BOTANY



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Botany (Ha, Morrow, and Algiers)

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1: INTRODUCTION TO BOTANY

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1.1: INTRODUCTION

Biology is the scientific study of living organisms and their interactions with one another and their environments. This is a very broad definition because the scope of biology is vast. Biologists may study small organisms, such as the microscopic blue-green algae that give us clues about the evolution of plants, or biomes such as the Mojave desert, shown here with a Joshua Tree in the foreground (Figure 1.1.1). Plant biology is the study of plants and their interactions with their environment.

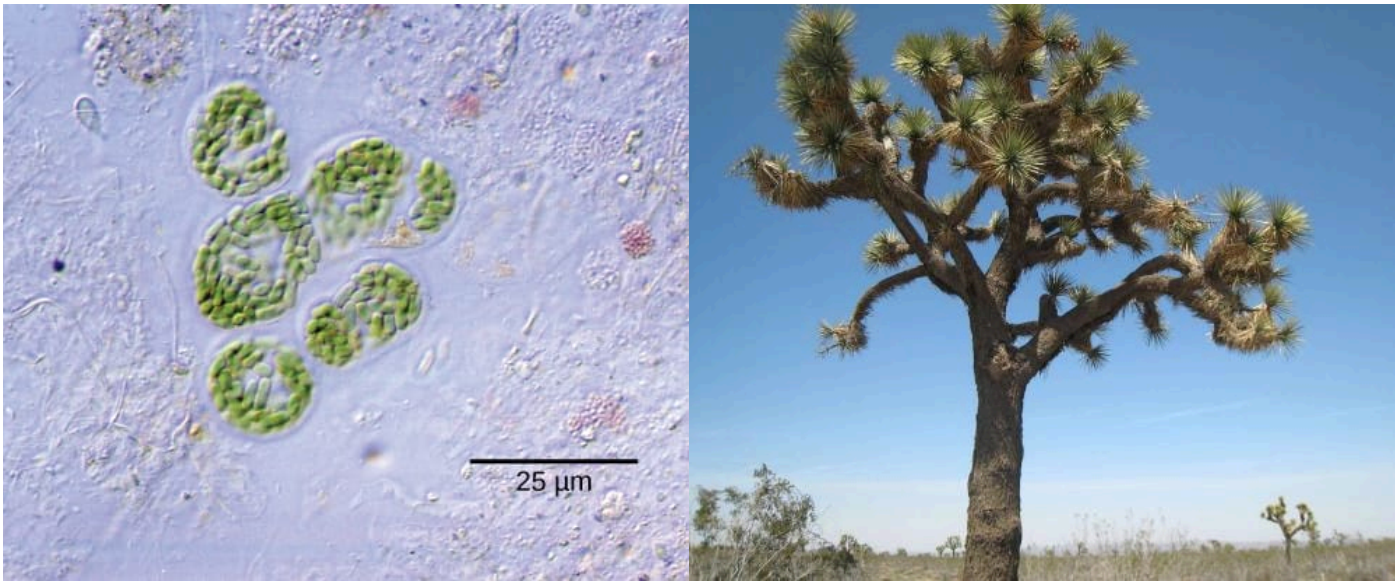


Figure 1.1.1: (a) Cyanobacteria, shown here at 300x magnification under a light microscope, are some of Earth's oldest life forms. (b) A Joshua Tree in the Mojave Desert. Credit a: modification of work by NASA; Credit b: Kammy Algiers (CC-BY).

Science (from the Latin scientia, meaning "knowledge") can be defined as knowledge of the physical or natural world through observation or experimentation. Scientists seek to understand the world and the way it operates. To do this, they use two methods of logical thinking: inductive reasoning and deductive reasoning. Biologists study the living world by posing questions about it and seeking science-based responses. The scientific method is a method of research with defined steps that include experiments and careful observation.

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1.1.1: The Scientific Method

Learning Objectives

- Identify the shared characteristics of the natural sciences.
- Summarize the steps of the scientific method.
- Compare inductive reasoning with deductive reasoning.
- Describe the goals of basic science and applied science.

The Process of Science

Science includes such diverse fields as astronomy, biology, computer sciences, geology, logic, physics, chemistry, and mathematics (Figure 1.1.1.1). However, those fields of science related to the physical world and its phenomena and processes are considered natural sciences. Natural sciences could be categorized as astronomy, biology, chemistry, earth science, and physics. One can divide natural sciences further into life sciences, which study living things and include biology, and physical sciences, which study nonliving matter and include astronomy, geology, physics, and chemistry. Some disciplines such as biophysics and biochemistry build on both life and physical sciences and are interdisciplinary. Natural sciences are sometimes referred to as "hard science" because they rely on the use of quantitative data; social sciences that study society and human behavior are more likely to use qualitative assessments to drive investigations and findings.

Not surprisingly, the natural science of biology has many branches or subdisciplines. Cell biologists study cell structure and function, while biologists who study anatomy investigate the structure of an entire organism. Those biologists studying physiology, however, focus on the internal functioning of an organism. Some areas of biology focus on only particular types of living things. For example, botanists explore plants, while zoologists specialize in animals.

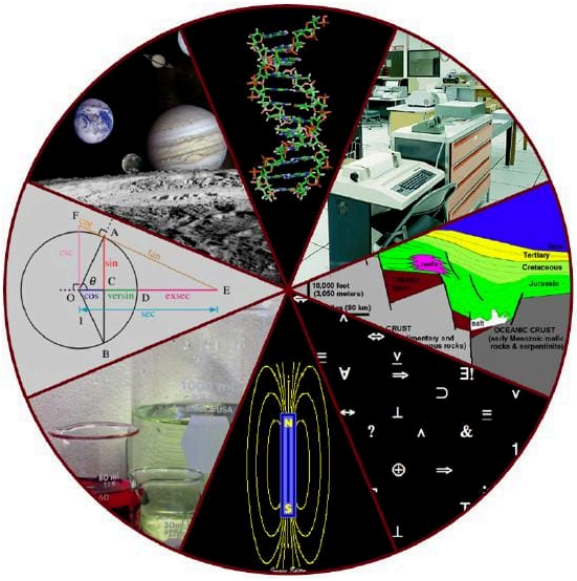


Figure 1.1.1.1: The diversity of scientific fields includes astronomy, biology, computer science, geology, logic, physics, chemistry, mathematics, and many other fields. (credit: "Image Editor"/Flickr)

Scientific Reasoning

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. To do this, they use two methods of logical thinking: 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 (numeric), 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.

Deductive reasoning, or deduction, is the type of logic used in hypothesis-based science. In deductive reason, the pattern of thinking moves in the opposite direction as compared to inductive reasoning; that is, specific results are predicted from a general premise. 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. Studies in climate change can illustrate this type of reasoning. For example, scientists may predict that if the climate becomes warmer in a particular region, then the distribution of plants and animals should change. These predictions have been made and tested, and many such changes have been found, such as the modification of arable areas for agriculture, with change based on temperature averages.

Inductive and deductive reasoning are often used in tandem to advance scientific knowledge (Example 1.1.1.1). 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**, which is usually inductive, aims to observe, explore, and discover, while **hypothesis-based science**, which is usually deductive, begins with a specific question or problem and a potential answer or solution that one can test. The boundary between these two forms of study is often blurred, and most scientific endeavors combine both approaches.

1.1.1.1 Exa

Here is an example of how the two types of reasoning might be used in similar situations.

In inductive reasoning, where a conclusion is drawn from a number of observations, one might **observe** that members of a species are not all the same, individuals compete for resources, and species are generally adapted to their environment. This observation could then lead to the **conclusion** that individuals most adapted to their environment are more likely to survive and pass their traits to the next generation.

In deductive reasoning, which uses a general premise to predict a specific result, one might start with that conclusion as a general premise, then predict the results. For example, from that premise, one might predict that if the average temperature in an ecosystem increases due to climate change, individuals better adapted to warmer temperatures will outcompete those that are not. A scientist could then design a study to test this prediction.

The Scientific Method

Biologists study the living world by posing questions about it and seeking science-based responses. The **scientific method** is a method of research with defined steps that include experiments and careful observation. The scientific method was used even in ancient times, but it was first documented by England's Sir Francis Bacon (1561–1626; Figure 1.1.1.2), who set up inductive methods for scientific inquiry. The scientific method is not exclusively used by biologists but can be applied to almost all fields of study as a logical, rational problem-solving method.

It is important to note that even though there are specific steps to the scientific method, the process of science is often more fluid, with scientists going back and forth between steps until they reach their conclusions.



Figure 1.1.1.2: Sir Francis Bacon (1561–1626) is credited with being the first to define the scientific method. (credit: Paul van Somer)

Observation and Question

Scientists are good observers. In the field of biology, naturalists will often will make an observation that leads to a question. A **naturalist** is a person who studies nature. Naturalists often describe structures, processes, and behavior, either with their eyes or with the use of a tool such as a microscope. A naturalist may not conduct experiments, but they may ask many good questions that can lead to experimentation. Scientists are also very curious. They will research for known answers to their questions or run experiments to learn the answer to their questions.

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?"

Proposing a Hypothesis

A **hypothesis** is an educated guess or a suggested explanation for an event, which can be tested. Sometimes, more than one hypothesis may be proposed. Once a hypothesis has been selected, the student can make a prediction. A prediction is similar to a hypothesis but it typically has the format "If . . . then . . . .".

For example, one hypothesis might be, "The classroom is warm because no one turned on the air conditioning." However, there could be other responses to the question, and therefore one may propose other hypotheses. A second hypothesis might be, "The classroom is warm because there is a power failure, and so the air conditioning doesn't work." In this case, you would have to test both hypotheses to see if either one could be supported with data.

A hypothesis may become a verified **theory**. This can happen if it has been repeatedly tested and confirmed, is general, and has inspired many other hypotheses, facts, and experimentations. Not all hypotheses will become theories.

Testing a Hypothesis

A valid hypothesis must be testable. It should also be **falsifiable**, meaning that it can be disproven by experimental results. Importantly, science does not claim to "prove" anything because scientific understandings are always subject to modification with further information. This step—openness to disproving ideas—is what distinguishes sciences from non-sciences. The presence of the supernatural, for instance, is neither testable nor falsifiable. To test a hypothesis, a researcher will conduct one or more experiments designed to eliminate one or more of the hypotheses. 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. The **control group** contains every feature of the experimental group except that it was not manipulated. Therefore, if the results of the experimental group differ from the control group, the difference must be due to the hypothesized manipulation, rather than some outside

factor. Look for the variables and controls in the examples that follow. To test the first hypothesis, the student would find out if the air conditioning is on. If the air conditioning is turned on but does not work, there should be another reason, and this hypothesis should be rejected. To test the second hypothesis, the student could check if the lights in the classroom are functional. If so, there is no power failure, and this hypothesis should be rejected. Each hypothesis should be tested by carrying out appropriate experiments. 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 1.1.1.3). Using the scientific method, the hypotheses that are inconsistent with experimental data are rejected.

While this “warm classroom” example is based on observational results, other hypotheses and experiments might have clearer controls. For instance, a student might attend class on Monday and realize she had difficulty concentrating on the lecture. One observation to explain this occurrence might be, “When I eat breakfast before class, I am better able to pay attention.” The student could then design an experiment with a control to test this hypothesis.

Visual Connection

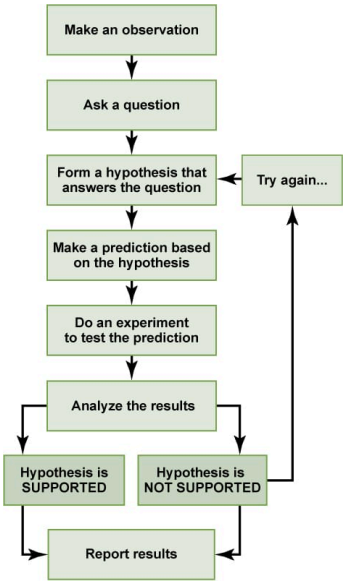


Figure 1.1.1.3: The scientific method consists of a series of well-defined steps. In step 1, an observation is made. In step 2, a question is asked about the observation. In step 3, an answer to the question, called a hypothesis, is proposed. In step 4, a prediction is made based on the hypothesis. In step 5, an experiment is done to test the prediction. In step 6, the results are analyzed to determine whether or not the hypothesis is correct. If a hypothesis is not supported by experimental data, one can propose a new hypothesis. In either case, the results are reported.

The scientific method may seem too rigid and structured. It is important to keep in mind that, although scientists often follow this sequence, there is flexibility. 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. Notice, too, that the scientific method can be applied to solving problems that aren’t necessarily scientific in nature (Example 1.1.1.2).

1.1.1.2 Exa

In the example below, the scientific method is used to solve an everyday problem. Match the scientific method steps (numbered items) with the process of solving the everyday problem (lettered items). Based on the results of the experiment, is the hypothesis correct? If it is incorrect, propose some alternative hypotheses.

Steps of the Scientific Method

1. Observation
2. Question
3. Hypothesis (answer)
4. Prediction
5. Experiment
6. Result

Process of Solving an Everyday Problem

A. There is something wrong with the electrical outlet.
B. If something is wrong with the outlet, my coffee maker also won't work when plugged into it.
C. My toaster doesn't toast my bread.
D. I plug my coffee maker into the outlet.
E. My coffee maker works.
F. Why doesn't my toaster work?

Two Types of Science: Basic Science 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 to 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 a practical 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 or find a cure for a particular disease. 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 wide knowledge foundation 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, DNA makes new copies of itself, shortly before a cell divides. 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 their genome.) Other less complex organisms have also been studied as part of this project in order to gain a better understanding of human chromosomes. The Human Genome Project (Figure 1.1.1.4) relied on basic research carried out with simple organisms and, later, with the human genome. An important end goal eventually became using the data for applied research, seeking cures and early diagnoses for genetically related diseases.

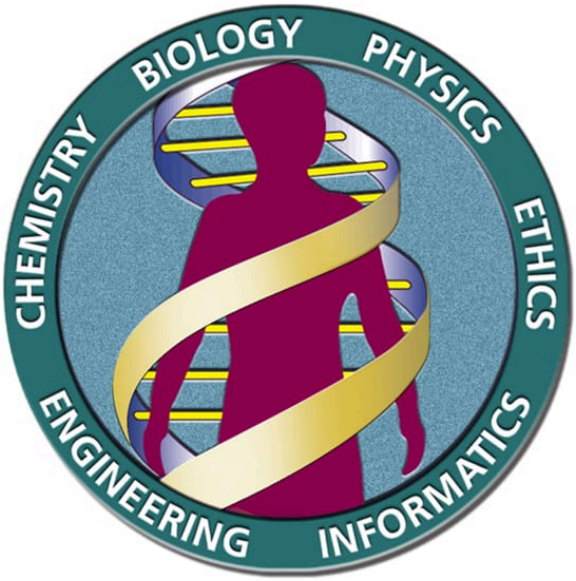


Figure 1.1.1.4: The Human Genome Project was a 13-year collaborative effort among researchers working in several different fields of science. The project, which sequenced the entire human genome, was completed in 2003. (credit: The U.S. Department of Energy Genome Programs)

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 on the dish, 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 in order for other researchers to expand and build upon their discoveries. Collaboration with other scientists—when planning, conducting, and analyzing results—are all important for scientific research. For this reason, important aspects of a scientist's work are communicating with peers and disseminating results to peers. Scientists can share results by presenting them at a scientific meeting or conference (Figure 1.1.1.5), but this approach can reach only the select few who are present. Instead, most scientists present their results in **peer-reviewed manuscripts** that are published in scientific journals. Peer-reviewed manuscripts are scientific papers that are reviewed 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.



Figure 1.1.1.5: Scientific conferences are one means of reporting scientific findings. Often, scientists present findings that they plan to publish or have recently published at conferences. These are the recipients of PLANTS Grant for undergraduates to attend BOTANY 2018, a conference organized by the Botanical Society of America. Image by The Botanical Society of America (CC-BY-NC-SA).

A scientific paper is very different from creative writing. Although creativity is required to design experiments, there are fixed guidelines when it comes to presenting scientific results. First, scientific writing must be brief, concise, and accurate. A scientific paper needs to be succinct but detailed enough to allow peers to reproduce the experiments.

The scientific paper consists of several specific sections—introduction, materials and methods, results, and discussion. This structure is sometimes called the "IMRaD" format, an acronym for Introduction, Method, Results, and Discussion. There are usually acknowledgment and reference sections as well as an **abstract** (a concise summary) at the beginning of the paper. There might be additional sections depending on the type of paper and the journal where it will be published; for example, some review papers require an outline.

The **introduction** starts with brief, but broad, background information about what is known in the field. A good introduction also gives the rationale of the work; it justifies the work carried out and also briefly mentions the end of the paper, where the hypothesis or research question driving the research will be presented. The introduction refers to the published scientific work of others and therefore requires citations following the style of the journal. Using the work or ideas of others without proper citation is considered plagiarism.

The **materials and methods** section includes a complete and accurate description of the substances used, and the method and techniques used by the researchers to gather data. The description should be thorough enough to allow another researcher to repeat the experiment and obtain similar results, but it does not have to be verbose. This section will also include information on how measurements were made and what types of calculations and statistical analyses were used to examine raw data. Although the materials and methods section gives an accurate description of the experiments, it does not discuss them.

Some journals require a results section followed by a discussion section, but it is more common to combine both. If the journal does not allow the combination of both sections, the results section simply narrates the findings without any further interpretation. The **results** are presented by means of tables or graphs, but no duplicate information should be presented. In the **discussion** section, the researcher will interpret the results, describe how variables may be related, and attempt to explain the observations. It is indispensable to conduct an extensive literature search to put the results in the context of previously published scientific research. Therefore, proper citations are included in this section as well.

Finally, the **conclusion** section summarizes the importance of the experimental findings. While the scientific paper almost certainly answered one or more scientific questions that were stated, any good research should lead to more questions. Therefore, a well-done scientific paper leaves doors open for the researcher and others to continue and expand on the findings.

Review articles do not follow the IMRaD format because they do not present original scientific findings (they are not primary literature); instead, they summarize and comment on findings that were published as primary literature and typically include extensive reference sections.

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1.1.2: 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 1.1.2.1) 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 1.1.2.1: 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 1.1.2.2).



Figure 1.1.2.2. 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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1.1.3: 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 1.1.3.1: 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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1.1.4: 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 1.1.4.1).

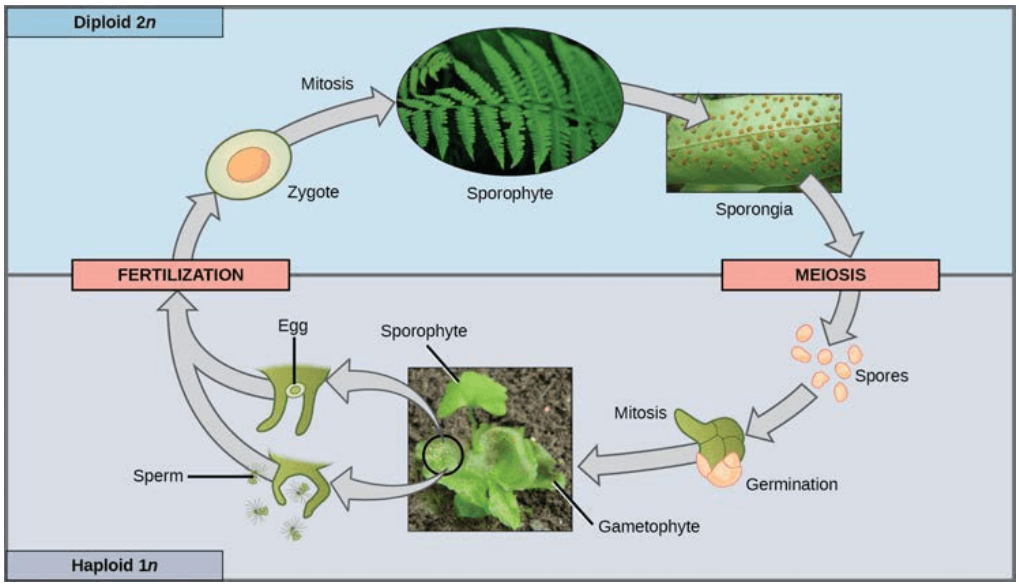


Figure 1.1.4.1: The plant life cycle is haplodiplontic (alternations of generations). Fern is shown as an example. The haploid (n) multicellular life stage is called the gametophyte as it produces gametes (egg and sperm cells) that fuse during fertilization to form a diploid (2n) zygote. This zygote 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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1.1.5: 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 1.1.5.1). 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.

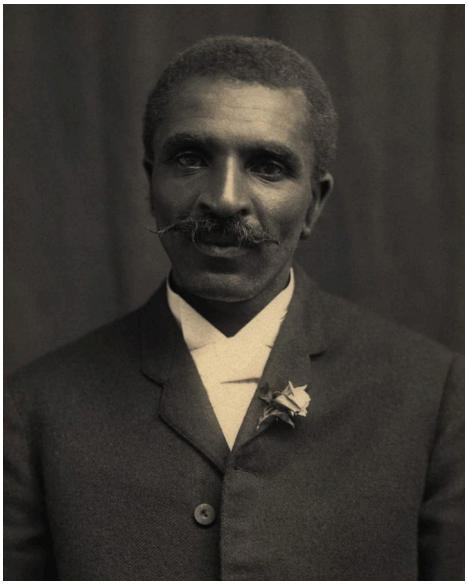


Figure 1.1.5.1: George Washington Carver was an American agricultural scientist and inventor who promoted crop rotation to prevent soil depletion. He was the most prominent Black scientist of the early 20th century. (Wikipedia; Public Domain)

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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1.1.6: Chapter Summary

Biology is the science that studies living organisms and their interactions with one another and their environments. **Plant biology** is the study of plants and their interactions with their environment. **Science** (from the Latin scientia, meaning “knowledge”) can be defined as knowledge of the physical or natural world through observation or experimentation. Science attempts to describe and understand the nature of the universe in whole or in part by rational means. Science has many fields; those fields related to the physical world and its phenomena are considered **natural sciences**.

Scientists seek to understand the world and the way it operates. To do this, they use two methods of logical thinking: inductive reasoning and deductive reasoning. **Inductive reasoning** uses particular 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**, a step-based process that consists of making observations, defining a problem, posing **hypotheses**, testing these hypotheses, and drawing one or more conclusions. The testing uses proper controls. 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 science**, however, is to solve practical problems.

A scientific **research paper** consists of several well-defined sections: introduction, materials and methods, results, and, finally, a concluding discussion. **Review papers** summarize the research done in a particular field over a period of time.

Plants are 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. They have a **haplodiplontic life cycle**, which alternates between two multicellular life stages: the haploid **gametophyte** and the diploid **sporophyte**. Fungi, photosynthetic prokaryotes, algae, and some heterotrophic "protists" are also commonly studied as part of **botany**.

The history of life on Earth goes back more than three and a half billion years. 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 mechanisms that is responsible for the diversity of species on Earth today.

A few examples of subfields of plant biology are **ethnobotany**, **agriculture science**, **phytochemistry**, **systematic botany**, and **plant ecology**.

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

- Identify the shared characteristics of the natural sciences.
- Summarize the steps of the scientific method.
- Compare inductive reasoning with deductive reasoning.
- Describe the goals of basic science and applied science.
- Describe the importance of plants in the study of botany and list other organisms that typically included in the study of botany.
- Describe the role of evolution in the history of life.
- Describe the role of natural selection in evolution.
- Describe the role of ploidy in the haplodiplontic (alternation of generations) life cycle of plants.
- Compare and contrast gametophyte and sporophyte generations.
- Describe the various subdisciplines of plant biology.

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2: BIODIVERSITY (ORGANISMAL GROUPS)

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

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

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



Figure \(\PageIndex{1}\): This photo includes many of the organisms mentioned above. The central mushrooms are part of a lichen relationship, *Lichenomphalia umbellifera*, which includes a fungus and a green alga. The mushrooms are surrounded by mosses (of the bryophytes), ferns (from the seedless vascular plants), and a branch from a conifer (belonging to the gymnosperms) lays across them. Among the mosses, microscopic diatoms can likely be found living epiphytically, as well as free-living cyanobacteria. Uncharacteristically, one of the few lineages not pictured here is angiosperms. Perhaps they are all growing upon a fallen tanoak or some other hardwood tree. Photo Credit: Richard Tehan, CC BY-NC.

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2.1.2: Organizing Life on Earth

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2.1: SYSTEMATICS

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2.1.1: Introduction

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



Figure 2.1.1.1: The life of a bee is very different from the life of a flower, but the two organisms are related. Both are members the domain Eukarya and have cells containing many similar organelles, genes, and proteins. (credit: modification of work by John Beetham)

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2.1.2: Organizing Life on Earth

Learning Objectives

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

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

Phylogenetic Trees

Scientists use a tool called a phylogenetic tree to show the evolutionary pathways and connections among organisms. A phylogenetic tree is a diagram used to reflect evolutionary relationships among organisms or groups of organisms. Scientists consider phylogenetic trees to be a hypothesis of the evolutionary past since one cannot go back to confirm the proposed relationships. In other words, a “tree of life” can be constructed to illustrate when different organisms evolved and to show the relationships among different organisms (Figure 2.1.2.1).

Unlike a taxonomic classification diagram, a phylogenetic tree can be read like a map of evolutionary history. Many phylogenetic trees have a single lineage at the base representing a **common ancestor**. Scientists call such trees **rooted**, which means there is a single ancestral lineage (typically drawn from the bottom or left) to which all organisms represented in the diagram relate. Notice in the rooted phylogenetic tree that the three domains— Bacteria, Archaea, and Eukarya—diverge from a single point and branch off. The small branch that plants and animals (indicated with a "you are here" star in Figure 2.1.2.1) occupy in this diagram shows how recent and miniscule these groups are compared with other organisms. **Unrooted** trees don’t predict a common ancestor but do show relationships among species.

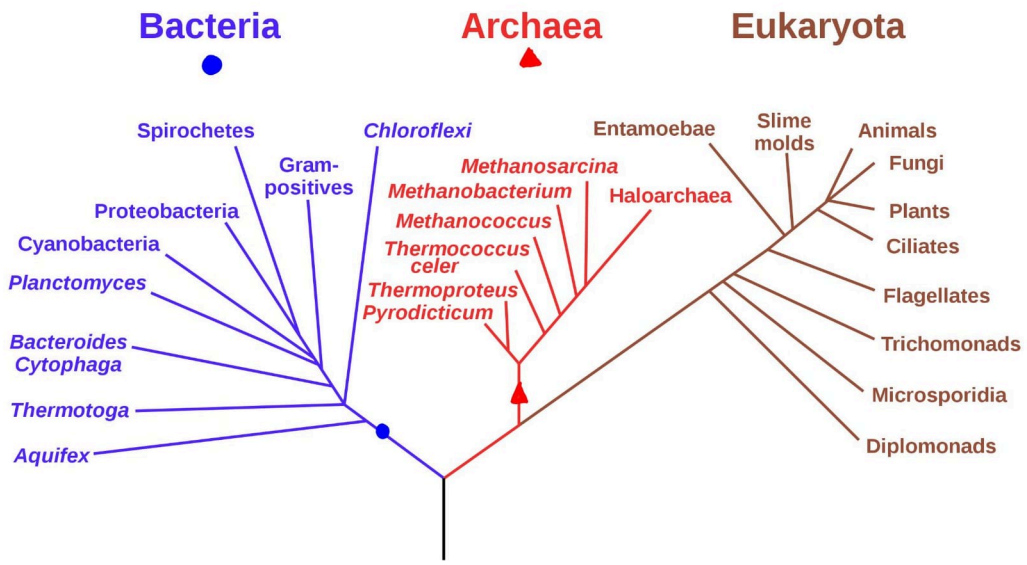


Figure 2.1.2.1: The phylogenetic tree in part a is rooted and resembles a living tree, with a common ancestor indicated as the base of the trunk. Two branches form from the trunk. The left branch leads to the domain Bacteria. The right branch branches again, giving rise to Archaea and Eukarya. Smaller branches within each domain indicate the groups present in that domain. The phylogenetic tree in part B is unrooted. It does not resemble a living tree; rather, groups of organisms within the Archaea, Eukarya, and Bacteria domains are arranged in a circle. Lines connect the groups within each domain. The groups within Archaea and Eukarya are then connected together. A line from the Archaea/Eukarya domains, and another from the Bacteria meet in the center of the circle. There is no root, and therefore no indication of which domain arose first. Both of these phylogenetic trees shows the relationship of the three domains of life—Bacteria, Archaea, and Eukarya—but the (a) rooted tree attempts to identify when various species diverged from a common ancestor while the (b) unrooted tree does not. (credit a: modification of work by Eric Gaba)

In a rooted tree, the branching indicates evolutionary relationships (see Figure 2.1.2.2). The point where a split occurs, called a **branch point** or node, represents where a single lineage evolved into a distinct new one. A lineage that evolved early from the root and remains unbranched is called a **basal taxon**. When two lineages stem from the same branch point, they are called **sister taxa**. A branch with more than two lineages is called a **polytomy** and serves to illustrate where scientists have not definitively determined all of the relationships. It is important to note that although sister taxa and polytomy do share an ancestor, it does not mean that the groups of organisms split or evolved from each other. Organisms in two taxa may have split apart at a specific branch point, but neither taxa gave rise to the other.

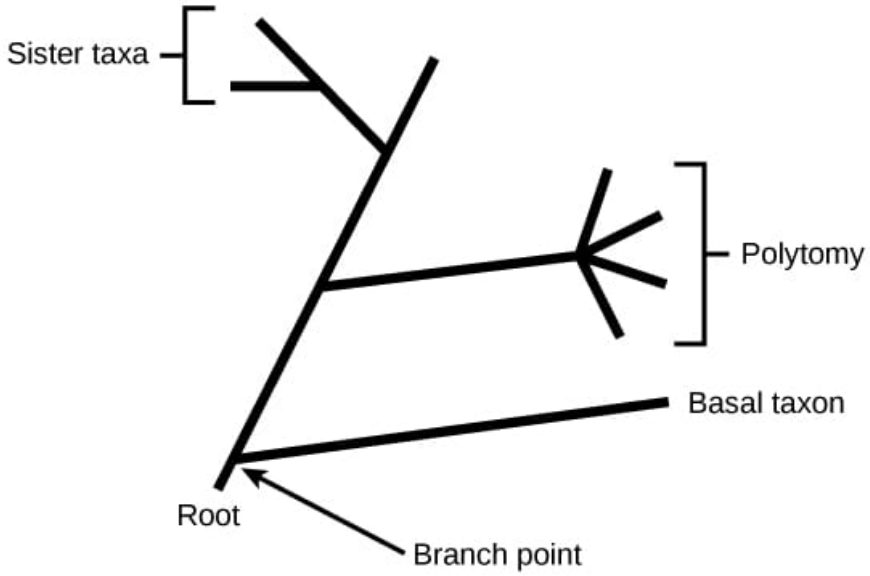


Figure 2.1.2.2: The root of a phylogenetic tree indicates that an ancestral lineage gave rise to all organisms on the tree. A branch point indicates where two lineages diverged. A lineage that evolved early and remains unbranched is a basal taxon. When two lineages stem from the same branch point, they are sister taxa. A branch with more than two lineages is a polytomy. Descriptive text: A phylogenetic tree that starts at a root, indicating that all organisms on the tree share a common ancestor. Shortly after the root, the tree branches out. One branch gives rise to a single, basal lineage (basal taxon), and the other gives rise to all other organisms on the tree. The next branch forks at one point into four different lineages, an example of polytomy. The final branch gives rise to two lineages, an example of sister taxa.

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

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

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

Examples of Simple Trees

In Figure 2.1.2.3 and Figure 2.1.2.4, some example trees are drawn to show how to interpret the structure of a phylogenetic tree.

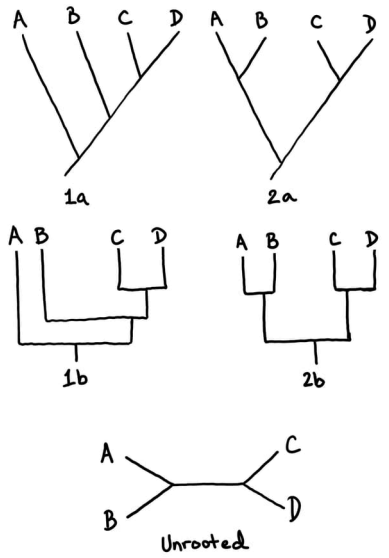


Figure 2.1.2.3: These diagrams show hypotheses for four different taxa: A, B, C, and D. These taxa could represent individuals, different species, or any other level of classification. Trees 1a and 1b are drawn differently but represent the same hypothesis: C and D are most closely related (sister taxa) and A is the most ancestral lineage. Trees 2a and 2b represent a slightly different hypothesis: C and D are sister taxa, but A and B are also sister taxa; neither lineage is depicted as "older" than the other. This last relationship is also represented in the "Unrooted" tree: there is no hypothesis in this tree for which group is most ancestral (no "root"). Images drawn by Maria Morrow, CC-BY-NC.

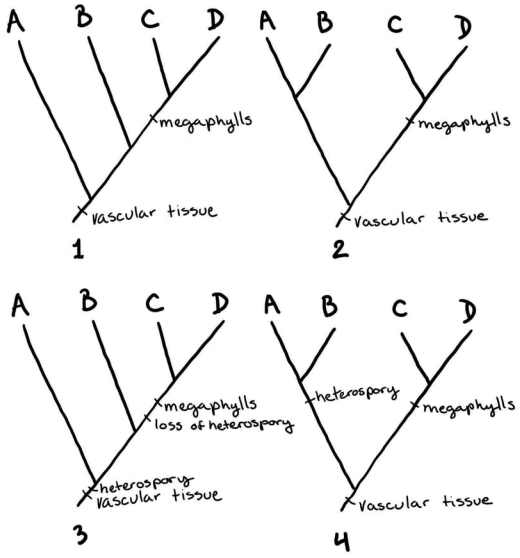


Figure 2.1.2.4. Vascular tissue appears on the root of the trees as an ancestral trait. This means that A, B, C, and D all have vascular tissue. Megaphylls appears in both trees as a shared derived characteristic (synapomorphy) of C and D. This means C and D have megaphylls, but A and B do not. Both tree 1 and tree 2 are equally parsimonious. In trees 3 and 4, a third trait has been added: heterospory. In addition to the information from trees 1 & 2, we now see that A and B are heterosporous, while C and D are not. In tree 3, heterospory appears as an ancestral trait which is lost in C and D. In tree 4, heterospory is a synapomorphy of A and B. Tree 3 has four changes, while tree 4 only has three. This means that tree 4 is more parsimonious and therefore more likely (though not necessarily correct!). Images drawn by Maria Morrow, CC-BY-NC.

The Levels of Classification

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

The taxonomic classification system (also called the Linnaean system after its inventor, Carl Linnaeus, a Swedish botanist, zoologist, and physician) uses a hierarchical model. Moving from the point of origin, the groups become more specific, until one branch ends as a single species. As you saw in Figure 2.1.2.1, scientists divide organisms into three large categories called **domains**: Bacteria, Archaea, and Eukarya. Within each domain is a second category called a **kingdom**. Each domain might encompass many kingdoms. For example, kingdom Plantae, kingdom Animalia, and kingdom Fungi represent three of the many kingdoms contained within domain Eukarya. After kingdoms, the subsequent categories of increasing specificity are: **phylum, class, order, family, genus,** and **species** (Figure 2.1.2.5).

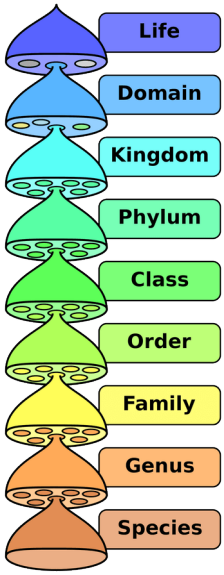


Figure 2.1.2.5: The taxonomic classification system uses a hierarchical model to organize living organisms into increasingly specific categories. Within what we have currently described as life, there are three domains. Within each domain, there are kingdoms. Within each kingdom, there are phyla. Within phyla there are classes, within classes there are orders, within orders there are families, within families there are genera, and within genera there are species. Diagram by Pengo, Public domain, via Wikimedia Commons.

The kingdom Plantae stems from the Eukarya domain. For the shore pine (*Pinus contorta var. contorta*), the classification levels would be as shown in Figure 2.1.2.6. Therefore, the full name of an organism technically has multiple terms associated. For the shore pine, it is: Eukarya, Plantae, Pinophyta, Pinopsida, Pinales, Pinaceae, *Pinus*, *Pinus contorta,* and var. *contorta*. Notice that each name is capitalized except for the specific epithet (contorta), and the genus and species names are italicized. Notice also the underlined endings of the words. In plant taxonomy, the underlined portion is always used for those taxonomic levels: phyla end in -phyta, classes end in -opsida, orders end in -ales, and families end in -aceae.

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

Figure 2.1.2.6 shows how the levels move toward specificity with other organisms. Notice how the shore pine (leftmost image) shares a domain with the widest diversity of organisms, including plants, fungi, algae, and animals. At each sublevel, the organisms become more similar because they are more closely related. Historically, scientists grouped similar organisms using characteristics, but as DNA technology developed, more precise relationships have been determined.

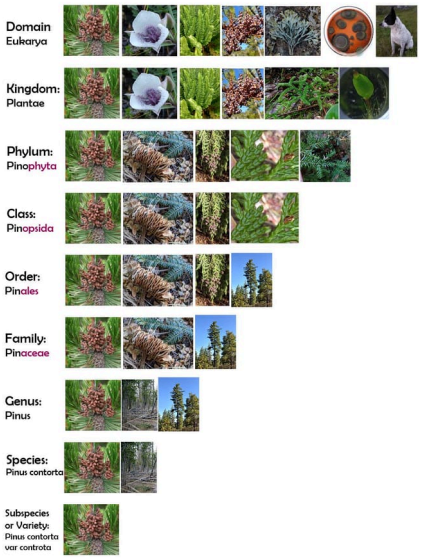


Figure 2.1.2.6: At each sublevel in the taxonomic classification system, organisms become more similar. Author's note: The reduction is slightly artificial in this diagram, as Pinales is the only order within Pinopsida. Figure and images by Maria Morrow, CC-BY-NC, except: the lodgepole pine, which comes from the public domain in the Wikimedia Commons, retrieved from the following page [1] of the Yellowstone Digital Slide Files archives; the *Pinus contorta* var *contorta* image, by Janice S, CC-BY-NC.

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

Summary

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

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2.1.3: Determining Evolutionary Relationships

Learning Objectives

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

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

Two Options for Similarities

In general, organisms that share similar physical features and genomes tend to be more closely related than those that do not. Such features that overlap both morphologically (in form) and genetically are referred to as **homologous structures** and stem from developmental similarities that are based on evolution. For example, the bones in the wings of bats and birds have homologous structures (Figure 2.1.3.1), as do the leaves of monocots and eudicots (Figure 2.1.3.2).

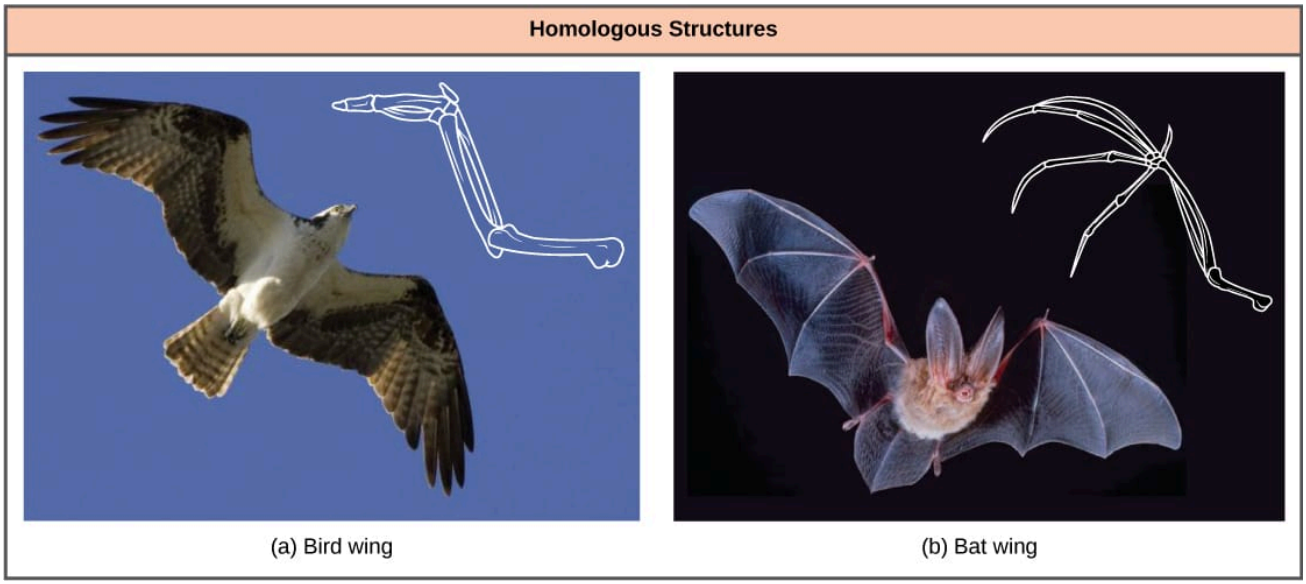


Figure 2.1.3.1: Bat and bird wings are homologous structures, indicating that bats and birds share a common evolutionary past. Both the bird wing and the bat wing share common bones, analogous to the bones in the arms and fingers of humans. However, in the bat wing, the finger bones are long and separate and form a scaffolding on which the wing's membrane is stretched. In the bird wing, the finger bones are short and fused together at the front of the wing. (credit a: modification of work by Steve Hillebrand, USFWS; credit b: modification of work by U.S. DOI BLM)

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

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

leaves have similarities due to shared ancestry, though they may appear outwardly different.

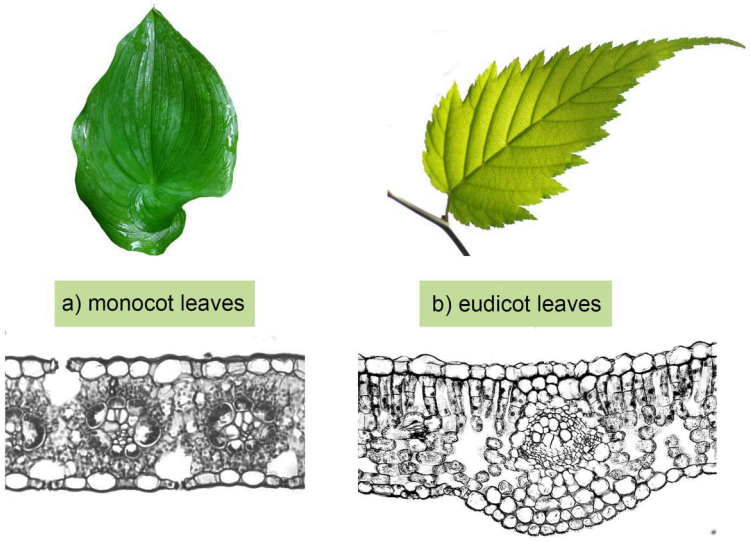


Figure 2.1.3.2: Monocots and eudicots are two major divisions within flowering plants. The leaves of these plants have differences in anatomy and morphology that allow us to distinguish between the two groups. However, the overall structure is very similar. This is because their leaves are homologous, derived from a shared common ancestor but diverging in appearance over evolutionary time. Figure created by Maria Morrow with modification of work by Simon A. Eugster (eudicot leaf), CC BY-SA 4.0, via Wikimedia Commons.

Misleading Appearances

Some organisms may be very closely related, even though a minor genetic change caused a major morphological difference to make them look quite different. Similarly, unrelated organisms may be distantly related, but appear very much alike. This usually happens because both organisms were in common adaptations that evolved within similar environmental conditions. When similar characteristics occur because of environmental constraints and not due to a close evolutionary relationship, it is called an analogy or homoplasy. For example, insects use wings to fly like bats and birds, but the wing structure and embryonic origin is completely different. These are called **analogous structures** (Figure 2.1.3.3 and Figure 2.1.3.4).

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

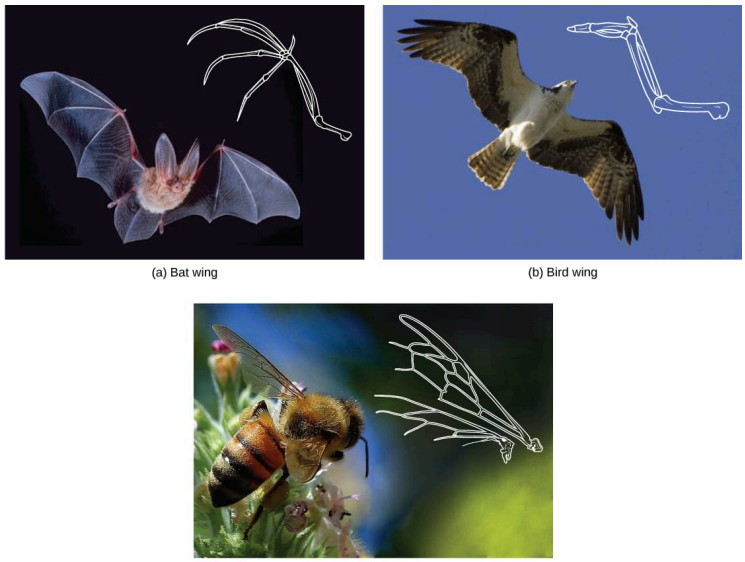


Figure 2.1.3.3: The (c) wing of a honeybee is similar in shape to a (b) bird wing and (a) bat wing, and it serves the same function. However, unlike the bat and bird wings, the honeybee wing is not composed of bones and has a distinctly different structure and embryonic origin. These wing types (insect versus bat and bird) illustrate an analogy—similar structures that do not share an evolutionary history. (credit a: modification of work by Steve Hillebrand, USFWS; credit b: modification of work by U.S. DOI BLM; credit c: modification of work by Jon Sullivan)

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

Analogous structures are often caused by **convergent evolution** of structures used for similar functions. For example, there are many different groups of unrelated organisms that photosynthesize. Plants are one lineage of photosynthetic organisms, whose ancestors are shared with the green and red algae. The brown algae have a completely different evolutionary history and do not share a common ancestor with plants (they are more closely related to water molds). However, many brown algae form flat, leaf-like structures similar to plants, as both groups use these structures for photosynthesis. Many brown algae, such as the kelps, also form stem- and root-like structures (see Figure 2.1.3.4).



Figure 2.1.3.4: Analogous structures. Brown algae, such as this sea palm (*Postelsia palmaeformis*) are not closely related to plants. However, because they have a similar nutritional strategy (photosynthesis), they have evolved similar looking features. Sea palms have an anchorage system called a holdfast that looks like roots emerging from the base. A stem-like stipe holds the leaf-like blades aloft. Photo by Peter Pearsall/U.S. Fish and Wildlife Service, USFWS - Pacific Region, Public domain, via Wikimedia Commons.

Molecular Comparisons

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

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



Figure 2.1.3.5: This image shows amino acid sequences for the same protein (VEGF) in humans and mice. Each line represents the sequence of a different individual. Each letter represents an amino acid. The sequences have been aligned to find similarities and differences. The bars across the sequences show amino acids that are unchanged across the organisms tested. These positions are considered shared ancestral characteristics. At all other locations, there may be differences in the amino acids between organisms. We can use these as synapomorphies to build a tree, assuming that organisms who share more similar sequences are more closely related. This information has revolutionized the way phylogenies are built. "Alignment of the VEGF Homology Domain of representative VEGFs (all mammalian VEGFs from human and mouse plus one VEGF-E (viral) and one VEGF-F (snake venom)" Mjeltsch, CC BY-SA 4.0, via Wikimedia Commons.

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

A research team in China identified a segment of DNA thought to be common to some medicinal plants in the family Fabaceae (the legume family) and worked to identify which species had this segment (Figure 2.1.3.6). After testing plant species in this family, the team found a DNA marker (a known location on a chromosome that enabled them to identify the species) present. Then, using the DNA to uncover phylogenetic relationships, the team could identify whether a newly discovered plant was in this family and assess its potential medicinal properties.



Figure 2.1.3.6: Dalbergia sissoo (D. sissoo) is in the Fabaceae, or legume family. Scientists found that D. sissoo shares a DNA marker with species within the Fabaceae family that have antifungal properties. Subsequently, *D. sissoo* was shown to have fungicidal activity, supporting the idea that DNA markers can be used to screen for plants with potential medicinal properties.

Building Phylogenetic Trees

How do scientists construct phylogenetic trees? After the homologous and analogous traits are sorted, scientists often organize the homologous traits using a system called cladistics. This system sorts organisms into **clades**: groups of organisms that descended from a single ancestor. For example, in Figure 2.1.3.7, all of the organisms in the orange region evolved from a single ancestor that had amniotic eggs. Consequently, all of these organisms also have amniotic eggs and make a single clade, also called a **monophyletic** group. Clades must include all of the descendants from a branch point.

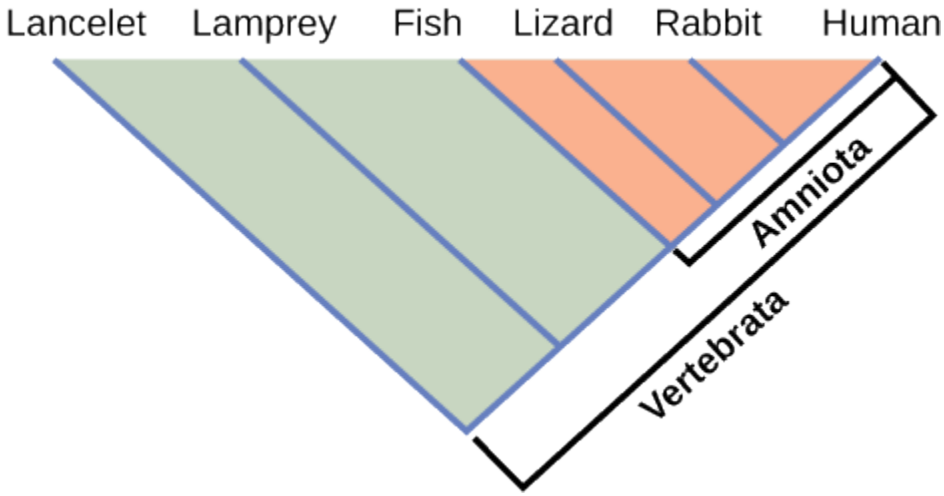


Figure 2.1.3.7: A phylogeny of vertebrates. Lizards, rabbits, and humans all descend from a common ancestor that had an amniotic egg. Thus, lizards, rabbits, and humans all belong to the clade Amniota. Vertebrata is a larger clade that also includes fish and lamprey. Descriptive text: Lancelets are at the left tip of the V, and humans are at the right tip. Four more lines are drawn parallel to the lancelet line; each of these lines starts further up the right arm of the V than the next. At the end of each line, from left to right, are lampreys, fish, lizards, and rabbits. Lizards, rabbits, and humans are in the clade Amniota, which form a small V nested in the upper right-hand corner of the V-shaped Vertebrata clade.

Clades can vary in size depending on which branch point is being referenced. The important factor is that all of the organisms in the clade or monophyletic group stem from a single point on the tree. This can be remembered because monophyletic breaks down into “mono,” meaning one, and “phyletic,” meaning evolutionary relationship. Figure 2.1.3.8 shows various examples of clades. Notice how each clade comes from a single point, whereas the non-clade groups show branches that do not share a single point.

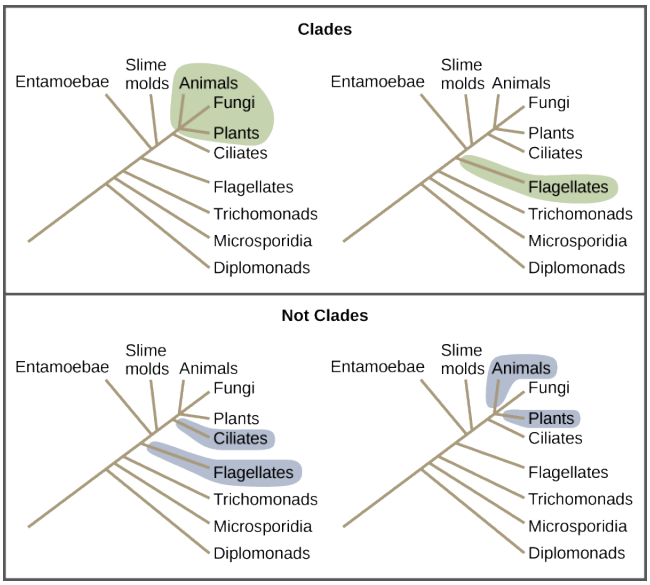


Figure 2.1.3.8: All the organisms within a clade stem from a single point on the tree. A clade may contain multiple groups, as in the case of animals, fungi and plants, or a single group, as in the case of flagellates. Groups that diverge at a different branch point, or that do not include all groups in a single branch point, are not considered clades. Descriptive text: In order from the bottom, these are diplomonads, microsporidia, trichomonads, flagellates, entamoebae, slime molds, and ciliates. At the top of the tree, animals, fungi and plants all branch from the same point and are shaded to show that they belong in the same clade. Flagellates are on a branch by themselves, and they also form their own clade and are shaded to show this. In another image, Flagellates and ciliates are shaded to show that they branch from different points on the tree and are not considered clades. Likewise, a grouping of animals and plants but not fungi would not be considered a clade cannot exclude a branch originating at the same point as the others.

Phylogenetic trees can be constructed by scoring similarities and differences between the taxa of interest (check out this supplementary video to see how it is done). These traits can be morphological or developmental features (Figure 2.1.3.7) or genetic traits called **single nucleotide polymorphisms** (SNPs, or snips, for short). Taxa with the most similarities are placed into the same clade.

Shared Characteristics

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

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

If a characteristic is found in the ancestor of a group, it is considered a **shared ancestral character** because all of the organisms in the taxon or clade have that trait. The vertebrate in Figure 2.1.3.7 is a shared ancestral character. Now consider the amniotic egg characteristic in the same figure. Only some of the organisms in Figure 2.1.3.7 have this trait, and to those that do, it is called a **shared derived character** because this trait derived at some point but does not include all of the ancestors in the tree.

The tricky aspect to shared ancestral and shared derived characters is the fact that these terms are relative. The same trait can be considered one or the other depending on the particular diagram being used. Returning to Figure 2.1.3.8, note that the amniotic egg is a shared ancestral character for the Amniota clade, while having hair is a shared derived character for some organisms in this group. These terms help scientists distinguish between clades in the building of phylogenetic trees.

Choosing the Right Relationships

Imagine being the person responsible for organizing all of the items in a department store properly—an overwhelming task. Organizing the evolutionary relationships of all life on Earth proves much more difficult: scientists must span enormous blocks

of time and work with information from long-extinct organisms. Trying to decipher the proper connections, especially given the presence of homologies and analogies, makes the task of building an accurate tree of life extraordinarily difficult. Add to that the advancement of DNA technology, which now provides large quantities of genetic sequences to be used and analyzed. Taxonomy is a subjective discipline: many organisms have more than one connection to each other, so each taxonomist will decide the order of connections.

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

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

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

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

Summary

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

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2.1.4: Perspectives on the Phylogenetic Tree

Learning Objectives

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

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

Many phylogenetic trees have been shown as models of the evolutionary relationship among species. Phylogenetic trees originated with Charles Darwin, who sketched the first phylogenetic tree in 1837 (Figure 2.1.4.1a), which served as a pattern for subsequent studies for more than a century. The concept of a phylogenetic tree with a single trunk representing a common ancestor, with the branches representing the divergence of species from this ancestor, fits well with the structure of many common trees, such as the oak (2.1.4.ab). However, evidence from modern DNA sequence analysis and newly developed computer algorithms has caused skepticism about the validity of the standard tree model in the scientific community.



Figure 2.1.4.1: The (a) concept of the "tree of life" goes back to an 1837 sketch by Charles Darwin. Like an (b) oak tree, the "tree of life" has a single trunk and many branches. (credit b: modification of work by "Amada44"/Wikimedia Commons)

Limitations to the Classic Model

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

adding a layer of complexity to the understanding of phylogenetic relationships.

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

Horizontal Gene Transfer

Horizontal gene transfer (HGT) is the introduction of genetic material from one species to another species by mechanisms other than the vertical transmission from parent(s) to offspring. These transfers allow even distantly related species to share genes, influencing their phenotypes. It is thought that HGT is more prevalent in prokaryotes, but that only about 2% of the prokaryotic genome may be transferred by this process. Some researchers believe such estimates are premature: the actual importance of HGT to evolutionary processes must be viewed as a work in progress. As the phenomenon is investigated more thoroughly, it may be revealed to be more common. Many scientists believe that HGT and mutation appear to be (especially in prokaryotes) a significant source of genetic variation, which is the raw material for the process of natural selection. These transfers may occur between any two species that share an intimate relationship (Table 2.1.4.1).

Table 2.1.4.1**:** Summary of Mechanisms of Prokaryotic and Eukaryotic HGT.

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

HGT in Prokaryotes

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

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

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

More recently, a fourth mechanism of gene transfer between prokaryotes has been discovered. Small, virus-like particles called **gene transfer agents** (GTAs) transfer random genomic segments from one species of prokaryote to another. GTAs have been shown to be responsible for genetic changes, sometimes at a very high frequency compared to other evolutionary processes. The first GTA was characterized in 1974 using purple, non-sulfur bacteria. These GTAs, which are thought to be bacteriophages (viruses that infect bacteria) that lost the ability to reproduce on their own, carry random pieces of DNA from one organism to another. The ability of GTAs to act with high frequency has been demonstrated in controlled studies using marine bacteria. Gene transfer events in marine prokaryotes, either by GTAs or by viruses, have been estimated to be as high as 10^{13} per year in the

Mediterranean Sea alone. GTAs and viruses are thought to be efficient HGT vehicles with a major impact on prokaryotic evolution.

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

HGT in Eukaryotes

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

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

In animals, a particularly interesting example of HGT occurs within the aphid species (Figure 2.1.4.2). Aphids are insects that vary in color based on carotenoid content. Carotenoids are pigments made by a variety of plants, fungi, and microbes, and they serve a variety of functions in animals, who obtain these chemicals from their food. Humans require carotenoids to synthesize vitamin A, and we obtain them by eating orange fruits and vegetables: carrots, apricots, mangoes, and sweet potatoes. On the other hand, aphids have acquired the ability to make the carotenoids on their own. According to DNA analysis, this ability is due to the transfer of fungal genes into the insect by HGT, presumably as the insect consumed fungi for food. A carotenoid enzyme called a desaturase is responsible for the red coloration seen in certain aphids, and it has been further shown that when this gene is inactivated by mutation, the aphids revert back to their more common green color (Figure 2.1.4.2).



(a) (b)

Figure 2.1.4.2: (a) Red aphids get their color from red carotenoid pigment. Genes necessary to make this pigment are present in certain fungi, and scientists speculate that aphids acquired these genes through HGT after consuming fungi for food. If genes for making carotenoids are inactivated by mutation, the aphids revert back to (b) their green color. Red coloration makes the aphids a lot more conspicuous to predators, but evidence suggests that red aphids are more resistant to insecticides than green ones. Thus, red aphids may be more fit to survive in some environments than green ones. (credit a: modification of work by Benny Mazur; credit b: modification of work by Mick Talbot)

Endosymbiosis, Genome Fusion, and the Evolution of Eukaryotes

Scientists believe the ultimate in HGT occurs through genome fusion between different species of prokaryotes when two

symbiotic organisms become **endosymbiotic**. This occurs when one species is taken inside the cytoplasm of another species (see Figure 2.1.4.3), which ultimately results in a genome consisting of genes from both the endosymbiont and the host. This mechanism is an aspect of the Endosymbiont Theory, which is accepted by a majority of biologists as the mechanism whereby eukaryotic cells obtained their mitochondria and chloroplasts. However, the role of endosymbiosis in the development of the nucleus is more controversial. Nuclear and mitochondrial DNA are thought to be of different (separate) evolutionary origin, with the mitochondrial DNA being derived from the circular genomes of bacteria that were engulfed by ancient prokaryotic cells. Mitochondrial DNA can be regarded as the smallest chromosome. Mitochondrial DNA is usually inherited from the mother only. The mitochondrial DNA degrades in sperm when the sperm degrades in the fertilized egg or in other instances when the mitochondria located in the flagellum of the sperm fails to enter the egg. However, recent studies suggest fathers also occasionally contribute their mitochondrial DNA to their offspring as well (See this Nature Article).

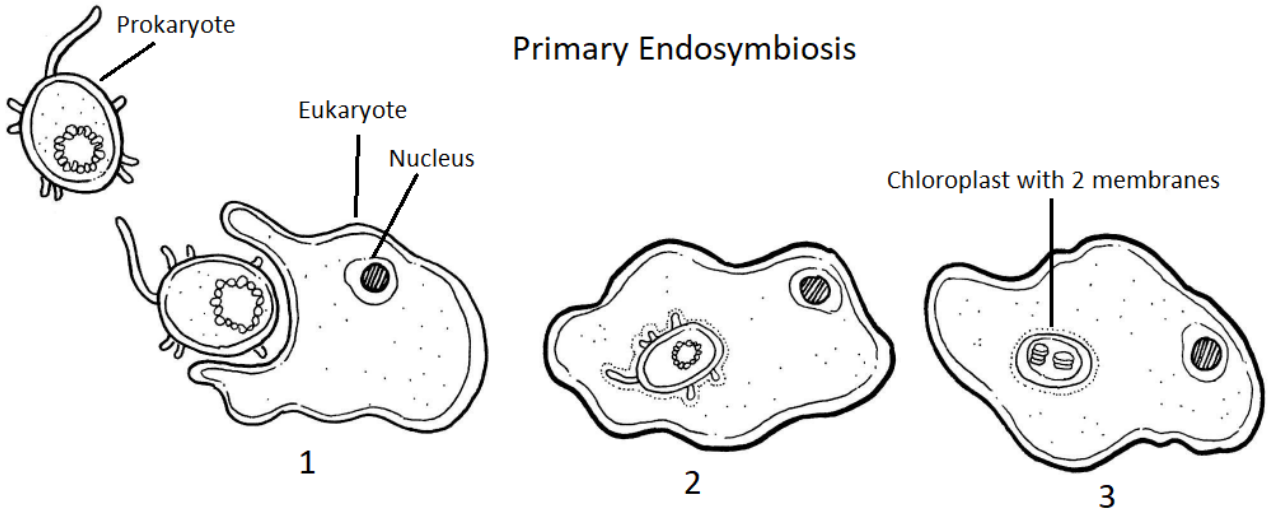


Figure 2.1.4.3: This diagram shows a prokaryotic cell on the far left. In step one, this cell is engulfed by a eukaryotic cell. In step two, we see the prokaryotic cell trapped within the eukaryotic cell, though it still looks the same as before it was engulfed. It is surrounded by a membrane of the eukaryote (dotted line). In step three, assumedly after a long period of evolution and intermediate stages, we see a fully formed chloroplast with two membranes. Artwork by Nikki Harris CC BY-NC with added labels by Maria Morrow.

Within the past decade, the process of genome fusion by endosymbiosis has been proposed by James Lake of the UCLA/NASA Astrobiology Institute to be responsible for the evolution of the first eukaryotic cells (Figure 2.1.4.4a). Using DNA analysis and a new mathematical algorithm called conditioned reconstruction (CR), his laboratory proposed that eukaryotic cells developed from an endosymbiotic gene fusion between two species, one an Archaea and the other a Bacteria. As mentioned, some eukaryotic genes resemble those of Archaea, whereas others resemble those from Bacteria. An endosymbiotic fusion event, such as Lake has proposed, would clearly explain this observation. On the other hand, this work is new and the CR algorithm is relatively unsubstantiated, which causes many scientists to resist this hypothesis.

More recent work by Lake (2.1.4.4b) proposes that gram-negative bacteria, which are unique within their domain in that they contain two lipid bilayer membranes, indeed resulted from an endosymbiotic fusion of archaeal and bacterial species. The double membrane would be a direct result of the endosymbiosis, with the endosymbiont picking up the second membrane from the host as it was internalized. This mechanism has also been used to explain the double membranes found in mitochondria and chloroplasts. Lake's work is not without skepticism, and the ideas are still debated within the biological science community. In addition to Lake's hypothesis, there are several other competing theories as to the origin of eukaryotes. How did the eukaryotic nucleus evolve? One theory is that the prokaryotic cells produced an additional membrane that surrounded the bacterial chromosome. Some bacteria have the DNA enclosed by two membranes; however, there is no evidence of a nucleolus or nuclear pores. Other proteobacteria also have membrane-bound chromosomes. If the eukaryotic nucleus evolved this way, we would expect one of the two types of prokaryotes to be more closely related to eukaryotes.

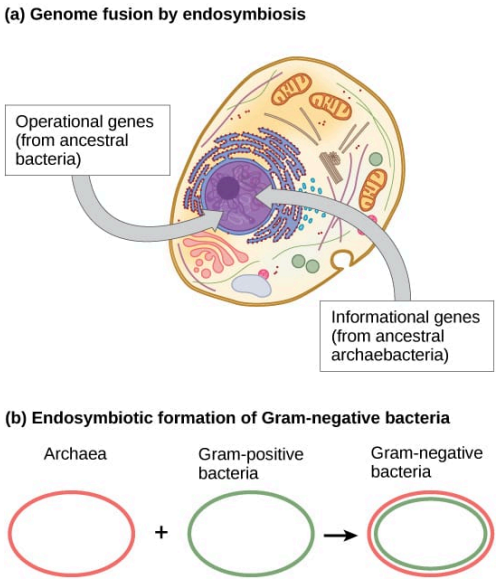


Figure 2.1.4.4: The theory that mitochondria and chloroplasts are endosymbiotic in origin is now widely accepted. More controversial is the proposal that (a) the eukaryotic nucleus resulted from the fusion of archaeal and bacterial genomes, and that (b) Gram-negative bacteria, which have two membranes, resulted from the fusion of Archaea and Gram-positive bacteria, each of which has a single membrane. Descriptive text: The illustration indicates that, within the nucleus, operational genes were inherited from an ancestral Eubacteria, and informational genes were inherited from an ancestral Archaebacteria. Part B indicates that the outer membrane of Gram-negative bacteria is derived from Archaea, and the inner membrane is derived from Gram-positive bacteria.

The nucleus-first hypothesis proposes that the nucleus evolved in prokaryotes first (2.1.4.5a), followed by a later fusion of the new eukaryote with bacteria that became mitochondria. The mitochondria-first hypothesis proposes that mitochondria were first established in a prokaryotic host (2.1.4.5b), which subsequently acquired a nucleus, by fusion or other mechanisms, to become the first eukaryotic cell. Most interestingly, the eukaryote-first hypothesis proposes that prokaryotes actually evolved from eukaryotes by losing genes and complexity (2.1.4.5c). All of these hypotheses are testable. Only time and more experimentation will determine which hypothesis is best supported by data.

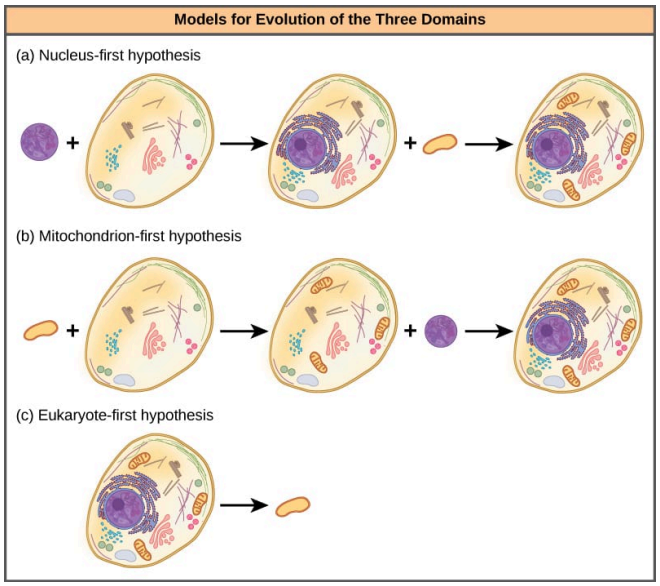


Figure 2.1.4.5: Three alternate hypotheses of eukaryotic and prokaryotic evolution are (a) the nucleus-first hypothesis, (b) the mitochondrion-first hypothesis, and (c) the eukaryote-first hypothesis. In the nucleus-first hypothesis, a primary endosymbiotic event resulted in an ancestral eukaryotic cell acquiring a nucleus, and a secondary endosymbiotic event resulted in the acquisition of a mitochondrion. In the mitochondrion-first hypothesis, the mitochondrion was acquired before the nucleus, but both were acquired by endosymbiosis. In the eukaryote-first hypothesis, prokaryotes evolved from eukaryotic cells that lost their nuclei and organelles.

Web and Network Models

The recognition of the importance of HGT, especially in the evolution of prokaryotes, has caused some to propose abandoning the classic “tree of life” model. In 1999, W. Ford Doolittle proposed a phylogenetic model that resembles a web or a network more than a tree. The hypothesis is that eukaryotes evolved not from a single prokaryotic ancestor, but from a pool of many species that were sharing genes by HGT mechanisms. As shown in Figure 2.1.4.6a, some individual prokaryotes were responsible for transferring the bacteria that caused mitochondrial development to the new eukaryotes, whereas other species transferred the bacteria that gave rise to chloroplasts. This model is often called the “web of life.” In an effort to save the tree analogy, some have proposed using the *Ficus* tree (Figure 2.1.4.6b) with its multiple trunks as a phylogenetic to represent a diminished evolutionary role for HGT.

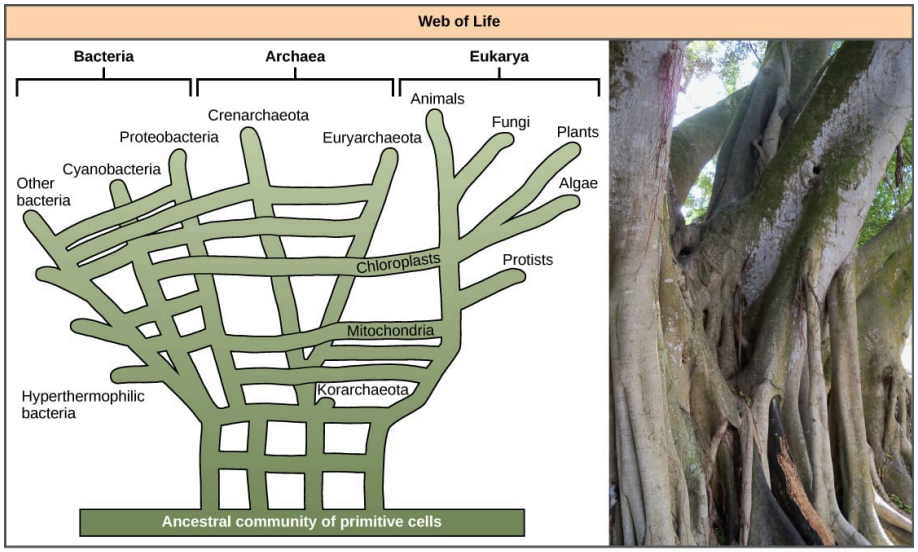


Figure 2.1.4.6): Web of life model showing the three domains of life. In (a), branches of the tree of life are connected laterally by genome transfer events (mitochondria and chloroplasts are labeled). Instead of appearing as a tree with distinct pathways to follow, the evolutionary "branches" form an interconnected web or net-like structure. At the base of the web, several paths emerge from a shared ancestral community of primitive cells. In (b), the complex aerial roots of a tropical tree cross and attach to each other, forming a similar structure to (a). (credit b: modification of work by "psyberartist"/Flickr) Illustration (a) shows the web of life.

Ring of Life Models

Others have proposed abandoning any tree-like model of phylogeny in favor of a ring structure, the so-called “ring of life” (Figure 2.1.4.7); a phylogenetic model where all three domains of life evolved from a pool of primitive prokaryotes. Lake, again using the conditioned reconstruction algorithm, proposes a ring-like model in which species of all three domains—Archaea, Bacteria, and Eukarya—evolved from a single pool of gene-swapping prokaryotes. His laboratory proposes that this structure is the best fit for data from extensive DNA analyses performed in his laboratory, and that the ring model is the only one that adequately takes HGT and genomic fusion into account. However, other phylogeneticists remain highly skeptical of this model.

