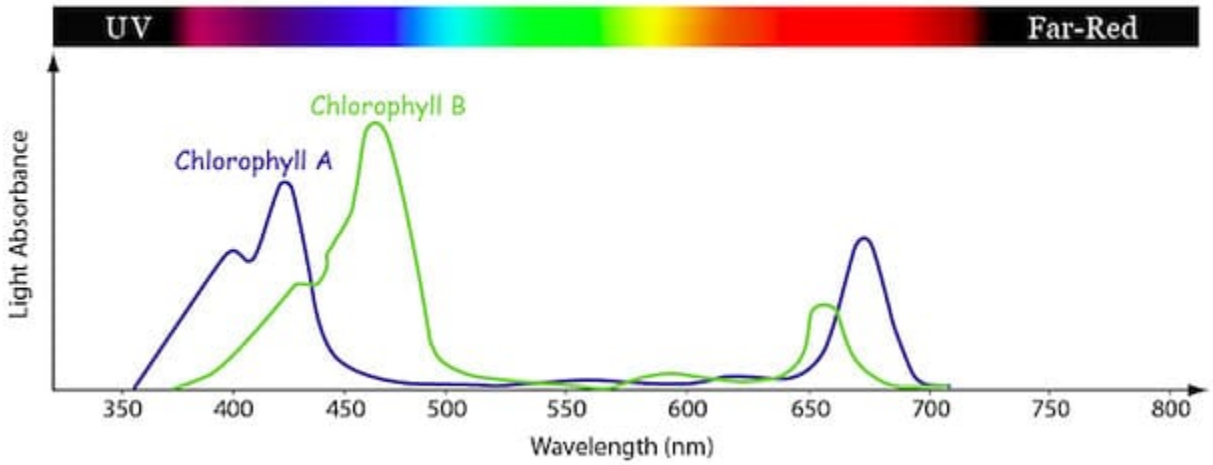
water + carbon dioxide -> oxygen, water, and simple sugars

$$12H_20 + 6CO_2 \rightarrow 6O_2 + 6H_2O + C_6H_{12}O_6$$

This balanced equation tells us that 12 molecules of water plus 6 molecules of carbon dioxide, in the presence of chlorophyll, accessory pigments, and light, produces 6 molecules of oxygen gas, returns 6 molecules of water back to the cell, and produces one molecule of a simple sugar like glucose or fructose.

Two reactions make up photosynthesis: the Light Reaction (abbreviated LR) and the Light Independent Reaction (abbreviated LIR). As the names suggest, the LR requires light while the LIR does not. The LR uses light energy to split water, which transforms the energy from the sun into hydrogen ions and electrons. The LIR uses that energy to grab the carbon from carbon dioxide and use the carbon to build simple sugars.

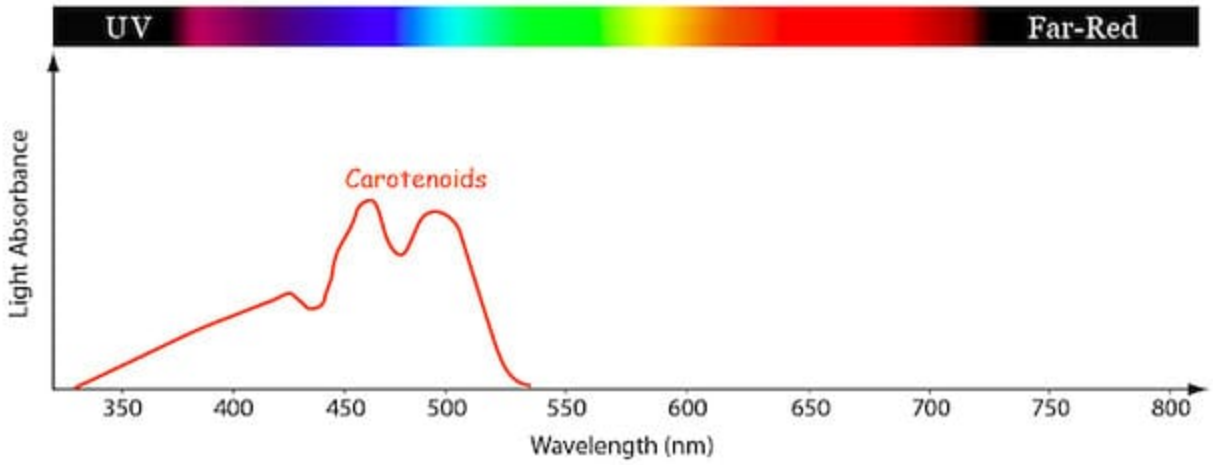
Let's start with the light reaction. You've heard of chlorophyll, and may recognize this molecule as a green pigment that captures light for photosynthesis. There are two chlorophyll pigments in plants that are critical for absorbing light: Chlorophyll *a* and Chlorophyll *b*.



Chlorophyll A & B Absorption Spectrum. byr7. CC BY 2.0

The graph above shows % absorbance of different wavelengths by these two chlorophylls. The Y axis (the vertical one) shows the percentage of the light that is absorbed (rather than reflected). High levels of absorption mean that the chlorophyll molecule uses that wavelength of light for energy. Low absorption means that the molecule does not use that wavelength, and is thus reflected away. The X axis indicates the wavelength of light in nanometers (nm) (the wavelength of green light, roughly 500 nm). The bar at the top represents the color of the light at the wavelength shown. The blue line is a typical absorption curve for chlorophyll a, while the green line shows chlorophyll *b*.

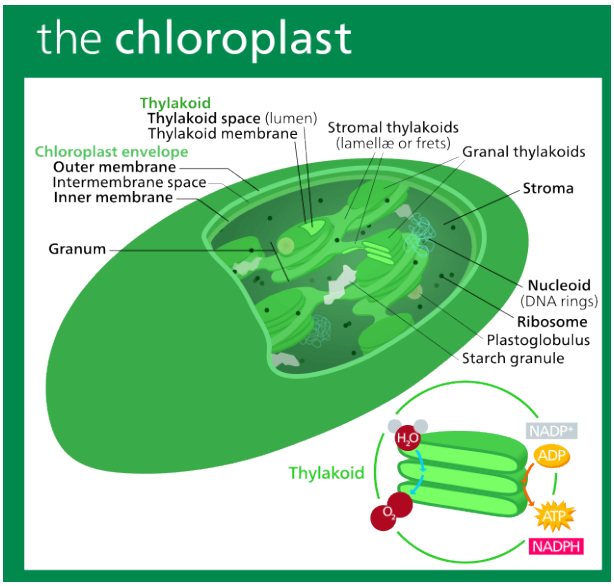
High absorbance at a particular wavelength means that pigment is collecting that light at that wavelength to harvest energy. Low absorbance means that the plant is reflecting that light back. Both chlorophyll *a* and *b* absorb blue and red light wavelengths and reflect green. Chlorophyll *a* has a peak in the violet and red regions and chlorophyll *b* in the blue and orange regions. Notice how their absorbance is very low in the green region. That's why we think of chlorophyll as green, and why we perceive leaves, which have chlorophyll as the predominant pigment, as green. Also notice that chlorophyll reflects some yellow wavelengths, but when the yellow and deep green wavelengths are mixed, we see the green leaf color.



Carotenoids absorption spectrum. byr7. CC BY 2.0

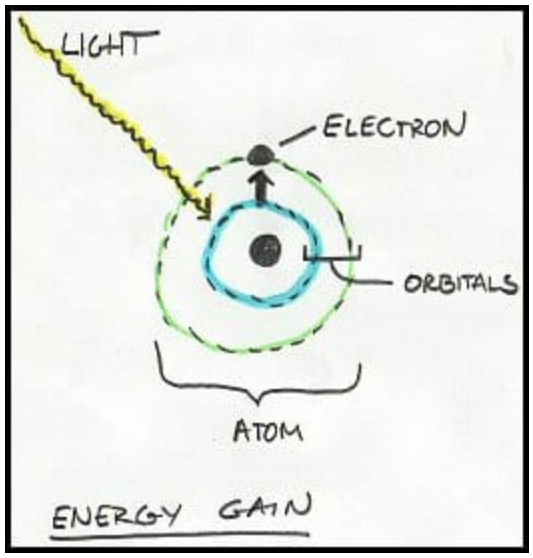
The graph above shows the absorbance of carotenoid pigments, which are present throughout the growing season. Carotenoids are called an accessory pigment in photosynthesis. They assist chlorophyll in light capture and energy transfer, and contribute to the regulation and moderation of excessive excitation of pigment molecules during intense sunlight, including exposure to UV light. Carotenoids absorb light in the green range, but reflect in yellow and red. We don't see these pigments during the growing season because they are much lower in concentration than the chlorophylls, so the green reflected light overwhelms the orange, and we see green. But when the chlorophyll fades in the fall, due to decomposition of chlorophyll, the orange can be seen in beautiful fall leaf colors.

Chlorophyll *a* and *b*, as well as the accessory pigments, are found in the chloroplasts, which are membrane-bound organelles within cells. The highest concentration of chloroplasts is most commonly found in the palisade mesophyll cells of the leaf.



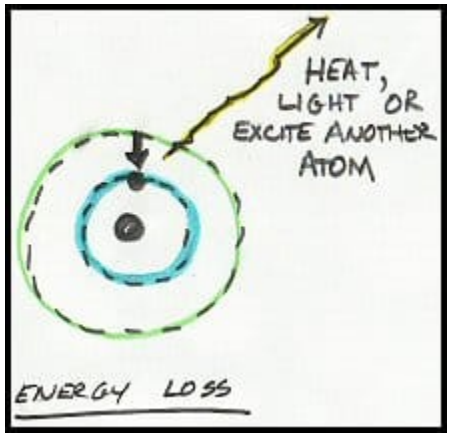
Chloroplast. Kelvinsong. CC BY 3.0

The above illustration of a chloroplast labels the internal structures. The chloroplast has a double membrane. The interior of the chloroplast is called the stroma. Within the stroma are coin-like thylakoids. The stacks of thylakoids are called grana. The thylakoids are also surrounded by a membrane, called the thylakoid membrane. The green chlorophyll pigment that you associate with photosynthesis, as well as the accessory pigments, are embedded in the thylakoid membranes and arranged in a structure called the antenna complex — given this name because it captures and routes the energy from sunlight to a collector called a reaction center.



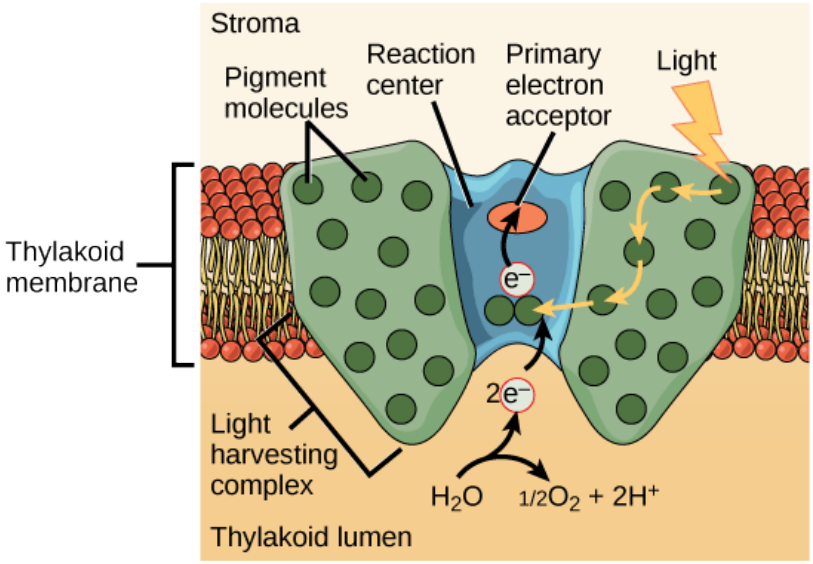
Energy gain. Tom Michaels

As shown above, when light hits a pigment molecule in the antenna complex, the energy from the light photon promotes (pushes up) an electron in one of the pigment's atoms to a higher orbital as seen in the cartoon and energy is gained.



Energy loss. Tom Michaels

The electron can't stay in that higher orbital indefinitely, and when it drops back to its home orbital it releases the energy it absorbed from light, denoted as **energy loss**. This released energy can be passed to another pigment molecule. This process of one pigment capturing the photon's energy and passing that energy onto adjacent pigment molecules is the crucial step in energy transformation that takes place in photosynthesis. This is the step that takes light energy and converts it into chemical energy — one of the only known biological processes that allows this type of energy transformation.



Light harvesting complex. OpenStax. CC BY 4.0

A light photon excites an electron of one pigment molecule in the antenna complex, or light harvesting complex, and by resonance this energy is transferred from pigment molecule to pigment molecule The energy transfer makes its way to the reaction center, where the first major chemical reaction in photosynthesis — splitting water — takes place. This reaction is called the **light reaction** or **light-dependent reaction** because it requires light. Water is split when the reaction center grabs electrons from water, which separates water into oxygen gas (O_2), hydrogen ions (H^+), and electrons (e^-).

To reiterate, the light is captured by the light harvesting complex (antenna complex) where electrons in the chlorophyll atoms are excited and jump up to a higher orbital. When the electron drops back, the energy is transferred to an adjacent pigment atom. This resonance energy travels down the antenna complex to the reaction center, where the captured energy pulls electrons out of water molecules, and water is split into oxygen gas, hydrogen ions, and electrons. The energy that was present in the photons of light has been transferred to the hydrogen ions and the electrons. We'll see more of how that energy is used in the next section.

Review questions

1. What wavelength(s) of light does chlorophyll a absorb? Chlorophyll b? What wavelengths do these two molecules reflect?
2. What pigments make up the antenna complex?
3. How is the energy in light transformed in the Light Reaction?

Recall that the overall equation for photosynthesis is:

water + carbon dioxide -> oxygen, water, and simple sugars

$$\mathbf{12H_20 + 6CO_2 \rightarrow 6O_2 + 6H_2O + C_6H_{12}O_6}$$

This equation is made up of two parts called **half-reactions**. The first half-reaction is an equation summarizing the Light Reaction, where energy from sunlight is used to split water molecules into oxygen gas, some electrons, and some hydrogen ions. The energy from sunlight is transferred from the pigments to these hydrogen ions and electrons. The half-reaction for the Light Reaction is as follows:

$$\mathbf{12H_2O \rightarrow 6O_2 + 24e^- + 24H^+}$$

Light independent reaction

The Light-Independent Reaction (LIR) is the second part of photosynthesis. It takes place in the stroma of the chloroplast. Unlike the Light Reaction, it does not require light. In the LIR, two compounds, NADPH and ATP, carry the energy from light that was

originally transformed into hydrogen ions and electrons through the splitting of water. The NADPH and ATP, along with carbon dioxide from the atmosphere, enter a process called the **Calvin Cycle**, where the energy is used to fix carbon into a molecule abbreviated G3P. This process requires the help of an important protein abbreviated RuBisCO (Ribulose-1,5-bisphosphate carboxylase/oxygenase) that catalyzes the step in the process where the carbon from atmospheric CO_2 is incorporated into an organic molecule. RuBisCO is the most abundant protein in leaves and, given the number of leaves in the world, likely the most abundant protein on the planet. The G3P produced by the carbon fixation process is called a triose phosphate, meaning it is a 3-carbon sugar (triose) with phosphorus and oxygen atoms (phosphate) attached. Triose phosphate moves out of the chloroplast into the mesophyll cell's cytoplasm, where two of these three-carbon molecules are combined to produce the 6-carbon molecules glucose and fructose. The glucose and fructose molecules then combine to form sucrose, a 12-carbon organic molecule. Sucrose is important because it is the sugar that is transported by the phloem throughout the plant to provide energy and building blocks for other organic molecules like starch and cellulose.

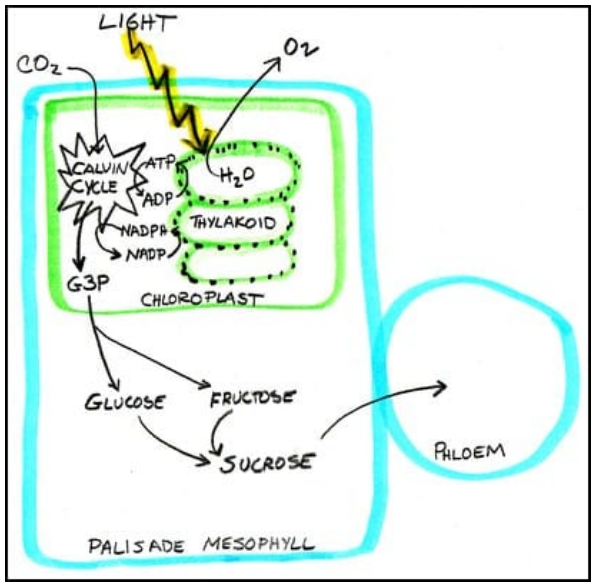
The half-reaction for the LIR is:

$$24H^+ + 24e^- + 6CO_2 \rightarrow C_6H_{12}O_6 + 6H_2O$$

Review questions

1. Does the Light Independent Reaction require darkness?
2. What sugar is moved throughout the plant through the phloem?

Photosynthesis summary



Mesophyll cell. Tom Michaels

When we add the two half-reaction equations for LR and LIR together, we get back to the summary equation for photosynthesis:

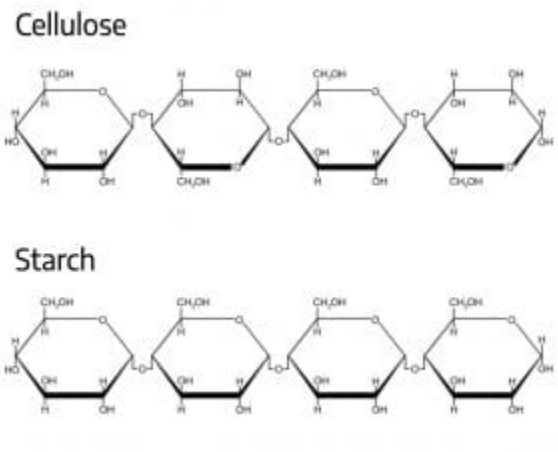
$$12H_2O + 6CO_2 \rightarrow 6O_2 + 6H_2O + C_6H_{12}O_6$$

The illustration above is a summary of what happens in a mesophyll cell. The rectangular blue outline represents a palisade mesophyll cell in a leaf. Inside the cell is a green rectangle, representing a chloroplast. Inside the chloroplast is a stack of green ovals with black dots. These ovals are the thylakoids, and the stacks are grana. The black dots in the green thylakoid membrane represent the antenna complexes. Light hits the antenna complex and transfers its energy to pigments, and the energy is funneled to the reaction center where water (H_2O) is split in the light reaction to form the energy carriers ATP and NADPH. This is the Light Reaction. The waste product formed at this stage is oxygen, which might be waste for the plant, but is quite useful for us.

In the Light Independent Reaction the energy is carried to the Calvin Cycle, represented by the multi-pointed star in the

chloroplast, which uses the energy in ATP, the NADPH, and CO_2 from the atmosphere to form the three-carbon G3P triose phosphate with the help of RuBisCO. Triose phosphate leaves the chloroplast and passes into the cytoplasm of the mesophyll cell to be transformed into glucose and fructose, which are combined into sucrose that is exported from the mesophyll cell to the phloem.

Cellulose and starch



Cellulose and starch molecules. FreeSVG. CC0 1.0

Within a plant, the regions of photosynthesis and sugar production are called the **source**. Leaves are typically the main source within the plant, since that is where most photosynthesis takes place. Those regions that do not support photosynthesis (like roots), but that still need organic molecules to survive, are called **sinks**. Movement of solutes (molecules dissolved in water) like sucrose from source to sink through the phloem is called translocation. Translocation of sucrose through the phloem to the sink provides cells with a source of stored energy, and also building blocks for organic molecules, as noted earlier. Sucrose can be broken down to glucose and fructose, building blocks used to form other extremely useful organic compounds. Two particularly useful compounds result from the production of long glucose chains: starch, a key energy storage compound in plant cells, and cellulose, the main constituent of the cell wall and key to a plant's structural integrity. Wood, for instance, is primarily made up of the cellulose-rich cell walls of dead xylem. Both starch and cellulose are long chains of glucose, but they differ in the way the glucose molecules are linked together.

Cellulose is the molecule into which carbon extracted from atmospheric CO_2 is sequestered for long-term storage. Starch sequesters carbon for a much shorter period of time because it is either eaten, used by the plant for new growth, or decomposed by bacteria and fungi that can utilize starch for energy.

Review question

1. Define translocation — what molecules are being transported?

To review

- In the light reaction, pigments in the thylakoid membrane capture energy from sunlight.
- The energy is used to split water, which releases oxygen to the atmosphere.
- The energy used to split water is transferred into electrons and hydrogen atoms, and eventually to ATP and NADPH.
- In the light independent reaction, the ATP and NADPH power the Calvin cycle that captures carbon from atmospheric CO_2 and incorporates it into simple sugar molecules.
- These simple sugars can be translocated to sinks, where they are used for energy, converted into energy storage compounds, or converted into structural molecules.

Some of the explanations and pictures used in this lecture came from Introduction to photosynthesis and other pages at that McDaniel College site. For additional explanations, an overview of the chemical reactions of photosynthesis, and another

description of the properties of light and pigments, navigate to the pages listed at the top of that web page.

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17.3: Terms

These are the important terms from this chapter to be sure to know. You might also find these in later chapters.

Accessory pigments	Light-absorbing pigments, other than chlorophyll, that are found in chloroplasts.
Adhesion	A force where dissimilar molecules stick together; in plants this force of adhesion between water and the walls of the xylem helps hold the water in the xylem against the downward force of gravity.
Antenna complex	Structure of chlorophyll and accessory pigments that are embedded in the thylakoid membranes; captures and routes energy from sunlight to a collector called a reaction center.
Apoplast	Space outside the cell membrane where water and minerals can move freely; interrupted by the casparian strip in roots.
ATP	A principle molecule for storing and transferring energy in cells; created in the LR.
Carotenoid pigments	Accessory pigments that absorb green light and reflect yellow and red light; overtaken by chlorophyll during the growing season, so we do not see the yellow-red reflection.
Cellulose	A long chain of glucose that is a main constituent of the cell wall and key to a plant's structural integrity; sequesters atmospheric CO_2 for long-term storage.
Chlorophyll	Green photosynthetic pigment found in plants, algae, and cyanobacteria that captures light for photosynthesis.
Chlorophyll a	Type of chlorophyll; mainly absorbs violet and red light while reflecting green light.
Chlorophyll b	Type of chlorophyll; mainly absorbs blue and orange light while reflecting green light.
Chloroplasts	Membrane-bound organelles found within cells that house chlorophylls and accessory pigments.
Cohesion	A force where similar molecules stick together; in plants this occurs with water molecules bonding together.
Evapotranspiration	Movement of water in the plant from the root through the stem to the leaf and out the stomata to the atmosphere; also called transpiration.
Fructose	Simple sugar; can be produced via photosynthesis.
Gas exchange	Movement of oxygen and carbon dioxide through stomata in the plant.
Glucose	Simple sugar; can be produced via photosynthesis.
Grana	Stacks of thylakoids.
Guttation	Dew-like drops of water that are forced out of the leaves of some plants due to root pressure.
Hydrogen bond	When water molecules are near each other and the negative region of one molecule is attracted to the positive region of another; a weaker bond than covalent bonds.
Light absorption	Process in which light is absorbed and converted to energy.
Light Independent Reaction (LIR)	Second half-reaction in photosynthesis; occurs without the presence of light and uses the energy produced in the Light Reaction to grab the carbon from carbon dioxide and use the carbon to build simple sugars.
Light Reaction (LR)	First half-reaction in photosynthesis; occurs with the presence of light and uses light energy to split water, which transforms the energy from the sun into hydrogen ions and electrons.
Light reflectance	Light wavelengths that are not absorbed, but are reflected back.
Light wavelength	Length of the wave from one peak to the next; measured in nanometers.
NADPH	Energy created in the LR; used to drive the LIR.
Palisade mesophyll	Densely packed, columnar-shaped, elongated cells full of chloroplasts; analogous to cortex parenchyma cells in the stem, but in the leaf they are specialized for light energy capture.

Photoautotrophs	Name given to living things, namely plants, that use energy from light to produce organic molecules with which they build their cells and store energy; self-nourishing.
Photon	Particle representing a quantum of light; provides the energy that drives photosynthesis.
Photosynthesis	Process of capturing light energy and producing carbon-based organic molecules.
Reaction center	Complex of pigments, proteins, and other factors that execute the primary energy conversion reactions of photosynthesis, primarily where water is split in the LR to form the energy carriers ATP and NADPH.
Resonance	Energy that is passed from one molecule to the next.
Rubisco	One of the most abundant proteins on earth; catalyzes the step in the process where carbon from atmospheric CO_2 is incorporated into an organic molecule; full name: Ribulose-1,5-bisphosphate carboxylase/oxygenase.
Simple sugars	Monosaccharides; examples include glucose and fructose.
Starch	Key energy storage compound in plant cells; a long glucose chain that sequesters atmospheric carbon for short-term use.
Stroma	Interior of the chloroplast; site of the LIR.
Sucrose	Sugar that is transported by the phloem throughout the plant to provide energy and building blocks for other organic molecules like starch and cellulose.
Symplast	Interior to the cell membrane, where water and minerals are transported through cells.
Tension	Differential pressure; in plants this occurs as water molecules are pulled through the plant via transpiration.
Thylakoid membrane	Membrane that surrounds the thylakoid.
Thylakoids	Membrane-bound compartments inside chloroplasts and cyanobacteria; the site of the light-dependent reactions of photosynthesis.
Transpiration	Movement of water in the plant from the root to stem to leaf and out through the stomata to the atmosphere; also called evapotranspiration.
Triose phosphate	A 3-carbon sugar (triose) with phosphorus and oxygen atoms (phosphate); G3P is an example.
Turgor pressure	Water pressure inside of cells.

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18: ROOTS AND THE MOVEMENT OF WATER - HOW IS WATER MOVED THROUGH A PLANT?

Learning Objectives

- Understand what influences the weird behavior of water, particularly tonicity, adhesion, and cohesion
- Learn how transpiration drives the movement of water through a plant and which environmental factors influence transpiration rates
- Predict the movement of water in different situations and explain why it moved the way it did
- Draw and describe the flow of water as it moves through a plant from the soil environment to the atmosphere

This chapter explores how water moves through plants, starting from the soil and traveling up to the leaves. It introduces the unique physical properties of water—such as cohesion, adhesion, and tonicity—and explains how these contribute to water transport. Key processes like diffusion, osmosis, and pressure differences are discussed in the context of how plants absorb, move, and regulate water.

18.1: Material movement and diffusion's multiple roles in plant biology

18.2: Water and Solute Transport

Contributors and Attributions

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18.1: Material movement and diffusion's multiple roles in plant biology

In addition to needing materials, organisms need to move materials: materials need to be moved from where they are acquired or synthesized to other places where they are utilized; materials may need to be transported to storage sites and also retrieved from storage sites; chemical signals may need to move from a place of sensation to a place of response.

Materials are moved in three basic ways in organisms, two of which occur in non-living systems as well: (1) materials move by diffusion, which is a consequence of the fact that all molecules at a temperature above absolute zero (i.e., all molecules!) are moving in a random thermal way; (2) fluid materials (i.e., gases and liquids) move by mass flow, from high pressure to low as long as there is an open pathway that allows the fluid to move; (3) materials move as the result of chemical interactions unique to biological entities, the so-called motor proteins, which can use chemical energy to do physical work (i.e., pushing or pulling a molecule, applying force over a distance) or the rotary motors of flagella that create a rotational movement that 'runs on' proton movement down an electrochemical gradient. Motor proteins are highly significant within cells where they can produce cytoplasmic streaming, a process that is significant to larger cells because diffusion is ineffective except over very short distances. The larger cells found in some of the algae, and especially in the coenocytic/siphonaceous cells are highly dependent on the ability of motor proteins to transport material within the cell. But for this course, we are more interested in the ability of larger, multicellular organisms, especially plants, to move materials within the organism, a process that is accomplished by a combination of diffusion and pressure flow.

TOPICS

- Diffusion
  - A simple but insufficient model
  - Osmosis—the diffusion of solvents, including water
  - Effects of pressure on diffusion
  - Combining the effects of purity and pressure
- Plants and Fungi use manipulations of pressure and osmosis multiple ways
  - Structurally
  - Growth
  - Guard cell movements
  - Leaflet movements
  - Long-distance transport
    - In the phloem
    - In the xylem
      - the patterns
      - the mechanisms
      - the problem of cavitation and trade-offs in xylem anatomy
      - rare cases of pressurized xylem

Diffusion

A simple but insufficient model

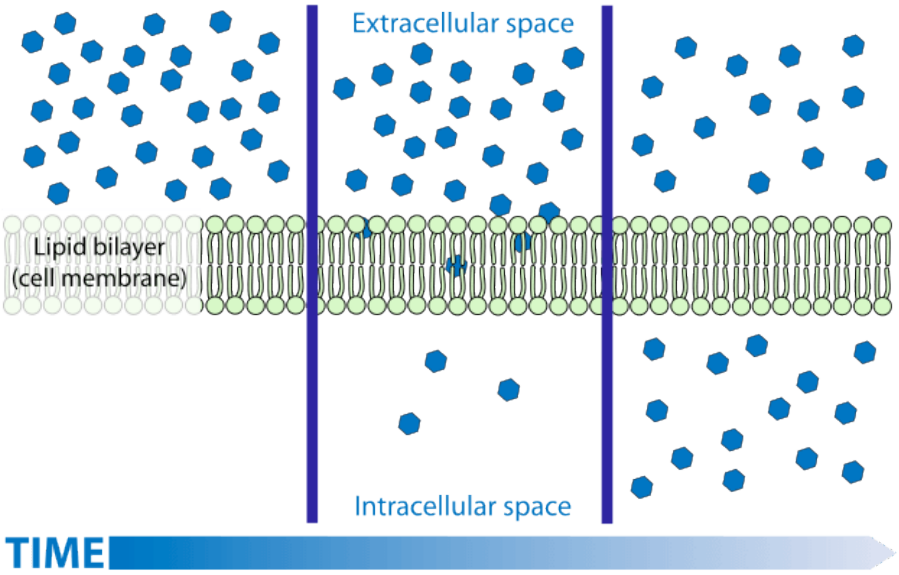


Figure 1 Diffusion of a solute across a cell membrane—random thermal motion results in a net movement

Diffusion is a process familiar to most. While the diffusion of gases and solutes is easily understood by simplistic models, the understanding of the diffusion of liquids, in particular water, is much more challenging and is often muddled by the imprecise application of terminology. The diffusion of gases and solutes is described as a spontaneous movement from regions of higher concentration to regions of lower concentration. The explanation for this spontaneous process is easily linked to kinetic theory—molecules move in a random way because of thermal energy. A s a consequence of this random movement, there is a net flow of matter from places where there are more molecules (i.e., higher concentrations) to regions where there are fewer molecules (lower concentrations). If dealing with mixtures (a gas with more than one component), each component will move independently of the others.

Liquid water diffusion (osmosis) is NOT always from 'high concentration to low'

However, this model (explanation) is not readily applied to liquid waterwith solutes, or tosolutions in general, largely because the idea of 'concentration' varies Concentration is not as precise a term as one might think, it can be expressed in several different ways (mass concentration, number concentration, molarity, molality, mole fraction). In the simplistic model of diffusion, the most appropriate measure would appear to be (number) concentration (number of molecules per unit volume) since random movement would move molecules from where they have more molecules per unit volume to where they have fewer molecules per unit volume. However, when considering the solvent (not the solute), the number concentration is not an accurate predictor of diffusion. For water and for most solvents the number concentration of the solvent changes very little as solutes are added, yet adding solutes can have a substantial influence on the diffusion of solvent. And while water volume changes little as solutes are added, the extent that it does change varies with different solutes, yet the effect on the diffusion of water is not controlled by the specific solute added but only on how much solute (number of particles) was added.Consider that while the addition of most solutes causes the water to slightly increase in volume (the number concentration goes down—the same number of water molecules are now in a largervolume), the addition of some solutes can cause water to contract (i.e., the number concentration goes up—the same number of water molecules are now in a smaller volume). If the (number) concentration of water is what directs its movement one would expect different solutes to have different effects on the diffusion of liquid, depending upon how much they caused the solution to change volume (and number concentration). And you actually would expect that some solutions (the ones that cause water to shrink) would have water diffuse fromthe solution intopure water. This never happens! Keeping all other factors constant, water alwaysdiffuses from where it is pure into any solution, regardless of the solute. And, at low concentrations, there is little to no effect of the particular solute—they all have the same effect on diffusion regardless of their impact on water 's number concentration.Itis the concentration of the solute NOT the concentration of water molecules that are directing diffusion: all other factors being held constant, water always diffuses from where there is a lower solute concentration to where there is a higher solute concentration. From this, one can conclude that itis the purity of water, not itsconcentration, that drives diffusion. This may

seem like a subtle difference but it actually reflects some very profound features related to the laws of thermodynamics. Purity relates to entropyand entropy is known to' drive 'spontaneous processes. Moreover, our' mental image ', i.e., model, of what causes diffusion, doesn' t work—solventmolecules do NOT go from where there are more of them to where there are less of them, they tend to go from where they are purer to where they are less pure.

The effect of pressure on diffusion

A second key reason that the description/model that describes diffusion as occurringfrom 'high concentration to low' is deficient is that it fails to consider the effects of pressure. Pressure is the most familiar reason that fluids move (wind, water flow in pipes, blood flow in animals) but these movements are not diffusion, they are something called 'mass flow' , a movement that depends only on pressure differences, and a movement that will occur whenever there are pressure differences and an open path for fluid flow. But when mass flow is impossible (because there is no 'open path') pressure can also influence diffusional movement: water will diffuse from areas of high pressure to areas of low pressure. This is especially important for cells possessingboth a cell membrane and a cell wall. While the membrane allows there to be different purities of the solvent (water) inside vs. outside the cell, the wall allows there to be different pressures inside vs. outside the cell, and bothpurity and pressure are important in dictating the diffusion of water.

Combining the effects of purity and pressure

All other things being equal, water moves by diffusion from regions of higher pressure to regions of lower pressure and also from regions of high purity to regions of low purity. These two factors can 'balance' each other and it is possible to have NO diffusion between an area of low purity and high pressure connected toan area of low pressure and high purity. Looking at this another way, if you have water of low purity confined in a rigid container (i.e., a cell with a cell wall) and it is put into pure water, water will move into the cell, increasing the pressure in the cell. Eventually, pressure will be reached where there is no more diffusion into the cell. At this point, the pressure differences between the inside and outside are matching the purity differences between the inside and outside.

Unfortunately, there is no easily conceptualized model for the diffusion of liquid wateras there is for the diffusion of gases and solutes. A rigorous model of the diffusion of liquid water requires the application of concepts from a thermodynamic parameter called water potential. The basic idea is relatively simple: osmosis (the diffusion of liquid water) is a spontaneous process and any spontaneous process must result in a decrease in the amount of energy available to do work (the 'free energy'). Generally, two key factors affect the free energy of water (its water potential): thepressure (which increases its water potential) and the presence of solutes (which decreases its water potential). Liquid water diffuses from areas of high water potential to areas of low water potential just as heat flows from warm areas to cold areas.

Forall organisms, and in particular those without a cell wall, the cell membrane and cellular activity allow solute concentration differences to develop between the inside and the outsideof the cell, resulting in differences in water purity between the inside of the cell and the outside. Whenpurity differences develop, water will flow in or out by diffusion. As long as the purity differences are small this movement can eliminate the purity differences by making the inside less pure(if water flows out)or more pure(if water flows in). However, such water movement will also cause the cell to change volume and if the cell swells or shrinks too much it can cause irreparable damage to the membrane, thereby destroying cell functioning. As a consequence, organisms without a cell wall must either live in areas where water purity is similar to what is found inside their cells or they must have structures/ mechanisms that lessen diffusion and/or have the ability to either eliminate the water that diffuses in (e.g., the contractile vacuole of *Paramecium*) or to acquire water to replace that being lost by diffusion (generally this is accomplished by acquiring the 'salty' water and eliminating the salts).



Figure 2 Wilted cucumber plants show loss of structure when deprived of water.

For cells with a wall (e.g., plants and fungi), the wall allows a new 'solution' to living in areas where the cell is more concentrated in solutes than the external environment (this is the normal situation for most non-marine habitats: fresh-water lakes and streams and terrestrial habitats where organisms are immersed partially or totally in soil whose water is generally quite pure, i.e., with few solutes). For these organisms, the rigid wall allows pressure to increase as water flowsinto the cells. This pressure acts to reduce the inward diffusion of water and eventually a dynamic equilibrium is reached where the high pressure and low purity inside the cell balance the lower pressure and higher purity outside the cell. Water moves (diffuses, i.e., moves by osmosis) in and out at the same rate.

Plants and fungi use 'osmotic systems ' in a number of ways

Structurally

Water can be used as 'building blocks' when it is confined in a structure that will not expand. Living cells, with the combination of a cell membrane and a cell wall, are structurally strong and plants and fungi use them to form rigid structures that can withstand gravitational and wind forces (also discussed in chapter 3). Evidence for the structural importance of water comes from the observation of wilting: if plants are deprived of a source of water to replace that being lost by evaporation, they lose structural integrity. Some plants and fungi produce some structures (e.g., trees, bracket fungi) that don 't collapse when deprived of water, but for many plantsaccess to water is essential to' standing up'because it is the pressurization of cells that provides rigidity. Central to this ability is a cell wall that has high tensile strength and resists expansionand consequently allows for pressurization.