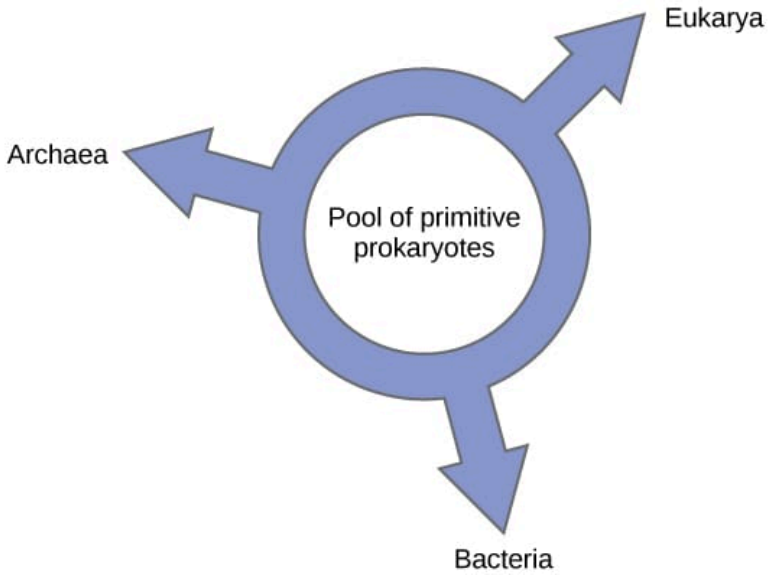


Figure 2.1.4.7: According to the “ring of life” phylogenetic model, the three domains of life evolved from a pool of primitive prokaryotes. No distinct root is present in this model. a ring with the words “pool of primitive prokaryotes” in the middle.

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

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

Summary

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

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2.1.5: Chapter Summary

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

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

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

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

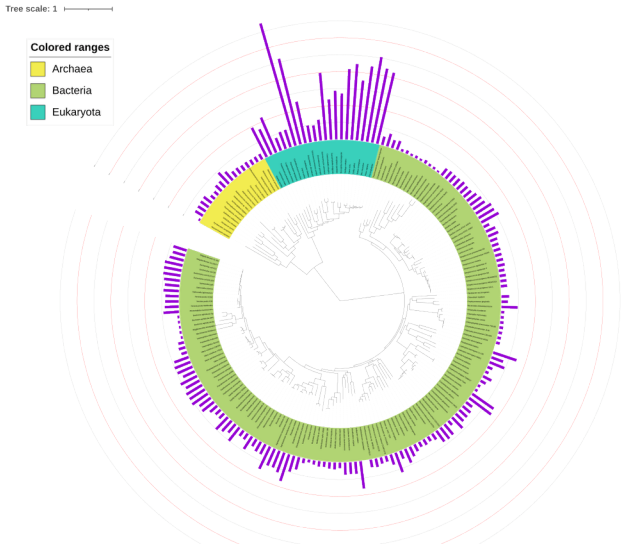


Figure 2.1.5.1: An unrooted phylogeny for all organisms whose entire genome had been sequenced, as of 2006. As sequencing technology has advanced exponentially, many more organisms currently have fully sequenced genomes. The purple bars on the outiside represent the size of the genome for that organism. The eukaryotes have much larger genomes. What might this have to do with the number of prokaryotes vs. eukaryotes sequenced in these early days? This image was generated using iTOL: Interactive Tree Of Life, an online phylogenetic tree viewer and Tree Of Life resource.

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

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

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

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2.2: PROKARYOTES AND VIRUSES

Most organisms on Earth, and in fact most of the cells in your body, are prokaryotic. These unicellular organisms are ubiquitous across ecosystems and organisms, involved in every aspect of ecology. Prokaryotes can be divided into two major groups: Bacteria and Archaea. Unlike prokaryotes, viruses are acellular, and so are not considered living. However, they are distinct biological entities with important roles in evolutionary history and the life histories of organisms.

2.2.1: Prokaryotes

2.2.1.1: Cell Structure

2.2.1.2: Archaea

2.2.1.3: Bacteria

2.2.1.3.1: Cyanobacteria

2.2.1.3.2: Root Nodules

2.2.2: Viruses

2.2.3: Chapter Summary

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2.2.1: PROKARYOTES

Scientists have studied prokaryotes for centuries, but it wasn't until 1977 that Carl Woese discovered two distinct lineages within the prokaryotes: Bacteria and Archaea.

Prokaryotes have an important role in changing, shaping, and sustaining the entire biosphere. They can produce proteins and other substances used by molecular biologists in basic research and in medicine and industry. For example, the bacterium *Shewanella* lives in the deep sea, where oxygen is scarce. It grows long appendages, which have special sensors used to seek the limited oxygen in its environment. It can also digest toxic waste and generate electricity. Other species of prokaryotes can produce more oxygen than the entire Amazon rainforest, while still others supply plants, animals, and humans with usable forms of nitrogen; and inhabit our body, protecting us from harmful microorganisms and producing some vitally important substances.

Prokaryotes are everywhere, playing important roles in the transformation and exchange of nutrients in every ecosystem. In 1966, scientist Thomas Brock discovered that certain bacteria can live in boiling water. This led many to wonder whether prokaryotes may also live in other extreme environments, such as at the bottom of the ocean, at high altitudes, or inside volcanoes, or even on other planets. This chapter will examine some of the diversity, structure, and function of prokaryotes.



Figure 2.2.1.1: Extremophiles in Owens Lake, California. This astronaut photograph highlights the mostly dry bed of Owens Lake, located in the Owens River Valley between the Inyo Mountains (upper left corner) and the Sierra Nevada (bottom). Shallow groundwater, springs, and seeps support minor wetlands and a central brine pool. Two bright red areas along the margins of the brine pool indicate the presence of halophilic (salt-loving) organisms known as archaeans. Gray and white materials within the lake bed are exposed sediments and salt crusts. The nearby towns of Olancha and Lone Pine are marked by the presence of green vegetation, indicating a more constant availability of water. Photograph and caption text from ISS Expedition 28 crew, Public domain, via Wikimedia Commons. Descriptive text: An aerial view of what looks to be a dried up lake bed. There are areas of whitish-grey salt crusts surrounding red pools. A few patches of green can be seen on the borders of the image and in a series of artificial-looking (angular) ponds.

2.2.1.1: Cell Structure

2.2.1.2: Archaea

2.2.1.3: Bacteria

2.2.1.3.1: Cyanobacteria

2.2.1.3.2: Root Nodules

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2.2.1.1: Cell Structure

Learning Objectives

- Explain the distinguishing characteristics of prokaryotic cells
- Describe common cell morphologies and cellular arrangements typical of prokaryotic cells and explain how cells maintain their morphology
- Describe internal and external structures of prokaryotic cells in terms of their physical structure, chemical structure, and function
- Compare the distinguishing characteristics of bacterial and archaean cells

Cell theory states that the cell is the fundamental unit of life. However, cells vary significantly in size, shape, structure, and function. At the simplest level of construction, all cells possess a few fundamental components. These include **cytosol** (a gel-like substance composed of water and dissolved chemicals needed for growth), which is contained within a **plasma membrane** (also called a cell membrane or cytoplasmic membrane); one or more **chromosomes** (condensed DNA and proteins), which contain the genetic blueprints of the cell; and **ribosomes**, organelles used for the synthesis of proteins.

Beyond these basic components, cells can vary greatly between organisms, and even within the same multicellular organism. The two largest categories of cells—**prokaryotic cells** and **eukaryotic cells**—are defined by major differences in several cell structures. Prokaryotic cells (Figure 2.2.1.1.1) lack a nucleus surrounded by a complex nuclear membrane and generally have a single, circular chromosome located in a **nucleoid**. Prokaryotic microorganisms are classified within the domains Archaea and Bacteria.

The structures inside a cell are analogous to the organs inside a human body, with unique structures suited to specific functions. Some of the structures found in prokaryotic cells are similar to those found in some eukaryotic cells; others are unique to prokaryotes. Although there are some exceptions, eukaryotic cells tend to be larger than prokaryotic cells. The comparatively larger size of eukaryotic cells dictates the need to compartmentalize various chemical processes within different areas of the cell, using complex membrane-bound organelles. In contrast, prokaryotic cells generally lack membrane-bound organelles; however, they often contain inclusions that compartmentalize their cytoplasm. Figure 2.2.1.1.1 illustrates structures typically associated with prokaryotic cells. These structures are described in more detail in the next section.

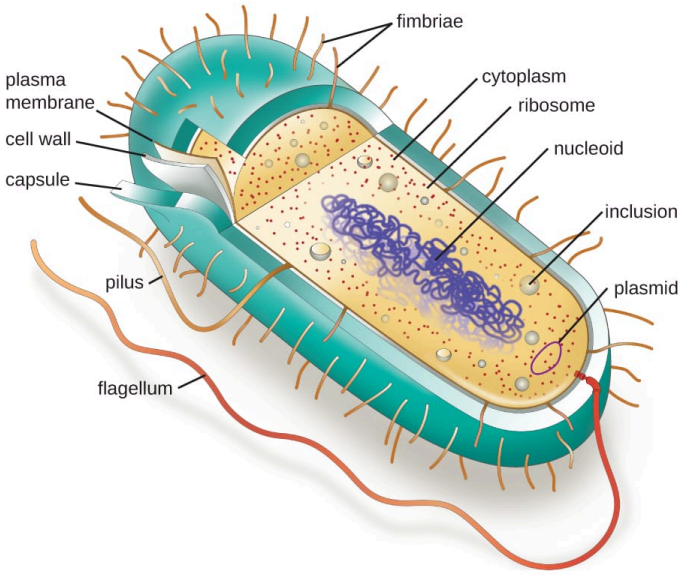


Figure 2.2.1.1.1: A typical prokaryotic cell contains a cell membrane, chromosomal DNA that is concentrated in a nucleoid, ribosomes, and a cell wall. Some prokaryotic cells may also possess flagella, pili, fimbriae, and capsules. Descriptive text: The thick outer layer is called the capsule, inside of that is a thinner cell wall and inside of that is an even thinner plasma membrane. Inside of the plasma membrane is a fluid called the cytoplasm, little dots called ribosomes, small spheres called inclusions, a small loop of DNA called a plasmid, and a large folded loo of DNA called the nucleoid. Long projections start at the plasma membrane and extend out of the capsule; these are called flagella (singular: flagellum). A shorter projection is labeled pilus. And many very short projections are labeled fimbriae.

Common Cell Morphologies and Arrangements

Individual cells of a particular prokaryotic organism are typically similar in shape, or **cell morphology**. Although thousands of prokaryotic organisms have been identified, only a handful of cell morphologies are commonly seen microscopically. Figure 2.2.1.1.2 names and illustrates cell morphologies commonly found in prokaryotic cells. In addition to cellular shape, prokaryotic cells of the same species may group together in certain distinctive arrangements depending on the plane of cell division. Some common arrangements are shown in Figure 2.2.1.1.3.

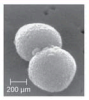
Common Prokaryotic Cell Shapes			
Name	Description	Illustration	Image
Coccus (pl. cocci)	Round		
Bacillus (pl. bacilli)	Rod		
Vibrio (pl. vibrios)	Curved rod		
Coccobacillus (pl. coccobacilli)	Short rod		
Spirillum (pl. spirilla)	Spiral		
Spirochete (pl. spirochetes)	Long, loose, helical spiral		

Figure 2.2.1.1.2: Cell morphologies commonly found in prokaryotic cells. Descriptive text: The term Coccus (plural: cocci) is the name given to round, spherical shapes. The term bacillus (plural: bacilli) is the name given to rod shaped cells. These cells are shaped like long rounded rectangles. The term vibrio (plural vibrios) is the name given to curved rods, these cells have a shape like a long comma. The term coccobacillus (plural coccobacilli) is the name for short rods; these cells look like ovals. The term spirillum (plural spirilla) is the name for long spiral cells; these look like cork screws. The term spirochete (plural spirochetes) is the name for long, loose helical spiral shaped cells. These look similar to the spirillum but are more floppy. (credit “Coccus” micrograph: modification of work by Janice Haney Carr, Centers for Disease Control and Prevention; credit “Coccobacillus” micrograph: modification of work by Janice Carr, Centers for Disease Control and Prevention; credit “Spirochete” micrograph: modification of work by Centers for Disease Control and Prevention)

Common Prokaryotic Cell Arrangements		
Name	Description	Illustration
Coccus (pl. cocci)	Single coccus	
Diplococcus (pl. diplococci)	Pair of two cocci	
Tetrad (pl. tetrads)	Grouping of four cells arranged in a square	
Streptococcus (pl. streptococci)	Chain of cocci	
Staphylococcus (pl. staphylococci)	Cluster of cocci	
Bacillus (pl. bacilli)	Single rod	
Streptobacillus (pl. streptobacilli)	Chain of rods	

Figure 2.2.1.1.3: Common cell arrangements of prokaryotes. Descriptive text: The term Coccus (plural cocci) is the name for a single coccus (a single round cell). The term diplococcus (plural diplococci) is the name for a pair of two cocci (two spheres attached together). The term tetrad (plural tetrads) is the name for a grouping of four cells arranged in a square. The term streptococcus (plural streptococci) is the name for a chain of cocci; the spheres are connected into a long chain. The term staphylococcus (plural staphylococci) is the name for a cluster of cocci; the spheres are connected into a bundle. The term bacillus (plural bacilli) is the name for a single rod. The term streptobacillus (plural streptobacilli) is the name for a chain of rods; the rectangles are connected into a long chain.

Prokaryotic Cell Structures

The Nucleoid

All cellular life has a DNA genome organized into one or more chromosomes. Prokaryotic chromosomes are typically circular,

haploid (unpaired), and not bound by a complex nuclear membrane. Prokaryotic DNA and DNA-associated proteins are concentrated within the nucleoid region of the cell (Figure 2.2.1.1.4). In general, prokaryotic DNA interacts with **nucleoid-associated proteins** (NAPs) that assist in the organization and packaging of the chromosome. In bacteria, NAPs function similar to histones, which are the DNA-organizing proteins found in eukaryotic cells. In archaea, the nucleoid is organized by either NAPs or histone-like DNA organizing proteins.

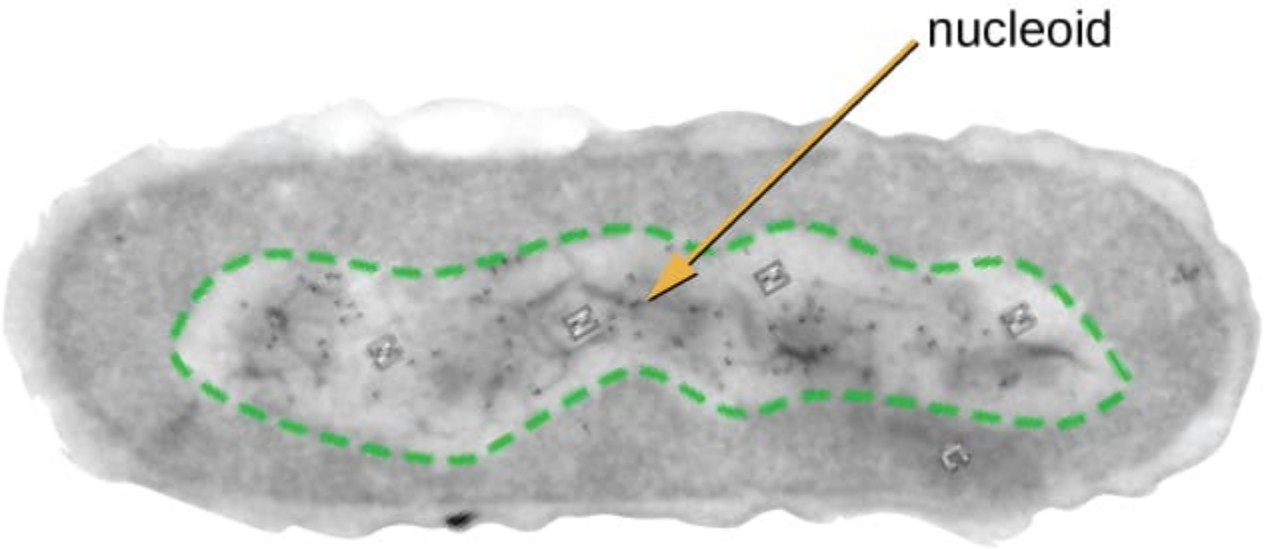


Figure 2.2.1.1.4: The nucleoid region (the area enclosed by the green dashed line) is a condensed area of DNA found within prokaryotic cells. Because of the density of the area, it does not readily stain and appears lighter in color when viewed with a transmission electron microscope.

Plasmids

Prokaryotic cells may also contain extrachromosomal DNA, or DNA that is not part of the chromosome. This extrachromosomal DNA is found in **plasmids**, which are small, circular, double-stranded DNA molecules. Cells that have plasmids often have hundreds of them within a single cell. Plasmids are more commonly found in bacteria; however, plasmids have been found in archaea and eukaryotic organisms. Plasmids often carry genes that confer advantageous traits such as antibiotic resistance; thus, they are important to the survival of the organism.

Ribosomes

All cellular life synthesizes proteins, and organisms in all three domains of life possess ribosomes, structures responsible protein synthesis. However, ribosomes in each of the three domains are structurally different. Ribosomes, themselves, are constructed from proteins, along with ribosomal RNA (rRNA). Prokaryotic ribosomes are found in the cytoplasm. They are called 70S ribosomes because they have a size of 70S (Figure 2.2.1.1.5), whereas eukaryotic cytoplasmic ribosomes have a size of 80S. (The S stands for Svedberg unit, a measure of sedimentation in an ultracentrifuge, which is based on size, shape, and surface qualities of the structure being analyzed). Although they are the same size, bacterial and archaeal ribosomes have different proteins and rRNA molecules, and the archaeal versions are more similar to their eukaryotic counterparts than to those found in bacteria.

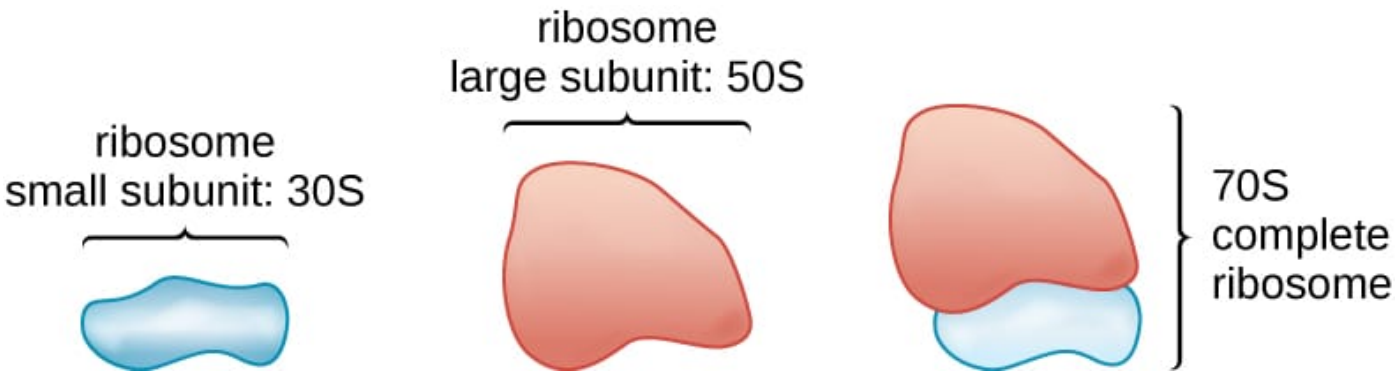


Figure 2.2.1.1.5: Prokaryotic ribosomes (70S) are composed of two subunits: the 30S (small subunit) and the 50S (large subunit), each of which are composed of protein and rRNA components. The small subunit has a size of 30S, the large subunit has a size of 50S and the complete ribosome (containing both the small and large subunit) has a size of 70S. Note that 30+50 does not equal 70. This is because the unit "S" is not necessarily a unit that measures size, but a unit that measures sedimentation rates (the Svedberg coefficient).

Plasma Membrane

Structures that enclose the cytoplasm and internal structures of the cell are known collectively as the cell envelope. In prokaryotic cells, the structures of the cell envelope vary depending on the type of cell and organism. All cells (prokaryotic and eukaryotic) have a plasma membrane (also called cytoplasmic membrane or cell membrane) that exhibits selective permeability, allowing some molecules to enter or leave the cell while restricting the passage of others.

The structure of the plasma membrane is often described in terms of the fluid mosaic model, which refers to the ability of membrane components to move fluidly within the plane of the membrane, as well as the mosaic-like composition of the components, which include a diverse array of lipid and protein components (Figure 2.2.1.1.6). The plasma membrane structure of most bacterial and eukaryotic cell types is a bilayer composed mainly of phospholipids formed with ester linkages and proteins. These phospholipids and proteins have the ability to move laterally within the plane of the membranes as well as between the two phospholipid layers.

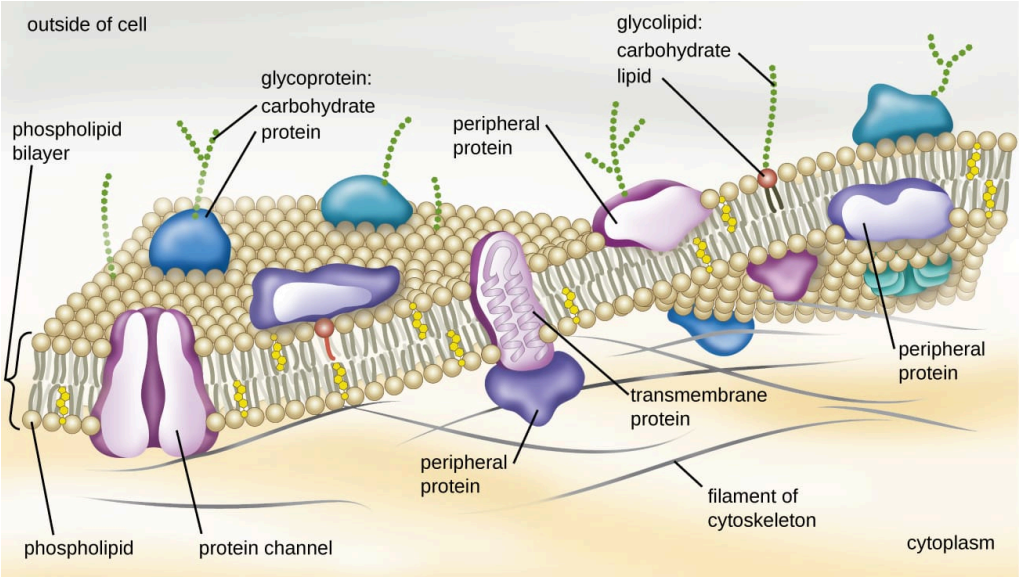


Figure 2.2.1.1.6: The bacterial plasma membrane is a phospholipid bilayer with a variety of embedded proteins that perform various functions for the cell. Note the presence of glycoproteins and glycolipids, whose carbohydrate components extend out from the surface of the cell. The abundance and arrangement of these proteins and lipids can vary greatly between species. Descriptive text: The top of the diagram is labeled outside of cell, the bottom is labeled cytoplasm. Separating these two regions is the membrane which is made of mostly a phospholipid bilayer. Each phospholipid is drawn as a sphere with 2 tails. There are two layers of phospholipids making up the bilayer; each phospholipid layer has the sphere towards the outside of the bilayer and the two tails towards the inside of the bilayer. Embedded within the phospholipid bilayer are a variety of large proteins. Protein channels span the entire bilayer and have a pore in the center that connects the outside of the cell with the cytoplasm. Peripheral proteins sit on one side of the phospholipid bilayer. Transmembrane proteins span the bilayer. Glycolipids have long carbohydrate chains (shown as a chain of hexagons) attached to a single phospholipid; the carbohydrates are always on the outside of the membrane. Glycoproteins have a long carbohydrate chain attached to a protein; the carbohydrates are on the outside of the membrane. The cytoskeleton is shown as a thin layer of line just under the inside of the phospholipid bilayer.

Archaeal membranes are fundamentally different from bacterial and eukaryotic membranes in a few significant ways. First, archaeal membrane phospholipids are formed with ether linkages, in contrast to the ester linkages found in bacterial or eukaryotic cell membranes. Second, archaeal phospholipids have branched chains, whereas those of bacterial and eukaryotic cells are straight chained. Finally, although some archaeal membranes can be formed of bilayers like those found in bacteria and eukaryotes, other archaeal plasma membranes are lipid monolayers.

Proteins on the cell's surface are important for a variety of functions, including cell-to-cell communication, and sensing environmental conditions and pathogenic virulence factors. Membrane proteins and phospholipids may have carbohydrates (sugars) associated with them and are called glycoproteins or glycolipids, respectively. These glycoprotein and glycolipid complexes extend out from the surface of the cell, allowing the cell to interact with the external environment (Figure 2.2.1.1.6). Glycoproteins and glycolipids in the plasma membrane can vary considerably in chemical composition among archaea, bacteria, and eukaryotes, allowing scientists to use them to characterize unique species.

Plasma membranes from different cells types also contain unique phospholipids, which contain fatty acids. Phospholipid-derived fatty acid analysis (PLFA) profiles can be used to identify unique types of cells based on differences in fatty acids. Archaea, bacteria, and eukaryotes each have a unique PFLA profile.

Photosynthetic Membrane Structures

Some prokaryotic cells, namely cyanobacteria, have membrane structures that enable them to perform photosynthesis. These structures consist of an infolding of the plasma membrane that encloses photosynthetic pigments such as green chlorophylls and bacteriochlorophylls. In cyanobacteria, these membrane structures are called **thylakoids**; in other photosynthetic bacteria, they are called chromatophores, lamellae, or chlorosomes.

Cell Wall

The primary function of the **cell wall** is to protect the cell from harsh conditions in the outside environment. Most (but not all)

prokaryotic cells have a cell wall, but the makeup of this cell wall varies.

The major component of bacterial cell walls is called **peptidoglycan** (or murein); it is only found in bacteria. Structurally, peptidoglycan resembles a layer of meshwork or fabric. Since peptidoglycan is unique to bacteria, many antibiotic drugs are designed to interfere with peptidoglycan synthesis, weakening the cell wall and making bacterial cells more susceptible to the effects of osmotic pressure. In addition, certain cells of the human immune system are able to “recognize” bacterial pathogens by detecting peptidoglycan on the surface of a bacterial cell; these cells then engulf and destroy the bacterial cell, using enzymes such as lysozyme, which breaks down and digests the peptidoglycan in their cell walls.

Filamentous Appendages

Many bacterial cells have protein appendages embedded within their cell envelopes that extend outward, allowing interaction with the environment. These appendages can attach to other surfaces, transfer DNA, or provide movement. Filamentous appendages include **fimbriae**, **pili**, and **flagella**.

Fimbriae and Pili

Fimbriae and pili are structurally similar and, because differentiation between the two is problematic, these terms are often used interchangeably. The term fimbriae commonly refers to short bristle-like proteins projecting from the cell surface by the hundreds. Fimbriae enable a cell to attach to surfaces and to other cells. For pathogenic bacteria, adherence to host cells is important for colonization, infectivity, and virulence. Adherence to surfaces is also important in biofilm formation.

The term pili (singular: pilus) commonly refers to longer, less numerous protein appendages that aid in attachment to surfaces (Figure 2.2.1.1.7). A specific type of pilus, called the F pilus or sex pilus, is important in the transfer of DNA between bacterial cells, which occurs between members of the same generation when two cells physically transfer or exchange parts of their respective genomes (see How Asexual Prokaryotes Achieve Genetic Diversity).

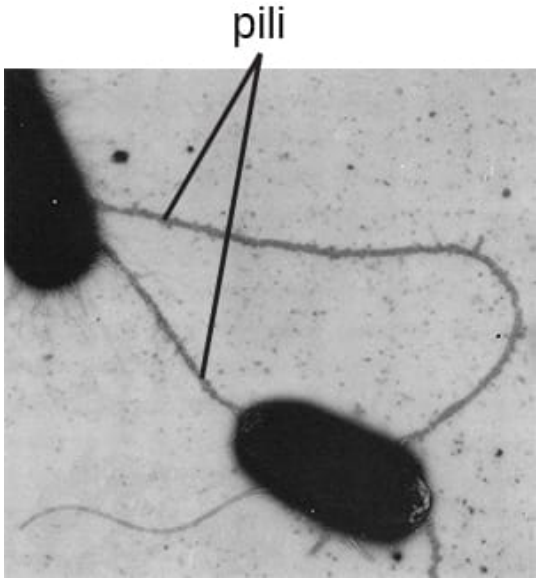


Figure 2.2.1.1.7: Bacteria may produce two different types of protein appendages that aid in surface attachment. Fimbriae typically are more numerous and shorter, whereas pili (shown here) are longer and less numerous per cell. (credit: modification of work by American Society for Microbiology)

Flagella

Flagella are structures used by cells to move in aqueous environments. Bacterial flagella act like propellers. They are stiff spiral filaments composed of flagellin protein subunits that extend outward from the cell and spin in solution. Different types of motile bacteria exhibit different arrangements of flagella (Figure 2.2.1.1.8).

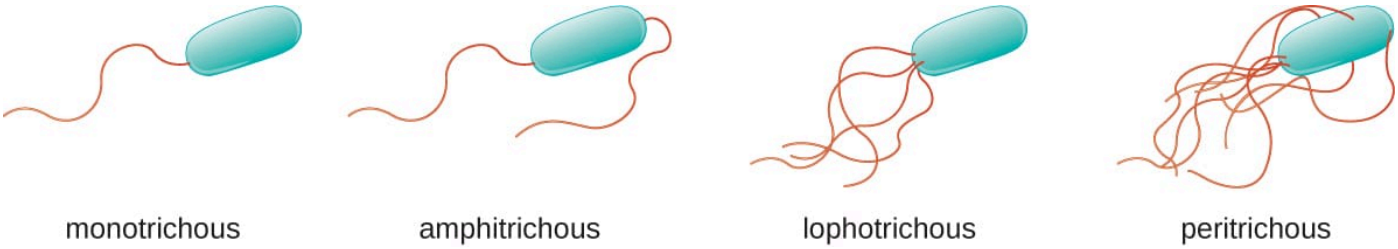


Figure 2.2.1.1.8: Flagellated bacteria may exhibit multiple arrangements of their flagella. Common arrangements include monotrichous, amphitrichous, lophotrichous, or peritrichous. Monotrichous bacteria have a single flagellum at one end. Amphitrichouls bacteria have one flagellum at each end. Lophotrichous bacteria have a tuft of flagella at one end. Peritrichous bacteria have flagella all the way around the outside of the cell.

Summary

- Prokaryotic cells differ from eukaryotic cells in that their genetic material is contained in a **nucleoid** rather than a membrane-bound nucleus. In addition, prokaryotic cells generally lack membrane-bound organelles.
- Prokaryotic cells of the same species typically share a similar **cell morphology** and **cellular arrangement**.
- Most prokaryotic cells have a **cell wall** that helps the organism maintain cellular morphology and protects it against changes in osmotic pressure.
- Outside of the nucleoid, prokaryotic cells may contain extrachromosomal DNA in **plasmids**.
- Prokaryotic **ribosomes** that are found in the cytoplasm have a size of 70S.
- Bacterial membranes are composed of phospholipids with integral or peripheral proteins. The fatty acid components of these phospholipids are ester-linked and are often used to identify specific types of bacteria. The proteins serve a variety of functions, including transport, cell-to-cell communication, and sensing environmental conditions. Archaeal membranes are distinct in that they are composed of fatty acids that are ether-linked to phospholipids.
- Prokaryotic cell walls may be composed of **peptidoglycan** (bacteria) or **pseudopeptidoglycan** (archaea).
- Some prokaryotic cells have **fimbriae** or **pili**, filamentous appendages that aid in attachment to surfaces. Pili are also used in the transfer of genetic material between cells.
- Some prokaryotic cells use one or more **flagella** to move through water.

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2.2.1.2: Archaea

Learning Objectives

- Describe why the Archaea have been difficult to place on the tree of life
- Explain what it means to be an extremophile

When these microscopic organisms were first separated from bacteria in 1977. When their ribosomal RNA was sequenced, it became obvious that they bore no close relationship to the bacteria and seemed to be more closely related to the eukaryotes. For a time they were referred to as archaebacteria, but to emphasize their distinctness, we now call them Archaea.

Diversity of Archaea

Though archaeans are involved in many important ecological processes and present across Earth's ecosystems, they are most known for being **extremophiles**, existing in conditions that prevent most organisms from functioning:

- **thermophiles** live at high temperatures
- **hyperthermophiles** live at really high temperatures (present record is 121°C!)
- **psychrophiles** (also called cryophiles) like it cold (one in the Antarctic grows best at 4°C)
- **halophiles** live in very saline environments (like the Dead Sea)
- **acidophiles** live at low pH (as low as pH 1 and who die at pH 7!)
- **alkaliphiles** thrive at a high pH.

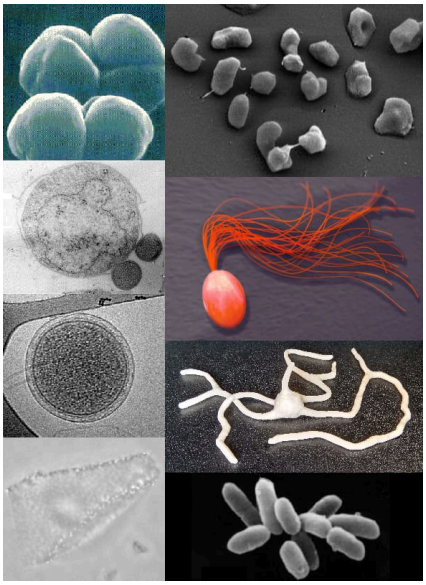


Figure 2.2.1.2.1: Diversity of Archaea. Image by Maulucioni, CC BY-SA 4.0, via Wikimedia Commons.

Methanogens

Methanogens are chemoautotrophs that use hydrogen as a source of electrons for reducing carbon dioxide to food. This process produces methane ("marsh gas", CH_4) as a byproduct. These are found living in such anaerobic environments as:

- the muck of swamps and marshes
- the rumen of cattle (where they live on the hydrogen and CO_2 produced by other microbes living along with them)
- our colon (large intestine)

- sewage sludge
- the gut of termites

Two methanogens that have had their complete genomes sequenced are *Methanocaldococcus jannaschii* and *Methanothermobacter thermoautotrophicus*.

Crenarchaeota

The first members of this group to be discovered like it really hot and so are called **hyperthermophiles**. One can grow at 121°C (the same temperature in the autoclaves used to sterilize culture media, surgical instruments, etc.). Many like it acidic as well as hot and live in acidic sulfur springs at a pH as low as 1 (the equivalent of dilute sulfuric acid). These use hydrogen as a source of electrons to reduce sulfur in order to get the energy they need to synthesize their food (from CO_2).

Aeropyrum pernix is one member of the group that has had its genome completely sequenced. Other members of this group seem to make up a large fraction of the plankton in cool, marine waters and the microbes in both soil and the ocean that convert ammonia into nitrites (nitrification).

Evolutionary Position of the Archaea

The Archaea have a curious mix of traits characteristic of bacteria as well as traits found in eukaryotes (discussed in Chapter 2.1). Table 2.2.1.2.1 summarizes some of them.

Table 2.2.1.2.1**:** Traits that the Archaea have in common with Eukarya (left) and Bacteria (right).

Eukaryotic Traits	Bacterial Traits
• DNA replication machinery • Histones • Nucleosome-like structures • Transcription machinery ◦ RNA polymerase ◦ TFIIB ◦ TATA-binding protein (TBP) • Translation machinery ◦ initiation factors ◦ ribosomal proteins ◦ elongation factors ◦ poisoned by diphtheria toxin	• Single, circular chromosome • Operons • No introns • Bacterial-type membrane transport channels • Many metabolic processes ◦ energy production ◦ nitrogen-fixation ◦ polysaccharide synthesis

Economic Importance of the Archaea

Because they have enzymes that can function at high temperatures, considerable effort is being made to exploit the Archaea for commercial processes such as providing enzymes to be added to detergents (maintain their activity at high temperatures and pH) and an enzyme to covert corn starch into dextrins. Archaea may also be enlisted to aid in cleaning up contaminated sites, e.g., petroleum spills.

There are no known pathogenic Archaea.

Summary

Archaea are a group of prokaryotes that were distinguished from Bacteria in the late 1970s. These organisms often exist in extreme environments and have diverse metabolic processes, including anaerobes that produce methane. Archaea are difficult to place in the phylogenetic tree of life. Though they share many prokaryotic traits with Bacteria, they seem to be genetically closer to Eukarya, including the processes used to replicate DNA and synthesize proteins.

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2.2.1.3: BACTERIA

Learning Objectives

- Describe some of the important ecological roles performed by bacteria
- Explain a few ways bacteria interact with plants
- Differentiate between oxygenic and anoxygenic photosynthesis

Bacteria are prokaryotes that, along with several other distinctions, have peptidoglycan in their cell wall. These unicellular organisms are incredibly diverse and involved in all ecological processes across every ecosystem. Though most are too small to see with the naked eye and thus easily overlooked, some bacteria, such as the myxobacteria (in the order Myxococcales), collaborate to produce multicellular structures (see Figure 2.2.1.3.1). This section will address some select bacterial taxa relevant to botany.



Figure 2.2.1.3.1: Myxobacteria on decaying wood. These clonal bacteria form nearly macroscopic structures (these are still quite tiny!). Photo by Alison Pollack, CC-BY-NC.

Phototrophic Bacteria

The phototrophic bacteria are a large and diverse category of bacteria that do not represent a taxon but, rather, a group of bacteria that use sunlight as their primary source of energy. This group contains both Proteobacteria and nonproteobacteria. They use solar energy to synthesize ATP through photosynthesis. When they produce oxygen, they perform **oxygenic photosynthesis**. When they do not produce oxygen, they perform anoxygenic photosynthesis. With the exception of some cyanobacteria, the majority of phototrophic bacteria perform anoxygenic photosynthesis.

One large group of phototrophic bacteria includes the purple or green bacteria that perform photosynthesis with the help of bacteriochlorophylls, which are green, purple, or blue pigments similar to chlorophyll in plants. Some of these bacteria have a varying amount of red or orange pigments called carotenoids. Their color varies from orange to red to purple to green (Figure 2.2.1.3.2), and they are able to absorb light of various wavelengths. Some green sulfur bacteria are able to photosynthesize at the bottom of the ocean using the light wavelengths emitted from geothermally heated rocks around hydrothermal vents![1] Traditionally, photosynthetic bacteria are classified into sulfur and nonsulfur bacteria; they are further differentiated by color (e.g. purple sulfur bacteria).

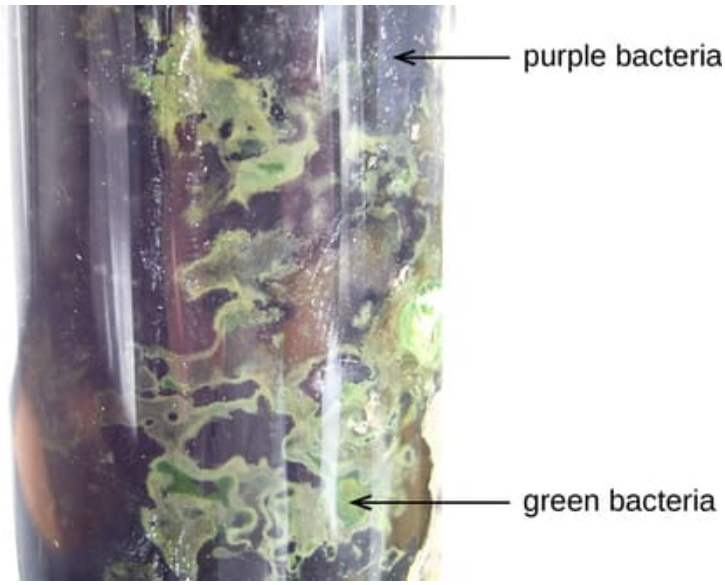


Figure 2.2.1.3.2: The purple and green sulfur bacteria shown in this Winogradsky column use bacteriochlorophylls to perform photosynthesis.

The sulfur bacteria perform anoxygenic photosynthesis, using sulfites as electron donors and releasing free elemental sulfur. Nonsulfur bacteria use organic substrates, such as succinate and malate, as donors of electrons.

The purple sulfur bacteria oxidize hydrogen sulfide into elemental sulfur and sulfuric acid and get their purple color from the pigments bacteriochlorophylls and carotenoids. Bacteria of the genus *Chromatium* are purple sulfur Gammaproteobacteria. These microorganisms are strict anaerobes and live in water. They use carbon dioxide as their only source of carbon, but their survival and growth are possible only in the presence of sulfites, which they use as electron donors. *Chromatium* has been used as a model for studies of bacterial photosynthesis since the 1950s.

The green sulfur bacteria use sulfide for oxidation and produce large amounts of green bacteriochlorophyll. The genus *Chlorobium* is a green sulfur bacterium that is implicated in climate change because it produces methane, a greenhouse gas. These bacteria use at least four types of chlorophyll for photosynthesis. The most prevalent of these, bacteriochlorophyll, is stored in special vesicle-like organelles called chlorosomes.

Purple nonsulfur bacteria are similar to purple sulfur bacteria, except that they use hydrogen rather than hydrogen sulfide for oxidation. Among the purple nonsulfur bacteria is the genus *Rhodospirillum*. These microorganisms are facultative anaerobes, which are actually pink rather than purple, and can metabolize ("fix") nitrogen. They may be valuable in the field of biotechnology because of their potential ability to produce biological plastic and hydrogen fuel.

The green nonsulfur bacteria are similar to green sulfur bacteria but they use substrates other than sulfides for oxidation. *Chloroflexus* is an example of a green nonsulfur bacterium. It often has an orange color when it grows in the dark, but it becomes green when it grows in sunlight. It stores bacteriochlorophyll in chlorosomes, similar to *Chlorobium*, and performs anoxygenic photosynthesis, using organic sulfites (low concentrations) or molecular hydrogen as electron donors, so it can survive in the dark if oxygen is available. *Chloroflexus* does not have flagella but can glide, like *Cytophaga*. It grows at a wide range of temperatures, from 35 °C to 70 °C, thus can be thermophilic.

Another large, diverse group of phototrophic bacteria compose the phylum Cyanobacteria; they get their blue-green color from the chlorophyll contained in their cells (Figure 2.2.1.3.3). Species of this group perform oxygenic photosynthesis, producing megatons of gaseous oxygen. Scientists hypothesize that cyanobacteria played a critical role in the change of our planet's anoxic atmosphere 1–2 billion years ago to the oxygen-rich environment we have today. This group is discussed further in 3.1.3.1.

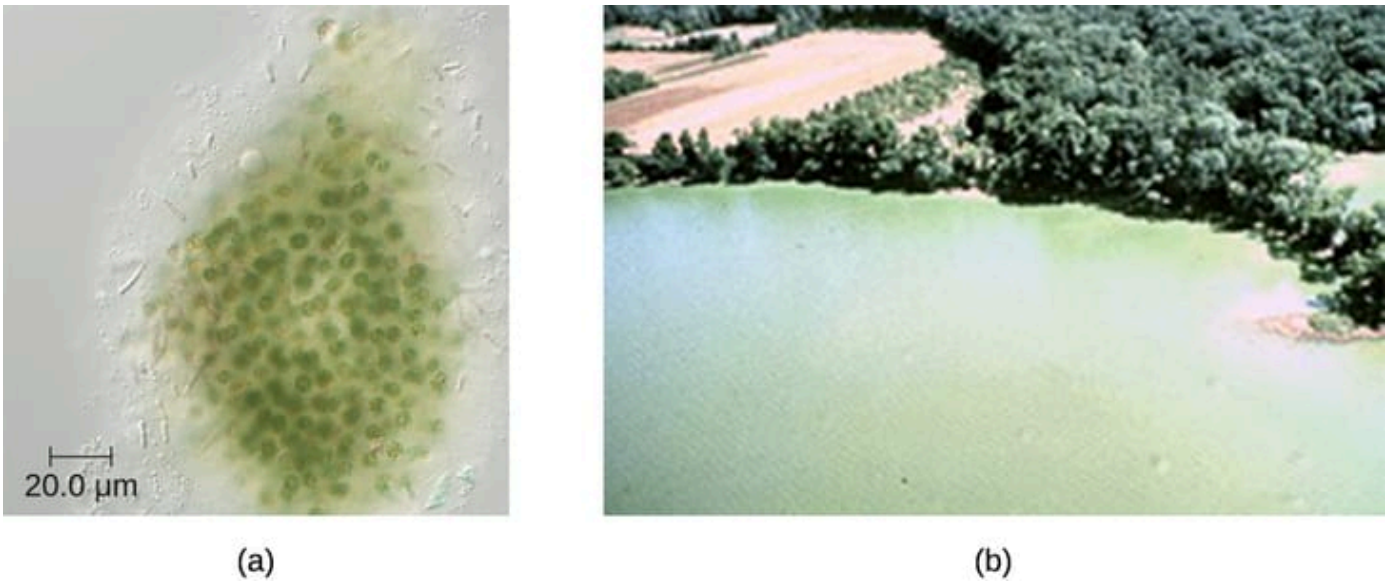


Figure 2.2.1.3.3: (a) *Microcystis aeruginosa* is a type of cyanobacteria commonly found in freshwater environments. (b) In warm temperatures, *M. aeruginosa* and other cyanobacteria can multiply rapidly and produce neurotoxins, resulting in blooms that are harmful to fish and other aquatic animals. (credit a: modification of work by Dr. Barry H. Rosen/U.S. Geological Survey; credit b: modification of work by NOAA)

Table 2.2.1.3.2 summarizes the characteristics of some important groups of phototrophic bacteria.

Table 2.2.1.3.2: Characteristics of Phototrophic Bacteria.

Phylum	Class	Example Genus or Species	Common Name	Oxygenic or Anoxygenic	Sulfur Deposition
Cyanobacteria	Cyanophyceae	*Microcystisaeruginosa*	Blue-green bacteria	Oxygenic	None
Chlorobi	Chlorobia	*Chlorobium*	Green sulfur bacteria	Anoxygenic	Outside the cell
Chloroflexi (Division)	Chloroflexi	*Chloroflexus*	Green nonsulfur bacteria	Anoxygenic	None
Proteobacteria	Alphaproteobacteria	*Rhodospirillum*	Purple nonsulfur bacteria	Anoxygenic	None
	Betaproteobacteria	*Rhodocyclus*	Purple nonsulfur bacteria	Anoxygenic	None
	Gammaproteobacteria	*Chromatium*	Purple sulfur bacteria	Anoxygenic	Inside the cell

Bacteria and Plants

Some important plant diseases are caused by pathogenic bacteria. For example, members of the genus *Agrobacterium* infect a variety of plants. Much like viruses, these bacteria insert part of their own genome into their host, causing the infected plant to produce a large gall (Figure 2.2.1.3.4). This genus is particularly famous for its use in the genetic engineering of plants. Scientists can insert a gene into the *Agrobacterium* genome, which will then be inserted into the plant after infection. Other pathogenic bacteria can cause rot, blight, and even death of some host species. Species like *Pseudomonas syringae* and *Erwinia herbicola* are capable of inducing the formation of ice (ice nucleation), injuring plant tissues.



Figure 2.2.1.3.4: A gall on white paper birch caused by *Agrobacterium radiobacter* infection. Photo by Erik Barr, CC-BY-NC.

In addition to diseases, many bacteria live within plant tissues, either freely or within endophytic fungi that live between the plant cells. These endophytic and/or endohyphal bacteria may play important roles in plant physiology, defense, and other aspects of plant biology by the production of a wide array of chemical compounds. Some bacteria are capable of nitrogen-fixation, converting atmospheric nitrogen into plant available forms. Plants in the bean family and alders have a mutualistic relationship with nitrogen-fixing bacteria and form structures called **root nodules** (see 3.1.3.2).

- Topic hierarchy

2.2.1.3.1: Cyanobacteria

2.2.1.3.2: Root Nodules

Summary

- Phototrophic bacteria are not a taxon but, rather, a group categorized by their ability to use the energy of sunlight. They include Proteobacteria and nonproteobacteria, as well as sulfur and nonsulfur bacteria colored purple or green.
- Sulfur bacteria perform anoxygenic photosynthesis, using sulfur compounds as donors of electrons, whereas nonsulfur bacteria use organic compounds (succinate, malate) as donors of electrons.
- Some phototrophic bacteria are able to fix nitrogen, providing the usable forms of nitrogen to other organisms.
- **Cyanobacteria** are oxygen-producing bacteria thought to have played a critical role in the forming of the earth's atmosphere.
- Plants have complex symbiotic relationships with bacteria, including parasites, commensalists, and mutualists.

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2.2.1.3.1: Cyanobacteria

Learning Objectives

- Explain the role of Cyanobacteria in changing Earth's atmosphere
- Describe a few mutualistic relationships formed with Cyanobacteria
- Distinguish between different Cyanobacterial cell types and describe their functions

Stromatolites

The earliest fossils are interpreted to be unicellular organisms similar to modern day cyanobacteria, sometimes referred to as blue green algae. The most widely accepted of these fossils dates back to 3.4 billion years ago from the Strelley Pool Formation in Western Australia. These particular fossils are called **stromatolites** and are composed of alternating layers of fossilized cells and calcium carbonate (Figure 2.2.1.3.1.1). We can use evidence from modern day stromatolite formation in Western Australia to infer that these fossilized cells were doing a process called photosynthesis, using dissolved CO_2 in the water to form sugar molecules. This causes calcium to precipitate out of the seawater, forming hardened layers of calcium carbonate on top of the colony of organisms. Because they need access to light to continue photosynthesizing, living cells begin forming a new layer on top of the calcium carbonate. This process continues, making a ringed pattern as the formation grows, much like we see in trees and corals.



Figure 2.2.1.3.1.1: The images above show stromatolites. The first image shows present day stromatolites formed on the coast of Western Australia. The second image shows a fossil stromatolite with the rings of growth formed by successive layers of Cyanobacteria. First photo by AndyGo, CC-BY-NC. Second image: Stromatolite Fossil from Wyoming by James St. John via Wikimedia Commons. CC-BY 2.0.

Cyanobacteria perform oxygenic photosynthesis. The ancestors of modern day cyanobacteria are responsible for the initial production of our oxygen-rich atmosphere. In addition to these initial inputs, cyanobacteria are the origin of chloroplasts in all eukaryotic phototrophs, including plants. In an event called **primary endosymbiosis**, a cyanobacterium was engulfed by a heterotrophic eukaryote. Instead of being digested, the prokaryote lived within the larger cell. Over time, genes were exchanged between the prokaryote and the eukaryote, eventually resulting in the first chloroplasts.

Modern Cyanobacteria

Cyanobacteria can be found free-living, often in colonies, or living in symbiotic relationships with other organisms, such as fungi

and plants.

Free-Living

Cyanobacteria can be found in a vast diversity of places, from floating in the ocean to living in cryptobiotic crusts in the desert. *Nostoc* is a type of cyanobacteria that can often be found living in gelatinous colonies in wet, terrestrial environments. The colony secretes a **mucilaginous sheath** that provides a protective barrier and allows for the exchange of materials between cells in the colony.



Figure 2.2.1.3.1.2: Each of these glassy orbs contains a colony of *Nostoc pruniforme* surrounded by a mucilaginous sheath. The bacteria are not visible to the naked eye, so appear as a single organism. Photo by René Stalder, CC-BY-NC.

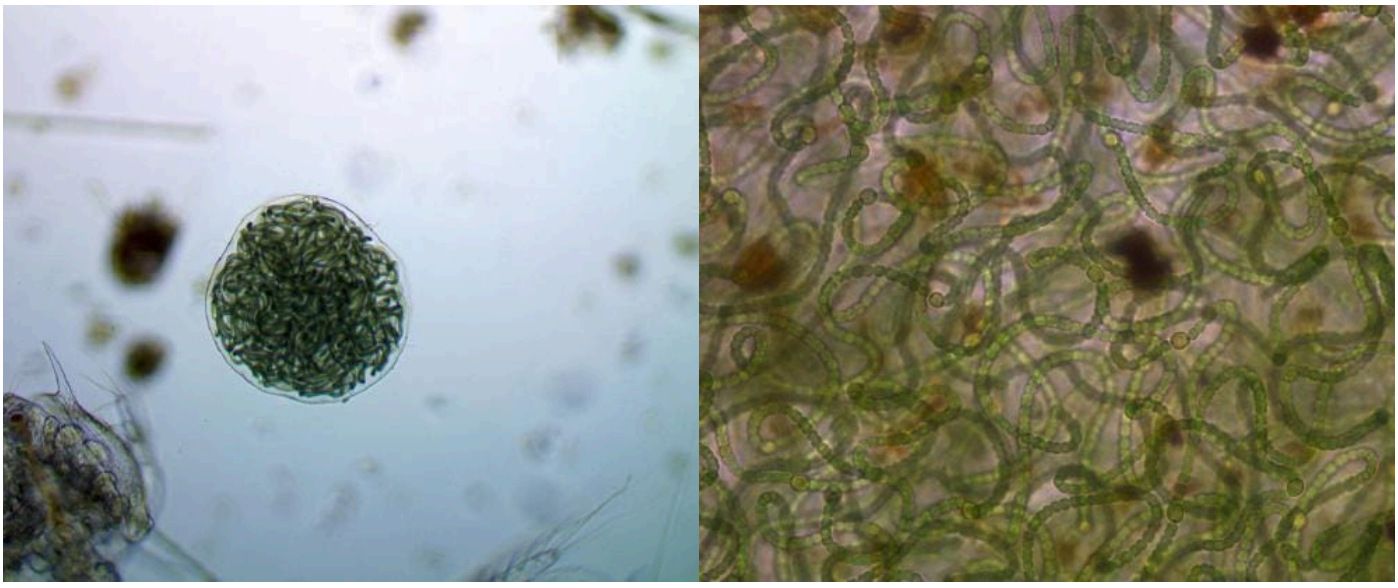


Figure 2.2.1.3.1.3: A view of a *Nostoc* colony through a microscope. The colony consists of chains of individuals, wrapped together into a ball. This ball is coated by a transparent mucilaginous sheath (visible in the first photo, left). The green color of the ball is due to the photosynthetic pigments in the cyanobacteria. In the photo on the right, a colony is shown at a higher magnification. Individuals can be distinguished, including some larger, yellow cells. These latter individuals have converted into heterocysts. First photo (left) by Ivan, CC-BY. Second photo (right) by Mindy Morales, CC-BY-NC.

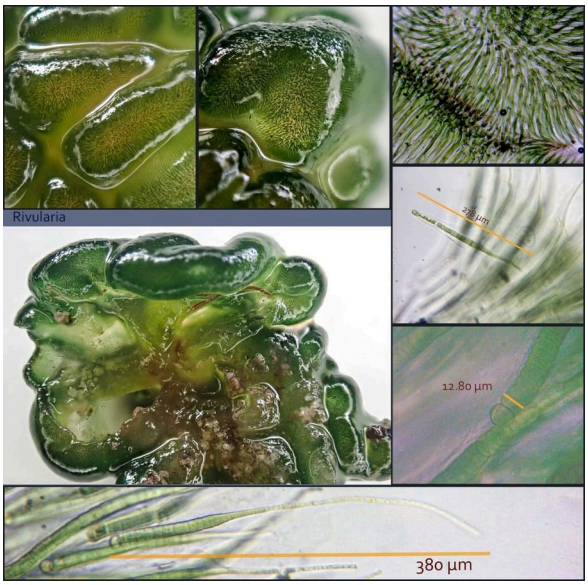


Figure 2.2.1.3.1.4: Multiple views of a gelatinous colony formed by *Rivularia polyotis*. At lower magnification, colonies are not easily distinguished, surrounded by a thick gelatinous layer. As images reach higher magnification, individual chains can be distinguished, composed of flat, disc-like cells.The thick mucilaginous sheath is visible in the two images in the upper left corner, as well as the central image on the left. Chains of individuals can be distinguished, looking like hairy projections. Photos by Luigi, CC-BY-NC.

Mutualists

Many cyanobacteria that you'll see in botany will be in mutualistic relationships. *Anabaena* is a colonial cyanobacterium that lives within the water fern *Azolla*, fixing nitrogen in the fern's relatively nutrient-poor aquatic environment. *Nostoc* is another colonial cyanobacterium capable of fixing nitrogen. It can be found free-living in gelatinous colonies shown above or, as you are likely to see it in your botany course, in compartments of a hornwort thallus. Cyanobacteria can also be found in a mutualistic relationship with fungi in cyanolichens.



Figure 2.2.1.3.1.5: Darkly colored lichens, such as this Peltigera (left) and Nephroma (right), often have a cyanobacterial partner. Photos by Maria Morrow, CC-BY-NC.

Anabaena

If you were to chop up a sample of *Azolla* and look at it under the microscope, you'd see what looked like strings of green beads.

Each bead is an individual cyanobacterium of the genus *Anabaena*. However, even though each one is an individual, some cells will specialize to provide a service for the colony, as a whole.

- **Heterocysts** are thick-walled, chlorophyll-free cells that are fixing atmospheric nitrogen into bioavailable forms using the enzyme nitrogenase. Heterocysts cannot do photosynthesis, as that process produces oxygen and nitrogenase cannot function in the presence of oxygen.
- **Akinetes** are individuals that still perform photosynthesis, but also function as a sort of failsafe. Akinetes store large amounts of lipids and carbohydrates so that they have enough energy to begin a new colony if conditions become too cold or too dry for survival. Their formation is triggered by these conditions (dry or cold), so you may not see them from a fresh water fern leaf, as this is a relatively stable, comfortable environment.

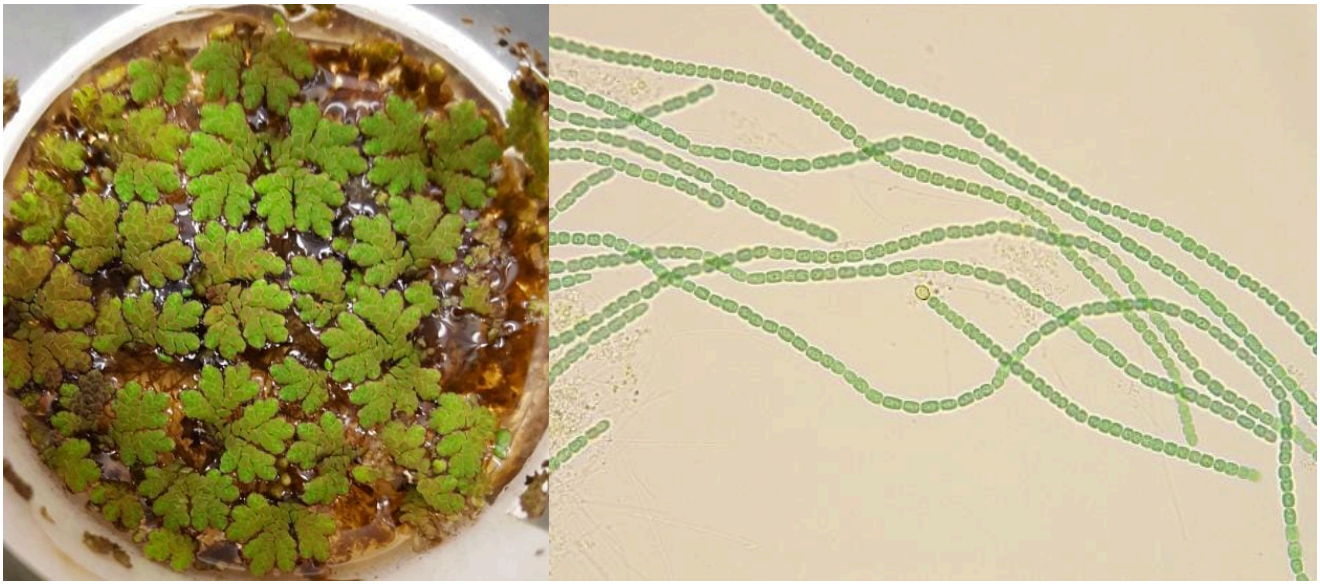


Figure 2.2.1.3.1.6 : In the image on the left, many *Azolla* plants can be seen floating in a dish of shallow water. Each fern is about the size of a dime (approx. 1 cm across). In the image on the right, individual *Anabaena* cells are strung together in colonies. These cells were once inside the leaves of the water fern. Photo credit: Melissa Ha, CC BY-NC.

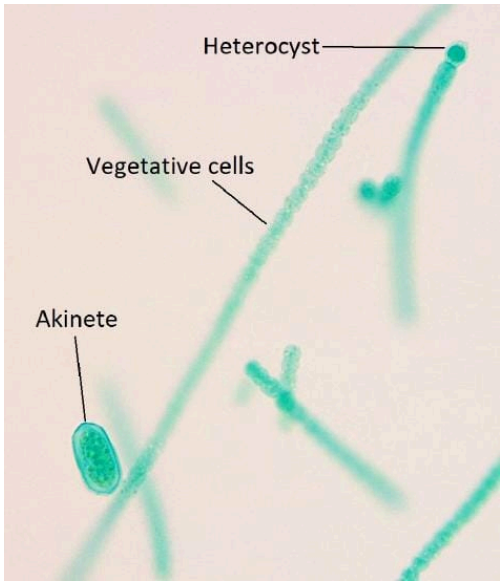


Figure 2.2.1.3.1.7: Three different cell types are visible in this *Anabaena* colony. There is one large, thick-walled akinete in the lower left. In the upper right, there is a smaller, round heterocyst that is about the size of two vegetative cells. The rest of the cells distinguishable in the image are "normal" vegetative cells. Photo credit: Melissa Ha, CC BY-NC.

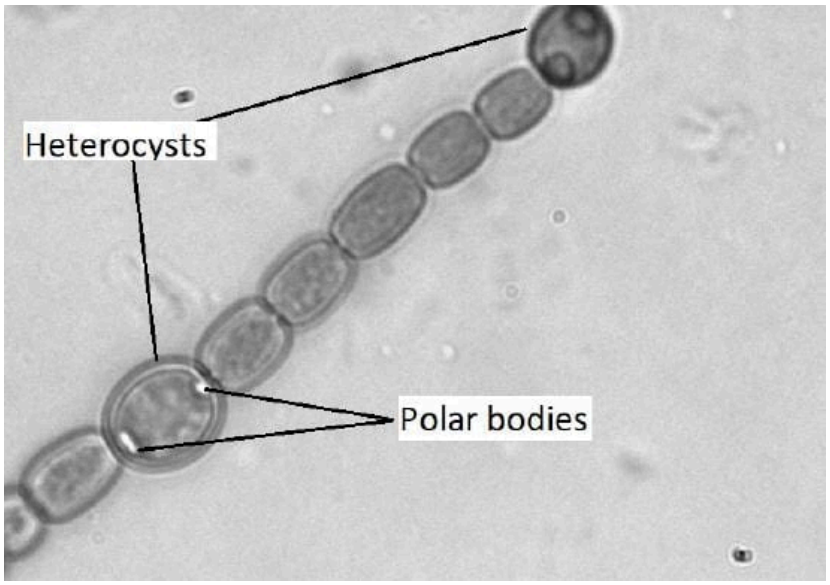


Figure 2.2.1.3.1.8: Heterocysts usually appear yellow and are more round than the vegetative cells. However, beginners often confuse the larger ones for akinetes (particularly when no akinetes are present. Something that makes heterocysts easier to distinguish from akinetes is the presence of polar bodies. Heterocysts have two distinct regions on either side called polar bodies. Akinetes don't have these and appear more granular. Photo by Maria Morrow, CC-BY-NC.

Summary

Cyanobacteria are a group of bacteria that perform oxygenic photosynthesis. The ancestors of modern cyanobacteria were responsible for the initial input of large amounts of oxygen into Earth's atmosphere. Evidence of these early cyanobacteria can be found in fossilized structures called stromatolites, which are still formed in some regions of the world. Cyanobacteria can be found free-living or as mutualists within the tissues of other organisms. Colonies of individuals are often encased within a protective mucilage. Within a colony, individual cells might specialize to fix nitrogen (heterocysts) or to survive cold and/or dry conditions (akinetes).

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2.2.1.3.2: Root Nodules

Learning Objectives

- Describe the root nodule symbiosis between plants and bacteria
- Explain why plants cannot get nitrogen from the nitrogen-rich atmosphere

Several different groups of prokaryotes form mutualistic relationships with plant roots. Nitrogen is an essential nutrient for plants, yet it is difficult to obtain in many ecosystems. Though it is abundant in our atmosphere, this form a nitrogen (N_2) is triple-bonded to itself, a bond which most organisms cannot break. However, certain bacteria have an enzyme called nitrogenase that can break the triple bond and convert nitrogen into usable forms for plants, such as ammonia (NH_3). These bacteria can be found free-living in the environment or in mutualistic relationships with certain plants. A common relationship between plants and these nitrogen-fixing bacteria is the formation of root nodules--swellings in the plant roots that connect to the vascular tissue, allowing for the exchange of sugars and nutrients between the two different organisms.

Rhizobiales and Legumes

Plants in the bean family (*Fabaceae*) form mutualistic relationships in the form of root nodules with nitrogen-fixing bacteria in the order *Rhizobiales*.



Figure 2.2.1.3.2.1: Nodules formed on the roots of *Robinia* provide a safe place and plenty of sugars for the nitrogen-fixing *Rhizobium* bacteria living inside. Photo by Thomas Koffel, CC-BY-NC.



Figure 2.2.1.3.2.2: Root nodules from a leguminous plant. In the first image, several amorphous nodules can be seen emerging from the roots. In the second image, one of these nodules has been removed. The nodules appear pinkish due to the activity of leghemoglobin transporting oxygen away from the nodule, indicating that the enzyme nitrogenase is actively fixing nitrogen inside. Photos by Olive Long, CC-BY-NC.

Frankia and Alder

Frankia is a genus of bacteria that grows filamentously, called an actinomycete. Root nodules present on alder and few other groups of woody plants contain *Frankia*.



Figure 2.2.1.3.2.3: The first image shows excavated roots from a living alder tree (*Alnus rubra*). There are many yellow-orange nodules in clusters on the roots where *Frankia* is actively fixing nitrogen. In the second image, a dead alder tree is washed up on the beach in California. The arrow is indicating clusters of root nodules that were formed when the tree was alive and housed nitrogen-fixing *Frankia*. Photos by Maria Morrow, CC BY-NC.

Summary

Some plants form a mutualistic relationship with bacteria for access to nitrogen. The bacteria infect the root hairs of the plant, forming a nodule. Within the nodule, the bacteria converts atmospheric nitrogen to a plant-available form. In return, the plant supplies the bacteria in the nodule with sugars.

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2.2.2: Viruses

Learning Objectives

- Describe the general characteristics of viruses
- Describe the range of effects viral infections can have on plants

Viruses are microscopic (see Figure 2.2.2.1 for scale), acellular, and contain nucleic acids. Despite their small size, which prevented them from being seen with light microscopes, the discovery of a filterable component smaller than a bacterium that causes tobacco mosaic disease (TMD) dates back to 1892.[1] At that time, Dmitri Ivanovski, a Russian botanist, discovered the source of TMD by using a porcelain filtering device first invented by Charles Chamberland and Louis Pasteur in Paris in 1884. Porcelain Chamberland filters have a pore size of 0.1 µm, which is small enough to remove all bacteria ≥0.2 µm from any liquids passed through the device. An extract obtained from TMD-infected tobacco plants was made to determine the cause of the disease. Initially, the source of the disease was thought to be bacterial. It was surprising to everyone when Ivanovski, using a Chamberland filter, found that the cause of TMD was not removed after passing the extract through the porcelain filter. So if a bacterium was not the cause of TMD, what could be causing the disease? Ivanovski concluded the cause of TMD must be an extremely small bacterium or bacterial spore. Other scientists, including Martinus Beijerinck, continued investigating the cause of TMD. It was Beijerinck, in 1899, who eventually concluded the causative agent was not a bacterium but, instead, possibly a chemical, like a biological poison we would describe today as a toxin. As a result, the word *virus*, Latin for poison, was used to describe the cause of TMD a few years after Ivanovski's initial discovery. Even though he was not able to see the virus that caused TMD, and did not realize the cause was not a bacterium, Ivanovski is credited as the original discoverer of viruses and a founder of the field of virology.

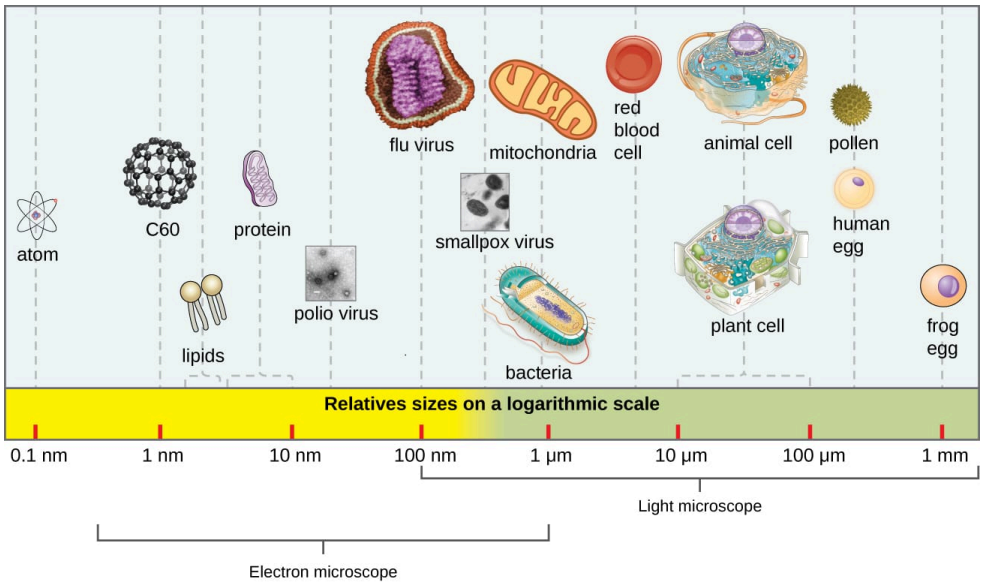


Figure 2.2.2.1: The size of a virus is small relative to the size of most bacterial and eukaryotic cells and their organelles. Descriptive text: The largest object is a frog egg ad 1 mm. Human egg cells and pllen are approximately 400 µm. Typical plant ant animal cells reange from 10 to 100 µm. Red blood cells are uner 10 µm. Mitochondria and bacteria are approximately 1 µm. Smallpox is approximately 500 nm. Flu virus is approximately 100 nm. Polio virus is approximately 50 nm. Proteins range from 5 – 10 nm. Lipids range from 1 – 5 nm. Atoms are approximately 0.1 nm.

Today, we can see viruses using electron microscopes (Figure 2.2.2.2) and we know much more about them. Viruses are distinct biological entities; however, their evolutionary origin is still a matter of speculation. In terms of taxonomy, they are not included in the tree of life because they are acellular (not consisting of cells). In order to survive and reproduce, viruses must infect a cellular host, making them obligate intracellular parasites. The genome of a virus enters a host cell and directs the production of the viral components, proteins and nucleic acids, needed to form new virus particles called virions. New virions are made in the host cell by assembly of viral components. The new virions transport the viral genome to another host cell to carry out another round of

infection. Table 2.2.2.1 summarizes the properties of viruses.

Table 2.2.2.1: Properties of viruses.

Characteristics of Viruses
Infectious, acellular pathogens
Obligate intracellular parasites with host and cell-type specificity
DNA or RNA genome (never both)
Genome is surrounded by a protein capsid and, in some cases, a phospholipid membrane studded with viral glycoproteins
Lack genes for many products needed for successful reproduction, requiring exploitation of host-cell genomes to reproduce

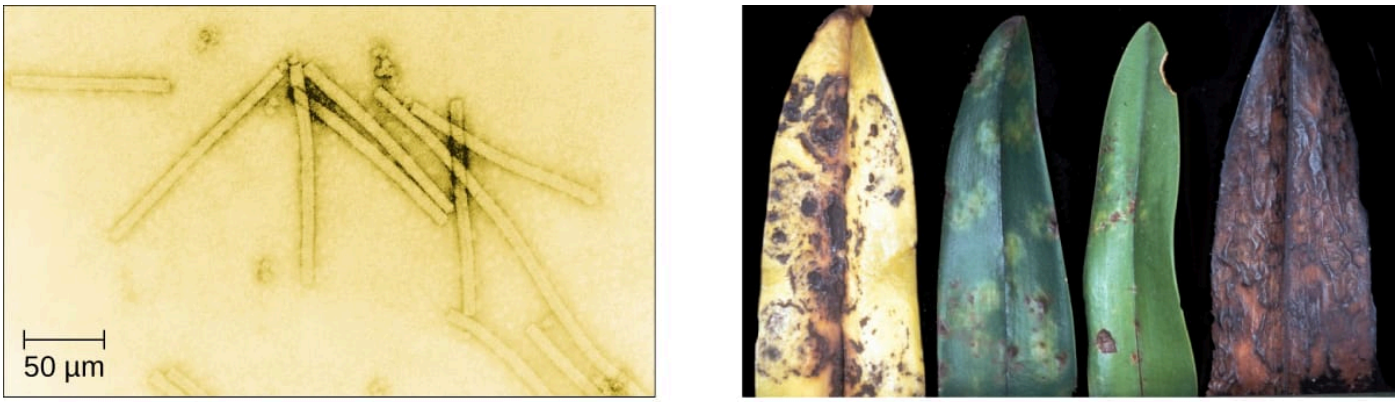


Figure 2.2.2.2: (a) Long, rod-shaped structures are tobacco mosaic virus (TMV) viewed with transmission electron microscope. (b) Plants infected with tobacco mosaic disease (TMD), caused by TMV. Leaves have necrotic lesions and chlorosis (yellowing). (credit a: modification of work by USDA Agricultural Research Service—scale-bar data from Matt Russell; credit b: modification of work by USDA Forest Service, Department of Plant Pathology Archive North Carolina State University)

Viruses and Plants

Viruses can infect every type of host cell, including those of plants, animals, fungi, protists, bacteria, and archaea. Most viruses will only be able to infect the cells of one or a few species of organism. This is called the **host range**. However, having a wide host range is not common and viruses will typically only infect specific hosts and only specific cell types within those hosts. The viruses that infect bacteria are called bacteriophages, or simply phages. The word *phage* comes from the Greek word for devour. Other viruses are just identified by their host group, such as fungal or plant viruses. Once a cell is infected, the effects of the virus can vary depending on the type of virus. Viruses may cause abnormal growth of the cell or cell death, alter the cell's genome, or cause little noticeable effect in the cell. Some viruses, like TMV, cause disease and inhibit plant growth (Figure 2.2.2.2). In other cases, scientists are finding that viruses can confer adaptive traits to their hosts, such as heat tolerance in the grass geyser's Panicum (see Figure 2.2.2.3).



Figure 2.2.2.3: Dicanthelium thermale, also called geyser's Panicum, is a grass species that is able to grow near hot pools and geysers. The heat tolerance in this grass is due to an infection by a fungus (*Curvularia protuberata*) which is, in turn, infected by a virus (*Curvularia* thermal tolerance virus). Neither the grass nor the fungus can tolerate soil temperatures above 38 degrees Celsius when grown alone, and grasses infected with the virus-free fungus cannot tolerate heat stress.[2] All three partners in the symbiosis are required for growing in this extreme environment. Photos by Christian Schwarz, CC-BY-NC.

Viruses can be transmitted through direct contact, indirect contact with contaminated materials, or through a vector: an animal that transmits a pathogen from one host to another. Arthropods such as mosquitoes, ticks, and flies, are typical vectors for viral diseases, and they may act as mechanical vectors or biological vectors. Mechanical transmission occurs when the arthropod carries a viral pathogen on the outside of its body and transmits it to a new host by physical contact. Biological transmission occurs when the arthropod carries the viral pathogen inside its body and transmits it to the new host through biting. Most plant viruses are transmitted by aphids (see Figure 2.2.2.4).

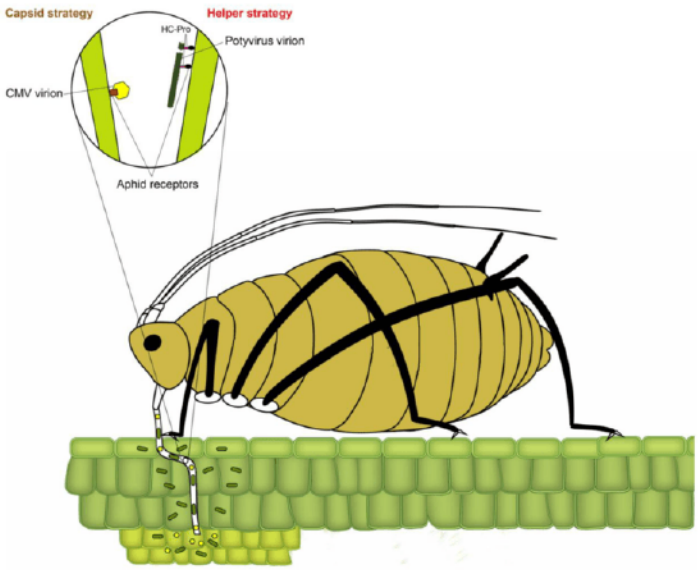


Figure 2.2.2.4: Aphids as viral vectors. This diagram shows an aphid piercing through the tissue in a leaf with a stylet to read the vascular tissue. Viral particles can be seen moving through the aphid stylet and into the plant. Original caption text: " A model depicting two strategies of binding of non-persistent viruses to aphid receptors. The circle represents an enlarged view of the tip of the aphid stylet, showing virion binding through capsid and helper strategies. In capsid strategy (the left side of circle), amino acids in the coat protein of nonpersistent stylet-borne viruses such as Cucumber mosaic cucumovirus (CMV) bind to aphid receptors (e.g., Stylin-01 receptor of Acyrthosiphon pisum and Myzus persicae). In helper strategy (right side of the circle), helper component proteinase (HC-Pro) acts as a “molecular bridge” between coat protein of non-persistent potyviruses and aphid receptors." Diagram and original caption text by Kiran R. Gadhave , Saurabh Gautam, David A. Rasmussen, and Rajagopalbabu Srinivasan, CC BY 4.0, via Wikimedia Commons.

Summary

Viruses are acellular, obligate intracellular parasites. They are composed of a nucleic acid (either DNA or RNA), a protein coat, and occasionally lipids. Viruses are not considered living because they are not composed of cells. However, viruses have important impacts on the life histories of organisms. As agents of disease, viruses contribute to top-down population control. They can also influence host biology in positive ways, such as thermal tolerance in panic grasses. Viruses can be spread from host to host by vectors. Sucking insects like aphids are important viral vectors for plants, as they transmit viruses into the vascular system.

Footnotes

[1] H. Lecoq. "[Discovery of the First Virus, the Tobacco Mosaic Virus: 1892 or 1898?]." *Comptes Rendus de l'Academie des Sciences – Serie III – Sciences de la Vie* 324, no. 10 (2001): 929–933.

[2] L.M. Marquez, R.S. Redman, R.J. Rodriguez, and M.J. Roossinck. (2007) A virus in a fungus in a plant: Three-way symbiosis required for thermal tolerance. *Science*. Vol 315. DOI: 10.1126/science.1137195

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2.2.3: Chapter Summary

Prokaryotes are unicellular organisms with circular DNA that lack a nucleus or other membrane-bound organelles. These organisms can be divided into two distinct evolutionary lineages: Bacteria and Archaea. Though Bacteria and Archaea share many traits, Archaea are considered more closely related to eukaryotes due to their cellular processes. Both groups of prokaryotes have complex and essential roles in ecosystems across the globe.

With regard to plants, Bacteria are particularly important for their role in converting atmospheric nitrogen into plant-available forms. Some of these nitrogen-fixing bacteria can be found in root nodules or other specialized compartments (e.g. cephalodia), while others are free-living. Additionally, without the original endosymbiotic event of a photosynthetic bacterial ancestor, "plants" would not exist!

Viruses are biological entities that are not classified as organisms because they are not composed of cells. They have an obligate intracellular relationship with their hosts. Most viruses that we are aware of are disease-causing, such as the Tobacco Mosaic Virus. However, as we learn more about virology, other outcomes are emerging, such as the heat tolerance observed in some grasses.

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

- Explain the distinguishing characteristics of prokaryotic cells
- Describe common cell morphologies and cellular arrangements typical of prokaryotic cells and explain how cells maintain their morphology
- Describe internal and external structures of prokaryotic cells in terms of their physical structure, chemical structure, and function
- Compare the distinguishing characteristics of bacterial and archaean cells
- Describe why the Archaea have been difficult to place on the tree of life
- Explain what it means to be an extremophile
- Describe some of the important ecological roles performed by bacteria
- Explain a few ways bacteria interact with plants
- Differentiate between oxygenic and anoxygenic photosynthesis
- Explain the role of Cyanobacteria in changing Earth's atmosphere
- Describe a few mutualistic relationships formed with Cyanobacteria
- Distinguish between different Cyanobacterial cell types and describe their functions
- Describe the root nodule symbiosis between plants and bacteria
- Explain why plants cannot get nitrogen from the nitrogen-rich atmosphere
- Describe the general characteristics of viruses
- Describe the range of effects viral infections can have on plants

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2.3: FUNGI

Kingdom Fungi includes an enormous variety of living organisms. While scientists have identified about 150,000 species of fungi, this is only a fraction of the several million species of fungi likely present on Earth. Organisms in this group are heterotrophic eukaryotes that eat by external digestion, then absorption. Fungi can be unicellular (yeasts) or composed of filamentous cells called hyphae, which taken together form a thallus called the mycelium.

2.3.1: Introduction to Fungi

2.3.2: Characteristics of Fungi

2.3.3: Ecology of Fungi

2.3.4: Microfungi

2.3.5: Macrofungi

2.3.6: Importance of Fungi in Human Life

2.3.7: Chapter Summary

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2.3.1: Introduction to Fungi

The word *fungus* is from the Latin word for mushroom, which is also similar to the Greek word for sponge. Indeed, the familiar mushroom is a reproductive structure used by only some of the fungi. There are many fungal species that don't produce mushrooms at all. The kingdom Fungi includes an enormous variety of living organisms collectively referred to as Eucomycota, or true Fungi. While scientists have identified almost 150,000 species of fungi as of 2020,[1] this is only a fraction of the millions of fungal species likely present on Earth.

Though understudied, kingdom Fungi is filled with fascinating organisms. An individual *Armillaria ostoyae* fungus in Oregon is one of the oldest and largest organisms on Earth, spreading across almost 10 km^2 of forest, with a mass anywhere from 6,800 to 30,000 metric tons and an estimated age between 1,900 to 8,500 years old, depending on estimates of growth rate. The fungus *Pilobolus* can shoot its spores twice as fast as a rifle bullet, many fungal species glow in the dark, others control the minds of insects, and still others negotiate the distribution of carbon, nitrogen, phosphorus, and other materials between trees in the world's forests.



Figure 2.3.1.1: Most people associate fungi with the reproductive structures they make. The rainbow of mushrooms shown in this image belong to the Basidiomycota, just one of the major lineages of fungi. On the right hand side, a few Ascomycota fruiting bodies can be seen: bright blue apothecia of *Chlorociboria* and the black, spatulate fruiting bodies of the earth tongues *Trichoglossum* and *Geoglossum*. The Ascomycota and Basidiomycota are generally considered macrofungi because most make fruiting bodies that we can see. The other fungi are often called the microfungi, forming microscopic fruiting structures. Photo by Maria Morrow, CC-BY-NC. Note: These were all found in my backyard on a single outing.

Fungi were once considered plant-like organisms and so are studied under the umbrella of botany. Though they are more closely related to animals than plants, fungi were not moved into their own kingdom until 1969, the same year we landed on the moon. Fungi are not capable of photosynthesis: they are heterotrophic, using complex organic compounds as sources of energy and carbon. These sources of carbon are digested externally, then absorbed. Some fungal organisms multiply only asexually, whereas others undergo both asexual reproduction and sexual reproduction. Most fungi produce a large number of spores, which are haploid cells that can undergo mitosis to form multicellular, haploid individuals. Like bacteria, fungi participate in nearly every role in an ecosystem. They are often decomposers and participate in the cycling of nutrients by breaking down organic materials to simple molecules.

Fungi are frequently found in symbiotic relationships with other organisms. For example, most terrestrial plants form a mutualistic symbiosis with fungi; the roots of the plant connect with the underground parts of the fungus forming **mycorrhizae**. Through mycorrhizae, the fungus and plant exchange nutrients and water, greatly aiding the survival of both species. Lichens are another association between a fungus and a photosynthetic partner (usually an alga), where they form a single body that might contain two to many different organisms. Fungi also cause serious infections in plants and animals. For example, Dutch elm disease, which is caused by the fungus *Ophiostoma ulmi*, is a particularly devastating type of fungal infection that destroys many native species of

elm (*Ulmus* sp.) by infecting the tree's vascular system. The elm bark beetle acts as a vector, transmitting the disease from tree to tree. Accidentally introduced in the 1900s, the fungus decimated elm trees across the continent. Many European and Asiatic elms are less susceptible to Dutch elm disease than American elms.

The close evolutionary relationship between fungi and animals makes fungal infections in humans a challenging to treat. Unlike bacteria, fungi do not respond to traditional antibiotic therapy because they are eukaryotes. Fungal infections may prove deadly for individuals with compromised immune systems.

Fungi have many commercial applications. The food industry uses yeasts in baking, brewing, and wine making. Cheeses and cured meats are products of fungal metabolism. Many industrial compounds are byproducts of fungal fermentation. Fungi are the source of many commercial enzymes, as well s the main source of citric acid production. Fungi are important to the health industry. Antibiotics were originally discovered in the fungus *Penicillium notatum* and many current medications, such as some antibiotics or the immunosuppressant Cyclosporine, are derived from fungi.

What is a mycologist?

Mycologists are biologists who study fungi. Many mycologists start their careers with a degree in botany, microbiology, or even ecology. To become a lab mycologist, a bachelor's degree in a biological science (preferably majoring in microbiology) and a master's degree in mycology are often necessary. Mycologists can specialize in taxonomy and fungal genomics, molecular and cellular biology, plant pathology, fungal ecology, biotechnology, or biochemistry. Some medical microbiologists concentrate on the study of infectious diseases caused by fungi (mycoses). Mycologists collaborate with zoologists and plant pathologists to identify and control difficult fungal infections, such as the devastating chestnut blight, the mysterious decline in frog populations in many areas of the world, or the deadly epidemic called white nose syndrome, which is decimating bats in the Eastern United States.

Government agencies hire mycologists as research scientists and technicians to monitor the health of crops, national parks, and national forests. Mycologists are also employed in the private sector by companies that develop chemical and biological control products or new agricultural products, and by companies that provide disease control services. Because of the key role played by fungi in the fermentation of alcohol and the preparation of many important foods, scientists with a good understanding of fungal physiology routinely work in the food technology industry. **Oenology**, the science of wine making, relies not only on the knowledge of grape varietals and soil composition, but also on a solid understanding of the characteristics of the wild yeasts that thrive in different wine-making regions. It is possible to purchase yeast strains isolated from specific grape-growing regions. The great French chemist and microbiologist, Louis Pasteur, made many of his essential discoveries working on the humble brewer's yeast, thus discovering the process of fermentation.

Perhaps because mycology is often given short shrift within higher education (many institutions do not even offer mycology courses), many mycologists become teachers. This includes those employed as professors, as well as those who write books, teach workshops, give lectures, or provide other forms of education. As the field of mycology grows, so to do the possibilities for mycologists!

Footnote

[1] Figure from the 2020 Species Fungorum database. More information can be found in this open-access paper.

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2.3.2: Characteristics of Fungi

Learning Objectives

- List the characteristics of fungi.
- Describe the composition of the mycelium.
- Describe the mode of nutrition of fungi.
- Explain sexual and asexual reproduction in fungi.

The Fungal Body

Fungi have well-defined characteristics that set them apart from other organisms. Most multicellular fungal bodies are made up of filaments called **hyphae**. Hyphae can form a network called a **mycelium**, which is the thallus (body) of the fungus (Figure 2.3.2.1). Fungi are heterotrophs that excrete enzymes to digest food externally, then absorb the digested food. Because of this feeding strategy, fungi tend to live within whatever their food substrate is. The thin, filamentous hyphal structure allows for maximal surface area and thus, maximal contact with the food substrate.



Figure 2.3.2.1: The mycelium of a fungus fans out across a woody substrate, branching successively. Photo by Dr Mary Gillham Archive Project, CC BY 2.0, via Wikimedia Commons.

Hyphae that have walls (**septa**) between the cells are called **septate hyphae**; hyphae that lack walls and cell membranes between the cells are called nonseptate or **coenocytic hyphae** (Figure 2.3.2.2 – 3). Early diverging lineages of fungi have coenocytic hyphae, while later lineages (often referred to as "higher fungi") have septate hyphae.

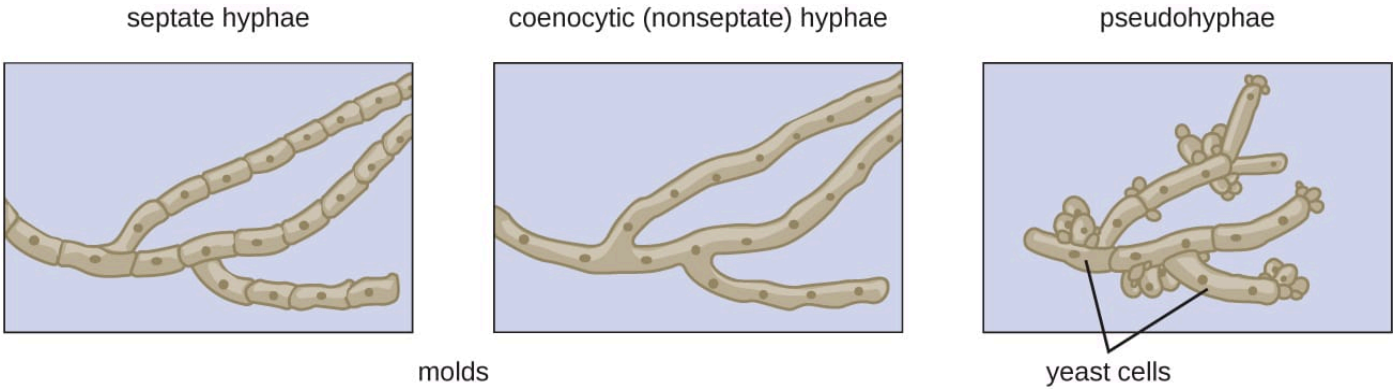


Figure 2.3.2.2: Multicellular fungi form hyphae, which may be septate or nonseptate. Septate hyphae have distinct cellular compartments separated by walls called septa. These septa can allow the fungus to keep nuclei (shown as dark dots in the diagram) contained in specific regions. Coenocytic hyphae lack septa and contents of the hyphae can move freely. Unicellular fungi (yeasts) can sometimes form pseudohyphae from individual yeast cells. The evolution of multicellularity is sometimes studied in yeasts producing pseudohyphae.



Figure 2.3.2.3: In the image above, there are several long, transparent, thread-like structures (hyphae). In this particular fungus, the hyphae are septate. There are four arrows in the image, each one is pointing to a septum. Photo by Maria Morrow, CC-BY-NC.

In contrast to filamentous fungi, **yeasts** are unicellular. The budding yeasts reproduce asexually by **budding** off a smaller daughter cell (Figure 2.3.2.4); the resulting cells may sometimes stick together as a short chain or pseudohypha (Figure 2.3.2.2). *Candida albicans* (Figure 2.3.2.5) is a common yeast that forms pseudohyphae; it is associated with various infections in humans, including vaginal yeast infections, oral thrush, and candidiasis of the skin.

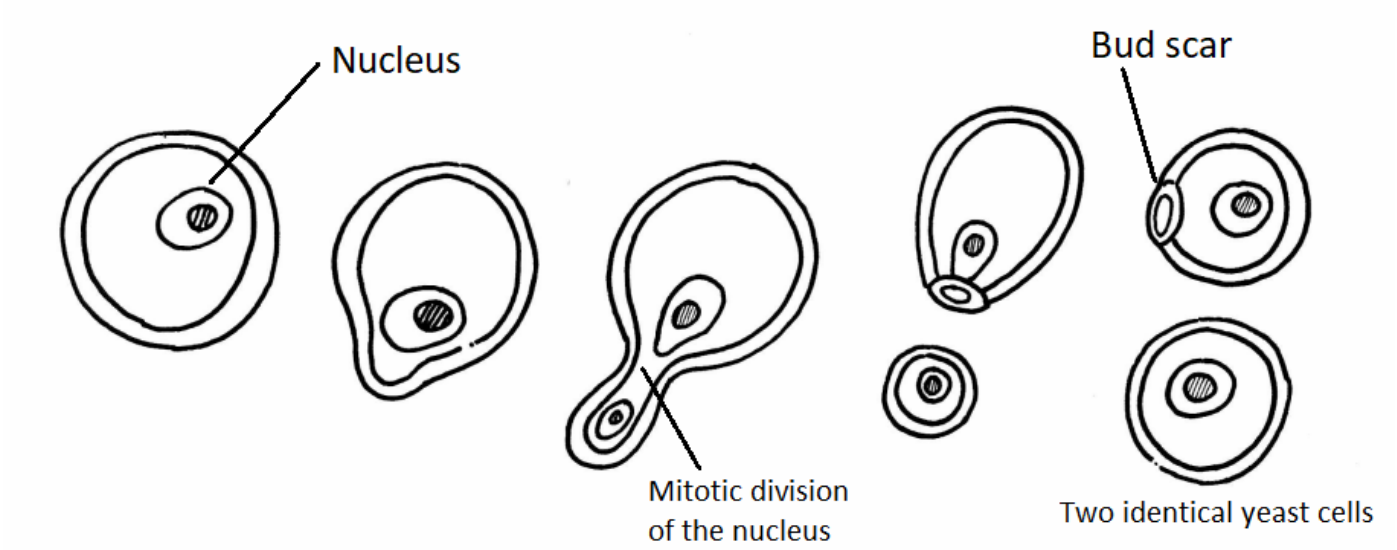


Figure 2.3.2.4: In the diagram above, a yeast cell reproduces by budding. On the far left is the parent yeast cell (the nucleus is labeled). Moving from left to right, the yeast cell forms a protrusion, then produces a copy of the nucleus by mitosis. In the next frame, a cell wall has formed between the protrustion (bud) and the parent cell, and they have physically separated. In the final frame, the two yeast cells are equal in size and genetically identical, but the parent cell can be identified by the presence of a circular bud scar. Artwork by Nikki Harris, CC-BY-NC.

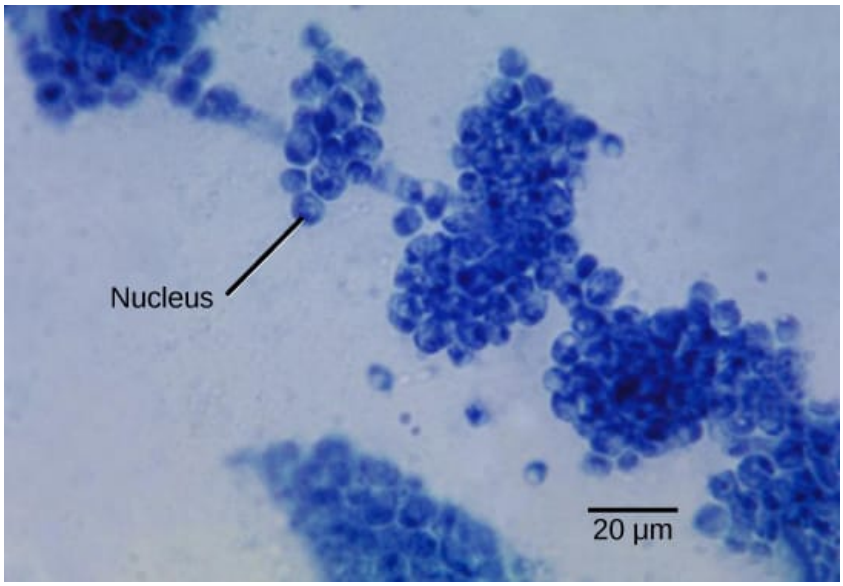


Figure 2.3.2.5: Candida albicans is a yeast cell and the agent of candidiasis and thrush. This organism has a similar morphology to coccus bacteria; however, yeast is a eukaryotic organism (note the nucleus). (credit: modification of work by Dr. Godon Roberstad, CDC; scale-bar data from Matt Russell)

Some fungi are **dimorphic**, having more than one appearance during their life cycle. These dimorphic fungi may be able to appear as yeasts or filamentous forms, which can be important for infectivity. They are capable of changing their appearance in response to environmental changes such as nutrient availability or fluctuations in temperature, growing as a mold, for example, at 25 °C (77 °F), and as yeast cells at 37 °C (98.6 °F). This ability helps dimorphic fungi to survive in diverse environments.

Cell Structure and Function

Fungi are eukaryotes, and as such, have a complex cellular organization. As eukaryotes, fungal cells contain a membrane-bound nucleus. The DNA in the nucleus is wrapped around histone proteins, as is observed in other eukaryotic cells. A few types of fungi have structures comparable to bacterial plasmids (loops of DNA); however, the horizontal transfer of genetic information from one mature bacterium to another rarely occurs in fungi. Fungal cells also contain mitochondria and a complex system of internal membranes, including the endoplasmic reticulum and Golgi apparatus.

Unlike plant cells, fungal cells do not have chloroplasts or chlorophyll. Many fungi display bright colors arising from other cellular pigments, ranging from red to green to black, though none of these are for photosynthesis. The poisonous *Amanita muscaria* (fly agaric) is recognizable by its bright red cap with white patches (Figure 2.3.2.6). Pigments in fungi are associated with the cell wall and some play a protective role against ultraviolet radiation. Some fungal pigments are toxic.



Figure 2.3.2.6: Amanita muscaria is a fungus that produces bright pigments. The skin of the caps (pileipellis) of these mushrooms is bright red due to the interaction of several pigments. Fungal pigments are, as yet, still poorly understood. (Photo credit: Christine Majul)

Like plant cells, fungal cells have a thick cell wall. The rigid layers of fungal cell walls contain complex polysaccharides called **chitin** and glucans (unlike the cell walls of plants, which contain cellulose). Chitin, also found in the exoskeleton of insects, gives structural strength to the cell walls of fungi. The wall protects the cell from desiccation and predators. Fungi have plasma membranes similar to other eukaryotes, except that the structure is stabilized by **ergosterol**, a steroid molecule that replaces the cholesterol found in animal cell membranes. Ergosterols are often exploited as targets for antifungal drugs.

Most members of the kingdom Fungi are nonmotile. Flagella are produced only in the chytrids. Motile cells have a single, whiplash flagellum, placing these organisms in the Opisthokonts (along with animals).

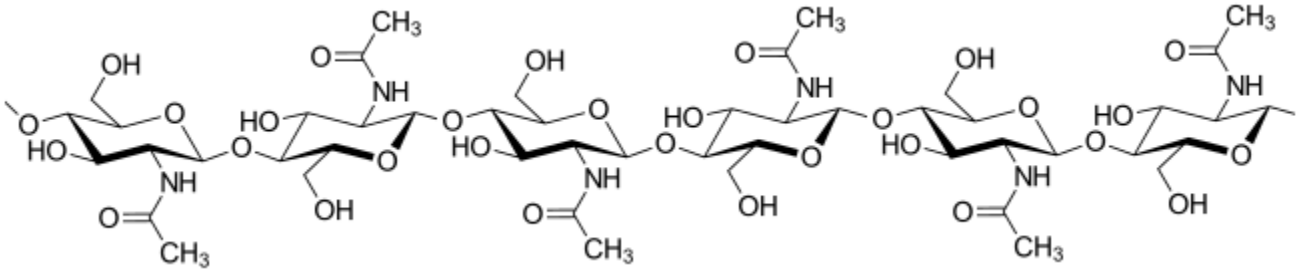


Figure 2.3.2.7: Chemical structure of chitin. As a polysaccharide, chitin is composed of chains of sugar monomers. However, unlike cellulose or starch, these glucose monomers each have an additional amide group attached.

Growth

For filamentous fungi, a fungal spore germinates and grows apically. The mycelium is often highly branched and the fungus grows from the apex of each hypha, forming a radial growth pattern (Figure 2.3.2.8). Because fungi grow within their substrate, we often do not see the mycelium, only the fruiting structures. In Figure 2.3.2.9, a circle of mushrooms called a fairy ring has formed in a grassy lawn. The original spore would have been deposited in the center of that ring and the mycelium grew outward from there. The mushrooms are produced at the edge of the mycelium.

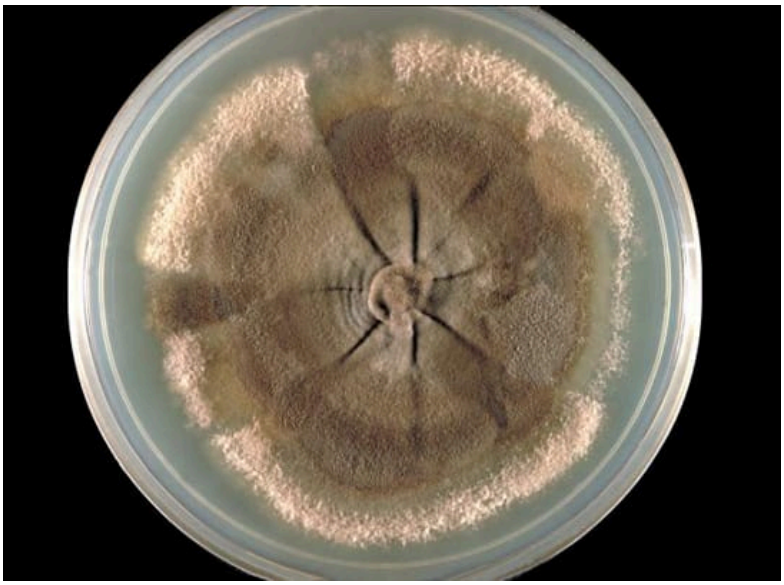


Figure 2.3.2.8: The mycelium of the fungus *Neotestudina rosati* growing in a petri plate. The fungus was transferred to the plate at a point in the center, then grew outward toward the edges of the plate. Descriptive text: The fungus, which is about 8 centimeters in diameter, has the appearance of wrinkled round skin surrounded by powdery residue. A hub-like indentation exists at the center of the fungus. Extending from this hub are folds that resemble spokes on a wheel. (credit: CDC)



Figure 2.3.2.9: A fairy ring of white mushrooms, demonstrating the radial growth of the mycelium. Photo by Aviddoghug at English Wikipedia (Original text: David Gough), Public domain, via Wikimedia Commons.

Nutrition

Like animals, fungi are heterotrophs; they use complex organic compounds as a source of carbon, rather than fix carbon dioxide from the atmosphere as plants do. In addition, fungi do not fix nitrogen from the atmosphere. Like animals, they must obtain it from their diet. However, unlike most animals, which ingest food and then digest it internally in specialized organs, fungi perform these steps in the reverse order; digestion precedes ingestion. First, exoenzymes are transported out of the hyphae, where they process nutrients in the environment. Then, the smaller molecules produced by this external digestion are absorbed through the large surface area of the mycelium. As with animal cells, the polysaccharide of storage is **glycogen**, rather than starch, as found in plants.

Fungi are mostly **saprotrophs**, organisms that derive nutrients from decaying organic matter. They obtain their nutrients from dead or decomposing organic matter, mainly plant material. Fungal exoenzymes are able to break down insoluble polysaccharides, such as the cellulose and lignin of dead wood, into readily absorbable glucose molecules. The carbon, nitrogen,

and other elements are thus released into the environment. Because of their varied metabolic pathways, fungi fulfill important ecological roles and are being investigated as potential tools in bioremediation. For example, some species of fungi can be used to break down diesel oil and polycyclic aromatic hydrocarbons (PAHs) due to their chemical similarity to the lignin found in wood. Other species take up heavy metals, such as cadmium and lead.

Some fungi are parasitic, causing infections in other organisms. Many important plant parasites are rusts, fungi in the Basidiomycota with complex life cycles. In environments poor in nitrogen, some fungi resort to predation of nematodes (small non-segmented roundworms). Species of *Arthrobotrys* fungi have a number of mechanisms to trap nematodes. One mechanism involves constricting rings within the network of hyphae. The rings swell when they touch the nematode, gripping it in a tight hold. The fungus penetrates the tissue of the worm by extending specialized hyphae called haustoria. Many parasitic fungi possess haustoria, as these structures penetrate the tissues of the host, release digestive enzymes within the host's body, and absorb the digested nutrients.

Some fungi live in a mutually beneficial symbiotic relationship with another organism, often a photosynthetic organism such as a plant or alga. The association of fungus and plant root is called **mycorrhizae**. Over 90% of land plant species benefit from symbiotic mycorrhizal relationships. The plant benefits by more-efficient mineral (e.g. phosphorus) uptake and the fungus benefits by the sugars translocated to the root by the plant.

Mycorrhizal fungi may also form conduits for nutrients **between** plant species, for better or worse. The colorless, and hence heterotrophic ghost pipe (*Monotropa uniflora* - pictured in Figure 2.3.2.10) is an angiosperm that must secure all its nourishment from mycorrhizal fungi that are attached at the same time to the roots of some autotrophic plant such as a pine tree. Radioactive carbon administered to the pine (as CO_2) soon turns up in carbohydrates in nearby ghost pipes.



Figure 2.3.2.10: Mycoheterotrophic plants like *Monotropa uniflora* (ghost pipe) do not have chlorophyll and so cannot make their own food. Instead they steal sugars from their mycorrhizal partners.

Reproduction

Fungi disperse themselves by releasing **spores** (haploid, in most cases). Fungal spores are present almost everywhere (and are a frequent cause of allergies). Spores of the wheat rust fungus have been found at 4000 m in the air and more than 1450 km (900 miles) from the place they were released. No wonder then that many fungi seem to have a worldwide distribution.

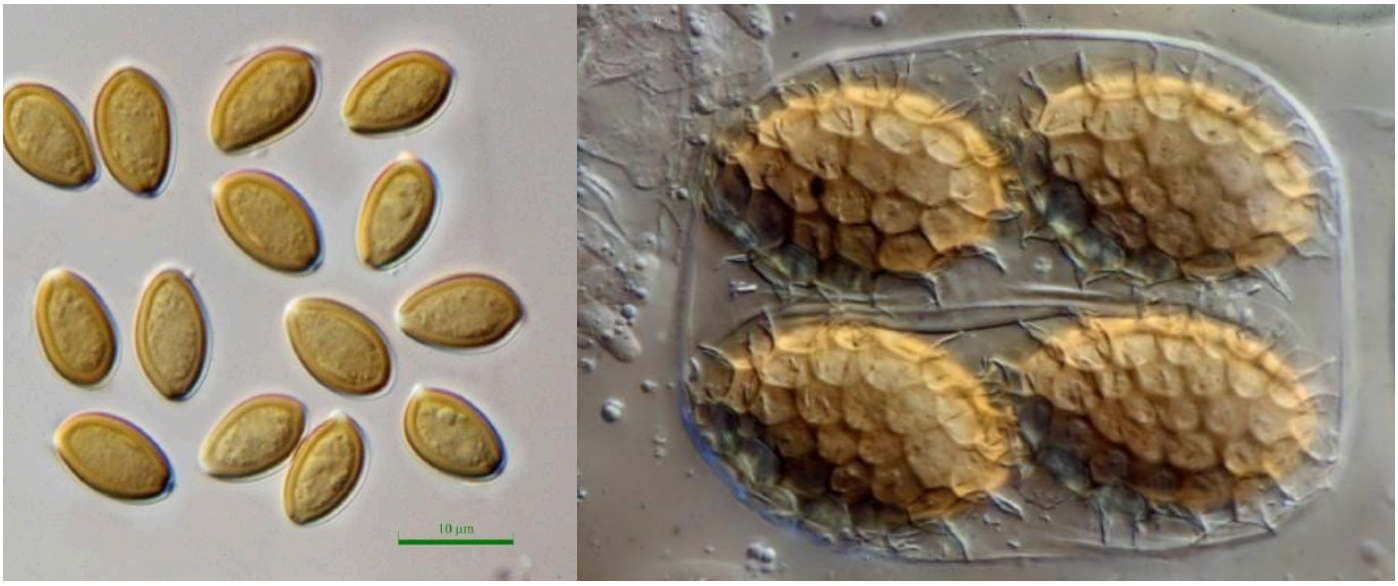


Figure 2.3.2.11: Spores produced by *Psilocybe cyanescens*, Basidiomycota (left) and *Tuber gibbosum,* Ascomycota (right). Photos by Alan Rockefeller, CC-BY-NC.

Fungi reproduce sexually and/or asexually. Fungi may exhibit asexual reproduction by mitosis with budding (Figure 2.3.2.13), fragmentation of hyphae, and formation of asexual spores by mitosis (Figure 2.3.2.14). Depending on the taxonomic group, sexually produced spores are known as zygospores (in the former Zygomycota), ascospores (in Ascomycota), or basidiospores (in Basidiomycota).

In both sexual and asexual reproduction, fungi produce spores that disperse from the parent organism by floating on the wind, hitching a ride on an animal, or some other means. Fungal spores are microscopic and often produced in large numbers. When the giant puffball mushroom bursts open, it releases trillions of spores. The huge number of spores released increases the likelihood of landing in an environment that will support growth (Figure 2.3.2.12).



Figure 2.3.2.12: The (a) giant puff ball mushroom releases (b) a cloud of spores when it reaches maturity. (credit a: modification of work by Roger Griffith; credit b: modification of work by Pearson Scott Foresman, donated to the Wikimedia Foundation)

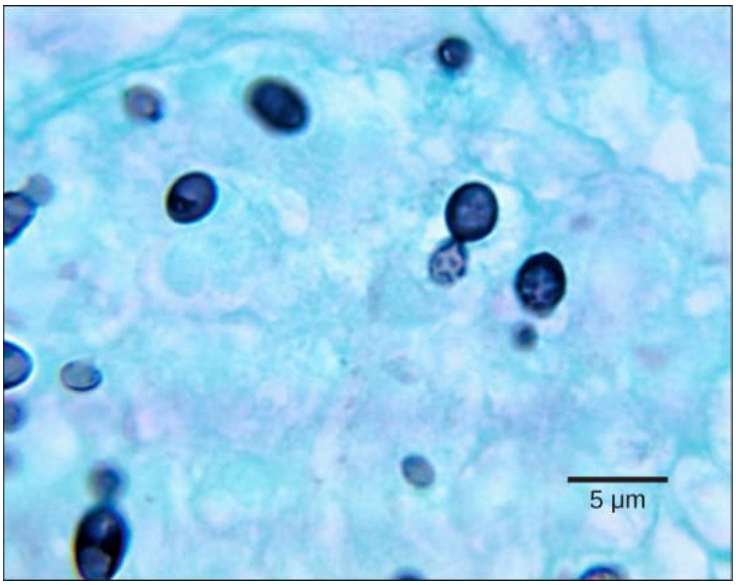


Figure 2.3.2.13: The dark cells in this bright field light micrograph are the pathogenic yeast *Histoplasma capsulatum*, seen against a backdrop of light blue tissue. *Histoplasma* primarily infects lungs but can spread to other tissues, causing histoplasmosis, a potentially fatal disease. Descriptive text: The parent cells are stained dark blue and round, with smaller, teardrop shaped cells budding from them. The cells are about 2 microns across and 3 microns long. (credit: modification of work by Dr. Libero Ajello, CDC; scale-bar data from Matt Russell)

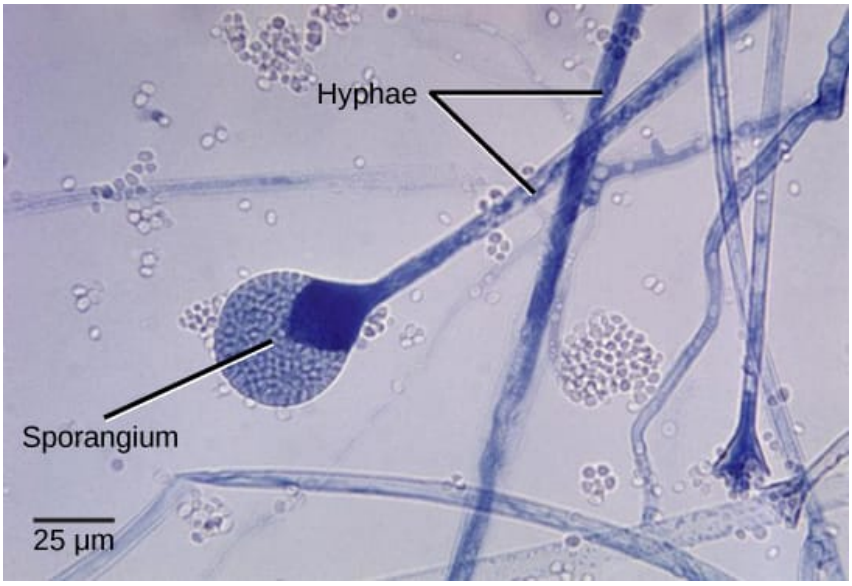


Figure 2.3.2.14: This bright field light micrograph shows the release of spores from a sporangium at the end of a hypha called a sporangiophore. The organism is a *Mucor* sp. fungus, a mold often found indoors. Descriptive text: One hypha has a round sporangium, about 35 microns in diameter, at the tip. The sporangium is dark blue at the neck, and grainy white–blue elsewhere. Spores that have already been released appear as small white ovals. (credit: modification of work by Dr. Lucille Georg, CDC; scale-bar data from Matt Russell)

Fungal life cycles are unique and complex, though fungi are typically said to have a **haplontic life cycle** (Figure 2.3.2.15). In a generalized fungal life cycle, haploid mycelia of different mating types either form hyphae that have gametes at the tips or fuse directly (somatogamy). The cytoplasm fuses in an event called **plasmogamy**, producing a cell with two distinct nuclei (a dikaryotic, or n+n, cell). At some point later, the nuclei fuse (in an event called **karyogamy**) to create a diploid zygote. The zygote undergoes meiosis to form haploid spores that germinate and grow into a new haploid mycelium. How these events occur is one of the major ways we classify fungi, and the life cycles of different fungal groups contrast significantly.

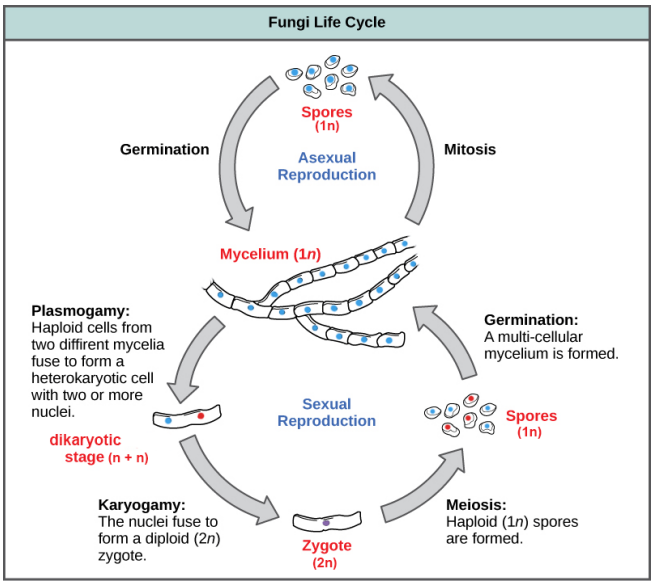


Figure 2.3.2.15: Fungi may have both asexual and sexual stages of reproduction. The life cycle is, in general, haplontic: the multicellular stage is haploid. In the asexual life cycle, a haploid (1n) mycelium undergoes mitosis to form spores. Germination of the spores results in the formation of more mycelia. In the sexual life cycle, the mycelium undergoes plasmogamy, a process in which haploid cells fuse to form a heterokaryon (a cell with two or more haploid nuclei). This is called the heterokaryotic stage. The dikaryotic cells (cells with two more more nuclei) undergo karyogamy, a process in which the nuclei fuse to form a diploid (2n) zygote. The zygote undergoes meiosis to form haploid (1n) spores. Germination of the spores results in the formation of a multicellular mycelium. Original diagram altered by Maria Morrow.

Review the characteristics of fungi by visiting this interactive site from Wisconsin-online.

Summary

Fungi are eukaryotic organisms that appeared on land more than 450 million years ago. They are heterotrophs and contain neither photosynthetic pigments such as chlorophyll, nor chloroplasts. Fungi are important decomposers that release essential elements into the environment. However, they have many other important roles in ecosystems as parasites and mutualists. External enzymes digest nutrients that are then absorbed by the mycelium of the fungus, which is composed of filamentous cells called hyphae. A thick cell wall made of chitin surrounds the hyphae. Unicellular fungi are called yeasts and reproduce by budding. Fungi can reproduce asexually (typically referred to as molds) and/or sexually. One of the primary ways fungi were classified into phyla was based on the life cycle and type of sexual structures produced.

Characteristics of Fungi:

- Eukaryotic
- Heterotrophic by absorption
- Morphology: Unicellular or a thallus composed of hyphae. If present, motile cells have only a single, whiplash flagellum.
- Cell walls: Chitin
- Storage carbohydrate: Glycogen
- Life cycle: Haplontic (though this one gets a bit weird)
- Ecology: Many fungi are decomposers, primarily in terrestrial ecosystems. Other groups of fungi live in symbiosis with other organisms as parasites, mutualists, or commensalists.

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2.3.3: Ecology of Fungi

Learning Objectives

- Describe some of the roles of fungi in ecosystems.
- Describe mutualistic relationships of fungi with plant roots and photosynthetic organisms.
- Describe the beneficial relationship between some fungi and insects.

Fungi play a crucial role in the maintenance of ecosystems. They are found in most habitats on Earth, though they are largely moisture-dependent. Their ability to exist in such a wide variety of habitats is often facilitated by symbiotic relationships with other organisms, whether these are parasitic, mutualistic, or commensal. Fungi are not obvious in the way large animals or tall trees appear, in part because they live within their food, digesting it externally before absorbing it. Like bacteria, they are the major recyclers of organic matter.

Habitats

Although fungi are primarily associated with humid and cool environments that provide a supply of organic matter, they colonize a surprising diversity of habitats, from seawater to human skin and mucous membranes. Fungi have been found living inside rocks and rocky substrates in marine ecosystems[1], high in the Andes mountains on salt crusts[2], in the hot springs of the Jurassic period[3], and inside just about any organism you can think of. Chytrids are found primarily in aquatic environments. Other fungi, such as *Coccidioides immitis*, which causes pneumonia when its spores are inhaled, thrive in the dry and sandy soil of the southwestern United States. Fungi that parasitize coral reefs live in the ocean. However, most members of the kingdom Fungi grow on the forest floor, where the damp environment is rich in decaying debris from plants and animals. In these environments, fungi play a major role as decomposers and mutualists, facilitating the transfer of nutrients to members of the other kingdoms.

Decomposers and Recyclers

The food web would be incomplete without organisms that decompose organic matter (Figure 2.3.3.1). Some elements—such as nitrogen and phosphorus—are required in large quantities by biological systems, and yet are not abundant in the environment. The action of fungi releases these elements from decaying matter, making them available to other living organisms. Trace elements present in low amounts in many habitats are essential for growth, and would remain tied up in rotting organic matter if fungi and bacteria did not return them to the environment via their metabolic activity.



Figure 2.3.3.1: Fungi are an important part of ecosystem nutrient cycles. These small stalked structures are the fruiting bodies of the fungus Pilobolus, one of the zygospore-forming fungi. They receive their nutrients through their hyphae, which are embedded in this nitrogen-rich deer scat. The black spore packages are shot from the fruiting bodies, sticking to adjacent blades of grass where they may be again eaten by an ungulate and deposited elsewhere in the form of scat. Photo by Maria Morrow, CC-BY-NC.

The ability of fungi to degrade many large and insoluble molecules is due to their mode of nutrition. As seen earlier, digestion precedes ingestion. Fungi produce a variety of exoenzymes to digest nutrients. The enzymes are either released into the substrate or remain bound to the outside of the fungal cell wall. Large molecules are broken down into small molecules, which are transported into the cell by a system of protein carriers embedded in the cell membrane. Because the movement of small molecules and enzymes is dependent on the presence of water, active growth depends on a relatively high percentage of moisture in the environment.

As saprotrophs, fungi help maintain a sustainable ecosystem for the animals and plants that share the same habitat. In addition to replenishing the environment with nutrients, fungi interact directly with other organisms in beneficial, and sometimes damaging, ways (Figure 2.3.3.2).



Figure 2.3.3.2: Shelf fungi, so called because they grow on trees in a stack, break down the woody tissues of a tree. While some shelf fungi are found only on dead trees, others can parasitize living trees and cause eventual death, so they are considered serious tree pathogens. This photo shows a root disease fungus fruiting from the base of a broken tree. Photo by Maria Morrow, CC-BY-NC.



Figure 2.3.3.3: Fungi are some of the only organisms that can decompose wood. When they do, it changes the texture of the wood. In the first photo, th appears white and is separated into layers (laminated white rot). In the second photo, the wood appears brown and is breaking into cubes (cubical bro Photos by Maria Morrow, CC-BY-NC.

Fungi are essential to the turnover of carbon locked up in woody materials. **Lignin** is a component of the secondary cell wall in plants, composing much of what we call **wood**, and is notoriously difficult to break down. Wood decay fungi are generally divided into two major groups: white rotters that break down both lignin and cellulose and brown rotters that have lost their ability to degrade lignin (Figure 2.3.3.3). The lignin-rich material left behind by brown rotters provides moisture retention and a springy, lightness to the soil substrate in forest ecosystems.

Mutualistic Relationships

Symbiosis (*sym* - shared, *bio* - life) is the ecological interaction between two or more organisms of different species that live together in a close physical association. The definition does not describe the quality of the interaction. When both members of the association receive a net benefit, the symbiotic relationship is called **mutualistic**. When one partner benefits at the expense of the other, it is **parasitism**. If one partner benefits but the other is unaffected, it is **commensalism**. Mutualistic relationships, however, are rarely so clear cut. Instead, these relationships often exist somewhere along the **parastism-mutualism continuum**, displaying elements of each. Fungi form these complex mutualistic associations with many types of organisms, including cyanobacteria, algae, plants, and animals.

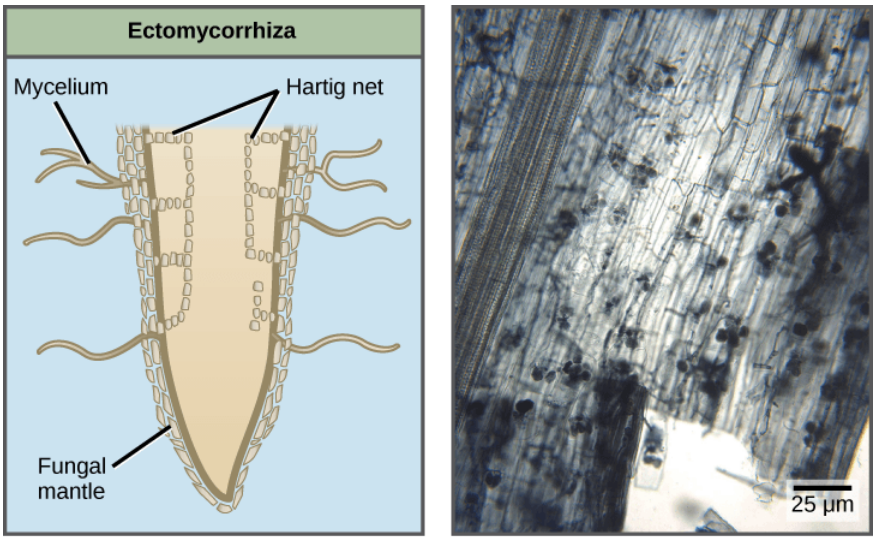
Mycorrhizal Relationships

One of the most remarkable associations between fungi and plants is the establishment of **mycorrhizae**. Mycorrhiza, which comes from the Greek words *myco* meaning fungus and *rhizo* meaning root, refers to the association between vascular plant roots and their symbiotic fungi. Around 90 percent of all plant species form mycorrhizal relationships with fungi. In a mycorrhizal association, the fungal mycelia use their extensive network of hyphae and large surface area in contact with the soil to channel water and minerals from the soil into the plant. In exchange, the plant supplies the products of photosynthesis to fuel the metabolism of the fungus.

There are a number of types of mycorrhizae. **Ectomycorrhizae** (“outside” mycorrhiza) form when fungi envelope the roots in a sheath (called a **mantle**) and a **Hartig net** of hyphae that extends into the roots between cells (Figure 2.3.3.4 a and Figure 2.3.3.5 a). The fungal partner can belong to the Ascomycota, Basidiomycota or occasionally one of the zygospore-forming Endogonales. Ectomycorrhizal relationships tend to be present in temperate and boreal forest trees, though their importance in tropical forests is currently being elucidated. In a second type, fungi in the Glomeromycota form arbuscular mycorrhiza (called **endomycorrhizae**). The fungi form **arbuscules,** highly branched hyphal structures that penetrate root cell walls and are the site of the metabolic exchanges between the fungus and the host plant (Figure 2.3.3.4 b and Figure 2.3.3.5 b). The arbuscules (from the Latin word for little trees) have a shrub-like appearance due to increase surface area for exchange across membranes.

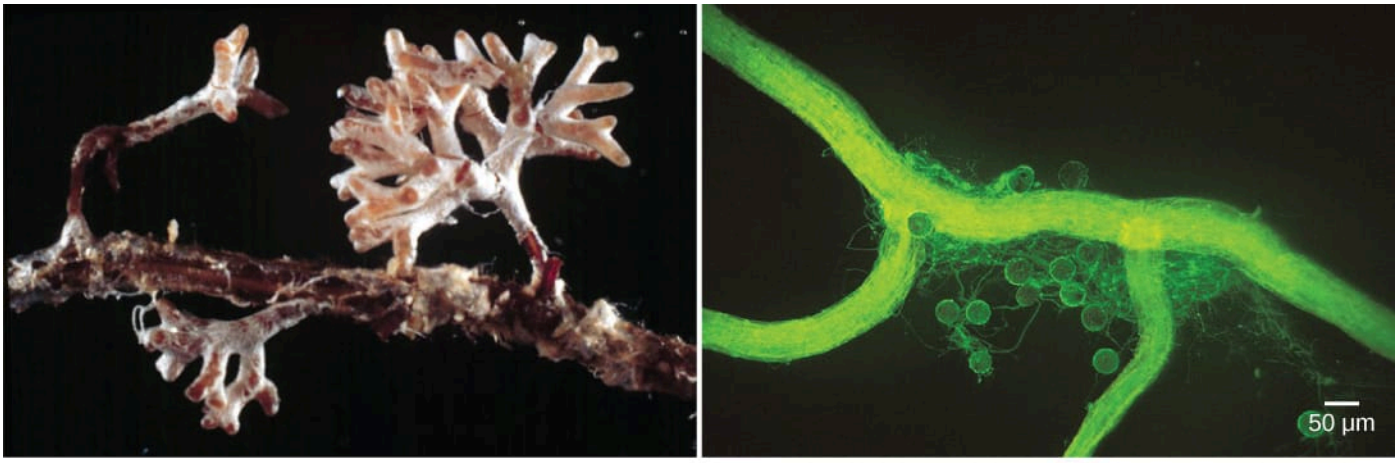
Orchids rely on a third type of mycorrhiza. Orchids are a group of plants, often living as epiphytes, that form tiny seeds without much storage to sustain germination and growth--the black specks in vanilla bean ice cream are the seeds of an orchid. Their seeds will not germinate without a mycorrhizal partner (usually a Basidiomycete). The orchid seed attracts a mycorrhizal fungus via chemical signals, then when the relationship is established, begins lysing the fungal cells to gain nutrients from the fungus. It is not until the orchid produces its leaves and can successfully photosynthesize that sugars begin being transferred to the fungus. Plants in the Ericaceae (heath family) represent at least two different types of mycorrhiza: Ericoid and Monotropoid.

Art Connection



(a) (b)

Figure 2.3.3.4: (a) Ectomycorrhiza forming a fungal mantle and Hartig net in a plant root and (b) arbuscular mycorrhiza forming arbuscules. In ectomycorrhiza, fungal hyphae form a structure called a Hartig net inside the root. The Hartig net forms rows of cells that extend straight down, and branch toward the outside of the root. A fungal mantle surrounds the root. Mycelia extend from the fungal mantle. In arbuscular mycorrhiza, the fungi form finger-like clusters that are connected to mycelia that extend from the root into the soil. (credit b: MS Turmel, University of Manitoba, Plant Science Department)



(a) (b)

Figure 2.3.3.5: The (a) inoculation of *Pinus radiata* (Monterey pine) roots by the hyphae of *Amanita muscaria* (fly amanita) causes the pine tree to produce many small, branched rootlets. The Amanita hyphae cover these small roots with a white mantle. (b) Spores (round bodies) and hyphae (thread-like structures) are evident in this light micrograph of an arbuscular mycorrhiza between a fungus and the root of a corn plant. (credit a: modification of work by Randy Molina, USDA; credit b: modification of work by Sara Wright, USDA-ARS; scale-bar data from Matt Russell)

Evolution Connection

Mycorrhizae are the mutually beneficial symbiotic association between roots of vascular plants and fungi. A well-accepted theory

proposes that fungi were instrumental in the evolution of the root system in plants and contributed to the success of angiosperms. The bryophytes (mosses and liverworts), which are considered the most primitive plants and the first to survive on dry land, do not have a true root system; some have vesicular–arbuscular mycorrhizae and some do not. They depend on a simple rhizoid (an underground organ) and cannot survive in dry areas. True roots appeared in vascular plants. Vascular plants that developed a system of thin extensions from the rhizoids (found in mosses) are thought to have had a selective advantage because they had a greater surface area of contact with the fungal partners than the mosses and liverworts, thus availing themselves of more nutrients in the ground.

Fossil records indicate that fungi preceded plants on dry land. The first association between fungi and photosynthetic organisms on land involved moss-like plants and endophytes. These early associations developed before roots appeared in plants. Slowly, the benefits of the endophyte and rhizoid interactions for both partners led to present-day mycorrhizae; up to about 90 percent of today's vascular plants have associations with fungi in their rhizosphere. The fungi involved in mycorrhizae display many characteristics of primitive fungi; they produce simple spores, show little diversification, do not have a sexual reproductive cycle, and cannot live outside of a mycorrhizal association. The plants benefited from the association because mycorrhizae allowed them to move into new habitats because of increased uptake of nutrients, and this gave them a selective advantage over plants that did not establish symbiotic relationships.

Lichens

Lichens are typically defined as a symbiotic relationship between a fungal partner (the **mycobiont**, typically an ascomycete) and an alga or cyanobacterium (the **photobiont**). The mycobiont forms the thallus, wrapping a thin layer of photobiont cells in fungal tissue. The fungus therefore houses the photobiont, while the photobiont makes sugars via photosynthesis that the fungus feeds on. The fungus controls the reproduction of the photobiont and when the photobiont gets to eat. The fungus is, in essence, farming the photobiont. Would you consider this a parasitism or mutualism?

This association forms a unified thallus that appears to be a single organism, thus lichens have species names. However, the more scientists look, the more interacting organisms they seem to find in lichens. Tripartite lichens contain two photobionts: an alga and a cyanobacteria. Many lichens have been found to contain a second mycobiont (typically a basidiomycete yeast), endohyphal bacteria, and other organisms whose role in the lichen relationship we do not yet understand. See Chapter 3.7 in the Photographic Atlas for a deeper dive into lichens.



Figure 2.3.3.6: California's state lichen, *Ramalina menziesii,* the lace lichen. This lichen forms draping nets dangling from tree branches, sometimes completely covering trees in the coastal dunes. Because lichens often grow on dying trees, people occasionally think they are causing this decline. However, lichens are generally too slow-growing to compete with trees and often filter nutrients from the air, which then drip off the lichens toward the roots of the tree, potentially helping fertilize it. Photo by JJ Johnson, CC-BY-NC.

Other examples of fungus–plant mutualism include the **endophytes**: fungi that live inside tissue without damaging the host plant. Endophytes release toxins that repel herbivores, or confer resistance to environmental stress factors, such as infection by microorganisms, drought, or heavy metals in soil.

Fungal-Animal Mutualism

Fungi have evolved mutualisms (and parasitisms!) with numerous insects in phylum Arthropoda: jointed, legged invertebrates. Arthropods depend on the fungus for protection from predators and pathogens, while the fungus obtains nutrients and a way to disseminate spores into new environments. The association between species of Basidiomycota and scale insects is one example. The fungal mycelium covers and protects the insect colonies. The scale insects foster a flow of nutrients from the parasitized plant to the fungus. In a second example, leaf-cutting ants of Central and South America literally farm fungi. They cut disks of leaves from plants and pile them up in underground gardens (Figure 2.3.3.7). A basidiomycete fungus (*Leucoagaricus gongylophorus*) is cultivated in these disk gardens from bits of mycelium from the queen's original colony, meaning the fungi within these gardens are all genetically quite similar (a monoculture, if you will). The fungus digests the cellulose in the leaves that the ants cannot break down, then produces nutrient-rich structures called gongylidia on which the ants feed. The ants patrol their garden, tending their fungi. There are actinomycetes (filamentous bacteria) that live on the surface of the ant, within its cuticle, that produce antifungal compounds specific to another parasitic fungus (an ascomycete) that often invades these fungal gardens. Both ants and fungi benefit from the association. The fungus receives a steady supply of leaves and freedom from competition, while the ants feed on the fungi they cultivate. Watch this process in action in Video 2.3.3.1.



Figure 2.3.3.7: A leaf cutting ant transports a piece of a leaf that will feed a farmed fungus. (credit: Scott Bauer, USDA-ARS)

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 2.3.3.1: Leaf cutter ants and their fungal gardens. Sourced from YouTube.

Fungivores

Animal dispersal is important for some fungi because an animal may carry spores considerable distances from the source. Fungal spores are rarely completely degraded in the gastrointestinal tract of an animal, and many are able to germinate when they are passed in the feces. Some dung fungi actually require passage through the digestive system of herbivores to complete their lifecycle. The black truffle—a prized gourmet delicacy—is the fruiting body of an underground mushroom. Almost all truffles are ectomycorrhizal, and are usually found in close association with trees. Animals eat truffles and disperse the spores. In Italy and France, truffle hunters use female pigs to sniff out truffles. Female pigs are attracted to truffles because the fungus releases a

volatile compound closely related to a pheromone produced by male pigs.

Fungal Parasites of Plants

Parasitism describes a symbiotic relationship in which one member of the association benefits at the expense of the other. Both parasites and pathogens harm the host; however, the pathogen causes a disease, whereas the parasite usually does not.

The production of sufficient good-quality crops is essential to human existence. Plant diseases have ruined crops, bringing widespread famine. Many plant pathogens are fungi that cause tissue decay and eventual death of the host (Figure 2.3.3.8). In addition to destroying plant tissue directly, some plant pathogens spoil crops by producing potent toxins. Fungi are also responsible for food spoilage and the rotting of stored crops. For example, the fungus *Claviceps purpurea* causes ergot, a disease of cereal crops (especially of rye). Although the fungus reduces the yield of cereals, the effects of the ergot's alkaloid toxins on humans and animals are of much greater significance. In animals, the disease is referred to as ergotism. The most common signs and symptoms are convulsions, hallucination, gangrene, and loss of milk in cattle. The active ingredient of ergot is lysergic acid, which is a precursor of the drug LSD. Smuts, rusts, and powdery or downy mildew are other examples of common fungal pathogens that affect crops.



Figure 2.3.3.8: Some fungal pathogens include (a) green mold on grapefruit, (b) powdery mildew on a zinnia, (c) stem rust on a sheaf of barley, and (d) grey rot on grapes. In wet conditions *Botrytis cinerea*, the fungus that causes grey rot, can destroy a grape crop. However, controlled infection of grapes by Botrytis results in noble rot, a condition that produces strong and much-prized dessert wines. (credit a: modification of work by Scott Bauer, USDA-ARS; credit b: modification of work by Stephen Ausmus, USDA-ARS; credit c: modification of work by David Marshall, USDA-ARS; credit d: modification of work by Joseph Smilanick, USDA-ARS)

Aflatoxins are toxic, carcinogenic compounds released by fungi of the genus *Aspergillus*. Periodically, harvests of nuts and grains are tainted by aflatoxins, leading to massive recall of produce. This sometimes ruins producers and causes food shortages in developing countries.

Summary

Fungi occupy nearly all environments on Earth, but are frequently found in cool, moist places with a supply of decaying material. Fungi are saprotrophs that decompose organic matter, mutualists, and parasites. Many successful mutualistic relationships involve a fungus and another organism. Some groups of fungi establish complex mycorrhizal associations with the roots of plants. Approximately 90% of all plant species form some type of mycorrhizal relationship and it is likely that this symbiosis aided early plants in their transition onto land. Lichens are a symbiotic relationship between a fungus and a photosynthetic organism, usually an alga or cyanobacterium. The photosynthetic organism provides energy derived from light and carbohydrates, while the fungus supplies minerals and protection. Some animals that consume fungi help disseminate spores over long distances.

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2.3.4: Microfungi

Learning Objectives

- Use characteristics to distinguish between groups of microfungi.
- Describe some of the roles microfungi have in ecosystems.
- Explain the relationship between plants and members of Glomeromycota.
- Identify structures in the "zygomycete" life cycle and know their ploidy.

Chytrids

This small group (~1000 species) is thought to be the most primitive of the fungi. Once all classified as Chytridiomycota, these early, aquatic fungi are now grouped into Blastocladiomycota, Chytridiomycota, and Neocallimastigomycota. Unlike all the other fungi, its members produce flagellated gametes (for sexual reproduction) and flagellated zoospores (for asexual reproduction). They are mostly aquatic.

The evolutionary record shows that the first recognizable chytrids appeared during the late pre-Cambrian period, more than 500 million years ago. Like all fungi, chytrids have chitin in their cell walls, but one group of chytrids has both cellulose and chitin in the cell wall. Most chytrids are unicellular; a few form multicellular thalli with filamentous hyphae, which have no septa between cells (coenocytic). They produce gametes and diploid zoospores that swim with the help of a single flagellum.



Figure 2.3.4.1: A parasitic chytrid thallus (the globose structure indicated by the arrow) on a diatom. Photo by Thijs Frenken, CC-BY-NC.

Chytrids usually live in aquatic environments, although some species live on land or as mutualists in the rumens of ungulates. Some species thrive as parasites on plants, insects, or amphibians (Figure 2.3.4.3), while others are saprotrophs. The chytrid genus *Allomyces* (Figure 2.3.4.2) is well characterized as an experimental organism; fungal sex horomones (specifically sirenin) were first discovered in this group. Its reproductive cycle includes both asexual and sexual phases. *Allomyces* produces diploid or haploid flagellated zoospores in a sporangium.



Figure 2.3.4.2: Chytrids in the genus *Allomyces* are aquatic decomposers. The first image (top) shows sesame seeds floating in pond water with fungus growing off of them. The second image (bottom left) shows a microscopic image of a zoosporangium produced at the end of a hyphal filament (asexual reproduction). The final image (bottom right) shows two resting sporangia, the result of sexual reproduction. Photos by Tom Bruns, CC-BY-NC.

Parasitic Chytrids

Many chytrids are parasites, perhaps due to their need for an aqueous environment. Some chytrid species are parasites of other chytrids (*Rozella allomycis* is a parasite that lives within *Allomyces*), some are parasites of algal species (Figure 2.3.4.3 and Figure 2.3.4.4), some are parasites of plants (Figure 2.3.4.5, while still others are parasites of animals (Figure 2.3.4.6. The most infamous chytrid species is a parasite on amphibians, discussed in the following section.

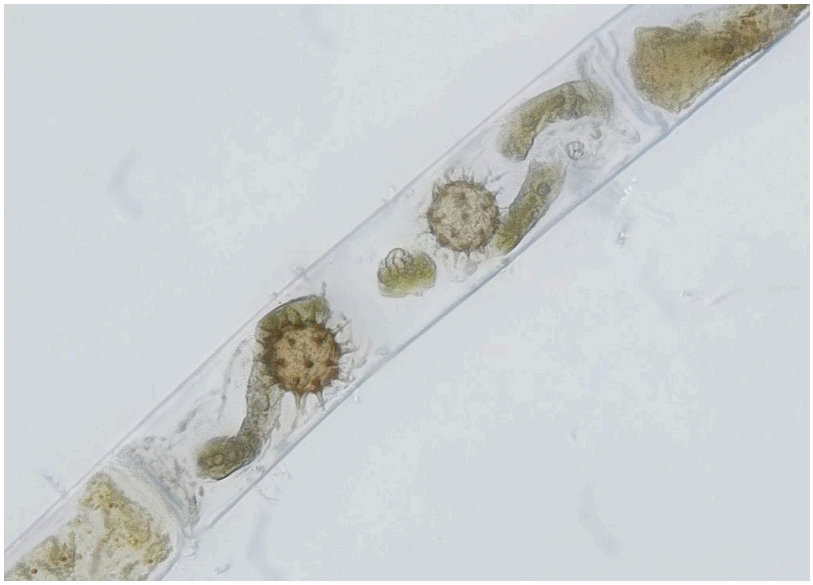


Figure 2.3.4.3: This image shows *Micromyces zygogonia* (Chytridiomycota), a parasite with spiky structures (prosori), inside the cells of the alga *Spirogyra*. Photo Credit Fahrenheit_66 (iNaturalist username), CC-BY-NC-SA.

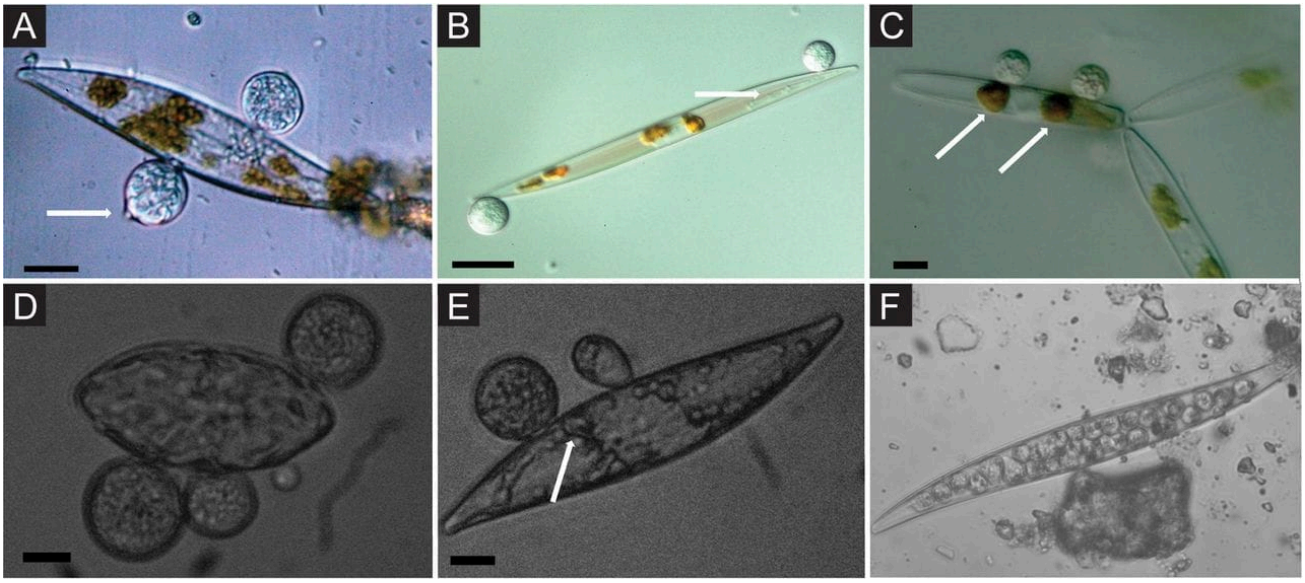


Figure 2.3.4.4: In these images, the part of the chytrids you can see is the large, globose struture attached to the outside of the diatom. This is the part of the thallus where spores are made. "Chytrid parasites of marine diatoms. (A) Chytrid sporangia on *Pleurosigma* sp. The white arrow indicates the operculate discharge pore. (B) Rhizoids (white arrow) extending into diatom host. (C) Chlorophyll aggregates localized to infection sites (white arrows). (D and E) Single hosts bearing multiple zoosporangia at different stages of development. The white arrow in panel E highlights branching rhizoids. (F) Endobiotic chytrid-like sporangia within diatom frustule. Bars = 10 µm. For more details see: Hassett BT, Gradinger R (2016) "Chytrids dominate arctic marine fungal communities". *Environ Microbiol*, **18**(6):2001–2009." CC BY 4.0, via Wikimedia Commons.



Figure 2.3.4.5: A parasite on Geranium, this *Synchytrium papillatum* (Chytridiomycota) is forming pink growths on the calyx and peduncle of these flowers. Photo Credit: James Bailey, CC BY-NC.



Figure 2.3.4.6: Likely the most infamous chytrid, *Batrachochytrium dendrobatidis* (Chytridiomycota) causes a lethal skin infection in many amphibians. This now widespread invasive pathogen is contributing to global amphibian declines and extinctions. Photo by Jonathan (JC) Carpenter, CC BY-NC.