Growth

Cellular growth occurs when the internal pressures exceed the strength of the cell wall and thusyields to the pressure inside it. Organs (fungal filaments, roots and shoots) grow as a result of the expansion of individual cells and the internal pressure not only has to push out the cell wall but may also haveto push away (compress) soil in its path. Thus for plants (both roots and sometimes shoots)and fungi, growth may require the production of a significant amount of force. The force to power this growth comes from the diffusion of water (osmosis) and very significant forces can be created as the result of the movement of water down its water potential gradient. Pressures of 2-4 bars (= 0.2-0.4 MPa [megapascals] = 2-4 atmospheres of pressure = 30-60 pounds per square inch) are common and can be quite effective, as anyone who has observed a dandelion coming up through a sidewalk may have realized.

Guard cells and stomates

The opening and closing of stomates come about as a result of changes in the pressure of specialized cells, guard cells, that surround the pore. Pressurization of the guard cells, as a result of solute accumulation and subsequent water diffusion into the

guard cells, causes the cells to swell and form an opening (a stomate) inbetween them. Adecrease in solutes in the guard cellswill cause a movement of water out of the cell, resulting in adrop in pressure and consequently stomatal closure. The triggers that stimulate guard cells to accumulate or lose solutes have been extensively studied and include light and the concentration of carbon dioxide. The exact controls may not be the same for all species. At least some plants are able to regulate internal carbon dioxide levels at a 'set point' that allows photosynthesis to proceed with little inhibition due to a lack of carbon dioxide, while at the same time minimizing the amount of water lost due to transpiration.

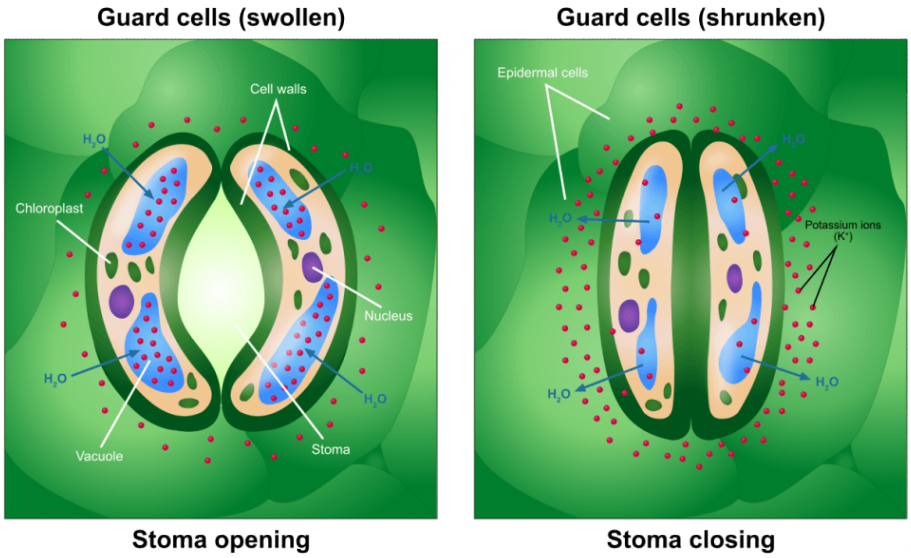


Figure 3 Stomatal pores are formed when guard cells take on water and are pressurized.

Leaflet movement

Similar to the action of guard cells, a number of plants have leaves or leaflets that move in response to environmental cues such as light, touch and drought, resulting in leaves or leaflets whose orientation varies depending upon circumstances. A common example is 'sleep movements' where leaves are horizontal during the day and vertical at night. These movements are the results of changes in the pressure of 'pulvinar' cells, located at pivot points. Relatively small changes in the size of these cells are leveraged as a result of their location and can cause substantial changesposition of organs involved. (see http://www.youtube.com/watch?v=U-PK13JEgk8 below)

Watch



A YouTube element has been excluded from this version of the text. You can view it online here: pb.libretexts.org/sdt34b/?p=302

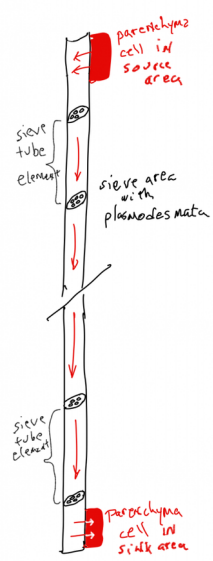


Figure 4 A model of phloem transport.

Long-distance transport

Phloem

Both transport systems in plants, xylem and phloem transport, operate as the result of pressure differences created in the 'pipes' found in these tissues. The pressure differences are created as the result of the diffusion of water. In the phloem, pressures are created as a result of the addition of solutes (sugars) to the pipe cells, a process known as phloem loading, that occurs in regions of the plant called 'source' areas. As a consequence of the phloem loading, water flows into the sieve tube elements of the source area, and the pressure increases, triggering a flow in the pipes. The pressure differences and the flow are maintained because solutes are not just loaded at 'source' areas, they are also removed at 'sink' areas, the locations that solutes are being transported to;thus a continuous pressure gradient occurs in the phloem, from sources that provide sugars, to sinks that consume or store sugars. The exact locations that serve as sources or sinks can change depending upon whether a location is producing sugars (sucrose) or consuming them.Phloem movement can be up the plant (e.g., from storage sites in the root to shoot apical meristems) or down the plant (e.g., from photosynthesizing leaves to storage sites in the root). Loading of sucrose requires metabolic energy as ATP is used to move sucrose from where it is less concentrated to where it is more concentrated. As was the case in guard cells, water movement into the sieve tubes is passive once the solutes have been added. Because it is a mass flow, not just sucrose but any solute that is in the sieve tube will be transported to the sink. The most common of these other solutes are amino acids, but other nitrogen-containing compounds are transported in the phloem along with some mineral elements (e.g., K^+, Mg^{2+}, Ca^{2+})

Xylem

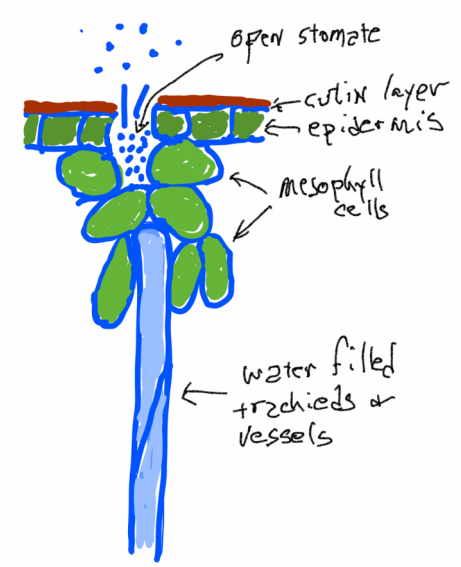


Figure 5 Xylem transport occurs in response to water loss from the leaves or as a result of water entry into growing cells.

Water transport in the xylem is also the result of 'pressure' differences but these are actually differences in tension rather than differences in pressure. While pressure compresses fluids, the tension pulls liquids apart, just as pulling on a string exerts a force that acts to break the molecules of string. Surprisingly, in certain situations, water has substantial tensile strength and can indeed be pulled. The cell walls of all the cells in a leaf are infused and coated with water because of the adhesion of water to the cell walls and the cohesion of water to itself. When water leaves a leaf by evaporation the remaining water is 'stretched' , put under tension, because the remaining smaller volume of water is covering the same original volume of cells. This tension is transmitted to the water in the conducting cells of the xylem and creates a 'pressure' difference (actually a tension difference) that can pull water up the (non-living) pipe cells. What is generally driving the water movement up the pipes (trach ei ds and vessels) is a tension created as water is lost due to transpiration. However, water flow up the xylem can also occur even if there is little transpiration as long as growth is occurring: the diffusion of water into expanding cells can create a tension to pull water up plants in the spring when plants lack leaves and transpiration rates are very low.

Water loss from the leaf is simple diffusion: water vapor at high concentrations (high humidity of the air inside the leaf) diffuses through open stomata to where the humidity is lower outside the leaf. The humidity of the air inside the leaf is maintained because liquid water in the cell walls of mesophyll cells evaporates and replaces water that has been lost. The tensions generated by water loss causes the tracheids and vessels to be slightly compressed as the pressure outside is 'normal' (one atmosphere) but the pressure inside is lower. Note that this is in contrast to the situation in living mesophyll cells which are pressurized because they have a membrane that allows them to concentrate solutes. If the tension in the water column of becomes too great cavitation occurs as air bubbles form when the water column is broken or when water breaks away from the sides of the tracheid or vessel. In either case, the cell is 'cavitated' and is no longer useful for water transport.

In both transpiration-driven and growth-driven situations, and in phloem transport, there is a short-distance diffusional movement that creates a pressure difference that can result in a long-distance movement. In both the xylem and phloem the movement withinthe pipes is NOT diffusion, it is a much more familiar process called bulk flow. Bulk flow is a much more effective means to transport materials over long distances than diffusion, which is only effective oververy small distances (tenths of a mm for liquids). Bulk flow is blocked by cell membranes and is impeded, but not prevented, by cell walls. The pits found in the cell walls of tracheids and vessel tube elements provide a relatively low resistance path for water to move between adjacent cells. Water flows even more readily through the perforation plates of vessels because they are completely open. In the (living) conducting cells of the phloem, plasmodesmata connect the individual cells and phloem sap (which is essentially cytoplasm lacking organelles) bulk flow occurs from cell to cell through the plasmodesmata. Bulk flow is also significant in the soil where there are passageways for water to flow through and where both gravity and the 'pull' by movement into plants can create pressure differences.

The pressures and tensions found in vascular tissue reflect these mechanisms. If a sieve tube is penetrated, phloem sap flows out because the pressure inside the cell is greater than atmospheric, just as you will bleed if your skin is severed. Under most circumstances, if a tracheid or vessel is penetrated water does NOT flow out , rather air flows in, reflecting the fact that the water inside the tracheid /vessel was under tension. In fact, if one measures the volume of a tracheid /vessel as tensions develop,

it slightly decreases because of compression from the outside. Because of this, tree trunks exhibit a measurable decrease in circumference during the day as transpiration and tensions increase and they rebound overnight as the tensions are relieved and the plant is rehydrated during times of little or no transpiration.

On rare occasions the water in the xylem is pressurized.

This condition is described as 'root pressure' and only occurs under certain circumstances. 'Root pressure' is by the 'bleeding' (exudation) from a decapitated stem. Under these same special conditions, if one punctures an individual xylem vessel or tracheid it will also bleed, unlike the more normal situation described above. Root pressure only occurs if the soil is moist, roots are actively growing, and transpiration is low (at night or when no leaves are present). Under these conditions solutes (mineral ions) accumulate in the xylem of the root because of the actions of root cells, and because the endodermis collectively behaves like a membrane and is a barrier that prevents solutes accumulated in the root xylem from leaking back out of the xylem tissue. Hence, like a living individual plant cell which can pressurize because the cell membrane allows solutes to be accumulated, the entire root xylem can accumulate ions and pressurize. This phenomenon is rare, both because roots are generally not active enough to accumulate sufficient ions in xylem tissue and also because a pull from the top (created by transpiration or growth) prevents a pressure buildup from occurring.

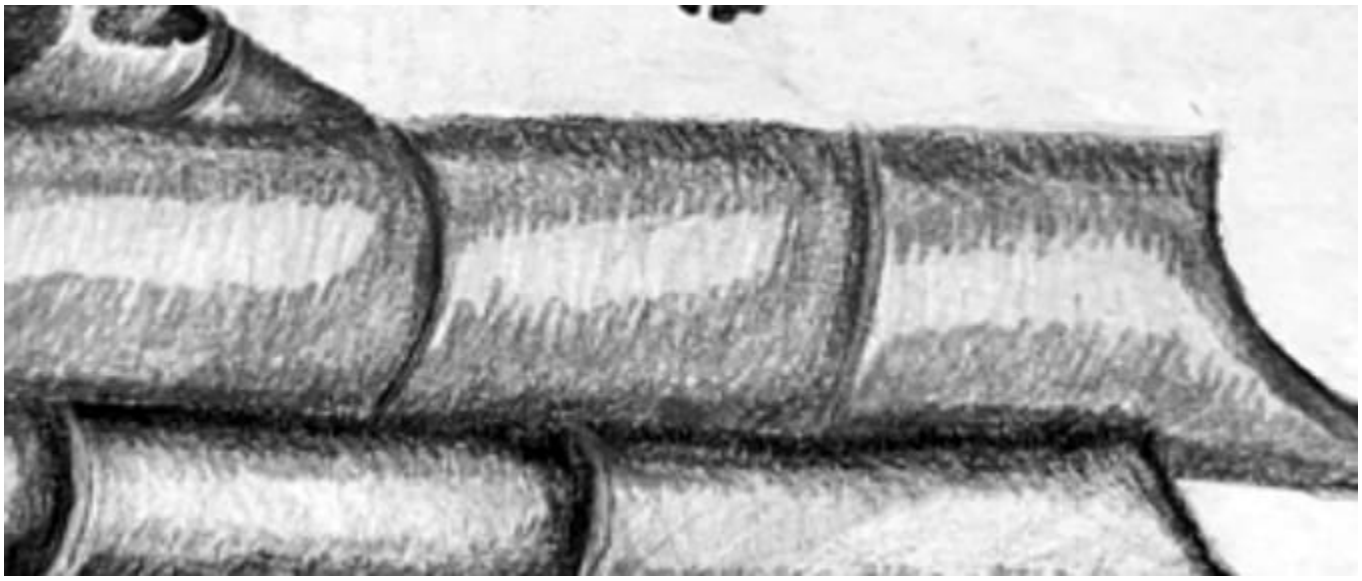
A final situation where the xylem is pressurized is the one that causes sap to flow (out) in maple tree trunks in the late winter and early spring. 'Tapping' , inserting a cylinder, into the xylem, results in the bleeding of sap that can be collected, concentrated and used as a source of sugar. Maple sap flow does NOT require root activity — it can be observed in stems removed from the root system. Maple sap flow DOES require freeze/thaw cycles because these somehow allow the xylem to become pressurized. The sugars found in the xylem sap are coming from xylem rays whose starch is converted into sucrose in late winter. Why only maples, and a few other species of trees, exhibit this behavior is generally attributed to aspects of their wood anatomy. Most tree species do not pressurize when exposed to freeze/thaw cycles.

Although phloem tissue is penetrated when maple is tapped and although phloem tissue is pressurized and transports sucrose, extremely little of the sap collected from maples is derived from the phloem. The living cells (sieve tube elements) of the phloem tissue are capable of rapidly plugging holes to prevent 'bleeding' and consequent sugar loss. Maple trees that are tapped will bleed from the xylem tissue for several months, as long as they are exposed to proper conditions and as long as there isn 't a' pull 'from the top of the plant caused by growth or evaporation from leaves. Maple sap flows when leaves aren' t present and growth is not occurring. If one could tap into the phloem tissue it would be found to have a much, much higher sugar concentration (comparable to maple syrup) than maple sap, whose sweetness is barely detected by humans until it is concentrated.

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18.2: Water and Solute Transport



Aquaporins, water channels in plant cell plasma membranes, play an important role in plant survival and growth. In return, they can be important players from increased temperatures to photosynthesis in plant life.

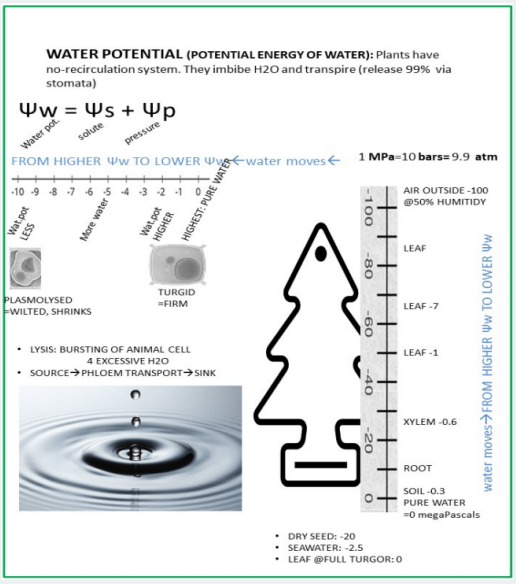
Moreover, solutes are also transported via plasma membranes and critical to plant growth and health. In recent years, substantial research has been carried out to elucidate highly complex transport systems of nutrients such as zinc (Zn), iron (Fe), and nitrogen (N).

Furthermore, osmosis and diffusion help plant water and solute uptake, respectively.

18.2.1. Student Learning Outcomes (SLOs)

- **SLO 14.01:** Apply the best practices for learning plant transport
- **SLO 14.02:** Describe the components of water potential
- **SLO 14.03:** Describe the characteristics of passive and active transport
- **SLO 14.04:** Compare plasmolyzed and turgid plant cells
- **SLO 14.05:** Identify given plant species with their scientific names based on their key features
- **SLO 14.06:** Explain the differences between hypertonic and hypotonic solutions
- **SLO 14.07:** Explain the differences between diffusion and osmosis

18.2.2. Big Picture



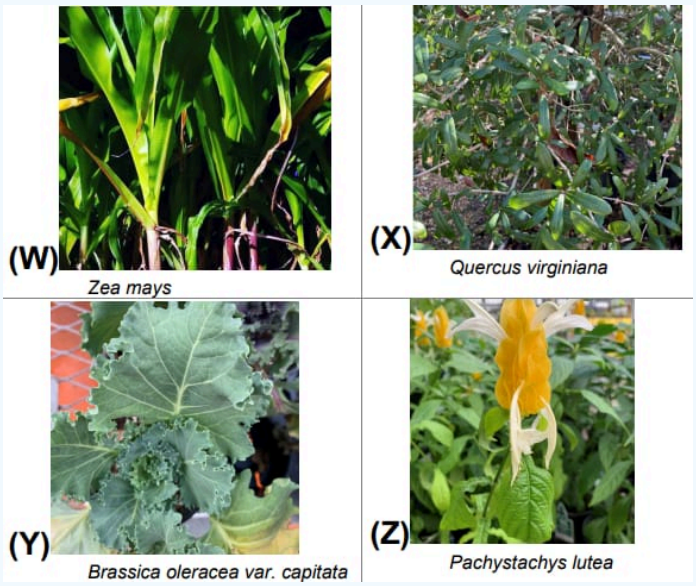
18.2.3. Vocabulary and Key Concepts

Camellia (*Camellia japonica*)	Alabama state flower
Water	• Water >> more than>> land on Planet Earth (in the air + surface + ground) • 2.5% Freshwater (1% drinking H_2O) + 97% saltwater (most H_2O)
3 Water Forms	• H_2O Vapor (gas) @0 °C • H_2O Liquid (water) @0 to 100 °C • H_2O Solid (ice) @100 °C (71 °C at top of Mt. Everest due to atmospheric pressure <1 atm) • GAS→*condensation*→LIQUID→*freezing/solidifying*→ICE→*heat/melting*→LIQUID→*heat/evaporation*→GAS • SOLID/ICE→*sublimation*→GAS→*deposition*→SOLID/ICE
Plant Cells (80%+ H_2O)	• Plant cells must maintain TURGOR (0-3 MPa water pressure) with enough H_2O for growing and functioning by stem/leaf tissue rigid (not wilted) (e.g., hypotonic)
Diffusion (ions movement)	• Moving substances in /out of cell from high concentration to low concentration.
Osmosis (H_2O molecules movement)	• Absorption of H_2O into root cells because there is more [solutes] in root cells >> soil water. A membrane required therefore only water passes through (but not solids).
Active transport (+energy)	• Movement into high concentration and may require a transporter. ATP energy required.
Translocation	• Long distance water (via xylem vessels) and nutrients (via phloem vessels) transport
Stomata (leaf epidermis pores)	• TRANSPIRATION: Loss of water via transpiration to atmosphere
Phloem sugar transport (translocation) SOURCE TO SINK	• Sugars move from "sugar sources" to "sugar sinks" • SUGAR SOURCES: Mature leaves • SUGAR SINKS: root, stem, fruit, flower, seed, young leaves

18.2.4. Test Your Knowledge

- Assessment 1: TRUE or FALSE: Xylem is dead at maturity while phloem is alive.
- Assessment.2: TRUE or FALSE: In phloem translocation, sugars move to organs that most needed.
- Assessment.3: Compare and contrast osmosis, diffusion, and active transport.
- Assessment 4: TRUE or FALSE: Guttation is loss of liquid droplets that contain substances [at night] while transpiration is loss of vapors of pure water [during the day].

18.2.5. Can You Spot These Plants?



18.2.6. Check Your Answers

1. TRUE
2. TRUE
3. While all three are movement of particles, diffusion and osmosis are passive transport only
4. TRUE

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19: SOILS, FERTILITY, AND PLANT GROWTH

Learning objectives

- Understand how the texture, structure, and fertility of soil affect plant growth.
- Appreciate the different types of soil and manufactured soil-less media for growing plants.

When a plant grows in soil or potting mix it removes nutrients as well as water from the soil. Although a plant produces (fixes) its own carbon-based molecules from photosynthesis, all other nutrients are taken up by the roots from soil. As we harvest plant material and dead plant material decomposes, these nutrients are depleted. This lesson discusses how this process changes soil structure, texture, and fertility.

19.1: Soils, Fertility, and Plant Growth

19.2: Plant Nutrition

19.3: Terms

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19.1: Soils, Fertility, and Plant Growth

Learning objectives

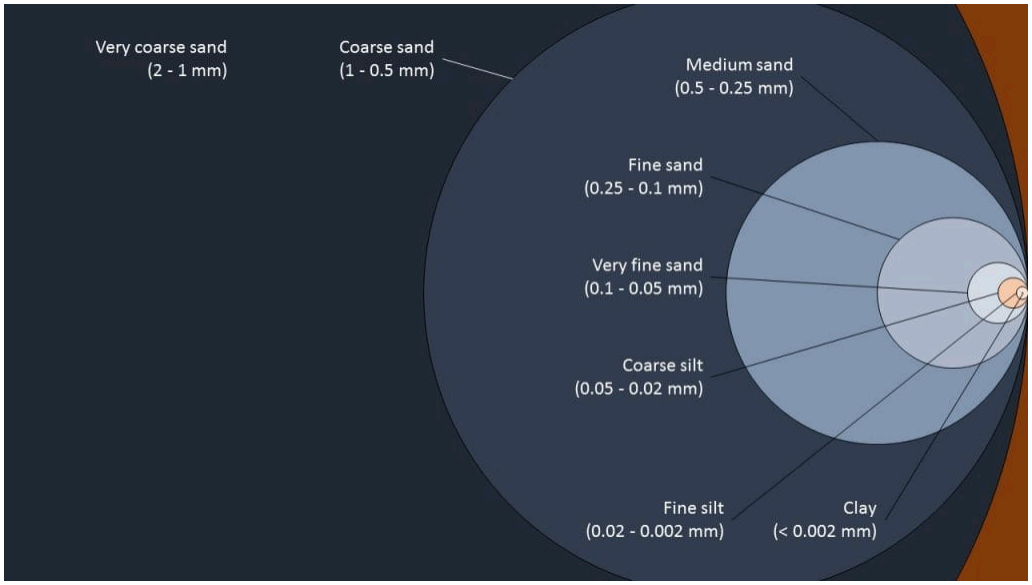
- Describe how soil texture and soil structure affect plant growth.
- Use simple tests to determine the texture of soil.
- Determine the meaning and impact of the three numbers typically displayed on fertilizer labels.

This is a course about plant propagation, but propagation is only useful if you can successfully grow the plants you propagate. Soil, light, and water are key to growing healthy plants. Here you'll have a brief introduction to soils and soil fertility — a huge area of knowledge and study.

Watch this video for an explanation of soil texture and soil structure (1:06)

Soil texture

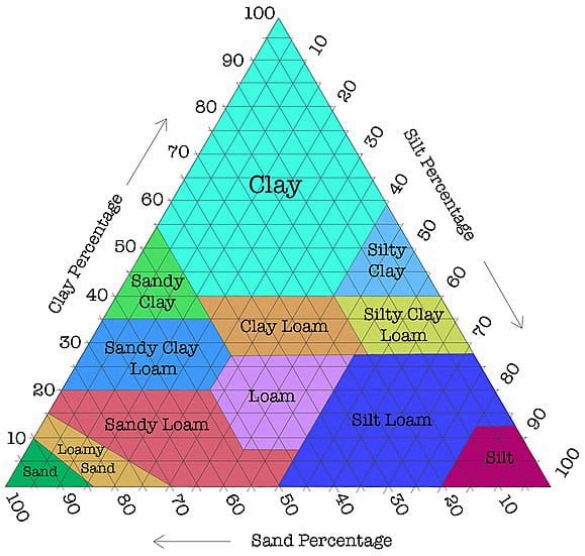
Soil has two key properties: texture and structure. Soil texture refers to the relative proportion of sand, silt, and clay particles in the soil. Sand, silt and clay are the three sizes of mineral particles (originating from rock rather than from previously living material) that make up soil. Sand is the largest particle, silt is intermediate, and clay is very small. In relative terms, if sand is a 55-gallon barrel, silt is the size of a plate, and clay is the size of a dime.



Soil particle size. Antonio Jordán. CC BY-SA 3.0

This mixture of different-sized particles is called **texture** because of how different combinations of these particle types make soil feel when you rub a sample between your thumb and forefinger. High amounts of sand makes a soil sample feel gritty, more silt makes it feel floury, and lots of clay makes it feel like velvet when dry and sticky when wet.

You can get a good idea of the texture of a field soil by doing a simple "jar test:" put soil in a jar, add water, shake the jar, then wait a few days to see the layers of different size particles settle.



Soil texture triangle. Lewi1224. CC BY-SA 4.0

The USDA Soil Texture Triangle, above, indicates the type of soil for different percentages of sand, silt, and clay. Notice that there are lines running through the triangle; these are to help you associate the percentages on the margins of the triangle with locations in the interior. The numbers on the margins are angled so that they are roughly parallel to the associated index lines. For example, the 60% clay index line is a horizontal line extending to the right of the 60 on the percent clay margin. The 20% silt index line runs from the upper right to the lower left of the triangle. And the 20% sand index line runs up from the lower right to upper left; all three lines are marked with a red arrow. These lines intersect at the red dot in the middle of the Clay area, indicating that a soil with 60% clay, 20% silt, and 20% sand is classified as a clay soil. When farmers talk about their field soil they often use the terms in the texture triangle rather than the percentages of sand, silt, and clay. This approach is much less common when talking about the potting mix used in greenhouses, as there is very little real mineral soil (sand, silt, clay) in these mixes.

Soils high in sand have great drainage and aeration so that roots are exposed to air in the soil and don't rot as easily. Roots can penetrate sandy soil easily. But sandy soils are poor at holding moisture when the weather turns dry, and sands don't hold nutrients well. Nutrients and moisture hang on to a soil best when the soil particles have a lot of surface area, and sand has the least surface area (relative to particle volume) of the three particle types.

Clay, in contrast, holds on to water so tenaciously that it is tough for the plant to get the water for itself. Wet clay is sticky, and clay packs together so tightly that when it dries it clumps together and turns into hard clods. Roots have difficulty penetrating a dry, clay soil. But clay does have a lot of surface area for its volume, and holds nutrients better than other particles. Clay soils tend to be fertile.

Watch this video to take a look at clay soil aggregates (2:15)

Silt has intermediate properties between sand and clay, as you might expect. An ideal soil has some of each type. A silt loam soil with 60% silt and 20% each of clay and sand is perfect for growing corn, wheat, and soybeans. But crops whose economically valuable part is in the ground, like potatoes and peanuts, do well in a sandy soil, because the tubers and pods come out of the ground cleaner and with less mechanical effort than they would from a soil with higher clay or silt.



Soil. Natural Resources Conservation Service Soil Health Campaign. CC BY 2.0

All soil textures have advantages and disadvantages, depending on climate, topography, and crop. The soil texture of large areas, like fields, can't really be modified to suit a particular crop, so a crop must be chosen that does well in the available soil. For example, if you have a field with sandy soils you aren't going to truck in tons of clay and silt to make the soil suitable for corn. Instead, you'll grow a crop like potato that does reasonably well on a lighter, sandy soil. For crops grown in greenhouses or containers, however, you can choose the soil texture to suit the crop you want to grow.

Review questions

1. What are the three particles that make up soil texture?
2. Which is smallest? Largest?
3. Is a loam soil high or low in clay relative to the other particles?
4. How do you determine soil texture using a soil jar?

Soil structure

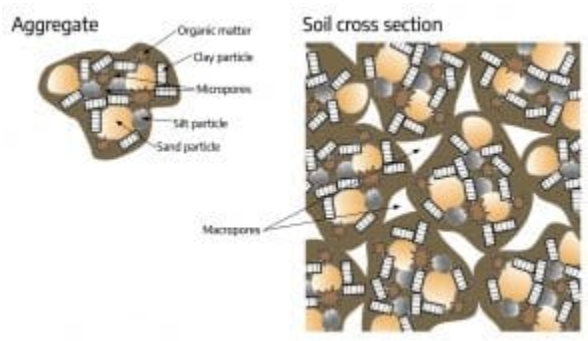


Soil structure. Soil Science. CC BY 2.0

Soil structure refers to the way in which the soil particles and other materials like the organic matter in the soil bind together into clumps. These clumps are called aggregates. Pure sand does not clump together into aggregates at all (think about how hard it is to get sand at a beach to stick together for a sand castle). When sand, silt, clay, and organic matter interact to form small aggregates, like the ones shown below, they create what is called a **granular structure**. Large holes in the aggregates provide spaces for gasses and water to pass through, while smaller holes hold water. The need for water is obvious, but the need for gas exchange may not be. As you know, root cells are growing, which means they require oxygen and give off carbon dioxide as a waste product. Oxygen needs to be available in the root zone, and carbon dioxide needs to be vented. If soils are waterlogged, plants die because too much carbon dioxide builds up around the roots and the roots are starved of oxygen. It is therefore important for soils to have these holes in the aggregates for gas exchange. This is called the **aeration-porosity** of the soil. Organic matter,

which in this case refers to decaying bits of formerly living material, helps build the aggregates by gently sticking the soil particles together. The space between and within aggregates provides aeration-porosity.

The illustration below includes a cross section of soil, showing several soil aggregates packed together. Each aggregate is built from sand, silt, clay, and organic matter (also called humus). Note the micro- and macropores for water and gas exchange.



Soil aggregation. Queensland Government. CC BY 4.0

Soil with granular aggregation that favors plant growth by holding water and nutrients, yet allows for drainage and gas exchange, is said to have good tilth. The soil hangs together (unlike sand), doesn't form hard clumps (unlike clay), and breaks apart into crumbly moist chunks when you turn over a spade of earth. While gardeners are usually stuck with whatever soil texture they might have in their gardens., one of the most important and readily accomplished tasks a gardener can take on to improve garden soil is to improve the soil structure by:

- increasing the soil organic matter, and
- reducing soil compaction.

Increasing soil organic matter will improve and stabilize soil aggregation. Reducing compaction, like foot traffic through the garden, will maintain the macro-and micropores in the soil to promote drainage, moisture retention, and gas exchange.

Watch this video to take a close look at a sandy soil (2:41)

Review questions

1. What makes up the glue that holds the soil particles into aggregates?
2. Why is gas exchange in soils important for plant growth?

Soil organic matter

Soil organic matter refers to carbon-based material in the soil that was originally a living organism, whether plant, animal, or microbe. Sometimes, soil organic matter also refers to organisms such as bacteria, fungi, insects, and worms that are still living in the soil, but this discussion refers to the materials that were once alive and are now dead and decomposing. Leaves, stems, and roots eventually die, are incorporated into the soil, and decompose. Soil organisms decompose the former living material and transform it into material called **humus**. Humus is sticky, and helps bind soil particles together into aggregates, as noted above. Humus also can absorb and hold up to six times its weight in water, so it is very important in improving light (sandy) soils. The decomposing organic matter also releases nitrogen and other nutrients that the plant can take up for growth. And finally, humus, like clay, holds nutrients in the soil through electrochemical charge; organic matter is negatively charged, so it holds positively charged cations like calcium that are important for plant growth.

In summary, organic matter is formerly living matter that is transformed in the soil into humus. Humus helps stick soil particles together to improve soil structure, holds water in droughty soils, and holds plant nutrients. Decomposing organic matter makes nutrients such as nitrogen available to plants.

Organic matter is added to soils in several forms:

Compost

For gardeners, this may be the most familiar form of organic matter. Leaves, weeds, grass clippings, and other organic material are mixed together and occasionally turned to promote decomposition. This results in humus that, when added to the soil, builds soil structure. Most of the nutrients have been used by the organisms that are decomposing the organic matter, are lost to the air, or are leached away by rain, so compost isn't very effective as a nutrient source. Its main purpose is to build soil structure and assist in retaining available moisture and nutrients.



Compost pile. nancybeetoo. CC BY 2.0

Green manure, or cover cropping

A crop grown with the sole purpose of tilling the crop into the land to increase the organic matter is called green manure. Green manure crops are used to change soil structure by incorporating organic matter directly into the soil. This technique is also used extensively in horticultural crop production to reduce soil-borne pathogens, and these crops serve a very useful purpose of smothering weeds.



Mixed species green manure crop. UGA CAES/Extension. CC BY-NC 2.0

Incorporating crop residues

After a crop is harvested, it is good agricultural and horticultural practice to incorporate the remaining plant material into the soil. Sometimes this is done with a moldboard plow to completely bury the residue, but the more modern method is to use the

bare minimum of tillage, or to leave the residue on the top of the soil and plant over the dead material the next spring. The latter method, called **no-till**, is particularly useful for minimizing soil erosion caused by soil particles blowing away with the wind or moving with flowing water.

The addition of too much organic matter that has too much carbon and not enough nitrogen can deplete the soil of nitrogen and harm plant growth. For instance, if you try to improve the organic matter of your soil by tilling in bales of straw or sawdust (both of which are almost all cellulose, which is very high in carbon), when the microbes begin to break the straw down they need to absorb nitrogen from the soil just for their own growth. If instead you add manure to the soil, which is a blend of straw (high carbon) and animal waste (high nitrogen), the microbes can use the nitrogen from the manure for their own growth as they decompose the organic matter and make more nitrogen available to plants.

Review questions

1. Why add organic matter to the soil?
2. Is all organic matter of the same value when added to soil, or are some types of organic matter better than others? Why?

Containers and raised beds

Garden soil cannot be used for container gardens, sa it compacts too tightly in pots and has terrible drainage. Instead, it is best to a soil-less mix like those available at nurseries, or to make a mix that is high in an organic matter like peat moss or rice hulls, to increase aeration porosity.

Watch this video to take a close look at a soilless container growing medium (0:58)



Salad table before planting. Tom Michaels

Author Dr. Tom Michaels developed this salad table, above, which has great potential for use in urban areas with smaller areas for growing greens, including apartment patios. This table is made with 2×4 lumber for the sides and legs, with hardware cloth and landscape fabric for the bottom of the table. The growth medium is normally a peat-based potting mix. A table this size supplies enough salad greens throughout the summer for two adults. You could modify it to have deeper soil so that you can raise a tomato or pepper plant.



Salad table with plants. Tom Michaels

Since the growing medium is potting mix, it dries out quickly. You can see a few modifications in this Hydroponic Salad Table, also created by Dr. Michaels. It's about 2′ x 4′ x 7.5″ deep and made with lumber, a plastic liner, and a styrofoam lid. About 30 gallons of nutrient solution is added to the box, the box is covered with a lid, and salad green seedlings like lettuce, spinach, chard, and kale are placed in holes in the lid. The plants yield greens for most of the summer and little or no water needs to be added.

To see more about the hydroponic salad table, see the Hydroponic Salad Table website, where Dr. Micheals has posted more information about how you can make a table like this.

You might find that salad tables, container gardens, or raised beds can keep you in touch with the food you eat while you retain your urban lifestyle.

The big three on fertilizer bags

Fertilizer bags and containers display a series of three numbers separated by dashes. This is called the fertilizer's analysis. The numbers represent the percentage of the fertilizer that is nitrogen (N), phosphorus (P), and potassium (K) — always in that order. N, P, and K are the elements needed by plants in the greatest quantities. Nitrogen is a key element found in protein, phosphorus is an important component in energy transfer molecules like ATP and as part of the DNA backbone, and potassium is an essential part of the mechanism for moving nutrients into and out of cells. Other elements can also be important in small quantities and in special circumstances, but N, P, and K are the most common plant nutrients.



Fertilizer bag. Pixabay. Pixabay license

A 10-10-10 general purpose garden fertilizer has 10% nitrogen, 10% phosphorus, and 10% potassium. The rest is filler, like sand or fine gravel. In Minnesota, fertilizers available to homeowners typically have no phosphorus because of legislation aimed at reducing phosphorus runoff into our lakes. Phosphorus is considered to be the limiting factor in algae growth, so if phosphorus runs off yards and gardens into lakes it causes algae blooms. In addition, our garden soils normally have sufficient phosphorus. A general fertilizer analysis without phosphorus would be 10-0-10. Nitrogen is usually the nutrient most limiting for plant growth, so it is worth it to read through the labels.