Bd (*Batrachochytrium dendrobatidis*)

Batrachochytrium dendrobatidis, commonly called Bd, is a chytrid fungus that infects the skin of amphibians. The infection causes hardening of the permeable skin, making it difficult for the animal to breathe. Swimming spores are produced in lesions on the skin and are easily spread through aquatic environments. Amphibians, who must spend part of their life cycle in water, are highly susceptible to this parasite, particularly as other stressors like climate change and pollution lower their resistance. Bd is contributing to a worldwide decline in many amphibian species (though there are numerous other contributing factors), particularly frogs.

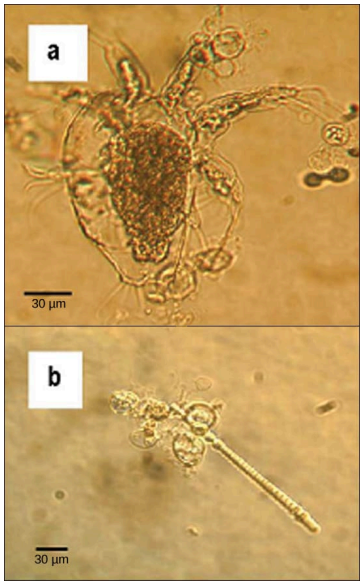


Figure 2.3.4.7: The chytrid *Batrachochytrium dendrobatidis* is seen in these light micrographs as transparent spheres growing on (a) a freshwater arthropod and (b) algae. This chytrid causes skin diseases in many species of amphibians, resulting in species decline and extinction. Descriptive text: Micrograph A shows an arthropod, which is a teardrop-shaped transparent organism about 90 microns across and 120 microns long. Tentacle-like appendages jut out from the front, wide end of the organism, and clusters of cilia-like appendages just out from either side and the back. Transparent oval organisms about 20 microns across cling to the arthropod. Micrograph B shows a similar oval transparent organisms clinging to rod-shaped algae about 5 microns across and 200 microns long. (credit: modification of work by Johnson ML, Speare R., CDC)

Neocallimastix

Neocallimastix is an anaerobic chytrid that lives in the rumen of some ungulates. Cows and other grazing animals can't actually break down the cellulose in the plants they eat. Instead, this plant material first travels to a pre-stomach called a rumen. A community of anaerobic organisms breaks down the cellulose, producing methane. When the pre-digested plant matter has been transformed into compounds that the cow can break down, it then moves to the stomach of the cow. The methane released by cows is due to this anaerobic activity in the rumen.

Zygospore-forming Fungi

Characteristics

Fungi in the former Zygomycota were recently split into several lineages because they are a paraphyletic group. These fungi produce a large sexual structure called a **zygospore** and so are called "zygomycetes". They are mainly saprotrophs with coenocytic hyphae and haploid nuclei. They produce haploid **sporangiospores** by mitosis during asexual reproduction. The group name comes from the zygospores that they use for sexual reproduction (Figure 2.3.4.8), which have hard walls formed from the fusion of reproductive cells from two individuals. Zygomycetes are important for food science and as crop pathogens. One example is *Rhizopus stolonifer* (Figure 2.3.4.8), an important bread mold that also causes rice seedling blight. *Mucor* is a genus of fungi that can potentially cause necrotizing infections in humans, although most species are intolerant of temperatures found in mammalian bodies.

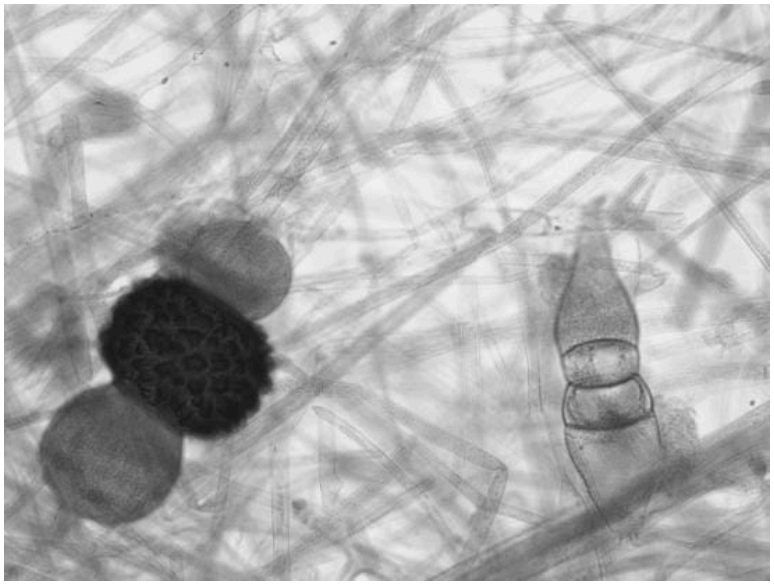


Figure 2.3.4.8: *Rhizopus* sexually reproducing. The large, warty zygosporangium (left) is being held by two suspensors, one from each mycelial parent. On the right side of the image, suspensors hold gametangia that would soon fuse to form a zygosporangium. Photo by Maria Morrow, CC BY-NC.



Figure 2.3.4.9: These images show asexually produced spores. (a) This brightfield micrograph shows the release of spores from a sporangium at the end of a hypha called a sporangiophore. The organism is a *Mucor* sp. fungus, a mold often found indoors. (b) Sporangia grow at the ends of stalks, which appear as the white fuzz seen on this bread mold, *Rhizopus stolonifer*. The tips of bread mold are the dark, spore-containing sporangia. (credit a: modification of work by Centers for Disease Control and Prevention; credit b right: modification of work by "Andrew"/Flickr)

Life Cycle

Zygomycetes have a thallus of coenocytic hyphae in which the nuclei are haploid when the organism is in the vegetative stage. Asexual reproduction occurs through mitosporangia that produce sporangiospores by mitosis. These can germinate and develop into a new haploid mycelium that is genetically identical to the parent. The black tips of bread mold are the swollen sporangia packed with black spores (Figure 2.3.4.8). Sexual reproduction starts when conditions become unfavorable. Two different mating strains (type + and type –) must be in close proximity for **gametangia** from the hyphae to be produced and fuse (**plasmogamy**), forming a multinucleate **zygosporangium**. Many sets of haploid nuclei fuse (karyogamy) to form diploid nuclei. The developing diploid zygospores have thick coats that protect them from desiccation and other hazards. They may remain dormant until environmental conditions are favorable. When the zygospore germinates, it undergoes meiosis and produces haploid spores from a sporangium. To differentiate between the sporangia produced in sexual and asexual reproduction, you must trace them back to the base. Did it emerge from a zygospore or from a hypha? Both types of spores are haploid and can germinate to form a new haploid mycelium. Spores that germinate from the sporangium of the zygospore will be genetically distinct from the parent mycelia.

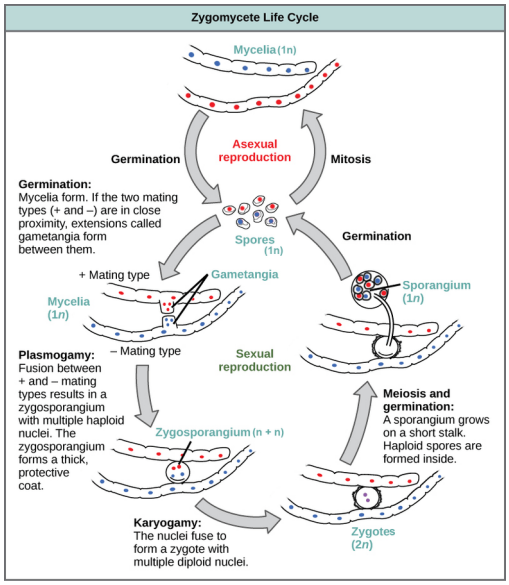


Figure 2.3.4.10: "Zygomycetes" have asexual and sexual life cycles. In the asexual life cycle, 1n spores undergo mitosis to form long chains of cells called mycelia. Germination results in the formation of more spores. In the sexual life cycle, spores germinate to form mycelia with two different mating types: plus and minus. If the plus and minus mating types are in close proximity, extensions called gametangia form between them. In a process called plasmogamy, the gametangia fuse to form a dikaryotic (n+n) zygosporangium with multiple haploid nuclei. A thick, protective coat forms around the zygosporangium. In a process called karyogamy, the nuclei fuse to form a zygote with multiple diploid (2n) nuclei. The 2n zygotes undergo meiosis. A sporangium grows on a short stalk and the haploid spores are formed inside. The spores germinate, ending the cycle. Original diagram altered by Maria Morrow.

Glomeromycota

Glomeromycota represent the arbuscular endomycorrhizal fungi. These fungi form a mutualistic relationship with plant roots, forming hyphal structures within the plant cell walls (Figure 2.3.4.12), branching to maximize contact with the plasma membrane. Outside of the direct interaction between these fungi and plants, the fungi themselves are not well understood.

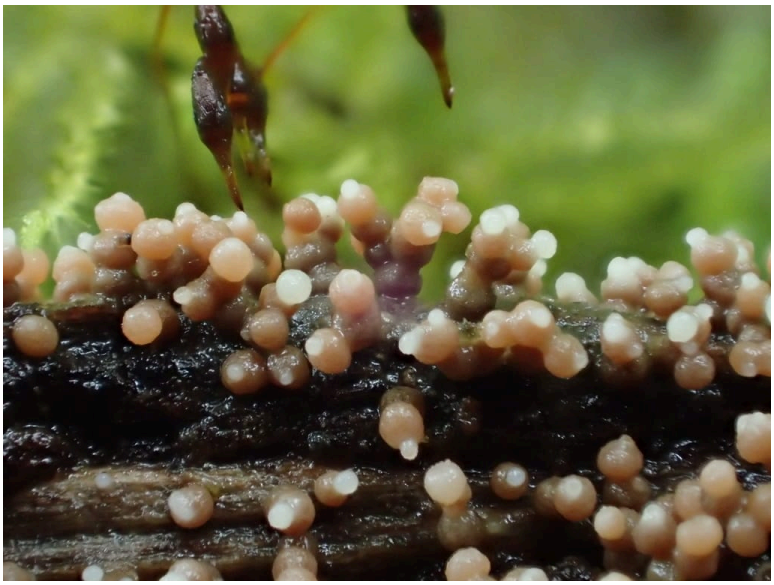


Figure 2.3.4.11: Glomus coremioides forming sporocarps, an unusual characteristic in this fungal phylum. The white to tan ones are still forming. Spores are produced within these structures. The ecology of this species is a bit mysterious. Photo by Damon Tighe, CC-BY-NC.

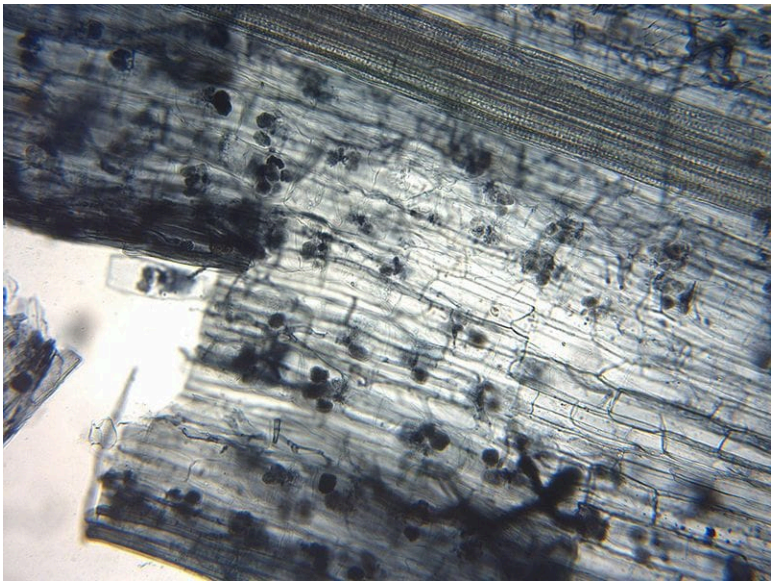


Figure 2.3.4.12: Endomycorrhizal fungi can form arbuscules (branching structures) and vesicles (globose structures). In this micrograph, a root has been stained and viewed at high magnification. The hyphal structures of the fungus can be seen within the root cells, particularly the vesicles, which stain darker. Msturmel, Public domain, via Wikimedia Commons.

Molds

Molds are fungi that are asexually reproducing or sometimes growing vegetatively. If a mold is coenocytic, it is likely from the zygospore-forming lineages. If the mold is septate, it could be a member of the Ascomycota or Basidiomycota. Spores produced by molds are called conidia (sing. **conidium**) and the structures they are produced on are called **conidiophores** (Figure 2.3.4.13). Molds are important decomposers and pathogens. Commercially, molds are important for a variety of uses, such as food production (e.g. cheese making, soy sauce, or the production of citric acid), food spoilage, and the production of antiobiotics.

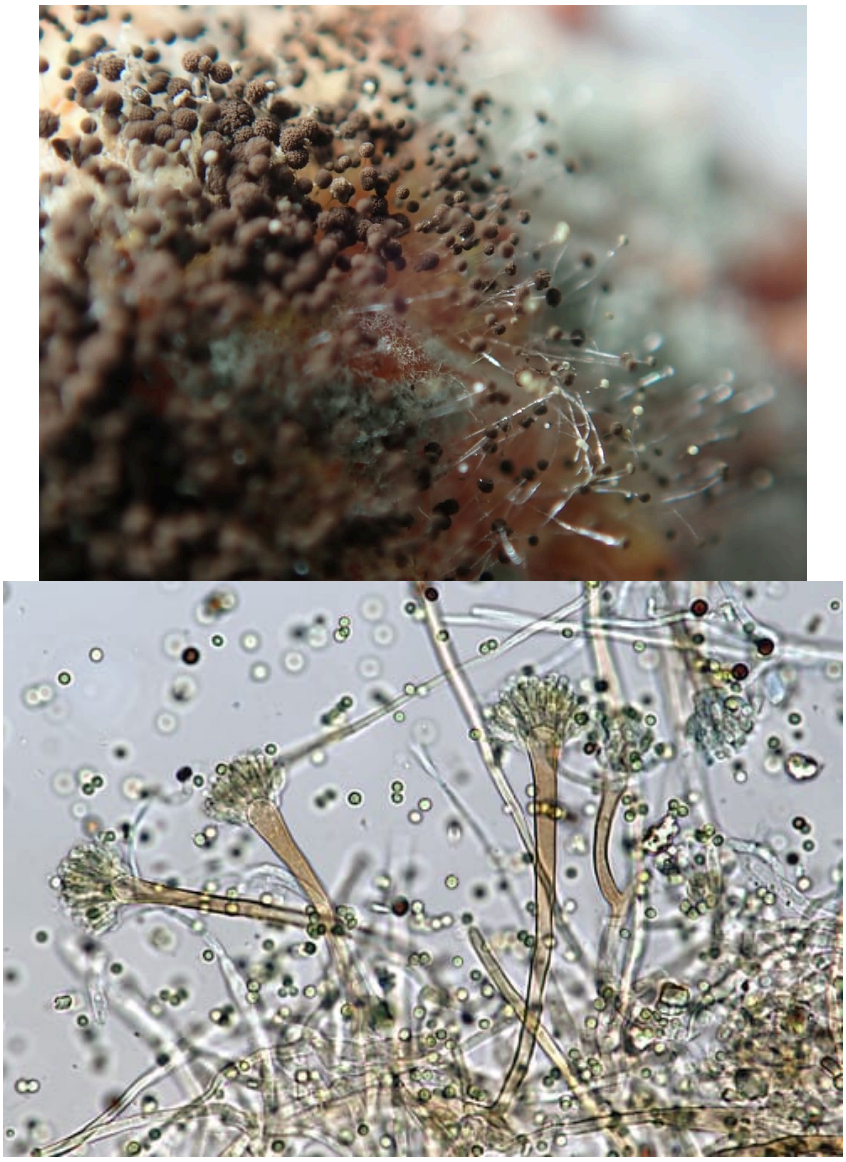


Figure 2.3.4.13: Aspergillus spp. conidiophores. In the first photo, the conidia appear brown and the conidiophores are hyaline (clear, lacking color). The younger conidiophores have whitish tops. In the second photo, the conidiophores appear brown with swollen ends. From these swollen ends, small, globose conidia are produced. The conidia appear almost greenish. First photo by Denis Makhnovsky, CC-BY-NC. Second photo by Kathie Hodge, CC BY-NC-SA.

Summary

Microfungi is a term used to refer to groups of fungi that form microscopic reproductive structures. The chytrids are early diverging lineages of fungi that have swimming spores with a single flagellum. These lineages are primarily aquatic, but some have evolved to live terrestrially. They have important roles as decomposers, mutualists, and parasites, including one causing worldwide declines in amphibians.

The zygospore-forming fungi, formerly classified as zygomycetes, have a haplontic life cycle and some can reproduce asexually by mitosis. When they sexually reproduce, they form a multinucleate zygosporangium that is often thick-walled and highly ornamented. These fungi are commonly found on sugary substrates like fruits or nutrient-dense substrates like dung. Some lineages are pathogens of arthropods.

The Glomeromycota are a strange group of fungi that form endomycorrhizal relationships with plants. These fungi penetrate the cells within plant roots and form highly branched structures called arbuscules to increase surface area for nutrient exchange. The plants transfer sugars to the fungus, while the fungus supplies nutrients like phosphorus and nitrogen, as well as water, from the

soil substrate.

Molds are fungi reproducing asexually and can be from the lineages of microfungi (coenocytic hyphae) or higher fungi (septate hyphae).

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2.3.5: Macrofungi

Ascomycota

Learning Objectives

- Use life history traits and morphological features to distinguish between Ascomycota and Basidiomycota.
- Identify structures in the Ascomycota life cycle and know their ploidy.
- Differentiate between different types of ascocarps; locate fertile surfaces within those structures.

The majority of described fungal species belong to the Phylum Ascomycota. Fungi in this group have simple septate hyphae and most produce fruiting bodies called ascocarps (Figure 2.3.5.1) for sexual reproduction. Some genera of Ascomycota either only reproduce asexually via conidia or the sexual phases have not been discovered or described. These were referred to as the Fungi Imperfecti or Deuteromycota. When ascomycetes reproduce sexually, they produce haploid **ascospores** (usually 8) within a sac-like structure called an **ascus** (Figure 2.3.5.2).

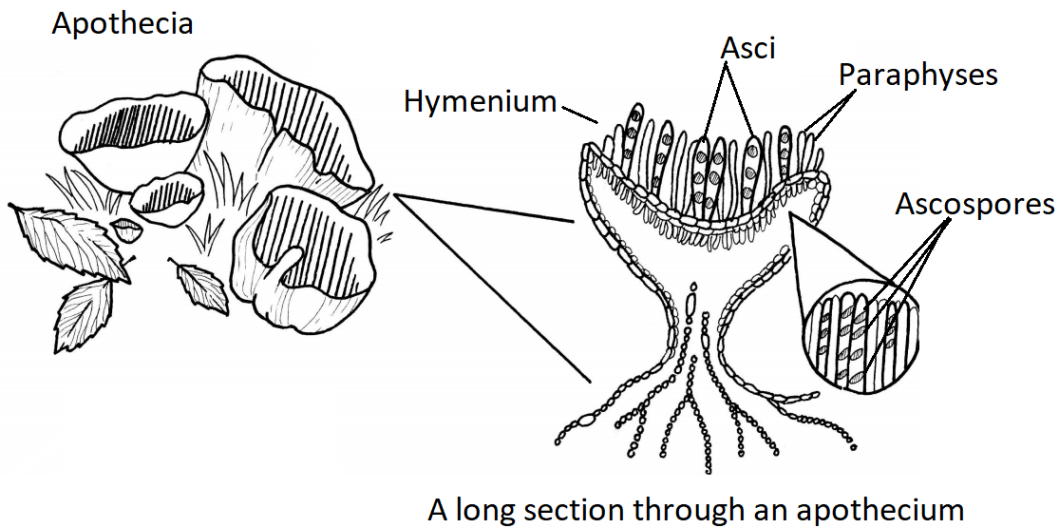


Figure 2.3.5.1: Ascomycetes are called the cup fungi after the cup-shaped fruiting body formed by many of the larger organisms in this group, the apothecium. A few apothecia are shown on the left side of the diagram. The right side shows a long section through an apothecium. Septate hyphae comprise most of the structure. On the interior surface of the cup is the hymenium, which is composed of asci and paraphyses. Ascospores are produced by meiosis within each ascus. Diagram by Nikki Harris, CC-BY-NC.

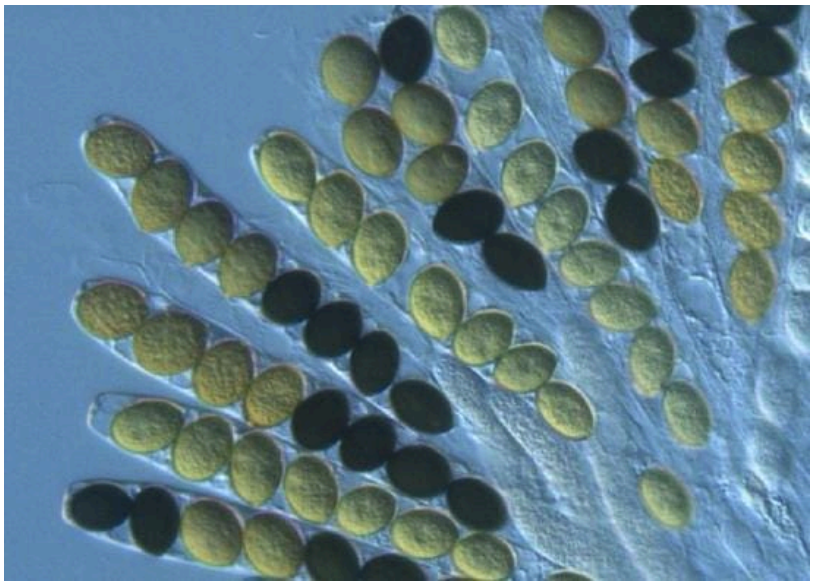


Figure 2.3.5.2: In this photo, light and dark colored ascospores are produced inside the asci of the fungus *Sordaria macrospora*. This demonstrates the linear division of the spores, as pairs of genetically identical light or dark spores are adjacent, produced after mitosis occurs within the ascus. Photo by Aurora Storlazzi, CC BY 4.0, via Wikimedia Commons.

The Ascomycota include some ectomycorrhizal fungi (*e.g.* truffles and morels), fungi that are used as food, others that are common causes of food spoilage (bread molds and plant pathogens), and still others that are human pathogens. Some notable examples of ascomycetes include:

- ***Saccharomyces cerevisiae*** one of the **budding yeasts**. It ferments sugar to **ethanol** and **carbon dioxide** and thus is used to make alcoholic beverages like beer and wine, to make ethanol for industrial use and in baking (it is often called **baker's yeast**). Here, it is the carbon dioxide that is wanted (to make bread and cakes "rise" and have a spongy texture). Yeast is also used in the commercial production of some vitamins and in the production - using recombinant DNA technology - of some human therapeutic proteins.
- ***Neurospora crassa***, another favorite "model" organism in the laboratory.
- The fungal partner in most **lichens** is an ascomycete.
- Powdery mildews that attack ornamental plants.
- The chestnut blight, which in a few decades killed almost all of the mature American chestnut trees in the Appalachians of North America.
- The Dutch elm disease, which has killed many of the American elms in the United States.
- ***Pneumocystis jirovecii***, which is a major cause of illness in immunosuppressed people, e.g., patients with AIDS.
- The **truffle** and the **morel**, both highly-prized food delicacies. Truffles establish a symbiotic relationship with the roots of such trees as oaks.



Figure 2.3.5.3: A truffle. It might not look like much, but truffles are some of the most highly prized fungal fruiting bodies! (Public Domain).

Ascomycete Life Cycle

Asexual reproduction is frequent and involves the production of conidiophores that release haploid conidia. Sexual reproduction starts with the development of special hyphae from either one of two types of mating strains. One strain produces an **antheridium** and a strain of a complementary mating type develops an **ascogonium**. At fertilization, the antheridium and the ascogonium combine in plasmogamy without nuclear fusion. Dikaryotic **ascogenous hyphae** arise, in which pairs of nuclei migrate: one from each parent strain. In each ascus mother cell, two nuclei fuse (karyogamy). During sexual reproduction, thousands of **asci** may fill a fruiting body called the ascocarp. The diploid nucleus gives rise to four haploid nuclei by meiosis. In most ascomycetes, this is followed by a round of mitosis, producing 8 **ascospores**. The ascospores are then released, germinate, and form haploid hyphae that are disseminated in the environment and start new mycelia (Figure 2.3.5.4).

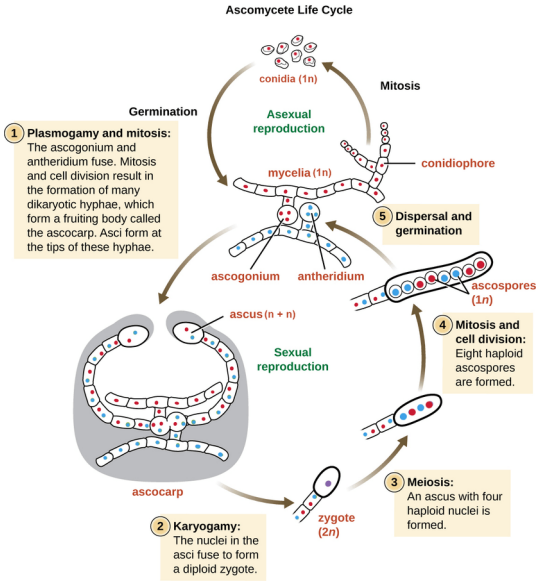


Figure 2.3.5.4: The life cycle of an ascomycete is characterized by the production of asci during the sexual phase. The haploid phase is the predominant phase of the life cycle. In asexual reproduction, haploid (1n) mycelia produce conidiophores which use mitosis to asexually produce spores. These spores then germinate into new haploid mycelia. Sexual reproduction begins when one mycelium produces an ascogonium and another produces an antheridium. In plasmogamy, the ascogonium and antheridium fuse. Mitosis and cell division result in the formation of many dikaryotic (n+n) hyphae, which form a fruiting body called the ascocarp. Asci form at the tips of these hyphae. In karyogamy, the nuclei in the asci fuse to form a diploid (2n) zygote. Then meiosis produces four haploid (1n) nuclei within the ascus. Then mitosis and cell division results in eight haploid ascospores in the ascus. These haploid (1n) ascospores then disperse and germinate into new mycelia. Original diagram altered by Maria Morrow.

Types of Ascocarps

Apothecium

Apothecia are cup-shaped with the asci fully exposed, lining the interior of the cup. Normally, these asci are microscopic. However, in the fungus *Ascobolus*, the large asci with dark ascospores can be seen with the naked eye or a handlens (Figure 2.3.5.5). The typical cup shape can be inverted and take on strange morphologies (see Figure 2.3.5.6).





Figure 2.3.5.5: In the first photo, apothecia of *Ascobolus furfuraceus* have asci appear black due to their dark spores. In the second photo, a magnified view of *Ascobolus immersus* shows the dark ascospores. First photo by Salvatore Bacciu and Paola Mereu, (CC-BY-NC). Second photo by Jerry Cooper, some rights reserved (CC-BY).



Figure 2.3.5.6: Two apothecia of *Helvella* in the image on the left. This ascomycete, much like a morel, has an apothecium at the end of a stalk. The apothecium at the top of the stalk is not cup-shaped because the cup has been inverted. The spores are produced on the surface of the apothecium that you can see in this image. The image on the right shows another ascoymcete, *Heyderia abietis*, with a similar strategy. The inverted cup shape makes a smooth tongue-like structure on the top of the stalk. These are only about 1 cm tall. Photos by Maria Morrow, CC-BY-NC.

Perithecium

A **perithecium** is a flask-shaped fruiting structure (Figure 2.3.5.7), often microscopic and embedded within either the substrate it is fruiting in or a fungal structure called a stroma (Figure 2.3.5.8). The asci are almost entirely closed off from the external environment, excepting a small hole in the top of the perithecium called an **ostiole**. Many plant parasites, such as the causal agents of Dutch elm disease, American chestnut blight, and ergot, are perithecial ascomycetes.

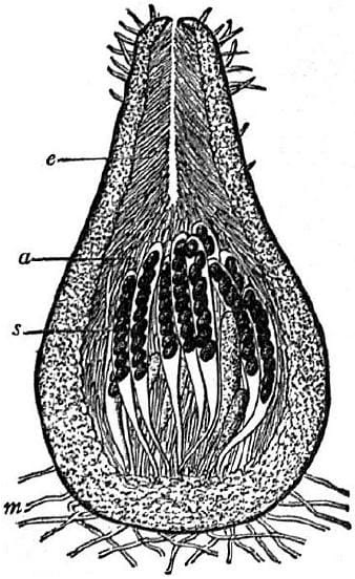


Figure 2.3.5.7: A diagram of a perithecium. m=the mycelium, s=asci with black ascospores inside, a=paraphyses (sterile cells surrounding the asci), e=the ostiole (opening). From Strasburger's Lehrbuch der Botanik. After v. Tavel., Public domain, via Wikimedia Commons.



Figure 2.3.5.8: Xylaria species produce perithecia embedded in sterile fungal tissue called a stroma. In *Xylaria tucumanensis*, the perithecia are large and are not surrounded by much stroma. In the first photo (left), each lumpy projection has a distinct dot in its center; this is the ostiole (opening) of the perithecium. The second photo (right) shows a long section through a fruiting structure. The white tissue is the stroma. The black, concave structures are the perithecia. Photos by Danny Newman, CC-BY-NC-SA.

Cleistothecium

A cleistothecium is a fully-enclosed fruiting structure. These typically have bag-like asci (Figure 2.3.5.9). Some (chasmothecia) split open to release their spores. This type of fruiting body can be found in the powdery mildews, a group of plant pathogenic fungi in the order Erysiphales (Figure 2.3.5.10).

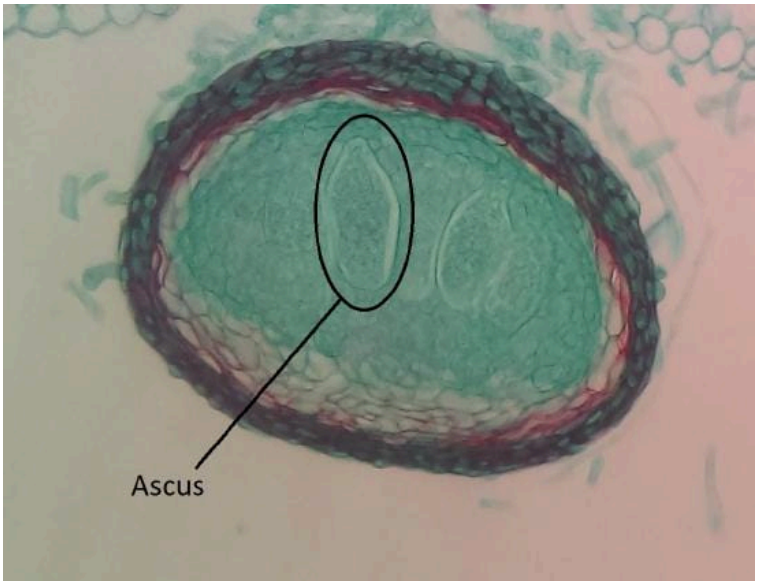


Figure 2.3.5.9: A section through a cleistothecium with an ascus circled. A cleistothecium is a fully enclosed fruiting body, generally microscopic, that encloses many bag-like asci. Photo by Melissa Ha, CC-BY-NC with labels added.



Figure 2.3.5.10: Powdery mildews (Erysiphales) are plant parasites that form cleistothecia. They get their name from the powdery white look they give to the surface of plants they are parasitizing (first). Sometimes within this powdery white fluff (mycelium), cleistothecia can be seen with some magnification (second). Photos by ðejay (Orkney), CC-BY-NC.

Lichenized Fungi

Learning Objectives

- Explain the lichen symbiosis.
- Identify structures in the lichen thallus.

Lichens are fungi that live in a symbiotic association with a green alga or cyanobacterium (the "**photobiont**"), or both. The primary fungal partner (the "**mycobiont**") in most lichens (98% of them) is an ascomycete. Basidiomycetes make up the remainder. The relationship is often characterized as mutualistic; that is, both partners benefit. However, evidence (see "The British Soldier" below) suggests that while the fungus is dependent on its autotrophic partner, the photobiont is often perfectly content to live alone. Recently many lichens have been found to harbor a second fungal partner, a basidiomycete yeast. Its function remains to be discovered, though the presence of the basidiomycete can change the outward appearance of the lichen (e.g. color).

The British Solder

The below image is of the colorful lichen called British soldier. The fungus is *Cladonia cristatella*, an ascomycete. Its name is the name given to the lichen. The photobiont is *Trebouxia erici*, a green alga. It is found in many other lichens as well, and also can be found growing independently. The algal cells eventually are killed by the fungus, but are continuously replaced by new ones. So, the relationship in this lichen is one of controlled parasitism rather than mutualism.



Figure 2.3.5.11: British soldier lichen, Cladonia cristatella.

The red cap produces the spores of the fungus, but these alone cannot form new lichens. Other structures (e.g., soredia), containing both partners, are needed to disperse the lichen to new locations. Some lichens release only fungal spores. These mycobionts depend for their continued survival on finding an acceptable photobiont released from other lichens. Phylogenetic trees, based on both ribosomal RNA genes and many protein-coding genes, as well as **fossils** indicate that lichens have been present on the earth for at least 600 million years.

Today about 14,000 species of fungi are known to form lichens. Lichens display a range of colors and textures and can survive in the most unusual and hostile habitats, though they are extremely sensitive to air pollution.. They cover rocks, gravestones, tree bark, and the ground in the tundra where plant roots cannot penetrate. Lichens can survive extended periods of drought, become completely desiccated, and then rapidly become active once water is available again. In part because of this ability, as well as the pigments in some lichens that protect from UV radiation, lichens are some of the only living things to survive exposure to conditions in space.

Explore the world of lichens using this site from Oregon State University.



(a) (b) (c)

Figure 2.3.5.12: Lichens have many forms. They may be (a) crust-like, (b) hair-like, or (c) leaf-like. Descriptive text: Different lichens are shown. Part A shows a lichen that appears like brown flecks on gray rock. Part B shows a moss-like lichen hanging from a tree. Part C shows lichen that have a wide, flat, convoluted shape. (credit a: modification of work by Jo Naylor; credit b: modification of work by "djpmapleferryman"/Flickr; credit c: modification of work by Cory Zanker)

The body of a lichen, referred to as a **thallus** (Figure 2.3.5.13), is formed of hyphae wrapped around the photosynthetic partner. The photosynthetic organism provides carbon and energy in the form of carbohydrates. If cyanobacteria are involved, they fix nitrogen from the atmosphere, contributing nitrogenous compounds to the association. In return, the fungus supplies minerals and protection from dryness and excessive light by encasing the algae in its mycelium. The fungus also attaches the symbiotic organism to the substrate.

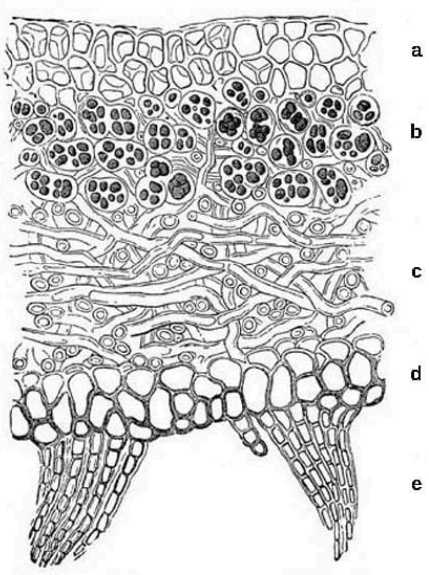


Figure 2.3.5.13: This cross-section of a lichen thallus shows the (a) upper cortex of fungal hyphae, which provides protection; the (b) algal zone where photosynthesis occurs, the (c) medulla of fungal hyphae, and the (d) lower cortex, which also provides protection and may have (e) rhizines to anchor the thallus to the substrate. Descriptive text: The lichen has multiple layers. The top layer, or cortex, is made up of irregularly shaped cells. Beneath this layer, the cells in the algal zone hyphae wrap around the cyanobacteria. Beneath the algal zone, long, thread-like mycelia occur. Beneath the mycelia is the lower cortex, which is similar in appearance to the upper cortex, but with larger cells. Projections beneath the lower cortex anchor the lichen to its substrate.

The thallus of lichens grows very slowly, expanding its diameter a few millimeters per year. Both the fungus and the alga participate in the formation of dispersal units for reproduction. Some lichens produce **soredia** (Figure 2.3.5.14), clusters of algal cells surrounded by mycelia, for asexual reproduction. Soredia are dispersed by wind and water and form new lichens. To reproduce sexually, the fungus makes spores that must find a new photosynthetic partner shortly after germinating.



Figure 2.3.5.14: A foliose lichen with marginal **soralia**. The powdery regions on the edges of this lichen are called soralia. In these soralia, the lichen is producing many soredia--loose bundles of fungal hyphae and algal cells that allow the lichen to reproduce asexually. Three of these soralia have been indicated by white arrows. Photo by Maria Morrow, CC-BY-NC.

Basidiomycota

Learning Objectives

- Use life history traits and morphological features to distinguish between Ascomycota and Basidiomycota
- Identify the parts of a mushroom
- Identify structures in the Basidiomycota life cycle and know their ploidy

The Basidiomycota (basidiomycetes) are fungi that produce haploid **basidiospores** (spores produced through budding) from club-shaped cells called **basidia** (Figure 2.3.5.13). These are typically formed within fruiting bodies called **basidiocarps**. They are important as decomposers (particularly of wood), plant pathogens, mutualists, and food sources for many animals. Basidiomycetes include the group of fungi that forms mushrooms, the rusts, and the smuts. **Mushrooms** are basidiocarps formed from masses of interwoven hyphae growing up from the mycelium. The basidia develop on fertile surfaces of the mushroom and release their spores (typically four from each basidium) into the air.

They hyphae of basidiomycetes are septate with **clamp connections** where the septa form (Figure 2.3.5.14). The septal structure is more complex than in ascomycetes. The septum is swollen around the pore (a **dolipore septum**) and is flanked by structures called **parenthesomes** (Figure 2.3.5.15).

Fungi with the following structures can be placed in the Basidiomycota*:

*It is important to note that these features may look different or not be present at all in some groups of Basidiomycota, such as the rusts (Pucciniomycotina) and smuts (Ustilagomycotina) -- see Chapter 3.6.4: Rusts & Smuts in the Photographic Atlas. However, there are many physiological and genetic similarities that support grouping these organisms together in the Basidiomycota.

Basidia and Basidiospores

Both karyogamy and meiosis occur within a cell called the basidium (Figure 2.3.5.15). Haploid basidiospores from atop projections on the basidum called sterigmata (sing. sterigma). There are generally four spores, as shown in the image below, though the number of spores produced can vary by species. For example, the mushroom you are likely most familiar with, *Agaricus bisporus* (though you probably know it as a crimini or button mushroom at its immature stage and portobello at maturity), only produces two spores on each basidium (bi- meaning two).



Figure 2.3.5.15: A section through the gills of a mushroom. On the left, a basidium has four basidiospores sitting atop its four sterigmata. On the right, the spores have been released and the sterigmata are easier to distinguish. Photo by Maria Morrow, CC-BY-NC.

Clamp Connections

Basidiomycetes maintain their dikaryotic (n+n) state in each hyphal compartment by making structures called clamp connections (Figure 2.3.5.16). These are not always present, but provide a helpful identification feature when they are!

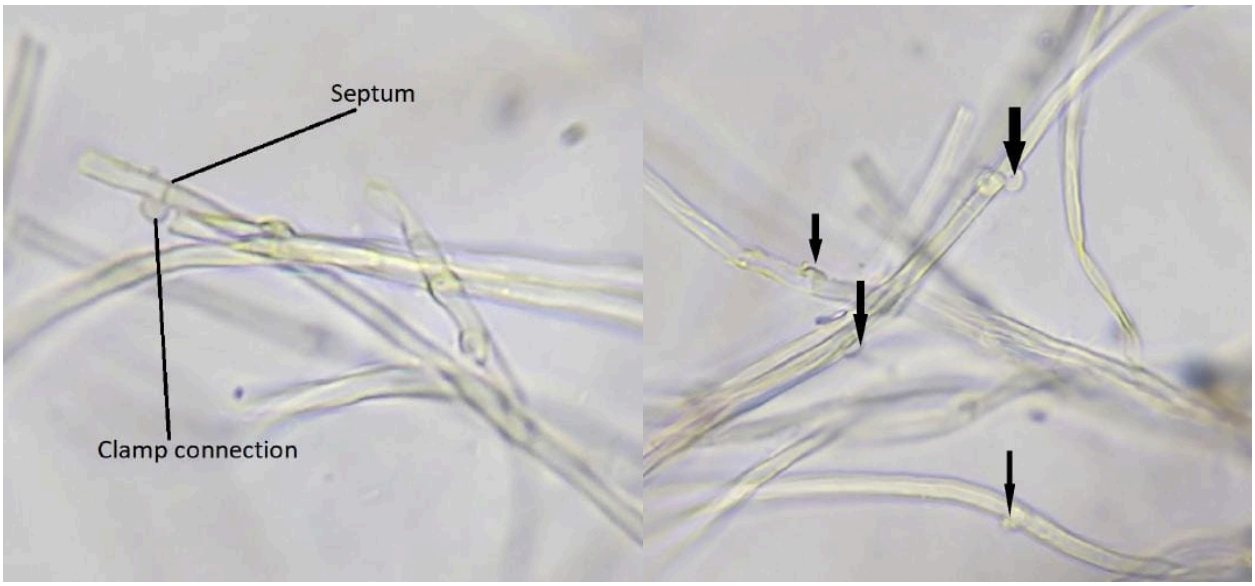


Figure 2.3.5.16: These two images show hyphae from a mushroom. In the image on the left, a clamp connection is visible at the septum. In the image on the right, four clamp connections are indicated by arrows. Photos by Maria Morrow, CC-BY-NC.

Complex Septations

Complex septations are shown in Figure 2.3.5.17.

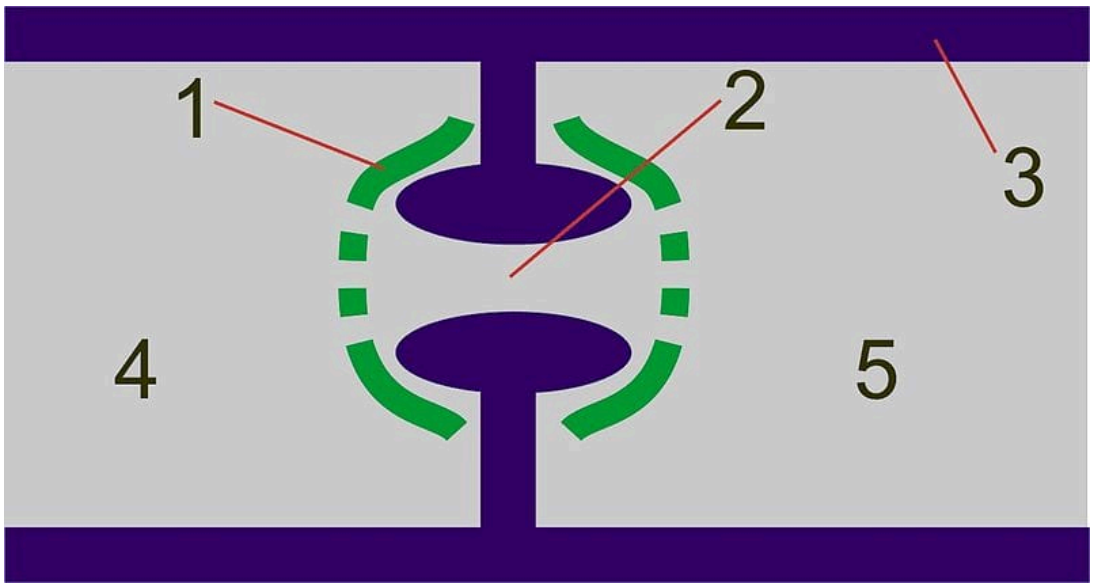


Figure 2.3.5.17: The complex dolipore septum found in basidiomycetes. This is not a feature that can be seen with the naked eye or in a standard microscope. "In hyphae of basidiomycete fungi, parenthesomes (1) "cap" a dolipore septum (2). The cell wall (3) swells around the septal pore to form a barrel-shaped ring. Perforations in the parenthesome allow cytoplasm to flow between (4) and (5)." Miguelferig, CC0, via Wikimedia Commons.

General Mushroom Anatomy

Though only a subset of basidiocarps look this way, they are the model for how we describe "mushrooms". In mycology, this type of basidiocarp is called "agaricoid" or "agaric" because it is the general form we see in the genus *Agaricus*. A more complex version of the agaric mushroom is seen in the genus *Amanita* (Figure 2.3.5.18).

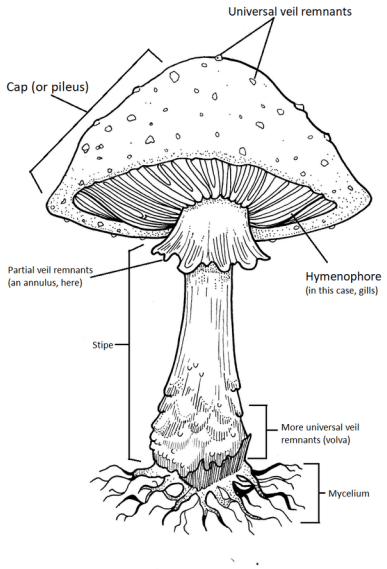


Figure 2.3.5.18: The anatomy of an *Amanita muscaria* basidiocarp. The cap (also called the pileus) protects the spore producing region, the hymenophore. The diagram shows a hymenophore composed of gills. However, you might see mushrooms with pores, teeth, or other types of spore-producing surfaces. The partial veil covers the hymenophore while the mushroom develops. When the cap extends as the mushroom grows, the partial veil is pulled and can either end up as an annulus or attached to the edges of the cap. Not all mushrooms have a partial veil and those that do often look quite different from this one! The universal veil (only present in a few mushrooms) covers the entire mushroom when it is young. As the mushroom expands, the universal veil is also pulled apart. Here, the cap has tiny fragments of the universal veil (warts) and the rest is at the base of the stipe (forming a volva). The stipe is the "stem" or "stalk" of the mushroom. Artwork by Nikki Harris, CC-BY-NC.

Basidiomycete Life Cycle

The life cycle of basidiomycetes involves an extension of the dikaryotic phase (Figure 2.3.5.19). Mycelia of different mating strains combine (plasmogamy) soon after germination and produce a secondary, dikaryotic mycelium that contains haploid nuclei of two different mating strains (a **dikaryon**). This is the dikaryotic stage of the basidiomycete life cycle, and it is the dominant stage. Eventually, the secondary mycelium generates a basidiocarp. The basidiocarp can vary greatly in morphology, but in the sense of a standard mushroom (Figure 2.3.5.15), the developing basidia are produced on the surface of gills located under cap.Within the club-shaped basidium, meiosis occurs and a diploid zygote is formed (karyogamy). The zygote divides by meiosis to produce four haploid nuclei. The haploid nuclei migrate into basidiospores, which germinate and generate monokaryotic hyphae. The mycelium that results is called a primary mycelium.

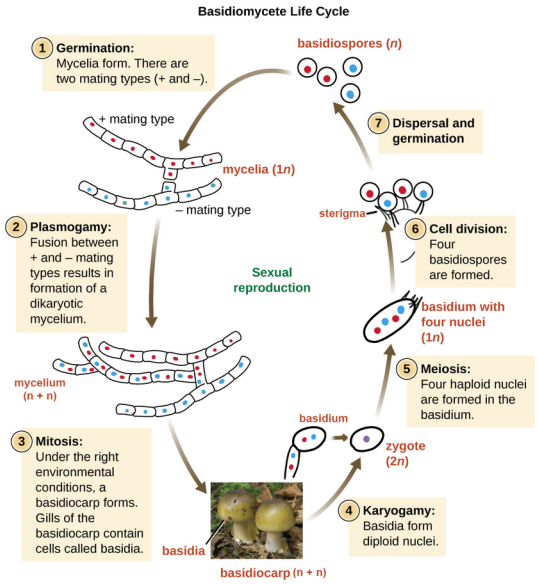


Figure 2.3.5.19: The life cycle of a basidiomycete alternates a haploid generation with a prolonged stage in which two nuclei (dikaryon) are present in the hyphae. Haploid (1n) basidiospores germinate to form haploid mycelia. In this diagram, there are two mating types (+ and -). In plasmogamy, fusion between + and – mating type mycelia results in formation of a dikaryotic (n+n) mycelium. Within the dikaryotic mycelium, one nucleus of each type (+ and -) is maintained between each septation. Under the right environmental conditions, a basidiocarp forms via mitosis. Gills of the basidiocarp contain cells called basidia. A photo of a mushroom labels the mushroom as basidiocap and basidia within the gills. Basidia form diploid nuclei via karyogamy; this produces a diploid zygote. Four haploid nuclei are formed in the basidium via meiosis. Cell walls are formed to produce four haploid (1n) basidiospores as they are pushed out the sterigmata. These spores then disperse and germinate into new haploid mycelia. Original diagram altered by Maria Morrow.

Summary

Macrofungi are represented by two major groups that can form macroscopic fruiting structures. However, many lineages within these groups might only reproduce asexually, form yeasts, or form microscopic fruiting structures (such as the rusts and smuts).

Ascomycetes typically form 8 ascospores within a structure called an ascus. In most lineages, these are produced within an ascocarp, which can be an apothecium (cup), perithecium (flask), or cleistothecium (ball). Ascomycetes have hyphae with simple septations. Their life cycle involves an extended dikaryotic phase that takes place within the ascocarp, forming dikaryotic ascogenous hyphae. These hyphae will eventually form asci, where karyogamy will take place, followed shortly after by meiosis, and usually mitosis.

Basidiomycetes typically form 4 basidiospores externally on a basidium. In the Agaricomycotina, these are produced on or in a basidiocarp, what we call mushrooms, specialized for spore dispersal. The basidiomycete life cycle is almost entirely dikaryotic. Haploid spores germinate, form a monokaryon, then must fuse with another monokaryon shortly afterward. These forms a dikaryotic mycelium with dolipore septations and clamp connections. Karyogamy only takes place within the basidia, follow promptly by meisosis to produce basidiospores.

Both ascomycetes and basidiomycetes for relationships with photosynthetic partners, such as algae or cyanobacteria, to form lichens. In this mutualism, the photobiont provides sugars from photosynthesis, while the mycobiont forms a protective thallus. In the case of cyanobacteria, these may also provide nitrogen fixation.

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2.3.6: Importance of Fungi in Human Life

Learning Objectives

- Describe the importance of fungi to the balance of the environment.
- Summarize the role of fungi in food and beverage preparation.
- Describe the importance of fungi in the chemical and pharmaceutical industries.
- Discuss the role of fungi as model organisms.

Although we often think of fungi as organisms that cause disease and rot food, fungi are important to human life on many levels. As we have seen, they influence the well-being of human populations on a large scale because they are part of the nutrient cycles in ecosystems. They have other ecosystem roles as well. As animal pathogens, fungi help to control the population of damaging pests. These fungi are very specific to the insects they attack, and do not infect animals or plants. Fungi are currently under investigation as potential microbial insecticides, with several already on the market. For example, the fungus *Beauveria bassiana* is a pesticide being tested as a possible biological control agent for the recent spread of emerald ash borer. It has been released in Michigan, Illinois, Indiana, Ohio, West Virginia and Maryland (Figure 2.3.6.1).



Figure 2.3.6.1: The emerald ash borer is an insect that attacks ash trees. It is in turn parasitized by a pathogenic fungus that holds promise as a biological insecticide. The parasitic fungus appears as white fuzz on the body of the insect. (credit: Houping Liu, USDA Agricultural Research Service)

The mycorrhizal relationship between fungi and plant roots is essential for the productivity of farm land and healthy forests. Without the fungal partner in root systems, most plants would either not survive or have a diminished fitness. The transfer of nutrients and mediation of community structure in forests is increasingly attributed to the regulation of mycorrhizal fungi. Transmission of defense signals and other more nuanced communication between plants via their mycorrhizal partners is currently under investigation.

We also eat some types of fungi, whether we are aware of it or not. Mushrooms figure prominently in the human diet of some countries: morels, matsutake, porcini, chanterelles, and truffles are considered delicacies (Figure 2.3.6.2). Molds of the genus *Penicillium* ripen many cheeses and cure meats. They originate in the natural environment such as the caves of Roquefort, France, where wheels of sheep milk cheese are stacked in order to capture the molds responsible for the blue veins and pungent taste of the cheese. Fermentation of *Aspergillus* is used to produce soy sauce, miso, and citric acid.

Fermentation—of grains to produce beer, and of fruits to produce wine—is an ancient art that humans in most cultures have practiced for millennia. Wild yeasts are acquired from the environment and used to ferment sugars into CO_2 and ethyl alcohol

under anaerobic conditions. It is now possible to purchase isolated strains of wild yeasts from different wine-making regions. Louis Pasteur was instrumental in developing a reliable strain of brewer's yeast, *Saccharomyces cerevisiae*, for the French brewing industry in the late 1850s. This was one of the first examples of biotechnology patenting.



Figure 2.3.6.2: The morel mushroom is an ascomycete much appreciated for its delicate taste. (credit: Jason Hollinger)

Many secondary metabolites of fungi are of great commercial importance. Antibiotics are naturally produced by fungi to kill or inhibit the growth of bacteria, limiting their competition in the natural environment. Important antibiotics, such as penicillin and the cephalosporins, are isolated from fungi. Valuable drugs isolated from fungi include the immunosuppressant drug cyclosporine (which reduces the risk of rejection after organ transplant), the precursors of steroid hormones, and ergot alkaloids used to stop bleeding. Psilocybin is a compound found in fungi such as *Psilocybe cyanescens,* which have been used for their hallucinogenic properties by various cultures for thousands of years. Psilocybin-producing fungi (though currently illegal to use in most states within America) are currently being investigated as treatment for conditions like depression, anxiety, and even migraines.

Fungi are important model research organisms for eukaryotic systems. Many advances in modern genetics were achieved by the use of the mold *Neurospora crassa*. Additionally, many important genes originally discovered in *S. cerevisiae* served as a starting point in discovering analogous human genes. As a eukaryotic organism, the yeast cell produces and modifies proteins in a manner similar to human cells, as opposed to the bacterium *Escherichia coli,* which lacks the internal membrane structures and enzymes to tag proteins for export. This makes yeast a much better organism for use in recombinant DNA technology experiments. Like bacteria, yeasts grow easily in culture, have a short generation time, and are amenable to genetic modification.



Figure 2.3.6.3: Yarns dyed with mycopigments, including extracts from the dyer's polypore, *Phaeolus schweinitzii*. Photo by Leslie Seaton from Seattle, WA, USA, CC BY 2.0, via Wikimedia Commons

In addition to the cultural uses you might be more familiar with, fungi are being explored for their use in constructing biodegradable packaging, insulation, and even leather-like material for clothing. Pigments can be extracted from some fungi and lichens, which can then be used to make watercolors or dyes for fabrics (Figure 2.3.6.3). Due to their amazing metabolic diversity, fungi are being used to remediate ecosystems contaminated with organic compounds and heavy metals. Check out Video 2.3.6.1 from Science Friday for some of the current innovations using mycelium.

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 2.3.6.1: This video explores how innovators are using mycelium fed on waste products to make fungal leather.

Summary

Fungi are important to everyday human life. Fungi are important decomposers in most ecosystems. Mycorrhizal fungi are essential for the growth of most plants. Fungi, as food, play a role in human nutrition in the form of mushrooms, and also as agents of fermentation in the production of bread, cheeses, alcoholic beverages, and numerous other food preparations. Secondary metabolites of fungi are used as medicines, such as antibiotics and anticoagulants. Fungi are model organisms for the study of eukaryotic genetics and metabolism.

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2.3.7: Chapter Summary

Fungi are heterotrophic eukaryotes with cell walls made of chitin and plasma membranes containing ergosterol. They can be unicellular (yeasts) or filamentous, forming a hyphal thallus called a mycelium. The hyphae can be coenocyctic or septate (with cross walls). Many fungi reproduce asexually (molds), producing spores called conidia by mitosis. Sexual reproduction in fungi varies greatly in different evolutionary lineages: several lineages of fungi produce multinucleate zygospores, ascomycetes produce ascospores within asci, and basidiomycetes produce basidiospores externally on basidia. Overall, the general life cycle can be classified as haplontic, though there is a dikaryotic stage that is extended in ascomycetes and extended even further in basidiomycetes.

Fungi live within their food substrate, exuding enzymes to digest externally, then absorbing it. They have diverse metabolic strategies and are capable of degrading a wide-range of compounds, making them incredibly important to decomposition and recycling of nutrients. The metabolic diversity of fungi has also lead to their use in the production of foods and medicines. Fungi are not just saprotrophs and have important roles as parasites and mutualists, namely lichens and mycorrhizae.

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

- List the characteristics of fungi.
- Describe the composition of the mycelium.
- Describe the mode of nutrition of fungi.
- Explain sexual and asexual reproduction in fungi.
- Describe some of the roles of fungi in ecosystems.
- Describe mutualistic relationships of fungi with plant roots and photosynthetic organisms.
- Describe the beneficial relationship between some fungi and insects.
- Use characteristics to distinguish between groups of microfungi.
- Describe some of the roles microfungi have in ecosystems.
- Explain the relationship between plants and members of Glomeromycota.
- Identify structures in the "zygomycete" life cycle and know their ploidy.
- Use life history traits and morphological features to distinguish between Ascomycota and Basidiomycota.
- Identify structures in the Ascomycota life cycle and know their ploidy.
- Differentiate between different types of ascocarps; locate fertile surfaces within those structures.
- Explain the lichen symbiosis.
- Identify structures in the lichen thallus.
- Use life history traits and morphological features to distinguish between Ascomycota and Basidiomycota
- Identify the parts of a mushroom
- Identify structures in the Basidiomycota life cycle and know their ploidy
- Describe the importance of fungi to the balance of the environment.
- Summarize the role of fungi in food and beverage preparation.
- Describe the importance of fungi in the chemical and pharmaceutical industries.
- Discuss the role of fungi as model organisms.

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2.4: "PROTISTS"

Protists are an artificial group of eukaryotes that are neither animals, fungi, nor plants. They represent the vast diversity of eukaryotic organisms, and thus span the breadth of possibilities with regard to life history traits. They can be heterotrophs or autotrophs, unicellular to massively multicellular (though rarely with any specialized tissue organization), and can be found across ecosystems worldwide. Photosynthesis within protists is the result of multiple separate endosymbiotic events.

2.4.1: Introduction to Protists

2.4.2: Heterotrophic "Protists"

2.4.2.1: Slime Molds

2.4.2.2: Oomycota

2.4.3: Photosynthetic "Protists"

2.4.3.1: Dinoflagellates

2.4.3.2: Brown Algae and Diatoms

2.4.3.3: Red and Green Algae

2.4.4: Chapter Summary

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2.4.1: Introduction to Protists

Learning Objectives

- Explain how organisms were originally classified under Protista.
- Describe the diversity of metabolic strategies and other life history traits within this artificial group.
- Identify evolutionary relationships between "protists" using a phylogenetic tree.

What are Protists?

The term "protist" is a general description for eukaryotic organisms that are not animal, plant, or fungus. These organisms were formerly classified in Kingdom Protista. As we have come to learn about genetics and the evolutionary history of organisms, we have discovered that these organisms come from many distinct evolutionary groups, some of which are closer to fungi and animals than to plants or each other. There are over 100,000 described living species of "protists", and it is unclear how many undescribed species may exist. Since many of these organisms live as commensals or parasites within other organisms, and these relationships are often species-specific, there is a huge potential for diversity that matches the diversity of hosts. As the catchall term for eukaryotic organisms that are not animal, plant, or fungus, it is not surprising that very few characteristics are common to all protists.

- They are **eukaryotes** because they all have a **nucleus**.
- Most have **mitochondria** although some have later lost theirs. Mitochondria were derived from aerobic alpha-proteobacteria that once lived within their cells.
- Many have **chloroplasts** with which they perform photosynthesis. These chloroplasts were derived from photosynthetic **cyanobacteria** originally, though have been acquired via secondary endosymbiotic events in several lineages.
- Many are unicellular and all groups (with one exception) contain some unicellular members.
- The name Protista means "the very first", and some of the 80-odd groups of organisms that we once classified as protists may well have had long, independent evolutionary histories stretching as far back as 2 billion years. Genome analysis added to other criteria show that other lineages are derived from more complex ancestors; that is, some are not "primitive" at all.
- Genome analysis also shows that many of the groups placed in the Protista are not at all closely related to one another; that is, the protists do not represent a single clade.
- So we consider them here as a group more for our convenience than as a reflection of close kinship, and a better title for this page would be **"Eukaryotes that are neither Animals, Fungi, nor Plants"**.

Evolutionary Relationships

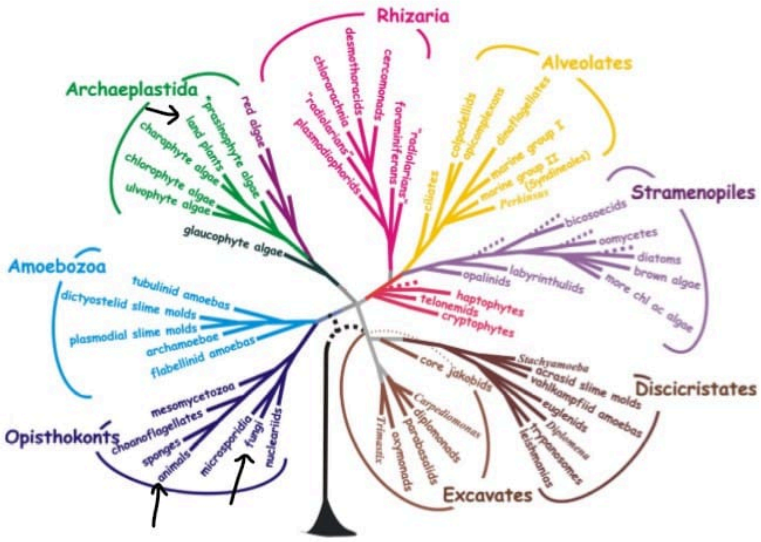


Figure 2.4.1.1: This phylogeny of eukaryotic organisms was published in a paper by Sandra L. Baldauf (2008). Three black arrows have been added to the original figure, pointing at the other three eukaryotic kingdoms: plants, fungi, and animals. Fungi and animals are located quite close together in a group called the Opisthokonts, indicating a shared evolutionary history that is more recent than many of the other lineages. Land plants can be found in a group called the Archaeplastida, which is shared with the green algae, red algae, and glaucophytes. All other lineages in this diagram had previously been lumped into the group "protists" and are still often referred to as such. Image credit: Sandra L. BALDAUF. An overview of the phylogeny and diversity of eukaryotes. J Syst Evol, 2008, 46 (3): 263-273. doi: 10.3724/SP.J.1002.2008.08060

In the phylogenetic tree above (Figure 2.4.1.1), protists do not share a common ancestry. Slime molds share a more recent evolutionary history with fungi and animals, while red and green algae are more closely related to land plants than they are to the brown algae (located in the Stramenopiles group). The evolutionary history of protists is not a single story of descent, but rather encompasses the evolutionary history of eukaryotes, in its entirety.

Because groups of protists do not share a common ancestor with each other that is not also shared with plants, fungi, and animals, "protists" represent a **polyphyletic** group. Only the characteristic of being eukaryotic unites, but is not exclusive to, this group. In the following sections, you will see some of the diversity of life history traits represented by protists.

Cell Structure

The cells of protists are among the most elaborate of all cells. Most protists are microscopic and unicellular, but some true multicellular forms exist (such as in the brown algae, Phaeophyta). A few protists live as colonies that behave in some ways as a group of free-living cells and in other ways as a multicellular organism. Still other protists are composed of enormous, multinucleate, single cells that look like amorphous blobs of slime, or in other cases, like ferns. In fact, many protist cells are multinucleated; in some species, the nuclei are different sizes and have distinct roles in protist cell function.

Single protist cells range in size from less than a micrometer to three meters in length to hectares. Protist cells may be enveloped by animal-like cell membranes or plant-like cell walls. Others are encased in glassy silica-based shells or wound with pellicles of interlocking protein strips. The pellicle functions like a flexible coat of armor, preventing the protist from being torn or pierced without compromising its range of motion.

Metabolism

Protists exhibit many forms of nutrition and may be aerobic or anaerobic. Protists that store energy by photosynthesis belong to a group of **photoautotrophs** and are characterized by the presence of chloroplasts. Other protists are **heterotrophic** and consume organic materials (such as other organisms) to obtain nutrition. Amoebas and some other heterotrophic protist species ingest particles by a process called **phagocytosis**, in which the cell membrane engulfs a food particle and brings it inward, pinching off an intracellular membranous sac, or vesicle, called a food vacuole (Figure 2.4.1.2). The vesicle containing the ingested particle, the phagosome, then fuses with a lysosome containing hydrolytic enzymes to produce a phagolysosome, and the food particle is

broken down into small molecules that can diffuse into the cytoplasm and be used in cellular metabolism. Undigested remains ultimately are expelled from the cell via exocytosis.

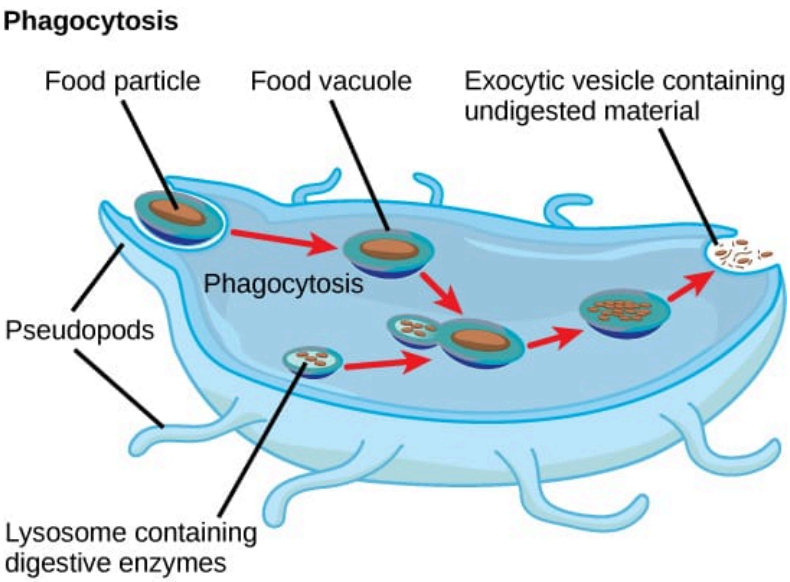


Figure 2.4.1.2: The stages of phagocytosis include the engulfment of a food particle, the digestion of the particle using hydrolytic enzymes contained within a lysosome, and the expulsion of undigested materials from the cell. Descriptive text: A eukaryotic cell is shown consuming a food particle. As the food particle is consumed, it is encapsulated in a vesicle. The vesicle fuses with a lysosome, and proteins inside the lysosome digest the food particle. Indigestible waste material is ejected from the cell when an exocytic vesicle fuses with the plasma membrane.

Subtypes of heterotrophs, called **saprotrophs**, absorb nutrients from dead organisms or their organic wastes. Some protists can function as **mixotrophs**, obtaining nutrition by photoautotrophic or heterotrophic routes, depending on whether sunlight or organic nutrients are available.

Motility

The majority of protists are motile, but different types of protists have evolved varied modes of movement (Figure 2.4.1.3). Some protists have one or more flagella, which they rotate or whip. Others are covered in rows or tufts of tiny cilia that they coordinately beat to swim. Still others form cytoplasmic extensions called pseudopodia anywhere on the cell, anchor the pseudopodia to a substrate, and pull themselves forward. Some protists can move toward or away from a stimulus, a movement referred to as taxis. Movement toward light, termed **phototaxis**, is accomplished by coupling their locomotion strategy with a light-sensing organ.

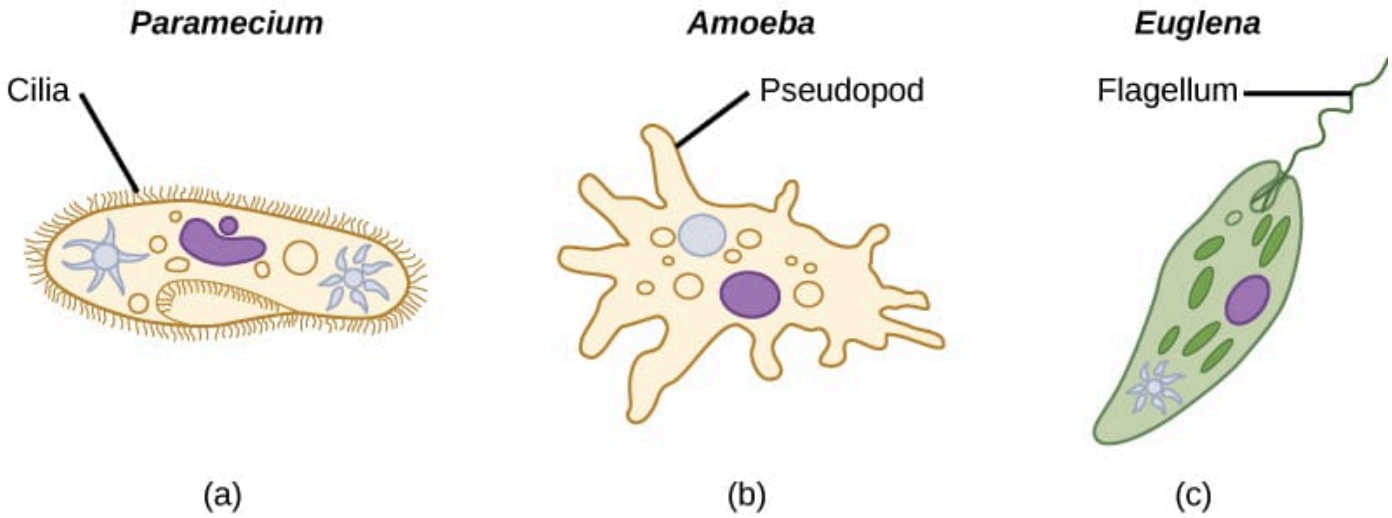


Figure 2.4.1.3: Protists use various methods for transportation. (a) Paramecium waves hair-like appendages called cilia to propel itself. (b) Amoeba uses lobe-like pseudopodia to anchor itself to a solid surface and pull itself forward. (c) Euglena uses a whip-like tail called a flagellum to propel itself. Descriptive text: Part a shows a shoe-shaped Paramecium, which is covered with fine, hair-like cilia. Part b shows an Amoeba, which is irregular in shape with long extensions of cytoplasm jutting out from the main body. The extensions are called pseudopods. Part c shows an oval Euglena, which has a narrow front end. A long, whip-like flagellum protrudes from the back end.

Life Cycles

Protists reproduce by a variety of mechanisms. Most undergo some form of asexual reproduction, such as binary fission, to produce two daughter cells. In protists, binary fission can be divided into transverse or longitudinal, depending on the axis of orientation; sometimes *Paramecium* exhibits this method. Some protists such as the true slime molds exhibit multiple fission and simultaneously divide into many daughter cells. Others produce tiny buds that go on to divide and grow to the size of the parental protist. Sexual reproduction, involving meiosis and fertilization, is common among protists, and many protist species can switch from asexual to sexual reproduction when necessary. Sexual reproduction is often associated with periods when nutrients are depleted or environmental changes occur. Sexual reproduction may allow the protist to recombine genes and produce new variations of progeny that may be better suited to surviving in the new environment. However, sexual reproduction is often associated with resistant cysts that are a protective, resting stage. Depending on their habitat, the cysts may be particularly resistant to temperature extremes, desiccation, or low pH. This strategy also allows certain protists to “wait out” stressors until their environment becomes more favorable for survival or until they are carried (such as by wind, water, or transport on a larger organism) to a different environment, because cysts exhibit virtually no cellular metabolism.

Protist life cycles range from simple to extremely elaborate. Certain parasitic protists have complicated life cycles and must infect different host species at different developmental stages to complete their life cycle. Some protists are unicellular in the haploid form and multicellular in the diploid form, a strategy employed by animals. Other protists have multicellular stages in both haploid and diploid forms, a strategy called alternation of generations that is also used by plants.