A caution: seeking the best value per pound of N isn't always the right strategy. Sometimes the form of the nutrient is important. If you are interested in growing a hydroponic salad table, the plants need a particular form of nitrogen called nitrate, which is not usually found in big, cheap bags of fertilizer; it's more likely to be found at a hydroponic shop, and costs more per pound of N than other forms.

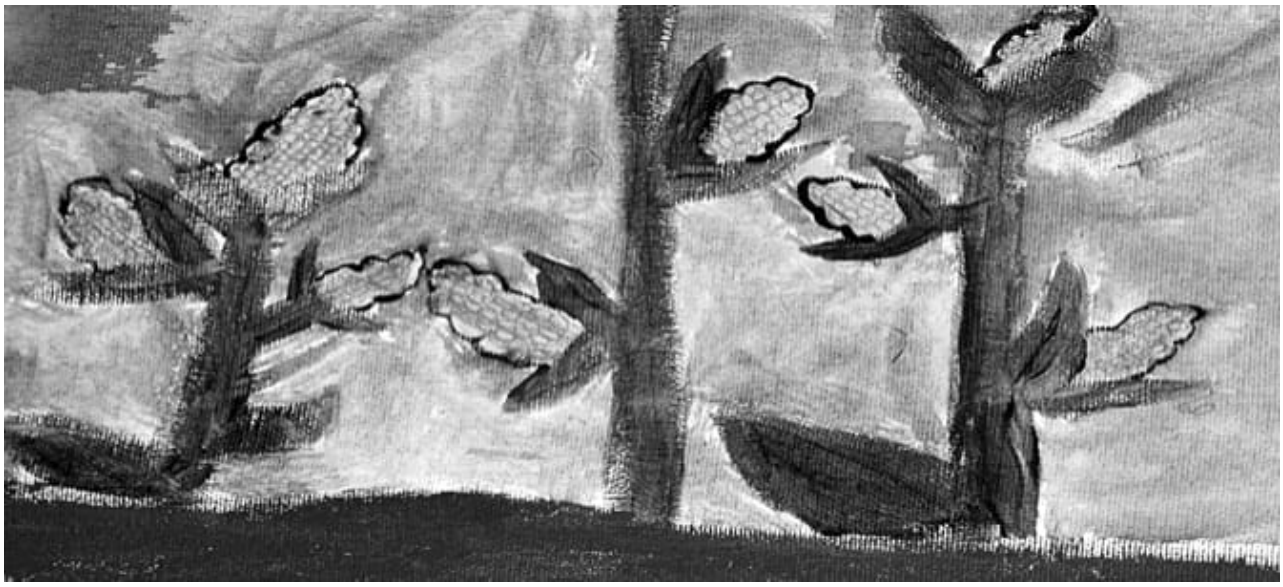
Review question

1. Is a 20-pound bag of 10-0-0 fertilizer that costs $10 a better value than a 10-pound bag of 46-0-0 that costs $20? Why or why not?

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19.2: Plant Nutrition



Learning Objectives

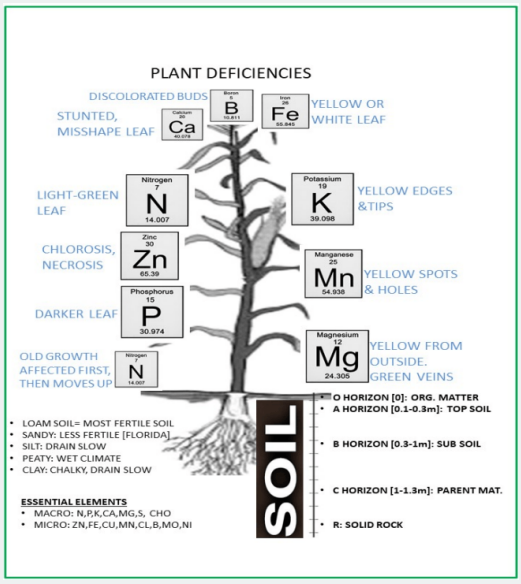
- Apply the best practices for learning plant mineral nutrition
- Describe the characteristics of N (nitrogen), P (phosphorus), and K (potassium)
- Describe the importance of zinc (Zn) in plants
- Explain some of the common symptoms of nutrient deficiencies
- Identify given plant species with their scientific names based on their key features
- Define soil components
- Describe mycorrhizae and Rhizobia for plant P and N

Nutrition has a critical impact from soil to plants to people levels. Essential nutrients are required by life but cannot be synthesized by the organism. For plants, essential mineral nutrients can be divided into two distinct groups, and they are all required for growth and production:

1. Macronutrients (needed in larger amounts): nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), and sulfur (S)
2. Micronutrients (trace elements, needed in smaller amounts): zinc (Zn), copper (Cu), iron (Fe), chloride (Cl), manganese (Mn), molybdenum (Mo), boron (B), nickel (Ni), selenium (Se), iodine (I)

Climbing of world population to 10 billion by 2050 will clearly require not only more food production but also higher enhanced efficiency of nutrient usage since they

19.2.2. Big Picture



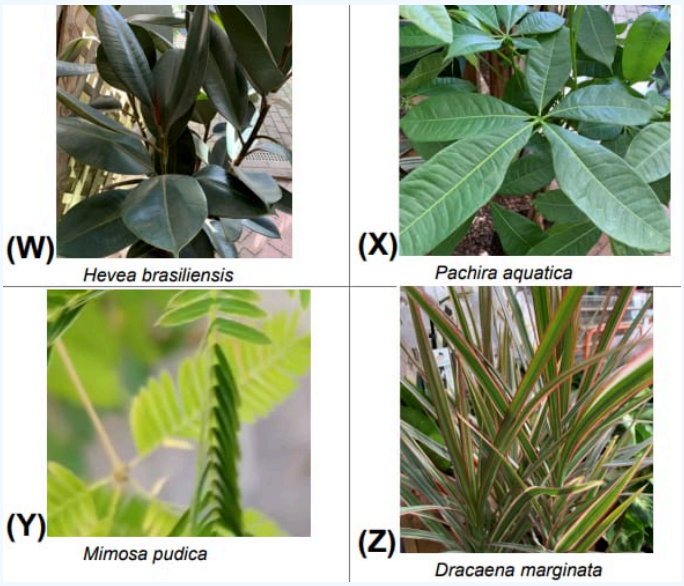
19.2.3. Vocabulary and Key Concepts

Dogwood (*Comus florida*)	Virginia state flower
17 Essential elements	CHO N P K Ca Mg S Zn Fe Cu Mn B Co Ni Cl **Macronutrients** **micronutrients**
Soil pH variation	**ACIDIC SOILS** pH: 0-7 — Azalea, blackberry, hydrangea **ALKALI SOILS** pH: 7-14 — Palms, geranium, olive
Deficiency symptoms 	• Yellowing old leaves: N, K, Mg, Zn • Yellowing young leaves: Fe, Mn • Burned old leaf tips: N, Zn • Necrosis: K, Mg, Zn, Fe, Mn • Death growing tips: B, K
Meat eating plants (Plants eat animals- carnivorous plants) 	• Venus flytrap • Pitcher plant • Butterwort • Sundew • Bladderwort • Cobra plant • Waterwheel plant
Plant Foods (Fertilizers)  	Fertilizers are plant food added to soil to supply plant nutrient(s) for crops. • Organic fertilizers: manure, compost, bone meal, tree leaves, eggshells, coffee grounds • Synthetic fertilizers (N-P-K ratio as %)

19.2.4. Test Your Knowledge

- Assessment 1: TRUE or FALSE: Essential nutrients are the most important for the plant life cycle.
- Assessment 2: NAME THE DEFICIENCY: Old leaf chlorosis, necrotic spots, stunted plants, especially in maize, sorghum, beans, potatoes
- Assessment 3: NAME THE DEFICIENCY: Old leaf yellowing, light-green whole plant, most common nutrient deficiency.
- Assessment 4: NAME THE DEFICIENCY: Burnt leaf tips, purple/dark green old leaf, second most common deficiency.

19.2.5. Can You Spot There Plants?



19.2.6. Check Your Answers

1. TRUE
2. Zn (zinc deficiency)
3. N (nitrogen deficiency)
4. P (phosphorus deficiency)

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19.3: Terms

These are the important terms from this chapter to be sure to know. You might also find these in later chapters.

Aggregates	“Clumps” in the soil; see soil structure definition.
Clay	Smallest particle in soil; has high nutrient holding capacity.
Compost	A type of organic matter that builds soil structure and assists in retaining moisture and nutrients.
Cover cropping	Crop used to benefit the soil rather than the main crop species.
Fertilizer analysis	N-P-K content of a bag of fertilizer; shown in percentages by weight.
Granular aggregation	Interaction of small soil aggregates; it is important to have a mixture of large and small holes between the aggregates to allow for water and gas exchange.
Green manure	Crop grown to purposefully be tilled back into the soil to increase the organic matter (and thus change the soil structure); can also smother weeds.
Humus	Sticky material made from organic matter that helps bind soil particles together into aggregates; can absorb and hold up to 6x its weight in water, releases nitrogen, and holds positively charged cations for plant growth.
Nitrogen (N)	One of the most important elements for plant growth (by quantity); a key element found in protein.
Organic molecule	Chemical compound associated with living organisms that contain carbon atoms.
Organic material/ matter	Material that has come from a recently living organism (such as plants) that may be partially or fully decomposed.
Phosphorus (P)	One of the most important elements for plant growth (by quantity); a key component in energy transfer molecules like ATP and as part of the DNA backbone.
Potassium (K)	One of the most important elements for plant growth (by quantity); a key part of the mechanism for moving nutrients into and out of cells.
Sand	Largest particle in soil; helps increase aeration.
Silt	Particle of intermediate size in soil.
Soil compaction	When the pore spaces between soil aggregates are compressed.
Soil organic matter	Carbon-based plant, animal, and/or microbe tissues that are in the process of breaking down; increasing soil organic matter improves and stabilizes soil aggregation.
Soil structure	The way in which the soil particles and other materials, like the organic matter in the soil, bind together into clumps.
Soil texture	Relative proportion of sand, silt, and clay particles in the soil.
Tillage	Process of incorporating the residue from the top of the soil into the soil; there are many types.

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20: INTRODUCTION TO AGRICULTURE

Learning Objectives

- Describe the origins and development of agriculture and crop domestication.
- Explain ecological principles and biotic interactions relevant to sustainable agriculture.
- Identify threats to agriculture from pests, pathogens, and invasive species, and understand plant defense mechanisms.
- Compare conventional, ecological, and genetically modified (GMO) approaches to crop and soil management.
- Evaluate the environmental and societal impacts of agricultural practices, including weed control and GMO use.

This chapter introduces agriculture as a recent but transformative human activity that began around 10,000 years ago, shaping ecosystems and societies through the domestication and cultivation of plants. It explores how key crops evolved, how modern practices like ecological management and genetic engineering have advanced agriculture, and how this ongoing interaction between humans and plants continues to impact the environment.

20.1: What is Agriculture?

20.2: Ecological Principles for Agriculture

20.3: Biotic Interactions

20.4: Interactions Involving Conditions

20.5: Soil Properties and Their Interrelationships

20.6: Ecological Crop and Soil Management

20.7: Threats to agriculture- insects and pathogens

20.8: Plant Defenses, Management Practices and Pests

20.9: Weeds and weed control

20.10: Invasive plants and GMOs

20.10.1: Invasive plants

20.10.2: GMOs

20.10.3: Terms

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20.1: What is Agriculture?



Figure 1 Van Gogh's Fields of Auberge, showing 19th century French agriculture.

What is agriculture? It is an activity whereby an organism actively cultures/cultivates/cares for other organisms with the intent of somehow utilizing these organisms directly or indirectly. While we are focused on the agricultural interactions involving humans, other organisms, specifically numerous ant species, carry out agriculture, culturing fungi, aphids and other organisms. Agriculture generally involves the 'domestication' , a genetic modification of organisms, both plants and animals, allowing them to be better utilized.

Agriculture involving humans and plants is certainly one of the most significant biotic interactions, an activity that influences vast expanses of land, roughly 12% of the earth's land surface. Although there is much less agricultural activity in aquatic/marine systems, there is some, and secondary effects from terrestrial activities, e.g. fertilizer run-off, also has an impact. Like all interactions, agriculture involves modifications of both partners. And while we will focus on the non-human component, generally flowering plants, it is important to keep in mind that agriculture has brought about tremendous changes in humans, with probably the most significant ones coming about as agriculture originated and humans altered their patterns of activity, movement and social interactions. It is significant to note that relative to the existence of humans, agriculture is a recent innovation, starting roughly 10, 00 years ago. For most of their 200, 000 year existence, humans were not involved with agriculture although they certainly did influence specific plants by their activities. It is also significant that agriculture apparently developed separately in multiple regions. Authorities now list eleven sites of agricultural origin, including the Middle East, Africa. the Far East and North, South and Central America. In each of these regions distinct species were utilized. The table below lists some of the earliest crops along with their region of origin:

Table 1.

crops	**site of domestication**
wheat, peas, lentils, flax, figs, chickpeas	Middle East
potato, tomato, pepper	South America

crops	site of domestication
corn, squash, beans	Mesoamerica
banana, sugarcane, taro	New Guinea
rice, mung beans, soy beans	China
millet, sorghum,	Africa
eggplant, mungo bean, pigeon pea	India

The majority of crops, and certainly the crops associated with the origin of agriculture, were wild plants that humans had already discovered to have desirable features (most commonly features related to eating but sometimes the features were mechanical, e.g. cotton, or chemical, e.g. a waterproof latex from tree bark). The next step was the appreciation that the plant could yield more product if it were somehow cared for, e.g. planted, pruned, etc. For most crops, the practice of collecting and planting seeds was crucial to crop development. Through time, many plant species were genetically modified by humans through selection of seeds from plants with particularly desirable traits, e.g. large seeds. Genetic modification of agricultural organisms (Darwin called this 'artificial selection') was most rapid when dealing with annual plants that could be selected for yearly. This chapter examines the histories of several crops that reveal interesting biological features.

TOPICS

- How do crops come to be?
  - Wheat
  - Strawberry
  - Naval oranges
  - Banana
  - Corn
- Hybrid seed
- Generating variability

Wheat



Figure 2 Bread wheat, the tip of the stem had multiple flowers that now have developed into fruits.

The plant known as 'wheat' actually includes three distinct species in the *Triticum*genus: einkhorn wheat, emmer wheat, and bread wheat. Each of these species has wild relatives that may be considered separate species or may be lumped with the domesticated form. These species are related evolutionarily in what is known as a polyploid series. Einkhorn has a diploid chromosome number of 14 and produces haploid gametes with seven chromosomes. Emmer wheat has 28 chromosomes, 14 of which came from Einkhorn wheat and 14 of which came from a related, but separate genus (*Aegilops,* although some workers have lumped *Aegilops*and *Triticum).* Bread wheat has 42 chromosomes, 28 of which come from emmer wheat and 14 from another species of *Aegilops*.

Polyploidy is common in plants and is an aspect in the history of multiple crops. It can come about several ways, the most common being a hybridization event where gametes of two separate species are combined. Viable gametes cannot be produced in the hybrid because meiosis is thwarted by the fact that there are no homologous chromosomes to pair, the chromosomes from one parent do not have 'matches' because the second parent was a different species with different chromosomes. Consequently, the hybrid is sterile; this ensures that the two parents are reproductively isolated, i.e. separate species.

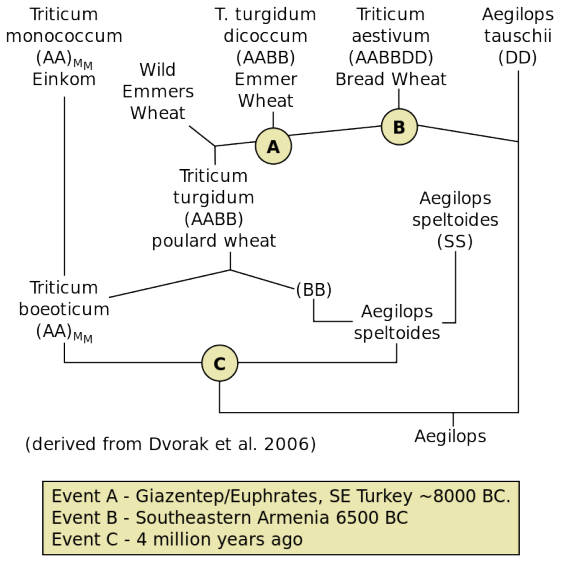


Figure 3 Evolution of wheat (Triticum) showing two diploid wheats (genome AA), three tetraploids (genome AABB) and one hexaploid (AABBDD) along with the approximate dates of origin. Note that the event A is before event B.

However, hybrid sterility can be overcome in several different ways. One is to produce functional gametes (i.e. cells that can fuse with other cells) without going through meiosis, i.e. to produce 'unreduced gametes' . If these 'unreduced gametes' find each other and fuse then a new species is created, one that has twice the chromosome number of its either of its parents. In the case of emmer wheat the new species has a diploid chromosome number of 28, 14 (seven pairs) coming from einkhorn wheat and 14 (seven pairs) coming from *Aegilops*. Another possibility is that the cells within the hybrid replicate their chromosomes (mitosis) but the cell does not divide, leaving a cell with double the number of chromosomes of its parents, and significantly, producing a cell that has a match for each chromosome. Such a cell (or derivatives of this cell) could go through meiosis because it does have pairs of chromosomes. In both of these situations a new 'polyploid' species is produced, for example emmer wheat. Polyploidy is also discussed in Chapter 31.

Bread wheat was produced by the same polyploid mechanism following hybridization between emmer wheat and another species of *Aegilops* . Hence, bread wheat possesses three genomes (sets of chromosomes), one from einkhorn wheat and two from two different species of *Aegilops*. Each set consists of seven chromosomes, thus dipoid cells of bread wheat have 42 chromosomes, two copies of each of the three sets of chromosomes. The origin of bread wheat is quite recent, less than 10, 000 years ago, and after both einkhorn and emmer wheat had been domesticated.

Strawberry



Figure 4 The commercial strawberry is a hybrid between two American species on from North America and one from South America.

The strawberries found in grocery stores have a very interesting heritage involving Chile, eastern North America and France. Strawberry is in the genus *Fragaria* and there are over 20 species occurring primarily in temperate regions of North America, Europe and the Far East. Most of these species have seen very limited agricultural utilization but are harvested in the wild. Although it has very limited commercial production, one European species, *F. vesca,* especially some clones with particularly large fruits, has been cultivated for over 500 years, primarily in parts of Turkey. A South American species with white fruits, *F. chiloensis,* , native to the west coast of North and South America was cultivated by native tribes in what is now Chile. In the early 1800 's six specimens of *F. chiloensis* were transported to France and propagated in several gardens alongside specimens of *F. virginiana* , a North American species. The two species hybridized, forming what is called ' garden strawberry ', *Fragaria x ananassa* (the ' x' in the name indicates that it is a hybrid). It is this hybrid that is now widely cultivated throughout the world, generally being propagated through cuttings.

Navel oranges

Another crop with a 'chance' origin is the navel orange. It occurred as a 'sport' , a mutant branch, on an orange tree growing in Brazil. Remember that branches originate from lateral buds, meristematic tissue left behind by the elongating shoot apical meristem. Occasionally, some of the lateral bud meristems possess mutations that cause them to produce a branch that grows abnormally or one that produces leaves that are unusual (a common manifestation is a branch that produces variegated leaves, leaves that are not uniformly green but are colored a variety of ways). In the case of the navel orange the branch was unusual

because its flowers, which normally occur singly, occured as pairs, with a second flower produced very close to the 'normal' flower. The proximity of the two flowers is manifested in an altered fruit development, producing not two distinct fruits but rather a single fruit with another fruit inside it. This is what produces the navel for which the plant is named. If one peels and opens up a navel orange, the second fruit is very evident at navel end. This fruit does not possess a skin and is much smaller than the normal fruit , typically less than an inch in diameter. But, like the normal fruit, it is composed of wedge-shaped sections. A second abnormality of navel oranges is that the pollen is sterile and consequently cannot fertilize flowers. Because of this, the fruits produced by navel oranges are seedless.

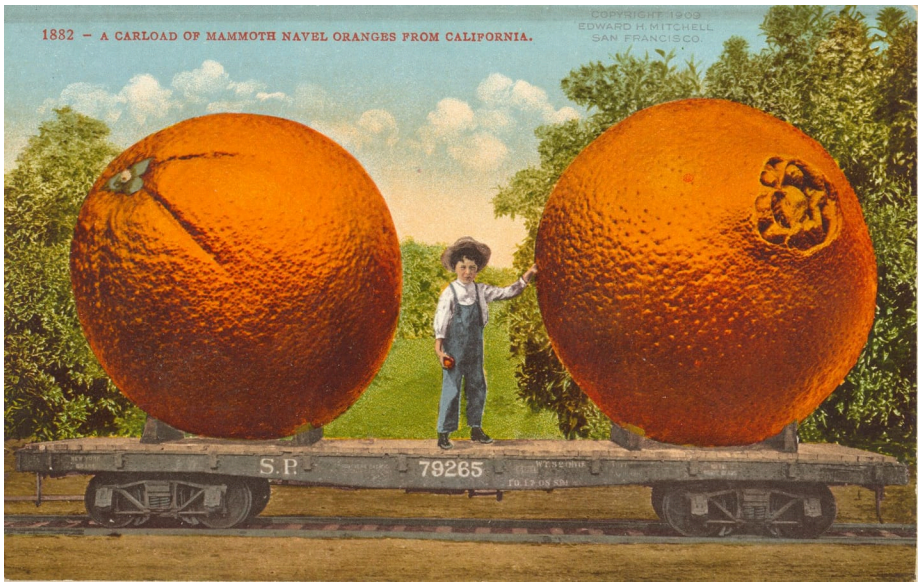


Figure 5 Navel oranges showing the characteristic 'navel' at the end opposite of the stem that attached it to the plant.

Navel oranges are perpetuated by cuttings, and all the navel oranges grown world-side are ultimately derived from to the original branch produced on the tree in Brazil. A cutting can be rooted to form a naval orange tree but are more commonly cuttings are grafted on to an existing root stock. A variety of species, generally close relatives, can be used as rootstocks and rootstocks can be selected for favorable characteristics, e.g. temperature, drought and pathogen tolerance. This allows horticulturalists to develop new varieties of rootstocks as pathogens evolve.

Banana

Unlike naval oranges which are propagated by grafting branches (called scions) on to a variety of rootstocks, bananas are propagated by cloning of whole plants, i.e. taking a cutting, usually a branch, and having it form roots. Cloning from cuttings is much less 'technological' than grafting and the utilization of cuttings as an agricultural technique goes back to the time when agriculture was developing. There are a large number of banana varieties and it is thought most appeared in the wild and were selected because of favorable features, in particular large fruits that lack seeds. Obviously a lack of seeds makes propagation by seed impossible, but cloning allows these favorable characteristics be perpetuated. Modern studies indicate that the many banana varieties are derived



Figure 6. Ripening banana fruits, each origination from a unisexual female flower.

from two species and polyploid derivatives of these species. Most bananas grown commercially are triploid, with a genetic constitution of AAB meaning that they possess two chromosome sets of one type and one chromosome set from the other. Such a triploid may be the result of a tetraploid (AAAA, that produces gametes that are AA) hybridizing with a (normal) diploid (BB, that produces gametes that are B). The offspring of this cross are sterile because meiosis is impossible, but cloning allows the plant to be perpetuated. Moreover, the sterility brought about by hybridization has created a favorable feature — no seeds. Triploids may also arise by the the union of an unreduced gamete from a diploid species (the species is AA but produces gametes that are AA instead of A) combining with a normal gamete from another species, e.g. a diploid species BB producing haploid gametes, B. The offspring is triploid, AAB, and sterile.

For most plant species the production of fruits is a consequence of the production of seeds, with the initiation of seed development triggering the initiation of fruit development. The production of fruits when seeds are not developing at all, or when seeds are initiated but soon aborted, is called parthenocarpy. It is generally considered to be evolutionarily unfavorable since the basic function of fruits is to promote seed dispersal and producing fruits without seeds is a waste of resources. Parthenocarpy can appear 'spontaneously' , but it generally will not be perpetuated, unless of course it is selected by early agriculturalists. More recently, parthenocarpy may be developed in breeding programs. An example is the seedless watermelon, which, like most bananas, is a sterile triploid, but it was produced by plant breeders crossing a tetraploid plant with a (normal) diploid plant. Seedless watermelons do have seeds but they are small and not fully developed. Seedless watermelons do require pollination to initiate the seeds but they soon abort. In some crops (e.g. some varieties of tomato) parthenocarpic varieties produce fruits even if pollination is lacking.

Corn

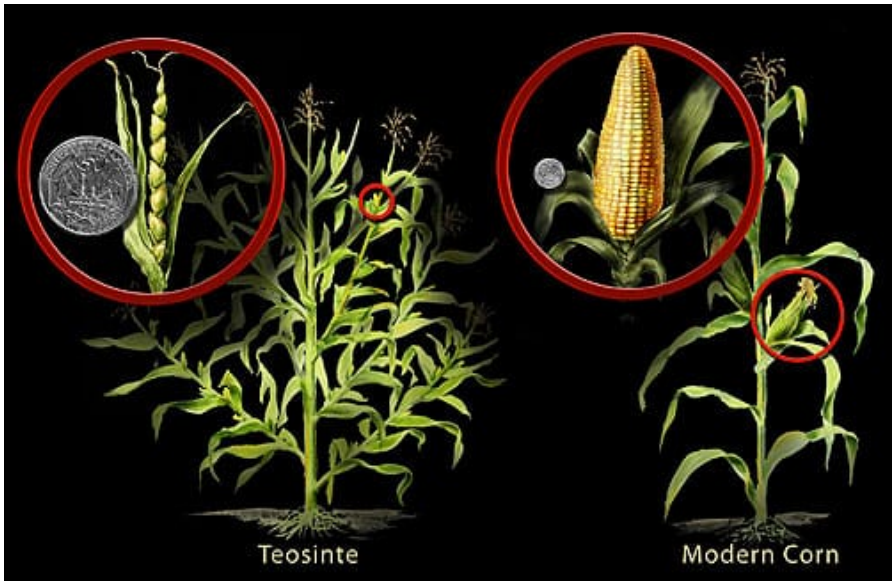


Figure 7 Teosinte, the ancestor of corn, compared to corn.

Corn 's origin as a crop has been a mystery because there had been no obvious ancestor, i.e. a species that looks like corn and could be considered to be something that primitive agriculturalists might manipulate to produce the entity that we know as corn. Research over the last 75 years has revealed that there is a close relative, called teosinte, but its proximity to corn is obscured by the fact that it ' looks ', i.e. has a morphology, that is substantially different from corn. Studies have revealed that corn and teosinte are actually the same species — they readily interbreed. The morphological difference between the two are actually the result of changes in only a few (less than 10) genes. It is now thought that selection on teosinte developed the variety (subspecies) that we now consider to be corn, a plant that unlike teosinte: does not branch, has much larger ' ears' (clusters of female flowers), and has seeds that are not enclosed in a rigid container but are relatively easily removed, allowing easier access to an edible structure.

Corn was responsible for dramatic changes in agriculture, in particular the development of seed companies, commercial entities that provide seed to individual farmers. Up until early in the 20th century most farmers provided seeds for themselves by storing seed from the previous crop. When storing seed for the next year 's crop, most farmers, passively or actively, selected for increased yield by saving seed from plants that were disease resistant, pest resistant and generally higher yielding. Early in the 20th century agriculture changed drastically in a number of ways, one of them being that farmers started to purchase seed from companies because they could provide seed that was better than what farmers had on hand. This better seed was the result of agricultural research occurring both in' land grant colleges '(who were charged with improving agriculture) and also in private companies when it was realized that that money could be made by supplying seeds to farmers. Corn was instrumental to this process because it is amenable to producing what is known as ' hybrid seed'.

Hybrid seed

Hybrid seed is seed that is produced by crossing two inbreed lines, where each inbreed line consists of plants produced by multiple generations of breeding with close relatives. Genetic research had shown that while inbreeding produced plants that grew and yielded poorly, a hybrid plant, produced by the crossing of two inbreed lines, was particular vigorous ('hybrid vigor'), more vigorous than either of the parental types before they were inbreed. 'Hybrid vigor' opened the door to seed companies, making them profitable for two reasons: (1) hybrid seed must be purchased anew each year because the seed from the hybrid crop is NOT particularly vigorous; it isn't a hybrid—both parents are essential the same, (2) developing hybrid seed was an activity that farmers growing crops for food probably would not want to take part in: they were interested in crops that could be grown in a season and sold to make a profit.

Corn is particularly amenable to producing hybrid seed because it has separate male and female flowers that are found on different parts of the plant. Corn tassels are clusters of male flowers. These can be removed and the pollen they produce can be used to fertilize specific plants. With corn, controlling who breeds with whom, which is essential to the production of hybrid seed, is relatively easy. The success of hybrid corn seed has spurred research into producing hybrid seed in a wide variety of plants including many that do not have separate male and female flowers. Seed producers have utilized a variety of techniques that

make hybrid seed production possible (see chapter 31)

Hybrid seed has several favorable features in addition to producing vigorous plants. The plants in a hybrid crop are more uniform than those produced from open pollinated seeds. Uniformity in size and time of maturation may greatly enhance harvesting. Hybrid crops also allow favorable traits developed in parental lines to be combined.

Generating variability

Whether or not one is utilizing hybrids, crop development requires variability followed by selection of plants with favorable features. Open pollinated crops generate variability both through naturally occurring mutations and also by chance shuffling of genes in the sexual process. Although there had been suspicions on the existence of sex in plants and the roles of pollen and pollination, the observations of Rudolf Cameraius late in the 17th century revealed the role of pollen and made possible the generation of variability by the intentional crossing of two related species. Often these efforts were stimulated by the botanical explorations and the collection of 'new' plants, e.g. the production of commercial strawberries described above. This allowed closely related plants to be grown together and crossed. Early in the 20th century workers discovered that they could generate variability with treatments that induce mutations: specific toxic chemicals or harsh radiation. And most recently modern molecular techniques allow for the most precise modifications of plant characteristics through the introduction, or occasionally removal, of specific genes. Although the later process is the only one described as 'genetic modification' , one should appreciate that crops have been genetically modified once they started to be cultivated. One should also appreciate that modern techniques are by far the most specific, meaning that the modifications are the most targeted, with the least amount of disruption of non-target genes and features (see chapter 31).

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20.2: Ecological Principles for Agriculture

Approaching agriculture and soil management from an ecological point of view means first understanding the characteristics that comprise resilient and relatively stable natural systems. Then, let's take a look at overall strategies that can contribute to similar resilience and health of crops, animals and farms. Finally, we'll briefly discuss practices that contribute to creating vital and strong agricultural systems (discussed in more detail in later chapters).

Managing Soils And Crops To Minimize Pest Problems

It is well established and known by most farmers that crop rotation can decrease many disease, insect, nematode and weed pressures. A few other examples of management practices that reduce crop losses:

- Insect damage can be reduced by avoiding excess inorganic nitrogen levels in soils by using precision nitrogen management.
- Adequate nutrient levels reduce disease incidence. For example, calcium applications have reduced diseases in crops such as wheat, peanuts, soybeans and peppers, while added potassium has reduced the incidence of fungal diseases in crops such as cotton, tomatoes and corn.
- Damage from insects and diseases (such as fungal diseases of roots) can be decreased by lessening soil compaction.
- The severity of root rots and leaf diseases can be reduced with composts that contain low levels of available nitrogen but still have some active organic matter.
- Many pests are kept under control by having to compete for resources or by direct antagonism from other insects (including the beneficials feeding on them). Good quantities of a variety of organic materials help maintain a diverse group of soil organisms.
- Root surfaces are protected from fungal and nematode infection by beneficial mycorrhizal fungi. Most cover crops, especially in reduced tillage systems, help keep mycorrhizal fungi spore counts high and promote higher rates of colonization by the beneficial fungi in the following crop.
- Parasitic fungal and nematode infections can be suppressed by selected cover crops.
- Weed seed numbers are reduced in soils that have high biological activity, with both microorganisms and insects helping the process.
- Weed seed predation by ground beetles is encouraged by reduced tillage and maintenance of surface residues. Reduced tillage also keeps the weed seeds at the soil surface, where they are accessible to predation by other organisms, such as rodents, ants and crickets.
- Residues of some cover crops, such as cereal rye, produce chemicals that reduce weed seed germination.

Ecological crop and soil management practices can be grouped under one or more of three strategies:

- grow healthy plants with strong defense capabilities
- suppress pests
- enhance beneficial organisms

These overall strategies are accomplished by practices that maintain and enhance the habitat both aboveground and belowground. And as the field habitat improves, so does the environment in general: less pollution of groundwater and surface water and more wildlife habitat in and surrounding the field.

Ecological approaches call for designing the field and farm to take advantage of the inherent strengths of natural systems. Most of this is done prior to, and during, planting a crop and has the goal of preventing problems from developing by contributing to one or more of the three overall strategies. In other words, it requires forethought and good planning.

Many natural, relatively undisturbed, systems are generally stable, and when disturbed by natural forces such as fire, wind or excess rain they are able to bounce back fairly rapidly. In other words, they are *resilient*. These resilient systems tend to have similar general characteristics:

Efficient.Natural systems have energy flows that efficiently use resources. The sun's energy captured by green plants is used by many organisms, as fungi and bacteria decompose organic residues and are then fed upon by other organisms, which are themselves fed upon by others higher up the food web. Natural ecosystems also tend to be efficient in capturing and using

rainfall and in mobilizing and cycling nutrients. This helps to keep the ecosystem from “running down” because of excessive loss of nutrients and at the same time helps maintain the quality of the groundwater and surface waters. Rainfall tends to enter the porous soil, rather than run off, providing water to plants as well as recharge to groundwater, slowly releasing water to streams and rivers.

Diverse. High biological diversity, both aboveground and in the soil, characterizes many resilient natural ecosystems in temperate and tropical regions. It provides nutrients to plants, checks on disease outbreaks, etc. For example, a diversity of plants—trees versus understory, grasses versus legumes—captures and supplies different resources. And competition for resources and specific antagonisms (such as antibiotic production) from the multitude of soil organisms usually keeps soilborne plant pathogens from causing diseases in a natural grassland or forest.

Self-sufficient.A consequence of efficiency and diversity in natural terrestrial ecosystems is that they become mainly self-sufficient, requiring only inputs of sunlight and rainfall.

Self-regulating.The great diversity of organisms decreases the risk of outbreaks (or huge population increases) of pathogens or insects severely damaging plants or animals. In addition, plants have a number of defense mechanisms that help protect them from attack.

These ecological characteristics provide a good framework for sustainable management of fields and farms, but we must also recognize that crop production (and even urban landscaping for that matter) is a process that greatly disturbs natural ecosystems in order to favor one or a few organisms (crop plants) over the competing interests of others. And systems are also disturbed in other ways to be able to produce crops. Routine management practices that occur during the season cause disturbances even if you have invested heavily in preventive management. For example, irrigation is frequently needed for high-value crops such as fresh market vegetables, even in humid regions. Some practices have little direct disturbance, such as scouting for pests and beneficial insects during the season. If an unanticipated problem, such as an insect outbreak, arises, remedial action, such as applying the most ecologically sound pesticide or releasing purchased beneficials into the field, may be required to reduce crop losses.

With currently available pesticides, the temptation exists to simply wipe out competitors—for example through soil fumigation or broad-spectrum herbicides like glyphosate—but this creates dependency on purchased materials from off the farm and weakens the overall resilience of the soil and cropping system. It also promotes genetically induced resistance to these chemicals and makes them less effective in the long run. The goal of ecological crop and soil management is to be *proactive* and *preventive* by creating conditions that help grow healthy plants, promote beneficials and suppress pests, and thereby minimize the extent of *reactive management* (which responds to unanticipated occurrences). The discussion below and in the rest of this book focuses on ways to maintain soil health and to enhance habitat in order to promote one or more of the three strategies listed above.

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20.3: Biotic Interactions

Interactions between individual organisms

Organisms interact with each other and these interactions can have significant consequences to the participants. Most students are familiar with the classification scheme below which organizes interactions into types based on the consequences of the interaction on the two participants:

	effect on the 'larger' organism			
		(-) negative	(0) neutral	(+) positive
effect on the 'smaller' organism	(-) negative	competition	amensalism	predation, herbivory
	(0) neutral	amensalism	'neutralism'	commensalism
	(+) positive	parasitism	commensalism	mutualism

There are multipleproblems with this scheme. It is not clear what level, organism or population, it is focused on or how effects might be measured. If considering at the individual level 'positive' might be monitored by organism size, growth rate, longevity or reproductive success. But if considering the population, level one might consider population density or population growth rate. Sometimes what is 'positive' and what is 'negative' may not be obvious. Some fungal endophytes substantially increase the growthof plants (positive effect) that they infect, yet at the same time reduce or eliminate the likelihoodof producing offspring (negative effect). Nitrogen-fixing bacteria infecting roots may benefit plants (faster growth, bigger plants) if soil nitrogen is low, but harm plants (slower growth, smaller plants) if nitrogen levels are high. Pollinator visits may benefit plants if they transport pollen to other members of the same species but not if their next visits are to different flower species.



Figure 1 Do wolves harm or benefit prey?