Life cycles can be generally classified as haplontic, diplontic, and haplodiplontic. In a **haplontic life cycle**, the multicellular stage is haploid and produces gametes from structures called gametangia. In plants and algae, these haploid organisms are sometimes referred to as gametophytes (meaning gamete plants). This life cycle is also called **zygotic meiosis**, because the zygote does not grow, but instead divides by meiosis to form haploid spores (see Figure 2.4.1.4).

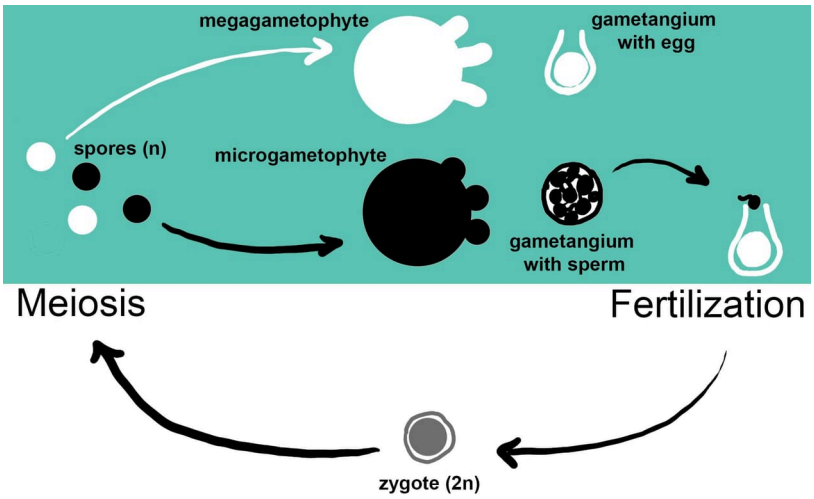


Figure 2.4.1.4: A haplontic life cycle. In this life cycle, there are spores that grow into two different types of multicellular haploids. One of these, the megagametophyte, produces a few large, nonmotile eggs. The other, the microgametophyte, produces many motile sperm. These gametes are heterogamous, because they have different morphology, and oogamous, because the egg is the larger, nonmotile gamete. Descriptive text: On the top half, there are four haploid spores (two white and two black). One of the white spores grows into a megagametophyte that produces a single large egg within a gametangium. One of the black spores grows into a microgametophyte that produces many sperm with flagella. A sperm fertilizes an egg to form a diploid zygote, shown as grey. The zygote has a thick wall. At some point, it divides by meiosis to produce spores. The zygote is the only stage in the lower half of the diagram. Diagram by Maria Morrow, CC BY-NC.

In a **diplontic life cycle**, the multicellular phase is diploid. The zygote grows by mitosis to form a diploid, multicellular organism. That organism might form sporangia for asexual reproduction. Spores would be diploid and could grow to form a new multicellular diploid organism. Sexual reproduction occurs in gametangia, where cells divide by meiosis to produce gametes. This life cycle is sometimes called **gametic meiosis** (see Figure 2.4.1.5).

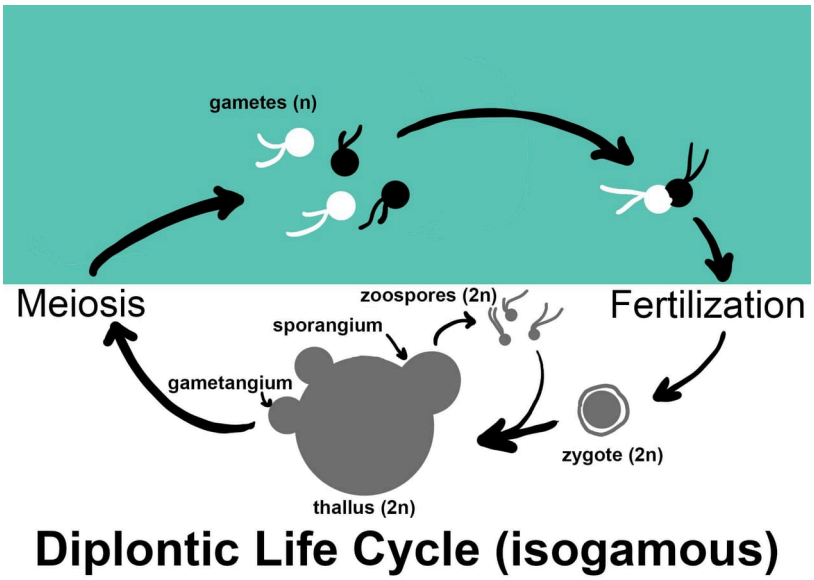


Figure 2.4.1.5: A diplontic life cycle. In this life cycle, the multicellular stage is diploid. The gametes that fuse to form the zygote. The gametes look the same, so are isogamous. Thy zygote grows into a diploid thallus. This is not a technical name for the diploid individual, but refers to a body not differentiated into complex tissues. The diploid organism can undergo asexual reproduction by producing diploid spores. In this diagram, they are called zoospores because they have flagella. Descriptive text: On the top half, there are four haploid gametes (two white and two black, each with two flagella and all about the same size). The gametes are the only stage on the top half of the diagram. A white gamete and a black gamete fuse to form a diploid zygote, shown as grey. The zygote has a thick wall. The zygote grows by mitosis to form a diploid thallus with a sporangium and several gametangia. Diploid, swimming zoospores (also grey) are produced from the sporangium, growing by mitosis to form a diploid thallus. In one of the gametangia, meiosis occurs to produce the spores. Diagram by Maria Morrow, CC BY-NC.

The **haplodiplontic life cycle**, also called **alternation of generations**, is the most complex. In this life cycle, there are multicelllular haploid and diploid phases. The zygote grows by mitosis to form a diploid **sporophyte**. The sporophyte, as its name implies, produces haploid spores by meiosis of cells within a sporangium. The spores grow into haploid **gametophytes**. The gametophytes produce gametes by mitotic division of cells within gametangia. These gametes then fuse to form the diploid zygote.

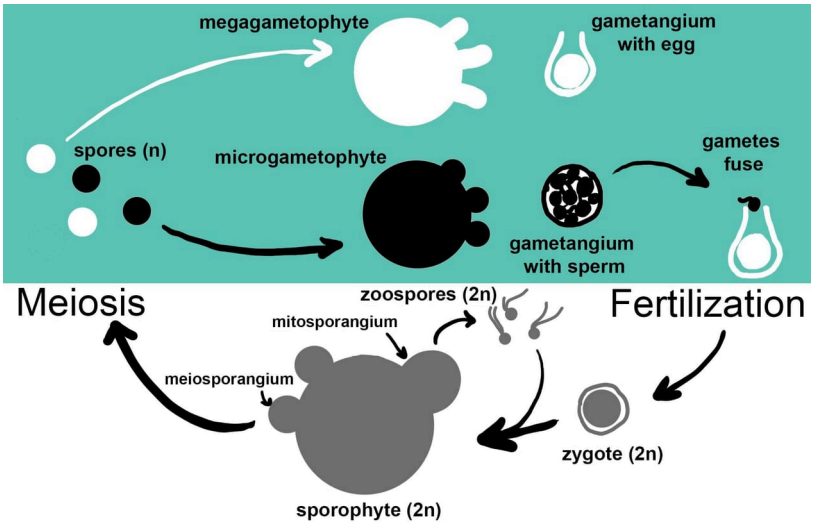


Figure 2.4.1.6: A haplodiplontic life cycle. In this life cycle, there are both haploid and diploid multicellular stages. The multicellular haploid stage is called the gametophyte, the multicellular diploid stage is called the sporophyte. The sporophyte might make spores by mitosis for asexual reproduction (here shown as zoospores). Descriptive text: On the top half, there are four haploid spores (two white and two black). One of the white spores grows into a megagametophyte that produces a single large egg within a gametangium. One of the black spores grows into a microgametophyte that produces many sperm with flagella. A sperm fertilizes an egg to form a diploid zygote, shown as grey. The zygote has a thick wall. The zygote grows by mitosis to form a multicellular sporophyte (grey) with a mitosporangium and several meiosporangia. Diploid, swimming zoospores (also grey) are produced from the mitosporangium, growing by mitosis to form a diploid thallus. In one of the meiosporangia, meiosis occurs to produce the spores. Diagram by Maria Morrow, CC BY-NC.

As you saw in Figures $2.4.1.d-f$, there are other distinctions that can be made in life cycles. **Isogamous** life cycles have gametes that look approximately the same. **Oogamous** life cycles are heterogamous (meaning the gametes look different, also called anisogamous) in a specific way: the egg is larger and nonmotile, while the sperm are smaller and motile. With all of the complexities in life cycles, it can be helpful to remember this simple rule: spores grow, gametes fuse. Gametes never grow my mitosis, but must fuse together to form a zygote. Spores tend to grow or germinate in some way.

Habitats

Nearly all protists exist in some type of aquatic environment, including freshwater and marine environments, damp soil, and even snow. Several protist species are parasites that infect animals or plants. A few protist species live on dead organisms or their wastes, and contribute to their decay.

Summary

Protists are extremely diverse in terms of their biological and ecological characteristics, partly because they are an artificial assemblage of phylogenetically unrelated groups. Protists display highly varied cell structures, several types of reproductive strategies, virtually every possible type of nutrition, and varied habitats. Most single-celled protists are motile, but these organisms use diverse structures for transportation.

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2.4.2: HETEROTROPHIC "PROTISTS"

Heterotrophic organisms must consume organic matter to obtain energy. Under the umbrella of protists, there are several heterotrophic groups. Some of these are closely related to photosynthetic lineages of protists that have obtained chloroplasts via endosymbiotic events, such as Oomycota and Phaeophyta. However, due to the relationship between nutritional strategies and ecological roles, it often makes more sense to discuss these lineages in groups of heterotrophs and autotrophs, rather than evolutionary relatedness.

This chapter will introduce slime molds and oomycetes, as these are groups commonly discussed in botany courses. However, it is important to note that there is a vast diversity of heterotrophic protist lineages not covered here with important and fascinating ecological roles.

- Topic hierarchy

2.4.2.1: Slime Molds

2.4.2.2: Oomycota

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2.4.2.1: Slime Molds

Learning Objectives

- Differentiate between the three major groups of slime molds.
- Differentiate between slime molds, fungi, and plants.
- Identify structures and phases in the myxomycete life cycle and know their ploidy.

Slime molds are an unusual group of organisms that have previously been classified as animals, fungi, and plants. Like plants, slime molds have **cellulose in the cell walls** of their spores. Unlike plants, slime molds are **heterotrophs**! Though they were formally classified as fungi, slime molds do not have chitin in their cell walls and have a **diplontic life cycle** (Figure 2.4.2.1.12). These organisms move about as amoebae engulfing bacteria (unlike fungi, who digest food externally). When conditions become unfavorable, whether due to lack of food or lack of moisture, they form spores. They can be found in damp substrates with ample bacteria and are most frequently found on decaying logs and forest duff.

There are several different lineages of organisms commonly referred to as slime molds. **Cellular slime molds** (dictyostelids, Figure 2.4.2.1.1(a)) are groups of unicellular amoebae that collaborate to form fruiting structures to disperse spores. **Protostelids** make small fruiting bodies that have cellular stalks. **Plasmodial slime molds** (classified as Myxogastria or Myxomycetes, Figure 2.4.2.1.1(b)) form a large, multinucleate amoeba with no cell wall that will eventually wall off individual nuclei to form spores.



Figure 2.4.2.1.1: (a) *Dictyostelium discoideum* is a cellular slime mold can be grown on agar in a Petri dish. In this image, individual amoeboid cells (visible as small spheres) are streaming together to form an aggregation that is beginning to rise in the upper right corner of the image. The primitively multicellular aggregation consists of individual cells that each have their own nucleus. (b) *Fuligo septica* is a plasmodial slime mold. This brightly colored organism consists of a single large cell with many nuclei.

Dictyostelids

The cellular slime molds exist as individual amoeboid cells that periodically aggregate. The individual amoebe can be seen aggregating in Figure 2.4.2.1.1(a). The aggregate then forms a fruiting body (Figure 2.4.2.1.2) that produces haploid spores. One cellular slime mold, *Dictyostelium discoideum*, has been an important study organism for understanding cell differentiation, because it has both single-celled and multicelled life stages, with the cells showing some degree of differentiation in the multicelled form. Watch Video 2.4.2.1.1 to see how these individuals aggregate into a single fruiting body.

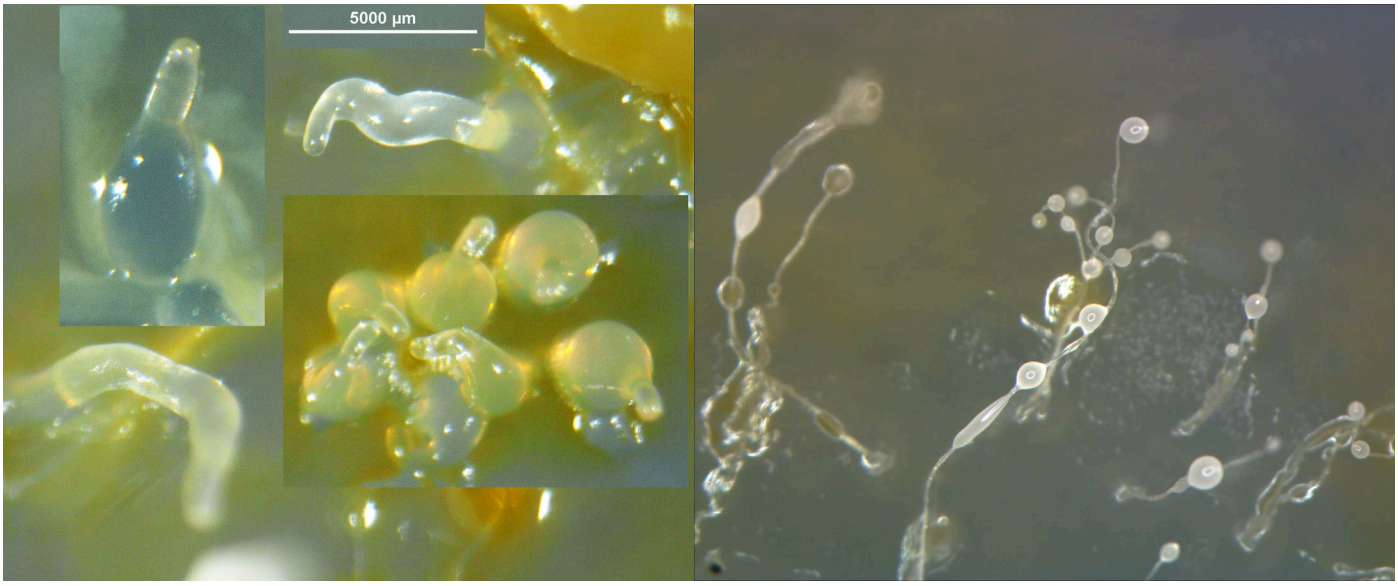


Figure 2.4.2.1.2: These images show a species of *Dictyostelium* developing fruiting bodies. In the first image, the culmination stages are visible. Many of these look like a settled teardrop with a point emerging. Others, in later stages, look more like a worm moving vertically. In the second image, several sporangia are in the process of forming, with individuals still migrating up the stalk to the apex. Only the individuals who end up in the sporangium will survive to "reproduce" as spores. Photos by Jerry Cooper, CC BY 4.0.

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 2.4.2.1.1: Watch the strange behavior of the cellular slime mold *Dictostelium discoideum* as individual amoebae respond to an aggregation signal (cAMP), form a mobile slug, and eventually produce a stalked fruiting structure and spores. Sourced from YouTube.

The organisms in this group have a complex life cycle (Figure 2.4.2.1.3) during the course of which they go through unicellular, multicellular, spore producing, and amoeboid stages. Thousands of individual amoebae aggregate into a slimy mass - each cell retaining its identity (unlike plasmodial slime molds). The aggregating cells are attracted to each other by the cyclic AMP (cAMP) that they release when conditions become stressful, such as a depletion in food. Individual amoebae respond to the chemical signal by moving to areas of higher cAMP concentration (**chemotaxis**), eventually aggregating into a single slug. The slug can respond to moisture and light gradients, navigating to a good spot for spore production. Some cells in the slug contribute to a 2–3-millimeter stalk, drying up and dying in the process. Cells atop the stalk form an asexual fruiting body that contains haploid spores. The spores are disseminated and can germinate if they land in a moist environment.

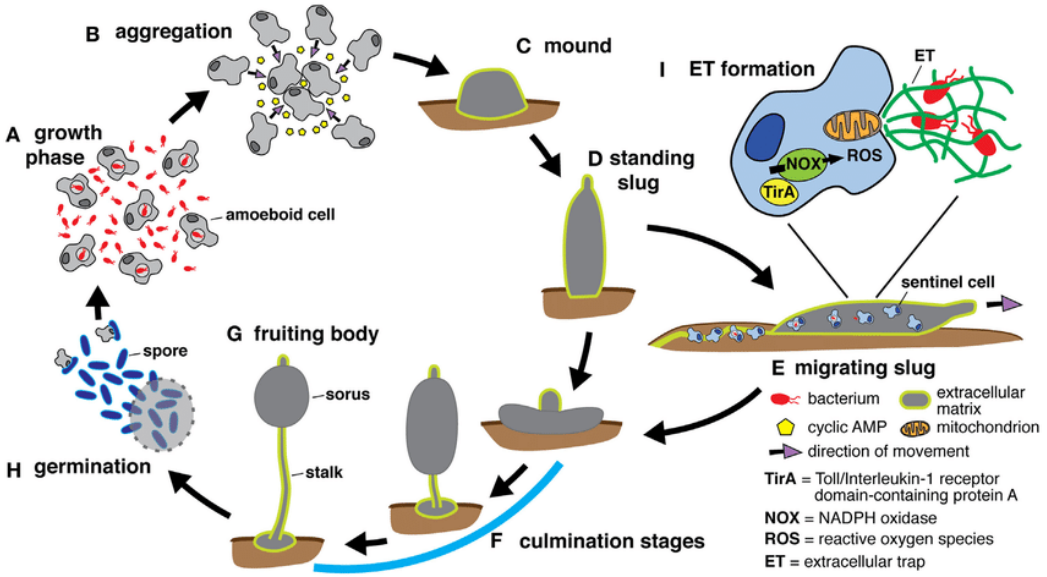


Figure 2.4.2.1.3: Dictyostelium life cycle (text from the original figure caption). "(A) During the growth phase of development, amoeboid cells feed on bacteria and replicate by binary fission. The development cycle is initiated upon resource depletion, and aggregation occurs when starving cells secrete cyclic AMP to recruit additional cells (B). The aggregating cells organize to form the mound stage enclosed within an extracellular matrix composed of cellulose and mucopolysaccharide (26) (C) and continue to develop into the standing slug (D). Depending on its environment, the standing slug either falls over to become a migrating slug that moves toward heat and light (e) or proceeds directly to the culmination stages (F) that ultimately produce the fruiting body, which consists of a spore-containing structure, the sorus, held aloft by a stalk of dead cells (g). Spores are released from the sorus and germinate into growing cells (H). Under optimal conditions, the developmental cycle takes around 24 h. If the slug forms underground, it migrates toward the surface to maximize spore dissemination. To protect itself from infection during migration, the slug possesses a rudimentary immune system comprising phagocytic sentinel cells. These cells move throughout the slug, take up bacteria and toxins, and are shed along with extracellular matrix as the slug moves (e). In response to bacteria, sentinel cells release extracellular traps, derived from mitochondrial DNA, via an unknown mechanism involving NADPH oxidase (NOX)-generated reactive oxygen species (ROS) and TirA, a soluble protein containing a toll/interleukin 1 receptor domain (i)." Figure sourced from the publication Eat Prey, Live: *Dictyostelium discoideum* as a model for cell-autonomous defenses. Dunn et al., (2018). CC BY 4.0 DOI: 10.3389/fimmu.2017.01906

Protostelids

Protostelids are a group that has received less attention than either the Dictyostelids or plasmodial slime molds, as each of the latter groups contains a model organism used to study a specific system. Protostelids make simple fruiting bodies, similar to the Dictyostelids, with a stalk and spores at the apex. The slime mold *Ceratiomyxa* looks more like a plasmodial slime mold, but closer inspection reveals that spores are formed on minute, stalked fruiting bodies covering the external surface of the tentacle-like structures (Figure 2.4.2.1.5). *Ceratiomyxa* may not actually be a protostelid, but the small, stalked fruiting bodies formed on the external surface are similar to what would be found in a true protostelid.



Figure 2.4.2.1.4: This image shows the slime mold *Ceratiomyxa fruticulosa*, which looks a bit like an organism you'd find under the sea. This slime mold (likely) belongs to the protostelid group because it makes its spores externally. Each coral-like extension of this slime mold is covered with tiny spores. Photo by Maria Morrow, CC BY-NC.



Figure 2.4.2.1.5: A close-up of *Ceratiomyxa fruticulosa*, showing the fruiting structures covering the outside of the strange, coralloid projections. Photo by Damon Tighe, CC BY-NC. See another great example here.

Plasmodial Slime Molds (Myxogastria)

Plasmodial slime molds represent a vast diversity of morphologies. While still a plasmodium (see Figure 2.4.2.1.6), they can be difficult to distinguish. However, once they have formed into a fruiting structure, they can form distinct, varied, and amazing shapes (see Figures 2.4.2.1.7 – 10)!

The Plasmodium

In their feeding stage, myxomycetes form one large amoeba called a **plasmodium** with many nuclei and no cell wall. This plasmodium moves over damp, decaying material looking for bacteria (and sometimes fungi) to engulf and digest. When it dries out or runs out of food, it begins to make fruiting structures called sporangia (sporangium, singular). Inside these sporangia, the diploid nuclei will undergo meiosis and haploid nuclei will be walled off to make spores for aerial dispersal. Dispersal by spores, heterotrophism, and glycogen as a storage carbohydrate originally classified this group within Kingdom Fungi, but this is the

end of the similarities. The spores have cell walls made of cellulose, like plants. When these spores land, they will germinate into haploid cells with two flagella (called swarm cells) or amoebae that will fuse together to form a diploid plasmodium. See Figure 2.4.2.1.11 for a diagram of this life cycle.



Figure 2.4.2.1.6: This image shows *Physarum polycephalum* exploring some decaying wood. This is the feeding **plasmodium**. During this stage, the giant, multinucleate amoeba moves over the substrate engulfing bacteria. The veins allow for streaming of the cytoplasm and efficient connections between sources of food. Photo by Daniel Folds, CC BY-NC.

Sporocarp Diversity

The diversity of sporulating structures, or **sporocarps**, has led many to fall in love with this group of organisms. In *Hemitrichia serpula,* the plasmodium forms into a network of veins that then become fruiting structures (a **plasmodiocarp,** see Figure 2.4.2.1.7). In some slime molds, like *Fuligo* and *Lycogala*, the entire plasmodium forms a cushion that dries and produces spores (an **aethalium,** see Figure 2.4.2.1.8). In other slime molds, individual sporangia are so closely clustered together, they appear to be a single fruiting structure (a **pseudoaethalium,** see Figure 2.4.2.1.9). The last type of sporocarp is more familiar, forming many distinct stalked **sporangia** (see Figure 2.4.2.1.10).



Figure 2.4.2.1.7: Hemitrichia serpula forms an uncommon fruiting body called a **plasmodiocarp**. The feeding stage accumulates its protoplasm into the veins of the plasmodium, forming strange linear, intertwining shapes. Photo by Roman Providukhin, CC-BY-NC.



Figure 2.4.2.1.8: Fruiting bodies of the plasmodial slime mold *Lycogala epidendrum* form into cushion-like structures called **aethalia**. The plasmodium has formed into pink ball-like structures on the surface of a rotten log. One of these structures has been popped and is oozing a pink slime, full of immature spores. This pink slime gives *Lycogala* its name, wolf's milk. Photo by Maria Morrow, CC BY-NC.



Figure 2.4.2.1.9: Another option for a fruiting structure is the **pseudoaethalium,** where there are distinct sporangia but they still form together like a cushion. This is the type of fruiting structure formed by *Tubifera ferruginosa*, the red raspberry slime mold. Photo by Hiromi Karagiannis, CC BY-NC.



Figure 2.4.2.1.10: Fruiting bodies of *Diachea leucopodia* have a distinct stalk and **sporangium**. The stalk in this species is white, while the elongate sporangium displays an oil-sheen rainbow of colors. Photo by Sypster, CC BY-NC.

Life Cycle

The life cycle of plasmodial slime molds is best classified as diplontic: the "multicellular" (actually just multinucleate) phase is diploid. Haploid cells that germinate from spores (amoebae or biflagellate **swarm cells**) do not grow until after they have fused with another haploid cell. In some myxomycetes, amoebae or swarm cells produced from the same parent plasmodium can fuse together to form a new plasmodium. This is called **homothallism** (homo- meaning same, thallus). In other myxomycetes, these gametes must be from different individuals (**heterothallism**, hetero- meaning other). The discovery of different mating types in myxomycetes, as well as the genes that determine mating type, was made by O'Neil Ray Collins (Figure 2.4.2.1.11).

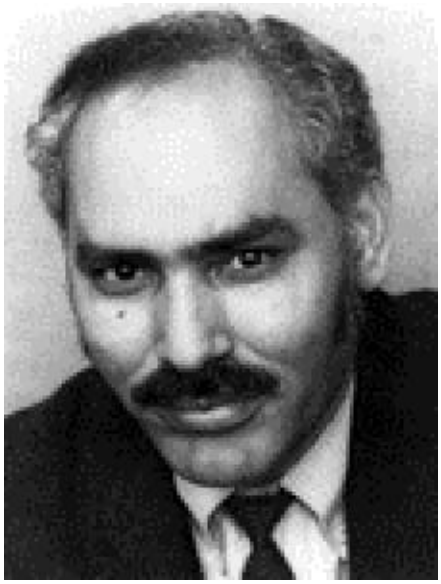


Figure 2.4.2.1.11: O'Neil Ray Collins (1931-1989) was an American mycologist and botanist. He is well known for his research on slime-mold genetics and was the first African-American biologist to hold a tenured position at University of California, Berkeley. In addition to discovering the existence of mating types and the associated alleles in slime molds, Collins's work to increase diversity and support minority students are important components of his legacy at UC Berkeley. (Credit: Public Domain)

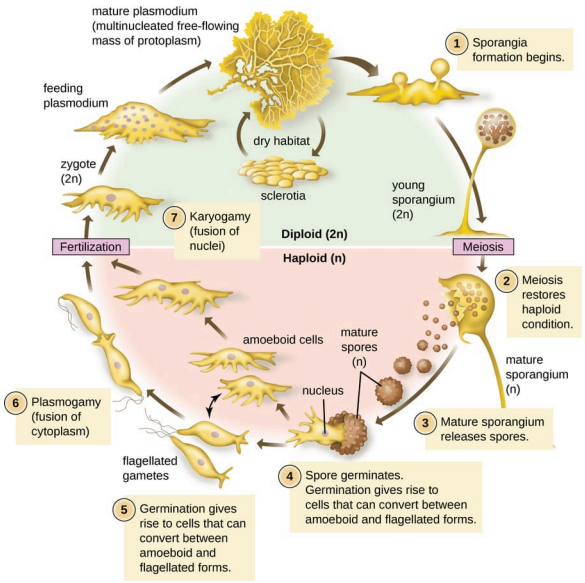


Figure 2.4.2.1.12: Plasmodial slime molds exist as large amoebae filled with many diploid (2n) nuclei. When conditions signal the amoeba to end its vegetative phase (lack of food or moisture), the plasmodium coalesces into a fruiting structure (sporocarp). Inside the sporocarp, the nuclei undergo meiosis to produce haploid spores. Spores are released and germinate when conditions are right. The spore might germinate to produce an amoeba or a flagellated swarm cell. Swarm cells and amoebae are able to transition between these stages. At some point, these haploid (1n) cells will fuse to produce a diploid amoeboid zygote. Plasmogomy is the fusion of cytoplasm of two cells. Karyogamy is the fusion of nuclei and leads to the production of a diploid zygote. The zygote will grow, replicating the nuclei with no cytokinesis, to form the multinucleate plasmodium. A mature plasmodium (multinucleated free-flowing mass of protoplasm) can produce sclerotium (small cells) in a dry habitat.

Summary

Slime molds represent several different lineages: the cellular slime molds (Dictyostelids), Protostelids, and plasmodial slime molds (Myxomycetes). These organisms move about as amoebae consuming bacteria until conditions become unfavorable, at which point they form spores. They can be found in damp substrates with ample bacteria and are most frequently found on decaying logs and forest duff.

Dictyostelids are model organisms for studying altruism. They are unicellular, but collaborate to form multicellular structures where only some of the individuals involved go on to make spores. Protostelids are less well-understood and form a single sporangium at the tip of a cellular stalk. Plasmodial slime molds (the myxomycetes) form a large, multinucleate amoeba during their feeding stage called a plasmodium. They have diplontic life cycles and there is a lot of morphological diversity of sporocarps represented in this group. Some organisms in this group are studied for their ability to solve mazes and spatial puzzles.

Though these organisms seem primitive, they have complex interactions with each other and their environments.

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2.4.2.2: Oomycota

Learning Objectives

- Compare and contrast oomycetes with plants and fungi.
- Explain some of the roles oomycetes have in both terrestrial and aquatic ecosystems.
- Identify structures in the *Saprolegnia* life cycle and know their ploidy.

The water molds, phylum Oomycota (“egg fungus”), were so-named based on their **filamentous morphology** and their use of **glycogen** as a storage carbohydrate. However, molecular data have shown that the water molds are not closely related to fungi. As diploid spores, many oomycetes have **two flagella** (one ornamented and one smooth) for locomotion, placing them in the **Heterokonts** (hetero- different, kont- flagella). The oomycetes are heterotrophic eukaryotes characterized by a **cellulose-based cell wall** and an extensive network of filaments that allow for nutrient uptake. This group of organisms has a **diplontic life cycle**. Most oomycetes are aquatic and are important decomposers in these ecosystems, but some have evolved to parasitize terrestrial plants (though these still rely on water). One particularly famous plant pathogen is *Phytophthora infestans*, the causal agent of late blight of potatoes, which caused the nineteenth century Irish potato famine.

Some notable water molds:

- Some species (e.g., *Saprolegnia* and *Achlya*) are parasites of certain fish and can be a serious problem in fish hatcheries.
- **Downy mildews** (Peronosporaceae) damage grapes and other crops.
- ***Phytophthora infestans***, the cause of the "late blight" of potatoes. In 1845 and again in 1846, it was responsible for the almost total destruction of the potato crop in Ireland. This led to the great Irish famine of 1845–1860. During this period, approximately 1 million people starved to death and many more emigrated to the New World. By the end of the period, death and emigration had reduced the population of Ireland from 9 million to 4 million.
- ***Phytophthora ramorum***, which is currently killing tanoaks and several species of true oaks in California. This pathogen is capable of infecting hundreds of species of plants and was likely introduced to California from ornamental *Rhododendron*.



Figure 2.4.2.2.1: A saprobic oomycete engulfs a dead insect. (credit: modification of work by Thomas Bresson)

Saprolegnia

Saprolegnia is a genus of primarily saprotrophic water molds. This genus is often studied for the life cycle features of oomycetes. This organism reproduces asexually by producing **zoospores** (zoospores are spores that swim, zoo- meaning ‘to live’ refers to its

motility) inside of an elongated sac called a **zoosporangium** (-angium meaning vessel, so a zoosporangium is what zoospores are produced inside of). These zoospores grow by mitosis into a diploid **thallus**, an undifferentiated body.

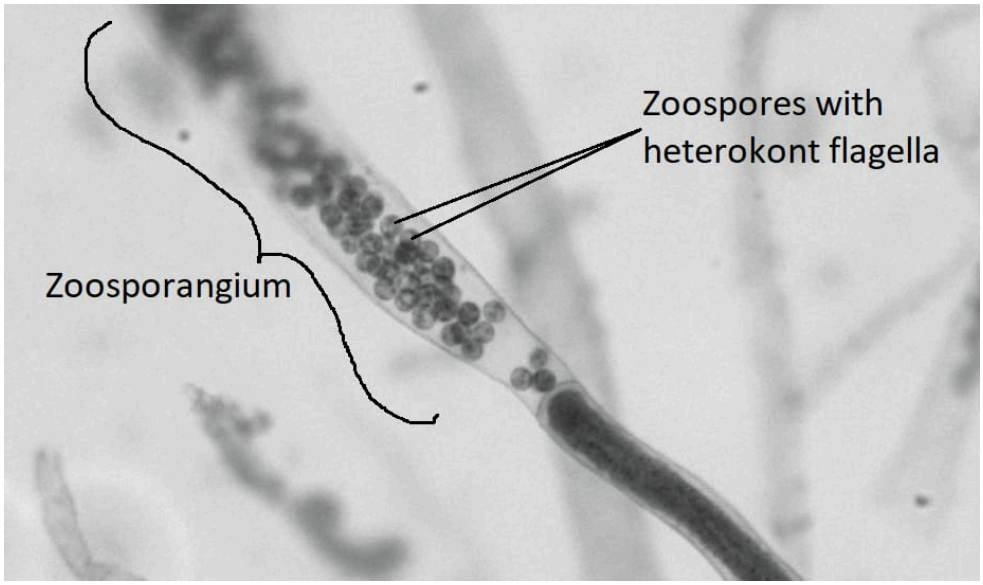


Figure 2.4.2.2.2: A zoosporangium of *Saprolegnia* with mature zoospores. The elongated, sac-like zoosporangium is partially visible in this image, located at the end of a filament of the thallus. Inside the zoosporangium are many small, round zoospores. Each of these would have two flagella: one whiplash and one tinsel. Photo by Maria Morrow, CC-BY-NC.

Saprolegnia's sexual reproducing structures include the globose **oogonium** and smaller, pad-like **antheridia** (singular, antheridium) that attach to the oogonium. Because these structures produce gametes--much like spores are produced in sporangia--the oogonia and antheridia are also referred to as **gametangia** (gametangium singular). The oogonium produces haploid **eggs** via meiosis. These eggs are fertilized by the haploid **male nuclei** produced by meiosis within the antheridium, creating a diploid, thick-walled zygote called an **oospore**.



Figure 2.4.2.2.3: Multiple antheridia can be seen appressed to the outside of the globose oogonium. In the center of the image is a spherical structure (oogonium) filled with smaller brown spherical structures (eggs or oospores). On the outside, there are empty-looking filaments with swollen ends (antheridia) appressed to it. Photo by Tom Bruns (pogon), CC-BY-NC.

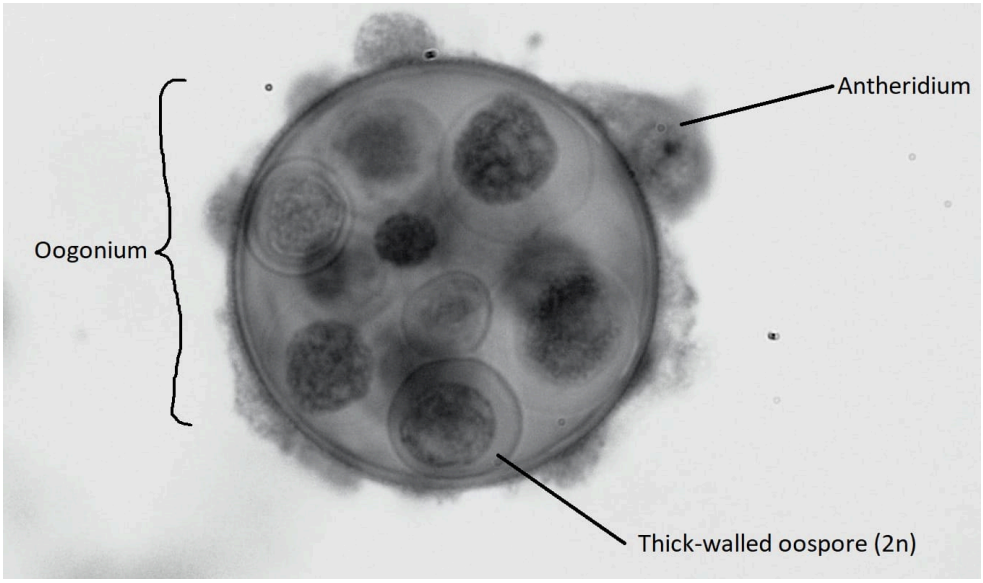


Figure 2.4.2.2.4: An oogonium of *Saprolegnia* with fertilized oospores. This large, globose oogonium would be located at the end of a filament on the thallus. Within the oogonium, there are many diploid oospores, which you can distinguish from unfertilized eggs by the thick wall that encloses them. On the outside of the oogonium, there are several antheridial pads apressed to the surface. The haploid nuclei within these antheridia have already been released into the oogonium. Photo by Maria Morrow, CC-BY-NC.

The oospore will be released and grow by mitosis to create a new multicellular **thallus**, completing the diplontic life cycle (Figure 2.4.2.2.5).

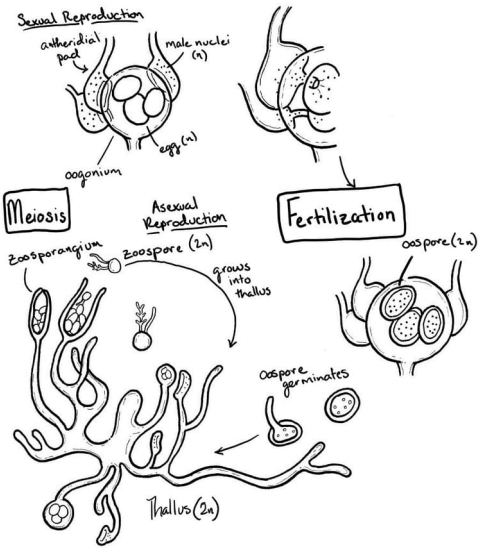


Figure 2.4.2.2.5: Saprolegnia life cycle. This life cycle is diplontic; the "multicellular" stage is the diploid thallus, though the filaments are coenocytic. The diploid thallus can reproduce by forming elongate zoosporangia where diploid zoospores are formed by mitosis. These zoospores have a whiplash flagellum and one decorated (hairy) flagellum (AKA zoospores with heterokont flagella). Zoospores can germinate and grow into a new diploid thallus, gentically identical to the parent. To sexually reproduce, the thallus can produce globose oogonia and/or filamentous antheridia. Within these structures, meiosis occurs to produce haploid eggs within the oogonium and haploid "male" nuclei within the antheridium. The antheridia adhere to the oogonium and deposit their nuclei inside. Some of these nuclei fuse with egg cells (completing fertilization) to form thick-walled, diploid oospores. When conditions are right, oospores may germinate to grow into a new thallus, genetically distinct from the parent(s). Diagram by Nikki Harris, CC BY-NC, with labels added by Maria Morrow.

Phytophthora

Phytophthora is a genus of water molds that parasitize plants. They have specialized zoosporangia that detach, allowing zoospores to be transported terrestrially and await germination until moisture is present. Some notable Phytophthoras are *P.*

ramorum (causal agent of sudden oak death, see Figure 2.4.2.2.6) and *P. infestans* (causal agent of late blight of potato and the Irish potato famine, see Figure 2.4.2.2.8).



Figure 2.4.2.2.6: Phytophthora ramorum can infect hundreds of different plant species, sometimes causing a leaf blight (as seen in the first photo), sometimes causing root disease. When it infects certain species of oak (*Quercus* spp.) and tanoak (*Notholithocarpus densiflorus*), it causes a lethal stem canker that oozes and stains a dark reddish color (second photo). First photo by Kerry Wininger, CC-BY-NC. Second photo by Chris Shuck, CC-BY-NC.



Figure 2.4.2.2.7: The first image shows two lemon-shaped sporangia, each at the end of a hyphal filament. These sporangia will release zoospores when conditions are favorable. The second image shows the leaf where these sporangia were produced, seen here as a discolored region with some white fuzz. Photos by 大肚魚, CC-BY-NC.

Phytophthora infestans is an oomycete responsible for potato late blight, which causes potato stalks and stems to decay into black slime (Figure 2.4.2.2.8). Widespread potato blight caused by *P. infestans* precipitated the well-known Irish potato famine in the nineteenth century that claimed the lives of approximately 1 million people and led to the emigration of at least 1 million more from Ireland. Late blight continues to plague potato crops in certain parts of the United States and Russia, wiping out as much as 70 percent of crops when no pesticides are applied.



Figure 2.4.2.2.8: These unappetizing remnants result from an infection with *P. infestans*, the causative agent of potato late blight. (credit: USDA)

Secondary Endosymbiosis

At some point in evolutionary history, a heterotrophic heterokont engulfed a red alga. This secondary endosymbiotic event resulted in several lineages of photosynthetic heterokonts, including the brown algae and diatoms. It is possible that the Oomycota also descended from this event, as there are apparent algal and cyanobacterial genes present in the nucleus of oomycetes. However, it is possible that these genes were acquired through horizontal gene transfer or evolved from homologs. As our understanding of genomes improves, so too will our interpretation of these events. Regardless, oomycetes currently live a chloroplast-free lifestyle and lack the vestigial plastids present in many lineages that have acquired and subsequently lost photosynthesis.

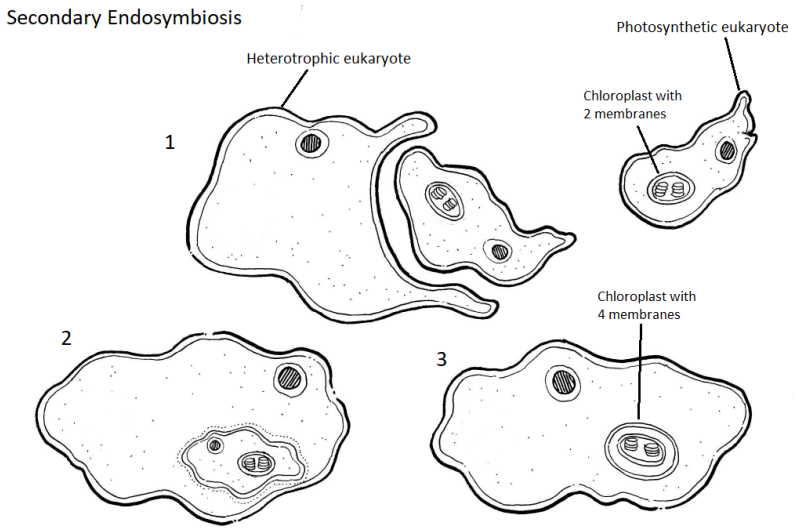


Figure 2.4.2.2.9: In the diagram above, we see a unicellular photosynthetic eukaryote with a 2-membrane chloroplast. In step one, this organism is engulfed by a heterotrophic eukaryote. In step two, we see the photosynthetic organism inside the heterotrophic organism. In step three, the original photosynthetic organism within the heterotroph has been reduced to a chloroplast with 4 membranes. The result is a new type of photosynthetic organism. Artwork by Nikki Harris CC BY-NC with added labels by Maria Morrow.

Summary

Oomycota, also called the water molds, is a group of fungus-like organisms with a history of living in aquatic ecosystems. These organisms have swimming spores and at least one stage in their life cycle has heterokont flagella: one whiplash flagellum and one decorated (hairy) flagellum. They have important roles as decomposers and parasites. Some have evolved to live terrestrially and are infamous parasites of plants, namely those in the genus *Phytophthora*. Among these is *Phytophthora infestans* the causal agent of late blight of potato and the Irish potato famine that resulted from an infestation during paricularly harsh, synergistic conditions in Ireland.

This group is closely related to the diatoms and brown algae. These photosynthetic lineages of heterokonts acquired their 4-membraned chloroplasts through secondary endosymbiosis of a red alga.

Members of this group share the following characteristics:

- Heterotrophic by absorption
- Morphology: Filamentous
- Cell wall composition: Cellulose
- Storage carbohydrate: Glycogen
- Life cycle: Diplontic

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2.4.3: PHOTOSYNTHETIC "PROTISTS"

Photosynthetic lineages can be found across the phylogenetic tree of protists. Most of the groups are unrelated to each other, as each major lineage acquired its chloroplast (and therefore the ability to photosynthesize) from different endosymbiotic events. For example, red and green algae belong to the same lineage (Archaeplastida). A red algal ancestor engulfed a cyanobacterial ancestor, leading to the first chloroplasts. These were inherited **vertically**--through reproduction and over evolutionary time--by the lineages of green algae. However, brown algae and diatoms inherited their chloroplasts from a secondary endosymbiotic event where their heterotrophic ancestor (something like an oomycete) engulfed a red alga. This is a **horizontal** transmission of chloroplasts between lineages, where genes (and here an organelle!) move between organisms through the environment, not through reproduction.

Endosymbiosis

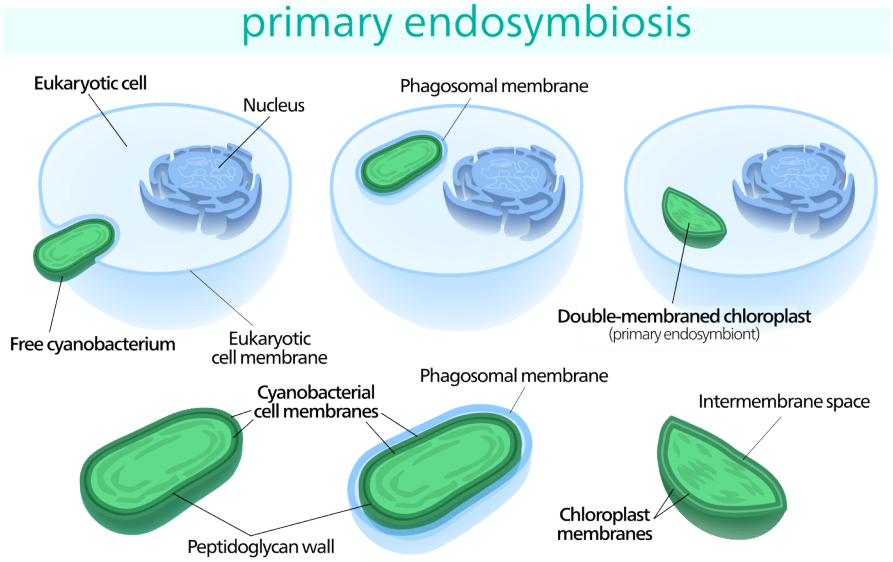


Figure 2.4.3.1: In primary endosymbiosis, a photosynthetic prokaryote (the free cyanobacterium) is engulfed by a heterotrophic eukaryote. After it is engulfed, the prokaryote is surrounded by a phagosomal membrane. The cyanobacterium is shown to have a peptidoglycan cell wall encompassed by two cell membranes. Eventually, genes are transferred between the cyanobacterium and eukaryote genomes. The phagosomal membrane disappears and we are left with a double-membraned chloroplast. Image by Kelvinsong, CC BY-SA 3.0, via Wikimedia Commons

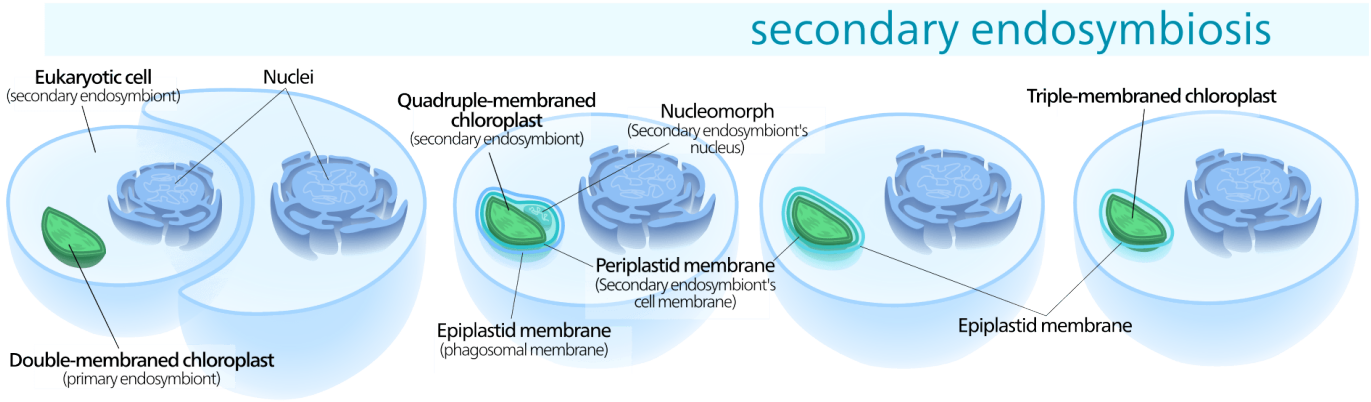


Figure 2.4.3.2: In secondary endosymbiosis, it is a photosynthetic eukaryote that is engulfed. After it is engulfed, it is surrounded by four membranes: the outer is the phagosomal membrane (epiplastid membrane), inside that is the cell membrane of the photosynthetic eukaryote that was engulfed (periplastid membrane), and inside that are the two membranes from the original chloroplast. In some secondary endosymbioses, the periplastid membrane is lost, resulting in a triple-membraned chloroplast. Image by Kelvinsong, CC BY-SA 3.0, via Wikimedia Commons

The horizontal transmission of chloroplasts between lineages via endosymbiosis resulted in several unrelated groups of photosynthetic protists. The lineages covered in this section are:

- Dinoflagellates (secondary endosymbiosis)
- Brown algae and diatoms (secondary endosymbiosis)
- Red and green algae (primary endosymbiosis)



-  Topic hierarchy

2.4.3.1: Dinoflagellates

2.4.3.2: Brown Algae and Diatoms

2.4.3.3: Red and Green Algae

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2.4.3.1: Dinoflagellates

Learning Objectives

- Explore some of the ecological roles of dinoflagellates.
- Describe the symbiosis between corals and zooxanthellae.
- Explain what happens in a red tide.

There are currently around 2,000 species of dinoflagellates. They are **unicellular**, though dinoflagellates exhibit extensive morphological diversity and can be photosynthetic, heterotrophic, or mixotrophic. In photosynthetic dinoflagellates, most use the pigments chlorophylls a and c. Many dinoflagellates are encased in interlocking plates of cellulose. Two perpendicular flagella fit into the grooves between the cellulose plates, with one flagellum extending longitudinally and a second encircling the dinoflagellate (Figure 2.4.3.1.1). Together, the flagella contribute to the characteristic spinning motion of dinoflagellates. Interestingly, dinoflagellates have a unique nucleus structure, where chromosomes are attached to the nuclear membrane. This is not found in other eukaryotes and so has received its own name: a **dinokaryon**.

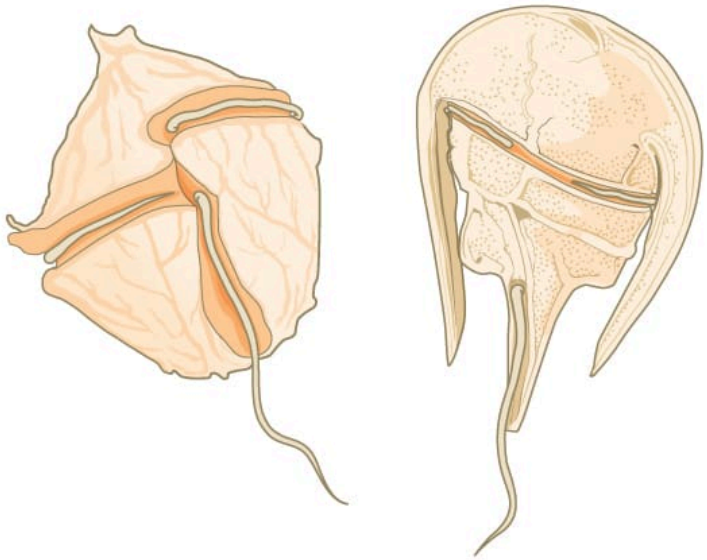


Figure 2.4.3.1.1: The dinoflagellates exhibit great diversity in shape. Many are encased in cellulose armor and have two flagella that fit in grooves between the plates. Movement of these two perpendicular flagella causes a spinning motion. Descriptive text: Two dinoflagellates. The first is walnut-shaped, with a groove around the middle and another perpendicular groove that starts at the middle and extends back. Flagella fit in each groove. The second dinoflagellate is horseshoe-shaped, with the body extending from the wide part of the horseshoe toward the narrow end. Like the first dinoflagellate, this one has two perpendicular grooves, each containing a flagellum.

These protists exist in freshwater and marine habitats, and are a component of **plankton**, the typically microscopic organisms that drift through the water and serve as a crucial food source for larger aquatic organisms. Some dinoflagellates generate light, called **bioluminescence**, when they are jarred or stressed. Large numbers of marine dinoflagellates (billions or trillions of cells per wave) can emit light and cause an entire breaking wave to twinkle or take on a brilliant blue color (Figure 2.4.3.1.2). For approximately 20 species of marine dinoflagellates, population explosions (also called blooms) during the summer months can tint the ocean with a muddy red color. This phenomenon is called a **red tide** due to the abundant red pigments present in dinoflagellate plastids. In some cases, such as the 2018/19 event on the Gulf Coast, these dinoflagellate species can secrete an asphyxiating toxin that can kill fish, birds, and marine mammals. Red tides can be massively detrimental to commercial fisheries, and humans who consume these protists may become poisoned.



Figure 2.4.3.1.2: Bioluminescence is emitted from dinoflagellates in a breaking wave, as seen from the New Jersey coast. (credit: "catalano82"/Flickr)

As plankton, dinoflagellates are essential sources of nutrition for many other organisms. In some cases, they are consumed directly. Others serve as producers of nutrition in a more indirect way. For instance, photosynthetic dinoflagellates called **zooxanthellae** use sunlight to fix inorganic carbon. In this symbiotic relationship, these protists provide nutrients for coral polyps (Figure 2.4.3.1.3) that house them, giving corals a boost of energy to secrete a calcium carbonate skeleton. In turn, the corals provide the protist with a protected environment and the compounds needed for photosynthesis. This type of symbiotic relationship is important in nutrient-poor environments. Without dinoflagellate symbionts, corals lose algal pigments in a process called coral bleaching, and they eventually die. This explains why reef-building corals do not reside in waters deeper than 20 meters: insufficient light reaches those depths for dinoflagellates to photosynthesize.



Figure 2.4.3.1.3: Coral polyps obtain nutrition through a symbiotic relationship with dinoflagellates. The dinoflagellate partners, called zooxanthellae, are what give corals their color.

Summary

Dinoflagellates are a group of morphologically and nutritionally diverse acquatic organisms, from the zooxanthellae that live inside coral polyps to the toxin-releasing microbes that cause red-tides. They have essential roles in marine food webs. They are typically unicellular, with cellulose plates and two flagella.

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2.4.3.2: Brown Algae and Diatoms

Learning Objectives

- Use life history, morphology, and cellular components to identify brown algae.
- Identify the components of a kelp thallus.
- Identify structures and events in the *Fucus* life cycle and know their ploidy.
- Identify structures and events in the *Laminaria* life cycle and know their ploidy.
- Use life history, morphology, and cellular components to identify diatoms.
- Classify diatoms based on symmetry and ecology.
- Describe sexual and asexual reproduction in diatoms.

Brown algae (class Phaeophyceae) and diatoms (class Bacillariophyceae) belong to the phylum Ochrophyta. They are the result of a secondary endosymbiosis between a heterokont and a photosynthetic eukaryote. Heterokonts, such as the Oomycota, are united by the presence of a textured, or "hairy," flagellum and an additional flagellum that lacks hair-like projections (Figure 2.4.3.2.1). Members of this subgroup range in size from single-celled diatoms to the massive and multicellular kelp.

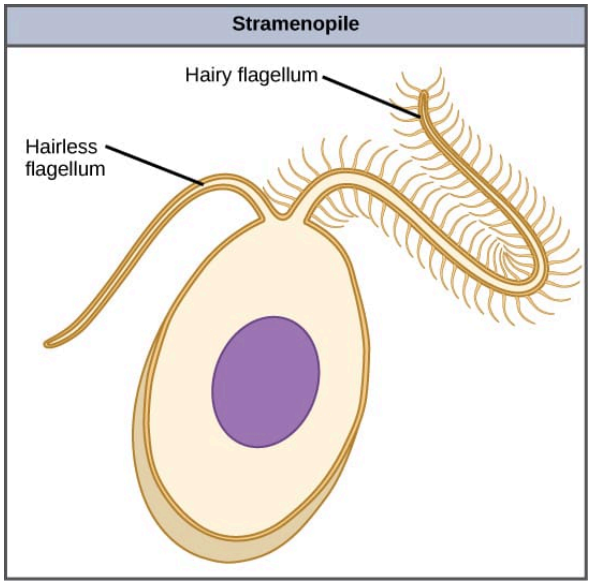


Figure 2.4.3.2.1: This stramenopile cell has a single hairy flagellum and a secondary smooth flagellum. This is sometimes referred to as having "heterokont flagella", as this morphology is unique to this group.

Brown algae, diatoms, and oomycetes belong to a single clade, the **stramenopiles** (aka heterokonts). The photosynthetic stramenopiles share the following characteristics:

- 4-membraned chloroplasts
- a yellow-brown pigment (which gives them their color). It is a carotenoid called **fucoxanthin**.
- chlorophylls a and c
- most have a diplontic life cycle (as you'll find below, *Laminaria* has a haplodiplontic life cycle)

Phaeophyceae

This group is commonly called the brown algae and includes rockweeds and kelps. Kelps are some of the fastest growing organisms on the planet! Brown algae are primarily marine and are often found in the intertidal zone. Members of this phylum are used for food in some coastal areas of the world and harvested in the U. S. for fertilizer and as a source of iodine.

Brown algae are brown due to the large amounts of carotenoids they produce, primarily one called **fucoxanthin**. These organisms are exclusively **multicellular** and have filamentous, multinucleate cells (much like oomycetes). They can get so large that they require special conductive cells to transport photosynthates from their blades down to the rest of their tissues. These conductive cells are called **trumpet hyphae** and have sieve plates and resemble sieve tubes found in flowering plants. Brown algae have cellulose cell walls and store carbohydrates in the form of laminarin. The polymer alginate can also be found in the cell walls of brown algae and is used commercially for a variety of purposes, including the high fidelity molds used in dentistry.

Kelp

Much like *Saprolegnia*, the body of an alga is termed a thallus because it is not differentiated into specialized tissues. The general morphology of a brown alga includes a **holdfast, stipe, gas bladder**(s)**,** and **blade**(s) (Figures $2.4.3.2.2 - 4$).



Figure $2.4.3.2.2$: In the diagram above, there are two kelp thalli. The one on the left side is labeled. At the bottom of the thallus is a network of root-like projections that make up the holdfast. The stem-like structure that travels up from the holdfast is the stipe, which terminates in an inflated gas bladder. There are several leaf-like structures attached to the gas bladder. These are blades. The thallus on the right has all of these components, but in a slightly different arrangement. Can you find them? Artwork by Nikki Harris CC-BY-NC with added labels by Maria Morrow.

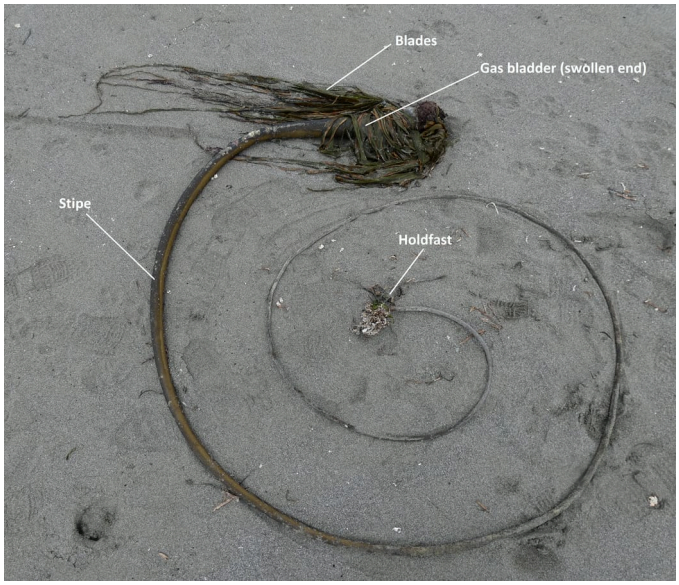


Figure $2.4.3.2.3$: A bull kelp thallus that was washed up on the beach and arranged in a spiral so all parts would be visible in one image. At the center of the spiral is the holdfast. This would be attached to the sea floor. A long stipe connects the holdfast to a gas bladder that is obscured by many thin blades, which all attach to the top of the gas bladder. Photo by Maria Morrow, CC-BY-NC.

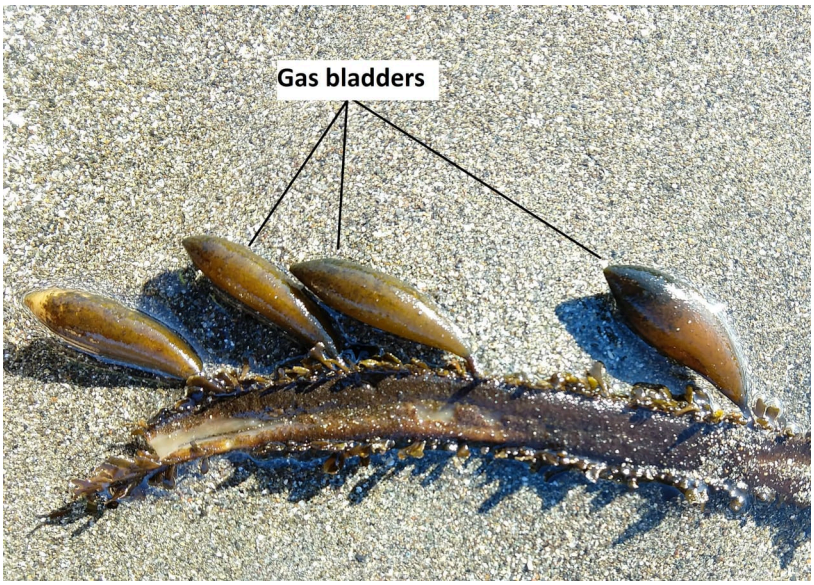


Figure 2.4.3.2.4: A piece of feather boa kelp with several small gas bladders. The four gas bladders shown all attach to the edge of the stipe. If the full thallus were visible, gas bladders would be attached down the entire length of both sides of the flattened stipe. Do you see any blades present? Photo by Maria Morrow, CC-BY-NC.

Fucus

A model organism for the Phaeophyta life cycle is *Fucus* (rockweed), which, like its relative *Saprolegnia,* has a diplontic life cycle. The *Fucus* thallus has dichotomous branching (forking into two equal branches) and swollen, heart-shaped reproductive tips of the branches. These swollen branch tips are called **receptacles** (Figure 2.4.3.2.5).

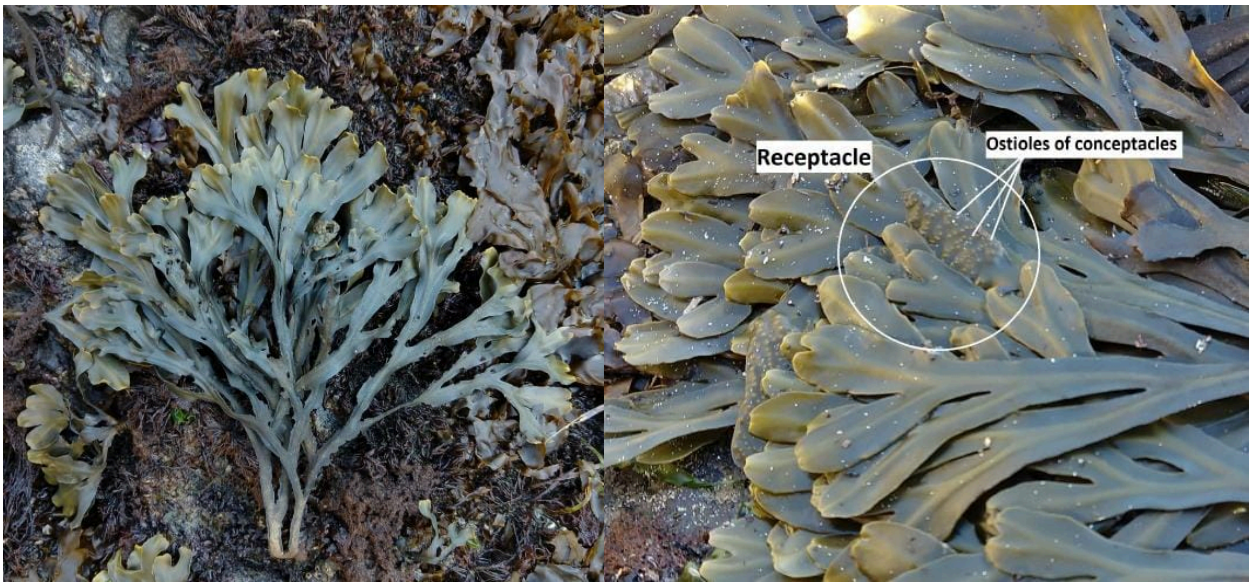


Figure 2.4.3.2.5: The first image shows a *Fucus thallus* (though a bit of the holdfast remained attached to the rock). The thallus branches dichotomously, making Y shapes each time it branches and forks into two equal pieces. The second image is a closer view of the ends of the branches. The swollen, heart-shaped ends are called receptacles. The bumps on these receptacles are the tops of the conceptacles--vase-like chambers embedded within the receptacle. Photos by Maria Morrow, CC-BY-NC.

The receptacles are covered in small bumps, each with a pore at the center of the bump called an **ostiole**. The bumps are **conceptacles**, chambers that house the gametangia (Figure 2.4.3.2.6). Phaeophyta produce **oognia**, globose gametangia that undergo meiosis to produce eggs, and **antheridia**, branched gametangia that undergo meiosis to produce sperm (Figure 2.4.3.2.7).

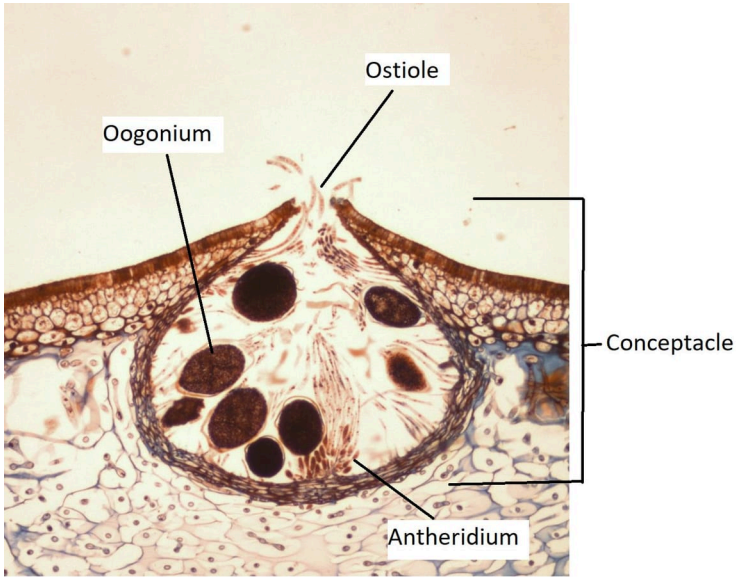


Figure 2.4.3.2.6: A cross section through a *Fucus* receptacle shows inside a conceptacle. The male and female gametangia are housed within the conceptacle chamber. The antheridia are branched structures that look like small trees. These produce sperm with heterokont flagella (not visible in this image). The oogonia are globose structures divided into sections as eggs are produced. The eggs will be fertilized by sperm that swim in through the ostiole, forming a diploid zygote that will be released in the marine water. This zygote will grow by mitosis into a multicellular, diploid thallus. Photo by Maria Morrow, CC-BY-NC.

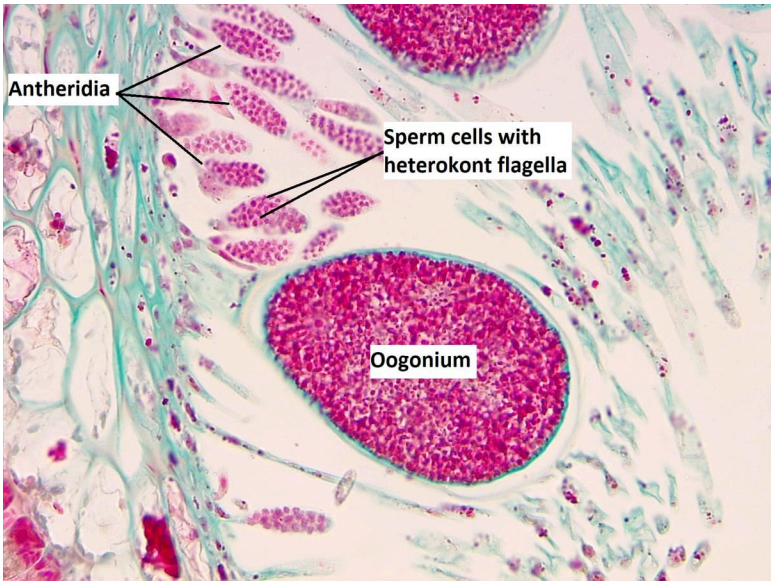


Figure 2.4.3.2.7: A closer view of the antherida and oogonium inside a *Fucus* conceptacle. There are no eggs distinguishable within the oogonium. However, individual sperm cells can be seen within the antheridia. These sperm cells would each have the typical heterokont flagella. Photo by Melissa Ha, CC-BY-NC.

Fucus Life Cycle

Fucus has a diplontic life cycle (Figure 2.4.3.2.8) where haploid gametes are produced from a diploid thallus. These haploid gametes do not grow, but fuse together to form a zygote. See Figure 2.4.3.2.9 for an example of alternation of generations in the Phaeophyta.

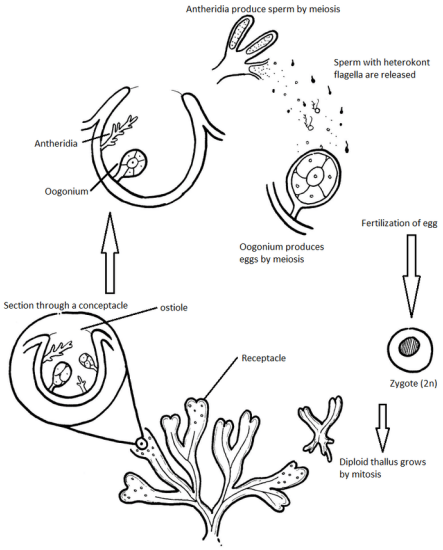


Figure 2.4.3.2.8: The diplontic life cycle of *Fucus*. If you start at the bottom of the diagram, there is a diploid thallus. The ends of the thallus branches are receptacles. A cross section through a receptacle shows us the inside of a conceptacle: the opening of the conceptacle is an ostiole. Within the conceptacle, there is a globose oogonium that has been divided into many compartments. These are egg cells and are the result of meiosis within the oogonium. The branched antheridia produce sperm by meiosis, all of which have heterokont flagella. The haploid sperm are released and swim to fertilize an egg, forming a diploid zygote. The zygote grows by mitosis into a diploid thallus, which brings us back to the beginning. Diagram by Nikki Harris, CC-BY-NC with labels added by Maria Morrow.

Laminaria Life Cycle

A variety of algal life cycles is represented by the stramenopiles, but the most complex is alternation of generations, in which both haploid and diploid stages involve multicellularity. Compare this life cycle to that of humans, for instance. Haploid gametes produced by meiosis (sperm and egg) combine in fertilization to generate a diploid zygote that undergoes many rounds of mitosis to produce a multicellular embryo and then a fetus. However, the individual sperm and egg themselves never become multicellular beings. Terrestrial plants also have evolved alternation of generations. In the brown algae genus *Laminaria*, haploid spores develop into multicellular gametophytes, which produce haploid gametes that combine to produce diploid organisms that then become multicellular organisms with a different structure from the haploid form (Figure 2.4.3.2.9). Certain other organisms, such as the red alga *Polysiphonia*, perform alternation of generations in which both the haploid and diploid forms look the same.