Perhaps the most significant biological context for the terms would be evolutionary (positive = enhanced reproductive success) but this may depend on circumstances that are difficult to evaluate. Predators would generally be thought to have a negative on prey populations, but in a number of situations, predators are thought to 'benefit' prey populations by preventing overpopulation (Figure 1). Another problem with the scheme is that it ignores the fact that the consequences of interactions may be very different at different levels of biological interaction. Seed predation (e.g., Clark's nutcracker eating pine seeds, Figure 2)) is clearly harmful to most individual pine organisms (i.e., the embryonic pine individual present in a seed) but apparently benefits the pine populations by allowing for dispersal.



Figure 2 Do individual pine seeds benefit from their interaction with Clark 's Nutcracker? Some do, some don' t, but it is thought that the population of limber pines does.

Another way to organize biotic interactions is not based upon arbitrary considerations of what 'benefits' or 'harms' the organisms/populations involved, instead, it is based upon the medium through which the interaction occurs:

- trophic interactions—one organism eats another or part of another, obtaining material (carbohydrates, proteins, fats) that can be used both for ener gy (i.e., burned in cellular respiration) or partially broken down and reformed into molecules of the consumer
- resources/ conditions interactions—Resources are materials (e.g., oxygen) that an organism either produces, making them available for other organisms or depletes/consumes, making them less available for other organisms . Conditions are physical

parameters, e.g., pH, temperature, humidity, light intensity. Conditions influence organism behavior and organisms can change conditions and thereby affect other organisms. Resources and conditions are combined here because several can be considered both as a resource and a condition. Oxygen can be considered a resource because oxygen can be produced or consumed but it also is a condition that has physical consequences, e.g., oxygen concentrations affect the solubility of ions in the soil solution. Similarly, light is a resource that plants ' consume ' , reducing its availability to the shaded plants below, but it also is a physical condition that influences all organisms in a number of ways.

- work interactions—one organism does work for another organism (work in the sense of physics, and chemistry, a process that requires the expenditure of energy, e.g., moving material from one place to another).

TOPICS

- Trophic interactions
  - Predation
  - Grazing
  - Parasitoids
  - Parasites
  - Leftovers
- Interactions involving resources and conditions
- Work interactions

Trophic Interactions

Although all trophic interactions are 'organism A eats organism B' , resulting in a transfer of material from A to B, the way the eating is done varies greatly and it may be the case that the most significant consequences of the interaction do not involve the transfer of material. Below are four categories of trophic interactions involving the organisms considered in this course. The categories are based on the consequences to the two 'players' of the trophic relationship: the organisms doing the eating ('eater') and the organism being eaten (the 'eatee'). Although it is generally the case that the eatee is harmed because it loses material, and the eater benefits because it gains material, this is not necessarily the case and sometimes other components of the interaction are even more significant.

Predation



Figure 3 Red crossbills have a specialized bill that allows them to open the cones of conifers and predate on the seeds inside.

The eating event kills the 'eatee' (the organism being eaten) and the eater consumes multiple prey items during its life (Figure 3). In plants, this generally only occurs when the plantsare small when they are seeds ('seed predation'), or the consumption of

seedlings. The embryonic plants found in a seed are particularly nutritious per unit weight because, compared to larger plants, they have relatively less structural material (i.e., cell walls) and relatively high concentrations of minerals and vitamins. The eater benefits from the nutrition obtained (assuming that eatee does not contain toxins that the eater cannot handle) and the eatee is eliminated. This interaction has driven evolutionary changes involving chemical, physical and phenological (timing) changes in plants, and consequent changes in predators, for as long as seed plants have been around. In a number of instances, the interaction has developed into a mechanism of seed dispersal, utilizing an eater 's mobility and perhaps its caching behavior (see the reading on pines and the Clark' s Nutcracker). Seed predationalso was probably a driving force in the development of (fleshy) fruits as a means of seed dispersal:plantsdeveloped features that would reward the eatee in a way that did not involve (permanently) consuming the seed and killing its embryo. Seed predation also accounts for fruit structure that most definitely doesprotect the seeds inside (e.g., nuts), although seed predators have responded by developing structures (sharp teeth of saki monkeys or beaks of goldfinch, Figure 4) and behaviors that allow them to open seeds, or digestive systems that grind the seed coat or fruit coat away. Although most of the organisms that we have studied are photosynthetic autotrophs (plants, algae) and are the eatees, we have also considered some organisms that are the eaters (cellular and plasmodial slime molds, and some of the euglenoids and dinoflagellates). Some fungi are predators in the classic sense (i.e., they capture prey and kill them, http://www.mykoweb.com/articles/FungalSnares.html), and a number of fungi are predators in a less classical sense, being capable of killing their food with toxins or other processes.



Figure 4 American Goldfinch is commonly feed on thistle or sunflower 'seeds' (actually fruits) at feeders, but can eat a wide variety of species, including many grasses.

Grazing

The eater (grazer) does not kill the eatee, but only eats part of it, and usually, the grazer eats parts of several individuals. Most familiar examples of herbivory (eating of plants) are grazing: cows and grass, deer and shrubs, J apanese beetles (Figure 5) and ornamental plants. While most grazing on plants is on their leaves, some organisms graze on other parts: pollen, flowers, ovaries, roots). Although p lants are the most common kind of organism



Figure 5 Japanese beetles damage but usually do not kill the plants that they feed upon.

grazed upon there are several other ' inanimate ' groups that are grazed: photosynthetic protists (' algae '), a few non-photosynthetic protists (plasmodial slime molds) and many fungi . Grazing is most likely to occur on organisms that have indeterminate growth. Most grazing on plants is on leaves and the eatee is affected both by the loss of photosynthetic area (and hence the ability to photosynthesize) and also because of the loss of nutrients (e.g., nitrogen and phosphorus) that are relatively hard to replace. Too much grazing can be fatal for the eatee but lesser amounts of grazing sometimes actually produce beneficial results; for instance, grazing of apical meristems can induce branching and produce a plant that actually produces more leaves, flowers and fruits.



Figure 6 A leaf hopper, a grazer that often spreads disease from one plant to another.

One particularly significant aspect of grazing is that it is a means of disease transmission between individuals , comparable to a mosquito (also a grazer) spreading malaria. Leafhoppers and aphids are both insects that have piercing mouthparts to acquire nutrients from phloem tissue in leaves and stems. If they move from an infected plant to another plant they can transmit pathogens (viruses, bacteria and others) in the process, and often this is the most significant aspect of their grazing (Figure 6).



Figure 7 Granary weevil—a seed predator of cereal grains (e.g., wheat, rice). Adult females drill through the wall of the fruit and deposit a single egg which, when hatched into a larva, consumes the seed contents and then emerges as an adult.

Parasitoids

The distinctive feature here is that the reproduction of the eater is obligatelyand directlyassociated with the trophic event and that the eatee dies as a result of the association. While any heteterotroph must consume food in order to acquire the matter and energy needed to reproduce, in the case of parasitoids the connection is direct because a propagule (usually a fertilized egg) is deposited on the eatee. The vast majority of parasitoid interactions involve insects, one as the eater and another as the eatee. But occasionally plants are parasitoid prey, sometimes by organisms consumingseeds (e.g., granary weevils (Figure 7) and acorn weevils http://video.nationalgeographic.com/video/animals/bugs-animals/beetles/weevil_acorn/) and also some fungi, termed necrotrophic fungi, who infect their hosts (plants), kill them with toxins and then feed on the dead tissue, eventually producing fungal reproductive structures.

Parasites



Figure 8 The orange strings are dodder, a parasitic plant that connects to the phloem tissue of its host to acquire nutrients.

As in grazing, the eater generally does not kill the eatee, but in contrast to grazing, the eater generally only feeds upon one host and thus is not typically a means of spreading disease from one eatee to another. Evolutionarily, one might argue that parasites

(and perhaps some grazers) adopt a strategy of keeping their host alive in order to assure a food supply for a longer time. There are a number of fungi called biotrophic fungi, including the important plant pathogenspowdery mildews and rusts, that feed off of living plant tissue and would be considered parasites. They produce structures called haustoria that penetrate the cell wall and interact with the plant cell plasma membrane, providing them with access to materials (e.g., sugars, amino acids) present in the cytosol. Dodder (Figure 9) a non-photosynthetic flowering plant, also produces haustoria. These penetrate into the phloem tissue of their hosts and provide them with nutrition. The fungal component of mycorrhizae would be considered parasites, as would be the nitrogen-fixing bacteria that form galls in some plants. Indeed, mostgall-forming organisms (insects, fungi, mites) would be considered parasites. The gall is an abnormal growth induced by the presence of the parasite. The parasite is fed by its host and ultimately exits the gall.

(As an example see www.wenatcheenaturalist.com/sagebrush-galls/ or www.fllt.org/inside-the-goldenrod-gall/). Most of these interactions are similar to parasitoids in that the reproduction of the eater is dependent on the interaction, however, the host is not killed. In most instances, the eatee suffers because of a loss of nutrients, and the eater benefits because it is provided with nutrition and often with protection as a result of the structure of the gall.



Figure 9 Galls on a sugar maple leaf. These galls are triggered by mites.

Saprophytes, i.e., eating 'leftovers'

All organisms are a source of food after they die and thereby represent an 'easily captured' prey item. Heterotrophs that consume material (plant, animal, fungal and others) that is already dead (i.e., they did not kill it) are termed saprophytes. Because plants are continually shedding leaves and roots (and in many cases stems), these discarded items are often abundant and provide food for a number of organisms. The nutrient quality of these discarded items is generally substantially below that of living tissues because the plant, in the process of senescence, recycles materials, retrieving much of the material present in the soon to be discarded item before it is actually shed. Leaf protein, nucleic acid and mineral concentrations all decline drastically before leaves are shed and the remaining material is much less digestible both because most of the molecules that remain(e.g., cellulose, lignin) are more difficult to degrade and because of the lack of nitrogen makes it hard to build up substantial populations of saprophytes. Organisms(especially larger ones. e.g., earthworms, insect larvae) feeding on dead organic material often obtain nutrition, perhaps most of their nutrition, from the consumption of much smaller organisms (e.g., bacteria, amoebae, fungi) that are present on the decaying material and not from theorganic material itself, i.e., they are really getting their nutrition from being predators, not saprophytes. Bacteria and fungi are the most significant saprophytes in the soil but other groups (cellular slime molds, plasmodial slime molds and heterotrophic forms of euglenoids) may also be saprophytic. In aquatic systems, a significant amount of organic material can be broken down to the point that it dissolves and ispresent as dissolved organic material, which some organisms are able to assimilate.

Conditions/Resources Interactions

All organisms change the resources and conditionsaround them. The extent to which this affects other organisms depends on:

how big the organism is (big things have more of an effect than small ones), how plentiful they are (i.e., their population size) and precisely what changes they bring about. Any organism is a 'producer, ' i.e., it grows and produces a resource (i.e., biomass) that some other organisms can eat. Therefore all organisms must provide resources. Plants (andmore generally autotrophs) are particularlyimportant in a resource sense because, being the base of food chains, their activity represents how many trophic resources are available to entire communities. Also, except for autotrophs who are self-feeders, all other organisms, i.e, . heterotrophs, eat something and can influence other species by depleting that resource. But there are many other ways that organisms interact with each other besides affecting trophic resources. Here are some examples:

The trees of a forest substantiallychange the conditions below them.Temperatures are moderated (cooler in the daytime, warmer at night). Wind is moderated. Rainfall/snowfall patterns are changed. For deciduous forests the annual deposit of leaves covers the ground surfaceand acts like insulation, keeping the soil warmer in the fall and cooler in the spring. In evergreen forests, leaves layer the ground but the fact that they do not come all at once alters the dynamics. Leaf litter affects soil chemistry. Thus different species can have different effects. The tipping over of a tree root system that occurs when trees are blown over changes the topography and exposes lower mineral layers. And some species (e.g., yellow birch) germinate best in mineral soil because the roots of seedlings are unable to penetrate a blanket of leaf litter.

Oxygen consumption by organisms in terrestrial habitats generally has little impact because the oxygen levels in the air are high (~20% of the air is oxygen) and because winds keep the air well-mixed and localized depletions are unlikely. In contrast, oxygen depletion in the soil and in some aquatic situations can havevery significant consequences. In waterlogged soil, oxygen consumption by roots, fungi and a host of soil organisms, coupled with reduced oxygen movement in soils water-filled pores, can make the soil anaerobic. Similarly, unless there are processes promoting mixing of the water column, respiration by heterotrophs at the bottom of the lake significantly lowersthe oxygen levels, potentially affecting all organismsliving there.



Figure 10 Red bog moss (Sphagnum capillifolium) is a common species in bogs. Note the densely packed stems.

A globally significant example of organisms changing oxygen availability and consequently affecting other organisms involves Sphagnummossand areas known as bogs. Sphagnum mosscan develop high population densities and this, coupled with their pattern of growth, creates a dense mat of stems elongatingat the top but withan extensive layer of dead stem and leaf material below. The stems and leaves hold substantial quantities of waterand water is also held in the spaces between plants, producing what is essentially a giant sponge. This creates a habitat of stagnant water, where there islittle mixing of the surface layer of water with the water below. Consequently, at a very shallow depth, the water becomes anaerobic because of oxygen consumption by saprophytes feeding on the dead plant material. In addition, the chemistry of sphagnum cell walls causes the waterto becomeacidic. The acidic conditions, combined with lack of oxygen, greatly reduce the decomposition of plant material, thereby reducingthe supply of nutrients(remember that nutrients become available to plants because of decomposition), and cause peat (un-decomposed plant material) to accumulate. The soil conditions prevent a large number of species (e.g., trees) from existing in the area or causes them to be stunted. Instead, bogs have a characteristic group of species, often members of the blueberry family, that are tolerant of the soil conditions.

One of the types of plants found in the nutrient-poor conditions of a bog are 'carnivorous' plants including pitcher plants, which nicely demonstrate the nutritional distinction between autotrophs and heterotrophs. Heterotrophs obtain both 'food' (a

carbohydrate supply for cellular respiration) and nutrients (e.g., nitrogen) from the material they consume. Carnivorous plants obtain energy through photosynthesis just as most plants do, making food in photosynthesis and then eating it. The significance of their predation is that it provides carnivorous plants with non-carbohydrate nutrients which are otherwise hard to come by because of the habitats where they dwell. There are a wide variety of devices for capturing prey (generally insects), including pitchers, snap traps, flypaper, bladders and lobster traps (https://earthsky.org/earth/lifeform-of-the-week-carnivorous-plants-are-out-for-blood).



Figure 11 An Ontario bog. The stunted trees are mostly larch and white pine. The red shrub is probably huckleberry. All of the plants are growing out of a waterlogged bed of Sphagnum.

Pitcher plants have a highly modified leaf whose petiole serves as a container for rainwater. The pitcher also possesses features that attract and capture insects who eventually drown there. The water develops a decomposition community of bacteria, fungi, water molds, amoebae, insect larvae and others. As a result of their activity, nutrients become available in a small enough form for the plant to absorb as they do in normal aerobic soil. In contrast, nutrients do not become available to the roots due to the waterlogged peat that pitcher plants are rooted in.

Dense growth of algal (usually cyanobacteria but sometimes green algae) can 'seal' the top of ponds, creating a situation comparable to sphagnum bogs because the wind is not able to inducemixing of the oxygen-rich top layers of the water with the lower layers. Because no light can penetrate the dense algal layer on top, no photosynthesis is possible except at the surface. These factors, coupled with the magnitude of dead plant material that is created by the algal growth and the decomposition of this material by heterotrophs below, cause the lower water levels to become anaerobiceventually drastically altering the species present and limiting the rate of decomposition.

Resources /conditions represent significant avenues whereby species can interact with each other. In particular , two species requiring the same resource can affect each other by making the resource less available for other organism/species. Plants interact with other plants by their consumption of light, nutrients and water. This is the classic explanation for an interaction described as 'competition' although there are other reasons besides resource depletion that might explain why the presence of one species might deter the growth of another species (or at the population level, the presence of one population lessens the population density of a second population).

Globally, two of the most important biotic consequences involving resources are the addition of oxygen to the atmosphere by photosynthetic organisms and the addition of simple mineral forms of nutrients into the soil or aquatic systems as a result of the decomposition carried out by heterotrophs.

Plants provide resources in other ways; their physical structure is important to many other other species : birds nest in trees ; many spiders use plant structures as a base for their webs; p arts of plants and pieces of lichens are often used as building materials for nests.



Figure 12 Plants don't just provide building materials (lumber) for humans, they provide them for a wide variety of organisms including osprey (above) and hummingbirds (below). The materials utilized include twigs, bark, vines, bits of leaves, parts of lichens. Many squirrels utilize branches and leaves to make their nests. Both birds and mammals utilize holes in tree trunks as nesting sites.



Figure 13 A female ruby-throated hummingbird on its nest which has an outside coating of lichens.

Work Interactions

A number of species interact with each other by providing services, i.e., doing work, for other species. For plants, the most significant of these results fromorganisms that provide mobility, mobility for male gametophytes in pollination and mobility for seeds. Animals transport seeds both 'passively' , when seeds or fruits stick to fur, and 'actively' when the plant attracts animals to a trophic reward (generally fruits, but sometimes seeds, Figure 14) with the mobile animal then transporting the seeds and depositing them (often by defecating) some distance away. For the most part, pollination is active with the plant advertising a trophic reward, which may be nectar (a sugar secretion) and/or may be pollen. In the case of pollinators, not only are some species capable of moving pollen but they can do it in a very directed way, transporting it to members of the same species of plant, thereby allowing cross-pollination and cross-fertilization to occur. This specificity (i.e., mobility to a specific, favorable location) occasionally is the case for seed transport, e.g., Clark's nutcrackers transport seeds to sites that are particularly favorable for the growth of the pines whose seeds they are transporting; certain ant dispersed species bring about movement of seeds to sites (ant nests) that are particularly favorable for seedling establishment (Figure 14).



Figure 14 Seeds of bloodroot have appendages called elaiosomes that are appealing to ants that collect the seeds and take them to their nest.

While the common interaction is a 'quid pro quo' with food provided by the plant 'in exchange for' work by the visitor, occasionally the plant is providing a non-food reward. Some orchids provide specific chemicals that serve as pheromones for the insects that acquire them. The Yucca plant provides not only food but also a shelter for larval yucca moths that develop from the eggs that the yucca moth deposits as it is pollinating the plant. Ficus trees provide food and nesting sites for pollinators.

Two excellent sites that consider these interactions are:

- Yucca moth: https://www2.palomar.edu/users/warmstrong/ww0902a.htm
- Ficus: https://www2.palomar.edu/users/warmstrong/pljune99.htm

[Both these links come from an outstanding website ('Wayne' s Word') that is an excellent source of botanical information. Take some time to explore it.]

There are a number of examples of 'cheating' by both the visitor and the plant. Some visitors can consume the food reward without picking up pollen and consequently without providing the plant with a service. Plants may attract visitors with visual displays but give them no rewards.

'Protection rackets' describe a relationship where the plant provides food and another species does work by protecting the plant from herbivores. This relationship is particularly well developed in some Acacia trees and shrubs where the plant not only provides food rewards but also provides nesting spots for colonies of ant defenders. Additionally, while the typical food reward (for pollination, seed dispersal and defense) is nectar, a compound that is cheap to produce, some Acacia species provide more complex food rewards, Beltian bodies, packets that are much more rewarding nutritionally because they contain lipids and proteins. These are much more expensive for the plant to make. An extension of this interaction is the three species interaction of plants, aphids and ants. Aphids are insect herbivores that tap into the plant 's phloem tissue using their stylet. Since phloem sap has abundant sucrose but scant amino acids, the aphid eats a lot of phloem sap to acquire the amino acids it needs and the excess sucrose is excreted as ' honeydew ', aka ' frass' (insect excrement). Ants have developed a relationship of defending the aphids from predators while acquiring the honeydew that the aphids produce.



Figure 15 The small insects on the top part of the leaf petiole are aphids whose stylets have penetrated into phloem tissue and are having phloem sap pumped into their mouth by the plants. The ants collect aphid frass and feed the ant colony with it. The ants also protect the aphids from potential predators.

Nitrogen-fixing bacteria do chemical work, the reduction of nitrate to ammonia, for their host plants, in exchange for food and a protected habitat. In nodule forming plants the protected habitat are galls on the roots. The aquatic fern *Azolla* forms small cavities on the surfaces of leaves that the nitrogen-fixing cyanobacterium *Anabaena* colonize. This relationship is utilized by rice farmers who encourage the growth of *Azolla,* a small aquatic plant that lives on the surface of bodies of water. Nitrogen fixed by the cyanobacterium becomes available to the rice when the *Azolla* dies and is decomposed.

A more 'one-sided' work interaction involvesinsects acquiring and utilizing chemicals that the plant synthesizes. Monarch butterflies acquire a poison from the milkweed plants that they eat. The plant gains nothing but the insect acquires a chemical that deters predation. A similar situation occurs with poison dart frogs. The frogs become poisonous because of the insects that they consume, with yet-to-be-determined plants eaten by the insects providing the specific chemicals. Plants can also be on the receiving end of defensive chemicals as is the case with some fungal endophytes who produce toxins that can affect herbivores.

A number of species utilize the work performed by one species in order to produce a particular structure. One might consider the role of coral animals and lichen fungi to be providing services (structure) for the dinoflagellates and algae that live inside them. Plants provide structural services for other plants as well; vines utilize the structure of other plants and thereby avoid the costs associated with producing structural cells (sclerenchyma fibers) that are needed to produce a rigid stem that can withstand the forces of gravity and wind. There are a group of plants called '**hemiparasites**' that utilize the root systems, the structure, of other plants. Their hosts supply them not with food (carbohydrates, which would be a trophic interaction and would require connecting to the phloem tissue) but with water and minerals, that move passively up the host's roots and into the stem of the hemiparasite. At least some of the benefits of mycorrhizal associations may involve a similar type of relationship, with the fungus providing structure to explore the soil to acquire water and nutrients, and the plant providing food for the fungus. In other mycorrhizal associations, there may be more specific actions involved, for example, the fungi may be producingenzymes that mobilize mineral elements and transfer them to their host.

Eating a plant is generally considered positive for the herbivore (the ' eater ') and negative for the plant (the ' eatee ') but plants may be poisonous to the herbivore and plants may ' benefit ' in a number of ways (e.g., increased growth, increased seed production) in response to being eaten.

Further Reading

“The Microbial World: Biotrophic plant pathogens” by Jim Deacon

- http://archive.bio.ed.ac.uk/jdeacon/microbes/biotroph.htm

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20.4: Interactions Involving Conditions

A particularly significant and interesting aspect of organismal life is its interaction with its surrounding environment. As indicated by the term, interaction implies that both components affect each other: the environment affects organisms and organisms affect the environment. The 'environment' includes components that are living, i.e., other organisms (the biotic environment), and components that are non-living such as rocks, clouds, water, dead organisms or parts of dead organisms. The environment has properties or conditions, such as temperature and oxygen concentration thatare commonly considered 'the abiotic environment' or the 'physical environment' . Conditions are the consequences of physical processes such as radiation, diffusion, convection;and these processes are sometimes strongly influenced bybiotic processes (Figure 1), such as respiration (generates heat and carbon dioxide, removes oxygen)and photosynthesis (absorbs light, adds oxygen and water, removes carbon dioxide). The conditions present on a sitecan dictate whether or not an organism can exist, and if it exists, how it behaves. This is sometimes described as an interaction between organisms and the physical, or abiotic, environment.



Figure 1 Sugar maple leaves interact with the physical environment (conditions) multiple ways: during the day they absorb light, lowering light intensity below the leaf; they also reduce the air 's CO_2 concentration, increase its O_2 and H_2O levels and heat it up by radiating long-wave radiation. At night leaves decrease the air' s oxygen level but increase its CO_2 and H_2O levels. If the sky is clear the leaves can significantly affect the temperature of objects below by 'shielding' them from the cold night-time sky.

Because organisms can affect conditions, they can interact with other organisms as a result. In addition to the interaction between organisms mediated through conditions, there are more direct interactions between organisms, such as one organism eating another or an insect transporting pollen from one plant to another. Interactions are fundamental to the discipline of ecology. Indeed one definition of ecology is 'a study of the interactions between living things and their environment' .

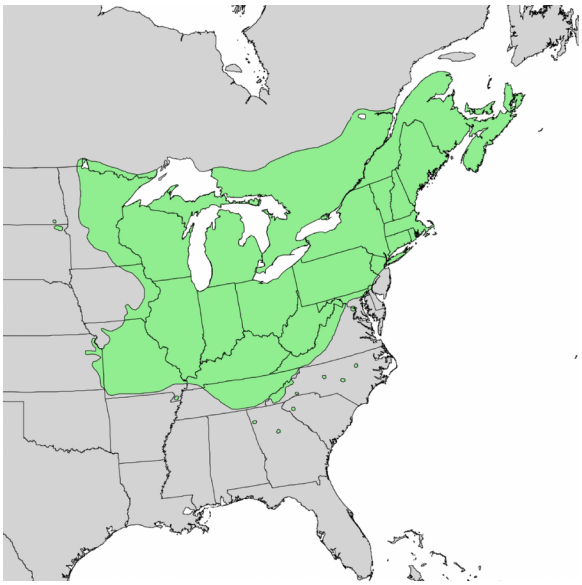


Figure 2 Sugar maple distribution: To the North, the population is limited by lower temperatures, to the West, by lower moisture levels and to the south, by multiple factors including higher temperatures, competition with other species, and perhaps disease.

Another common definition of ecology is 'a study of the distribution and abundance of organisms' (Figure 2). The distribution and abundance of organisms are controlled by interactions between organisms and their biotic and abiotic environment. For example, the distribution of a plant might be limited by the intensity of light. The amount of light available is a consequence of both the physical environment (latitude, degree of cloudiness, whether the site is facing south or north, etc.) and the biotic environment (presence or absence of tree species to intercept the light). The distribution and abundance of a particular plant (species 'A') might also be limited to the presence or absence of an organism that eats the plant or perhaps by an organism that pollinates the plant. In either of the latter cases, one might consider the factors that determine the distribution and abundance of the second species to be controlling the distribution and abundance of species A.

Another definition of ecology is “a study of biological organization above the level of individual.” As we have seen, organisms have a structure (form, size, organization of component parts), and also organisms have functions, they do things such as develop, reproduce, and exchange matter and energy with their environment. Similarly, groups of organisms (e.g. populations) have structural and functional features that can be described and categorized, and explanations can be sought as to what determines their organization. An important point is that life is not simply organized at the level of the cell and the level of an organism; there also is an organization involving groups of organisms and this is the level of study for the discipline of ecology.



Figure 3 A community ('northern hardwood forest') is defined in part by the presence of sugar maple. It is found in southern Canada, New England, parts of NY and Pennsylvania, and further south at higher elevations in the mountains.

Two entities that ecologists study are populations (groups of individuals of the same species) and communities (assemblages of species in a particular area). A population could certainly be considered a 'living thing' and its distribution across the landscape is a manifestation of biological organization and is a structural feature of this entity. The abundance of a species (how many individuals are present per unit of the environment) is another structural feature of a population. The fact that populations have patterns of distribution and abundance represents an organization, a structure, and the processes determining this structure are the same processes discussed above: interactions between organisms and their physical and biotic environments. Similar arguments can be made concerning the organization of communities.

I n our examination of the role of interactions in the biology of organisms , we will consider in this chapter the interactions between organisms and conditions, examining the key conditions that affect terrestrial and aquatic habitats, why these conditions affect an organism's function, and what factors cause these conditions to vary, including how organisms themselves may control conditions. In the next chapter, we will examine more direct interactions between organisms, trying to see fundamental similarities in the ways that organisms interact with each other. Finally, we will look at agriculture , an interaction that we all depend upon, and interactions (Chapters 28-30) that are critical to agriculture .

Our approach will be centered primarily on organisms, although many of the topics overlap with ecology and approach the topics from a broader scale.

TOPICS

- Temperature
  - Temperature's influences
  - Organism tolerances
  - Organism growth
  - Psychophiles and thermophiles
  - Fruit ripening
  - Temperature as a cue
  - Temperature's influence on other conditions
- Moisture
  - Terrestrial habitats
- Aquatic habitats
  - Salinity
  - Oxygen
  - Light
  - Currents
  - Nutrients

Temperature

Temperature is of critical importance to all organisms–it affects whether they can survive and what they do. Even for organisms who regulate their temperature at a set point, (i.e., homeotherms), temperature has significant consequences. But temperature is even more significant for the vast majority of organisms who do not regulate their temperature. For such organisms, termed poikilotherms, the thermal conditions of their environment control their metabolic activity. Although the temperature is important in all habitats, it is of relatively less importance in most aquatic systems because the thermal properties of water buffer temperature fluctuations. But organisms in terrestrial habitat s are immersed in a fluid (air) that absorbs very little heat energy and has a low heat capacity (i.e., little buffering ability). This makes the temperature of terrestrial systems much more dynamic in time and space than in most aquatic systems. One of the key reasons why temperature is important in terrestrial habitats is because it affects evaporation and moisture levels. While there are some terrestrial habitats where temperature is not a key determinant of activities, from a global perspective temperature and moisture are the major factor controlling what organisms are present and what they are doing.

Temperature's Influences on Organisms

All organisms have a range of temperatures in which they can carry out the functions that define and sustain them. Temperatures above and below this range alter their structure and functioning in several ways. The most important alterations are listed below.

Membranes and temperature

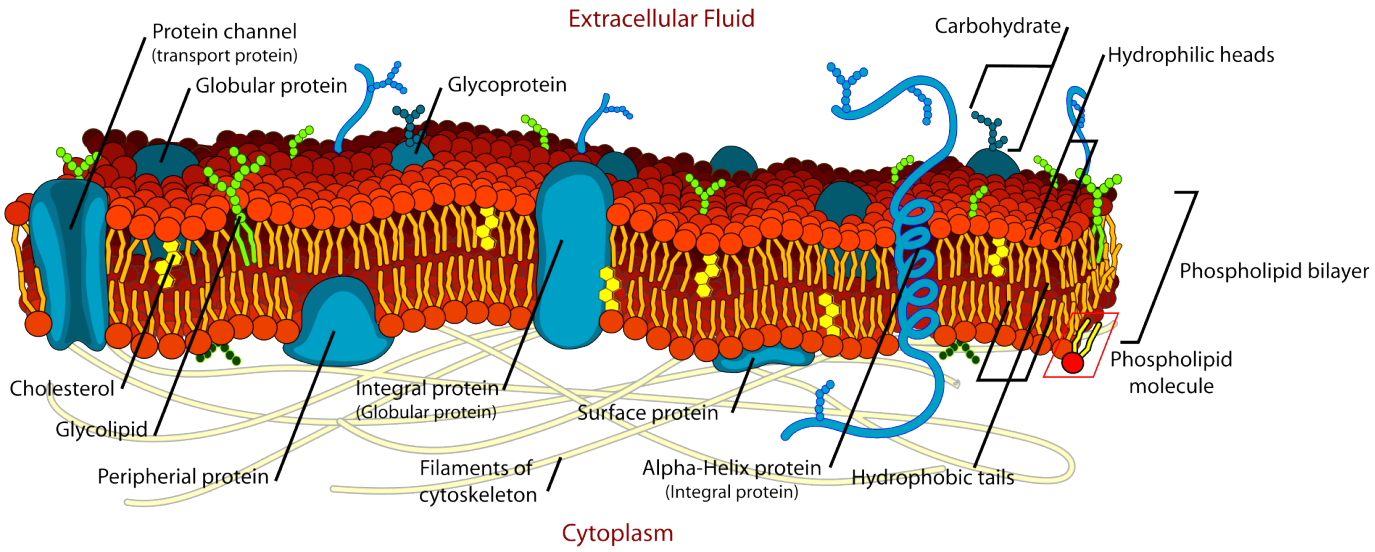


Figure 4 A model of a membrane, discussed in more detail in Chapter 3.

Membranes are essential for life, they regulate molecular movement and perform a variety of other functions. The physical nature of membranes is between a solid and a liquid; they can be described as “liquid crystals” because part of their nature is rigid and ordered while other parts are fluid-like (Figure 4, discussed also in Chapter 3). This duality of structure is important to their function; they need to be partly rigid because much of their functioning depends upon the organization of its parts; if these parts are out of place, functioning is disrupted. At the same time, membranes need to be able to change shape and membrane components do need to be able to move laterally; this is only possible because of membrane fluidity. Temperature disrupts the balance between fluidity and rigidity–high temperatures make membranes more fluid and low temperatures make them more rigid (crystalline). Shifts in either direction are damaging. Membrane characteristics of organisms found in habitats of different temperatures are different in predictable ways that relate to the maintenance of a certain degree of 'fluidity' . At higher temperatures, the lipids are more likely to contain longer chains of hydrocarbon and these chains are more likely to be more saturated. Both of these features make the membranes that they are found in more 'solid-like' at any particular temperature. Along the same lines, it has been found that some organisms that experience yearly variation in temperature adjust their membrane chemistry in a way that maintains a constant degree of fluidity in spite of changing temperatures. Thus, the range of temperature tolerance is partly determined by the chemical nature of an organism's membranes.

Coordinated chemical reactions and temperature

A second factor involved in both high and low-temperature disruptions of organism function is the balancing of the myriad chemical reactions that are taking place inside cells. The rate of nearly all chemical reactions is strongly influenced by temperature, with the rates going up as the temperature goes up. Most of these reactions are in some sort of a balance so that, in general, there is no build-up or depletion of metabolites. This balance can be upset at both high and low temperatures because the temperature sensitivity is not the same for all reactions–thus reactions that are 'in balance' at some temperatures may not be at higher or lower temperatures. The biochemistry of cells is such that control process (e.g., feedback loops) can operate to achieve balance in metabolic pathways, but there are limits to these control processes, and at least some of the problems with high and low temperatures may be attributed to problems with reactions becoming 'unbalanced' .

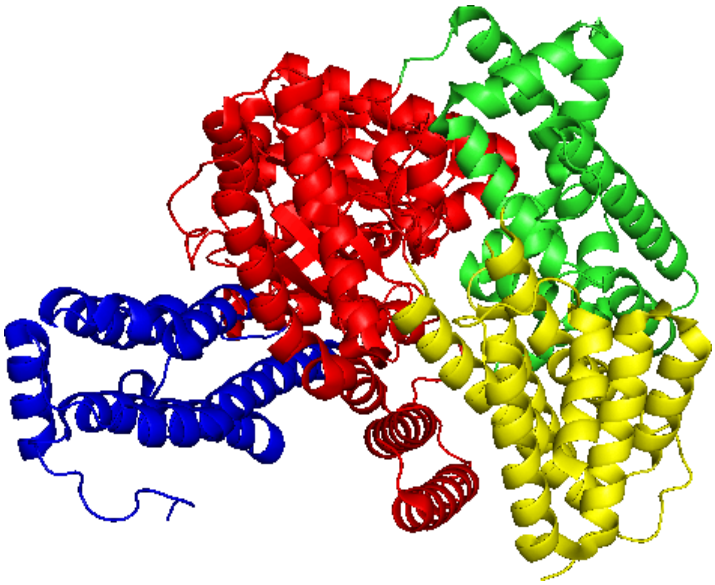


Figure 5 A model of enzyme structure. In order to perform its functions this three-dimensional structure needs to be maintained.

Enzymes and temperature

Enzyme functioning is dependent upon a three-dimensional structure. This structure can be disrupted, a process called denaturing, by high temperatures because the thermal motion is significant enough to break the relatively weak bonding that accounts for certain aspects of the enzyme structure. The temperature at which denaturing occurs varies with proteins but is in the range where temperatures become lethal to most organisms (25-40 C).

Problems with freezing

Not surprisingly, freezing causes a variety of problems for living things. The expansion associated with freezing can burst cells, destroying membranes and walls in the process. For plants and fungi, which have a substantial volume of their structure (the apoplast) that is outside of the membranes, freezing (especially if it occurs slowly) generally occurs first outside the cytosol, i.e., in the apoplast, because of its substantially lower solute concentration. The freezing outside causes the diffusion of water from the inside to the outside, resulting in desiccation damage on the inside. Because of these effects, a wide group of plants and fungi have their lower thermal limit at 0 C, or slightly below it.

In spite of this, plants and fungi do live in habitats where freezing occurs. For some, survival is the result of an overwintering part that is below-ground where temperatures are more moderate and never go below freezing. For others, e.g., trees and shrubs, the existence of perennial above-ground parts reflects an ability to withstand prolonged periods of sub-freezing temperatures. Tissues/cells may avoid freezing through two mechanisms, one involving freezing point depression and the other involving supercooling. Freezing point depression is one of the four 'colligative properties of solutions' — changes in the properties of a solution that occur with the addition of solutes, regardless of what solute is added. Although the presence of solutes in the cytosol does lower the freezing point, the effect is relatively small (up to -2 C, at the concentrations of solutes typically found in the cytosol), and protection against freezing by this mechanism is not significant for most organisms. Supercooling can result in much more substantial drops in the temperature at which freezing occurs. Supercooling describes a situation where liquid water exists at temperatures where it is usually frozen. Although supercooling can occur in pure, or nearly pure, water, especially if there are no sites for ice nucleation (e.g., under certain atmospheric conditions that cause supercooled raindrops), in living systems supercooling appears to be a consequence of specific antifreeze solutes, proteins or glycoproteins, that somehow prevent crystal formation. Such compounds are found not only in plants but also in fish and insects. The lower limit of supercooling is around -40 C (which is also -40 F!!!!), but for many species the limit of supercooling is well above this, in the range of -10 C.

An additional problem of freezing, significant to vascular plants, is that when water freezes dissolved air is excluding from the ice, creating bubbles of air in the ice. Upon thawing these bubbles remain. This is potentially a problem for xylem transport because the tensions that develop during xylem transport will cause expansion of the bubbles and cavitation (air locking) of vessels and tracheids, disrupting xylem water transport. This problem may be avoided by the production of new water-conducting cells in early spring, by pressurization of the xylem ('root pressure') that occurs in at least some species as a result of solute absorption in the

spring, or as a result of physical processes that can eliminate the bubbles.

Tolerances

All organisms have high and low thermal limits; if an organism reaches that temperature it dies. Chronic exposure to more moderate temperatures can also be lethal, in a manner connected to the length of exposure. Some plants will be killed by a short-term exposure at 38 C, while 36 C is lethal if exposure is longer than 60 minutes.

Extreme tolerances



Figure 6 Emerging from the inflorescence of wheat is a fungal sclerotium, a modified hyphal mass that is inactive and tolerant of extremes

The majority of organisms have high-temperature tolerances of around 40 C and low-temperature tolerances of 0 C but there are stages of many organisms that have a much wider range of tolerance. This tolerance is often associated with a stage in the organism 's life cycle that is devoted to dispersal, e.g., spores, seeds. These structures serve to perpetuate the organism through a time of unfavorable conditions. Along with tolerance to temperature extremes, there typically comes a tolerance to desiccation and to a number of' insults 'that would normally kill cells (e.g., ultraviolet radiation, extreme pH, lack of oxygen). This tolerance is a consequence of an altered cellular structure that simultaneously increases tolerance and decreases metabolic activity. In short, the structure of the cell(s) becomes more and more inanimate and less and less affected by extreme conditions. Usually this state of' suspended animation'involves several or all of the following: accumulation of materials such as starch or oils that serve as reserves of energy and reduced carbon, changes in membrane structure, changes in protein structure, changes in organelles (in eukaryotes), reduction in cytoplasmic volume, desiccation, and, for certain cells, a thickening of the cell wall (or sometimes the addition of a wall to a cell that previously lacked one).

Generally, these tolerant structures are single cells but in some organisms tissues or the entire organisms undergo comparable changes in structure and function. In the plant kingdom, such tolerant tissues are usually present in seeds and sometimes present in apical meristems. Such tolerance can occasionally be found in other structures and can also be found in entire plants, especially those found in freezing environments or deserts. The table below lists prokaryote, protist, fungal and plant structures that are particularly tolerant of extreme conditions. Although the table only tabulates low-temperature tolerances, it is important to realize that, in general, high-temperature tolerance, as well as desiccation tolerance, correlates with low-temperature tolerance. For example, most seeds readily tolerate prolonged exposure to frozen conditions; they also tolerate desiccation and exposure to high temperatures (e.g., 50 C) that would normally kill plants.

Table 1.

group	structure	notes
some bacteria	endospores	most are very resistant to high and low temperatures and survive for prolonged periods
most bacteria	microbial cyst (=exospore)	bacterial cells increase the thickness of the cell wall and contract the volume of the cytoplasm
cyanobacteria	akinete	an akinete is a specialized spore found only in some cyanobacteria
euglenoids	cyst	cyst formation is often triggered by changes in nutrient levels
dinoflagellates	cyst	cysts have no flagella and produce a cell wall with cellulose, features that are NOT normally present in dinoflagellates
diatoms	resting cells and spores	spores have thickened silica walls, resting cells do not; these structures may have requirements for germination. Spores of marine forms may be important components of the fossil record
zygomycetes	spores, zygospores	the zygospores that are associated with sex and are multinucleate have a much thicker cell wall and are more tolerant of abuse than normal cells
basidiomycetes	both asexual and sexual spores	in addition to spores, some forms produce sclerotia, desiccated and modified hyphae that are inactive and tolerant of extremes
ascomycetes	both asexual and sexual spores	(see above description for basidiomycetes)
mosses	whole plants, spores	the spores of most species are tolerant of a variety of treatments; in addition, the entire gametophyte plant of many mosses tolerates both freezing temperatures and desiccation

group	structure	notes
ferns and other seedless vascular plants	spores, rarely whole plants	unlike mosses and like most seed plants, ferns generally canNOT tolerate desiccation, although spores of ferns tolerate this and other extreme treatments. Only a few species have above-ground parts that overwinter in sub-freezing conditions.
conifers	pollen grains, seeds, whole plants	as a group, many conifers are more tolerant of freezing than most flowering plants, evidenced by the presence of conifers at high latitudes and elevations; however, spores are NOT especially tolerant; they generally only occur in hydrated tissues;
cycads	seeds only for most species	only a few can tolerate temperatures below freezing, most are restricted to warmer areas
gnetophytes	seeds only	only *Ephedra*tolerates freezing temperatures
ginkgo	pollen, seeds, above-ground parts	the tree is tolerant to the USDA's zone 3, which has temperatures down to -40
flowering plants	pollen, seeds, above-ground parts of some species	quite a number of flowering plants have adapted to temperatures well below freezing; there are also a number of species that can tolerate temperatures above 40 C

Temperature's Influences on Growth

Because temperature affects the rate of chemical reactions and because chemical reactions determine what an organism does, and in particular the **rate** at which things are done, the temperature has a profound effect on organism functioning. The combined effects of an organism 's chemical activity are termed metabolism and metabolic rates commonly double to triple with a 10 C (18 F) rise in temperature. While most students generally assume that the opportunity to' do more 'as a consequence of a higher metabolic rate is a desirable thing, this isn' t always the case. Higher metabolic rates require more food because an organism's metabolism runs on cellular respiration. To a certain extent, poikilotherms survive periods of low temperatures because it costs very little to maintain them under these conditions. Lower metabolic rates mean lower oxygen needs;consequently, many plants can survive low oxygen conditions (typically brought about by flooding) much more readily if temperatures are low.

Growth and growing degree days For any organism one of its most significant activities is growth, the acquisition of materials, and subsequent utilization of matter and energy to make the organism larger and ultimately coupled with the production of new organisms. The effect of temperature on growth is nicely seen in the concept of **growing degree days**, a statistic that integrates time and temperature and is used to predict the progress of a wide variety of crops during the season. While the details vary between crops, and even between different varieties of a specific crop, the basic idea is that you can predict the growth stage of a crop species by keeping track of the number of days that the crop has spent at different temperatures. For example, if the daily temperatures had a high of 86 F and a low of 70 F, corn might take 100 days to reach maturity (i.e., the time to harvest); if the temperatures were cooler, with a daily high of 80 F and the low of 60 F, it might take 140 days. Agronomists have developed

models to predict how long the crop will take to reach maturity based on the accumulation of something called a 'growing degree day' . Based on its temperature, each day is assigned a certain number of growing degree days (GDD's), with warm days earning more than cold ones. A typical formula that calculates growing degree days is the following:

$$GDD = [(Tmax + Tmin)/2] - 50$$

Given the days listed above, the warmer day is worth (86+70)/2–50 = 28 GDD, and the cooler day is worth (80+60) – 50 = 20 days. If corn needs 2800 GDD days to reach maturity it will do so in 2800/28 = 100 days at the warmer temperatures and 2800/20 = 140 days at the slightly cooler temperatures.

This is an example of an 'empirical model' , one that attempts to predict things based on observations but not necessarily based on an understanding of how a system operates. The fundamental basis for the model is the observation that crops grow faster when it is warmer. The model is successful in spite of the fact that it has a fairly crude approach to the relationship between growth and temperature. There are a number of features of the model that are useful to appreciate:

- a GDD represents a unit of growth and the basic idea is that plant development can be represented as an accumulation of these units of growth.
- a GDD also represents the product of time and temperature; although this is represented in its units ('degree-days'), it isn't obvious in the equation above because the time factor is always 1 day and is not included; the equation might be written:
  - GDD = [(Tmax + Tmin)/2 -50] degrees * [1.0] day
- the temperature term has two components, the first represents a type of average, a representation of a dynamic (changing with time) variable, in this case, temperature. This particular average (sum the extreme values and divide by 2) is convenient, as it is commonly used by meteorologists to reflect daily temperature. Although it is a crude type of average, based only on two values, it works well. The other temperature term (50 in the above equations) might be described as a 'base temperature' , the minimum temperature at which no growth occurs. Although the equation potentially predicts an impossible 'negative growth, ' if the average temperature is below the base temperature, this prediction is rarely the case because in most situations crops aren't planted until after average temperature daily temperature exceeds the base temperature.
- the GDD concept has been used successfully for a wide variety of crops and also with insects, generally with modifications of the 'base temperature' and/or changes in the average temperature term (e.g., letting the maximum temperature never exceed 86)

If one tried to devise a 'mechanistic model' , one that operates based on the mechanisms of growth, it would be much more challenging. Growth is a complex process that is a consequence of a variety of chemical reactions occurring simultaneously. Most of these are clearly affected by temperature but predicting the net effect of temperature on all of them would be particularly challenging. Certainly, the processes associated with growth are controlled by temperature, but the interrelationships associated with growth would be difficult to elucidate.

Variation in the temperature ranges for growth While the vast majority of fungi, plants and protists have an optimum temperature for growth in the range of 25-35 C, there are some exceptions. A number of plants have maximum rates of growth well below 35 C. Not surprisingly, these plants grow in cooler habitats. While there are a number of possible reasons for this, including the possibility that these organisms have membranes that function more appropriately at lower temperatures (see above), or the interaction between temperature and moisture (see below), another explanation involves the temperature sensitivity of photosynthesis and respiration. As mentioned above, respiration is closely tied to temperature and for most plants reaches a maximum in the 30-35 C range. The response of photosynthesis is different: it is generally less responsive to changes in temperature and, for C3 plants, it generally reaches a maximum at temperatures below 30 C, sometimes well below (Figure 7). The reason that photosynthesis is less responsive to temperature is partly due to the fact that some of the key chemistry is photochemical and photochemical reactions are not strongly dependent upon temperature. An additional factor is that carbon dioxide, a reagent in photosynthesis, must dissolve in water to make it to the site of photosynthesis (the chloroplast) and the solubility of carbon dioxide decreases as the temperature increases. Because of this, C4 plants, which have mechanisms to concentrate carbon dioxide, generally have higher temperatures for peak photosynthesis than C3 plants.

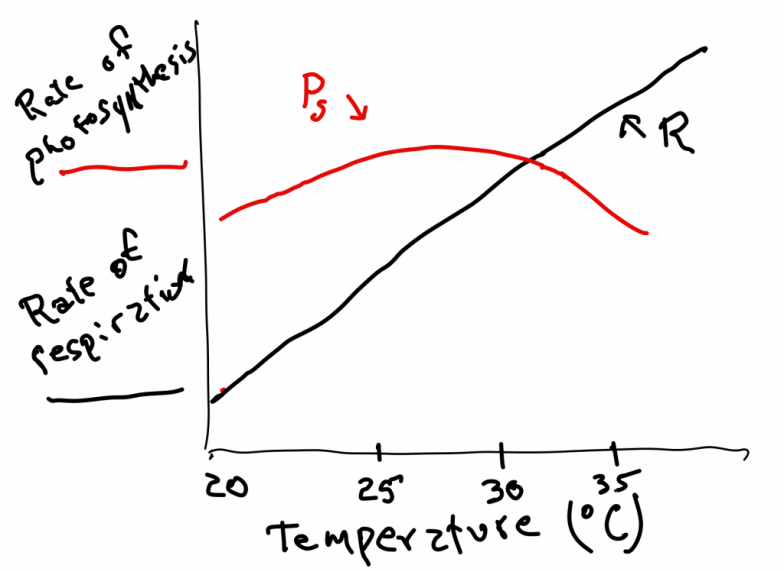


Figure 7 The influence of temperature on the photosynthetic and respiration rates of a typical C3 plant.

When considering the effects of temperature on photosynthesis, respiration and growth, one can consider photosynthesis as 'making food' and respiration as 'eating food' . As temperature increases in the 25-35°C range, plant appetite continues to increase rapidly while the rate of food production levels off or declines. The net effect of this is that at higher temperatures there is increasingly less food to power new growth. Consequently, plant growth often tails off at temperatures lower than one might expect.

Psychophiles, Cryophiles and Thermophiles



Figure 8 A dead bat with the characteristic 'white beard and mustache' caused by the hyphae of a psycophilic fungus.

A number of organisms, in particular certain bacteria but also some fungi and protists, are termed 'psychrophiles' or 'cryophiles' because they do best at low temperatures, sometimes at temperatures below freezing. While the basic pattern of increased activity with increased temperature holds, the range of activity is shifted to much lower temperatures: 0 to 10°C and sometimes -10 to 0°C. These organisms have modified membranes and, for the ones that operate below freezing, antifreeze compounds that allow them to operate at such low temperatures. Since a very common mechanism of food preservation is low/freezing temperatures, these organisms may pose problems for the food industry. A cryophilic fungus has turned out to be the culprit in the 'white-nose disease' of bats, a disease that has recently decimated populations of bats that overwinter in caves with temperatures in the 5-15°C range. The bat's behavior of lowering body temperature during the winter (in order to save energy) has provided these fungi with perfect conditions for growth.

At the other end of the tolerance range are thermophiles, who operate well above the normal activity range of 0-35°C. As with psychrophiles, the vast majority of thermophiles are prokaryotes, most often archaea, but there are some thermophilic eukaryotes, all of them fungi. Several of these thermophilic fungi are important components of large-scale composting operations important to the production of commercial mushrooms where the combined metabolic heat generation of the compost can elevate the temperature of the mulch to 80°C.

Fruit Ripening

One additional process affected by temperature will be mentioned because of its commercial significance: fruit ripening. In addition to the influence of temperature on the growth of fruits, the temperature continues to affect fruits after growth ceases, in the developmental process we describe as ripening. This process brings about important changes in characteristics (aroma, color, taste, texture) that are of significance to both consumers and producers. This developmental process is often controlled in various ways by temperature, and temperature can have a significant impact on the commercial value of a variety of fruit crops by influencing the appearance of both desirable and undesirable traits. In a more general sense, the temperature can influence the ecologically significant characteristics of fruits that affect their role in seed dispersal by influencing their attractiveness to frugivores.

Temperature as a Cue

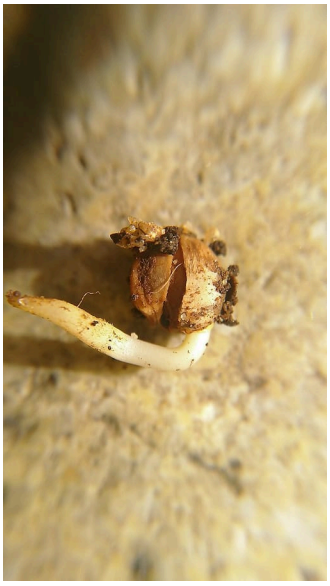


Figure 9 Germination of osage orange seed following cold temperature treatment

For many plants, and some fungi and protists, temperature provides an important cue that is used to coordinate growth and other activities with seasonal changes in conditions. Just as gravity organizes plant activity in space, the temperature can coordinate plant activity in time. In this situation, the temperature is not just a condition that the organism responds to, it is a signal that conveys information about what conditions will be like in the future, similar to the way that day length (photoperiod)can provide information about the coming seasons. However, since the noise in the temperature signal is substantial, using it to predict future conditions is more complicated: a return to warm conditions after cold ones could be a January thaw or it could be a real (spring) thing. For many plants, spring is sensed as a warm period after a measured period of cold. An example of this is seen in the germination patterns of many seeds. The seeds of most plants are shedin a dormant condition. Although some seeds don 't have specific germination requirements, they simply need a few weeks and they are able to germinate (this has been selected for in many crop species), many seeds require specific conditions or a series of specific conditions in order to germinate. Especially in temperate habitats, it is often a cold temperature treatment that will' break 'dormancy, i.e., allow the plant in the seed to resume growth (Figure 9). This pattern is beneficial because it would prevent seeds from germinating and thereby becoming susceptible to cold until after the harsh conditions of winter. Because the original horticultural practices developed to break seed dormancy involved layering seeds and keeping them moist and cool, such treatment is termed' stratification '. The key part of the treatment is the temperature treatment, not the layering. Contrary to the normal metabolic pattern, where activity is promoted by warmer temperatures (i.e., warmer temperatures produce more response than lower ones), in the stratification response activity is promoted by lower temperatures, with colder temperatures having greater effects than higher ones.Typically temperatures need to be below 50°F (10°C) to be effective and become more effective as the temperature decreases down to 0°C. Temperatures below

0°C, and temperature treatments when the seed is dried out, are not effective, indicating that metabolic activity is essential for the response. The process can be modeled in a manner similar to growing degree days, except in this case what is accumulated, termed' **chill units** ', requires temperatures below a certain threshold (typically 10°C), and more chill units are accumulated as the temperature decreases down to 0°C. When a seed accumulates enough chill units its dormancy is broken; at this point, the embryo' s behavior is typical of most organisms, and activity (growth) is promoted by warmer temperatures.

Besides breaking the dormancy of the embryos in seeds, cold treatments are also a very important cue in breaking the dormancy of shoot apical meristems (buds). Home gardeners often bring shoots of flowering trees and shrubs (e.g., apple) indoors to 'force' them to flower early (Figure 10). This practice works as long as the shoot has been exposed to cooler temperatures for a long enough length of time prior to warming it up. Shoots often will not force in December but will in February. The exact amount of 'chill time' that a shoot needs before it will respond to warmer temperatures varies. This phenomenon is sometimes the reason why certain trees may not be able to be grown in southern latitudes:they never receive enough cool temperatures to cause them to emerge from dormancy.



Figure 10 A stem from an apple tree that typically becomes active (breaks bud, starts growing, and flowers) in April can be induced to flower if stems collected in February are put in a warm environment. But twigs collected in January will not flower because they have not accumulated enough chill units.

Accumulation of chill units is also a cue for some plants to flower, a process termed '**vernalization.**' In some situations the cold treatment itself is the trigger for flowering; in other situations, the cold treatment simply flips a switch and allows the plant to flower in response to a second signal (e.g., photoperiod) that previously would not elicit any response.

Temperature's effect on other conditions

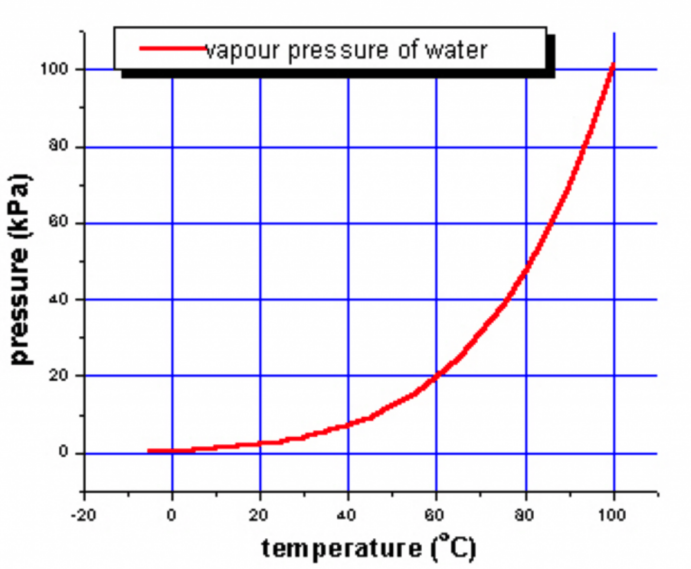


Figure 11 The effect of temperature on the vapor pressure of water, its tendency to evaporate.

Temperature is also important because it interacts with a number of other conditions. In terrestrial habitats, probably the most significant interaction is between temperature and moisture. Temperature affects evaporation, and occasionally condensation, rates. Evaporation occurs when an individual water molecule is moving fast enough to escape the cohesive forces of its neighbors. Since the velocity of molecules is a function of temperature, the warmer it is, the more likely evaporation is to occur. The tendency of a substance to evaporate is reflected in a property called vapor pressure, which measures the amount of the substance (in this case water) present in the vapor state when the liquid and air are in equilibrium. Figure 11 shows the very strong effect temperature has on vapor pressure. Under certain circumstances, evaporation will be directly related to vapor pressure and consequently would roughly double with each 10°C rise in temperature. In environments where lost water is difficult to replace, temperature can be of great significance to desiccation rates and the survival of organisms. For plants and fungi, the combined factors of temperature and water availability are of utmost importance in determining species abundance and activity. Note that although the temperature has a major influence on evaporation through its effect on vapor pressure, other factors are also important including the humidity of the air, the surface area of contact between the air and the water, and the degree of mixing (convection) of the air above the hydrated surface. Finally, although temperature affects evaporation, evaporation, in turn, affects temperature. In the case of plant leaves, evaporation can cause leaves to be significantly (over 2° C) cooler than the air temperature.

Temperature also affects the availability of certain compounds by affecting their solubility in water. While the solubility of many solids in water increases with higher temperatures, the opposite is true for gases, and in particular for carbon dioxide and oxygen. This is particularly significant for photosynthesis and, as described above, is part of the reason why the response of photosynthesis with increasing temperature is not comparable to that for respiration even though both involve a host of enzyme-mediated chemical reactions that generally are enhanced at higher temperatures.

Another situation where the decreased solubility of gases at high temperatures can be a problem is flooded soils. The effect of flooding is more damaging at high temperatures than at low ones. A variety of factors contribute to this: (1) decreased solubility of oxygen at higher temperatures, (2) increased rates of soil respiration at higher temperatures as carried out by the sum of organisms present in the soil (plant roots, fungi, bacteria, protozoans, etc.); increased respiration means decreased oxygen (3) increased oxygen requirements for plant roots because of the higher metabolic rates associated with higher temperatures.

Water and Terrestrial Habitats

Along with temperature, moisture is a key environmental variable dictating the distribution of organisms on terrestrial habitats. The reasons for this should be clear:

- water is an essential component of living tissues and a reagent in many essential reactions, including photosynthesis and ATP hydrolysis

- in terrestrial habitats, water is nearly always lost to the atmosphere in the process of evaporation
- for terrestrial autotrophs, who obtain carbon dioxide from the atmosphere, evaporation is all the more likely to occur since organisms must expose themselves to the atmosphere to acquire carbon
- for plants and animals, water is the medium in whichmaterials move when transportedand for animals, water is the basis for excretion

Tolerance to drying

The vast majority of organisms maintain their moisture conditions at a particular level through the familiar process of homeostasis. Most plants (and most organisms in general) would be considered **homiohydric**, i.e., they maintain their water levels at a 'set point' . To do this requires that an organism adjust either water gain or water loss. To a limited extent, plants adjust water gain: when they get drier, the driving force for water absorption is increased and this can result inan increased flux (remember the flux equation!). However, plants have only a fairly limited ability to 'get drier, ' and when they start to desiccate their most significant adjustments involve reducing water loss rather than increasing water gain. When plants experience water deficits their response is to reduce water loss by: (1) reducing the permeability of the plant to water by closing stomates, and (2) reducing the surface area for loss, generally by shedding leaves. Again, remember the flux equation and how these changes relate to it. Leaf loss is especially obvious in seasonally dry habitats where woody species lose all their leaves and herbaceous species spend the dry season as bulbs or other underground parts, both groups producing and possessing leaves only when conditions are more mesic.

These measures to reduce water loss come at the price of reducing a plant 's ability to feed itself. The very significant effect that moisture has on plant distributions reflects the fact that individual, population and species success involves balancing water loss and carbon gain. In some situations, a species may be successful by being able to acquire' its own'water source. Alfalfa and mesquite roots often penetrate deep enough to tap groundwater sources unavailable to other plants. However, a majority of plants in an area sharea common water source, the soil, i.e., the roots of many species are occupying the same volume of soil as other species, makingthe supply of water uniform for mostspecies living in an area. Consequently, conservation by one species or individual only leaveswaterthat can be taken by otherspecies. Species are successful by managing theiroverall growthand patterns of growth. This represents an area of diversification between different species.

Homeohydric organisms are intolerant of desiccation and die if their water status drops below a certain level ; most plants cannot recover from a loss of 10-15% of their water. Probably the main reason for this in vascular plants is 'catastrophic xylem dysfunction' which is a consequence of cavitation and positive feedback loops related to cavitation. Recall that individual vessels and tracheids may cavitate if the water in them is pulled too forcefully, the result of water loss at a time when there is a restriction of water acquisition as the soil dries. Cavitation results in a loss in a part of the xylem conducting system and this makes cavitation more likely in the remaining conducting elements (see the flux equation); increased resistance to flow as a result of cavitation means that there has to be a greater pull (higher tensions) in order to acquire the same amount of water. Thus there is a positive feedback loop: cavitation makes more cavitation likely which will make more cavitation likely. Catastrophic xylem dysfunction (no ability to transport water) may result quickly after the first cavitation event, leaving the plant with no ability to rehydrate itself.

There are a small number of organisms including a very few animals (tardigrades), some protists , and a few plants, that are poikilohydric: their water status is not strongly regulated but is allowed to assume the level dictated by the environment that they are in. Obviously, these organisms can only be successful (assuming that they live in an environment that dries out at least some of the time) if they are tolerant of desiccation, a phenomenon that is very rare in organisms, although they may produce parts like spores and seeds that are tolerant. Poikilohydric organisms can lose up to 90% of their water yet are still able to revive themselves when water again becomes available. The only plant group where desiccation tolerance is common is in non-vascular plants, many mosses and some liverworts, (ironically groups that are often considered to be restricted to moist environments); it is also present a few ferns and clubmosses and in a very few seed plants.



Figure 12 A dehydrated 'resurrection plant' , a type of clubmoss the rolls up into a ball when tolerating extreme drought.



Figure 13 The desert clubmoss after greening up and opening up..

While there are some mosses that are restricted to moist habitats, most are desiccation-tolerant and many are particularly prominent in arid situations, both arid habitats (deserts) and arid portions of more mesic habitats, e.g., growing on rocks that have no ability to store water. Some of these species do have features to lessen water loss, e.g., a drying response that involvescoiling of 'leaves' around the stem, lessening the surface area exposed to the atmosphere. Nonetheless, many mosses are capable of tolerating extreme desiccation and the whole organism, not just a select part, and can remain viable after undergoing repeated cycles of desiccation. They are inactive during dry periods but are able to quickly resume activity when moistened.



Figure 14 A desiccation tolerant fern shown in dry conditions



Figure 15 The same location as figure 14 but now under moist conditions.

Tolerance of flooding

At the other extreme, terrestrial organisms can be affected by excesses of water. Generally this is an indirect effect of a lack of oxygen was discussed above when considering the interactions between temperature and oxygen.

Water and Aquatic Environments

Salinity

One might assume that there are no problems associated with water in an aquatic environment since water is abundant. However, water does play an important role in dictating the organisms present in any particular aquatic environment, primarily because of the process of diffusion. Because water tends to diffuse from regions where it is purer to regions where it is less pure, living things are strongly affected by the purity of the water that they live in and this is primarily determined by the water 'ssalinity. All life has the ability to both accumulate and to generate solutes, and therefore the water in organisms is decidedly impure.Consequently, if organisms are placed in pure water, water diffuses into them. The influx of water has two potential results: one is chemical, the

cell solutes become so dilute that normal functioning is impeded; the second is mechanical, the influx of water can cause the organism to swell and ultimately burst. However, if the organism is enclosed in a rigid container the influx of water pressurizes the organism and the flowof water ceases with only modest changes in volume. Another possibility that allows organisms to live in' fresh'(i.e., pure) water is to have mechanisms that allow water to be expelled from the organism at the same rate that it enters.

The problems associated with the diffusion of water into organisms are eliminated if the purity of water is the same outside as it is inside the organism, and there are a number of organisms (many marine animals, some protists) that require such an environment where the purity of the cytosol is comparable to that of seawater.

There also are habitats, termed saline ('salty' , although the salt need not be NaCl) that have a water purity even less than that of most organisms. Most forms of life are excluded from such saline environments because diffusion causes them to lose water and they cannot tolerate the decrease in the internal water content that results from water loss. The organisms that are able to tolerate such environments do so by having more than the normal concentration of solutes in their cytosol, generally adding unique solutes that are typically not found in living things.

The problems of life in saline environments are not restricted to reduced water content. Additional problems stem from toxic concentrations of the solutes that make the habitat saline. Generally, this would be sodium and chloride ions but there are habitats where other solutes (e.g., potassium, calcium)are damaging. With the exception of sodium, which most plants don't require, these elements are essential for living things, but at high concentrations, they can interfere with normal cellular or organismal functioning and become toxic.

Oxygen and Aquatic Environments

Oxygen is of key importance in aquatic environments. Oxygen readily dissolves in water but its solubility is such that oxygen is generally less available than in terrestrial habitats. More significantly, its abundance varies much more in aquatic habitats than in terrestrial ones. When considering terrestrial environments, because of convectional mixing (winds) due to themuch lowerdensity of aircompared to water, and, to a lesser extent, because ofthe much more rapid rate of diffusion in gases, the oxygen levels of the air rarely change much. Processes (primarily biotic ones) may increase or decrease oxygen levels but rapid mixing with the huge reservoir of oxygen in the atmosphere as a whole, which is slightly less than 20% oxygen, rapidly returns the air in these areas to atmospheric values.

In contrast, liquid water is much denser, its movement is much more sluggish and consequently, the possibility of localized areas with oxygen concentrations substantially altered from that of the habitat as a whole is much more likely. Under certain situations aquatic habitats will be saturated with oxygen, i.e., holding all the oxygen that can dissolve in water, an amount that is temperature-dependent and decreaseswith increasing temperature. As would be expected, water is saturated with oxygen when the air and water are in close contact (i.e., the surface of bodies of water) or in situations where photosynthetic rates are high, thus increasing oxygen levels (generally theseareas are also close to the surface). However, there are lots of aquatic situations where the amount of dissolved oxygen is not at saturation. Generally, this is due to the depletion of oxygen by living things and the lack of mixing with water that is in contact with the air, a situation found at the bottom of lakes, in slow-moving streams, and waterlogged soils. Impediments to mixing will make oxygen depletion more likely. Two of the most common impediments are density gradients and solid materials. Sphagnum bogs usually have oxygen-depleted water at very shallow depths, depths where oxygen levels are usually much higher. This is the result of the fact that the sphagnum mat hinders the movement of the water column. Although the oxygen-rich atmosphere is centimeters away, oxygen levels drop to nearly zero. A similar thing can happen in ponds that are covered with a thick 'pond scum' of algae. Anothersignificant hindrance to water movement is density gradients set up by temperature. Less dense water 'floats' on more dense water and this will reduce oxygen transfer from the atmosphere to the denser water. The density of water decreases as the temperature increases from 4 C; hence, in this range, warmer water is less dense than cooler water. A consequence of this is that the water is layered ('stratified') during the times of the year that it is being heated from above, during the summer in northern latitudes, all year round in the tropics. The wind may cause turbulence in the water column but the penetration of this turbulence is limited by the density differences. The greater the temperature differences between the top and bottom, the more resistant the lake is to mixing. Because of this stratification, the bottom layers of a lake may become depleted of oxygen because they do not mix with the oxygenated water atthe surface. In tropical areas, low oxygen levels at the bottom of lakes occur year-round, but in temperate areas, mixing, and as a result aeration of the bottom layers, becomes increasingly likely during the fall. This is because, unlike the heating of the summer, which reinforces the stratification by making the top warmer, cooling breaks down the stratification by making the surface denser. As long as the lake is in a location that cools enough, the lake will eventually become 'isothermal' , i.e., the same temperature throughout the water column. Being isothermal also makes the lake the same density from top to bottom and, as long as the wind blows hard enough (how hard depends on the depth of the lake), the lake will 'mix' , bringing aerated water from the bottom to the top. This is significant from a nutritional standpoint because organic material settles to the bottom of the lake and decomposes there. Minerals released by

decomposition are only distributed throughout the water column when the lake is mixed. Further cooling of the lake once again results in stratification, as the density of water decreases(and the colder water floats on top)as the temperature drops from 4 to 0 C. If the lake freezes, the addition of an ice layer eliminates any wind-driven mixing whatsoever and oxygen levels at the bottom of the lake once again drop if respiration exceeds photosynthesis.Thisis usually the case(although some photosynthesis does take place in ice-covered lakes, it is relatively low because of decreased light penetration). In the spring (in the northern hemisphere) heating of the surface first eliminates the ice and then eliminates the stratification, making the lake uniform in temperature and density at 4 C, and again allowing for mixing by the wind. Further heating causes the lake to again becomestratified. Thus lakes in temperate habitats have an annual cycle that includes two brief periods in the fall and spring where mixing is very likely, so long as the wind blows and the lake is not too deep. This situation, termed spring and fall 'turnover' , is highly significant because it allows for mixing of the water column, bringing oxygenated water to the bottom of the lake (and also bringing minerals to the top of the lake (see below)).

Light and Aquatic Environments

As is the case in terrestrial environments, light plays an important role in dictating the distribution of photosynthetic organisms and it is even more important in aquatic environments because significant differences in oxygen concentrations can develop within the water column, depending upon the balance between photosynthesis and respiration. Light intensity is influenced by the depth and transparency of the water, the latter often being strongly influenced by the number of living things living in the water. Since aquatic photoautotrophs need light to survive, they need to be in the upper levels of the water, or, in the case of some flowering plants, float on the surface or even emerge from it. Phytoplankton (small photosynthetic organisms that 'float' in the water column) need to have features that prevent their settling. Features that are sometimes significant are large surface area to volume ratios (i.e., not spheres), oil or air bodies that decrease density, flagella and phototaxis (movement towards light (see cryptophytes). Some phytoplankton are known to migrate up and down diurnally, moving up to gain more light during the daylight hours.

Currents and Aquatic Environments

Currents are very significant in some aquatic environments and can have a strong influence on community structure. Currents are significant because they can mix portions of the water column, in particular, they can bring oxygen from the upper layers to the lower layers and nutrients from the lower layers to the upper layers. This is significant because oxygen may be limiting in the lower layers and nutrients may be limiting in the upper layers. Consequently, the current can substantially change the activities taking place.

Nutrients and Aquatic Environments

Nutrients are often limiting primary productivity and consequently total activity in aquatic situations. This is a result of the fact that most aquatic environments have two distinct parts: the upper layers where photosynthesis occurs and where inorganic nutrients are incorporated into biomass, and the bottom region, where there is typically little photosynthesis, but where biomass from the upper layers tends to settle, decomposition occurs , and nutrients are released. In such a system the activities of both the top and bottom can be limited by a lack of interaction between the two parts: the upper layers are limited by a lack of nutrients, hence little accumulation of biomolecules occurs; the bottom layer becomes limited by a lack of material to eat.

Nutrients transported into aquatic systems can be very important. Nutrients can be carried into aquatic systems by runoff from the surrounding land, especially agricultural land where nutrients are added through fertilization. Nitrogen and phosphorus often play key roles in determining the amount of primary production occurring and the total amount of biological activity taking place. However, as was the case in terrestrial systems , there are circumstances where other nutrients can play key roles.

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20.5: Soil Properties and Their Interrelationships

Healthy soils occur when their biological, chemical and physical conditions are all optimal (Figure 8.1), enabling high yields of crops and other important soil functions. When this occurs, roots are able to proliferate easily; plentiful water enters and is stored in the soil; the plant has a sufficient nutrient supply; there are no harmful chemicals in the soil; and beneficial organisms are very active and able to keep potentially harmful ones in check as well as stimulate plant growth.



Figure 8.1. Optimal chemical, biological and physical properties promote healthy soils.

A soil's various properties are frequently related to one another, and the interrelationships should be kept in mind. For example, when a soil is compacted, there is a loss of the large pore spaces, making it difficult or impossible for some of the larger soil organisms to move or even survive. (You often don't find earthworms in compacted soils.) In addition, compaction may make the soil waterlogged, causing chemical changes such as when nitrate (NO_3^-) is denitrified and lost to the atmosphere as nitrogen gas (N_2) and the greenhouse gas N_2O. When soils contain a lot of sodium, common in arid and semiarid climates, aggregates may break apart and cause the soils to have few pore spaces for air exchange as well as water drainage into the subsoil. Plants will grow poorly in a soil that has low organic matter content and degraded structure even if it contains an optimum amount of nutrients. Therefore, to prevent problems and develop soil habitat that is optimal for plants, we can't just focus on one aspect of soil but must approach crop and soil management from a holistic point of view.

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20.6: Ecological Crop and Soil Management

We'll discuss ecological crop and soil management practices as part of a general framework (Figure 8.2). The heart of the matter is that the strength of the system is enhanced by creating improved habitat both aboveground and in the soil. Although it is somewhat artificial to talk separately about aboveground and the soil habitat—many practices help both at the same time—it makes many issues clearer. Not all of the aboveground discussion refers directly to management of soil, but most does. In addition, the practices we'll discuss contribute to one or more of the overall strategies: 1) growing healthy plants with strong defense capabilities in healthy soils, 2) suppressing pests, and 3) enhancing beneficial organisms.