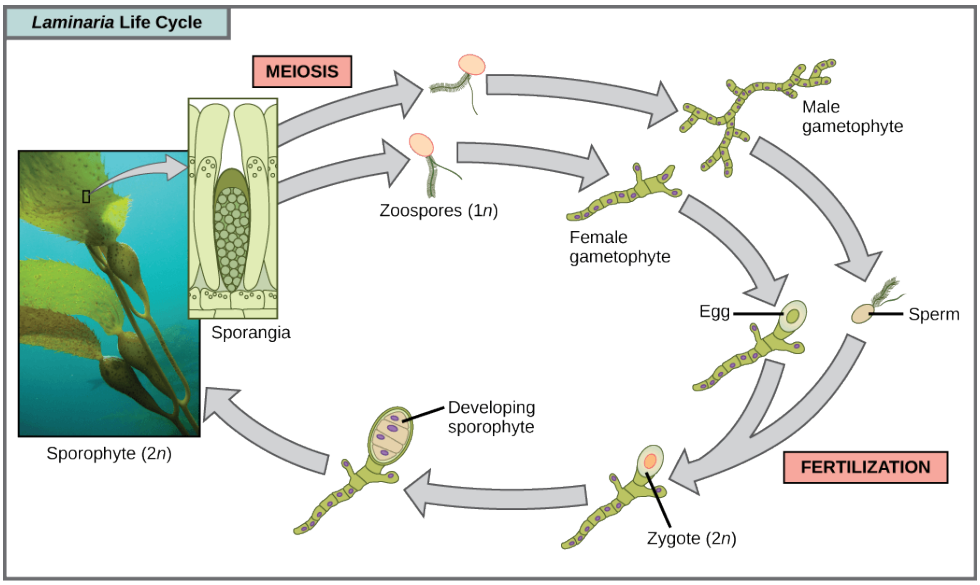


Figure 2.4.3.2.9: Several species of brown algae, such as the *Laminaria* shown here, have evolved life cycles in which both the haploid (gametophyte) and diploid (sporophyte) forms are multicellular. The gametophyte is different in structure than the sporophyte. The life cycle begins when sporangia undergo meiosis, producing 1n zoospores. The zoospores undergo mitosis, producing multicellular male and female gametophytes. The female gametophyte produces eggs, and the male gametophyte produces sperm. The sperm fertilizes the egg, producing a 2n zygote. The zygote undergoes mitosis, producing a multicellular sporophyte. The mature sporophyte produces sporangia, completing the cycle. A photo inset shows the sporophyte stage, which resembles a plant with long, flat blade-like leaves attached to green stalks via bladder-like connections. Both the blade and stalks are submerged. Sporangia are associated with the leaf-like structures. (credit "laminaria photograph": modification of work by Claire Fackler, CINMS, NOAA Photo Library)

Summary of Characteristics for Brown Algae

- Morphology: Multicellular thallus
- Cell wall composition: Cellulose and calcium alginate
- Chloroplasts: 4 membranes, pigments are chlorophyll a, chlorophyll c, and fucoxanthin
- Storage carbohydrate: Laminarin
- Life cycle: Primarily diplontic (alternation of generations in some species)
- Ecology: Marine

Bacillariophyceae

Diatoms are another photosynthetic lineage of photosynthetic heterokonts that was derived from the secondary endosymbiotic event. Diatoms are an incredibly diverse group of unicellular organisms containing anywhere from 20,000 to 2 million species. These organisms are unicellular and surrounded by a **frustule**, a silica shell made from two distinct valves that enclose the plasma membrane. Frustules are amazingly intricate, covered with small pores in an arrangement specially adapted for capturing sunlight (Figure 2.4.3.2.11). Some diatoms exhibit a slit in their silica shell, called a raphe. By expelling a stream of mucopolysaccharides from the raphe, the diatom can attach to surfaces or propel itself in one direction.

Like the brown algae, they have golden chloroplasts with 4-membranes (Figure 2.4.3.2.10). Diatoms store carbohydrates in the form of chrysolaminarin. The silica frustules of diatoms found in sediments (diatomaceous earth) are used for myriad commercial purposes, including toothpaste additives (as an abrasive), filters, and insulation.

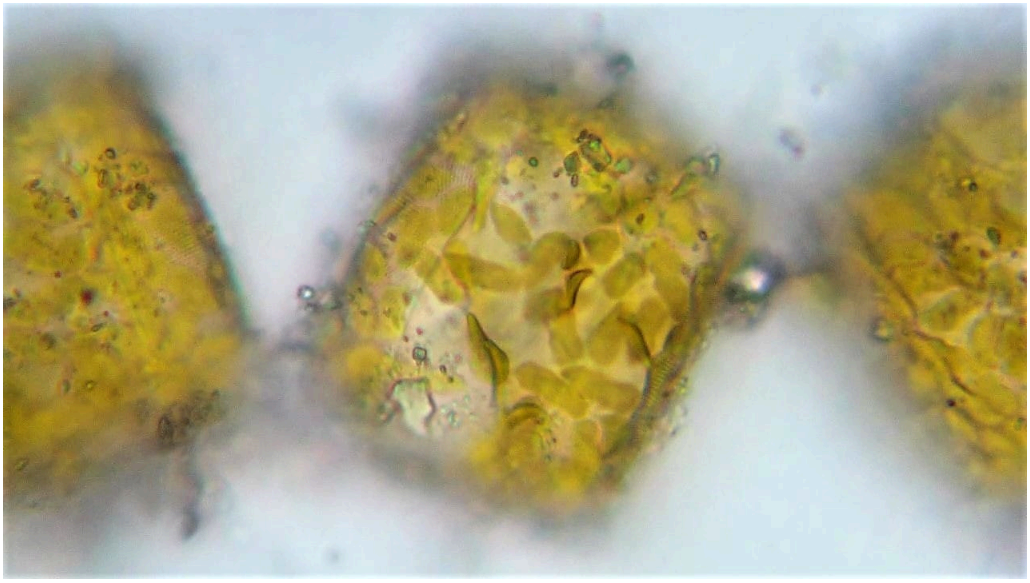


Figure 2.4.3.2.10: A diatom filled with golden organelles (chloroplasts). Photo by Vicente Franch Meneu, CC-BY-NC.

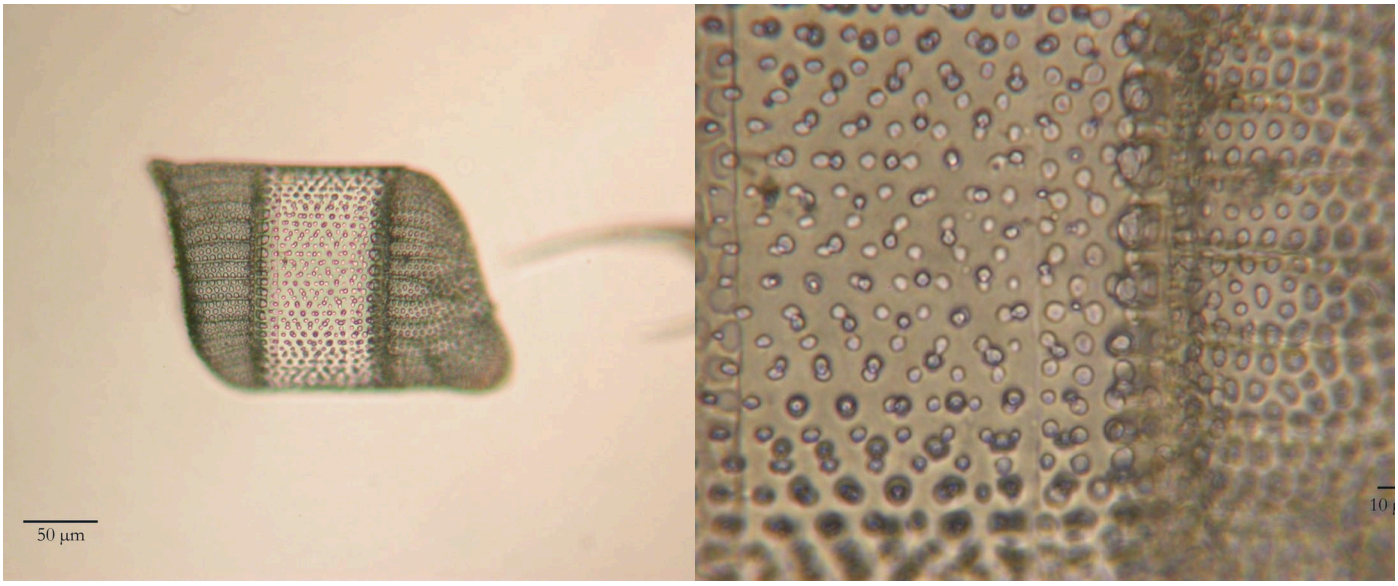


Figure 2.4.3.2.11: An *Isthmia nervosa* frustule showing the intricate pattern of pores. There appear to be multiple layers with a different pattern of pores to each. Scientists study these pore configurations when designing solar panels in an effort to mimic the sunlight harvesting abilities of diatoms. Photos by Lama Mark Webber, CC-BY-NC.

Morphology

We are still trying to figure out how to determine what a diatom "species" is and, so far, they have been classified based on the morphology of the frustule. Using this classification, historically there were two major groups of diatoms: **centric** (have radial symmetry, see Figure 2.4.3.2.12) and **pennate** (have bilateral symmetry, see Figure 2.4.3.2.13). These classifications have improved and increased in complexity, so here we will cover just the broad strokes. For a more in-depth look at current diatom morphological classification and fantastic images, check out this website.

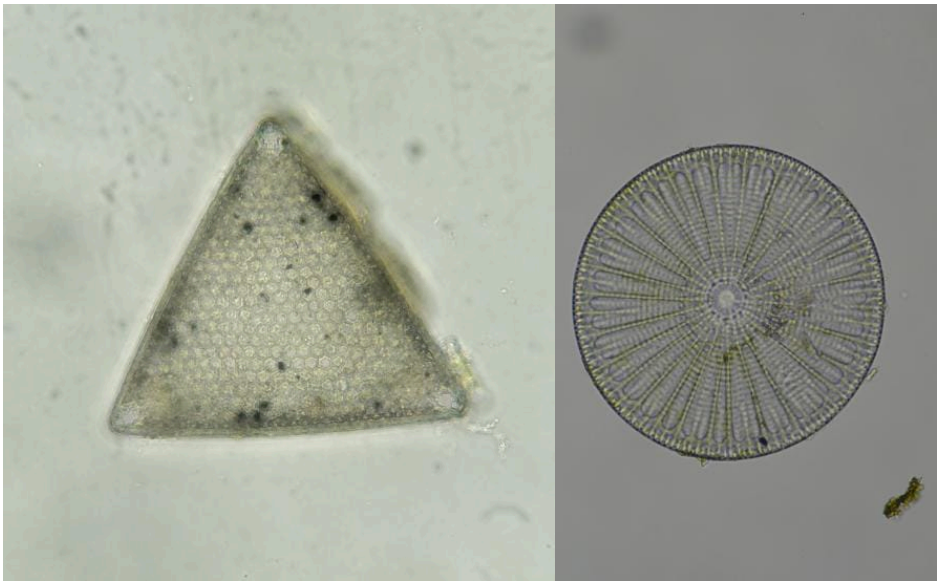


Figure 2.4.3.2.12: These images show centric diatoms. You can draw several lines of symmetry through each of these organisms. Centric is still a morphological description used for diatom genera. First: *Triceratium,* photo by Ryan Watson, CC-BY. Second: *Arachnoidiscus ehrenbergii* found on *Ulva,* photo by Randall, CC0.

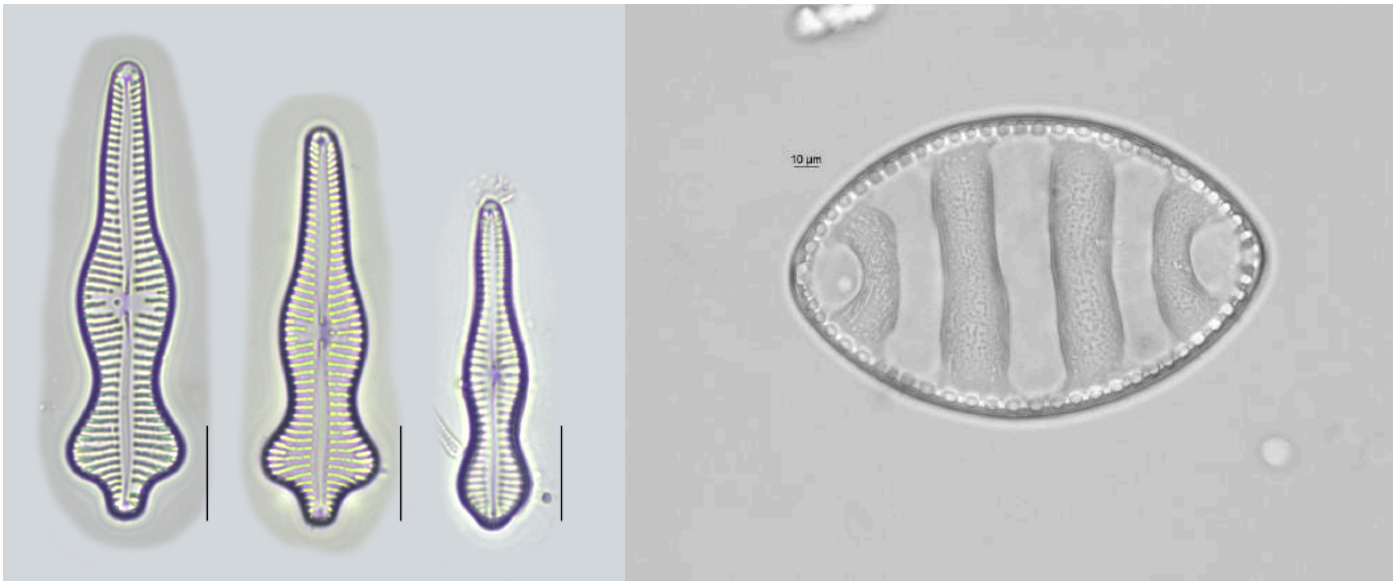


Figure 2.4.3.2.13: These images show a variety of "pennate" diatoms. This has historically classified many varieties of bilaterally symmetric diatoms which have since been further divided into better-described groups (some even asymmetrical). When considered three-dimensionally, only one line of symmetry can be drawn through this type of diatom. First: *Gomphonema acuminatum*, scale bar = 10 µm. Photo by Enviroethan, CC-BY-NC. Second: *Surirella undulata,* photo by Lila_137, CC-BY-NC.



Figure 2.4.3.2.14: Many diatoms live in colonies, where unicellular diatoms adhere together to make a more complex structure. This may make it easier to float in the water column (raft-formation) or make it more difficult to be engulfed by predators The examples above show colonies of diatoms in a variety of shapes. First: *Asterionella formosa*, a bilaterally symmetric diatom, forming a star-shaped colony. Photo by Mindy Morales, CC-BY-NC. Second: *Chaetoceros debilis*, a centric diatom forming a spiral-shaped colony. Photo by Sarka Martinez, CC-BY-NC.

Ecology

In addition to morphology, diatoms can also be classified by where they occur. Free-floating diatoms are **planktonic**. Diatoms attached to other organisms (like giant kelp) are **epiphytic** (Figure 2.4.3.2.15). Epiphytic diatoms can be found in aquatic ecosystems on algae and aquatic angiosperms like eelgrass, as well as terrestrial ecosystems, living in the damp crevices of tree bark. **Benthic** diatoms tend to dwell toward the bottom of a body of water. In general, these three categorizations refer to aquatic ecosystems. However, diatoms can be found just about anywhere there is water in terrestrial ecosystems. The community composition of diatoms varies depending on location. Because of this, diatoms have been used in forensic investigations to determine where someone drowned (depending on the diatom species present) and how long ago they drown (based on how far the diatoms had migrated into their tissues).

Diatoms are major **producers** in aquatic environments; that is, they are responsible for as much as 40% of the photosynthesis that occurs in fresh water and in the oceans. They serve as the main base of the food chains in these habitats, supplying calories to heterotrophic protists and small animals. These, in turn, feed larger animals. During periods of nutrient availability, diatom populations bloom to numbers greater than can be consumed by aquatic organisms. The excess diatoms die and sink to the sea floor where they are not easily reached by saprotrophs that feed on dead organisms. As a result, the carbon dioxide that the diatoms had consumed and incorporated into their cells during photosynthesis is not returned to the atmosphere. In general, this process by which carbon is transported deep into the ocean is described as the **biological pump**, because carbon is “pumped” to the ocean depths where it is inaccessible to the atmosphere as carbon dioxide. The biological carbon pump is a crucial component of the carbon cycle that maintains lower atmospheric carbon dioxide levels.

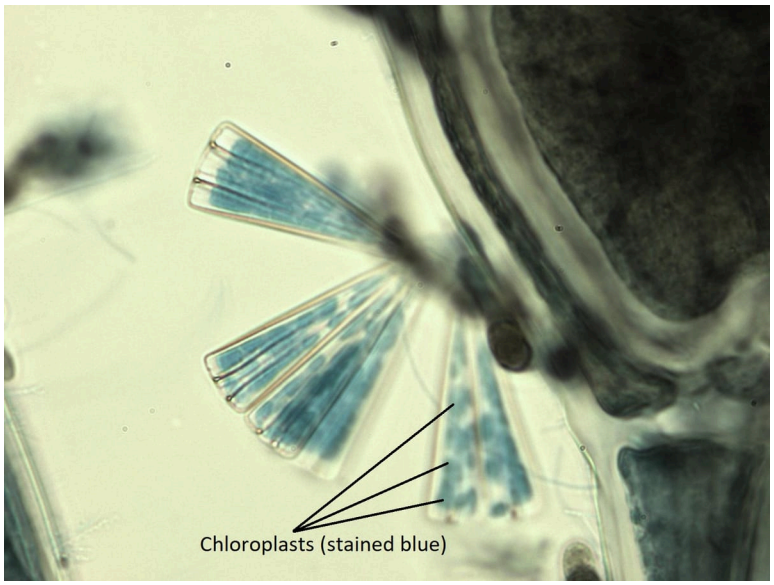


Figure 2.4.3.2.15: Epiphytic diatoms. These diatoms were photographed from a prepared slide of the red alga *Polysiphonia*. It is a fan-like colony of pennate diatoms that have attached to the surface of the red alga specimen used to make the slide. When the slide was made, it went through a staining bath. This turned the many golden chloroplasts within the diatoms blue. You can see the chloroplasts within the diatoms because the silica frustules are transparent, like glass. Photo by Maria Morrow, CC-BY-NC .

Reproduction

Diatoms primarily reproduce asexually by **binary fission**, similar to prokaryotes. During binary fission, the two valves of the frustule are separated and each new cell forms a new valve inside the old one. However, the new valve is always smaller. If diatoms only reproduce in this way, it results in a continual decrease in average size. When some minimal size is reached, this can trigger sexual reproduction. When diatoms sexually reproduce, they have a diplontic life cycle and produce a very large **auxospore** (Figure 2.4.3.2.16).



Figure 2.4.3.2.16: When diatoms sexually reproduce, they make a large structure called an auxospore. In this picture, the auxospore is a lightbulb-shaped cell located at the end of the colony of epiphytic diatoms. There are many golden chloroplasts visible each diatom. Photo by Maria Morrow, CC-BY-NC .

Diversity

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 2.4.3.2.1: This video shows some of the incredible diversity of diatom shapes and the amazing art Klaus Kemp makes with them. Sourced from YouTube.

Summary of Characteristics for Diatoms

- Morphology: Unicellular
- Cell wall composition: Silica frustule
- Chloroplasts: 4 membranes, pigments are chlorophyll a, chlorophyll c, and fucoxanthin
- Storage carbohydrate: Chrysolaminarin
- Life cycle: Diplontic
- Ecology: Everywhere! Marine, freshwater, and terrestrial.

Summary

Though brown algae and diatoms seem to have very little in common morphologically, they are descended from a common ancestor. Both of these groups have a diplontic life cycle during some stage of which a cell will have heterokont flagella. They have 4-membraned chloroplasts that contain the pigments chlorophyll a, chlorophyll c, and fucoxanthin. This latter pigment gives the chloroplasts in these groups a golden color. This is about where the similarities end.

Brown algae are exclusively multicellular and found in marine habitats, most typically in the intertidal zone. Their cell walls contain cellulose and they store their carbohydrates as laminarin.

Diatoms are exclusively unicellular and found in almost every habitat where there is water. Their single cell is surrounded by a silica frustule composed of two distinct valves. They store their carbohydrates as chrysolaminarin.

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2.4.3.3: Red and Green Algae

Learning Objectives

- Distinguish between different groups of algae using life cycle, morphological features, and cellular composition.
- Connect adaptations in the red and green algae to habitat characteristics and ecology.
- Identify structures and phases in the *Polysiphonia* and *Spirogyra* life cycles; know the ploidy of these structures.

Red algae and green algae are included in the supergroup Archaeplastida. It was from a common ancestor of these protists that the land plants evolved, since their closest relatives are found in this group. Molecular evidence supports that all Archaeplastida are descendants of an endosymbiotic relationship between a heterotrophic protist and a cyanobacterium. This primary endosymbiosis resulted in the chloroplasts of all photosynthetic eukaryotes discussed in this book! The red and green algae include unicellular, multicellular, and colonial forms.

Glaucophyta

Glaucophytes are unicellular, phototrophic eukaryotics found in freshwater ecosystems. Glaucophytes are likely an ancestral branch in the Archaeplastida and are often used as evidence of the cyanobacterial origin of chloroplasts. They have chloroplast-like organelles, called cyanelles or muroplasts, that have peptidoglycan between the two membranes. They have the same pigments as cyanobacteria and red algae: chlorophyll a and phycobilins. Much like the cyanobacteria, they appear blue-green due to the interaction of chlorophyll and phycocyanins (glauco- comes from the Greek glaukos meaning blue-green). Non-motile cells have a rigid cell wall composed of cellulose. Motile cells have two whiplash flagella. Sexual reproduction has yet to be documented in this group.

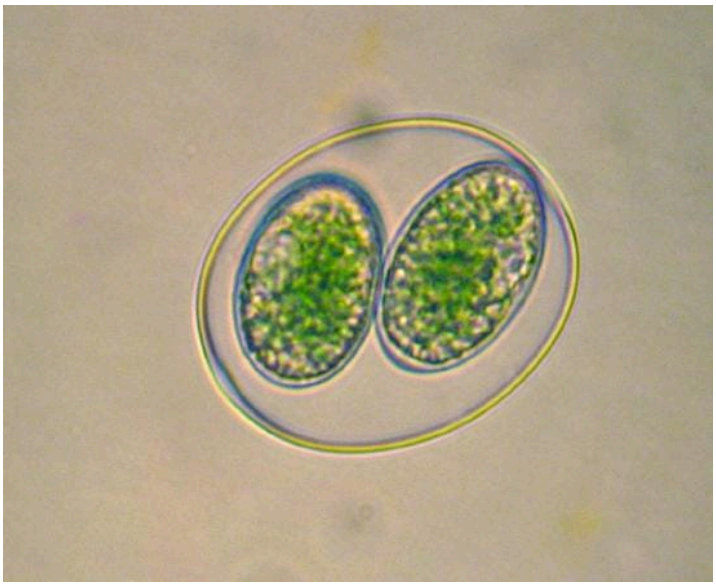


Figure 2.4.3.3.1: A nonmotile glaucophyte cell asexually reproducing. Two daughter cells are produced within the cell wall of the mother cell. Each daughter cell has a distinct cell wall and is filled with green cyanelles. Photo by James Tran, CC BY 2.0, via Wikimedia Commons

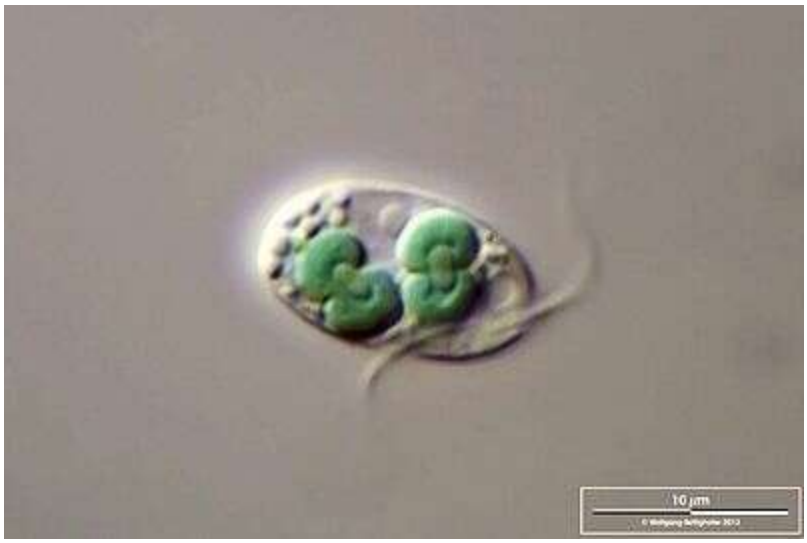


Figure 2.4.3.3.2: A motile cell (zoospore) of *Cyanophora paradoxa*. The green structures within this cell are cyanelles. Two flagella can be distinguished on the right side. Scale bar indicates 10 µm. From algae culture of University Duisburg-Essen (Germany), pictures were taken with Zeiss Axioplan and Canon 600D, CC BY-NC. Retrieved from EOL.org.

Rhodophyta

Red algae descended from the same endosymbiotic event as the Glaucophyta. The red algae are almost exclusively marine. Some are unicellular but most are multicellular. Approximately 6,000 species have been identified. They have true chloroplasts with two membranes (no remnant peptidoglycan) containing chlorophyll a. Like the cyanobacteria, they use phycobilins as antenna pigments - **phycoerythrin** (which makes them red) and **phycocyanin**. Red pigment allows the red algae to photosynthesize at deeper depths than the green or brown algae, harnessing more of the blue light waves that penetrate deeper into the water column. Unlike green algae and plants, red algae store carbohydrates as **Floridean starch** in the cytosol. Some are used as food in coastal regions of Asia. **Agar**, the base for culturing bacteria and other microorganisms, is extracted from a red alga.

Selection Pressures and Drivers

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

1. **Access to sunlight**: Most colors of light cannot penetrate into deeper water, as they are scattered by water molecules. The wavelengths of light that reach deepest into the ocean are blue and green. Many fish that live in the deep ocean are red. Because red light does not penetrate to the depths where they live, this makes them virtually undetectable by sight. Remember, we see things because of the light that bounces off of them. Red pigments reflect red light, so no red light, no reflected light. Red algae are using a similar strategy--absorb the wavelengths of light that are not red--with a different goal: to use that absorbed light to make food. The phycoerythrin in their chloroplasts reflects red light, giving them a red appearance, and absorbs the blue light that is able to penetrate to deeper areas in the water column.
2. **Fertilization**: The ocean is an expansive environment, often with large areas of open space between populations of organisms. In this environment, successful fertilization of an egg by a nonmotile sperm--red algae **lack flagella**--presents a challenge. Having multicellular haploid and diploid phases provides red algae more opportunities to produce gametes and spores. A diploid stage that clones the zygote, the **carposporophyte**, provides more opportunities to do meiosis from each fertilization event.
3. **Salinity:** Marine environments are relatively high in salinity. A possible adaptation for this is to have sulfated polysaccharides in the cell wall, such as the **galactans** present in Rhodophyta. This is a strategy present in (potentially all) marine algae and is inferred to be an adaptation for salinity-tolerance. See this open-access article for further information.



Figure 2.4.3.3.3: The red algae are a fascinating group that have evolved a diversity of morphologies and strategies. This red alga, *Asterocolax gardneri*, is a parasite on other red algae. Note that it lacks the color characteristic of the *Rhodophyta*. Because it feeds off other algae, it does not need to make its own food via photosynthesis and so does not require photosynthetic pigments. Photo by Chloe and Trevor, CC-BY-NC.

Morphology

Red algae have a diverse range of morphologies. Unicellular forms may live solitarily or as colonies but, unlike other members of the Archaeplastida, lack flagella. Flagella are absent from the Rhodophyta, lost at some point in their evolutionary history. Multicellular forms can be filamentous, leafy, sheet-like, coralloid, or even crust-like (some examples in Figure 2.4.3.3.4 and Figure 2.4.3.3.5). The strange coralline red algae have calcerous deposits in the cell walls that make the thallus hard, like a coral. These can take a variety of forms and are able to live at depths other algae cannot (over 500 feet deep for some!).



Figure 2.4.3.3.4: These images are all of multicellular red algae, which can range from filamentous (first image) to "leafy" (second image, left) to sheet-like (second image, right). The red color is due to an abundance of the red pigment phycoerythrin, which gives this group red chloroplasts. First image by Melissa Ha CC-BY-NC. Second image by Maria Morrow CC-BY-NC.



Figure 2.4.3.3.5: Examples of coralline red algae.The first image shows the thallus of a *Calliarthon tuberculosum* alga that has washed up on the beach. Having lost its characteristic pink color, the white, calcerous walls are more obvious. The second photo shows a crustose coralline red alga (species unknown to the author) forming pinkish blotches on a rock. There are a pair of forceps pointing at one of these blotches. First photo by Jennifer Rycenga, CC-BY-NC. Second photo by by Gsaunders, CC-BY-NC

Cells of multicellular species are connected via incomplete cytokinesis, resulting in **pit connections** (Figure 2.4.3.3.6).

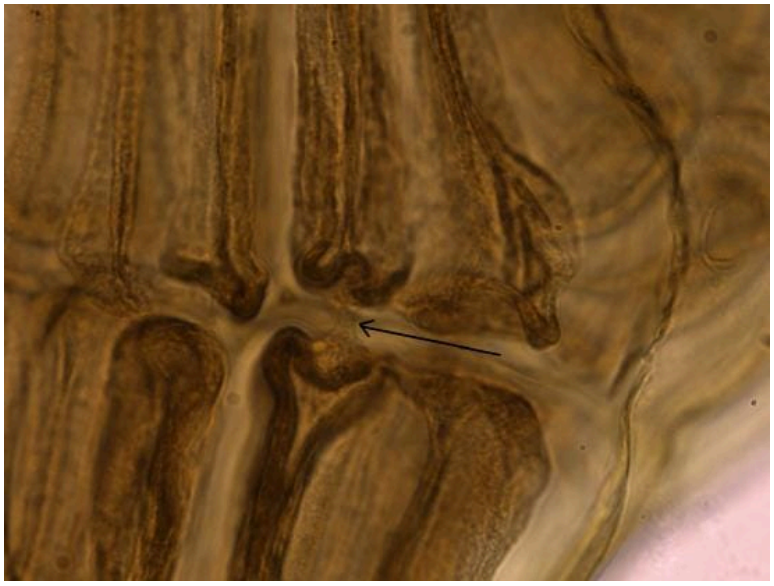


Figure 2.4.3.3.6: A pit connection between *Polysiphonia* cells. The images shows a channel (pit connection) connecting two adjacent cells, indicated by an arrow. This pit connection passes through the cell walls of both cells, as well as the middle lamellae. Photo by Maria Morrow CC-BY-NC.

Polysiphonia Life Cycle

Red algae have a haplodiplontic (**alternation of generations**) life cycle that has an extra diploid stage: the **carposporophyte**. *Polysiphonia* is the model organism for the Rhodophyta life cycle. The gametophytes of *Polysiphonia* are **isomorphic** (iso- meaning same, morph- meaning form), meaning they have the same basic morphology. Any difference you see in coloration of the images in this section is due to staining. They would all appear a deep red color in an unstained slide.



Figure 2.4.3.3.7: All stages of the *Polysiphonia* life cycle have the same basic morphology. If you were to see them without magnification, they would all look more or less like this: a small, red, finely branching thallus. The reproductive structures are used to differentiate the life stages: presence of spermatangia, cystocarps, or tetrasporangia. Photo by Gsaunders, CC-BY-NC.

Male Gametophyte

The male gametophyte has elongated structures that emerge from the tips of the thallus branches. These are **spermatangia**, where **spermatia** are produced by mitosis.



Figure 2.4.3.3.8: A *Polysiphonia* male gametophyte. In the first image, branches of the male gametophyte each terminate with several elongated structures that look almost like ears of corn. Each of these structures is a spermatangium. In the second image, a spermatangium is shown by itself, detached from the gametophyte. Cells in the spermatangum undergo mitosis to produce haploid, non-motile, unicellular gametes called spermatia. The image is not clear enough to distinguish individual spermatia. Photos by Maria Morrow, CC-BY-NC.

Female Gametophyte and Carposporophyte

The female gametophyte produces an egg that is contained within a structure called the **carpogonium**. This structure has a long, thin projection called a **trichogyne** (trich- meaning hair, -gyne meaning female). During fertilization, a spermatium fuses with the trichogyne and the nucleus of the spermatium travels down the tube to the **egg**. When the nucleus of the spermatium fuses with

the egg, a **zygote** is produced. This zygote is retained and nourished by the female gametophyte as it grows.

The globose structures you see growing from the female gametophyte thallus are called cystocarps. A **cystocarp** is composed of both female gametophyte tissue (n) and carposporophyte tissue (2n). The outer layer of the cystocarp, the **pericarp** (peri- meaning around) is derived from the female gametophyte and is haploid. The interior of the cystocarp consists of the **carposporophyte**, which is diploid, and produces structures called **carposporangia,** inside of which it produces **carpospores** by mitosis. All of these--carposporophyte, carposporangia, and carpospores--are diploid.

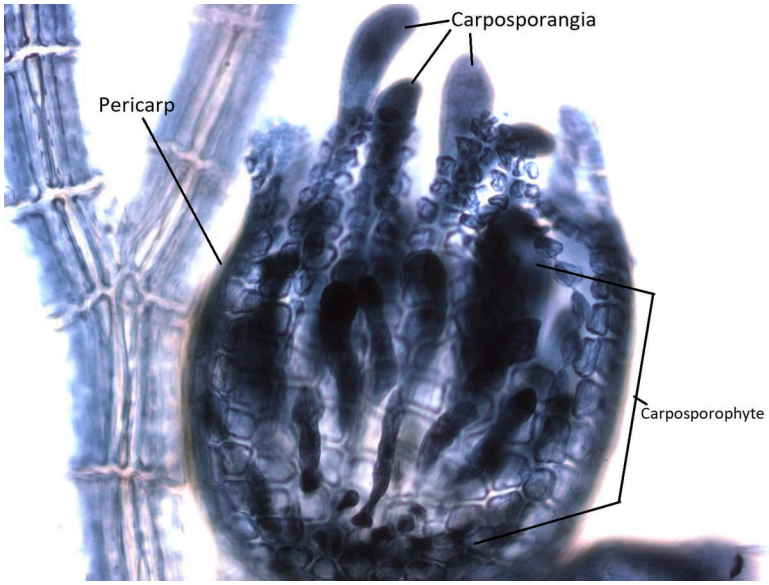


Figure 2.4.3.3.9: The image shows branches of the female gametophyte thallus on the left side. In the center, a globose cystocarp emerges from one of those branches. The cystocarp is composed of a haploid pericarp that forms the outside of the structure. The cells of the pericarp look blocky, almost scale-like. Within the pericarp, the tissues are diploid and belong to the carposporophyte. The carposporophyte is composed of many elongated carposporangia. Photos by Maria Morrow, CC-BY-NC.

Tetrasporophyte

The diploid carpospores are released into the ocean waters, where they will be carried on currents to another location. If a carpospore lands in an appropriate environment, it will grow by mitosis into a **tetrasporophyte** (2n). The tetrasporophyte produces **tetrasporangia** (2n) within the branches of the thallus. Each tetrasporangium produces four unique, haploid **tetraspores** by meiosis. Tetraspores (n) are released and will grow by mitosis into either male or female gametophytes, completing the life cycle.

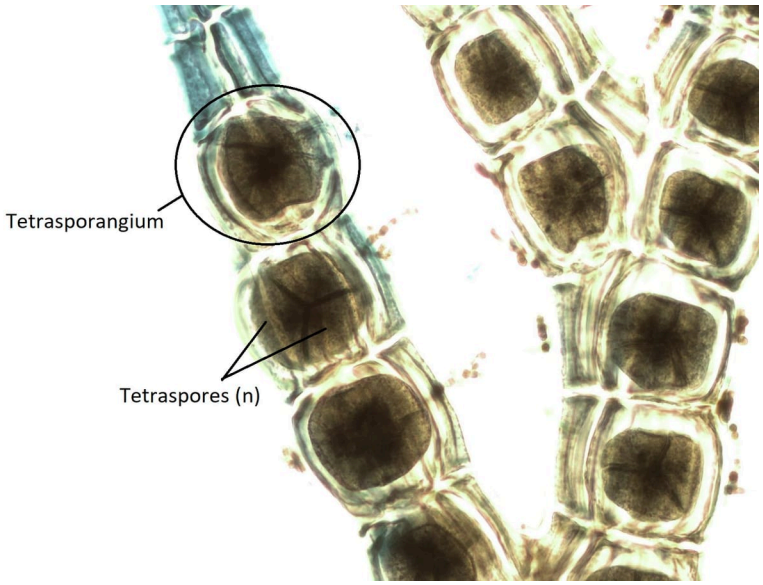


Figure 2.4.3.3.10: The image shows branches of the tetrasporophyte. Each of the compartments within the branches is filled with a globose tetrasporangium. In most of these, clear delineations can be seen where the tetrasporangium is dividing by meiosis into four distinct cells. These cells are haploid tetraspores. Photo by Maria Morrow, CC-BY-NC.

Full Life Cycle Diagram

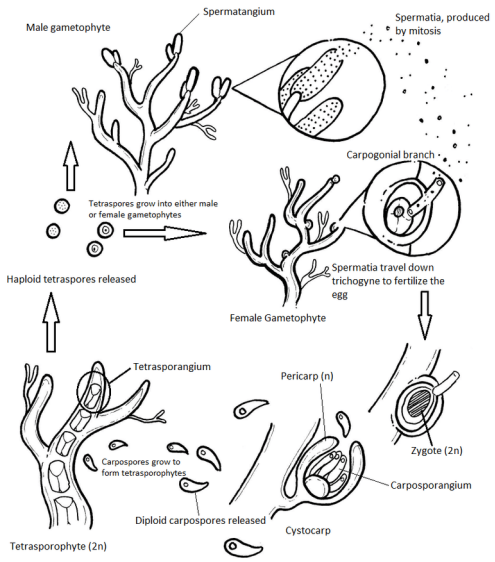


Figure 2.4.3.3.11: The alternation of generations life cycle of *Polysiphonia*. On the left side, in the center, there are four haploid tetraspores. These tetraspores grow by mitosis into haploid gametophytes, either "male" or "female". The male gametophyte produces spermatangia at the tips of its branches and these spermatangia produce haploid spermatia by mitosis. The female gametophyte produces carpogonial branches, which have an egg at the base and a long filament called a trichogyne that extends from the egg chamber. A spermatium fuses with a trichogyne and its nucleus travels down the trichogyne to fertilize the egg, making a diploid zygote. The zygote grows, still attached to the gametophyte, within a structure called the cystocarp. The cystocarp has an external layer called the pericarp that is formed from the female gametophyte's tissue (meaning it is haploid). Within the pericarp, the zygote has grown by mitosis into a carposporophyte making elongated carposporangia. Inside each carposporangium, diploid carpospores are produced by mitosis. Carpospores are released and grow by mitosis into tetrasporophytes. Within the branches of the tetrasporophyte, tetrasporangia are formed and undergo meiosis to produce four haploid tetraspores each. These tetraspores are released and we arrive back where we started. Diagram by Nikki Harris CC-BY-NC with labels added by Maria Morrow.

Summary of Characteristics for Red Algae

- Morphology: Unicellular to multicellular, no flagellated stages. Cells of multicellular species are connected via incomplete

cytokinesis, resulting in pit connections.
- Cell wall composition: Cellulose and galactans
- Chloroplasts: 2 membranes, pigments are chlorophyll a and phycobilins (primarily phycoerythrin, providing their red color)
- Storage carbohydrate: Floridean starch
- Life cycle: Alternation of generations with an extra diploid stage, the carposporophyte
- Ecology: Primarily marine (97% of species)

Green Algae

The most abundant group of algae is the green algae. The nature of the evolutionary relationships between the green algae are still up for debate. As of 2019, genetic data supports splitting the green algae into two major lineages: **chlorophytes** and **streptophytes**. The streptophytes include several lineages of green algae (such as the charophytes) and all land plants. Streptophytes and chlorophytes represent a monophyletic group called Viridiplantae (literally “green plants”). The green algae exhibit similar features to the land plants, particularly in terms of chloroplast structure. They have chlorophyll a and b, have lost phycobilins but gained carotenoids, and store carbohydrates as **starch inside plastids**. Although some of the multicellular forms are large, they never develop more than a few types of differentiated cells and their fertilized eggs do not develop into an embryo.

Green algae are an important source of food for many aquatic animals. When lakes and ponds are "fertilized" with phosphates and nitrates (e.g., from sewage and the runoff from fertilized fields and lawns), green algae often form extensive algal "blooms". Members of this group can be found in freshwater and marine habitats, and many have adapted to life on land, either inside of lichens or free-living (see Figure 2.4.3.3.12).



Figure 2.4.3.3.12: *Trentepohlia* is a genus of green algae that is found in terrestrial environments. It forms fluffy orange colonies on trees and is a photobiont in many lichens. One might not know they were looking at a green algae, due to the orange pigmentation. However, green algae have carotenoids. These terrestrial green algae produce an abundance of carotenoids, perhaps for protection from sun damage. Photo by Scott Loarie, CC0.

Selection Pressures and Drivers

1. **Sun Damage**. Green algae represent a diverse group of organisms with diverse life history traits, many of which are shared with land plants. The development of **carotenoids**-- yellow, orange, and red pigments that act in both light harvesting and sun protection--offers this group increased access to sunlight while simultaneously protecting against UV damage. UV rays do not penetrate very far into the water column, so organisms moving into shallower waters or terrestrial environments would need to deal with this new challenge. Many terrestrial species of green algae appear orange, rather than green, due to the production of large amounts of carotenoids.

Morphology

These algae exhibit great diversity of form and function. Similar to red algae, green algae can be unicellular or multicellular. Many unicellular species form colonies and some green algae exist as large, multinucleate, single cells. Green algae primarily inhabit freshwater and damp soil, and are a common component of plankton. *Chlamydomonas* is a simple, unicellular chlorophyte with a pear-shaped morphology and two opposing, anterior flagella that guide it toward light sensed by its eyespot (Figure 2.4.3.3.13). More complex species exhibit haploid gametes and spores that resemble *Chlamydomonas*.

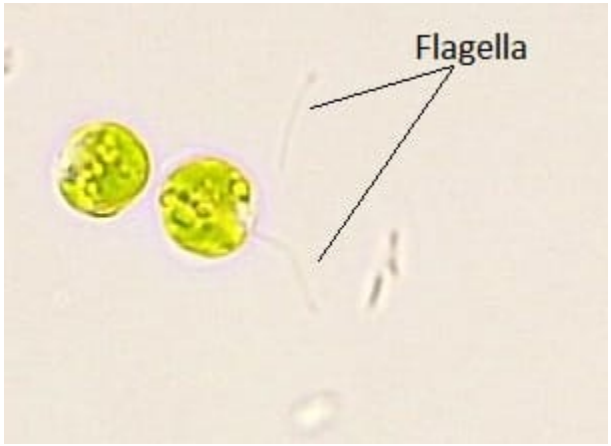


Figure 2.4.3.3.13: This image shows two unicellular green algae from the genus *Chlamydomonas*. They appear green due to the loss of phycobilins and evolution of chlorophyll b. They each have two whiplash flagella, though these are only visible on one of them in the picture. Photo by Melissa Ha, CC-BY-NC.

The alga *Volvox* is one of a colonial organism, which behaves in some ways like a collection of individual cells, but in other ways like the specialized cells of a multicellular organism (Figure 2.4.3.3.14). *Volvox* colonies contain 500 to 60,000 cells, each with two flagella, contained within a hollow, spherical matrix composed of a gelatinous glycoprotein secretion. Individual *Volvox* cells move in a coordinated fashion and are interconnected by cytoplasmic bridges. Only a few of the cells reproduce to create daughter colonies, an example of basic cell specialization in this organism.



Figure 2.4.3.3.14: *Volvox aureus* is a green alga in the supergroup Archaeplastida. This species exists as a colony, consisting of cells immersed in a gel-like matrix and intertwined with each other via hair-like cytoplasmic extensions. Descriptive text: The micrograph on the left shows a sphere about 400 microns across with round green cells about 50 microns across inside. The middle micrograph shows a similar view at higher magnification. The micrograph on the right shows a broken sphere that has released some of the cells, while other cells remain inside. (credit: Dr. Ralf Wagner)

Volvox can reproduce both asexually and sexually. In asexual reproduction, the gonidia develop into new organisms that break out of the parent (which then dies). In sexual reproduction, the presence of an inducing chemical causes the following:

- The gonidia of the males to develop into clusters of sperm.
- The gonidia of the females to develop into new spheres each of whose own gonidia develops into a pair of eggs.

- The sperm break out of the male parent and swim to the female where they fertilize her eggs.
- The zygotes form a resting stage that enables *Volvox* to survive harsh conditions (Figure 2.4.3.3.15).

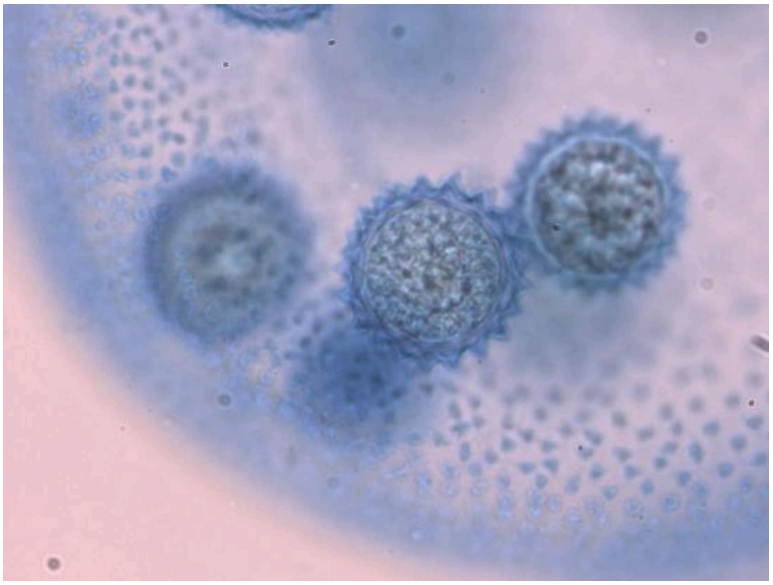


Figure 2.4.3.3.15: Volvox thick-walled, desiccation-resistant zygote. There is a larger sphere composed of many individuals (shown as blue dots). Within that larger sphere, there are several smaller spheres with thick, warty walls. Photo by Maria Morrow, CC-BY-NC.

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 2.4.3.3.1: This video shows how sexual reproduction occurs in the colonial green alga *Volvox*. Sourced from YouTube.

The genome of *Volvox carteri* consists of 14,560 protein-encoding genes - only 4 more genes than in the single-celled *Chlamydomonas reinhardtii*! Most of its genes are also found in *Chlamydomonas*. The few that are not encode the proteins needed to form the massive extracellular matrix of *Volvox*.

Species in the genus *Caulerpa* exhibit flattened fern-like foliage and can reach lengths of 3 meters (Figure 2.4.3.3.16). *Caulerpa* species undergo nuclear division, but their cells do not complete cytokinesis, remaining instead as massive and elaborate single cells.



Figure 2.4.3.3.16: Caulerpa taxifolia is a chlorophyte consisting of a single cell containing potentially thousands of nuclei, much like a plasmodial slime mold. (credit: NOAA)

True multicellular organisms, such as the sea lettuce, *Ulva*, are also represented among the green algae (Figure 2.4.3.3.17 and Figure 2.4.3.3.18).

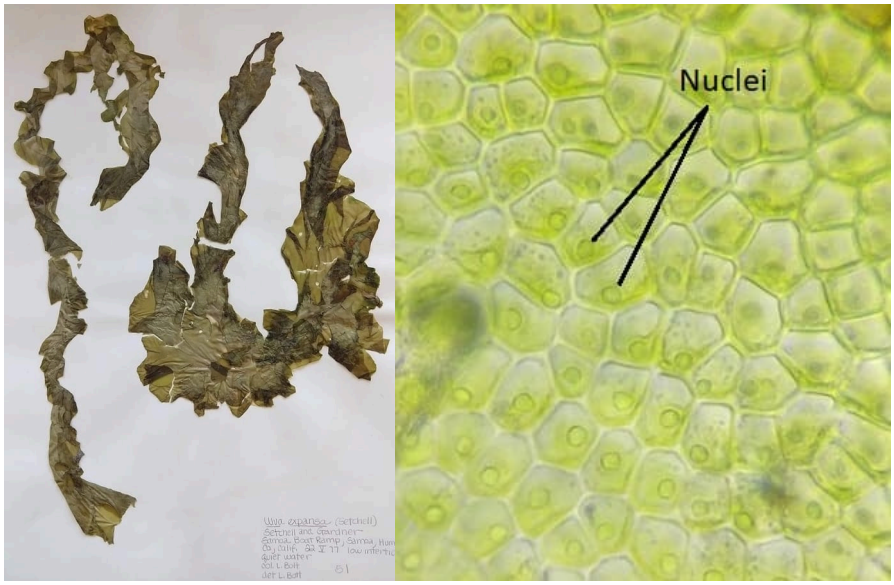


Figure 2.4.3.3.17: Ulva is a genus of multicellular marine green algae that forms flat sheets of cells. In the image on the left, there is a pressed sample of an *Ulva expansa* thallus that is serving as an herbarium specimen. In the image on the right, a piece of an *Ulva* thallus is being viewed through a microscope. Each cell contains green chloroplasts and a large nucleus, two of which are labeled in the image. Photos by Maria Morrow, CC-BY-NC.



Figure 2.4.3.3.18: Chaetomorpha coliformis, a marine green alga formed from chains of cylindrical cells (commonly called sea emeralds). Photo by Svenjah Heesch, (CC-BY-NC).

Spirogyra Life Cycle

Though green algae display a diversity of life cycles, many have a haplontic life cycle. A model organism for the green algae is *Spirogyra* (Figure 2.4.3.3.19). *Spirogyra* is a unicellular green algae that grows in long, filamentous colonies, making it appear to be a multicellular organism. Even though it is technically unicellular, its colonial nature allows us to classify its life cycle as haplontic. In the haploid vegetative cells of the colony, the chloroplasts are arranged in spirals, containing darkened regions called **pyrenoids** where carbon fixation happens. Each haploid cell in the filament is an individual, which makes sexual reproduction between colonies an interesting process.

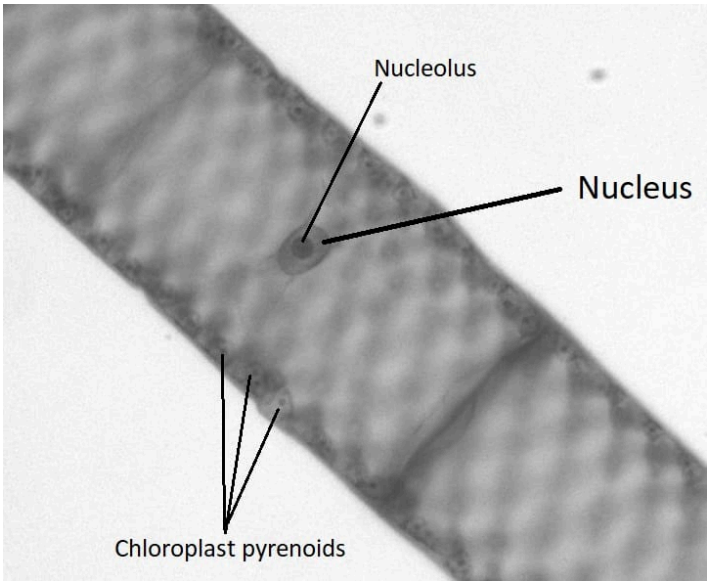


Figure 2.4.3.3.19: A vegetative cell in a *Spirogyra* colony. The nucleus is visible in the center of the cell, including a large, dark nucleolus. The chloroplasts are arranged in spirals around the cell and have dark regions called pyrenoids where carbon dioxide is fixed. Photo by Maria Morrow, CC-BY-NC.

When two colonies of *Spirogyra* meet that are of a complementary mating type (+/-), sexual reproduction occurs. The two colonies align, each cell across from a complementary cell on the other filament. A **conjugation tube** extends from each cell in one colony (Figure 2.4.3.3.20), inducing formation of a tube on the cells in the other colony. The conjugation tubes from each colony fuse together.

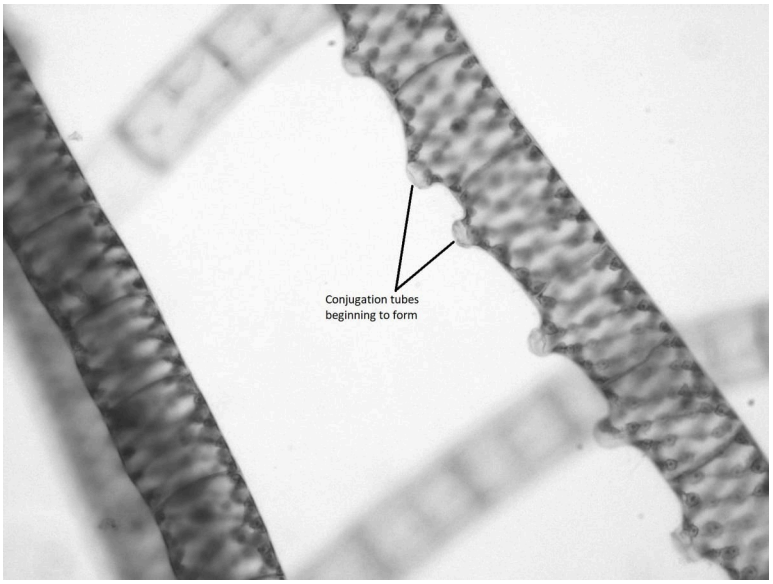


Figure 2.4.3.3.20: Spirogyra forming conjugation tubes. There are two vegetative colonies that are about to interact. The colony on the right has chemically sensed the presence of the colony on the right and has started to grow projections in the cell walls of each cell in the colony, extending them toward the other colony. These are the beginnings of conjugation tubes. Photo by Maria Morrow, CC-BY-NC.

The contents of one cell will move through the conjugation tube and fuse with the contents of the complementary cell, resulting in a diploid **zygote** (Figure 2.4.3.3.21). The zygote appears as a large, egg-like structure contained within the complementary cell. It has a thick wall that provides resistance to desiccation and cold, allowing colonies of *Spirogyra* to overwinter, when needed. The other colony is now a filament of empty cells that will be broken down by some decomposer. When conditions are right, the zygote undergoes meiosis to produce another vegetative colony of haploid cells.

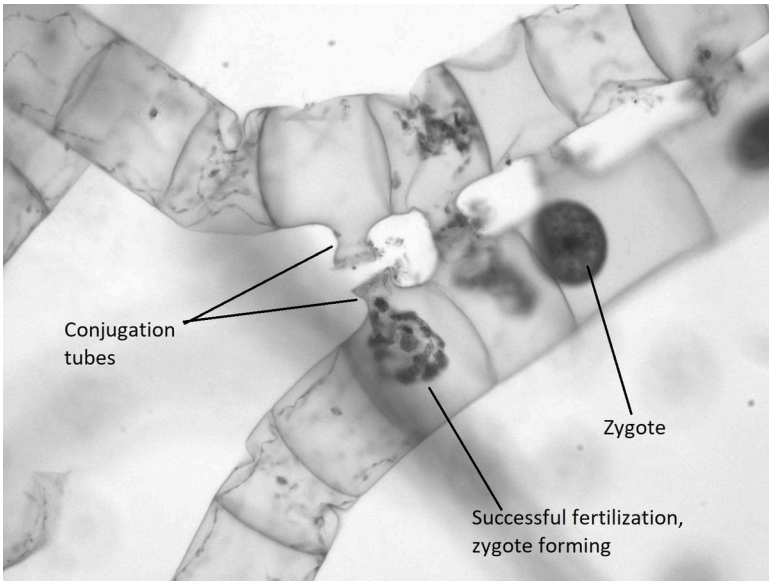


Figure 2.4.3.3.21: Cells in various stages of conjugation. Of the cells that have formed conjugation tubes and connected, the one farthest to the left has just recently finished the transfer and fusion of its cytoplasm, but the zygote hasn't fully formed yet. In the cell on the far right, there is a fully formed zygote. It is dark in color and has thick walls. The chloroplasts are not individually distinguishable within it. Photo by Maria Morrow, CC-BY-NC.

Full Life Cycle Diagram

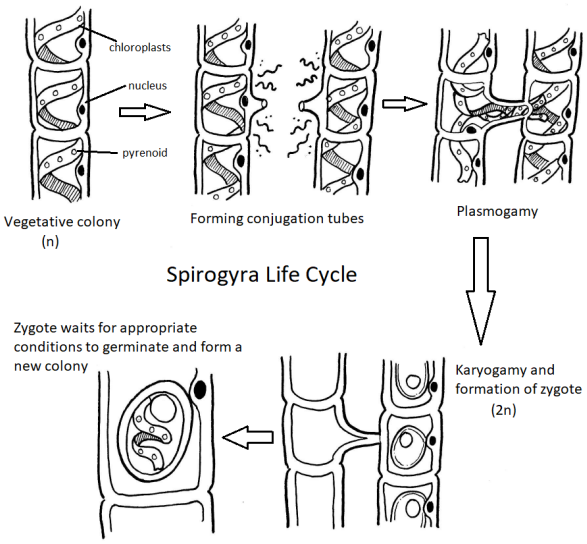


Figure 2.4.3.3.22: The haplontic life cycle of *Spirogyra*. Starting from the upper left corner and moving right, there is a single haploid vegetative colony of *Spirogyra*. The chloroplasts are drawn in as a single ribbon with circles representing pyrenoids. Each cell has a large, dark nucleus. Moving to the right, two colonies of complementary mating types begin to interact with each other through chemical signals and start forming conjugation tubes. In the next frame, the conjugation tubes have connected and the contents of one cell begins to transfer through the conjugation tube into a cell in the other colony. This is plasmogamy. Karyogamy occurs when the two nuclei fuse together and the diploid zygote is formed. This zygote waits for appropriate conditions to germinate, undergo meiosis, and form a new haploid colony. Diagram by Nikki Harris, CC BY-NC with labels added by Maria Morrow.

Summary of Characteristics for Green Algae

- Morphology: Unicellular to multicellular; two whiplash flagella on motile cells
- Cell wall composition: Cellulose
- Chloroplasts: 2 membranes, pigments are chlorophyll a, chlorophyll b, and carotenoids
- Storage carbohydrate: Starch
- Life cycle: Varies, but primarily haplontic. Some marine species have alternation of generations.
- Ecology: Freshwater, marine, and terrestrial species

Summary

Glaucophytes, red algae, and green algae are part of the Archaeplastida. These organisms are descended from the same primary endosymbiosis event. Glaucophytes are thought to be one of the earliest lineages to diverge due to the presence of remnant peptidoglycan between the membranes of its chloroplast-like cyanelles. Unsurprisingly, glaucophytes and red algae share the same pigments as Cyanobacteria.

Red algae (phylum Rhodophyta) are united by several synapomorphies (shared derived characteristics). They lack flagella, have pit connections between cells, and store carbohydrates as Floridean starch. The sulfated galactans in their cell walls allows them increased fitness in marine environments, while the pigment phycoerythrin allows them to photosynthesize deeper in the water column. They have an alternation of generations life cycle with an extra diploid phase, the carposporophyte, that clones the zygote. These characteristics can be connected to the environmental stressors presented by the marine habitats most red algae are found in.

Green algae represent several distinct lineages. Like plants, they store carbohydrates as starch within their plastids and have the pigments chlorophyll a and b, as well as carotenoids. Organisms in this group have haplontic (e.g. Spirogyra) or haplodiplontic (e.g. Ulva) life cycles. Many green algae are unicellular, forming complex colonies. Green algae can be found in marine, freshwater, and terrestrial environments (including within lichens!).

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2.4.4: Chapter Summary

Protists are an artificial grouping representing all eukaryotic organisms that aren't plants, animals, or fungi. Because of this, the life history traits of protists span the breadth of what is possible. In this book, protists have been divided into heterotrophs and photoautotrophs. The heterotrophic protists use glycogen as a storage carbohydrate, have cellulose in their cell walls (when present), and many have a diplontic life cycle. Despite these latter two traits, they were all formerly classified as fungi. Photoautotrophic protists are the result of endosymbiotic events (Figure 2.4.4.1). One lineage, including the diatoms and brown algae, derived from a secondary endosymbiotic event within the heterokonts. A second lineage, including the glaucophytes, red algae, and green algae, was derived from a primary endosymbiotic event. This latter lineage includes the ancestors of all land plants.

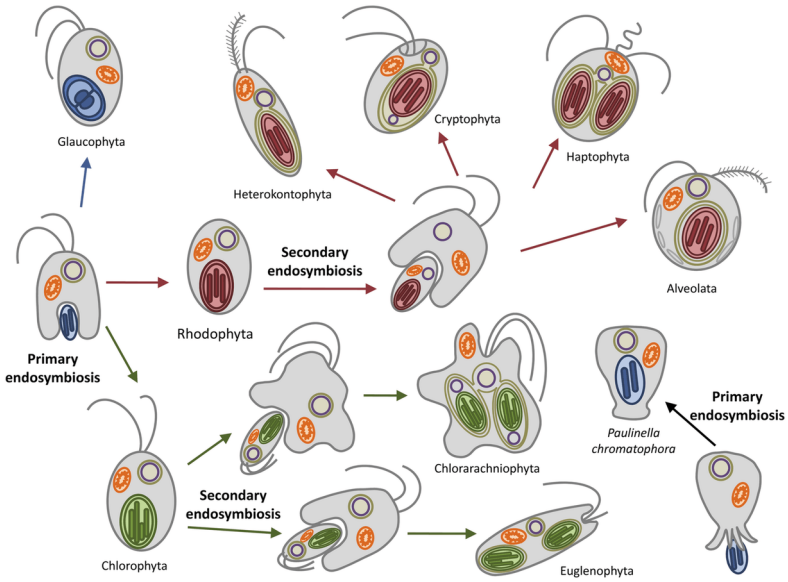


Figure 2.4.4.1: Endosymbiosis presents a complicated history for photosynthetic organisms. This diagram shows three lineages deriving from one primary endosymbiotic event (Glaucophyta, Rhodophyta, and Chlorophyta) and another unrelated lineage deriving from a separate primary endosymbiosis (*Paulinella chromatophora*). Secondary endosymbiosis occurs multiple times in this diagram. Involving a red alga, it leads to Heterokontophyta (heterokonts), Cryptophyta, Haptophyta, and Alveolata. Involving a green alga, there are two separate lineages, one leading to Euglenophyta and a second leading to Chlorarachniophyta. Diagram by Fabio Facchinelli, Andreas P. M. Weber, CC BY 3.0, via Wikimedia Commons.

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

- Explain how organisms were originally classified under Protista.
- Describe the diversity of metabolic strategies and other life history traits within this artificial group.
- Identify evolutionary relationships between "protists" using a phylogenetic tree.
- Differentiate between the three major groups of slime molds.
- Differentiate between slime molds, fungi, and plants.
- Identify structures and phases in the myxomycete life cycle and know their ploidy.
- Compare and contrast oomycetes with plants and fungi.
- Explain some of the roles oomycetes have in both terrestrial and aquatic ecosystems.
- Identify structures in the *Saprolegnia* life cycle and know their ploidy.
- Explore some of the ecological roles of dinoflagellates.
- Describe the symbiosis between corals and zooxanthellae.
- Explain what happens in a red tide.
- Use life history, morphology, and cellular components to identify brown algae.
- Identify the components of a kelp thallus.
- Identify structures and events in the *Fucus* life cycle and know their ploidy.

- Identify structures and events in the *Laminaria* life cycle and know their ploidy.
- Use life history, morphology, and cellular components to identify diatoms.
- Classify diatoms based on symmetry and ecology.
- Describe sexual and asexual reproduction in diatoms.
- Distinguish between different groups of algae using life cycle, morphological features, and cellular composition.
- Connect adaptations in the red and green algae to habitat characteristics and ecology.
- Identify structures and phases in the *Polysiphonia* and *Spirogyra* life cycles; know the ploidy of these structures.

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2.5: EARLY LAND PLANTS

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

2.5.1: Introduction to Early Land Plants

2.5.2: Bryophytes

2.5.2.1: Anthocerotophyta

2.5.2.2: Marchantiophyta

2.5.2.3: Bryophyta

2.5.3: Seedless Vascular Plants

2.5.3.1: Lycopodiopsida

2.5.3.2: Polypodiopsida

2.5.4: Chapter Summary

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2.5.1: Introduction to Early Land Plants

Learning Objectives

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

Land Plants

Land plants are sometimes referred to as “embryophytes” due to the evolution of the **embryo**, a zygote that is retained and nourished by the female gametophyte as it grows. Embryophytes share many common features, most corresponding to the selective pressures from the initial movement onto land. The embryo is one of these, providing higher likelihood of success for offspring in a new, harsh environment. In addition to the embryo, all plants have the same basic life cycle: **alternation of generations** (Figure 2.5.1.1). Much like the marine algae, the first plants were living in an environment where they needed to increase their chances of reproductive events. Multicellular stages on both sides of the life cycle increases the number of reproductive propagules. All plants are also **multicellular,** with **tissues** and **multicellular gametangia**.

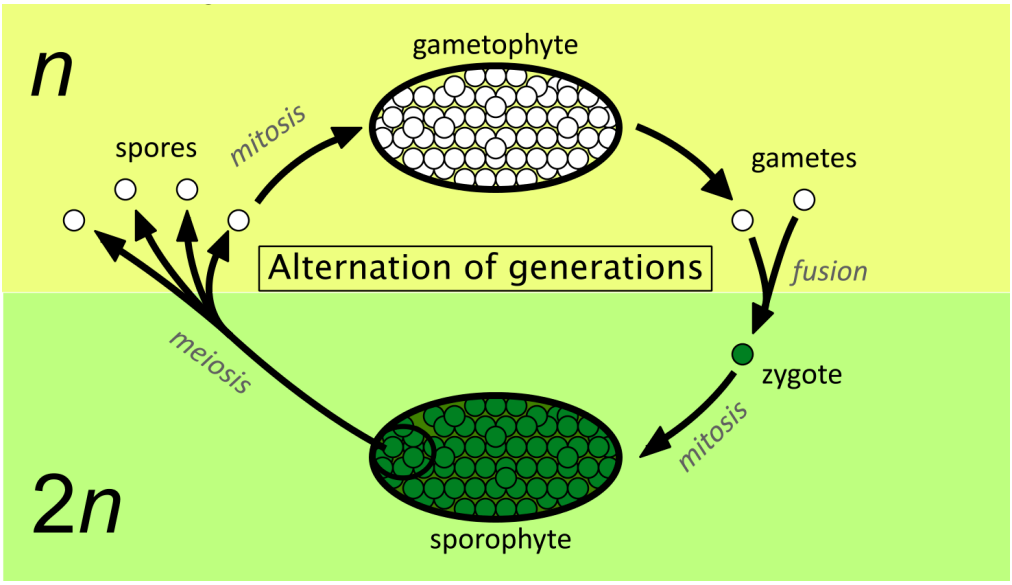


Figure 2.5.1.1: A generalized life cycle for plants. Alternation of generation involves two multicellular individuals. The top half is haploid and contains the spores, gametophyte, and gametes. The bottom half is diploid and contains the zygote and sporophyte. The multicellular haploid (n) individual is called the **gametophyte**. The gametophyte produces structures called **gametangia** where haploid **gametes** are produced by mitosis. Gametes do not grow, but instead must fuse together to form a diploid (2n) **zygote**. In plants, the zygote is retained on the megagametophyte as an **embryo**, where grows by mitosis into a multicellular diploid individual, the **sporophyte**. The sporophyte makes **sporangia** in which meiosis takes place, producing haploid **spores**. These spores are released and can grow by mitosis into haploid gametophytes. Diagram by Peter coxhead / derivative work: Peter coxhead, Public domain, via Wikimedia Commons.

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

Much like their green algal predecessors, plants store their carbohydrates as starch inside plastids, plastids with two membranes (the result of primary endosymbiosis), cell walls containing cellulose, and have the pigments chlorophyll a, chlorophyll b, and carotenoids. For this reason, along with genetic sequencing, land plants and green algae are grouped together in the Viridiplantae (Figure 2.5.1.2).

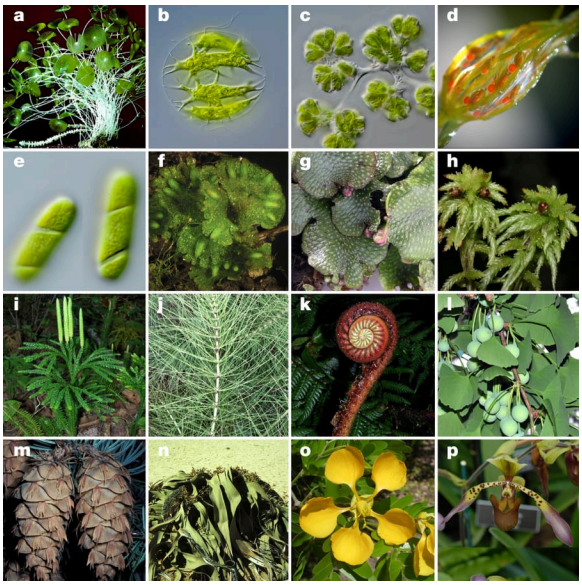


Figure 2.5.1.2: This figure represents the lineages contained within the Viridiplantae. It was retrieved from an open-access paper analyzing over 1,000 transcriptomes to assess the relationships between these lineages. The original caption follows: "**a**–**e**, Green algae. **a**, *Acetabularia* sp. (Ulvophyceae). **b**, *Stephanosphaera pluvialis* (Chlorophyceae). **c**, *Botryococcus* sp. (Trebouxiophyceae). **d**, *Chara* sp. (Charophyceae). **e**, '*Spirotaenia*' sp. (taxonomy under review) (Zygnematophyceae). **f**–**p**, Land plants. **f**, *Notothylas orbicularis* (Anthocerotophyta (hornwort)). **g**, *Conocephalum conicum* (Marchantiophyta (thalloid liverwort)). **h**, *Sphagnum* sp. (Bryophyta (moss)). **i**, *Dendrolycopodium obscurum* (Lycopodiophyta (club moss)). **j**, *Equisetum telmateia* (Polypodiopsida, Equisetidae (horsetail)). **k**, *Parablechnum schiedeanum* (Polypodiopsida, Polypodiidae (leptosporangiate fern)). **l**, *Ginkgo biloba* (Ginkgophyta). **m**, *Pseudotsuga menziesii* (Pinophyta (conifer)). **n**, *Welwitschia mirabilis* (Gnetophyta). **o**, *Bulnesia arborea* (Angiospermae, eudicot, rosid). **p**, *Paphiopedilum lowii* (Angiospermae, monocot, orchid). **a**, Photograph reproduced with permission of Thieme Verlag, Stuttgart[66]. **b**–**e**, Photographs courtesy of M. Melkonian. **f**–**j**, **l**–**n**, **p**, Photographs courtesy of D.W.S. **k**, Photograph courtesy of R. Moran. **o**, Photograph courtesy of W. Judd." One Thousand Plant Transcriptomes Initiative., Leebens-Mack, J.H., Barker, M.S. *et al*. One thousand plant transcriptomes and the phylogenomics of green plants. *Nature* **574,** 679–685 (2019).

The First Land Plants

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

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

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

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2.5.2: BRYOPHYTES

Learning Objectives

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

Introduction

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

Characteristics of Bryophytes

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



Figure 2.5.2.1: A thalloid liverwort gametophyte demonstrating the prostrate posture typical of bryophytes. It grows closely appressed to the surface of these rocks, sinking into the crevices to follow the path of the water. Photo retrieved from iNaturalist.org, posted by Alex Bairstow, CC-BY-NC.