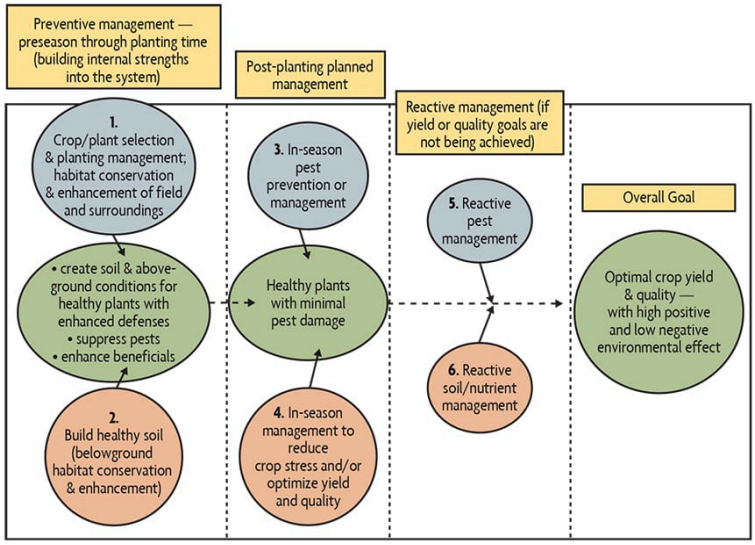


Figure 8.2. A whole-system approach to soil and crop management at the field level. Modified from Magdoff (2007).

Aboveground Habitat Management

There are numerous ways that the aboveground habitat can be improved:

- Select crops and varieties that are resistant to local pests (in addition to having other qualities such as yield, taste, etc.).
- Use appropriate planting densities (and companion crops) to help crops grow vigorously, smother weeds and (with companion crops) provide some protection against pests. In some cases, use blends of two or more varieties (cultivars) of the same crop. For example, combining one variety that is susceptible to a pest or drought but has a higher yield potential with one that's resistant and resilient has shown potential for increasing total yields for wheat and rice. Even though the farmer is growing the same crop, increased genetic diversity due to using different varieties seems to provide some protection. Perhaps there are possibilities for intercropping with rows of different crop types such as sunflowers with soybeans or peas.
- Plant perimeter (trap) crops that are more attractive to a particular pest than the economic crop(s) growing in the middle of the field and so can intercept incoming insects. This has been successfully practiced by planting Blue Hubbard squash on the perimeter of summer squash fields to intercept the striped cucumber beetle. The push-pull system practiced in East Africa goes a step further by planting the low-growing legume *Desmodium* within corn rows as a repellent plant for stem borers (push), and grasses along the field perimeter to attract the adult insect moths (pull), while also providing nitrogen and suppressing weeds.
- Create field boundaries and zones within fields that are attractive to beneficial insects. This usually involves planting a mix of flowering plants around or as strips inside fields to provide shelter and food for beneficials.
- Use cover crops routinely for multiple benefits, such as providing habitat for beneficial insects, adding nitrogen and organic matter to the soil, reducing erosion and enhancing water infiltration into the soil, retaining nutrients in the soil, and much more. It is possible to supply all of the nitrogen to succeeding crops by growing a vigorous winter legume cover crop, such as crimson clover in the southern United States and hairy vetch in the north.
- Use rotations that are complex, involve plants of different families and, if at all possible, include sod crops such as grass/clover hay that remain without soil disturbance for a number of years.

- Reduce tillage. This is an important part of an ecological approach to agriculture. Tillage buries residues, leaving the soil bare and more susceptible to the erosive effects of rainfall, while also breaking up natural soil aggregates. (The use of practices that reduce erosion is critical to sustaining soil productivity.) Some of these practices, such as the use of cover crops and more complex rotations, and reducing tillage, will also be mentioned below under “Enhancing Soil Habitat” and discussed in detail in later chapters.

Belowground Habitat Management

The general practices for improving the soil as a place for crop roots and beneficial organisms are the same for all fields and are the focus of our discussions in the next chapters. The real questions: which ones are best implemented, and how are they implemented in a specific situation (farm or other)? The approaches and practices are discussed in detail in Part 3 of this book, but Table 8.1 summarizes these management approaches and refers the reader to the appropriate chapters. In the final chapter (24) we discuss how all these considerations can be put together into an integrated soil health management approach.

Ch 12 Table 8.1 Management Goals, Approaches and Practices of Soil Health

OVERALL GOALS **grow healthy plants, suppress pests, enhance beneficial organisms, all while improving the surrounding environment**	
Management Approaches and Practices	**Where Discussed**
Minimize soil disturbance and reduce compaction using reduced tillage, better rotations, controlled field traffic, staying off wet soils, compaction remediation, etc.	**Chapters 11** (rotations), **14** (reducing runoff and erosion), **15** (addressing compaction), **16** (reducing tillage), **22** (urban soils)
Keep soil covered with crop residue, rotations with perennial forages, and by growing cover crops, which also helps to maintain continual presence of living roots in soil.	**Chapters 10** (cover crops), **11** (rotations), **16** (reducing tillage)
Maximize biodiversity in soil and aboveground through more complex rotations, frequent cover crops, integrated livestock and crop farming, and applying different types of organic matter amendments such as animal manures and composts.	**Chapters 10** (cover crops), **11** (rotations), **12** (livestock-crop integration), **13** (making and using composts)
Manage water to promote timely fieldwork and crop needs.	**Chapters 14** (reducing runoff and erosion), **15** (preventing and lessening compaction), **17** (irrigation and drainage)
Maintain pH within desired range and nutrients at levels that supply plants with sufficient amounts but without excess loss to the environment by routinely testing soils and applying nutrients, lime and other amendments based on results, frequently using cover crops, addressing salt problems, and integrating livestock and crop farming.	**Chapters 18** (nutrient management), **19** (managing nitrogen and phosphorus), **20** (nutrients, CEC, alkalinity, and acidity), **21** (soil tests and their interpretation), **23** (use soil health testing)

A Difficult Pest: Symphylans

Throughout this publication we emphasize the importance to soil health of organic matter and biodiversity, as well as of developing and maintaining good soil structure. However, there is a soilborne arthropod that thrives in soils with good organic matter content and that can cause major damage to a wide variety of crops. *Symphylans*, which are white and look like a centipede, feed mainly on root hairs and rootlets. They can move around easily with favorable soil structure, lots of old root channels and connecting pores. They occur usually with a spotty, circular distribution within certain parts of fields, and are more of a problem in certain geographic locations. Potatoes and beans appear to be less damaged by the pest, and it has been found that transplanted tomatoes do better than direct seeded ones when symphylans are present. While it is not established that other cover crops help reduce infestations, a spring oat cover crop may lessen damage to a subsequent crop. Increasing the planting density of squash has been shown to help maintain yields in the presence of the pest, though some thinning may be needed. Although some synthetic chemical controls are available, a lot more needs to be learned about how to manage this pest in ecologically sound ways. Care is essential when importing organic amendments: You do not want to introduce this pest by accident. And although there are organisms such as beetles, predatory mites and centipedes as well as fungal pathogens that feed on symphylans, a biologically active soil is not thought to be an adequate defense against this crop-damaging organism.

Conflicting Disease Management Advice?

In this book we promote reduced tillage and retention of crop residues at the soil surface. But farmers are often encouraged to incorporate crop residues because they can harbor disease organisms. Why the conflicting advice? The major difference is in the overall approach to soil and crop management. In a system that involves good rotations, conservation tillage, cover crops, other organic matter additions, etc., the disease pressure is reduced as soil biological diversity is increased, beneficial organisms are encouraged and crop stresses are reduced. In a more traditional system, the susceptibility dynamics are different, and a pathogen is more likely to become dominant, necessitating a reactive approach. A long-term strategy of building soil and plant health should reduce the need to use short-term cures.

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20.7: Threats to agriculture- insects and pathogens

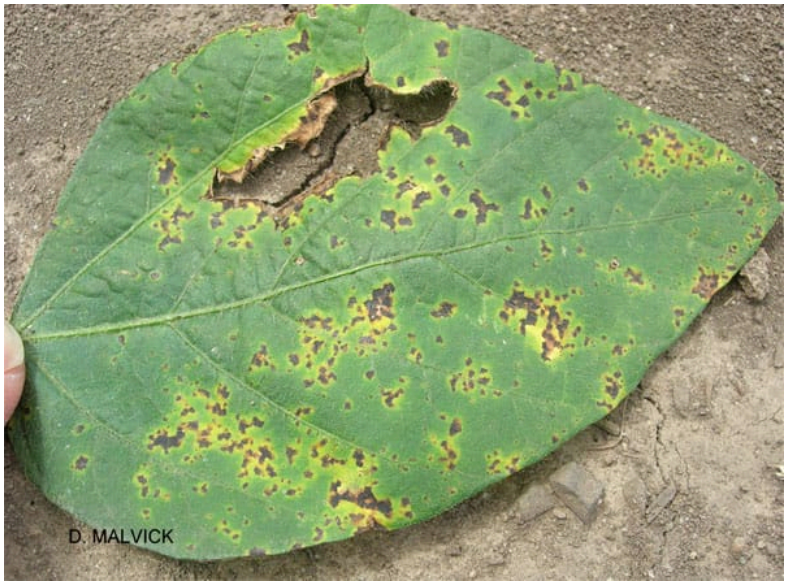


Figure 1 Bacterial blight on soybean leaf

As any farmer will tell you there are many threats to growing plants. Some of these have been covered in earlier chapters: extremes in temperature and moisture (Chapter 26); and interactions with other plants, i.e. weeds (Chapter 29). A large number of additional threats come from trophic interactions with a vast diversity of grazers, parasites and and predators. Certainly the most familiar of these are insects but other invertebrates (mites, nematodes, mollusks) and vertebrates can be significant obstacles to growing plants. Moreover, a large number of fungi, bacteria (Figure 1) , protists and viruses are also be important threats.

TOPICS

- Grazing herbivores
- Absorbing herbivores
- Plant defenses
- Boundary
- Chemicals
- Phenology
- A sampling of plant disease
- Phytoplasmas and defining disease
- Late blight of potato—the disease triangle
- Wheat rust disease—complex pathogen life cycles
- Corn smut disease—Mexican truffles
- Dutch elm disease —overreaction can kill you
- Rice blast disease—changing strategies
- Fire blight of apple—bacterial phytopathogens
- Crown gall disease—making a disease a tool
- Viral diseases—tobacco mosiac virus, cauliflower mosaic virus, ring spot disease of papaya

Grazing herbivores

Most animal herbivores, e.g. woodchucks and adult japanese beetles, are considered grazers, eating parts of the plant and using their mobility to get to other plants. However, a substantial number of insect herbivores have feeding stages (generally larvae, e.g. leaf min e rs, emerald ash borers , larval potato beetles) that are immobile to the extent of getting to new host plants. These might better be considered parasites because they feed solely on one host plant. Most non-animal herbivores (fungi, bacteria) are basically immobile and are considered parasites although some are capable of grow ing from one host to another and many are transported from one plant to another by wind, rain and insects.



Figure 2 Japanese beetles on peach leaves, an example of a grazing insect pest.

Most grazers on plants are ingesters (see Chapter 27), they remove and consume part of the plant, shred it to some extent and then digest the pieces in an internal tube, and ultimately excrete undigestible to their environment. Grazers, although they can severely reduce crop yields, rarely completely kill the plant it is eating both because they tend to specialize on only part of the plant (most commonly leaves) and because the plant is capable of replacing the organs/parts of organs that have been lost.

The plant material acquired by grazers is generally not very nutrient dense but varies substantially depending upon the part of the plant eaten. Nutritional quality is largely influenced by how many living cells are present (dead cells are basically all cell walls and are indigestible for most herbivores). Most herbivores specialize on one of the tissues listed below, but there are few generalists that feed on multiple tissues, e.g. browsers like moose and deer often eat stems, leaves and meristems.

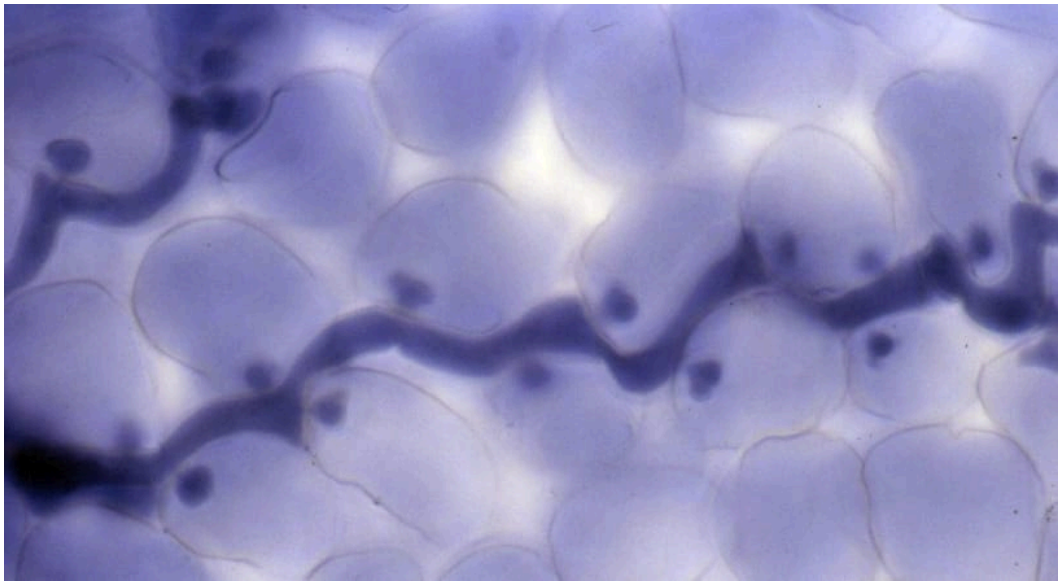
- primary growth of stems and roots — although stems and roots in primary growth have more living cells than those with secondary growth, they still are nutrient poor. Most of those cells that are living are not very metabolically active and consequently they are poorer in nutrients when compared to cells that are more metabolically active (e.g. leaf mesophyll cells).
- woody stems and roots, heartwood: Heartwood has no living cells and has increased levels of secondary chemicals. It generally has the lowest nutritional quality of any plant tissue, but there are heartwood specialists
- woody stems and roots, sap wood: Sapwood has some living cells (the rays) and these may be 'loaded' with starch and other nutrients, depending on the season. Hence sapwood is considerable more nutritious than heartwood but still is largely composed of cell wall material.
- woody stems and roots, vascular cambium — this meristematic tissue is nutrient rich and has relatively less cell wall material compared to mature cells. Moreover, it is more extensive that apical meristems, i.e. there is more material available to eat.
- the bark tissue of woody stems is nutrient poor with few living cells and an abundance of secondary chemicals. The portion of cells that are living decreases as the stem/root ages and hence bark of younger stems is more nutritious than the bark of older stems
- stems and roots that have been modified as storage structures — rhizomes, corms, bulbs, stolons. They are composed of living cells that are storing carbohydrates, usually in the form of starch. They are rich in digestible carbohydrates but may be deficient in amino acids (proteins) and other nutrients
- phloem feeders: These organisms (including aphids, leaf hoppers, mealy bugs and white flies , all significant agriculture pests) are not consuming any cells, but instead tap into the phloem transport system and acquire the materials that are being transported through it. Phloem sap has very high concentrations of sucrose along with much smaller concentrations of amino acids and some minerals. Because the ratio of carbohydrates to amino acids in phloem sap is so high most phloem feeders excrete 'honeydew' , essentially phloem sap — still rich in carbohydrates but with most of the amino acids removed. Honeydew is utilized by several other organisms, in particular some ant species and the sooty mold fungus.
- xylem feeders: Xylem sap has very few nutrients, almost no carbohydrates but with some of mineral ions. Also, while phloem feeders acquire sap passively because it is under pressure inside the phloem cells, xylem sap is under tension and requires 'sucking' (developing greater tensions than already present) in order for it to flow into xylem feeders. Nonetheless, there are some insects (larval cicadas, larval spittlebugs) which feed on xylem.



Figure 3 Emerald Ash borer larvae only eat the ash tree that the adult has chosen to lay an egg in.

Absorbing herbivores

In contrast to grazers, most non-animal plant herbivores are absorbers (see Chapter 27), absorbing nutrients from 'their environment' , with 'their environment' being the interior of a plant. Most of these organisms are bacteria and fungi, but some, like water molds, are protistsand a few are animals (e.g. nematodes, the larval stages of some insects). Most of these organisms are considered parasites and are generally considered to be plant pathogens. They invade plant tissues and then acquire materials in one of three ways: (1) the parasite feeds on materials that 'leak' from host cells.(2) the parasite kills host cells, causing cellular materials to become available. Organisms that feed this was are described as being necrotrophic (feeding off dead material). (3) the parasite and hostform a structure called an haustorium, a fusion of both the host cell membrane and the parasite cell membrane. (Note that the development of the haustorium generally requires breakdown of the cell walls of both the host and parasite.) Materials are transferred from host to parasite through the haustorium and both host and parasite stay alive. Organisms that feed this way are described as being biotrophic (i.e. feeding off living material). Some biotrophs are relatively benign herbivores (they benefit from keeping their host alive), and consequently many acquire relatively small amounts of resources from their hosts. But many biotrophs (e.g. rusts, smuts, downy mildew, powdery mildew) can be devastating to farmers as infestations often can reduce plant yields to next to nothing.


Figure 4 Downy mildew (oomycete) hyphae winding intercellularly between plant cells with haustoria (circular structures) penetrating intracellularly.

Plant defenses

An effective boundary:

> Except for large grazing animals, organisms need to get inside plant tissues in order to feed on the plant. The boundary makes this difficult by producing a surface that is hard to penetrate and inhospitable for life (see Chapter 3). For above ground primary growth, the boundary consists of epidermal cells that are tightly bound to each other, making it difficult to penetrate between cells. Additionally, above ground primary growth is coated with a cuticle that is difficult to pierce and hard to live on because it is hydrophobic. Below ground, mature primary roots have an endodermis that serves many of the same functions as the epidermis + cuticle does above ground. However, the youngest parts of roots have not developed an endodermis. This makes water acquisition easier but it also makes it easier for pathogens to enter.
>
> Pathogens/herbivores gain entry both by utilizing stomatal openings and also by having mouthparts that can penetrate the cuticle/epidermis, or having a needle-like or saw – like ovipositer (egg-laying organ) or, in the case of some fungi, producing an appressorium, a specialized cell type that is able to fuse with the epidermis and produce a structure that can penetrate it. Pathogens and herbivores also gain entry through wounds and openings in the epidermis as the result of growth processes, e.g. branch roots, the shedding of leaves and branches.

Chemistry:

> All plants produce diverse chemicals that influence herbivory and pathogens. Some are feeding deterrent chemicals that are poisonous or may advertise that poisons are present within the plant. At the same time, some chemicals produced by plants clearly attract certain herbivores. The assumption is that these chemicals had once served as feeding deterrents but that the herbivore has developed means to detoxify the poison and is now using the chemical to identify a host that relatively few competitors will be able to utilize. For example most insect herbivores will not eat milkweed but several insects (monarch butterfly larvae, the milkweed beetle and milkweed bugs) choose to feed on milkweed. Some even utilize the plant's poisons as their own, making them less likely to be consumed.
>
> Plants also produce chemicals because they recognize that they are under attack. The production of these 'induced' chemicals imply that the plant has an ability to sense the presence of the pathogen and the chemicals produced may: (1) kill the invader (phytoalexins) , (2) trigger defensive responses in neighboring plants and/or attract predators that may control the herbivore, or (3) elicit an 'hypersensitive response' , causing the invaded tissue to rapidly die. Note that the hypersensitive response may be effective in deterring biotrophic pathogens but actually benefits necrotrophic pathogens.

Phenology:

> Plants (and farmers) may be able to avoid herbivores/predators by adjusting the timing of seed germination, growth and flower / fruit production.

A Sampling of plant diseases:

Poinsettias, phytoplamas and the nature of plant disease

Poinsettia 's did not always look as most of them do now. The plant in the wild and the plant that was originally propagated as an ornamental plant was much taller plant and produced relatively few ' flowers ' (the structures that look like a flower are actually a cluster of flowers surrounded by colorful, usually red, bracts). Early in the 20th century a plant with a novel form appeared, one that was much shorter, branched much more frequently, and produced more flowers. This form could be propagated by cuttings and the assumption was that the original plant was a mutant, a ' sport ', like the original naval orange. Sports generally cannot be perpetuated by seed because the mutations making them distinctive are often recessive. But they often can be perpetuated by cuttings because cuttings are essentially continued growth of the original plant. There are other phenomena besides mutations that might account for an altered growth pattern that can be perpetuated by cuttings. Two possibilities are viruses and phytoplasmas (small bacteria lacking cell walls that live only in plant cells). Note that these three possibilities for the abnormal plant (mutation, viral infection phytoplasma infection) all could be described as ' plant disease' but that what is unusual is that the diseased plant is desirable not undesirable. It turns out that almost all the poinsettia produced today are diseased! And the culprit turns out to be a phytoplasma.



Figure 5 A diseased plant?? The desirable form of this plant is a consequence of a phytoplasma that has infected the plant.

So what is plant disease? In the poinsettia discussion it was associated with 'abnormal plants' A difficulty with this definition is that it is 'normal' for biological entities to be 'abnormal' . That is, if you look at a population (group of organisms) they aren 't all alike, they vary, some are ' outside the norm '. Additionally, ' normal ' is not readily defined. It can be defined statistically as a central tendency, e.g. abnormal is one more than one standard deviation from the mean. Although not perfect, the ' abnormal ' definition works with plants partly because the plants under consideration are typically those of economic importance and ' normal' is a type of plant that provides the most economic return. Additionally, most crops have been bred to be uniform.

Thus a diseased plant is recognized by abnormal structure or functioning. Common symptoms of diseased plants included stunted or deformed growth and yellowed (chlorotic) or dead (necrotic) leaves. But occasionally one might find a diseased plant that is 'bigger than normal' , that branches more than normal, or that has leaves that persist on the plant longe r than normal. In an arbitrary manner plant disease excludes insect herbivores even though have similarities with 'true' plant pathogens. Since this book is dealing with inanimate life we will not consider insect herbivores except as introduced above and as covered in the next chapter dealing developing new plants.

Late Blight of Potato and the ' disease triangle '



Figure 6 Late blight of potato, caused by the water mold *Phytophthora*

The causes of abnormal functioning, i.e. diseased plants, are legion, including: weather conditions, nutritional (soil) factors, genetic changes and a wide spectrum of disorders resulting from interactions with a variety of other organisms — bacteria, fungi, water molds, nematodes, insects and with biotic entities like viruses. With respect to these biotic causes of plant disease, plant pathologists describe what is called the 'disease triangle' where disease results from a combination of environmental conditions, host susceptibility, and disease-causing organism 's virulence. Disease is a consequence of a susceptible plant encountering a competent (i.e. virulent) pathogen under environmental conditions that favor the invasion and spread of the pathogen. A classic example of the disease triangle is late blight of potato, caused by the water mold *Phytophthora*. Potato is native to South America but was brought to Europe in the 17th century as a food crop. The disease organism, which also affects tomatoes, apparently originated in Mexico in the early 1800' s. The disease requires cool, moist conditions, a susceptible potato host and a virulent pathogen. The pathogen spread throughout North America in the early 19th century and made it to Europe probably as a result of importation of diseased potatoes to Belgium in 1845. It quickly spread throughout Europe, and in particular to Ireland, where potatoes were the primary food source and were grown extensively in monocultures. The cool moist conditions typical of Ireland were well-suited to the growth and reproduction of the pathogen. Moreover, the potatoes grown were genetically uniform and also highly susceptible to the blight. The result was devastating, over a million Irish died of starvation and another million emigrated, mostly to the United States. The severity of the blight varied over the next twenty years, primarily due fluctuations in environmental conditions. Note that crop failure not only eliminates food, it also eliminates 'seed potatoes' (potatoes saved to be planted the following year). Thus, even if favorable conditions might yield a relatively high crop (yield per acre), food shortages persist because fewer acres may have been planted. Late blight of potato continues to be a problem, with outbreaks tied to environmental conditions. There are partially resistant varieties but these are only temporary because the pathogen evolves to overcome the plant's resistance.



Figure 7 Phytopthora infestans on tomato, a close relative of potato.

The pathogen is an obligate biotrophic parasite, meaning it can only survive on a living host. It survives from year to year on potato tubers or potato plants left in the field. It spreads readily by spores (usually asexual) that require moisture to stay alive and are dispersed by wind and by raindrops. Pathogen growth and spread can be extremely fast if weather conditions are appropriate. The spores germinate quickly and enter susceptible plants through stomata, wounds, and directly through the cuticle. Once inside the leaf they produce hyphae that grow between cells and produce haustoria that penetrate the cell wall and interact with the host cell membrane and allow nutrients to pass to the fungus.

The disease requires a match between the host and the pathogen. *P. infestans* infects potato and also tomato, which is a close relative of potato. But many other close relatives are not suitable hosts. And there are other species of *Phytophthora* that affect other plant species but do not infect potatoes, e.g. *P. quercina* causes sudden oak death syndrome

Wheat rust — complex parasite life cycles

There are many different rust diseases that affect a variety of hosts, some do not utilize two different hosts , but all are host specific meaning that they can affect only a group of closely related plants: a variety, a species or several species from a single genus. The life cycle for wheat rust was introduced in Chapter 12 and a figure from that chapter is reproduced below. Note that

five different types of spores are produced that differ from each other by their ploidy level (diploid, dikaryon or haploid), what type of plant they are produced on, and what type of plant they can grow on (if any) and how they function.

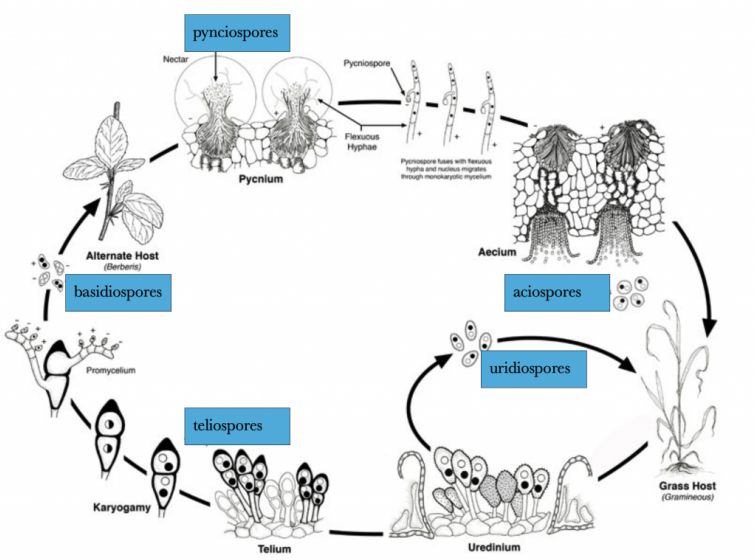


Figure 8 Life cycle of wheat rust, showing the five types of spores that are produced.

teliospores are dikaryon spores and the only stage of the life cycle that grows, albeit very temporarily, independent of a host. It also is the only stage that can overwinter.

basidiospores are haploid spores produced after the teliospore germinates and undergoes karyogamy to produce a diploid cell which then undergoes meiosis to produce haploid basidiospores. These spores are dispersed in the air and only germinate and grow on barberry plants.

pynciospores are haploid spores produced from hyphae produced in a structure emerging from the upper surface of barberry leaves. Also in this structure are haploid receptive hyphae which can receive pynciospores, fuse with them (plasmogamy) to form dikaryon hyphae. These grow to the lower surface of the leaf and form a structure called an aecium that produces dikaryon **aeciospores** that are dispersed by the wind and infect wheat plants.

Mycelial dikaryotic growth from the aeciospores can cause significant damage to the host wheat plant and also produces **urideospores**, produced in and orange structures called uremia. The uridospores spread *Puccinia graminis* to other wheat plants, facilitating disease spread through wheat crops.

As the wheat plant starts to senesce, both from the pathogen and from its natural, monocarpic cycle, the dikaryotic hyphae in the wheat plant produce **teliospores** , spores that can survive the winter and completing the life cycle.



Figure 9 *Puccinia graminis* on wheat stems—the orange structure are ureidia and produce urediospores that can infect other wheat plants.

Because wheat is an extremely important crop and because the disease spreads rapidly and evolves quickly, wheat rust is probably the most significant agricultural disease. Resistance to the disease involves genetics of both the fungus and the plant. Resistant plants have an ability to recognize invasion by the fungus and to respond to it. Recognition of the fungus is the result of the plant perceiving a chemical produced by the fungus is present. An avirulent fungus can become virulent by becoming unrecognizable, typically by not producing a specific chemical that that the avirulent (and thereby recognizable) fungi had been making. Hence virulence in the pathogen is typically recessive (inability to make something that the wild type does make). Plant resistance requires a dominant gene that gives the plant the ability to recognize and respond to the presence of the virus.

Corn smut — Mexican truffles

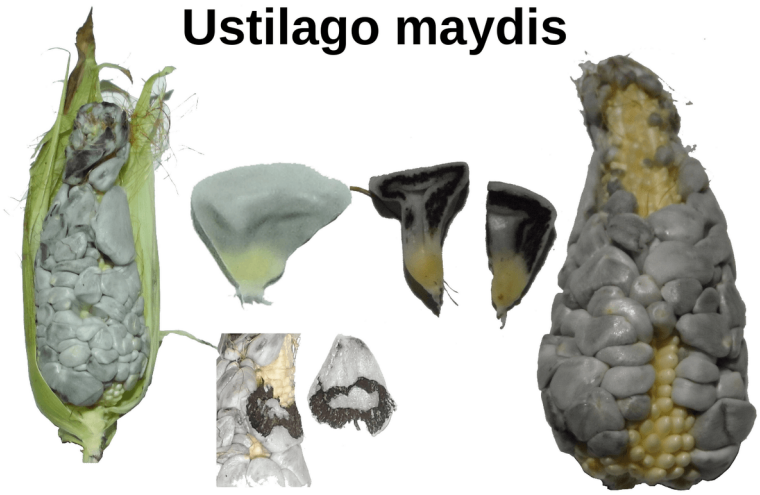


Figure 10 Corn smut. Infect plants produce deformed fruits (galls) instead of regular corn kernels.

Corn smut produces large, distinctive galls that are edible and highly desirable in Mexico. In other parts of the world the disease is very unwelcome, substantially reducing crop yields. Like the rusts, smut diseases are basidiomycetes and like the rusts the fungus is generally found in the dikaryon state, with cells possessing two haploid nuclei. Basidiomycetes only produce only a single diploid cell that immediately undergoes meiosis to form haploid spores. These germinate and grow into haploid hyphae that in smuts can produce new cells by budding (like yeast) and like yeast can be grown on an artificial medium, meaning that this stage is NOT biotrophic but acts like a saprophyte. However, when haploid hyphae of two different mating types find each other

and fuse and form a dikaryotic hyphae, it is now biotrophic, only able to survive on living cells of spe cific plants, in this case, corn and teosinte (a close relative of corn). Hence, to be a successful pathogen the haploid hyphae need to find each other on living corn (or teosinte) material. Additionally, the dikaryon hyphae only invade active tissues, most commonly the flowers, where they induce abnormal growth, galls, with greatly enlarged cells surrounded by hyphae. They do not form typical haustoria but do form structures that allow the transfer of materials from the plant to the fungus. As the galls mature they change color from silky white to black and also change textures, becoming softer. Although the galls look 'fungal' (if such a thing is possible!) they are actually mostly plant tissue. Inside the galls some fungal cells undergo karyogamy (fusion of the two haploid nuclei) to form a diploid cell and complete the sexual cycle. Corn smut is the most significant smut disease but there are other smut fungi that infect other agricultural grasses (sugarcane, barley, oats) as well as smuts that attack wild grasses and sedges.

Rice blast disease — changing pathogen strategies



Figure 11 Rice stems infected with rice blast disease

Rice blast is a devastating fungal disease that affects several cereals but is most significant in affecting rice. It is an ascomycete and the dikaryon stage is brief in time and extent. The pathogen is technically described as a hemibiotroph because initially it behaves like a biotroph, surviving with living plant cells, but eventually becomes a necrotroph, killing cells and obtaining nutrients from them. Haploid spores land on rice leaves, developing fruits, and other plant parts and are able to penetrate the cuticle by generating substantial pressures hydrostatically within a specialized cell called an appressorium. Once inside the fungus is able to spread by entering individual plant cells through plasmodesmata. After a certain amount of time that depends upon the tissue that has been invaded, the fungus shifts to a necrotrophic lifestyle, killing the host cells.

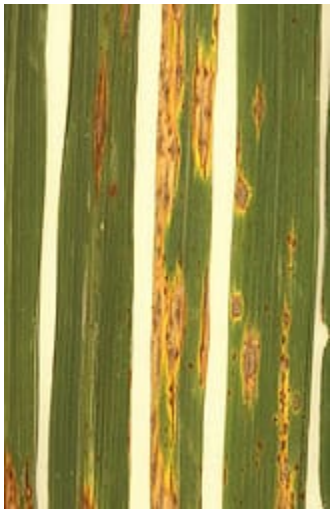


Figure 12 Rice leaves infected with rice blast disease.

Dutch elm disease — overreacting can be deadly

Dutch elm disease is caused by an ascomycete fungus that has a symbiotic relationship with a a bark beetle, a type of beetle that feeds on the vascular cambium and tissues (secondary xylem and phloem) that the vascular cambium produces. The fungus is transported from infected trees to new trees by the beetle and benefits not only by the transport but also by being placed inside the plant in the tissues that the fungus feeds on. The fungus feeds only on dying cells. but, unfortunately for the tree, its presence triggers the production of gums. Presumably such a response could help stop the spread of the fungus by making it more difficult to move. However, in elm trees the substances that are produced plug the vessels and trachieds of the host, making them unable to transport water up the plant. Like a number of human diseases, the damage of a pathogen stems mostly from the host response and less so from the actual activity of the pathogen. Dutch elm disease is one of many 'wilt diseases' caused by both fungi and bacteria that result in reduced water transport and wilting. In most of these the blocking of xylem tissue is the result of the plant response to the pathogen.



Figure 13 'Galleries' of bark beetle that spreads the fungal disease that causes elm death. The beetle feeds on the inner bark (phloem) and is able to carry spores from infected trees to uninfected trees.

Fire blight and bacterial phytopathogens

The majority of plant pathogens are fungal, but some, like late blight of potato, are oomycetes and some, like the phytoplasmas of poinsettias are bacteria. While phytoplasmas are unusual because they are obligate intracellular parasites, most bacterial diseases do not enter into the cell but they do produce 'effector' molecules that they are able to transfer into living cells and effect specific results such as hormonal responses that bring about tumors, exudation of materials, or cell death. Most bacterial plant pathogens are not easily classified as biotroph/necrotroph although clearly phytoplasmas are biotrophs, as is the gall-forming *Agrobacterium* (see below).Fire blight is interesting in this respect. It is caused by *Erwinia amylovora*that affects members of the rose family, in particular apples and pears, sometimes with catastrophic results. The bacteria can live as a harmless epiphyte living on sugars exuded by the stigmas of flowers and the nectaries at the base of flowers. From these locations *E.amylovora*can be spread by pollinators throughout a plant and throughout an entire orchard. At some point it is triggered to become a much less benign associate and it becomes necrogenic, killing host cells as a consequence of the effector molecules it produces.



Figure 14 Fire blight, a bacterial disease that kills members of the rose family, including apples and pears.

Crown gall disease — a disease used as a tool against disease



Figure 15 A 'crown gall' , an abnormal growth on a tree caused by the presence of *Agrobacterium tumifaciens*. **Crown gall disease affects a wide variety of plants, not just trees.**

Many plant diseases alter the growth pattern of plants, often producing characteristic structures called galls. The abnormal growth that is manifested in a gall usually is a consequence of changes in the amounts of plant growth regulators, aka hormones. This can be the result of the pathogen producing these chemicals (in fact one plant hormone, gibberellic acid, was first discovered as a result of it production by a fungal disease). But altered levels of plant growth substances can also be a consequence of the pathogen causing its host to produce more or less of a particular substance. The most common way this happens is that the pathogen alters gene expression in its host. *Agrobacterium tumifaciens* does this by actually altering the genes present in host cells via a process called transformation, a type of horizontal gene transfer. Among other genes that are transferred is one that codes for the production of the plant growth substance cytokinin which plays a role in the cell proliferation required for gall formation. The bacterium lives saprophytically in the soil but is able to recognize wounded plants when it contacts them and is transformed into a virulent form that makes its way into the plant. *A . tumifacien s* is a significant pathogen on several crop species, in particular perennial ones like walnut, apricot and plum. *A. tumifaciens* notable for its very broad range of hosts which is one of the reasons why it has proved useful in the genetic engineering of plants as it can be used to transfer specific genes from one organism to another (Chapter 31).