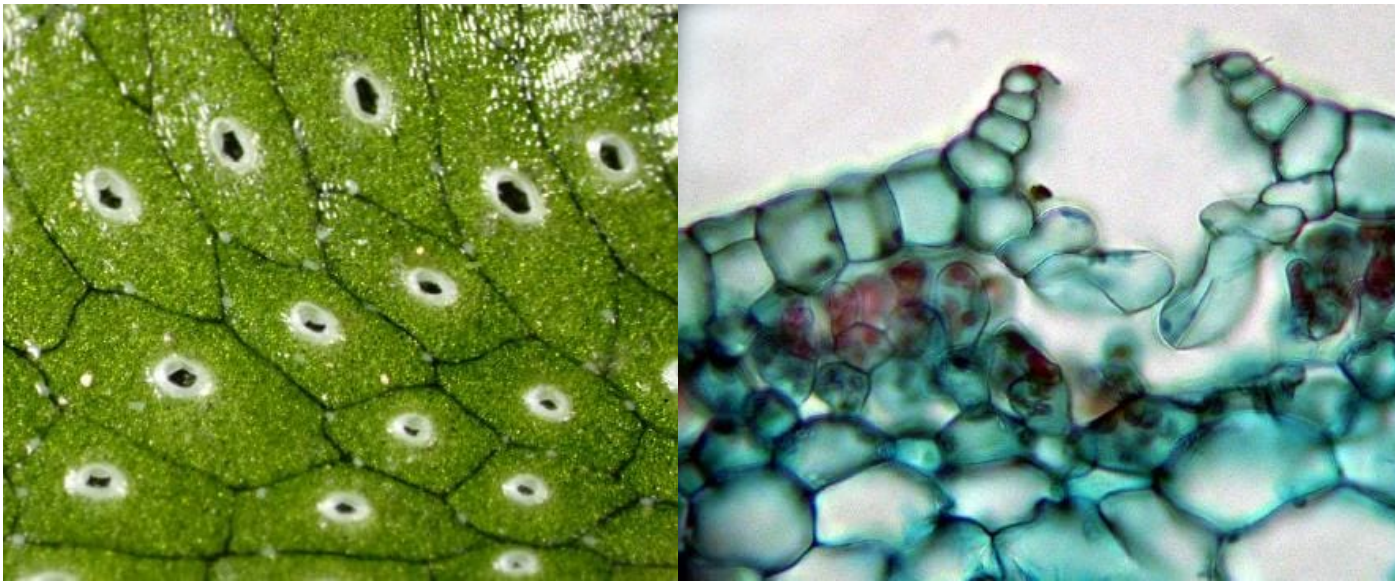


Figure 2.5.2.2: Simple pores on a thalloid liverwort. In the first photo, one simple pore can be seen in each section of the thallus, surrounded by a ring of lighter coloration. In the second photo, a cross section through a simple pore shows the smaller cells composing the epidermal layer surrounding the pore, as well as the lack of guard cells. Photos by George Shepherd, CC BY-NC-SA.

Selection Pressures and Drivers

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

1. **Sun exposure**. Sunlight provides the power that drives our biosphere, but some wavelengths of sunlight can be damaging to cellular structure and even DNA. High frequency wavelengths, such as ultraviolet (UV), X-rays, and gamma rays can penetrate outer protective layers like skin, through cell membranes, and causing damage to DNA, proteins, and other biomolecules. Fortunately for organisms on Earth, almost all of these wavelengths are filtered by the atmosphere before they reach us, though some UV rays still make it through. These last UV rays are filtered out for aquatic organisms, but terrestrial organisms need adaptations to protect against UV radiation. Humans have skin with melanin pigments. Terrestrial plants have an **epidermis** and **carotenoid pigments**.
2. **Desiccation**. Transitioning from a completely aquatic environment to a terrestrial one leads to challenges of drying out, also known as desiccation. Temperatures are more extreme outside of the water and evaporation from tissues into the relatively dry air is constant. Terrestrial plants quickly adapted a waxy covering on the epidermis, called a **cuticle**. This water-tight covering required the evolution of **simple pores**, and eventually **stomata**, to allow gas exchange with the outer environment. Because these plants lack vascular tissue, water can only be transported around the organism via osmosis. Thus, these plants must keep all tissues close to water access.
3. **Lack of a soil environment**. The first organisms to move onto land would have found a relatively barren, rocky landscape. Soils did not yet exist. The rocky substrate experienced physical weathering from rain and wind that would help break it down. Chemical weathering through acidic rain or the interaction of water with compounds in the rock could also assist in breakdown. However, up to this point, contributions from organic matter would be minimal. Bryophytes lack true roots, instead producing structures called **rhizoids** whose function is anchorage (Figure 2.5.2.3). There are genes present in bryophytes, as well as some fossil evidence, that indicate bryophytes likely had mycorrhizal relationships with fungi that helped them acquire nutrients in this new landscape.



Figure 2.5.2.3: Root-like projections emerge from gametophytes. In the image, these are shown as transparent filaments extendending from the underside of a green, thalloid gametophyte. Photo by Yuval, CC-BY-NC.

Bryophyte Lineages

This evolutionary group includes liverworts (phylum Marchantiophyta, Figure 2.5.2.4), mosses (phylum Bryophyta, Figure 2.5.2.5), and hornworts (phylum Anthocerophyta, Figure 2.5.2.6). There are approximately 23,000 known extant species, most of these belonging to the mosses. As of 2019, much is unresolved on the early lineages of plants and who was first on land. Recent genetic analyses interpret bryophytes as being monophyletic, all deriving from a common ancestor that branched from the main line of plants. Read this open-access paper for further information.



Figure 2.5.2.4: Liverworts, phylum Marchantiophyta, can be either leafy (first image) or thalloid (second image). Thalloid liverworts have no leaf-like structures, and look like a green, rubbery mat. Photo on the left by Maria Morrow, CC BY-NC. Photo on the right by Иван Матершев, CC-BY-NC-SA.



Figure 2.5.2.5: Mosses, phylum Bryophyta, are always leafy. Photo by Maria Morrow CC BY-NC.



Figure 2.5.2.6: Hornworts, phylum Anthoceratophyta, are always thalloid. Male gametophyte of *Phaeoceros laevis*. Photo by georgeg, CC-BY-NC.

- Topic hierarchy

2.5.2.1: Anthocerotophyta

2.5.2.2: Marchantiophyta

2.5.2.3: Bryophyta

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2.5.2.1: Anthocerotophyta

Learning Objectives

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

Hornworts, Phylum Anthocerotophyta

The name Anthocerotophyta means 'horn flower plant'. These strange plants, called the hornworts, get their name from the horn-like sporophytes they produce. Hornworts have a flattened thalloid gametophyte, out of which grow their long photosynthetic sporophytes (Figure 2.5.2.1.1), composed of a **sporangium** with a **columella** and **pseudoelaters**. The sporophyte grows from a basal meristem, with the oldest tissues at the apex. When spores have matured, the sporangium dries and dehisces, twisting open to release spores. The long, multicellular pseudoelaters (true elaters are a single cell) within the sporangium assist in dispersing the spores. Hornworts are somewhat rare and quite small, and they prefer shady and wet places. They are often found growing on the muddy sides of waterways, from small ditches to larger creeks.

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



Figure 2.5.2.1.1: Hornworts growing in a cluster. The gametophytes are the leafy green material growing closer to the surface. The sporophytes are the emergent structures. The appearance of the sporophytes is what gives the hornworts their name. Photo by Maria Morrow, CC-BY-NC.

Gametophyte Morphology

Hornwort gametophytes are exclusively thalloid, often with compartments of mutualistic cyanobacteria from the genus *Nostoc*. Cells within the gametophyte are **monoplastidic** (Figure 2.5.2.1.2), containing one large chloroplast in each cell. Similar to the green algae, hornwort chloroplasts contain a **pyrenoid** where starch storage is concentrated. On the exterior of the thallus, **simple pores** allow for gas exchange. Unlike stomata, simple pores have no guard cells, meaning they are permanently open. Some hornwort species house colonies of *Nostoc* within the gametophyte thallus, providing access to nitrogen fixed by the cyanobacterial colony.

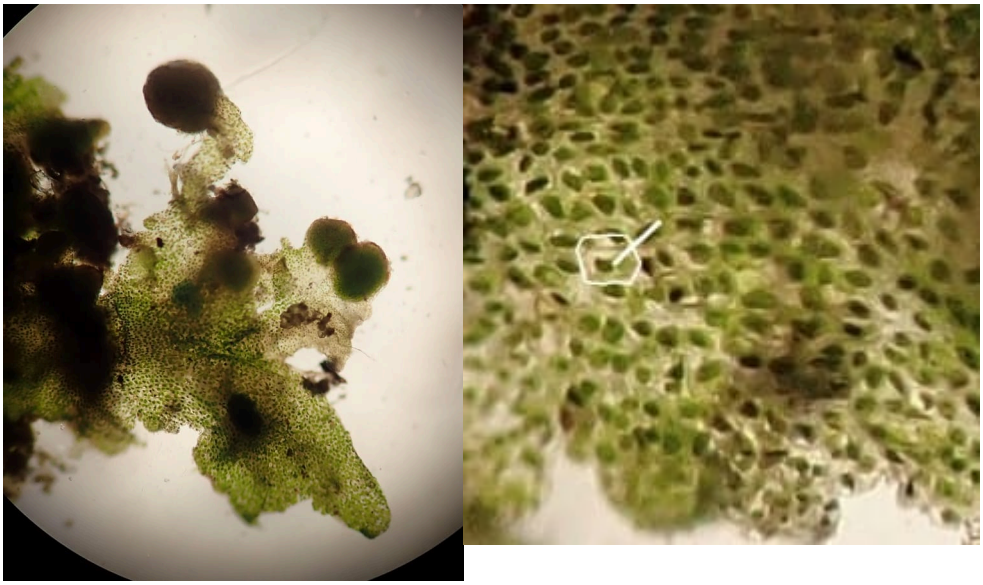


Figure 2.5.2.1.2: This image of part of a *Phaeoceros proskaueri* thallus shows the cells of the gametophyte each containing a single large plastid (monoplastidic). The second photo is a cropped view with a single cell encircled. A line indicates the single chloroplast within that cell. Photo by Amanda Heinrich, some rights reserved (CC-BY-NC).

Sporophyte Morphology

Hornwort sporophytes are comprised of a linear sporangium that lacks a seta. It grows from a **basal meristem**, meaning the cells at the apex are the oldest. When you see the sporangia mature, this becomes more obvious, as the tip dries out first and dehisces (Figure 2.5.2.1.3) to release the spores. Unlike the gametophyte, the sporophyte possesses true stomata for gas exchange, though stomata have been lost in some lineages. Notably, hornwort sporophytes are photosynthetic and capable of transferring photosynthates to the gametophyte. In other bryophyte lineages, the sporophyte is almost entirely dependent on the gametophyte for nutrition.

Within the sporgangium, there is a central columella (Figure 2.5.2.1.4) and often pseudoelaters and/or sterile cells that aid in spore dispersal by twisting when dry.

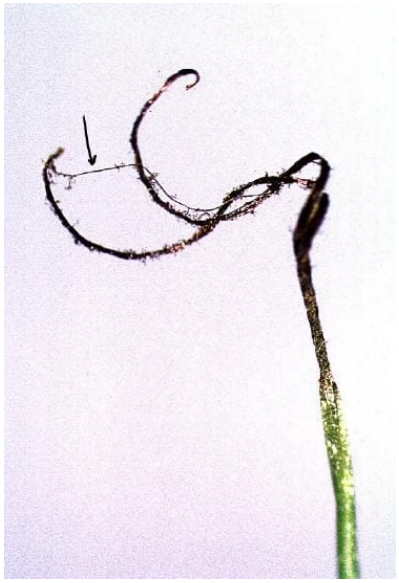


Figure 2.5.2.1.3: The sporophyte of *Phaeoceros* opens by two "valves", liberating the spores. Between the valves a structure known as the columella is found (indicated by arrow). It consists of a column of sterile tissue in the center of the spore-forming tissue. In this image, the columella is visible as a very slender, black, wire-like structure between the valves. Photo and caption text by George Shepherd, CC BY-NC-SA with arrow added by Maria Morrow. Descriptive text: The tip of the sporophyte is blackened and has split in two. There is a thin black strand emerging from the center, indicated by an arrow. The base of the sporophyte is still green.

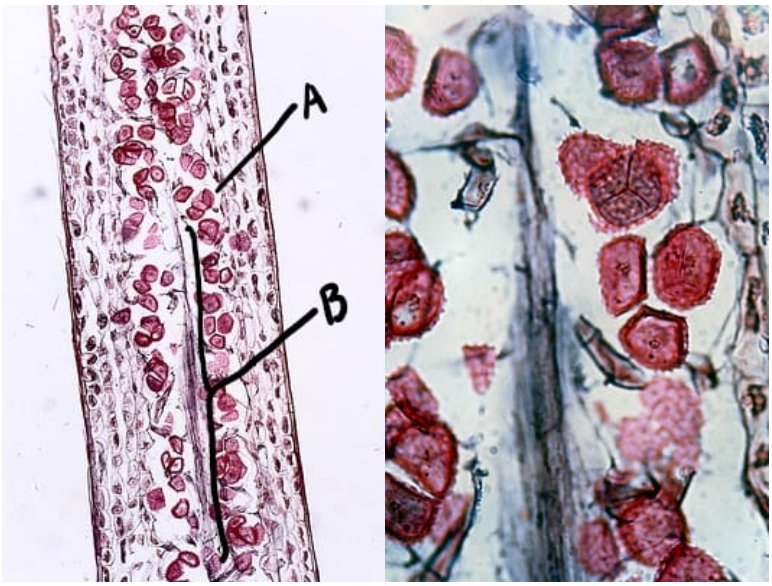


Figure 2.5.2.1.4: A cross section through an *Anthoceros* sporophyte. Spore tetrads (A) fill the sporangium and surround the central columella (B). The second photo shows the spore tetrads at a higher magnification. Photos by George Shepherd, CC BY-NC-SA with labels added by Maria Morrow.

Stomata on the sporophyte may assist in spore dispersal by allowing the sporangium to dry, providing conditions necessary for dehiscence. Figure 2.5.2.1.5 walks through the stages of sporophyte maturation, showing the appearance of the stomata at each stage.

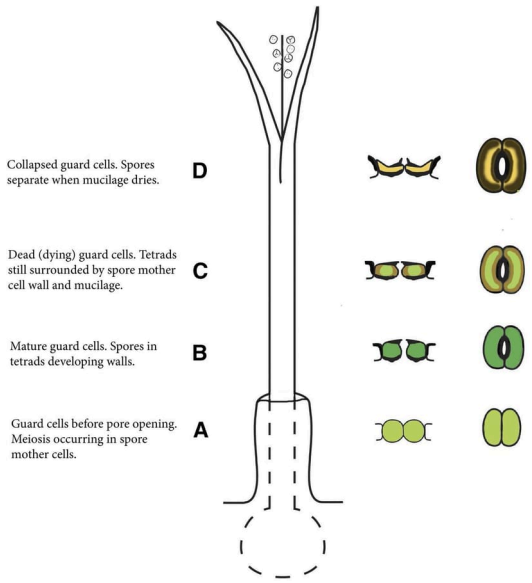


Figure 2.5.2.1.5: Diagrammatic representation of a hornwort sporophyte with progressive development and color of stomata indicated from the base upward. Once open, stomata never close, but the outer aperture increases slightly in width after guard cell collapse. The stomata color does not necessarily coincide with the overall color of the sporophyte because stomata die and collapse while the sporophyte is actively photosynthesizing. A, Developing stoma. B, Mature, living, and open stoma. C, Dead (dying) guard cells at the onset of collapse of the outer walls. D, Dead, collapsed, and slightly larger stoma. Above D, the sporophyte dries, leading to dehiscence into two valves along two parallel suture lines, mucilage dries around the spore tetrads, the spore mother cell wall adheres to the spore surfaces, and the spores separate for dispersal. Image and caption text from the open-access paper Hornwort Stomata: Architecture and Fate Shared with 400-Million-Year-Old Fossil Plants without Leaves by Karen S. Renzaglia, Juan Carlos Villarreal, Bryan T. Piatkowski, Jessica R. Lucas, Amelia Merced. Plant Physiology Jun 2017, 174 (2) 788-797.

Life Cycle

The hornwort life cycle, like all plants, is alternation of generations. The multicellular haploid stage, the gametophyte, is the longer-lived and larger phase of this life cycle. Most hornwort gametophytes are **monecious**, meaning both types of gametangia (antheridia and archegonia) are produced on the same gametophyte. The life cycle shown in Figure 2.5.2.1.6 features a monoecious gametophyte. If a hornwort is dioecious, the life cycle would have antheridia and archegonia produced on separate gametophytes and the sporophyte would grow from the gametophyte producing archegonia.

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

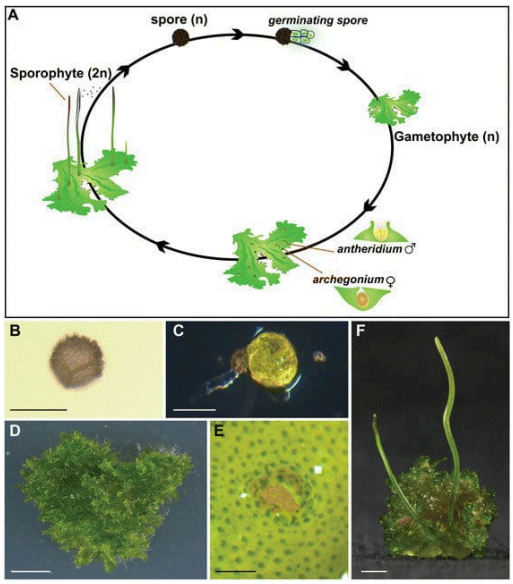


Figure 2.5.2.1.6: Life cycle of the hornwort *Anthoceros agrestis*. The life cycle of A. agrestis (A) starts with the spore (B) that germinates (C) and gives rise to the gametophyte (D). Gametophytes are monoecious and thus individual plants bear both male antheridia (E) and female archegonia. After fertilization of the egg by sperm from the antheridia, the zygote is retained within the archegonium. The resultant embryo develops into the sporophyte (F) in which spores are produced via meiosis. Scale bars = B: 40 µm; C: 100 µm; D: 2 mm; E: 200 µm; F: 2 mm. Caption text and image from Szövényi, Péter & Frangedakis, Eftychios & Ricca, Mariana & Quandt, Dietmar & Wicke, Susann & Langdale, Jane. (2015). Establishment of Anthoceros agrestis as a model species for studying the biology of hornworts. BMC Plant Biology. 15. DOI: 10.1186/s12870-015-0481-x. CC BY 4.0

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2.5.2.2: Marchantiophyta

Learning Objectives

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

Liverworts, Phylum Marchantiophyta

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

Gametophyte Morphology

There are two distinct type of liverwort gametophytes: leafy liverworts and thalloid liverworts. **Leafy liverworts** have leaves (though not true leaves, as they lack vascular tissue) without a central costa, which you will see in mosses. The leaves are arranged in a flat plane (Figure 2.5.2.2.1) with a set of smaller underleaves (Figure 2.5.2.2.2).



Figure 2.5.2.2.1: The leafy liverwort *Porella* has larger leaves running opposite each other down either side of the stem, making the liverwort look flat. The photo on the right shows a microscopic view of the leaves. Notice that there is no central rib on these leaves, which helps distinguish leafy liverworts from mosses. Photo on the left by Maria Morrow CC-BY-NC. Photo on the right by Rafael Medina, CC-BY-NC.

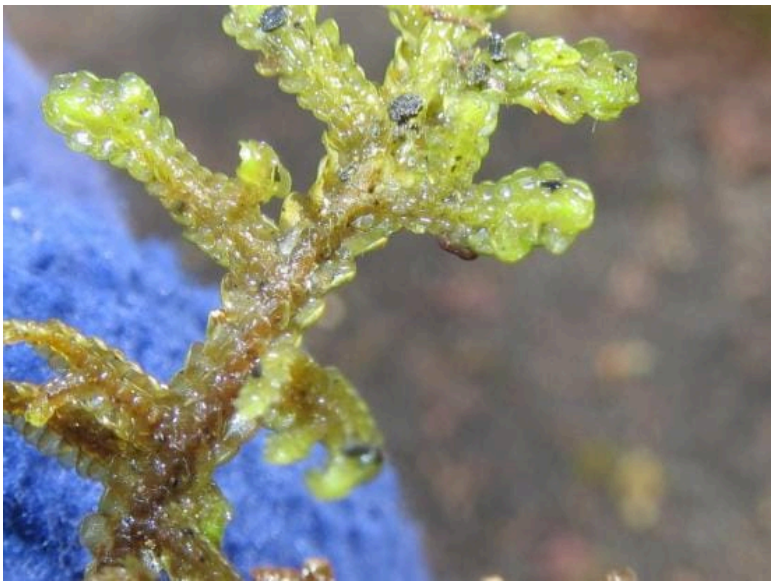


Figure 2.5.2.2.2: Another distinguishing feature of leafy liverworts are their underleaves. These are smaller, scale-like leaves that run along the center of the thallus on the underside. This image shows the underside of a *Porella navicularis* thallus covered with underleaves. Photo by Howard Bruner, CC-BY-NC.

Thalloid liverworts have no leaves and their gametophytes look more similar to hornwort gametophytes. Another similarity to hornworts is the presence of simple pores for gas exchange (no guard cells, meaning pores are permanently open). Unlike hornworts, liverwort cells have multiple chloroplasts. Rhizoids in this group are unicellular. Asexual clones, called **gemmae** (sing. gemma), are sometimes produced in structures called **gemmae cups** (Figure 2.5.2.2.3). These are haploid and genetically identical to the parent thallus.



Figure 2.5.2.2.3: The thalloid liverwort *Lunularia* has crescent-shaped gemmae cups. Several of these are present in the image above. The small green pebble-looking structures within them are asexual clones of the thallus called gemmae. Liverwort gametophytes do not have stomata. Instead, the thallus is covered in raised bumps where simple pores are located. Photo by Maria Morrow, CC-BY-NC.

The thalloid liverwort *Marchantia* has complex reproductive structures. Palm tree-like structures called **archegoniophores** are formed from the haploid gametophyte tissue. Archegonia are produced on the underside of the extending arms. When fertilized, the sporophyte will grow within the archegonium and emerge on the underside of the archegoniophore (see the right side of Figure 2.5.2.2.4). The antheridia are produced in a separate stalked structure with a flat top called an **antheridiophore** (see the left side of Figure 2.5.2.2.4). Water droplets splash onto the flat top, dispersing flagellated spores from the embedded antheridia.



Figure 2.5.2.2.4: This image shows gametangia producing structures from both gametophytes. The antheridiophore is on the left, with a flat surface that water can splash onto. This carries sperm from the embedded antheridia to other sufaces (hopefully, to an awaiting egg). On the right, there is a fertilized archegoniophore. The palmtree-like branches have lifted upward. Beneath them, yellow sporangia emerge at the tips of transparent setae. Photo by Felix Riegel, CC-BY-NC.

Sporophyte Morphology

Liverworts produce a single sporangium (also called a **capsule**) at the end of a **seta**, which is often fragile and transparent (Figure 2.5.2.2.5 – 6). The seta does not elongate until after the sporangium has formed. The sporangium dehisces, splitting into four valves (Figure 2.5.2.2.7). In thalloid liverworts, the sporophyte may emerge directly from the thallus or, as is the case with the genus *Marchantia*, from under archegoniophores. In leafy liverworts, the sporophyte often emerges laterally from the thallus. Within the sporangium, there are **elaters** (true unicellular elaters, Figure 2.5.2.2.8) that aid in spore dispersal. Unlike the hornworts, there is no columella. Unlike the mosses, the capsule lacks an operculum.

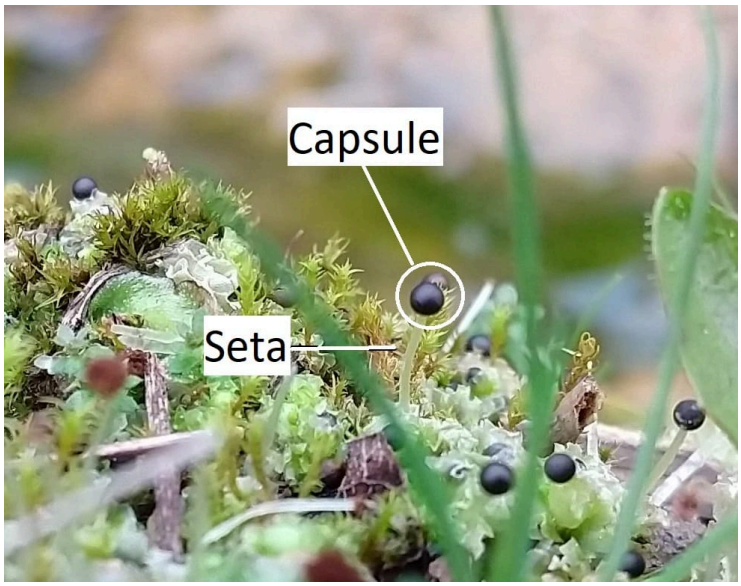


Figure 2.5.2.2.5: Liverwort sporophytes are comprised of a stalk called the seta and, at the top of the seta, a single capsule where spores are produced. In this liverwort (perhaps a *Fossombronia*), the sporophytes are short and stout with globose capsules. Photo by Maria Morrow, CC-BY-NC.

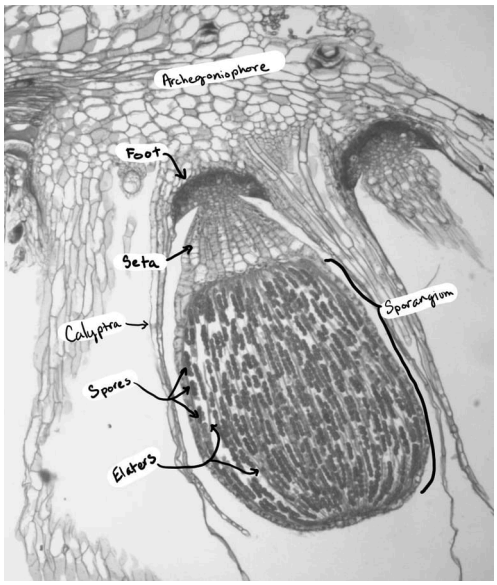


Figure 2.5.2.2.6: A sporophyte produced on the underside of an archegoniophore. It emerges upside-down and will eventually become more horizontal as the branches of the archegoniophore raise upward. The sporophyte attaches to the gametophyte at a region called the foot. It grows within the archegonium, now labeled as the calyptra. From the foot a short seta emerges, topped by a large sporangium. The sporangium is filled with rows of haploid spores produce by meiosis. Between these rows of spores, long elaters await the dehiscence of the sporangium to aid in spore dispersal. Photo by Maria Morrow, CC-BY-NC.



Figure 2.5.2.2.7: Noteroclada confluens capsule dehiscence. The capsule has split into four valves. Many elaters, as well as a few green spores, remain. Photo by George Shepherd, CC BY-NC-SA.



Figure 2.5.2.2.8: Noteroclada confluens elaters and spores. The elaters in the capsule are specialized elongated cells with a spiral thickening in their walls. In this case they are hygroscopic and twist and actively move as they dry out, helping to liberate the spores gradually. Photos and caption text by George Shepherd, CC BY-NC-SA.

Marchantia Life Cycle

Marchantia polymorpha is a thalloid liverwort with a complex life cycle (Figure 2.5.2.2.9). Asexual reproduction is accomplished through the production of haploid gemmae from the gametophyte thallus. Sexual reproduction occurs from dioecious gametophytes: archegoniophores and antheridiophores are produced on separate gametophytes. Sperm splashed from the antheridial head swim through the water with their dual flagella to reach an egg at the base of an archegonium. These archegonia are situated on the underside of the archegonial head. The diploid zygote grows within the archegonium, surrounded by its remaining tissue (the **calyptra**). As the sporangium develops, meiosis occurs simultaneously to produce haploid spores. A short seta extends to push the developed sporangium outward, lifting the arms of the archegoniophore. The sporangium dehisces into four valves, exposing the elaters to the external environment where they rapidly twist, flinging the haploid spores into the air. These haploid spores can germinate and grow into male or female gametophytes.

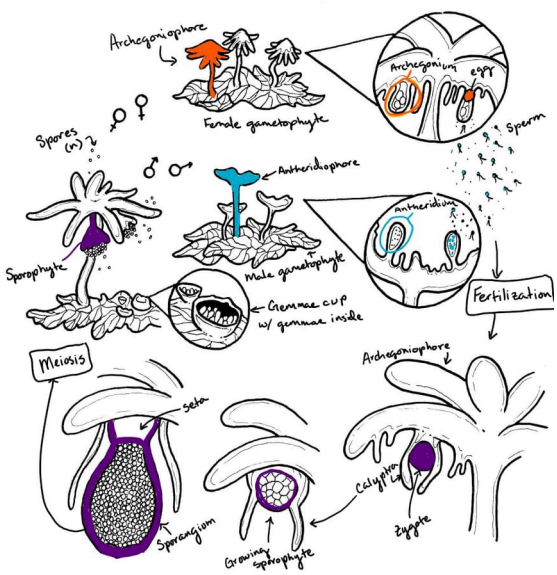


Figure 2.5.2.2.9: The *Marchantia polymorpha* life cycle. Starting with meiosis (left, center): Meiosis produces haploid spores which will grow by mitosis into either male or female gametophytes. Either of these gametophytes can produce **gemmae cups**--structures that hold asexually produced clones of the gametophyte (**gemmae**). Male gametophytes produce tall structures with flat tops called **antheriodiophores**. Many **antheridia** are embedded in the flat top of the antheridiophore. Antheridia produce biflagellate **sperm** by mitosis. Female gametophytes produce palm tree-like structures called **archegoniophores**. These archegoniophores produce **archegonia** on the underside of the 'branches', each with a single **egg** that was produced by mitosis. When water hits the flat top of the antheridiophore, it can splash sperm onto a female gametophyte. If the sperm are able to swim through the water to an egg, fertilization occurs producing a diploid **zygote**. The zygote grows into a **sporophyte** from within the archegonium. The remaining archegonial tissue is called the **calyptra**. A mature sporophyte will have a sterile stalk called a **seta** and a **sporangium** containing cells that will undergo meiosis to make haploid spores. Within the sporangium (not pictured), long twisted structures called **elaters** help disperse the spores aerially. Drawing by Nikki Harris, CC-BY-NC, with colors and labels added by Maria Morrow.

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2.5.2.3: Bryophyta

Learning Objectives

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

Mosses, Phylum Bryophyta

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



Figure 2.5.2.3.1: Gametophytes of *Dawsonia superba*, the world's tallest moss species, growing in New Zealand. Photo by Jacqui-nz, CC-BY-NC.

Sphagnum is an ancestral genus of mosses that grow in bogs and are commonly referred to as peat moss or peat, in its compressed form. They have large, empty cells (Figure 2.5.2.3.2) capable of absorbing around 20 times their dry weight in water and can exude compounds to make their environment more acidic. Because of this, and the compounds in their cell walls, the bogs where they grow have slow decomposition, allowing plant matter to accumulate and compress over time. This makes peat, a common source of fuel in higher latitudes. It's use as fuel, flavoring (the smoke), and in horticulture for its water holding capacity have contributed to its commercial importance. Many peat bogs are frozen over for most of the year, halting metabolic activity and slowing the release of methane from anaerobic decomposition. As the climate in northern latitudes warms, so do the peat bogs, increasing the release of methane.



Figure 2.5.2.3.2: Sphagnum gametophytes and cells. The gametophytes in the first photo are growing submerged in water. In the second photo, the strange, empty cells of *Sphagnum* leaves have algae growing within them! These large, empty cells give *Sphagnum* their immense water holding capacity. First photo by Tarpinian, CC-BY-NC. Second photo by Казаков Александр Павлович, CC BY 4.0, via Wikimedia Commons.

Gametophyte Generation

Moss gametophytes have spirally arranged leaves that emerge from all sides of the stem (Figure 2.5.2.3.3). In most mosses, the leaves have a central line of tissue called a **costa** that looks a bit like a midrib (though it is not, as bryophytes don't have lignified vascular tissue) and are only 1-2 cell layers thick. Rhizoids are produced at the base of the gametophytes. In the common haircap moss, *Polytrichum commune*, there are three kinds of gametophytes:

- **Female**, which develop **archegonia** at their tip. A single **egg** forms in each archegonium. (see Figure 2.5.2.3.6)
- **Male**, which develop **antheridia** at their tip. Multiple swimming **sperm** form in each antheridium. (see Figure 2.5.2.3.5)
- **Sterile**, which do not form sex organs.



Figure 2.5.2.3.3: A closer look at spiral leaf arrangement, this time with *Polytrichum commune,* the haircap moss. Note that leaves emerge from all directions of each gametophyte. Photo by Mizuki Maeda, CC-BY-NC.

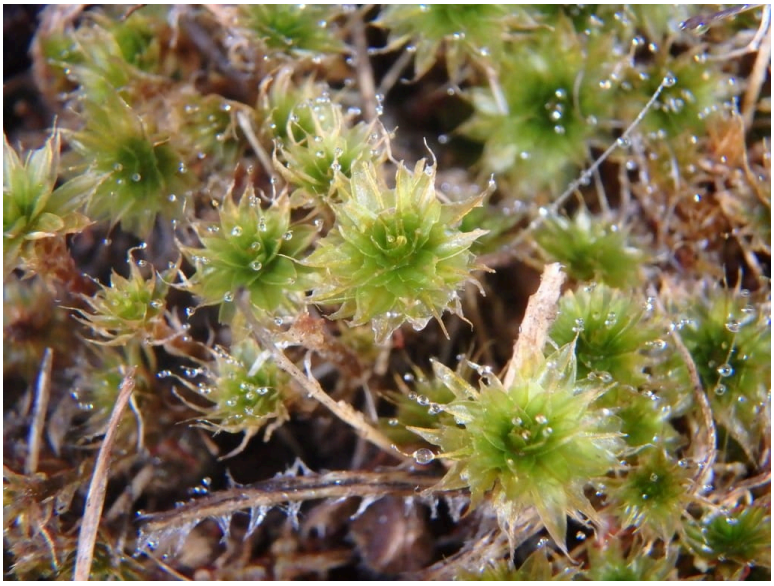


Figure 2.5.2.3.4: These moss gametophytes show spiral leaf arrangement and a distinct, tan costa that emerges on each leaf. Can you spot them? Photo by Geoffrey Cox, CC-BY-NC.

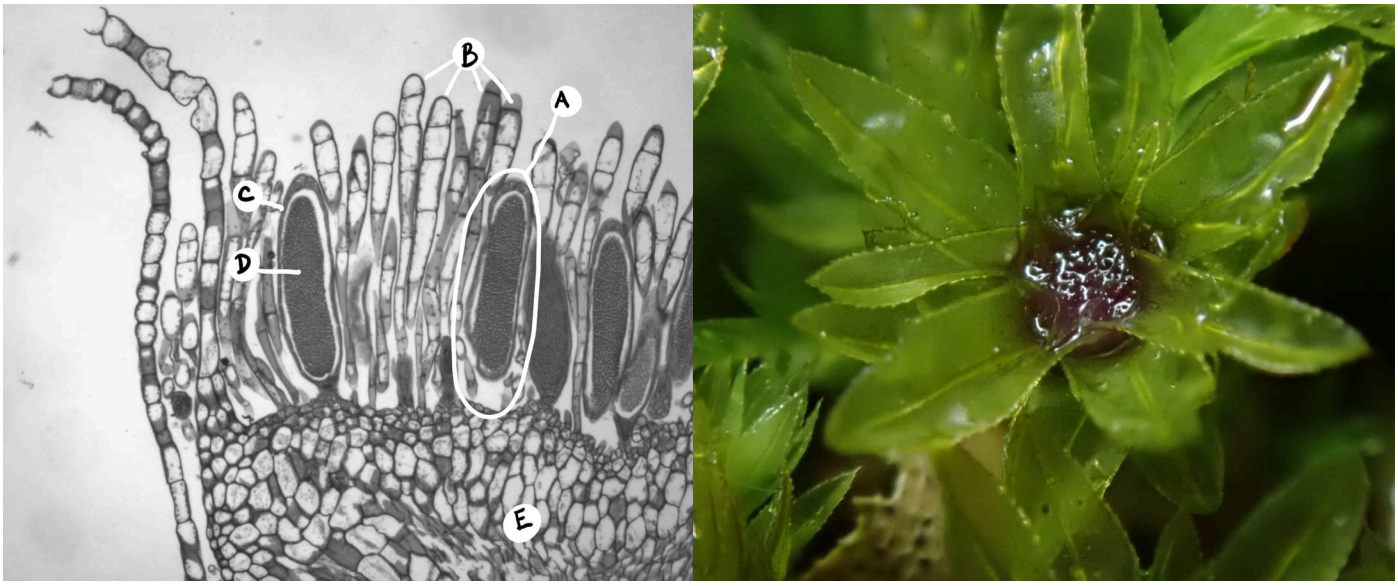


Figure 2.5.2.3.5: On the left is a labeled cross section of the antheridial head of a *Mnium* male gametophyte. On the right is an actual image of the splash cup (antheridial head) from a bird's eye view. The cross section is labeled as follows: A) An antheridium, B) paraphyses, C) sterile jacket of the antheridium, D) sporogenous tissue, E) male gametophyte. First photo by Maria Morrow, CC-BY-NC. Second photo by Bosmon, CC-BY-NC.

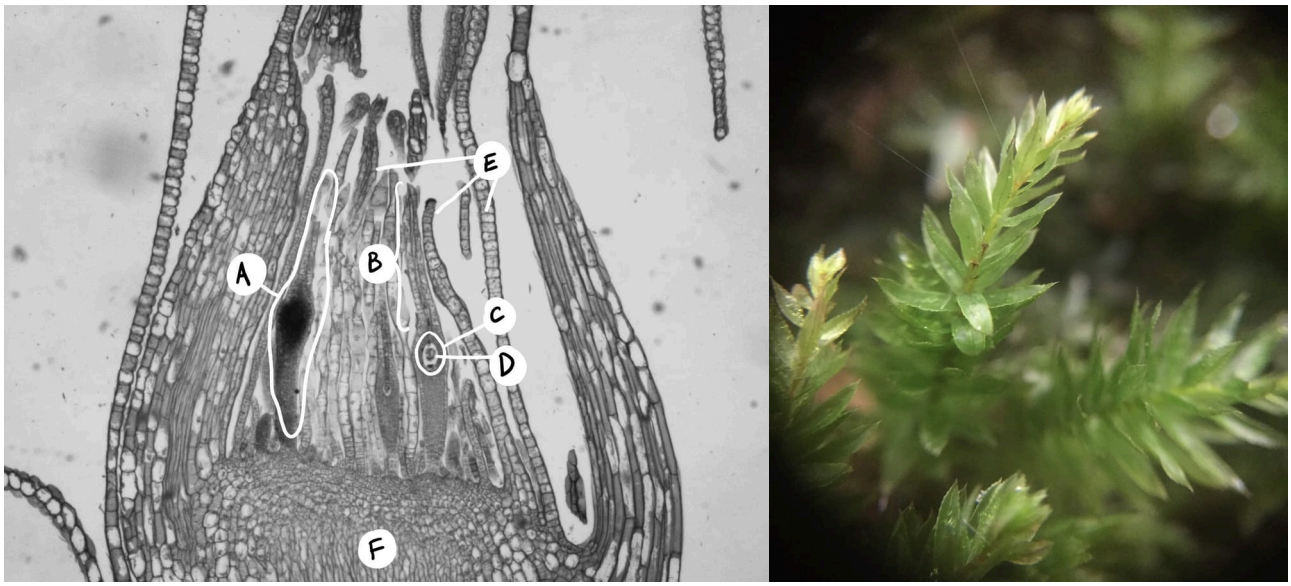


Figure 2.5.2.3.6: On the left is a labeled cross section of the archegonial head of a *Mnium* female gametophyte. On the right is an actual image of a female gametophyte. The cross section is labeled as follows: A) An archegonium, B) neck of the archegonium, C) venter, D) egg, E) paraphyses, F) female gametophyte. First photo by Maria Morrow, CC-BY-NC. Second photo by Tisrel, CC-BY-NC.

Sporophyte Generation

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

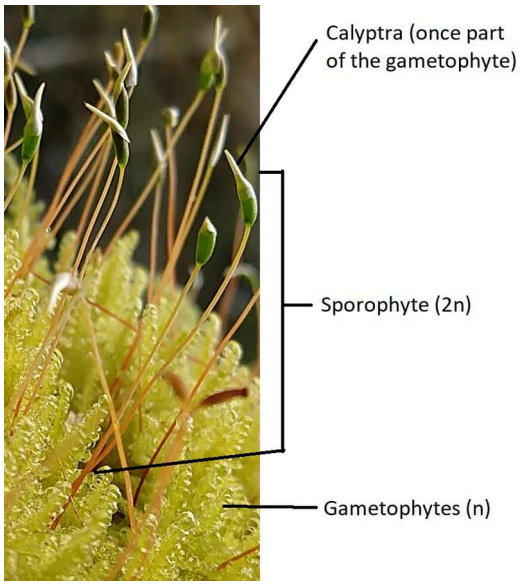


Figure 2.5.2.3.7: Moss sporophytes are composed of a seta and capsule, much like liverworts. When the sporophyte emerges from the archegonium, it brings a piece of that archegonium with it. This gametophyte remnant sits on the capsule like a cap, which is why it is called a calyptra. Photo by Maria Morrow, CC-BY-NC.

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



Figure 2.5.2.3.8: Moss sporophyte structures. In the first photo, the operculum of a *Polytrichum* sp. is visible. It is red and has a long, conical beak. In the second photo, the operculum of this moss has already popped off, revealing the peristome. There are two ranks of teeth in the peristome of this moss, the outer rank is bent and the tips are reaching inward. Green spores can bee seen clustered under the inner rank of teeth. Photos by George Shepherd, CC BY-NC-SA.

Tetraphis moss (*Tetraphis pellucida*) produces both asexual propagules (gemmae) and spores, which result from sexual reproduction (Figure 2.5.2.3.9). In 1991, Robin Wall Kimmerer found that spores were dispersed an average of 20 times farther from the parent plant than gemmae were, but gemmae established more easily. Each reproductive strategy thus served a different purpose: gemmae helped the plant spread locally, and spores were important for colonization of an entirely new location.



Figure 2.5.2.3.9: Sporophytes extend from the lush, green gametophyte in *Tetraphis pellucida*. The spores produced in the capsules of the sporophyte will function in long-distance dispersal. Photo by Nate Marineau, CC-BY-NC.

Mnium Life Cycle

Male gametophytes form antheridia at the top of the gametophyte in a structure called the perigonium or antheridial head (Figure 2.5.2.3.10). These are cup-shaped, and commonly referred to as splash cups. In early spring, raindrops splash sperm from male to female plants. These swim down the canal in the archegonium to the chamber containing the egg. The resulting zygote begins the sporophyte generation.

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

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

The sporangium is

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

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

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

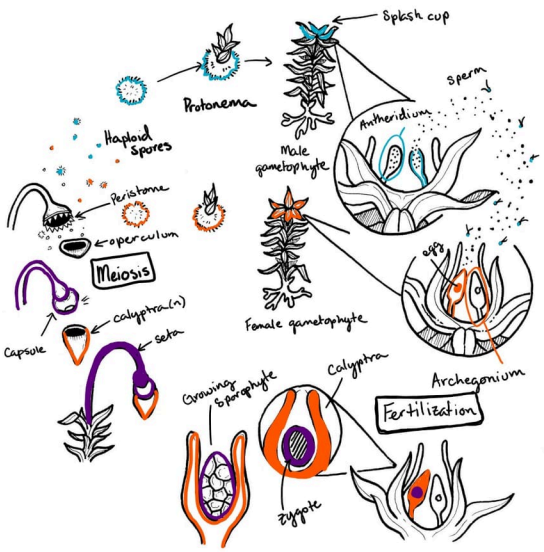


Figure 2.5.2.3.10: The *Mnium* life cycle. Starting with meiosis (left, center): Meiosis produces haploid spores which will grow by mitosis into either male or female gametophytes. Moss spores germinate and begin to grow into a chain of cells called a **protonema**. Male gametophytes are flat topped, called **splash cups**. Many **antheridia** are produced within the splash cup, surrounded by sterile cells called **paraphyses**. Antheridia produce biflagellate **sperm** by mitosis. Female gametophytes produce multiple **archegonia** at the top of the gametophyte. These are also surrounded by paraphyses. Each archegonium produces a single **egg** by mitosis. When water hits the splash cup, it can splash sperm onto a female gametophyte. If the sperm are able to swim through the water to an egg, fertilization occurs producing a diploid **zygote**. The zygote grows into a **sporophyte** from within the archegonium. The remaining archegonial tissue is called the **calyptra** and will remain on top of the sporophyte as a cap-like structure. A mature sporophyte will have a sterile stalk called a **seta.** Underneath the calyptra, there is a **capsule** containing cells that will undergo meiosis to make haploid spores. The capsule has a lid-like **operculum** that will pop off when the spores have matured. **Peristome** teeth along the opening of the capsule aid in spore dispersal. Drawing by Nikki Harris, CC-BY-NC, with colors and labels added by Maria Morrow.

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2.5.3: SEEDLESS VASCULAR PLANTS

Learning Objectives

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

Introduction

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

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

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

Characteristics

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

Selection Pressures and Drivers

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



-  Seedless Vascular Plants 

2.5.3.1: Lycopodiopsida
2.5.3.2: Polypodiopsida

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2.5.3.1: Lycopodiopsida

Learning Objectives

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

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

Characteristics

- **Microphylls**. Leaves with a single, unbranched vein of vascular tissue. Microphylls may have evolved from **enations**, scale-like appendages that later gained vascular tissue. Another possibility is that microphylls evolved from sporangia. Note: The term microphyll, confusingly, is not an indication of the size of the leaf.
- **Rhizomes**. Asexual propogation of the sporophyte through underground stems.
- **Strobili**. Cone-like structures where sporangia are produced on leaves called sporophylls (Figure 2.5.3.1.1).
- **Homosporous or heterosporous**. Haploid spores grow into bisexual gametophytes in *Lycopodium*. In Selaginella, **microspores** develop into **microgametophytes** that produce sperm and **megaspores** develop into **megagametophytes** that produce eggs.



Figure 2.5.3.1.1: A club moss, genus *Lycopodium*. The upright, yellowish structures are developing strobili.

Lycopodium

Members of this genus are homosporous, meaning they produce spores that develop into bisexual gametophytes, producing both

antheridia and archegonia on the same thallus.

Gametophyte Morphology

In seedless vascular plants, the sporophyte is the longer-lived, larger, leafy generation. This trend of sporophyte dominance throughout the evolutionary timeline of plants leads to continually smaller, less complex gametophytes. Gametophytes of this group are seldom seen. They are small and thalloid (Figure 2.5.3.1.2). In *Lycopodium*, the gametophyte grows from a homospore and is bisexual, producing both antheridia and archegonia.



Figure 2.5.3.1.2: Image of a preserved *Lycopodium* gametophyte. The flat thallus extending out to the right is the gametophyte. The sporophyte emerges from its left side, the root system developing downward and shoot system developing upward. Photo by Curtis Clark, CC BY-SA 3.0, via Wikimedia Commons

Sporophyte Morphology

Sporophytes branch dichotomously and have true roots, stems, and leaves due to the presence of lignified vascular tissue. This lignified vascular tissue provides rigid structural support, allowing sporophytes to grow tall. The leaves, called **microphylls**, have a single, unbranched vein of vascular tissue (Figure 2.5.3.1.3). Asexual propogation of sporophytes can occur via an underground stem that travels horizontally, called a **rhizome**.



Figure 2.5.3.1.3: A *Lycopodium* sporophyte growing vegetatively. The branches occur in Y-formations, showing dichotomous branching. There are many small, thin leaves (microphylls). Each one only has a single vein of vascular tissue, though this is not observable in this image. Photo by Maria Morrow, CC BY-SA 3.0.

To sexually reproduce, these plants produce cone-like structures at the end of their branches, called strobili. A **strobilus** is composed of leaves called **sporophylls** that bear sporangia (Figure 2.5.3.1.4). Meiosis occurs within the sporangia to produce haploid homospores. Unlike the bryophytes, a single sporophyte can produce many sporangia (Figure 2.5.3.1.5).

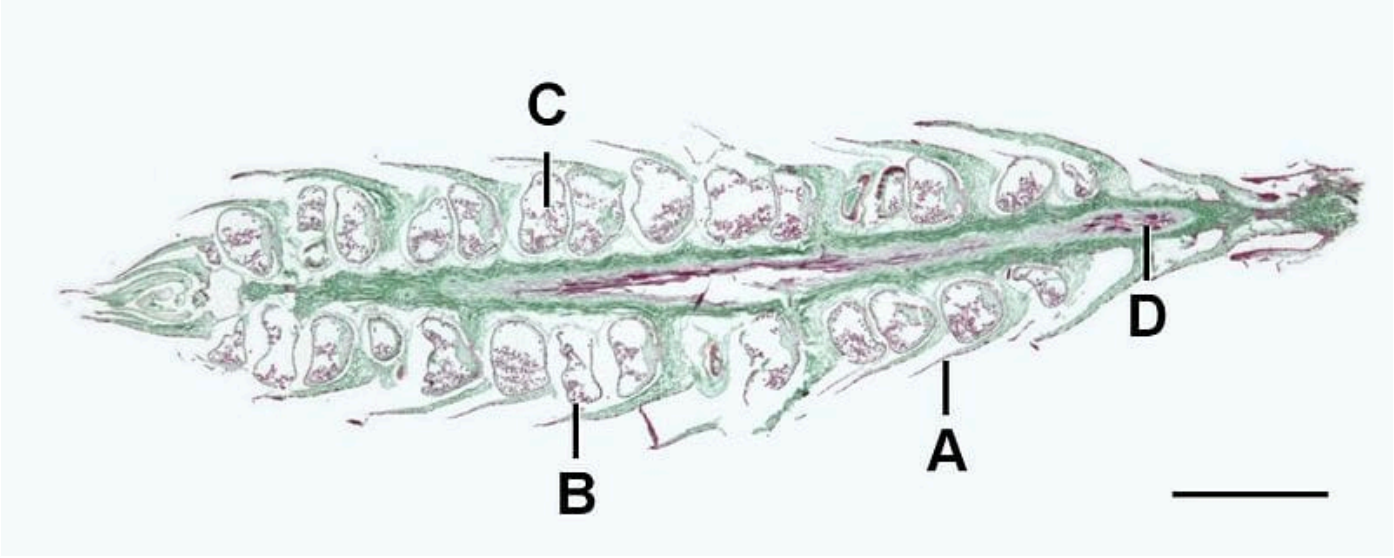


Figure 2.5.3.1.4: A longitudinal section of a *Lycopodium* strobilus, shown horizontally, and labeled as follows: A) sporophyll, B) sporangium, C) spores, D) cone axis. Scale bar represents 1.5mm Photo by Jon Houseman, CC BY-SA 3.0, via Wikimedia Commons

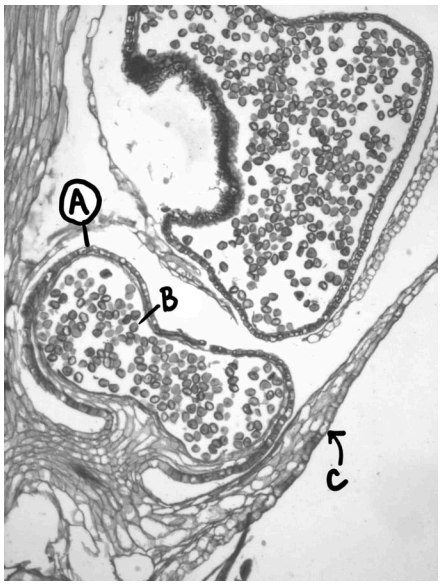


Figure 2.5.3.1.5: Lycopodium is homosporous. All spores produced are approximately the same size. A sporangium (A) is enclosing homosporous spores (B). This sporangium is attached at a point to a leaf (sporophyll, labeled C) that cups around it. Photo by Maria Morrow, CC BY-SA 3.0.

Selaginella

Members of the genus *Selaginella* are **heterosporous**, meaning they produce two different types of spores. Larger spores (megaspores) develop within **megasporangia** and are subtended by **megasporophylls**. Megaspores develop into gametophytes that produce archegonia. Smaller spores (microspores) develop within **microsporangia** and are subtended by **microsporophylls**. Microspores develop into gametophytes that produce antheridia. Megasporangia and microsporangia are found in the same strobilus (Figure 2.5.3.1.6)

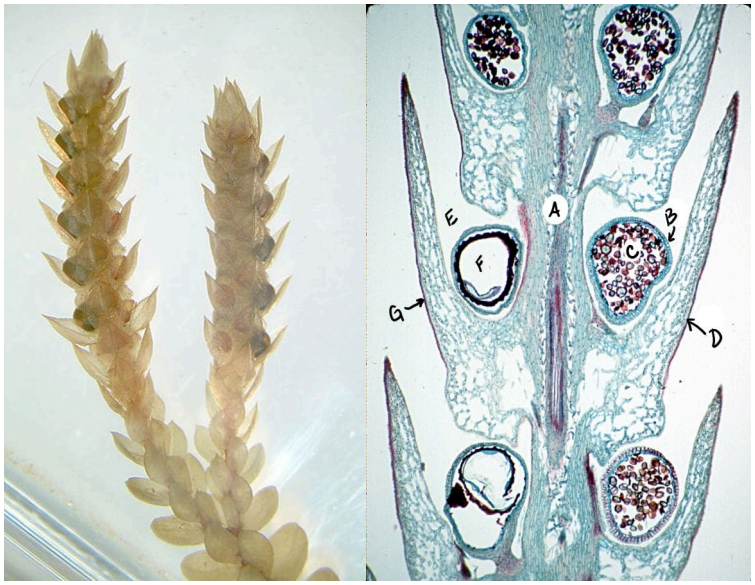


Figure 2.5.3.1.6: In the first image there are liquid-preserved strobili of *Selaginella*, showing mega- and microsporangia through translucent sporophylls. The two types of sporangia appear different and several large, dark spores can be seen through the wall of each megasporangium. The second image is a cross section through a strobilus. Notice that the spores contained within the sporangia are quite different in size. Labels are as follows: A) cone axis, B) microsporangium, C) microspores, D) microsporophyll, E) megasporangium, F) megaspore, G) megasporophyll. Photo on the left is by Curtis Clark, licensed as noted, CC BY-SA 2.5, via Wikimedia Commons. Photo on the right is by Curtis Clark, CC BY-SA 3.0, via Wikimedia Commons with labels added by Maria Morrow.

Extinct SVPs

Extinct lycophytes like *Lepidodendron* and *Sigillaria* grew into tall trees, branching dichotomously and producing a moss-like canopy of microphylls over 100 feet (30 m) in the air (Figures 2.5.3.1.7 – 8). Some of these microphylls were several feet long! Lycophytes first appear in the fossil record over 400 million years ago. By the Carboniferous period (around 300 mya), the landscape was covered with lycophyte forests and shallow swamps. Much of the fossil fuels we use today are derived from these extinct arboreal lycophytes falling into swamps, slowing decomposition and creating layers of carbon-rich material that we now find as coal seams.





Figure 2.5.3.1.7: In the first image there is fossil from a *Lepidodendron* tree on display at the State Museum of Pennsylvania. This extinct lycophyte genus was perhaps one of the dominant features in the landscape during the carboniferous period. On the right is an artist's reconstruction of *Lepidodendron,* showing dichotomous branching of the roots and shoots. Microphylls and pendant strobili emerge in the canopy. Photo of the fossil by Jstuby at en.Wikipedia, Public domain, via Wikimedia Commons. Artist's reconstruction by Tim Bertelink, CC BY-SA 4.0, via Wikimedia Commons.





Figure 2.5.3.1.8: In the first image there is fossil from a *Sigillaria* (possibly a root fragment) that is on display at State Museum of Pennsylvania. On the right is an artist's interpretation of what these plants looked like during the Carboniferous period. Photo of the fossil by Jstuby at en.Wikipedia, Public domain, via Wikimedia Commons. Artist's reconstruction by Tim Bertelink, CC BY-SA 4.0, via Wikimedia Commons.

An ancestor of modern-day *Equisetum*, *Calamites,* is thought to look much like the *Equisetum* species we see today, excepting

that it would have been 60 feet (20 m) tall (Figure 2.5.3.1.9). Most ancient pteridophytes appeared in Silurian period, they were rhyniophytes. Rhyniophyles had well-developed aboveground gametophytes and relatively short, dichotomously branched leafless sporophytes. The next important steps were formation of leaves and further reduction of gametophytes.



Figure 2.5.3.1.9: On the left are fossils of *Calamites*, an extinct relative of *Equisetum*, from the Sedgwick Museum's collection. On the right is an artist's interpretation of what these plants looked like. There is a large rhizome under the surface of the soil. The tree-like horsetail might have been 60 feet tall and has whorled branches with small leaves. Fossil photo by Verisimilus, CC BY 3.0, via Wikimedia Commons. Artist's reconstruction by Falconaumanni, CC BY-SA 3.0, via Wikimedia Commons.

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2.5.3.2: Polypodiopsida

Learning Objectives

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

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

Characteristics

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

Equisteum (subclass Equisetidae)

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

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

Gametophyte Morphology

Horsetail gametophytes are reduced and thalloid (figure 2.5.3.2.1). Gametophytes grow from homospores and can produce both antheridia and archegonia.

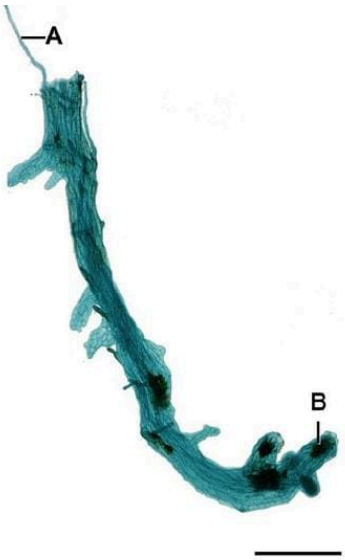


Figure 2.5.3.2.1: Whole mount of an *Equisetum* gametophyte. A indicates a long, thin rhizoid. B indicates one of several antheridia, each positioned on an extending lobe from the long, linear thallus. Scale=0.6mm. Jon Houseman, CC BY-SA 3.0, via Wikimedia Commons.

Sporophyte Morphology

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

Vegetative Shoots

On the vegetative shoot, the leaves are dark, papery and non-photosynthetic. Branches are photosynthetic and produced in whorls. Branches and leaves emerge at **nodes**, separated by regions of the main stem called **internodes**. Unlike most plants, the branches emerge below the leaves in the node (Figure 2.5.3.2.2 – 3). The epidermis of the stems contain **silica**, which has an abrasive texture.



Figure 2.5.3.2.2: A vegetative shoot of *Equisetum*. There are rings of long, thin, green branches emerging from each node. Above each whorl of branches, a ring of pointy brown leaves are pressed up against the main stem. Photo by Maria Morrow, CC-BY 4.0.

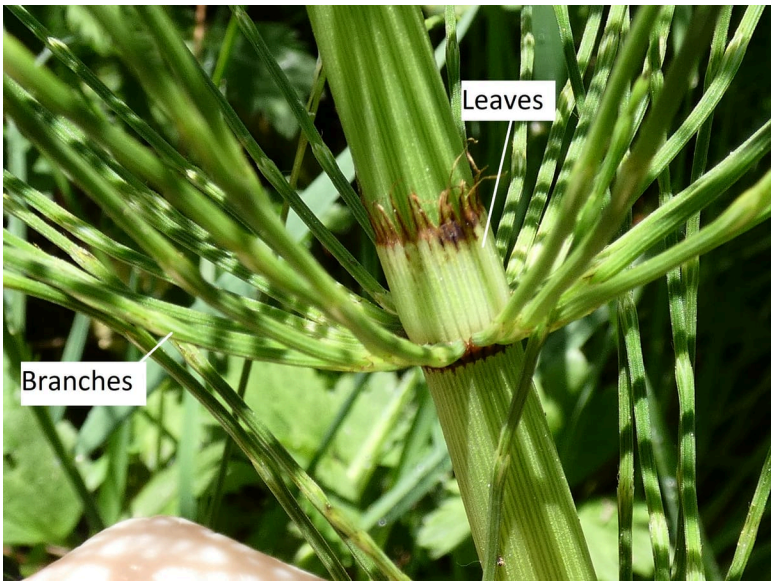


Figure 2.5.3.2.3: A close up of the vegetative shoot of *Equisetum*. In this image, you get a better view of the leaves. They start out as a united tube surrounding the main stem, then turn dry and brown, separating into individual, wispy points. The whorl of leaves looks a bit like a grassy crown encircling the stem. Photo by Maria Morrow, CC-BY 4.0.

Reproductive Shoots

Sporangia are produced in a terminal strobilus on the **reproductive shoot** (figure $2.5.3.2.4-5$). In some species, this reproductive shoot lacks chlorophyll and is instead fed through the rhizome of connected vegetative shoots. Spores are photosynthetic and have four hygroscopic arms called **elaters.**

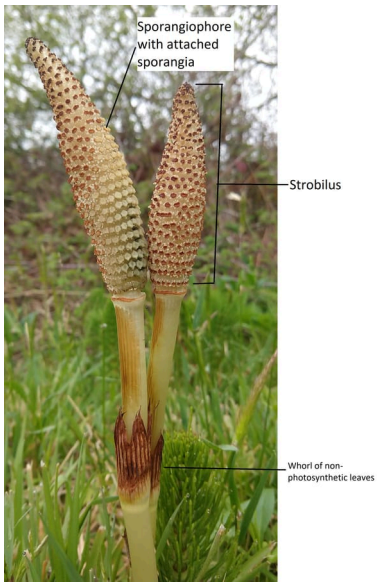


Figure 2.5.3.2.4: Two reproductive shoots of *Equisetum*. These shoots are a very pale yellow, lacking chlorophyll and unable to do photosynthesis. The leaves on the reproductive shoots still occur in whorls and are larger than on the vegetative shoots shown above. At the top of each shoot, there is an elongated structure that comes to a point and looks like it is covered in polka dots. These are the strobili. Each polka dot is the top of a sporangiophore, each of which bear many sporangia, perhaps visible to you as little white frills surrounding the polka dots. Photo by Maria Morrow, CC-BY 4.0.

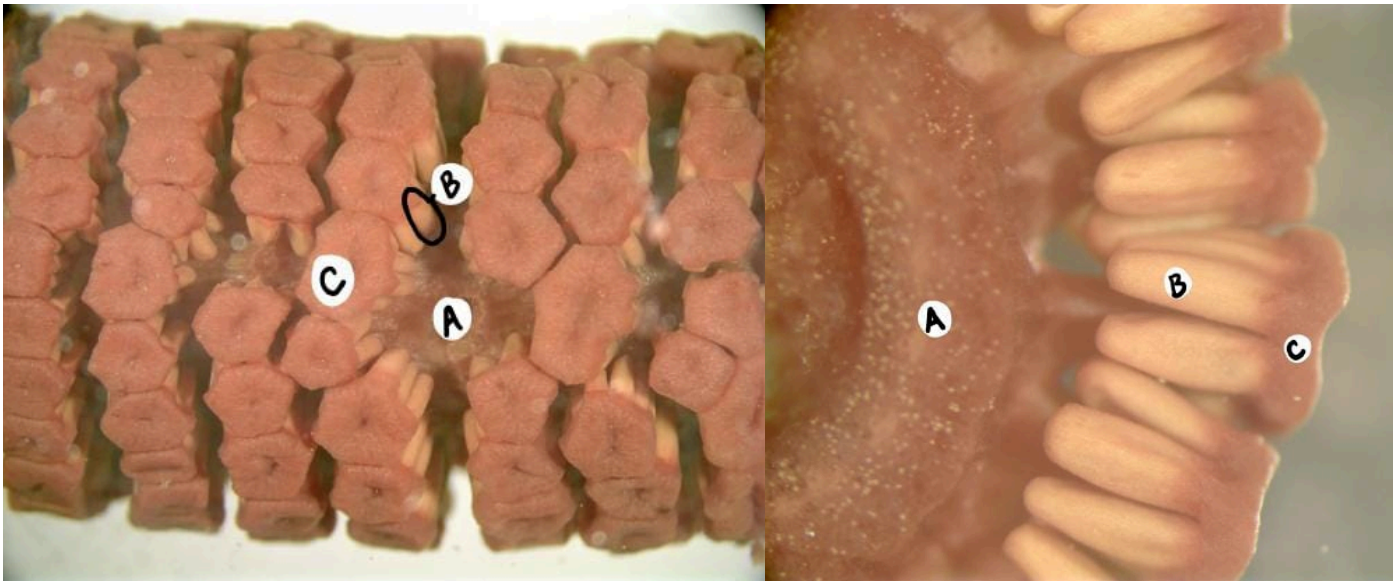


Figure 2.5.3.2.5: These images show a preserved strobilus. In the first image, e are looking straight at the tops of the sporangiophores (C), but some sporangia (B) are visible underneath them. There is a section where you can see the cone axis (A). In both images, the labels represent the same structures: A) cone axis, B) sporangium, C) sporangiophore. Copyright by Curtis Clark, licensed as noted, CC BY-SA 2.5, via Wikimedia Commons with labels added by Maria Morrow.

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

Ferns (subclass Polypodiidae)

Some 15,000 species of ferns live on earth today. Many of these are found in the tropics where some — the "tree ferns" — may grow to heights of 40 ft (13 m) or more. The ferns of temperate regions are smaller. They are usually found in damp, shady locations. They produce perennial rhizomes that can overwinter. Their leaves, called **fronds** due to apical growth, emerge from the rhizome each spring as coiled **fiddleheads** (Figure 2.5.3.2.6). These fiddleheads open through a process called **circinate vernation**, where the growing tissues are protected at the center of the coil and emerge last.

True ferns are **megaphyllous**: their leaves originated from flattened branches and have branching veins of vascular tissue. True ferns have unique sporangia: **leptosporangia** (Figure 2.5.3.2.6). Leptosporangia originate from a single cell in a leaf, they have long, thin stalks, and the wall of one cell layer. They also open actively: when sporangium matures (dries), a row of cells with thickened walls on the outside of the sporangium (called an **annulus**) will shrink slower than surrounding cells and finally would break and release all spores at once. Leptosporangia are grouped in clusters called **sori** which are often covered with umbrella- or pocket-like **indusia**. Gametophytes are minute and grow aboveground. While most ferns are homosporous, some genera of true ferns (like the water fern *Azolla*, water shamrock *Marsilea* and several others) are heterosporous (Figure 2.5.3.2.7).

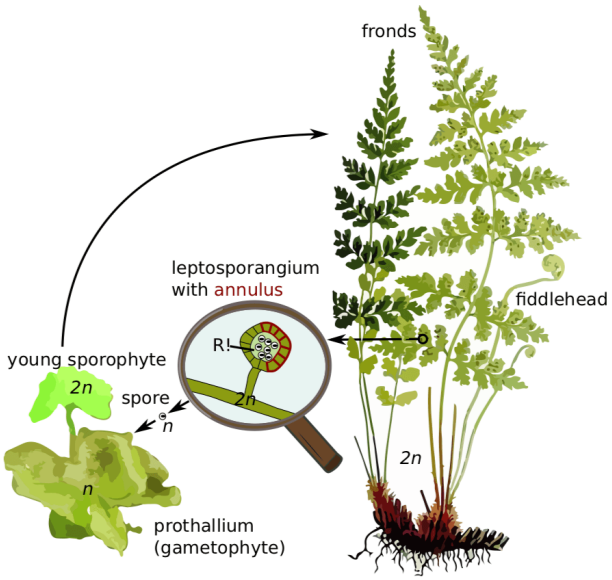


Figure 2.5.3.2.6: Selected stages of *Cystopteris* life cycle, representative of Pteridopsida. In this life cycle, a leptosporangium is featured in the middle. It has a thickened row of cells along the outside of the sporangium (the annulus) that will split the sporangium open as it dries. This produces a haploid (n) spore that develops into a prothallium (gametophyte, n). From the prothallium, a diploid (2n) sporophyte grows out. This then develops into several mature fronds and a developing fiddlehead.



Figure 2.5.3.2.7: *Salvinia natans* (left) is a heterosporous member of Polypodiidae. The hairs on the tops of the leaves repel water and help the leaves stay afloat. Kono Yasui (right), the first Japanese woman to earn her PhD, described the anatomy of this species in the *Annals of Botany*, making her the first Japanese woman to publish in a scientific journal centered outside of Japan. Over her career, she published 99 papers, including studies of plant cells (plant cytology), plant genetics, and even the formation of coal. Left image by Le.Loup.Gris, CC-BY-SA, and right image by 朝日新聞社 (public domain).

True ferns are highly competitive even to angiosperms. In spite of their “primitive” life cycle, they have multiple advantages: abilities to photosynthesize in deep shade (they are not obliged to grow fast), to survive high humidity, and to make billions of reproductive units (spores). Ferns do not need to spend their resources on flowers and fruits, and are also less vulnerable

to vertebrate herbivores and insect pests, probably because they do not employ them as pollinators and, therefore, can poison tissues against all animals.

Gametophyte Morphology

Fern gametophytes are reduced, thalloid, and heart-shaped (Figure 2.5.3.2.8). They are often referred to as a prothallus or **prothallium**. Rhizoids are produced from the underside of the thallus, just like in the bryophytes. Similar to the horsetails, whether a gametophyte produces antheridia or archegonia can be regulated by environmental cues (Figure 2.5.3.2.9). Each antheridium produces many swimming sperm, but archegonia produce only a single egg (Figure 2.5.3.2.10).

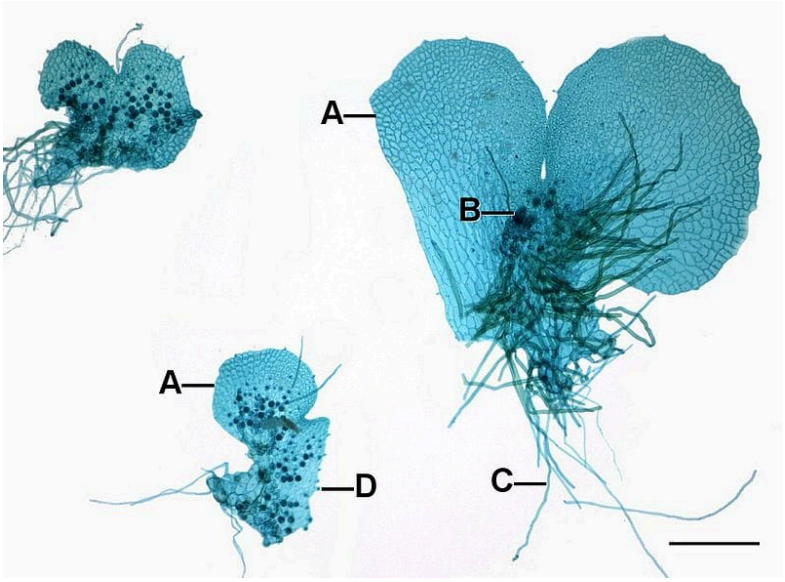


Figure 2.5.3.2.8: Three fern gametophytes that have been stained and so appear blue. The images are labeled as follows: A) Prothallus, B) Archegonium, C) Rhizoid, D) Antheridium. Scale=0.525mm. The rhizoids and archegonia emerge from the underside off the thallus. Descriptive text: A points to the flat, heart-shaped thallus, B points to structures with elongated necks close to the rhizoids, C points to long thin projections, D points to small dark structures spread across the thallus. Photo by Jon Houseman, CC BY-SA 4.0, via Wikimedia Commons.

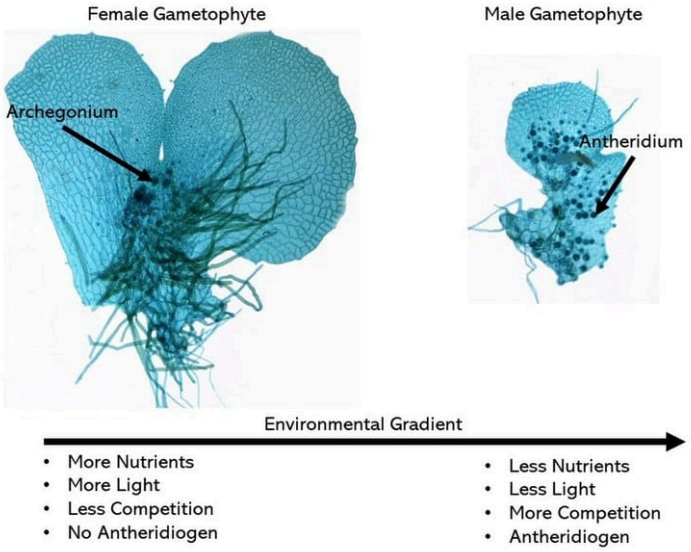


Figure 2.5.3.2.9: Fern gametophytes may develop either antheridia or archegonia based on environmental characteristics such as nutrients, competition, light, and antheridiogens. More nutrients, more light, less competition, and the absence of antheridiogen all select for the production of archegonia. Less nutrients, less light, more competition, and antheridiogen all select for the production of antheridia. Image by Jon Houseman, CC BY-SA 4.0, via Wikimedia Commons.