Tobacco mosaic virus, cauliflower mosaic virus, and ring spot disease of papaya

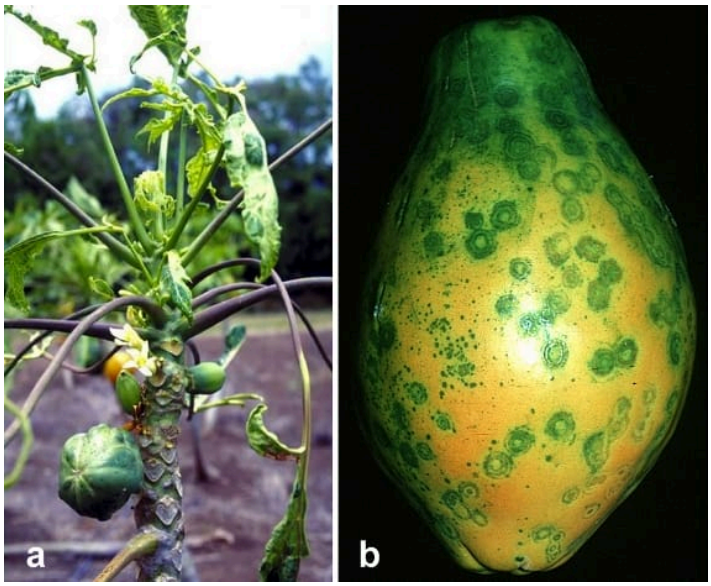


Figure 16 Ring spot virus on papaya

Plants are affected by a large number of viruses that can cause very significant crop losses. Tobacco mosaic virus (TMV) is not one of the most damaging viral pathogens but it is notable because of its role in the understanding of viruses and its use in bioengineering. TMV was the first virus to be isolated and purified and this allowed for the recognition that infectious agents need not be cellular in order for them to cause disease. Viruses are composed of both protein and genetic material (either DNA or RNA) and upon entry into a cell they insert genetic material that codes for the production of viral protein and genetic material. A critical part of the inserted viral genome is a region called a promoter that 'promotes' the expression of the genes downstream from it, thereby ensuring their expression. Genetic engineers have utilized this region of the genome of several viruses in order to insert desirable genes from one organism into another organism. In particular the cauliflower mosaic virus (CaMV) has proved to particular useful in producing 'genetically modified' organisms. One crop where the CaMV promoter was very useful was in the development of strains of papaya that are resistant to the ring spot disease of papaya, a disease that is caused by yet another virus that threatened to eliminate the papaya as a commercial crop.

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20.8: Plant Defenses, Management Practices and Pests

After discussing the key ecological principles and approaches to soil management, let's do a deeper dive and see how amazing plants really are.

They use a variety of systems to defend themselves from attack by insects and disease-causing pathogens. Sometimes they can just outgrow a small pest problem by putting out new root or shoot growth. Many plants also produce chemicals that slow down insect feeding. While not killing the insect, it at least limits the damage. Beneficial organisms that attack and kill insect pests need a variety of sources of nutrition, usually obtained from flowering plants in and around the field. However, when fed upon, by caterpillars for example, many plants produce a sticky, sweet substance from the wounds, called "extra-floral nectar," which provides some attraction and food for beneficial organisms. Plants under attack by insects also produce airborne (volatile) chemicals that signal to beneficial insects that the specific host it desires is on the plant. The beneficial insect, frequently a small wasp, then hones in on the chemical signal, finds the caterpillar and lays its eggs inside it (Figure 8.3). As the eggs develop, they kill the caterpillar. As one indication of how sophisticated this system is, the wasp that lays its eggs in the tomato hornworm caterpillar injects a virus along with the eggs that deactivates the caterpillar's immune system. Without the virus, the eggs would not be able to develop and the caterpillar would not die. There is also evidence that plants near those with feeding damage sense the chemicals released by the wounded leaves and start making chemicals to defend themselves even before they are attacked.

Plant Pests

A variety of organisms can harm crops, from pathogens such as viruses, bacteria and fungi to nematodes to insects to weeds. Even larger animals such as deer (or, in Africa, elephants) can significantly damage crops. There is nothing inherently bad about these organisms we commonly call pests. They're just doing what they naturally do in order to survive and reproduce. But when growing crops we need to minimize the damage done by such organisms. The key is doing so in environmentally sound ways: building healthy soils, using crop varieties with natural resistance, and using rotations and cover crops that suppress pests while providing many other benefits as well.

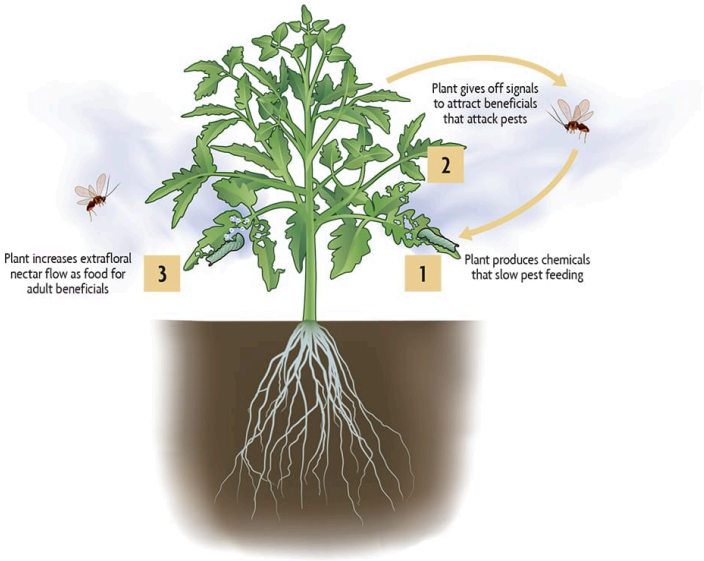


Figure 8.3. Plants use a number of defense strategies following damage by feeding insects. Modified from unpublished slide of W.J. Lewis. *Illustration by Vic Kulihin.*

Leaves are not the only part of the plant that can send signals that recruit beneficial organisms when under assault. When attacked by the western corn rootworm, a major pest, the roots of some varieties of corn have been shown to release a chemical that attracts a nematode that infects and kills rootworm larvae. During the process of breeding corn in the United States, this ability to signal the beneficial nematode has apparently been lost. However, it is present in wild relatives and in European corn varieties and is, therefore, available for reintroduction into U.S. corn varieties.

Plants also have defense systems to help protect them from a broad range of viral, fungal and bacterial pathogens. Plants frequently contain substances that inhibit a disease from occurring whether or not the plant is exposed to the disease organism. In addition, antimicrobial substances are produced when genes within the plant are activated by various compounds or organisms—or a pest—in the zone immediately around the root (the rhizosphere) or by a signal from an infection site on a leaf. This phenomenon is called "induced resistance." This causes the plant to form various hormones and proteins that enhance the plant's defense system. The resistance is called systemic because the entire plant becomes resistant to a pathogen, even far away from the infection site.

Plants have a number of defense systems that protect them from disease. Beneficial bacteria in soil surrounding the root (the rhizosphere zone) provide a first line of defense against soil-borne diseases by competition or antagonism. If the disease organism (let's say a fungus like *Rhizoctonia solani* that causes root diseases in seedlings of diverse crops such as wheat, rice, potatoes, tomatoes and sugarbeets) makes it through the rhizosphere and contacts the root surface, beneficial organisms living inside roots provide another line of defense by producing chemicals that attach the fungus.

Then the plant itself also can produce chemicals that help it resist the attack. There are two major types of induced resistance that are induced in response to signals from microorganisms: systemic acquired resistance (SAR) and induced systemic resistance (ISR) (Figure 8.4). SAR is induced when plants are exposed to a pathogen or even to some organisms that do not produce disease. Once the plant is exposed to the organism, it will produce the hormone salicylic acid and defense proteins that protect the plant from a wide range of pathogens. ISR is induced when plant roots are exposed to specific plant growth, promoting rhizobacteria (PGPR) in the soil. Once the plants are exposed to these, hormones (jasmonate and ethylene) are produced that protect the plants from various pests. Some organic amendments have been shown to induce resistance in plants, and farmers who have very biologically active soils high in organic matter may already be taking advantage of it, as well as of other ways pests are controlled in such soils. However, there currently are no reliable and cost-effective indicators to determine whether a soil amendment or soil is enhancing a plant's defense mechanisms. More research needs to be conducted before induced resistance becomes a dependable form of pest management on farms. Although the mechanism works very differently from the way the human immune system works, the effects are similar: the system, once it's stimulated, offers protection from attack by a variety of pathogens and insects.

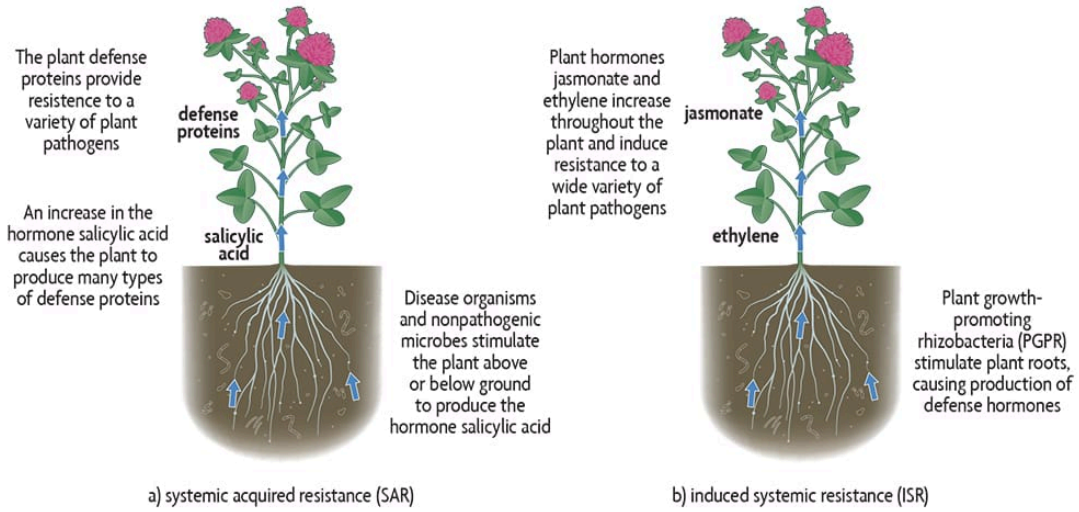


Figure 8.4. Types of induced resistance to plant diseases. Modified from Vallad and Goodman (2004) by Amanda Gervais. *Illustration by Vic Kulihin.*

Plant Defense Mechanisms

Plants are not passive in the face of attack by insects, nematodes or diseases caused by fungi and bacteria. Genes activated when plants are attacked or stimulated by organisms produce chemicals that

- slow insect feeding
- attract beneficial organisms
- produce structures that protect uninfected sites from nearby pathogens

- produce chemicals that provide a degree of resistance to pathogenic bacteria, fungi and viruses
- host organisms in roots that protect against pathogens

When plants are healthy and thriving, they are better able to defend themselves from attack and may also be less attractive to pests. When under one or more stresses, such as drought, nutrient limitations or soil compaction, plants may “unwittingly” send out signals to pests saying, in effect, “Come get me, I’m weak.” Vigorous plants, taller and with more extensive root systems, are also better competitors with weeds as they are able to shade them out or just compete well for water and nutrients.

Many soil management practices discussed in this chapter and in the other chapters in Part 3 help to reduce the severity of crop pests. Healthy plants growing in soils with good biological diversity can mount a strong defense against many pests (see text box). Ecological soil and plant management is so critical to plant health because it helps to suppress pest populations and also influences, as we have just seen, the ability of plants to resist pests. Developing optimal soil health is, therefore, the basis for management of crop pests on farms; it should be a central goal that underpins crop integrated pest management (IPM) programs.

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20.9: Weeds and weed control

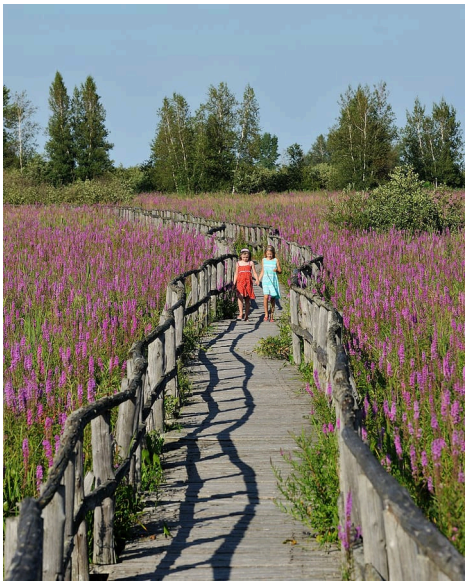


Figure 1 The pretty purple flowers are purple loosestrife, a plant brought to North America as an ornamental but it has escaped to become a problem weed it wetland areas.

Ralph Waldo Emerson defined a weed as 'a plant whose virtues have not yet been discovered' , but in fact a number of weeds were known to have 'virtues' and were spread by humans intentionally. Dyer's woad is a significant pest in the western U.S. but was brought to North America intentionally for its use a source of blue dye (hence the common name). Many weedy plants, e.g. purple loosestrife (Figure 1), were intentionally introduced by gardeners who found them attractive. A large number of weed organisms of all types are similarly the result of intentional introduction in new habitats (honeybees, earthworms, gypsy moth, starlings and many more).

Is there a better definition of weed? Ecologist consider organisms to be 'weedy' if they have a suite of characteristics (high reproductive potential, extensive dispersal abilities, rapid growth rate, ability to reproduce even under adverse conditions) that would make them likely to appear and survive in disturbed habitats. Disturbed habitats, sometimes called ruderal habitats, are areas that have once been populated but some disturbance, e.g. fire, has eliminated what once lived there. Significant for terrestrial habitats, they generally are sites with developed soils, as opposed to sites that were never vegetated and have no soil. So although ecological weeds are considered 'pioneer species' , they are not pioneering on to previous uninhabited land our very young soil. Ecological weeds can colonize and quickly dominate a disturbed site but may not persist because they often are unable to compete with other species that eventually arrive at the site.

But 'weed' is not used just by ecologists and its definition is both utilitarian and subjective:

> 'A plant that interferes with the management objectives at a particular location. It is a plant growing where it is not wanted. Under certain situations, the plant may not be totally undesirable.'

This definition focus on plants but undesirable organisms come from the entire spectrum of life, including the non-plant organisms considered in this book: cyanobacteria, green algae, red algae, diatoms, dinoflagellates and fungi.

Weeds are 'pests' , organisms that are undesirable for reasons that are specific to a particular situation and, as noted above, their undesirable nature depends upon situation.

- honeybees are pests when they nest in houses
- earthworms are desirable in agricultural situations but are weeds in native habitats where they can alter conditions and disrupt the native community
- dandelions are weeds in lawns, where some consider them unsightly, but are useful to pollinators and to foragers who eat their leaves and flowers
- sandbur is highly undesirable on beaches because of its sharp fruits that are painful to step on and stick to clothing

- dyer's woad clearly is (was) useful as a source of dye but if one is managing land for other purposes then it is a weed
- weeping willow trees are desirable as ornamentals but their roots can clog drainage systems
- the nitrogen fixing bacterium *Rhizobium* is desirable if it invades plant roots in habitats where nitrogen is relatively scarce. When nitrogen is abundant *Rhizobium* actually decrease plant growth because they are being fed by the plant

The last example highlights the fact that there is some overlap between 'weeds' and 'disease' , something that will be considered in the next chapter.

TOPICS

- Features of weeds
- Controlling weeds



Figure 2 Sandbur is a grass whose fruits have very sharp points.

Features of weeds

As mentioned above, weedy plants typically grow fast and reproduce both rapidly and abundantly. But given the flexible and utilitarian definition of weed a key feature of weeds is that they must have characteristics that someone might consider undesirable. Here are some examples:

- dandelions interrupt the smooth continuous texture of a lawn giving what some consider a an undesirable look.
- sandbur produces fruits that are very painful to step on or get caught in a stocking
- burdock, beggar's tickseed, stickseed and many others produce fruits that stick on clothing
- box-elder trees produce an unappealing form that readily sheds branches. Its abundant fruits clog gutters
- poison ivy, wild parsnip, giant hogweed, St. Johnswort are toxic to many human



Figure 3 Poison ivy, native to North America, is highly undesirable because it produces a chemical that is a skin irritant.

The foremost undesirable feature of agricultural weeds is that their presence in cropland deters the growth of whatever crops are being grown, an interaction that generally would be labelled competition, a concept that is easy to cite but is often much more difficult to pin down. The basic idea is that if two species utilize the same resources (water, light, nutrients) then the presence of of a competitor can reduce the availability of these resources and thereby diminish the growth of the crop. The phenomenon of decreased crop growth when in the presence of weeds is well established, but the exact mechanism is elusive and certainly may vary between different weeds. Note that the best competitor for any particular crop plant is another individual of the same type because it requires the same resources and acquires them in the same manner. Thus intraspecific competition (between individuals of the same species) may be hard to separate from interspecific competition (crop vs. weed). Keeping track of resources is often challenging and other interactions might account for the pattern. C ompetition could be due to factors such as allelopathy (the weed produces chemicals that deter the growth of the crop) or perhaps because the weed attracts insect pests/ disease organisms that may affect the crop. For these reasons competition is often defined without the specific requirement of resource depletion. Most agricultural weeds are plants that deter the growth of crop species for undetermined reasons.

What might make a particular plant likely to be an agricultural weed? Here there is large overlap with characteristics of ecological weeds:

- weeds seeds germinate readily with few or no specific germination requirements
- weeds grow quickly and since resource acquisition is strongly tied to plant size, growing quickly allows weeds to be very effective competitors
- weeds readily reproduce, allowing for their perpetuation on a site and producing a substantial 'seed bank' of seeds in the soil. Although most weed seeds germinate readily, not all do, and some seeds remain viable for tens of years, meaning that ungerminated weed seeds remain in the soil for prolonged time periods



Figure 4 Dyer's woad was introduced to eastern North America in colonial times. It is not a problem throughout most of the United States but is a problem in parts of the western states.

While the above apply to annual weeds, there are also perennial weeds which reproduce readily from fragmented roots which may be produced by tilling. Why till? because most crops are annuals and they would have a very hard time competing against already established plants. But note that tilling 'plays into the weed' s strength': it is a form of disturbance which is generally something that weeds require.

The characteristics listed above also would be desirable features of a crop plant: germinate readily, grow quickly, reproduce abundantly. Indeed, several crops are thought to have been domesticated from weeds (e.g. wheat, sunflower, barley, carrot).

Another feature that is commonly associated with weeds is that they are non-native, i.e. they were introduced into an area where they previously had not be present, generally because of human activity (both intentional and unintentional). While some would consider any non-native to be a weed, most would require that the introduced species must be invasive, i.e. spreading from where it was introduced. Many introduced species are invasive and this is generally attributed to the fact that 'natural controls' (herbivores, disease) are not simultaneously introduced with the weed. While this certainly explains the invasive nature of some introductions, other factors come into play. Dyer 's woad was introduced in the eastern U.S. and showed only a modest invasive nature as it spread westward and was restricted to repeatedly disturbed sites like the sides of roads. Arriving in California and Utah in contaminated alfalfa seed its behavior changed substantially, becoming much more invasive and entering habitats that are much less disturbed, replacing native plants. Part of this behavior is probably due to the fact that woad' s native habitat is much more similar to the arid west than to the more mesic eastern and central part of the country.



Figure 5 Indigo dye derived from the fruit of Dyer's woad. Most indigo is now made synthetically but until the 20th century the primary sources of blue dye (indigo) were Dyers woad and several other unrelated species.

An interesting invasive pattern is shown by black locust, a tree native to central and southeastern U.S. but not to the northeast. After it was intentionally introduced to the northeast it has become invasive as it has in several other parts of North America. What had limited its spread previously is unknown. Again appreciating that what a weed is is subjective, black locust might be considered a weed in the northeast but not in the areas where it is native.

Another interesting pattern is seen in *Phragmites australis* , common reed. Apparently a variety of this species was native to North America and was present when European's arrived. This native variety of the species is not invasive and does not form large monotypic stands. Ecologists noted that the behavior of the plant changed drastically in the 20th century, with the plant becoming much more invasive. What actually happened was that a European variety of the same species had been introduced and this was the plant was exhibiting the invasive behavior. The two varieties (non-invasive North American ; invasive European) are very closely related (same species) and very difficult to distinguish. Apparently minor genetic changes can be responsible for invasive behavior.



Figure 6 Phragmites australis, a grass with both weedy (invasive) and non weedy varieties.

However, lots of weeds are 'natives' (ragweed, giant ragweed, sunflower, Jerusalem artichoke, milkweed, New England Aster, goldenrod) and most of these have not invaded new habitats but have continued to occur in the disturbed habitats found in any particular region.

Weed control

In most situations weeds cannot be permanently eliminated but their populations may be controlled using three approaches: (1) chemical control, using pesticides (herbicides) to kill the weed (2) biological control, using biological agents (pathogens, herbivores) to reduce weed populations and (3) cultural control, modifying how the land is maintained in order to reduce weed populations.

Chemical control

Chemical control is a recent innovation, only becoming a significant control agent in the last eighty years. The basic idea is simple: find some chemical that kills weeds. The difficulty is that most chemicals that kill weeds are non-selective, i.e. they don't just kill weeds, they kill all or most plants, including those whose growth you are trying to promote. A wide variety of herbicides have been developed but the three below are widely used and show a degree of selectivity and therefore can be used in some situations without damaging the plants/crops one is trying to grow.

> **2, 4 D** (2, 4, dichlorophenoxyacetic acid) is the oldest widely used herbicide. Its discovery as a useful product, a weed killer, was the result of 'basic' research, i.e. research that was not focused on utility (developing a weed killer) but rather research that simply involved developing an understand of the natural world. In this case, workers were studying the effects of auxin, the first chemically identified plant hormone, originally studied by Darwin one hundred years earlier. The only naturally occurring auxin is indoleacetic acid, but early in the 1940 's workers discovered a number of chemicals, with structures similar to indoleacetic acid, that could produce similar effects on plant growth and development. One of these artificial auxins was 2, 4 D. It was up to Dr. Franklin D. Jones to do some ' applied ' science, i.e. apply basic research to a practical problem. Dr. Jones was looking for something to kill the poison ivy that was plaguing his children. He tried 2, 4 D and found it was very effective in killing poison ivy. Significantly, 2, 4 D is selective: it kills most broadleaf plants (dicots) but spares ' narrow-leaved' plants, grasses and similar species. Because this selectivity matches what one might look for eliminating lawn weeds and weeds of cereal grains (e.g. corn, wheat), 2-4 D has proved to be highly useful.
>
> **Roundup** (glyphosate) was developed in the 1970 's and is the most widely used herbicide both in agricultural situations and in home/garden situations. It is not at all selective, basically killing whatever plants to which it is applied. It is also a systemic herbicide, meaning that if it is applied to the leaves it can be transported to the roots and rhizomes and can kill them too. Selectivity was developed because resistance to Roundup, using genes from bacteria, has been genetically engineered (i.e. gene transfer) into several crop species, first soybeans (' Roundup Ready Soybeans), and later to corn and cotton. Fields with these specific crops can be treated with Roundup to kill all other plants.
>
> **Atrazine** is the second most used herbicide in the U.S., but mostly in agricultural situations and less in residential situations. It is selective, killing most broadleaf species and many weedy grasses, but being tolerated by several crop species: corn, sorghum, and sugar cane (all are grasses). Additionally, an atrazine resistant (GMO) canola variety has been developed as well.

Concerns about herbicides abound and include: human health concerns, ecological concerns and concerns about the development of herbicide resistant 'superweeds' . Both Roundup and Atrazine have been used extensively enough that there are new varieties of weeds that are unaffected by these chemicals, comparable to the evolution of antibiotic resistant bacteria.

Biological control

Biological control involves the use of other organisms to deter the growth of weeds. In general, this type of control is developed for introduced, invasive species of weeds and a search is made for herbivores or pathogens (see Chapter 30 on disease) that are native to where the introduction came from but are not present in the region that they have invaded. Care must be taken to avoid introducing species that might be harmful to existing native species. This is more likely if the biocontrol agents selected are 'specialists' in their feeding habits. Purple loosestrife is an example of an invasive weed that has been controlled (not eliminated) by introductions of insect herbivores, beetles and weevils that specialize on purple loosestrife. These species are common in purple loosestrife's native habitat (Europe and Asia) but were not introduced to North America when purple loosestrife was.

Cultural control

Cultural control By definition weeds are **always** a problem, at least a problem for someone. Although weeds can be an 'issue' in

native habitats, the vast majority of weed problems involve humans (gardeners, farmers) trying to raise specific plants, i.e. trying the 'culture' plants that are somehow desirable. The cultural practices that are followed can influence the magnitude of the weed problem. The choice of crops, the timing of planting, the seeding density, the distance between rows, the number of sequential seasons that a crop is planted, all are cultural practices that may influence the severity of weed problems. Because most crops are annuals, they need to be planted each year and planting involves disturbance, thereby encouraging weed growth. Indeed, some early 19th century farmers considered early versions of the plough to be 'poisoning the soil' and promoting weed growth. Appreciating that farmers are in a catch-22 condition, they need disturbance but disturbance promotes weed problems, there are cultural practices that can lessen the problem such as the timing of the ploughing and how intensive the ploughing is. A modern technique is called 'no-till' farming utilizes minimal tilling, thereby giving weeds less area to utilize and that area that is available is seeded with a crop that may out-compete the weeds. Perennial non-woody crops such as alfalfa, asparagus, strawberries, raspberries require different cultural practices that might include items like mulching, mowing, tilling or the intentional planting of understory plants that might suppress weedy growth. This is also true for woody perennial crops like grapes and apples. Cultural practices vary widely depending on the crop and its characteristics. For instance flooding is an effective means of weed control but can only be utilized if crops, e.g. rice, tolerate the flooding. Fire can be used for annual crops and for woody (tree) crops if it is a low intensity surface fire.



Figure 7 No till farming: Instead of ploughing the entire field, a narrow trench is 'drilled' where the seed is planted. Note last year's corn stalks.

Most weed management strategies utilize ' **Integrated Pest Management** ' , an approach that incorporates chemical, biological and cultural approaches to manage not only weeds but also insect pests and pathogens.

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20.10: INVASIVE PLANTS AND GMOS

Learning objectives

- Define what GMO technology is and how it is applied to plant improvement.
- Discuss why GMO technology is controversial and develop an informed opinion about it.
- Know several examples of non-native invasive plants and their impact on the environment.

Although the discovery of DNA as the genetic material seems like a long time ago (~1928), plant genetic modification has been going on for thousands of years as farmers make selections of individuals to tailor crops to their needs. We continue manipulating plants in the discipline of plant breeding. Genetically Modified Organisms (GMOs) are very recent, but offer a new way to improve plants. Although GMO technology is controversial, it has been rapidly adopted by farmers.

A short lesson on invasive plants introduces this issue and discusses how plant propagators can help. As consumers we must be aware of potential risks some plants pose to the environment.

20.10.1: Invasive plants

20.10.2: GMOs

20.10.3: Terms

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20.10.1: Invasive plants

Learning objectives

By the end of this lesson you will:

- Be able to explain the consequences of introducing non-native plants that become invasive.
- Be able to map how some plants become invasive.
- Know several examples of non-native invasive plants in Minnesota.

Overview

This lesson introduces some of the features and impacts of non-native invasive plants, using a Minnesota perspective. Be aware, however, that just as a plant native to an exotic continent may become a weedy invasive plant in Minnesota, some plants native to Minnesota have been taken to other continents and become invasive in their new homes. Invasive plants are defined by the U.S. Department of Agriculture as those non-native to an ecosystem whose introduction causes or is likely to cause economic or environmental harm or harm to human health. One example is the oriental bittersweet (*Celasturs orbiculatus*); the photo below shows, from near Red Wing, Minnesota, shows it smothering ground and tree vegetation.



Bittersweet. Ross. CC BY-NC-ND 2.0

Invasive plant species have contributed to the decline of about half of the endangered and threatened plant species in the U.S. Their impacts include, but are not limited to, the following:

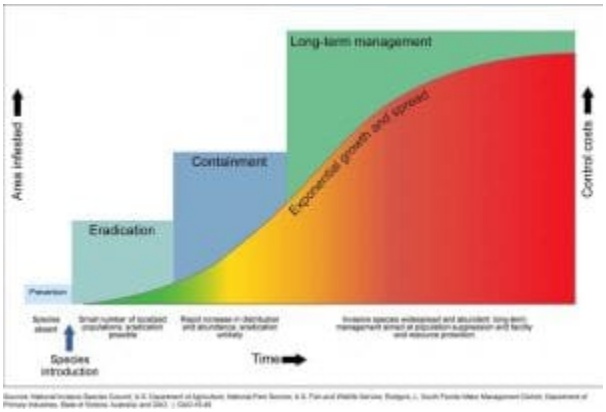
- Competition with native plant species for moisture, sunlight, nutrients, and space.
- Decrease in biodiversity.
- Degradation of wildlife habitat, agriculture lands, and water quality.
- Increase in soil erosion.
- Decrease in recreational opportunities.
- If sexually compatible native plants are present in the invaded regions, hybrids can form resulting in genetic contamination or pollution to native environments.

This lesson reviews some of the common features of invasive plants in Minnesota, and includes specific information about several species.

Where do invasive plants come from?

People and plants have a close relationship, evolving a co-dependence over thousands of years. As people move around the globe

they bring with them the plants that are useful for fuel, food, feed for their animals, enhancing the aesthetics of their new home, and providing fiber for clothing and construction. While most of these plants have been positive forces in the lives of people and do relatively no harm, some escape from cultivation and become invasive. In Minnesota, for example, the most reported invasive plant is common tansy (*Tanacetum vulgare*). It was likely first brought to the U.S. by John Winthrop, Governor of the Massachusetts Bay colony, about 400 years ago. Although humans are a primary dispersal means for invasive plants and often move them intentionally, such plants may also arrive unintentionally as contaminants in food plants or as seed contaminants in fodder that travels with people and their animals.



Invasion curve. US Government Accountability Office. Public domain.

The graph above shows the relationship between an invasive plant's spread and time. Initially, the spread is slow and is in a "lag phase" due to the small number of plants in the initial introduction. This lag phase (left third of the graph) is a period in which, if the plant is detected and addressed, control could result in its eradication. Most invasive plants, however, have a high rate of reproduction, either asexual or sexual. In many cases they spread by prolific fleshy fruit production (as with the bittersweet shown above) that is eaten by birds and other animals. As numbers of the invasive plant increase, it enters the exponential rate of spread (middle third of the graph). Think of exponential spread as a rate similar to 2, 4, 16, 256, 65536. If left unchecked, as some invasive plants are, spread will reach a maximum (shown in the last third of the graph). The horticultural industry is a common entry point for many invasive plants. The properties that make a plant attractive to growers and consumers for their yard or garden — including novelty, robust growth, abundant flowering over a long period of time, and easy sexual or asexual propagation — are the very qualities that make many ornamental introductions invasive.

In addition to large quantities of seed, invasive characteristics listed by the U.S. Department of Agriculture's Invasive Plant website include:

- Thriving on disturbed soil.
- Distribution by birds, wind, or humans over great distances.
- Aggressive root systems that spread long distances from a single plant.
- Root systems that grow so densely that they smother the root systems of surrounding vegetation.
- Production of chemicals in leaves or root systems that inhibit the growth of other plants around them (referred to as **allelopathy**).

As invasive plants spread they displace native vegetation, and can dramatically impact the ecosystem into which they are introduced.

Review questions

1. What is an invasive plant?
2. What is happening during the three phases of invasive plant spread?
3. What impacts do invasive plants have on the environment?
4. What are common properties of an invasive plant?
5. If genetic pollution occurred, could it be reversed?

Invasive plant examples

Common tansy (*Tanacetum vulgare*)

Tansy, an herbaceous perennial in the family Asteraceae, is the most reported invasive plant in Minnesota. It was introduced to North America from Eurasia about 400 years ago, and has been used as a medicinal plant and a funerary herb because of its aroma. Rumor has it that the first president of Harvard University was buried with tansy, and when his grave was moved almost 200 years later, the tansy was still fragrant. Tansy's invasion of pasture lands is problematic due to its toxicity to mammals. For more information on common tansy see the Minnesota Department of Agriculture website.



Tansy. Robert Flogaus-Faust. CC BY 4.0

Oriental bittersweet (*Celastrus orbiculatus*)

Oriental bittersweet was intentionally introduced as an ornamental for dried floral arrangements and fall decorations (left-hand photo, below). It is a woody vine that climbs trees and structures and is capable of girdling the trees as the vines tighten around the truck (right-hand photo). Girdling plus the accumulated growth of heavy vines can bring down large trees. Oriental bittersweet thrives in a wide range of habitats, light levels, and soil types, and can grow to over 20 meters (65 ft) in length. Although it is on the Minnesota Department of Agriculture's list of plants that are prohibited and must be eradicated, it is still grown and propagated in Wisconsin for use in floral arrangements.



American Bittersweet. Peggy. CC BY-ND 2.0


Bittersweet girdling a tree. mwms1916. CC BY-NC-ND 2.0

Knotweeds (*Fallopia sp.*)

The knotweed complex consists of two species and their hybrid, includes Japanese knotweed (*Fallopia japonica*), giant knotweed (*F. sachalinense*), and their hybrid Bohemian knotweed (*F.* × *bohemica*). (Remember that an "×" between the genus and specific epithet indicates an interspecific hybrid.) The knotweed was originally imported as a novel ornamental. With its fast growth and late fall flowering it can make a very showy specimen planting. Each taxa of knotweed has very rapid growth. As an herbaceous perennial it resumes growth from large rhizomes (an underground stem) that produce prolific shoots and adventitious roots, making it difficult to control with herbicides.



Japanese knotweed. David Short. CC BY 2.0.

Knotweeds can also cause damage to structures. With their long-lived rhizomes capable of adventitious rooting, and dioecious flowers capable of prolific seed set, knotweeds are a double threat to native plants and the environment.



Knotweed can grow through cracks in pavement, walls, and foundations, causing structural damage. Gordon Joly. CC BY-SA 2.0.

Japanese barberry (*Berberis thunbergii*)

As a popular landscape plant, Japanese barberry (*Berberis thunbergii*) has been extensively bred, and many crosses have been made with related and sexually compatible barberries. It is planted in most areas of the University of Minnesota Twin Cities campuses. Barberry produces a fleshy drupe that is consumed and dispersed by birds. It has many sharp spines along the shoots and forms dense thickets. These thickets can prevent students from cutting across landscapes and provide excellent protection to small rodents (mice). As barberry populations increase, so do those of mice and other small rodents. Increased mouse populations are associated with increased tick populations (ticks are small, blood-sucking parasitic bugs) that may increase tick-borne diseases.



Japanese Barberry. James Gaither. CC BY-NC-SD 2.0.

Winged burning bush or winged euonymus (*Euonymus alatus*)

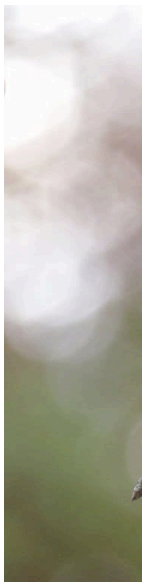
Winged burning bush or winged euonymus (*Euonymus alatus*) is small tree or shrub from eastern Russia, central China, Korea, and Japan. It is very popular for the interesting wings on its stems and its brilliant red fall foliage. Its popularity for shade or sun landscape planting and ability to escape from cultivation means that escaped populations often occur in nature. This video

shows a paddling trip to the Tellico River in Tennessee and the discovery of a large winged euonymus escaped from cultivation. Winged euonymus is adaptable to many growing conditions and forms dense canopies, reduces native native plant diversity. It is a popular landscape plant and still being propagated and sold in Minnesota. Fortunately, several researchers are breeding Euonymus cultivars with reduced or no seed set. How might these cultivars be propagated if they were sterile?



Euonymus alatus 'Compactus'. Leonora (Ellie) Enking. CC BY-SA 2.0


Winged burning bush young stem. Wisconsin First Detector Network. CC BY-NC 2.0.



Common buckthorn (*Rhamnus cathartica*)

Common buckthorn is native to Europe and Asia and is a highly invasive perennial understory shrub or tree. Although propagation and sale of common buckthorn (*Rhamnus cathartica*) are prohibited in Minnesota, it is common in both urban and natural habitats. There is, for example, a large and very old male buckthorn tree (a dioecious plant) at the corner of Cleveland Avenue North and Buford Avenue on "The Lawn" of the St. Paul Campus of the University of Minnesota.


Subopposite leaves on common buckthorn. Eli Sagor. CC BY-NC 2.0


Buckthorn fruit. Peter O'Connor. C

Buckthorn was introduced to North America as an ornamental shrub and used for living fence rows and wildlife habitat. It has since

spread aggressively across most of the northeast and upper Midwest through production and distribution of prolific fleshy fruit (middle photo, above). Common buckthorn has become a serious threat to native forest understory habitats, where it outcompetes native plant species. With such a large distribution, novel control methods are being tested such as goat grazing (above), which is showing success and has a reduced environmental impact compared to herbicide control.

These examples are a small sample of the plants that are known to be invasive in Minnesota. Fortunately for the horticulture industry, consumers, many scientists, and communities are engaged in eliminating invasive plants that have escaped into their environments.

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20.10.2: 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*.

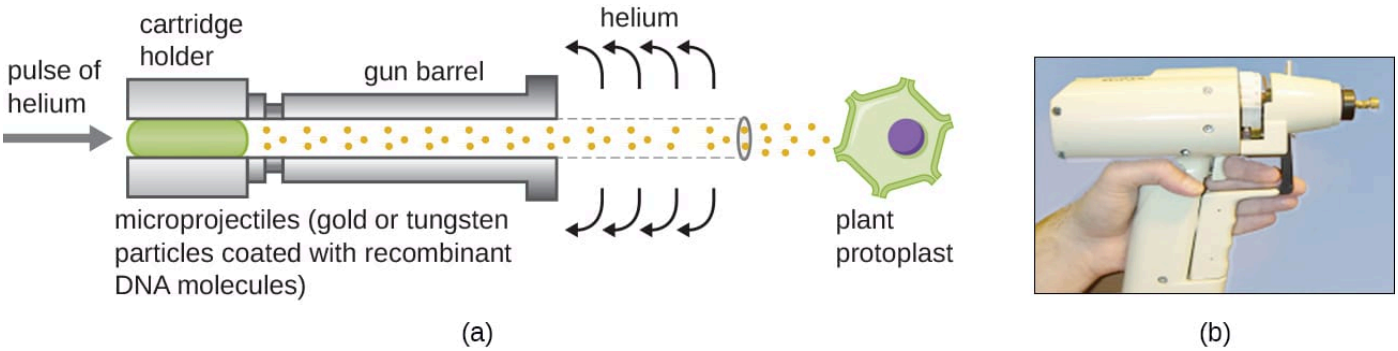


Diagram of gene gun process. OpenStax. CC BY 4.0.

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.

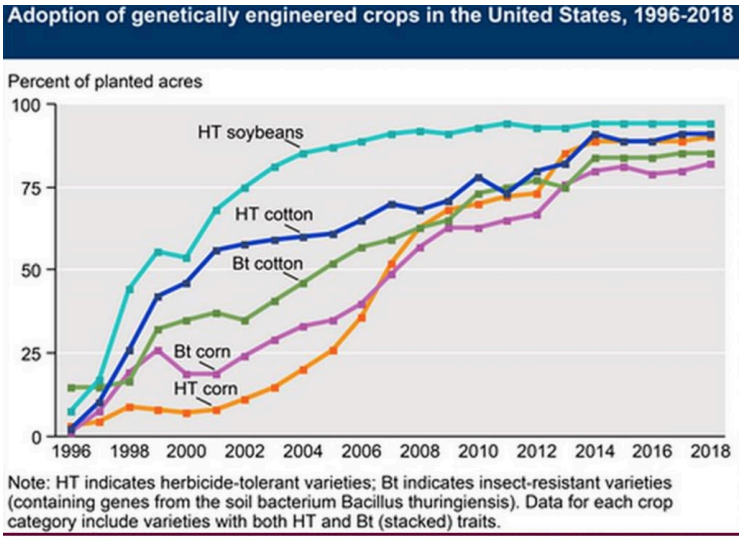
The art of GMO technology is discovering how non-plant organisms (virus, bacteria, fungi, insects, and so on) might contribute a gene to improve a plant, be it through weed control, increased nutrition in foods, or resistance to pests or viruses. GMO crops are produced by interdisciplinary teams with 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?

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20.10.3: Terms

These are the important terms from this chapter to be sure to know. You might also find these in later chapters.

Bi-parental cross	Cross between two different plants.
Conventional crop	Crop that is not GMO, with all of its genes originating from sexual reproduction.
Emasculate	Act of removing the anthers before pollen has been shed from a flower that is used as the female in breeding; used to reduce self-pollination when wanting to cross.
Exponential spread	Very rapid spread of an invasive plant as numbers and reproductive rates accelerate.
Genetic engineering	Manipulation and introduction of a transgene into a plant for a specific trait.
Genetic pollution	Where genes from GMO crops may escape to conventional crops or weedy relatives.
GMO	Genetically engineered organism or a plant containing a transgene .
Inbreeding	Producing seed by selfing over 5–7 generations to develop pure lines.
Invasive plant	Plant that is non-native to an ecosystem, and whose introduction causes or is likely to cause economic or environmental harm or harm to human health.
Lag phase	Phase during invasive plant spread that is slow due to a low number of plants being introduced.
Plant tissue culture	Method that uses synthetic growth media to provide the environment for mitotic cell divisions of plants and is used to regenerate a single cell into a whole plant.
Ploidy	Number of sets of homologous chromosomes in a cell.

Pure line	True breeding plant produced by inbreeding so it is homozygous at most loci and produces identical plants by seed .
Reciprocal cross	Matching cross where the pollinator becomes the female and female of the former cross becomes the pollen donor.
Rhizome	Horizontal stem growing just below the soil surface.
Super weed	Weed produced by crossing with a GMO crop; inherits the GMO trait, like herbicide tolerance.
Totipotent	Ability of a single plant cell to grow into a whole plant.
Transformation	Process of using the gene gun or *Agrobacterium tumefaciens* to introduce a transgene into a plant.
Transformed	Synonym for GMO, or plant carrying a transgene.
Transgene	Gene introduced into a plant from another organism, not through sexual reproduction.
Transgenic	Synonym for GMO, or plant carrying a transgene. .
Viral coat protein	Protein that surrounds the viral genome, protecting it; essential to virus replication. .

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21: PLANT BREEDING

Learning Objectives

- Understand the basic principles and goals of plant breeding, including hybridization and selection.
- Differentiate between sexual and asexual propagation methods and their impact on breeding strategies.
- Explain the role of emasculation in controlled crosses and identify when and how it is used.
- Compare breeding approaches for different crops, such as rose and tomato, based on their propagation and genetic characteristics.
- Recognize the historical development of plant breeding and the contributions of key figures and techniques.

This chapter introduces the fascinating world of plant breeding, showing how humans have shaped crops through both traditional and modern techniques. It explores how breeding strategies differ depending on whether a plant is propagated by seed (like tomatoes) or asexually (like roses). You'll learn about key practices like emasculation, hybridization, and selection, and how these methods are used to develop new plant varieties with desirable traits.

21.1: Plant Breeding

21.2: Propagating plants and developing new plants

21.3: Cataloging, Classification, and Deliberate Hybridizations

21.4: Terms

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21.1: Plant Breeding

Learning objectives

- 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)

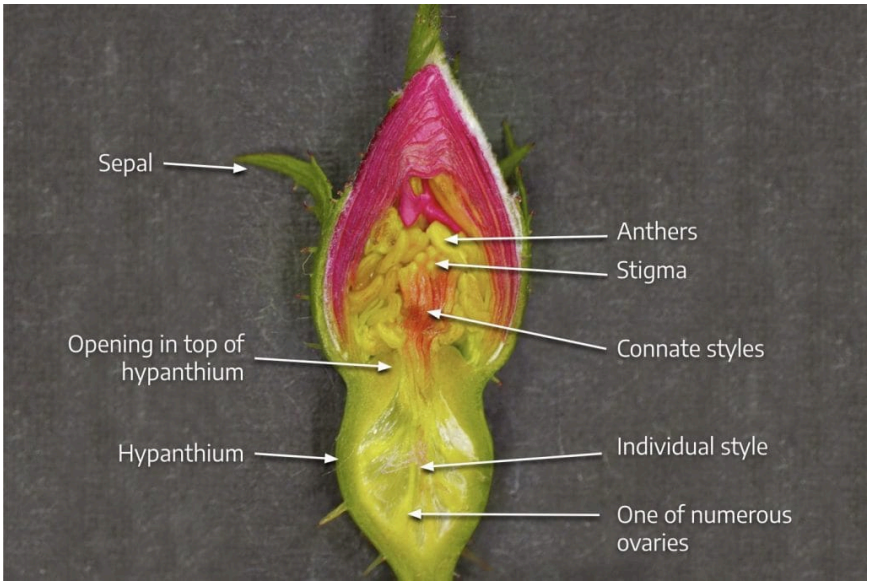


Photo by Eastfield College Microscopy Lab, Mesquite, TX, CC BY-NC.

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).



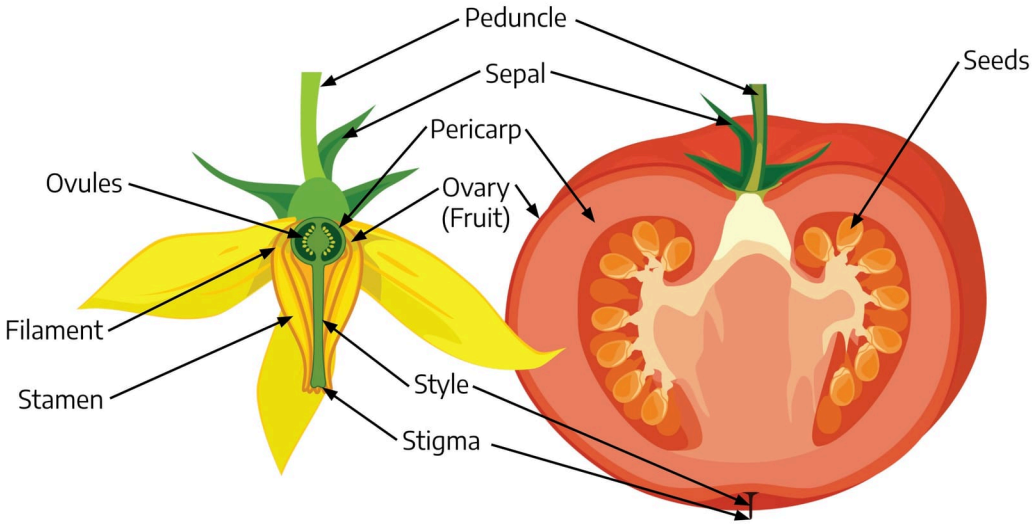
Nevada rose. T. Kiya. CC BY-SA 2.0

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?

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21.2: Propagating plants and developing new plants



Fig. 1 Propagating rice. Rice is an annual and must be replanted each year. In the above case, seeds are germinated, allowed to grow to a seedling and then transplanted to flooded fields. In other areas rice is grown on upland sites with seeds directly plant into the soil.

Ancient agriculture required plant propagation, making new plants. Plants don ' t live forever and many crops are annuals or are harvested less than a year after planting. Although the earliest agricultural efforts may not have involved intentionally propagating plants, fundamental to the development of agriculture was the acknowledgment that making new plants is an essential part of the process. The techniques used to propagate plant crops vary depending upon the crop. For most familiar crops it required storing some seed (i.e. not eating it) and planting it at some point in the future. For crops such as cereal grains and most legumes , where the seed is the part that is harvested and eaten, development of the ' store and plant ' technology was relatively straightforward and rapid. However crops such as tomato, squash and eggplant , where a fleshy fruit is harvested and the seeds are small and inconspicuous, required more technology: a recognition that seeds were present in the fruit and a method for processing of some of the fruit to obtain seeds for planting. Perennial plants do not require propagation each year, they could be maintained without propagation. But eventually they required some means of making new plants, especially if the agriculturalists are moving to a new area. For reasons discussed below, propagation of perennial plants often did not involve seeds but instead, asexual, means of propagation.

For most of its existence agriculture did not involve attempts to produce novel plants, plants with characteristics that distinguished them from their parents. However, the hope from the earliest onset of agriculture was that one might be able to improve the characteristics of the crop, producing crops that yielded more, tasted better, stored better, were easier to harvest, and were more tolerant of hardships, in particular, more tolerant of disease..Primitive farmers were happy when they found desirable novelties and also were able, knowingly or unknowingly, to gradually change the crops they grew. But they did not have the understanding and technology to intentionally create something novel. This has become possible over the last 100 years. Although an understanding of aspects of asexual reproduction was important for some crops, it was the recognition of the sexual process in pl ants, in particular the functioning of flowers and pollination , that has been critical to the development of the technologies of crop improvement (Figure 2). All of the major crops have been, and continue to be, intentionally modified. And this is one of the many factors that has changed, and made more complex, the business of agriculture. Where it was once basically controlled by a farmer who served both as a producer and salesman, it is now a vastly more complex system that depends on farmers, seed producers, researchers, fertilizer producers, equipment manufacturers, agricultural scientists, the government, and vast array of 'middle-men' .

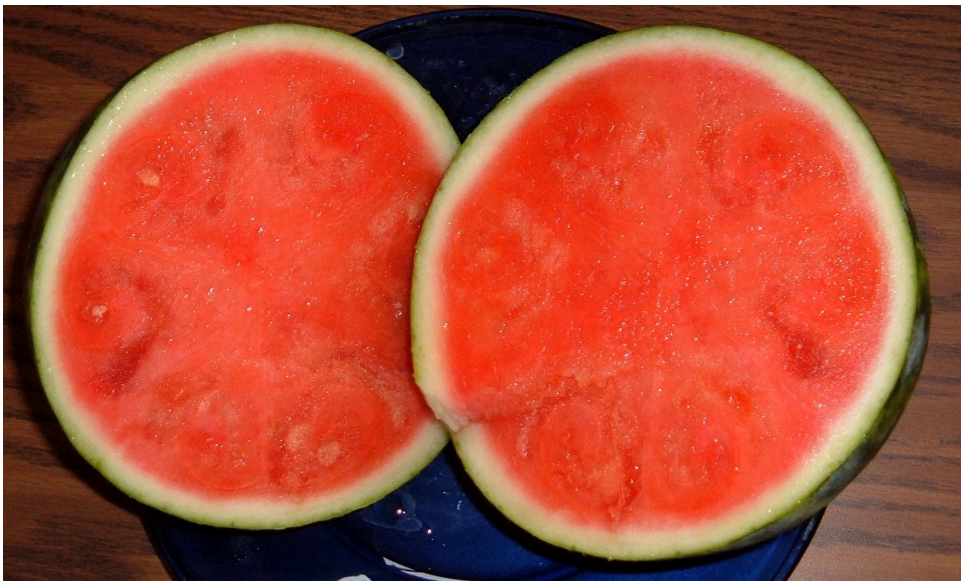


Figure 2 Seedless watermelon, a novel type of fruit developed recently that has the desirable feature of not producing seed. Although it produces no seed the plant that grew to produce this watermelon did come from a seed. It is a sterile hybrid, comparable to a mule.

TOPICS

- Asexual reproduction—propagation by cuttings
- Sexual reproduction by seeds and the importance of breeding system
- Hybrid seeds
- The green revolution
- Creating novel plants
  - grafting
  - generating variability
  - genetic engineering

Asexual reproduction

Most woody plants do not 'breed true' , meaning that if you plant a seed from your favorite apple tree, or from a 'wild' tree growing in the woods, it is highly unlikely that the seed will grow into a tree comparable to the parent. In fact, the apples that you might harvest will probably be less than desirable. Similar patterns would be found for grapes and olives, two ancient crops that have long been propagated not from seed but instead asexually. The easiest technique is 'rooting' , cutting a stem and placing it in moist soil in hopes that it will sprout roots (see the discussion adventitious roots in Chapter 8). A similar procedure can be done with roots, inducing them to produce new shoots. Since the middle of the 20th century an artificial plant hormone has been used to promote adventitious growth in shoots/roots that might not do so otherwise.

Obviously, asexual propagation does not produce novel material, it o nly perpetuates existing ones. It is important in a large number of vegetable crops including banana, pineapple, potato, sweet potatoes, cassava and many more. It also is the most common means of propagating of most ornamental flowering plants started in the greenhouse (e.g. geranium, begonia). For some of these plants (e.g. banana, naval oranges and some ornamental flowers) asexual reproduction is essential because the plant is a sterile hybrid and cannot produce viable seeds. For other species, e.g. potato (Figure 3), pineapple (Figure 4) and many others asexual reproduction is simply an easier means of propagation, eliminating the seedling stage which is sometimes more sensitive to conditions than cuttings are. A disadvantage of asexual propagation is that the clones are genetically uniform and thus crops are more susceptible to widespread failure (e.g. in late blight of potato). Another problem is that viral diseases are transmitted in cuttings but not through seeds.



Figure 3 Sprouts on a potato, these are branches growing from a modified stem (the potato). These will grow into new plants and is the primary means of propagating potato.



Figure 4 Pineapple is a monocarpic plant that dies after flowering. It is propagated by planting the 'top' of the fruit or by planting 'sprouts' that may appear at the base of the plant.

Sexual propagation —seeds and the significance of breeding system



Figure 5 Early 20th century seed catalog, showing several varieties of green beans.

Propagation by seeds is probably the most familiar process to most of us. For annual species grown as crops, propagation only requires the discipline to store seeds for the next season. Unlike asexual reproduction, sexual reproduction can result in variation. Variation has positive and negative effects on farming. On the one hand it allows for crop improvement and the production of novel plants (see below). On the other hand crop uniformity is generally helpful to agriculture because it makes cultural practices (e.g. planting and harvesting) more easily handled. Significant to crop variability is the breeding system of the crop. If the crop has a closed breeding system (Chapter 17) as the result of being apomictic or from having a bisexual flower and being self fertile, then offspring are likely to be the same as their parents and a crop may show little variation. Additionally, if a novel plant does appear, a closed breeding system makes it easier for a farmer to perpetuate plants with that specific feature. For instance, an important characteristic for cereal grains is to have 'non-shattering' heads, meaning inflorescences that do not shed their seeds, holding them on the plant and making harvesting easier. With a closed breeding system, seeds from non-shattering heads are likely to pass that feature on to their offspring since they may have no sexual process at all (apomixis) or are most likely to breed with themselves. In contrast, plants with a more open breeding system are more likely to be variable, with offspring that don 't all look alike and don' t necessarily look like their parent. And when a plant with favorable characteristics is found, it is more difficult to perpetuate these features through time. In fact, it is likely that these features will disappear quickly, from being 'washed out' by breeding with individuals that do not possess the feature. It is also significant that population size and reproductive isolation influence variability. A population of plants with an open breeding system may be very uniform if the population is small and reproductively isolated from other populations of the same plant, as can be the case for crop species.

Hybrid seed

Even before an understanding of the basis of genetics was developed the phenomenon of 'inbreeding depression' , had been noted: the decline in vigor in populations that are continually inbreeding. The degree to which this happens varies among species. It is probably not surprising that inbreeding depression is not a generally a problem for species with closed breeding systems. But for plants with open breeding systems, inbreeding can cause substantial reductions in crop yield. This was recognized by farmers and was part of the reason that seed companies, who took steps to avoid this problem, developed a clientele. Early in the 20th century plant breeders realized that although inbreed lines show reduced vigor, a 'hybrid cross' between two inbreed lines, produced plants that were more vigorous than either of the parental lines before they had been inbreed. Central to the production of hybrid seed is the need to control who breeds with whom. The technique requires that multiple generations bred only with close relatives, something that is easily accomplished by having populations isolated from each other. The next step is more difficult: ensuring that the inbreed lines NOT breed within the population but instead breed with individuals of another inbreed line. This was first done with corn, a plant with separate male and female flowers that are located in different parts of the plant. Crossing of inbreed lines can be accomplished by removing the male flowers (detasseling) from one inbreed line, thereby making these plants solely female and ensuring that if any seed is produced the male parent has come from a separate plant, usually from a second inbreed line that was planted nearby. Hybrid corn was first developed in the 1930's and became the dominant seed source by 1950, with yields increasing dramatically.

Large scale production of pure hybrid seed is nearly impossible in plants with perfect flowers (both male and female structures in the same flower). However, botanists discovered that it is possible to make plants with perfect flowers become unisexual. In the late 18th century workers noticed that not all pollen was viable and the ability to produce viable pollen sometimes often showed maternal inheritance. Later work indicated that there were cytoplasmic (i.e. non-nuclear) factors, inherited maternally (in plastids), that influence the production of viable pollen. Thus, geneticists were able to produce plants that were 'male sterile' , not able to produce viable pollen. Having plants that were unisexual (female) made the crosses that were needed to produce hybrid seed much more feasible. Hybrid seed production was further enhanced when 'restorer genes' were found that would restore the ability to make viable pollen. This allowed breeders to two cross two lines, one of which was unisexual, yet have the resulting hybrid produce flowers that are fully functional. Because of cytoplasmic male sterility the number of plants for which hybrid seed could be produced increased dramatically. Another means to the same end is the use of 'chemical hybridizing agents' , chemicals that make plants male (usually) sterile.

A negative consequence of planting hybrid seed is that seed cannot be stored year to year. Although the hybrid plant is vigorous, offspring of the hybrid plants are much less vigorous and also more variable. Growers utilizing hybrid seed need to purchase seed each year or switch to using open pollinated seeds instead of hybrid seed.

The Green Revolution

In the late 1960 's several scientists warned of an inevitable global famine, based in part on the assumption that crop yields could not be improved. Fortunately agricultural research, with a series of innovations that became known as the ' green revolution ' was able to drastically increase yield (Figure 6) and the global famine did not occur, although local famines continue to be a problem, usually the result of politics and war. Central to the green revolution were the efforts of Norman Borlaug, both as an agricultural researcher who developed high yielding varieties and as administrator who worked extensively to have new agricultural practices accepted by countries including Mexico, India and Pakistan. Central to the green revolution was hybrid seed and the development of new high yielding varieties of wheat and rice. Surprisingly, these varieties were actually dwarf plants. This had one direct effect: the problem of ' lodging' (plants being knocked over, usually as the result of wind) was lessened because the plants were shorter. But the new varieties also had a number of other features that helped to increase yield: increased seed production per plant, enhanced disease resistance (especially against rusts) and greater tolerance of drought or excessive rain. Also significant was that the new varieties would respond with increased yield to increased levels of fertilization. As a result of the new varieties and the new agricultural practices, crop yields more than doubled.

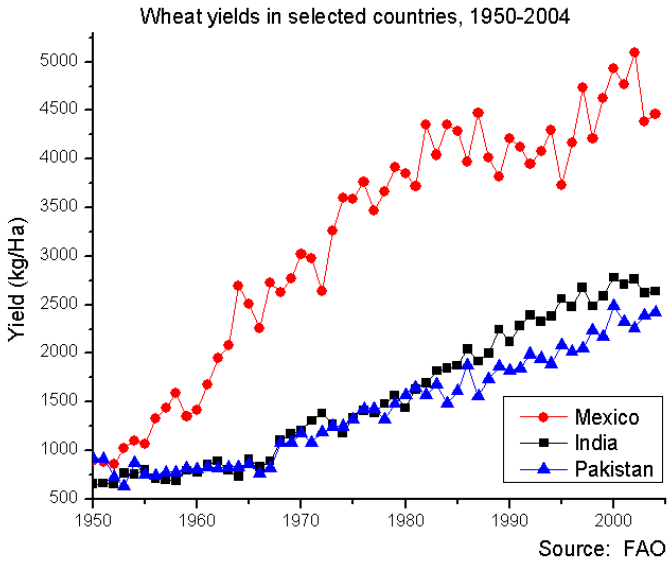


Figure 6 Changes in wheat yield in three countries during the 'Green Revolution'

How can crops be improved? And who does the work of crop development?

Crop development requires careful observations and recognition of individuals with favorable traits. By the end of the 19th century the importance of generating variability was increasingly recognized as being significant to crop development. However, in general, farmers desire crop uniformity because it makes growing and harvesting easier and their focus is on growing crops not

developing crops. During the 19th century, seeds were increasingly provided by the sources other than the farmer storing seeds or exchanging seeds with neighbors, and crop improvement was increasingly out of farmers'hands. During the latter half of the 19th century the federal government provided seed to anyone who asked for it. And, at the end of the century, land grant universities were charged with improving agriculture and this included developing improved varieties of crops. During this time period, private commercial seed companies became increasingly important as both a source of seeds and as a venue for improving crop quality.

Creating new plants using asexual methods of propagation

Although asexual reproduction is cloning, simply perpetuating what already exists, it has often been important in crop innovation. Novel plants are sometimes produced spontaneously by mutations of the seed or in branches of existing plants, and asexual reproduction of these mutants allows them to become new crops. This is what happened with navel oranges (Chapter 28), McIntosh apples (and many other apple varieties), poinsettia (Chapter 30), and a large number of ornamental plants. Cloning is also important as a means of perpetuating plants (generally hybrids) that have been created naturally (without human intervention) or artificially (with human intervention) that are unable to reproduce sexually.



Figure 7 Grafting two grapes together, the stem on the right comes from a North American rootstock. The stem on the left comes from a European variety that is valued for wine production. Successful grafting depends on the vascular cambium or the two plants fusing and then functioning normally as a lateral meristem.

Related to asexual reproduction is grafting, cutting a branch or bud off one plant and attaching it to a different plant, producing a novel organism, a chimera. There are a variety of reasons why this practice might be desirable, but one obvious one is in order to combine the favorable traits of two individuals into one individual, e.g. a good root system with a good shoot system. This is well represented by wine grape propagation. Stems from a European species are grafted on to root stocks from a North American species. The North American species produces inferior grapes for making wine but its root system can withstand attack from the insect pest *Phylloxera*. The root system of the European species is highly susceptible to *Phylloxera* but produces grapes of superior quality for wine. *Phylloxera* was mistakenly introduced from North America to Europe in the early 1800's and devastated European wine production. It was revived when workers were able to plant grapes composed of European shoots grafted on to North American rootstocks. Most fruit trees (apple, peach, plum) are similarly constructed with rootstocks that are vigorous and disease resistant grafted to shoots that produce desirable fruits.

Creating novel plants using the sexual process

Crossing with relatives

The relatives might be ancestral varieties that the crop originated from or species closely related to the crop. Technically, a crop species should should not hybridize with other species (i.e. it is an isolated gene pool, see Chapter 17) but sporadic seed production does occur. Although successful crosses may be infrequent, as long as there are some viable offspring, these

can be back-crossed to the original crop (i.e. cross the hybrid plants with plants from the parental population) with significant introduction of novel traits (i.e. variability) that may include desirable features. Occasionally, workers are successful crossing with more distant relatives (different genera, even different families). Part of this surprising possibility may be poor taxonomy (i.e. they actually are more closely related than depicted in the taxonomy) but apparently sometimes crosses can happen between plants that are not that closely related.

Polyploidy

For a cross to be successful the parents need to have the same chromosome number and the chromosomes of the two parents need to be similar enough that they can pair during meiosis. When hybrids between different species are produced they are generally sterile because of the inability to pair chromosomes during meiosis. Although the hybrid is sterile it is often possible to propagate it asexually , i.e. to clone the hybrid, . A number of ornamental plants are perpetuated this way. It also is what has occurred with banana, the plant that is cultivated is a sterile hybrid, unable to produce seed but thiis one of the features that make the commercial banana desirable! Another 'solution' to the problem of hybrid sterility is polyploidy, increasing the chromosome number. This sometimes happens without human involvement (see discussion of the evolution of wheat in Chapter 28) but in the last 100 years workers have developed techniques to promote polyploidy following hybridization, thereby creating a new species with characteristics of both parental lines.

Treatment with mutagens

A common means of generating variability, and perhaps producing favorable traits that can be selected for, is to treat the seeds with a chemical mutagen or radiation. Although most of the treated seeds do not survive or have unfavorable features, usually some seeds survive that may have desirable features. These plants can be crossed with existing varieties in hopes of introducing favorable features to the crop. The technique is also used with asexual propagation. The original ruby red grapefruit appeared as a sport on a normal grapefruit tree. Irradiation of branches of the original ruby red has produced the even redder varieties Rio Red and Star Ruby.

Genetically modified organisms

A much more focused technique of combining traits from different organisms is the production of 'GMO' s, genetically modified organisms; the phrase should be non-sensical to any trained biologist because all organisms are genetically modified, that is what evolution is about. But if we focus only on agricultural organisms the term has come to distinguish 'normal' agricultural organisms, all of which have a long and substantial history of genetic modification by humans from 'abnormal' agricultural organisms, ones produced using the relatively recent techniques of molecular biology that allow for much more focused genetic modification, with genes manipulated in various ways including: turned on, turned off, duplicated, removed and, in particular, moved from one organism to another. One famous example is 'golden rice' , rice to which additional genes, genes that would cause the rice produce beta-carotene, a vitamin D precursor, into the endosperm of the seed. A second example is 'Bt' corn, which has a gene derived from the bacterium *B acillus thuringiensis* , that produces a protein that is toxic to some insects, in particular the corn borer moth. Consequently 'Bt-corn' can avoid predation by corn borers. Interestingly, the bacterial toxins had been used by organic farmers, being mass produced by culturing *B. thuringiensis* , extracting the toxins and then spraying them on corn plants. A final example is 'Roundup ready' soybeans. Roundup is a commonly used herbicide that is effective because it blocks an important synthetic pathway. Plant molecular biologists were able to introduce genes into several crops, including soybean and cotton, that greatly reduced the the toxicity of roundup to these crops, making them 'roundup ready' . The advantage of modern molecular techniques is specificity: plants are modified in very specific ways. In contrast, developing new crops by hybridization or by chemical or radiational means will have multiple effects — yet the breeder is only paying attention to a small number of characters they are hoping to modify.

GMO 's have been vigorously opposed by a variety of groups for a variety of reasons. This opposition has decreased substantially in the last five years, partly because many of the problems that were cited have not appeared even though GMO plants have been in wide use over the last fifteen years. Any large-scale production of crops with novel characteristics will have possible risks but the GMO' s are probably one of the more benign techniques to generate variability. Consequently the production and use of GMO s is likely to increase in the coming years.

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21.3: 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).

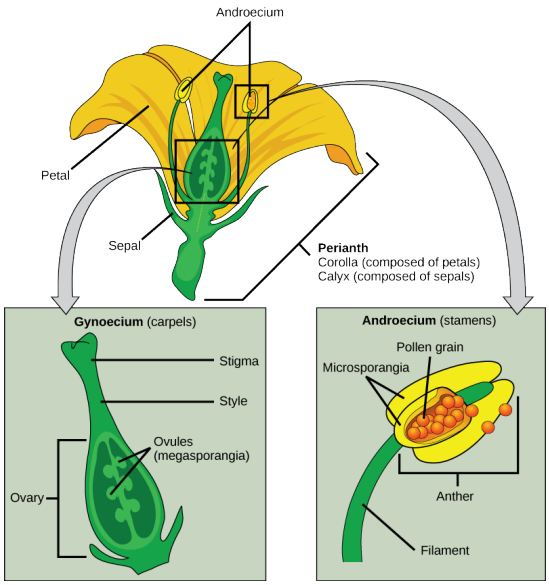


Fig 4.1 A flower is the reproductive organ of the angiosperms (flowering plants). A typical flower has four main parts—or whorls—known as the calyx, corolla, androecium, and gynoecium. The function of a flower is to produce gametes (egg cells and sperm cells), mediate the union of male and female gametes (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.

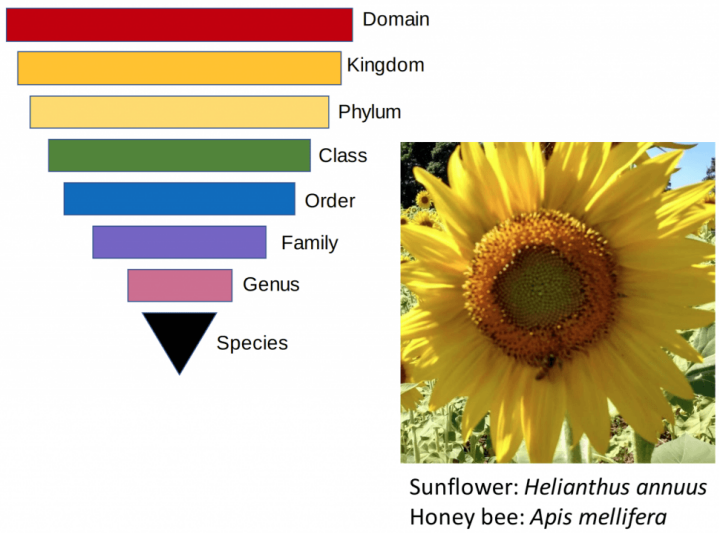


Fig 4.3 Binomial nomenclature proposed by Carl Linnaeus. "Binomial nomenclature" by Sushma Naithani is licensed under CC BY 4.0.

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.

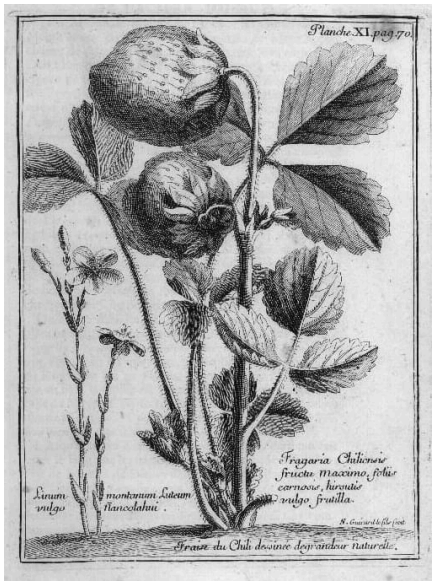


Fig 4.4 An illustration of Fragaria chiloensis (beach strawberry) by Amédée François Frézier (published in 'A voyage to the South-sea, and along the coasts of Chili and Peru, in the years 1712, 1713, and 1714'). "Planche XI" by Jean-Baptiste Scotin is in the public domain.

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.

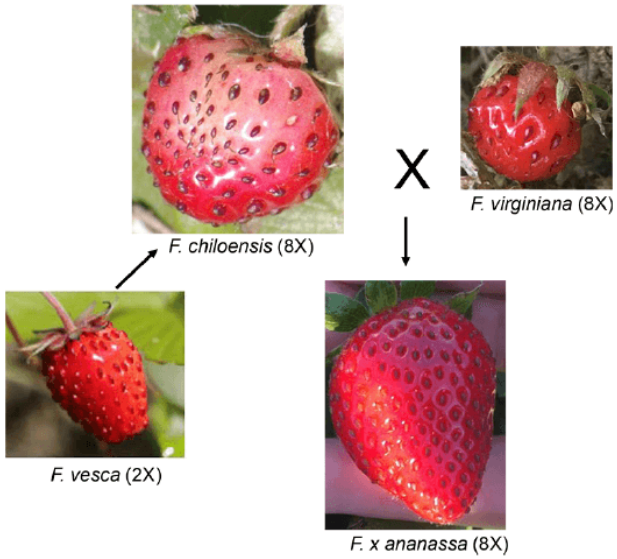


Fig 4.5 Garden strawberry, Fragaria x ananassa is an octoploid hybrid. "Garden Strawberry, Fragaria x ananassa" is a derivative of "Wild Strawberry – Fragaria vesca" by Björn S..., used under CC BY-SA 2.0, "Beach Strawberry Fragaria chiloensis" by Marisa Rafter, used under CC BY-NC 4.0, "Virginia Strawberry 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.

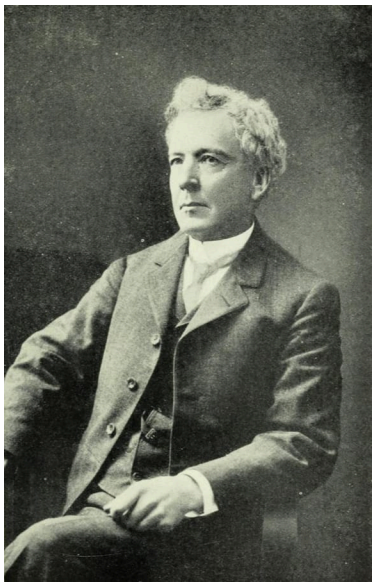


Fig 4.6 "Luther Burbank in 1915" by Gabriel Moulin is in the public domain.

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/

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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. ↵

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21.4: Terms

These are the important terms from this chapter to be sure to know. You might also find these in previous chapters.

Dominant allele	When one allele is expressed over the other alleles present.
Generative nucleus	Nucleus in the immature male gametophyte that will later divide by mitosis to produce two sperm cells.
Genes	Hereditary units consisting of a sequence of DNA that occupies a specific location on a chromosome (locus) and determines a particular characteristic in an organism. Genes undergo mutation when their DNA sequence changes.
Genotype	Genetic composition of an organism, including chromosomes of the nucleus and the DNA in chloroplasts and mitochondria.
Heritability	Measurement of a quantitative trait that passes from parent to offspring and is measured in high and low; high being similar between parent and offspring and low being dissimilar between parent and offspring.
Heterozygote	Plant with two different alleles of a particular gene and giving rise to varying offspring; offspring are generally more vigorous than offspring from homozygote.
Homozygote	Plant with identical alleles of a particular gene; gives rise to identical, or nearly identical, offspring.
Integument	Cells that form the ovary wall. Nucellus cells on the interior of the ovule wall develop into megaspore mother cells.
Linkage	When two genes are on the same chromosome.
Locus	Location on a chromosome where a particular gene is found.
Megaspornatium	Place in the ovary where the female gametophyte will be formed.
Mendel's First Law — the law of segregation	Principle that during gamete formation each member of the allelic pair separates from the other member to form the genetic constitution of the gamete; e.g., Ss diploid produces S and s gametes.
Mendel's Second Law — the law of independent assortment	Principle that during gamete formation the segregation of the alleles of one allelic pair is independent of the segregation of the alleles of another allelic pair.
Microsporangium	Place in the anther where the male gametophyte will be formed.
Phenotype	Physical appearance of an organism; expressed as Phenotype = Genotype + Environment
Punnett square	Simple database used to visualize the types of zygotes and their expected frequency that form from male and female gametes.
Qualitative differences	Large differences that can easily be seen or measured in qualitative terms; e.g. fruit color.
Quantitative differences	Small differences that are measured numerically; e.g. yield in kg/ha. Can be influenced by the environment.
Recessive allele	Allele(s) that are not expressed if a dominant allele is present; will be expressed if there is no dominant allele.
Suspensor	Produced by multiple mitotic cell divisions of the embryo's basal cell; the suspensor anchors the apical cell of the embryo to the ovule wall.
Synergid cells	Cells flanking the egg cell in the mature female gametophyte.
Tube nucleus, or vegetative nucleus	Nucleus in the male gametophyte that is associated with pollen tube growth.

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