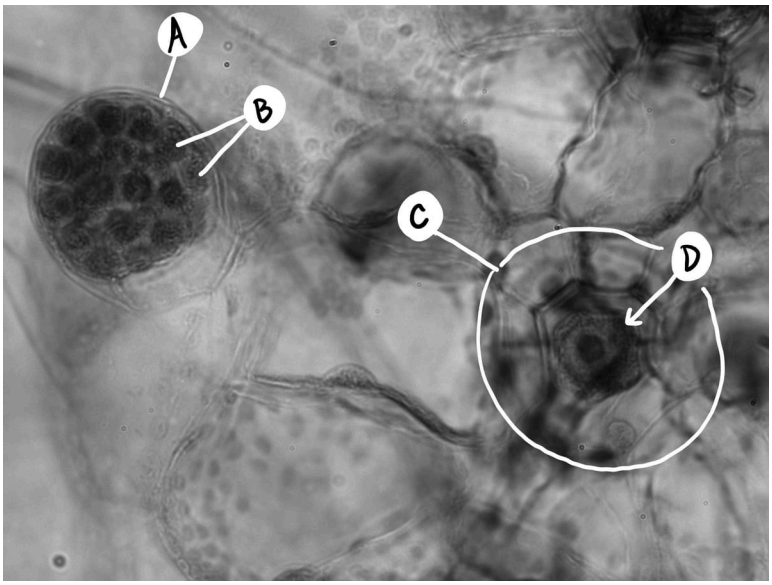


Figure 2.5.3.2.10: A magnified view of a fern gametophyte that has both antheridia and archegonia simultaneously. The antheridium (A) has many sperm inside (B) and does not appear three dimensional. The archegonium (C) is surrounded by enlarged cells--we are looking straight down the neck. At the center of the archegonium, there is only a single egg (D). Photo by Maria Morrow, CC-BY 4.0.

Sporophyte Morphology

Fern sporophytes are composed of megaphylls, often pinnately compound **fronds** that emerging as coiled **fiddleheads** in the spring. Sporangia are produced in clusters called **sori** (sorus, singular) on the fronds (Figure 2.5.3.2.11).



Figure 2.5.3.2.11: The underside of *Polypodium* frond. Each fuzzy-look orange region is a developing sorus (a cluster of sporangia). These sori are not protected by an indusium. Photo by Maria Morrow, CC-BY 4.0.

Circinate vernation is a term used to describe the development of the fern fiddlehead (Figure 2.5.3.2.12) into a frond. Because plants grow apically, it is important to protect the apical meristems in growing organs (as we have seen in both axillary and terminal buds with the protective bud scales). The fiddlehead is essentially a structure that tucks away the growing tips of the fronds. As the frond develops, it gradually unfurls, releasing the tips last.



Figure 2.5.3.2.12: The two images above show fiddleheads of two different types of ferns, a deer fern in the first image and a sword fern in the second. Each has the same basic shape--a long stalk that transitions in a tightly coiled knot containing the developing leaf tissues. Photo by Maria Morrow, CC-BY 4.0.

A sorus (plural, sori) is a cluster of sporangia, often protected by an umbrella-like structure called the **indusium** as the spores mature (Figure 2.5.3.2.13). Some sori are protected by an extension of the leaf called a **false indusium** (Figure 2.5.3.2.14), while others lack any protective covering. Each **sporangium** is lined by an inflated strip of cells called an **annulus**. When the spores have matured, the cells in the annulus begin to dry out, causing the cells to collapse and pull the sporangium open, releasing the spores.

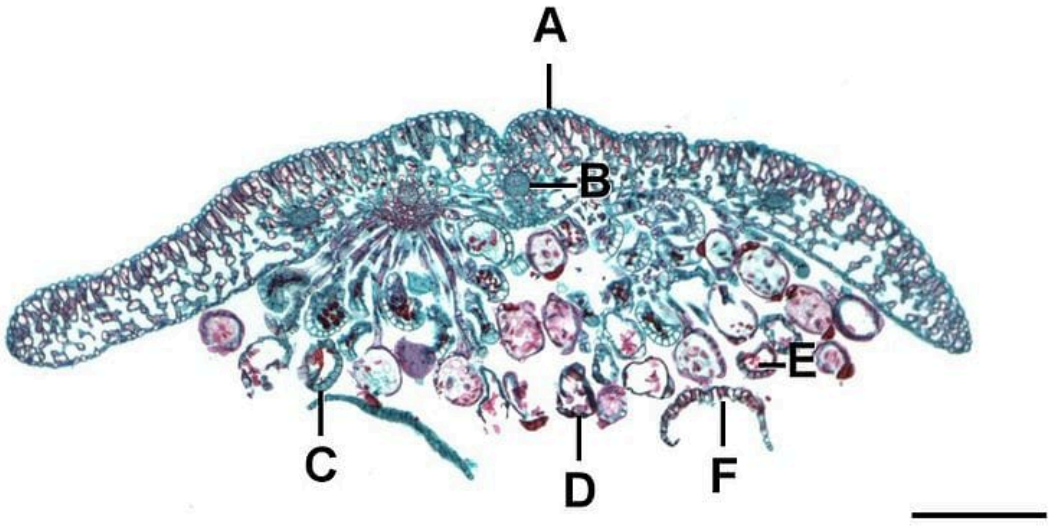


Figure 2.5.3.2.13: Cross section of a *Polystichum* sorus. The epidermis of the leaf (sporophyll) is labeled A. A large vascular bundle (B) is located in the center, as well as several others located along the length of the leaf. Under the leaf, a cluster of sporangia (D) are forming a sorus. Each sporangium is surrounded by a thickened layer of cells, the annulus (C). Within the sporangia, spores (E) are produced. The entire sorus was once covered by the residual structures labeled F, the indusium. Photo by Jon Houseman, CC BY-SA 3.0, via Wikimedia Commons.

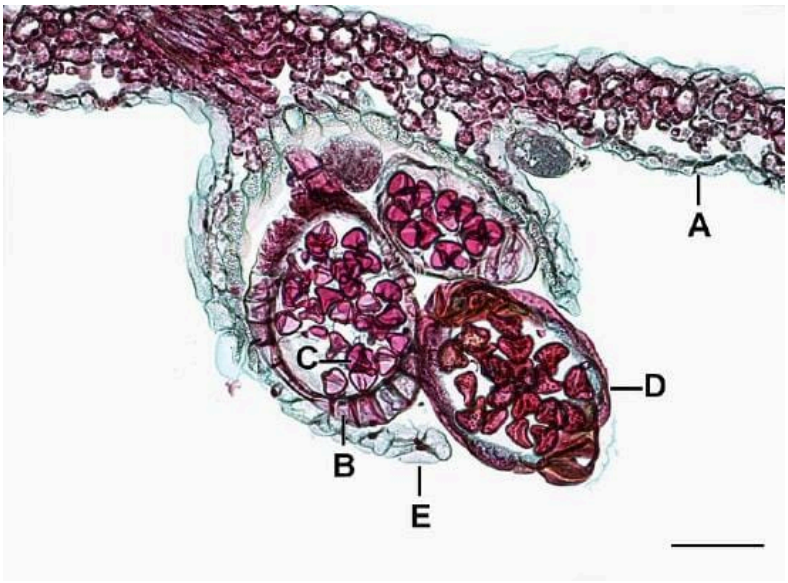


Figure 2.5.3.2.14: Cross section of a *Dicksonia* sorus. In this fern, the cluster of sporangia is enveloped by an extension of the leaf (E), a false indusium. A=Epidermis, B=Annulus, C=Spore, D=Sporangium, E=False indusium. Scale=0.1mm. Photo by Jon Houseman, CC BY-SA 3.0, via Wikimedia Commons.

Full Life Cycle Diagram

Ferns rely on water for dispersal of the sperm, which must swim into an archegonium to fertilize an egg (Figure 2.5.3.2.15). If moisture is plentiful, the sperm swim to archegonia - usually on another prothallus because the two kinds of sex organs generally do not mature at the same time on a single prothallus.

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

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

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

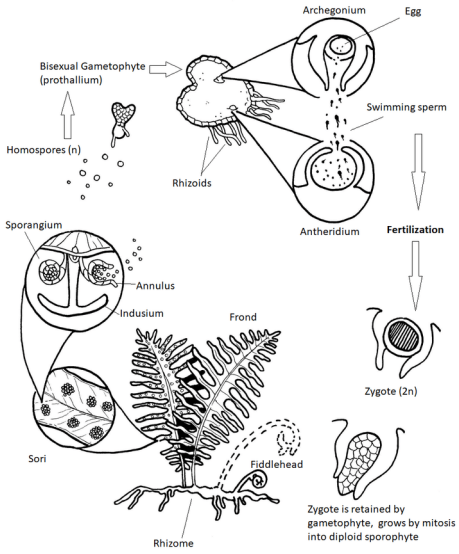


Figure 2.5.3.2.15: The diagram above shows the life cycle of a *Polypodium* fern. The gametophyte generation (n) is shown in the top half of the diagram and the sporophyte generation (2n) in the bottom half. Starting from the release of haploid homospores, these spores grow by mitosis into bisexual gametophytes. The gametophyte is heart-shaped, thalloid, and produces root-like structures called rhizoids. The antheridium produces many swimming sperm that are dispersed by water into an archegonium. A sperm swims down the neck/venter of an archegonium and fertilizes the single egg produced there. This produces a diploid zygote, which is retained on the gametophyte. The zygote grows by mitosis within the archegonium, producing a sporophyll (frond). When fully developed, the sporophyte will likely have multiple fronds and a rhizome. Fronds start as fiddleheads and uncoil by circinate vernation. The frond on the left is producing sori on the underside of the leaflets. Each sorus is a cluster of sporangia, which is protected by an indusium. Meiosis happens within the sporangia. Each sporangium has an inflated annulus to help release the spores when conditions are right. One of these has torn open to release its haploid homospores, which brings us back to the beginning. Diagram by Nikki Harris CC-BY 4.0 with labels added.

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2.5.4: Chapter Summary

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

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

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

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



Figure 2.5.4.1: Though not discussed in this chapter, you are likely to come across *Psilotum* in your botanical studies. These strange plants belong to the Polypodiopsida and are commonly referred to as whisk ferns. Oddly, they do not produce true leaves. Instead, photosynthesis is performed by the stems. These dichotomously branching stems extend underground, forming dichotomously branching rhizomes with projecting rhizoids. Their subterranean gametophytes parasitize mycorrhizal fungi, which later form a mutualism with the sporophyte generation. Fused sporangia are produced along the stems. Photo by Toshihiro Nagata, CC-BY-NC.

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

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

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

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2.6: SEED PLANTS

Fossil from the Devonian period reveal fernlike plants that were **heterosporous**; that is, produced two kinds of spores: **microspores** and **megaspores**. The megaspores were not released from the parent sporophyte. Fertilization took place within the tissue of the parent sporophyte thus freed from dependence on surface water. However, the necessity for the microspores to be carried from one plant to another in order to reach the megagametophyte robbed them of their value as agents of dispersal. This function was taken over by **seeds -** dormant, protected, embryo sporophytes.

2.6.1: Introduction to Seed Plants

2.6.2: Gymnosperms

2.6.2.1: Cycads and Ginkos

2.6.2.2: Conifers and Gnetophytes

2.6.3: Angiosperms

2.6.3.1: Flowers

2.6.3.2: Angiosperm Life Cycle

2.6.4: Chapter Summary

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2.6.1: Introduction to Seed Plants

Learning Objectives

- Explain how heterospory led to the evolution of seeds.
- Connect r- and k-strategies to propagules produced by plants (e.g. spores, gametes, pollen, and seeds).
- List a few ways gymnosperms and angiosperms differ in life history traits.

Fossil from the Devonian period reveal fernlike plants that were **heterosporous**; that is, produced two kinds of spores: **microspores** and **megaspores**. The megaspores were not released from the parent sporophyte. Fertilization took place within the tissue of the parent sporophyte thus freed from dependence on surface water. However, the necessity for the microspores to be carried from one plant to another in order to reach the megagametophyte robbed them of their value as agents of dispersal. This function was taken over by **seeds -** dormant, protected, embryo sporophytes.

Heterospory: The Next Big Step for Life on Land

Vertebrate animals became fully terrestrial only when their fertilization became completely independent from water. Plants started to perform the similar "evolutionary efforts" even earlier, but while reptiles actively approach the sexual partner, plants evolved different solutions. Instead of the active sex, plants use "carpet bombing" with spores; this increased the chance that two spores land nearby and the distance between sperm and egg cell will be minimal.

However, increasing the number of spores also results in a waste of resources, so plants minimized spore size; this will also allow for the longer distance of dispersal and fewer resources invested in each spore. On the other hand, some spores must remain large because the embryo (if fertilization occurs) will need the support from the feeding gametophyte. Consequently, plants ended up with division of labor: numerous, minuscule microspores that grow into microgametophytes with antheridia only, and a few large megaspores that make megagametophytes producing only archegonia (Figure 2.6.1.1). Megaspores are larger because they are rich in nutrients, ready to be fertilized and nourish a developing sporophyte.

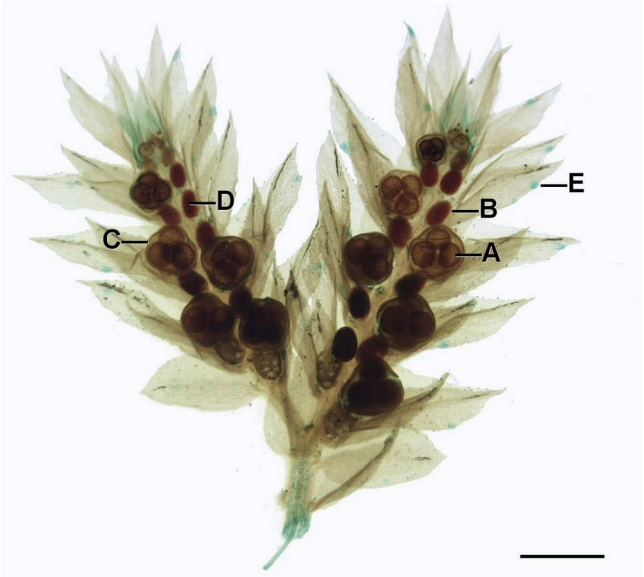


Figure 2.6.1.1: Selaginella, one of the seedless vascular plants, is heterosporous. A few megaspores (A) are produced within the megasporangium (C), while many microspores (B, too small to distinguish individually) are produced within the microsporangium (D). The megaspores will grow into gametophytes that produce archegonia (megagametophytes), while the microspores will develop into gametophytes that produce antherida (microgametophytes). Scale bar represents 0.7 mm. Photo by Jon Houseman, CC BY-NC, via Wikimedia Commons.

This **heterosporic** cycle makes fertilization less dependent on water and more dependent on spore distribution and gametophyte

features (Figure 2.6.1.2). It also allows for increased variations for selection to act upon. Division of labor allows resources to be used more efficiently and also restricts self-fertilization. In plant evolution, there was a high need for heterospory because it independently arose in several groups of seedless vascular plants (e.g. *Selaginella* and *Azolla*) and even among mosses.

As the evolutionary trajectory of heterospory progresses, some megaspores do not leave the mother plant and instead germinate there, waiting for the fertilization from a nearby microgametophyte: a step towards the first seeds. Male gametophytes become so small that they can easily be transported as a whole. Entire male gametophytes, rather than just gametes, start to be a mobile stage—this is origin of *pollination*.

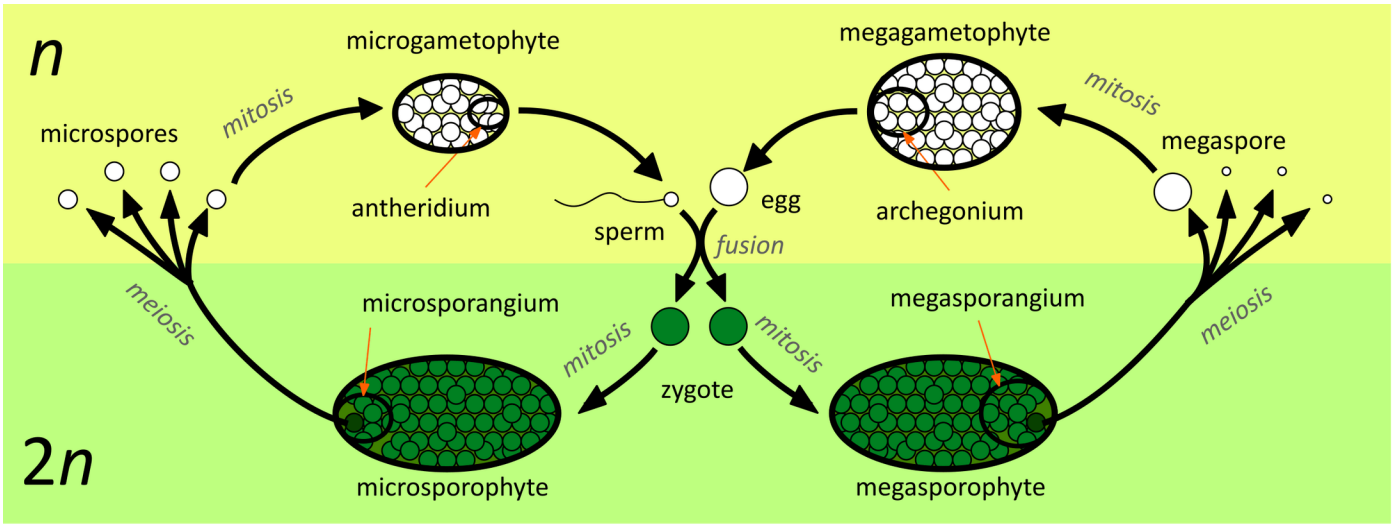


Figure 2.6.1.2: A heterosporic life cycle with dioecious sporophytes. Plant life cycles can get quite complex! In **dioecious** plants, microsporangia are produced on the microsporophyte and megasporangia are produced on the megasporophyte. In **monoecious** plants, microsporangia and megasporangia are produced on the same sporophyte. If two different types of sporangia are produced (mega- and micro-), the life cycle is heterosporic. Descriptive text: In this diagram, a microsporophyte produces microspores that grow into microgametophytes that produce sperm. A megasporophyte produces megaspores that grow into megagametophytes that produce eggs. Fertilization occurs and produces either a mega- or micro- sporophyte. Diagram by Peter Coxhead, Public domain, via Wikimedia Commons.

Getting Larger: Secondary Growth and the Transition From Seeds to Spores

When plants developed **secondary growth**, a type of growth that allowed for lateral expansion and accumulation of woody tissue, they were able to grow much larger. However, these giants faced a new problem. Big animals like elephants, lions, and whales tend to produce a small number of offspring but increase the child care to ensure survival. Another strategy, usually employed by smaller organisms, is to produce a large number of offspring with low investment in each (such as most fungal spores), though most of them will not survive (Figure 2.6.1.3).

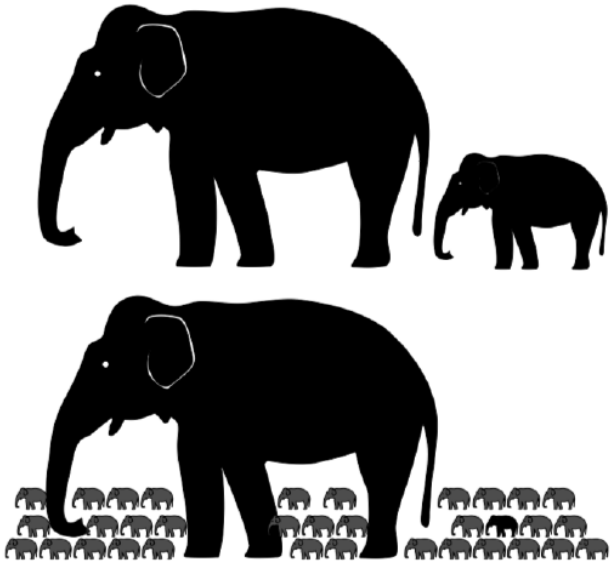


Figure 2.6.1.3: This image shows an elephant reproducing using two different strategies. While we may be familiar with the first elephant, the second type of elephant does not exist. Why might this be?

Imagine these big, secondary thickening spore plants: they made billions of spores with little nutrients or protection for the developing offspring. Naturally, only few from these billions would survive to become fertilized. Spore reproduction is cheap and efficient but results are unpredictable. Even worse, these spore tree forests were not at all stable: in accidentally good conditions, many spores would survive and make sporophytes, which would all start to grow simultaneously and then suppress each other. But if the environmental conditions are poor, then none of the gametophytes will survive so there would be no new saplings to replace the old trees.

Plants evolved a solution to this conundrum: the **seed**. The idea of a seed is to hide most of the heterosporous life cycle inside the parent plant. In seed plants, everything happens directly on the parent sporophyte: development of gametophytes, syngamy, and growing of offspring sporophyte. Consequently, the megaspore never leaves the sporangium. It germinates inside, waits for fertilization and then the zygote grows into and embryo, still inside the same sporangium. What will finally leave the mother plant is the entire megasporangium with the megagametophyte and embryo inside. This is the seed's chimeric construction: sporophyte, megagametophyte, embryo, and (in angiosperms) endosperm genotypes encased within a single structure.

One problem is still left. How will sperm reach the retained megagametophyte and egg cell? The target is now perhaps high above the ground, on a branch of the giant tree. The only possible solution is pollination. **Pollination** is the distribution of the whole male gametophytes, also called **pollen**. Plants aren't able to physically go find a mate, so they always need a third party to transport their pollen, usually wind or insects.

Once the pollen gets to the intended destination, how would the sperm then swim to the egg cell? Some seed plants excrete a drop of liquid from the top of the ovule (a **pollen drop**) to create a fluid connection between the pollen grain to the ovule. Another sperm delivery tool, the **pollen tube** (Figure 2.6.1.4), is made from one of the pollen grain cells in some plants. Fertilization with pollen tube is often called **siphonogamy**.

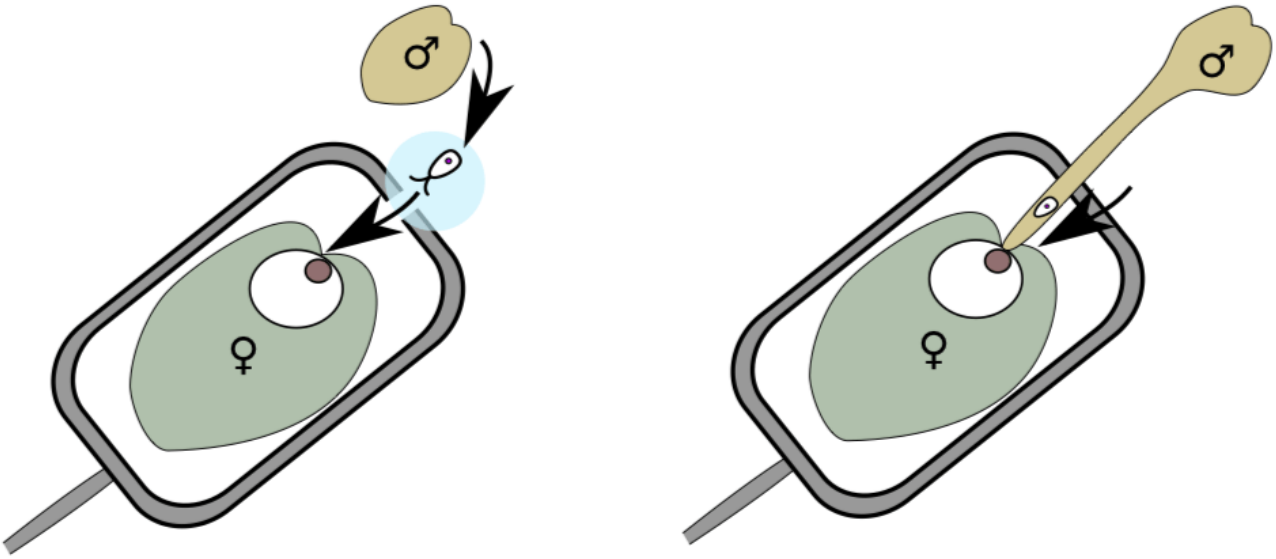


Figure 2.6.1.4: Open fertilization in seed plants (left) with the help of liquid extracted by mother plant; and fertilization with pollen tube (right), or siphonogamy, with the help of pollen tube growing from male gametophyte. Among extant seed plants, only cycads and ginkgo have the open fertilization.

Consequently, seed plants with the pollen tube do not have flagella on male gametes; these cells are **spermatia**: non-motile male gametes. A pollen tube allows only two male gametes per gametophyte. Male gametes are usually competing for fertilization—this selects the best genotypes; whereas in higher seed plants, competition is between pollen tubes. The haploid pollen tube grows inside alien tissue of diploid sporophyte, so this growth is extremely slow in many seed plants. However, angiosperms made their pollen tubes grow fast.

With all these revolutionary adaptations, seed plants were first to colonize really dry places, and, in turn, allowed all other life to survive in arid climates. Read more about the evolution of seeds in this article from September, 2020.

Gymnosperms and Angiosperms

Seed plants are composed of two major lineages: gymnosperms (meaning naked seed) and angiosperms (meaning covered seed). These two lineages represent major differences in life history traits connected to the evolutionary conditions during which each evolved.

Gymnosperm reproduction differs from that of angiosperms in several ways. In gymnosperms, the megagametophyte is contained within an ovule, present on exposed bracts of the megastrobilus, where seeds develop and are often passively released (though some are dispersed by animals). In angiosperms, the ovule is contained within an enclosed ovary. The ovary then develops into a **fruit**, specialized for seed protection and dispersal. **Double fertilization** is a key event in the life cycle of angiosperms, forming a second supply of nutrients for the developing embryo (the **endosperm**), but is absent in most gymnosperms. The gametophyte structures are produced in separate **strobili** in gymnosperms, whereas in angiosperms, they are often a part of the same **flower**. Wind plays an important role in pollination in gymnosperms because pollen is blown by the wind to land on the female cones. Although many angiosperms are also wind-pollinated, animal pollination is more common, resulting in specialized pollination syndromes present in flowers.

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2.6.2: GYMNOSPERMS

Learning Objectives

- Describe the shared derived characteristics of gymnosperms.
- Connect these adaptations to the stressors this group of plants would have faced.

Toward the end of the Carboniferous period, major changes in the climate occurred. The current day European and North American continents slammed together, forming the Appalachian mountains (which were taller, at that time, than the present-day Himalayas). Fossil and geologic records show a tendency toward a drier climate, with evidence of glaciation and lowered sea levels. Inland seas were increasingly diverted into distinct river channels as woody debris channelled the movement of waterways. In short, the terrestrial surface began to dry out and there was much more of it. The ancestors of birds, reptiles and mammals were adapting eggs that could survive outside of the water -- plants were working toward a similar strategy. Dry conditions would have selected for plants with thicker cuticles, leaves with less surface area to evaporate from, propagules that could survive through dry periods to germinate when water was available, and those that could grow taller than the current canopy. Around this time, a group of animals likely took flight for the first time -- the insects! This would present both new challenges and new opportunities for plants.

The plants that would become the gymnosperms evolved **xerophytic leaves** to prevent desiccation in the dry air (Figure 2.6.2.1).

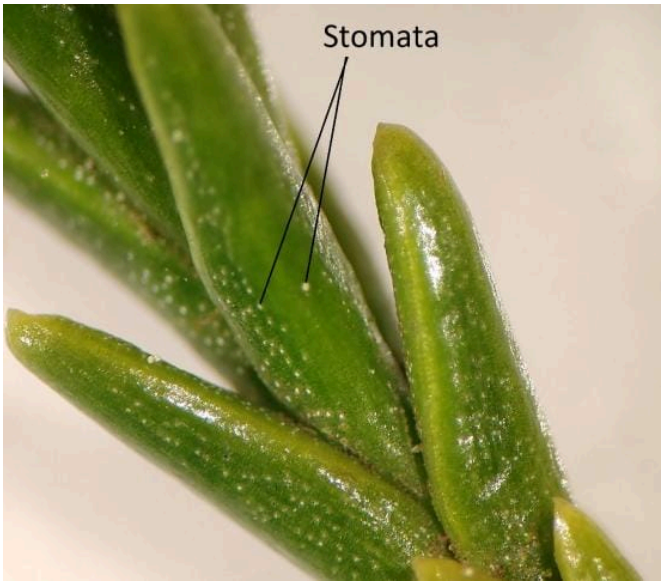


Figure 2.6.2.1: Xerophytic leaves tend to have a thick, waxy cuticle (note how shiny these giant Sequoia leaves are), a lower surface area to volume ratio with extra layers of densely packed cells, and sunken stomata. Photo by Maria Morrow, CC BY-NC.

These plants would have the ability to grow wider (and thus taller) via the production of a new layer of secondary xylem, AKA **wood**, each year. They could also produce exterior layers of dead cells, unlike the living epidermis, called **bark**. Together, the production of bark and wood are part of a process called **secondary growth** (Figure 2.6.2.2). These traits allowed some gymnosperms to adapt to extreme environments like the frozen tundra, high alpine, and deserts, to resist herbivory, and live thousands of years.



Figure 2.6.2.2: Secondary growth, viewed in a cross section through a woody stem. The outer layer is composed of bark, which surrounds the inner woody tissue. The wood is composed of lignified xylem cells. In gymnosperms, these cells would be tracheids. The bark forms a thick outer layer (red and fibrous) that surrounds the lighter, denser wood that composes the rest of the trunk. Photo by Maria Morrow, CC BY-NC, who is aware that this stump belongs to an angiosperm (in this case, an oak).

To increase the chances of fertilization in the absence of water, gametes began to be dispersed aerially via **pollen**. Perhaps most importantly, the zygote and female gametophyte were surrounded in a protective coating and dispersed as **seeds**. Both seeds and pollen develop within a structure called a **cone** (or strobilus, see Figure 2.6.2.3).



Figure 2.6.2.3: Megastrobilus and microstrobilus. The first photo shows a megastrobilus of *Araucaria*, where seeds are produced on each megasporophyll (distinguished by the curved bracts sticking out from under each one). The second photo shows a microstrobilus of *Pinus*. Each scale-like microsporophyll produces multiple microsporangia where the pollen grains develop. Photos by George Shepherd, CC BY-NC-SA.

The first fossil records of gymnosperms are from a period called the Permian, just after the Carboniferous. Gymnosperms used to have many more species, but it is likely that the event that wiped out most of the dinosaurs also represented the end for most of those lineages. Extant groups of gymnosperms include the conifers, cycads (similar in appearance to palms), gnetophytes, and single species from the ginkgophytes, *Ginkgo biloba*. Of the approximately 1000 species of gymnosperms alive today, about 600 of these are conifers, 58 of which are found in California. In fact, some of the oldest (bristlecone pine), tallest (coast redwood), and most massive (giant sequoia) organisms on the planet are conifers and all are native to California.

Many lineages of gymnosperms are currently threatened with extinction. Check out this open-access paper (Gymnosperms on the EDGE) for more information about gymnosperm conservation.

Selection Pressures and Drivers

1. **Competition for sunlight**. Seedless vascular plants were able to reach heights up to 100 feet tall. In the lineage leading to the gymnosperms and angiosperms, some plants developed the ability to grow wider as they grew taller. This secondary growth allowed for increased stability and, eventually, to reach heights over 300 feet.
2. **Drought**. Dry conditions would have selected for plants with thicker cuticles, leaves with less surface area to evaporate from, and propagules that could disperse without water and survive through dry periods to germinate when water was available.
3. **Herbivory**. In addition to leaves that could resist drought, the presence of insects would have driven selection for plants that could defend against herbivory. The thick cuticle and tough texture of xerophytic leaves made them difficult to eat, while resin canals in both leaves and stems provided another line of defense.

- Topic hierarchy

2.6.2.1: Cycads and Ginkos

2.6.2.2: Conifers and Gnetophytes

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2.6.2.1: Cycads and Ginkos

Learning Objectives

- Use morphological characteristics and life history traits to distinguish between ginkgos and flowering plants.
- Explain why *Ginkgo biloba* is called a living fossil.
- Use morphological characteristics and life history traits to distinguish between cycads and ferns.
- Define the term dioecious and provide an example.

Ginkgophyta

As of 2019, the most recent genetic studies have placed ginkgos as the oldest of the extant gymnosperms. This does not mean that it was the first gymnosperm. From the fossil record, it seems that most early gymnosperms went extinct. The sole remaining species in this group, *Ginkgo biloba*, is a living fossil virtually unchanged from its fossilized ancestors (see Figure 2.6.2.1.1). This plant is almost extinct in the wild--a few natural populations remain in China--but has a wide distribution as an ornamental tree. It is possible that this species was only kept alive due to cultivation efforts by Buddhist monks for its medicinal properties.



Figure 2.6.2.1.1: Ginkgo leaves have a distinctive shape that has remained relatively unchanged from their fossil record: a fan-shaped leaf that is often deeply dissected in the center (the specific epithet *biloba* means two lobes). The fossil leaf on the right is around 60 million years old. First image: *Ginkgo biloba* leaves, photo by Onidiras, CC-BY-NC. Second image: Fossil Ginkgo leaf by Anders Sandberg from Oxford, UK, CC BY 2.0, via Wikimedia Commons.

Ginkgo biloba is dioecious (as an exception among plants, *Ginkgo* has sexual chromosomes like birds and mammals) and the pollen is transported by wind to ovulate trees. The microstrobili are reminiscent of the catkins produced on some flowering plants (Figure 2.6.2.1.2). Pollen grains of ginkgos produce two multi-flagellate spermatozoa.



Figure 2.6.2.1.2: Male *Ginkgo biloba* trees produce microstrobili that look a bit like inflorescences. Inside these structures, pollen is produced. Photo by Belvedere04, CC-BY-NC.

Ovulate have paired ovules at the tips of branches that look much like fruits (Figure 2.6.2.1.3). The fleshy coating of the seed emits a foul odor as it decays, making staminate trees a more popular choice in ornamental settings.



Figure 2.6.2.1.3: Female *Ginkgo biloba* trees produce fruit-like megastrobili as fleshy, paired ovules. Each globose structure contains a developing seed. Apparently, they can smell quite putrid. Photo by Kim, Hyun-tae, CC-BY

This species is also long-lived, a single tree can live for thousands of years (the oldest is 3,500 years old!), and they are resistant to most pests. This pest resistance, as well as the medicinal properties, can be attributed to a wide variety of secondary metabolites produced in the leaves, including terpenes and flavonoids. A ginkgo tree at the Zenpuku temple in Tokyo, Japan is approximately 750 years old (Figure 2.6.2.1.4). Ginkgos were the first plants to regenerate after the Hiroshima bombing and were not found to contain any genetic abnormalities.



Figure 2.6.2.1.4: Ginkgos can be quite long-lived. This ginkgo tree is approximately 750 years old. It bears burn scars from WWII and has a complex trunk structure. It is sometimes referred to as the inverted or upside down tree due to the numerous aerial roots growing steadily downward. *Ginkgo biloba* at Zenpuku-ji in Azabu. Photo by Belvedere04, CC-BY-NC.

Cycadophyta

Although seed ferns are now extinct, some of their living descendants, the **cycads**, resemble them closely (Figure 2.6.2.1.5). Cycads are one of the more ancient gymnosperm lineages, appearing in the fossil record around 300 million years ago. Similar to *Ginkgo biloba*, cycads have sperm with multiple flagella that swim toward the egg. For plants, this is considered an ancestral trait. Cycads and ginkgos emerge as sister taxa that are ancestral to the conifers.



Figure 2.6.2.1.5: On the left is an image of what might be considered a "typical" cycad. The leaves are long, tough, and pinnately compound with long, thin leaflets arising from a central axis, like a feather. Unlike a fern, the leaves look tough. The plant in the photo on the right also shares these characteristics, yet it might not immediately stand out as a cycad. Left: *Dioon holmgrenii,* photo by Daniela Fernandez y Fernandez, CC-BY-NC. Right: *Bowenia spectabilis,* photo by kerrycoleman, CC-BY-NC.

Cycads produce leaves that are large and pinnately compound (have leaflets arising from a central axis, like a feather), making them appear frond-like. Unlike ferns, but like other gymnosperms, these leaves are xerophytic (Figure 2.6.2.1.6): tough, waxy, and more resistant to desiccation.



Figure 2.6.2.1.6: Each leaf blade shown here is a leaflet from the larger, pinnately compound leaf. There are many parallel veins of vascular tissue traversing each leaflet and the rachis of the leaf looks woody. *Zamia integrifolia,* photo by John C., CC-BY-NC.

Cycads are **dioecious.** The microstrobilus is produced on the "male" plant and consists of many microsporophylls bearing microsporangia. It is called a microstrobilus, not because *it* is small (these can be over a meter in height), but because the it produces smaller and more numerous spores than the megasporangium. Microstrobili are often larger than megastrobili in cycads (see Figure 2.6.2.1.7 and Figure 2.6.2.1.8). In cycads, pollen is carried to the megastrobilus by insects. The megastrobilus is produced on the "female" plant, and is composed of overlapping megasporophylls. In some cycads, such as *Cycas* spp., the megasporophylls do not form into a strobilus structure. Ovules are produced on megasporophylls (Figure 2.6.2.1.9); these ovules will develop into seeds after fertilization. Seeds are then dispersed by animals.



Figure 2.6.2.1.7: The large microstrobilus, the pollen-producing cone. Photo by BillyH, CC BY 3.0, via Wikimedia Commons.



Figure 2.6.2.1.8: A megastrobilus is composed of overlapping megasporophylls. Cycads are dioecious, meaning male and female strobili are produced on different individuals. These individuals are "female" and so produce a megastrobilus. Inside the megastrobilus, seeds are produced. These are visible in the photo on the right, the bright red structures that appear to be bubbling up from under the green megasporophylls. First: *Dioon merolae* Photo by Raul Ezequiel Gonzalez Trujillo, CC-BY-NC. Second: *Macrozamia macleayi,* photo by Blawson, CC-BY-NC.



Figure 2.6.2.1.9: From the megastrobilus, seeds are produced. In the first photo, rounded ovules are embedded on the edges of feathery megasporophylls of *Cycas*. In the second photo, a longitudinal section of a *Cycas* ovule shows the female gametophyte (A) surrounded by the nucellus (B) and the integument (C). The remains of the micropyle (D, the tube that runs from the outside into the ovule and through which the pollen grains are sucked) are visible, and this opens into the pollen chamber, where the pollen germinates and forms a pollen tube. Photos and caption text (modified) by George Shepherd, CC BY-NC-SA with labels added by Maria Morrow.

Descriptive text for the second image: The megagametophyte is gelatinous looking and at the center, connected to the exterior by the micropyle. The megagametophyte is surrounded by a pithy-looking nucellus, which is encased by a rind-like integument.

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2.6.2.2: Conifers and Gnetophytes

Learning Objectives

- Use morphological features and life history traits to distinguish conifers from other plants.
- Connect the adaptations of conifers to dry and/or cold environments.
- Identify structures and phases in the *Pinus* life cycle; know their ploidy.
- Use morphological features and life history traits to distinguish gnetophytes from other plants.
- Describe the traits gnetophytes share with angiosperms.

Though the gnetophytes have been difficult to place, phylogenetically, recent genetic studies place them as sister to the Pinaceae (pine family, emerging from within the conifers. See this open-access paper for recent genetic work on the evolutionary relationships between gymnosperms.

Conifers

Conifers are the most species-rich lineage of gymnosperms. From the fossil record, we think there were over 20,000 species of conifers. However, their diversity declined with the dinosaurs. Currently, there are around 600 extant species. These amazing plants represent some of the oldest, tallest, and most massive organisms on the planet. Though currently low in diversity, these amazing plants make up 30% of Earth's forests.

Conifers are the most widely known and economically important among gymnosperms. Conifers include the largest and the oldest of all living organisms. One redwood (*Sequoia sempervirens*) growing in California is almost 400 feet (122 meters) high. Bristlecone pines (*Pinus longaeva,* Figure 2.6.2.2.1) growing in the mountains of eastern California some are more than 5,000 years old. Giant sequioas (*Sequiadendron giganteum*) Most of them are temperate evergreen trees, but some are deciduous, such as larch (*Larix*) and the dawn redwood (*Metasequoia*). The stem has a large amount of xylem, a small cork, and minute pith. Seeds are distributed by wind and animals.



Figure 2.6.2.2.1: A bristlecone pine in the White Mountains of California. Gnarly, CC BY-SA 2.0, via Wikimedia Commons

Note: The Pinaceae is currently the largest family of conifers, so many of the examples for this group of gymnosperms will be from the type genus *Pinus* (pines).

Xerophytic Leaves in Conifers

Xerophytic leaves are adapted to withstand drought conditions. In conifers, we see a wide range of xerophytic leaves with different morphologies that can be shaped by their local environment. Consider the leaves of the coast redwood and the giant sequoia (Figure $2.6.2.2.2-3$). Though these two trees belong to different genera--*Sequoia* and *Sequoiadendron*, respectively--they are sister taxa. However, the coast redwood has adapted to life on the coast, where the giant sequoia has evolved in inland, higher elevation forests with much more extreme climatic conditions. How can this be seen in the structure of their leaves?



Figure $2.6.2.2.2$: The image on the left shows the adaxial (upper) side and the image on the right shows the abaxial (under) side of coast redwood leaves. Note that, particularly in the photo on the left, the leaves look shiny. This is due to the presence of a thick cuticle. The stomata are also concentrated on the underside of the leaf, as indicated by the black arrow in the image on the right. They are clustered in two silvery rows on each leaf, called a stomatal bloom. However, for xerophytic leaves, these are relatively flat, with a fairly standard surface area to volume ratio. Photos by Maria Morrow, CC-BY 4.0.

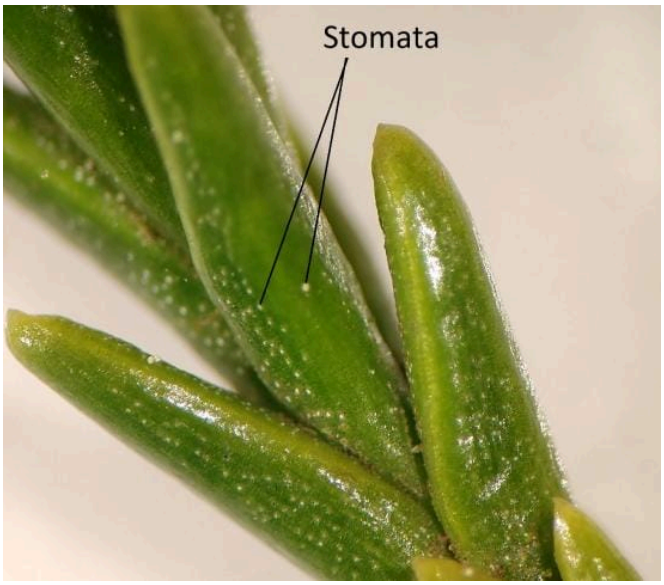


Figure \(\
PageIndex
{3}\):
These giant sequoia leaves were retrieved from a tree planted in a coastal environment, so the d
ifferences here represent evolutionary history, alone. Much like the coast redwood, these shiny leaves have a thick cuticle. The big difference to note is the thickness of these leaves, maintaining a much lower surface area to volume ratio than the coast redwood. The second thing to note is the orientation of the leaves. They are held much more closely together, reducing exposure to the wider environment. Two stomata are indicated in the image, though there are many. They are present on both adaxial and abaxial leaf surfaces.

Photo by Maria Morrow,
CC-BY 4.0
.

Figure 2.6.2.2.4), a thick cuticle surrounds the outside, coating the epidermis. Beneath the epidermis are several layers of tightly packed, small cells: the hypodermis. Stomata are sunken, located within the hypodermis. Under the hypodermis are the highly invaginated mesophyll cells. Further to the inside is a suberized ring of cells called the endodermis, just like in the root, which surrounds the vascular tissue. Transfusion tissue is located between the endodermis and the vascular tissue.

There are also resin canals that ring the needle, appearing as holes surrounded by small cells. These secrete **resin** to protect the plant. Resin is a sticky fluid rich in compounds that protect the plant. It flows through canals in the stems, roots, and leaves and can rush to fill a wound. The resin can gum up the mouth parts of herbivorous insects, offer chemical defense against pathogenic bacteria and fungi, and harden to close the wound (much like a scab).

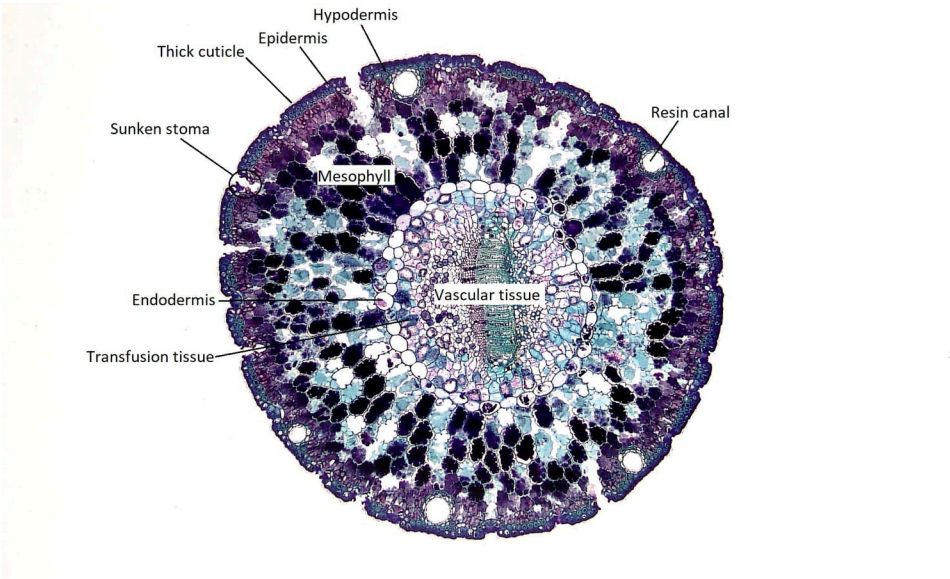


Figure 2.6.2.2.4: Most pine needles you see in botany are flat on one side, however, they also come in round. The tissues of this xerophytic leaf are labeled in the diagram. The epidermis is a single layer on the outside, coated by a thick cuticle. Under the epidermis, there are several layers of similar small, tightly packed cells (hypodermis). Within the hypodermis region, there are sunken stomata. Resin canals look like large holes and are present periodically around the cross section near the hypodermis. The highly invaginated mesophyll cells are between the hypodermis and endodermis. The endodermis is a single ring of cells that surrounds the vascular tissue. Within the endodermis, there is a single vascular bundle surrounded by transfusion tissue. Image by Fayette A. Reynolds M.S., Public Domain with labels added by Maria Morrow.

Reproduction in Conifers

Unlike other gymnosperms, conifers are **monoecious**, meaning megastrobili and microstrobili are produced on the same plant. In general, megastrobili tend to be larger and longer-lived, while microstrobili are smaller and ephemeral, disintegrating after pollen is dispersed (see Figure 2.6.2.2.5 – 6). Some conifers, like junipers (*Juniperus*) and yews (*Taxus*), lack woody cones and have fleshy scales. In all, conifer life cycle takes up to two years. Conifers do not have flagellate spermatozoa; their non-motile male gametes (spermatia) move inside long, fast-growing pollen tube.

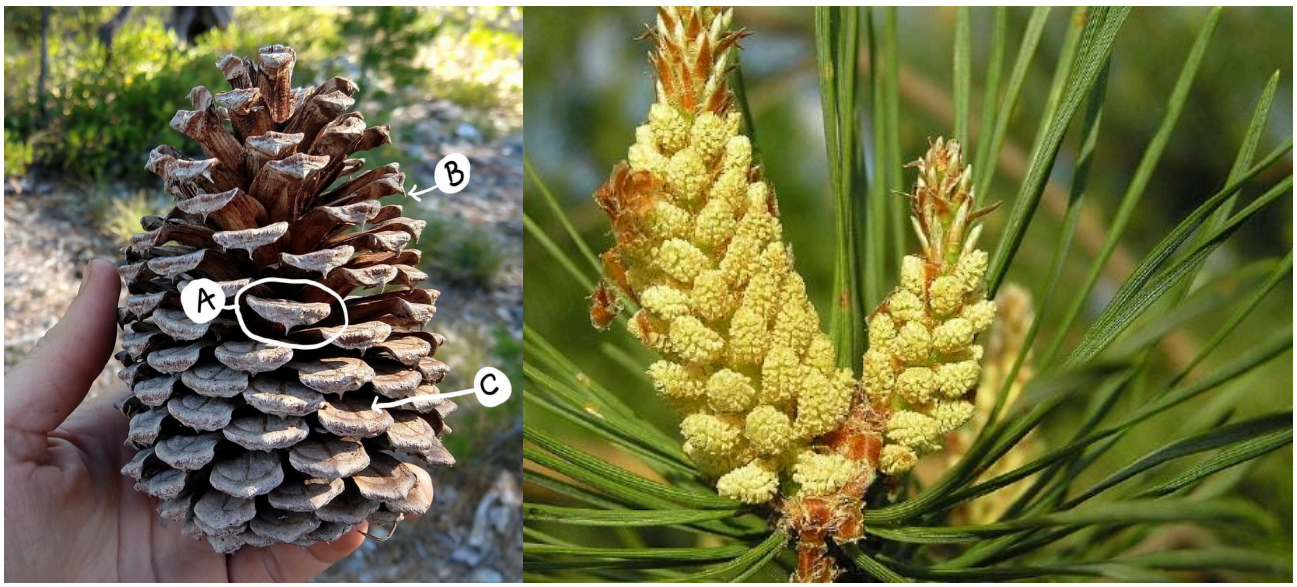


Figure 2.6.2.2.5: The two images above show the strobili of the genus *Pinus*. On the first image, a seed cone from a Jeffrey pine does not have visible bracts but it does showcase a pointy umbo (B) at the tip of the ovuliferous scale (A). Dual markings where two seeds developed on each scale (C). Pines tend to form woody megastrobili (seed cones) that decay slowly, the one pictured is likely over a year old. In contrast, the second image shows a cluster of microstrobili. They are small with papery scales that will fall off after the pollen has dispersed. First photo by Maria Morrow, CC-BY 4.0. Second photo by Beentree, CC BY-SA 3.0.

The female cones are larger than the male cones and are positioned towards the top of the tree; the small, male cones are located in the lower region of the tree. Because the pollen is shed and blown by the wind, this arrangement makes it difficult for a gymnosperm to self-pollinate.

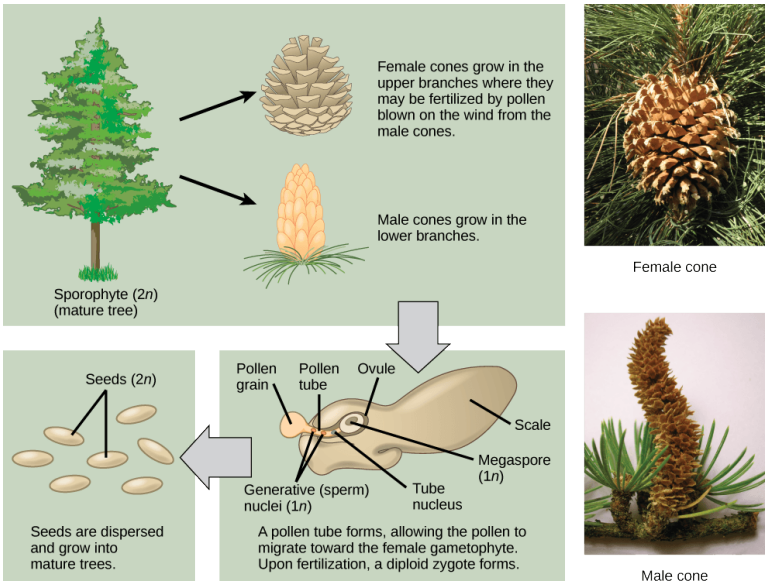


Figure 2.6.2.2.6: This image shows the life cycle of a conifer. Pollen from male cones blows up into upper branches, where it fertilizes female cones. Examples are shown of female and male cones. Descriptive text: The conifer life cycle begins with a mature tree, which is called a sporophyte and is diploid (2n). The tree produces male cones in the lower branches, and female cones in the upper branches. The male cones produce pollen grains that contain two generative (sperm) nuclei and a tube nucleus. When the pollen lands on a female scale, a pollen tube grows toward the female gametophyte, which consists of an ovule containing the megaspore. Upon fertilization, a diploid zygote forms. The resulting seeds are dispersed, and grow into a mature tree, ending the cycle. Both the male and female cone are made up of rows of scales, but the male the female cone is round and wide, and the male cone is long and thin with thinner scales. (credit “female”: modification of work by “Geographer”/Wikimedia Commons; credit “male”: modification of work by Roger Griffith)

Seed Cones

The megastrobilus, or seed cone, is composed of spirally arranged megasporophylls called ovuliferous scales (Figure 2.6.2.2.7). Each scale produces two megasporangia, which contain a diploid megasporocyte (also called a megaspore mother cell). Each megasporocyte undergoes meiosis. Only one of the four cells produced will survive to develop into a haploid megagametophyte and the other three will die. The megagametophyte is part of the ovule and contains archegonia, each with an egg cell inside (Figure 2.6.2.2.8). The megagametophyte is retained within the megasporangium, which becomes the nucellus. Surrounding the nucellus is the integument, which is initially continuous with the ovuliferous scale and has a small opening called a micropyle.

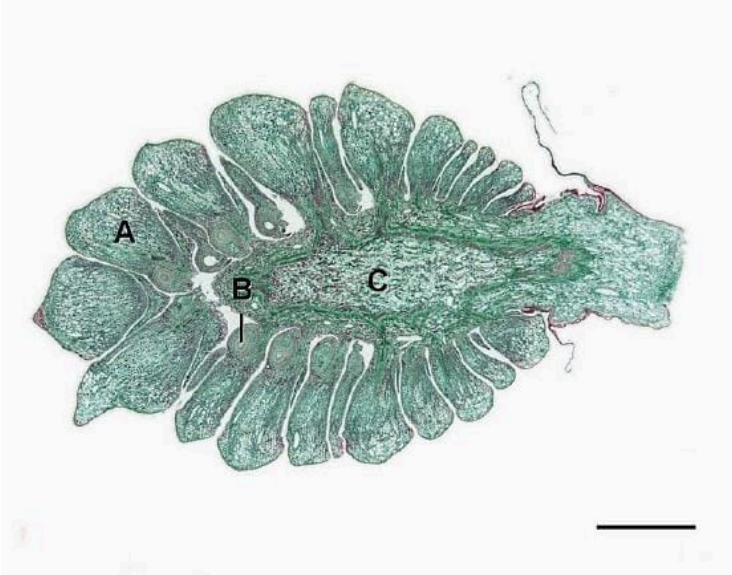


Figure 2.6.2.2.7: A micrograph of a longitudinal section through a yearling *Pinus* megastrobilus, labeled as follows: A=Ovuliferous scale, B=Megasporangium, C=Cone axis. Many ovuliferous scales surround the cone axis. Each scale has a megasporangium at its base, where it connects to the axis. Scale=1.0mm. Image by Jon Houseman, CC BY-SA 4.0, via Wikimedia Commons.

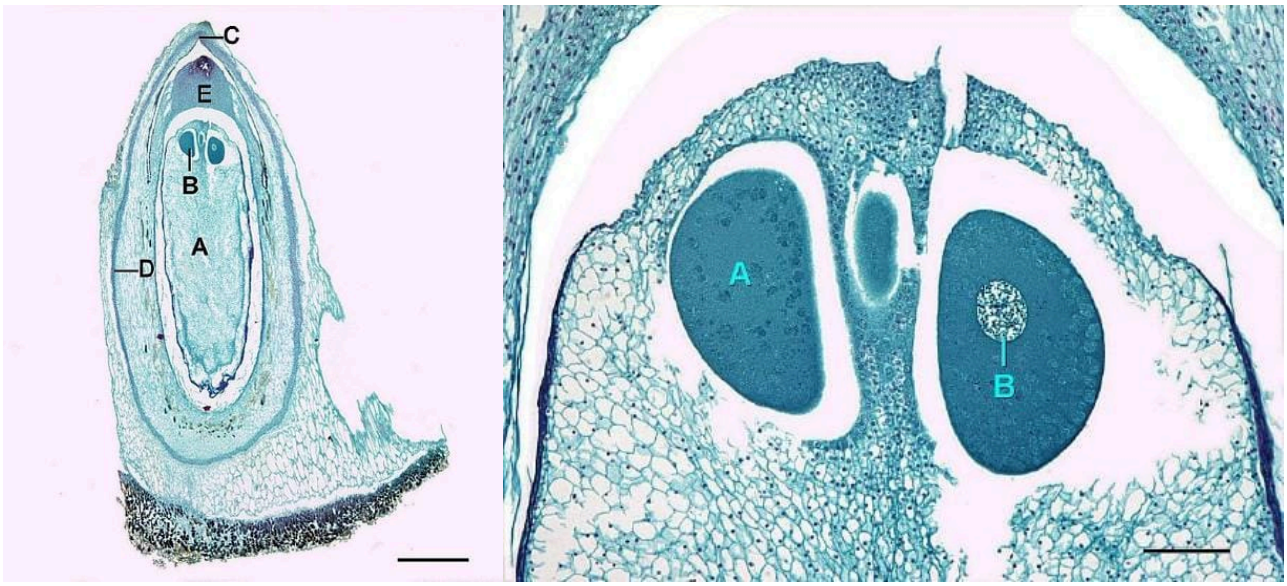


Figure 2.6.2.2.8: The first image is a micrograph of a *Pinus* ovule, labeled as follows: A=Gametophyte, B=Egg cell, C=Micropyle, D=Integument, E=Megasporangium. The integument lines the outside with a small hole at the tip (micropyle). Inside the integument is the megasporangium. The megasporangium surrounds the gametophyte, which has two egg cells within it, on the end closest to the micropyle. Scale=0.8mm. The second image is a closer view, showing the eggs within the megagametophyte, labeled as follows: A=Egg cell, B=Egg nucleus. The eggs are large and one has a nucleus visible. Scale=0.31mm. Images by Jon Houseman, CC BY-SA 4.0, via Wikimedia Commons.

Pollen Cones

Microstrobili (pollen cones) are formed from overlapping microsporophylls that bear multiple microsporangia. Within the microsporangium, there are microsporocytes (also called microspore mother cells), diploid cells that undergo meiosis to produce haploid microspores. Microspores grow by mitosis into microgametophytes, AKA pollen, within the microsporangium. The microgametophyte in gymnosperms is the four-celled, "winged" pollen grain.

Within the pollen grain (Figure 2.6.2.2.9), there is a **generative cell**, a **tube cell**, and two **prothallial cells**. On either side of the pollen grain, two wing-like structures called **air sacs** may help orient the pollen grain toward the ovule.



Figure 2.6.2.2.9: The first image is a long section through a pine microstrobilus that shows inside a microsporangium. Each microsporangium is produced on a leaf-like structure called a microsporophyll that emerges from the cone axis. Within the microsporangium, many mature pollen grains are visible. You can tell the pollen grains are mature at this magnification by the presence of the air sacs. In the second image, we see a closer image of pollen grains. The two ear-like air sacs flank the four cells enclosed in the center: the tube cell, generative cell, and two prothallial cells. The tube cell takes up most of the internal space and its nucleus is about the same size, if not a little bigger, than the entire generative cell. The two prothallial cells are squished against the edge opposite the air sacs and are not really distinguishable in this image. Photos by Maria Morrow, CC-BY 4.0.

A grain of pollen will be transported on the wind and, if lucky, it will land on a seed cone. The seed cone has a drop of sugary liquid (a **pollen drop**) that it secretes, then retracts, pulling the pollen in toward the ovule. This stimulates the tube cell to germinate a **pollen tube**, while the generative cell divides by mitosis to produce two **spermatia** (no flagella). These spermatia travel with the pollen tube, through the micropyle, and into an archegonium where one will fertilize an egg (Figure 2.6.2.2.10 – 11). It takes approximately one year for the pollen tube to grow and migrate towards the female gametophyte! When fertilization occurs, the micropyle closes and the integument becomes the **seed coat**.

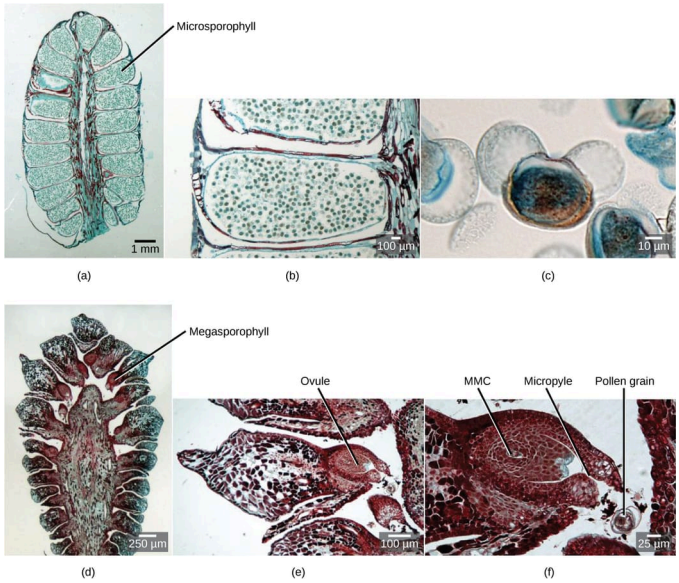


Figure 2.6.2.2.10: These series of micrographs shows male and female gymnosperm gametophytes. (a) This male cone, shown in cross section, has approximately 20 microsporophylls, each of which produces hundreds of male gametophytes (pollen grains). (b) Pollen grains are visible in this single microsporophyll. (c) This micrograph shows an individual pollen grain. (d) This cross section of a female cone shows portions of about 15 megasporophylls. (e) The ovule can be seen in this single megasporophyll. (f) Within this single ovule are the megaspore mother cell (MMC), micropyle, and a pollen grain. Descriptive text: Part a shows a cross section of a male cone, which is oval with a flattened bottom. A stem-like structure runs up the middle, and oblong microsporophylls radiate from either side. Migrograph b shows a blowup of a microsphorphyll, which is filled with round pollen grains. Micrograph C shows a blowup of a pollen grain, which is oval with two lobes and resembles Mickey Mouse. Part D shows a cross section of a female cone, which is similar in shape to the male cone but with a wider central structure. Megasporophylls radiate from either side of this structure. At the base the megasprophylls are narrow, and the widen out into a roughly diamond shape. Part E shows a blowup of the megasprophyll, which has an oval ovule at its base. Part F shows a blowup of the ovule. The megaspore mother cell is at the center. An opening called a micropyle allows entry of the pollen tube from the base. (credit: modification of work by Robert R. Wise; scale-bar data from Matt Russell)

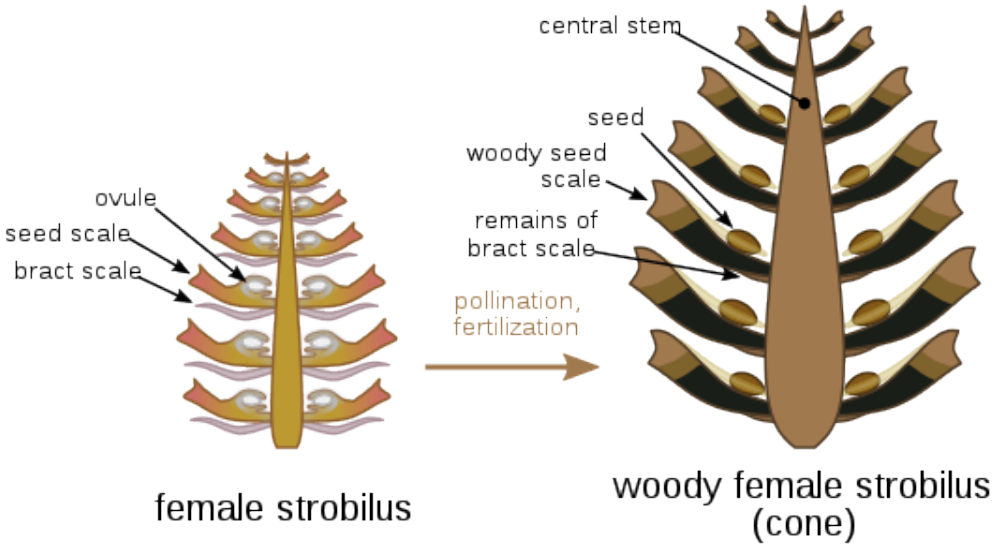


Figure 2.6.2.2.11: The megastrobilus before (left) and after (right) fertilization. In the unfertilized cone on the left, there is an ovule on top of each ovuliferous scale. In the fertilized cone on the right, the ovule has become a seed, the cone has become woodier, and the sterile bract has been reduced. Image by Nefronus, CC BY-SA 4.0, via Wikimedia Commons.

The zygote will grow and develop as an embryo within the seed, nourished by the megagametophyte tissue, as well as the nucellus (Figure 2.6.2.2.12). The scales of the cones are closed during development of the seed. Seed development takes another one to two years. Once the seed is ready to be dispersed, the bracts of the female cones open to allow the dispersal of seed; no fruit formation takes place because gymnosperm seeds have no covering. The seed will be dispersed by wind or animals and germinate to grow into a diploid pine tree once again.

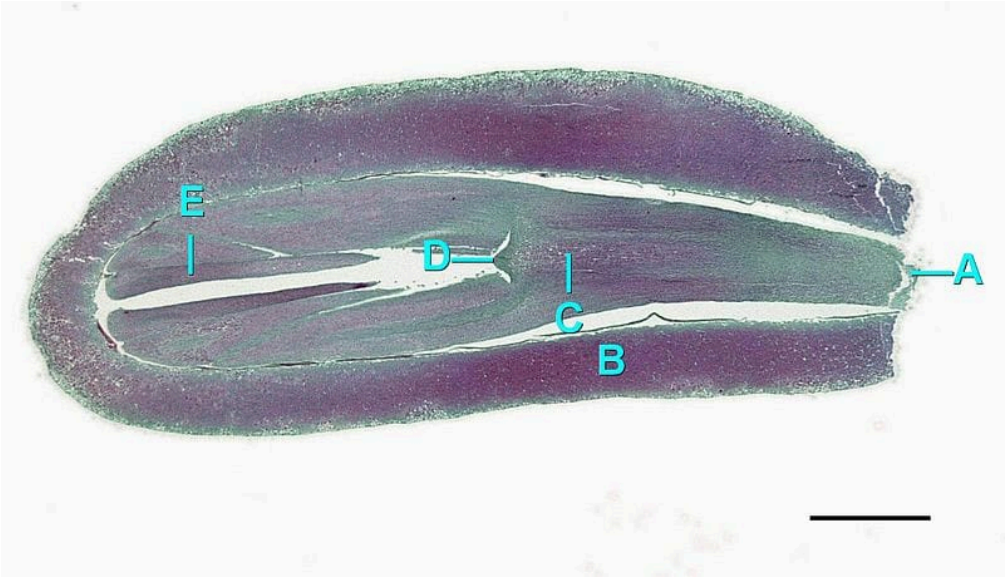


Figure 2.6.2.2.12: A longitudinal section through a fertilized pine seed. The embryo is developing within the integument, labeled as follows: A=Root cap, B=Integument, C=Hypocotyl-root axis, D=Shoot apical meristem, E=Cotyledons. The integument forms the outer layer, surrounding the embryo. The embryo has a root cap at one end, connected to the shoot apical meristem by the hypocotyl-root axis. Two arm-like cotyledons flank the shoot apical meristem. Scale=1.3mm. Photo by Jon Houseman, CC BY-SA 4.0, via Wikimedia Commons.

The Full Life Cycle

Video 2.6.2.2.1 is an extremely helpful narrated animation of the pine life cycle. You should watch this video or some other walkthrough of the pine life cycle before attempting to interpret the complex diagram (Figure 2.6.2.2.13).

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 2.6.2.2.1: A narrated video of the pine life cycle, sourced from Youtube.

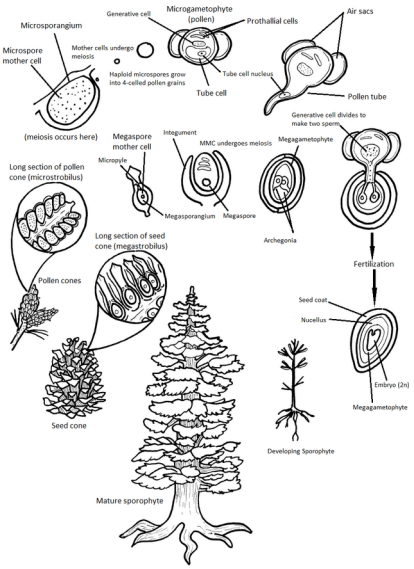


Figure 2.6.2.2.13: This is an illustrated diagram of the pine life cycle. Starting at the bottom of the image, there is a pine tree. This is the mature sporophyte (2n). It will produce both seed cones and pollen cones because it is monoecious. Seed cones will produce two megasporangia on each ovuliferous scale, each one surrounded by an integument. Within the megasporangium, a megaspore mother cell (2n) undergoes meiosis to produce four megaspores (n). Three die and one remains, developing by mitosis into the megagametophyte. The megagametophyte produces two archegonia, each with an egg. This trajectory occurs through the center of the diagram. Jumping back to the pollen cone, microsporangia are produced on each microsporophyll of the pollen cone. Initially, they are filled with microspore mother cells (2n) that then undergo meiosis to produce microspores (n). These microspores grow by mitosis (though only two rounds) into 4-celled microgametophytes: pollen. Each pollen grain is composed of two ear-like air sacs on the outside, a large tube cell, a small generative cell, and two tiny prothallial cells. The mature pollen grains are dispersed on the wind to seed cones where the tube cell will form a pollen tube into the megagametophyte by entering through a gap in the integument called the micropyle. The generative cell divides to produce to sperm cells, which travel down the pollen tube to fertilize an egg. Once fertilized, the integument closes, forming the seed coat. The embryo develops within the seed, consuming the megagametophyte and the megasporangium (now called the nucellus) as it grows. The seed is dispersed and, if in the right conditions, the embryo emerges from the seed coat and develops into a mature sporophyte. Diagram by Nikki Harris CC BY-NC with labels added.

Gnetophytes

Gnetophytes are a small group with only three genera that, excepting from their opposite leaves, seem not at all similar: *Ephedra*, *Welwitschia*, and *Gnetum*. *Ephedra* are horsetail-like desert leafless shrubs, *Gnetum* are tropical trees, and *Welwitschia* are strange desert plants that form two large, continuously growing leaves (Figure 2.6.2.2.14). Gnetophytes represent an anatomically and genetically difficult group to classify. They have several traits in common with angiosperms, such as vessel elements in the xylem, double fertilization, and a covering over their seeds. Even their leaves are angiosperm-like, with netted venation. However, these traits are convergently evolved, meaning that angiosperms and gnetophytes each evolved these traits separately. Genetically, recent studies have placed the gnetophytes as a sister group to the Pinaceae (pine family) within the conifers. This would mean that pines, firs, and spruces are more closely related to strange gnetophytes like *Ephedra* than they are to other conifers like redwoods, cedars, and Pacific yew. However, the true nature of this evolutionary relationship remains murky and contentious.



Figure 2.6.2.2.14: These three genera of plants represent the gnetophytes: *Ephedra* (left), *Gnetum* (center two) and *Welwitschia* (right). *Ephedra* has thin stems with scale-like leaves. *Gnetum* has large, flat leaves on very angiosperm-like plants. *Welwitschia* has just two leaves emerging opposite each other, no stem is visible.

Ephedra has archegonia, but in *Gnetum* and *Welwitschia* they are reduced. On the other hand, *Ephedra* and *Gnetum* have **double fertilization**, a process that you will see in angiosperms where both male nuclei fuse with cells of the one female gametophyte. Double fertilization in gnetophytes results in two competing embryos, and only one of them will survive in the future seed.

Both *Gnetum* and *Welwitschia* have vessel elements (like angiosperms). *Gnetum* also has angiosperm-like opposite leaves with netted venation, like the coffee tree (however, this probably is a result of modification of dichotomous venation). Ovules are solitary and covered with an additional outer integument; the male gametes are spermatia moving with the pollen tube instead of swimming (no flagella).

Welwitschia is probably most outstanding among gnetophytes. There is only one species and it occurs only in the Namibian desert. The best way to describe this plant is an “overgrown seedling.” It has a small trunk with two wide leaves that have parallel venation. The secondary thickening is anomalous, the wood has vessels. This plant is insect-pollinated and its winged seeds are dispersed by the wind. Fertilization is not double, but, along with pollen tubes, involves some interesting structures: prothallial tubes which grow from female gametophyte and meet with pollen tubes.

Characteristics of Gnetophytes

- Angiosperm-like features: vessel elements, double fertilization, fruit-like ovule coverings
- **Dioecious**. Female plants have covered ovules, while male plants have pollen cones.
- Leaves xerophytic with **opposite arrangement**
- Primarily insect pollinated; brightly colored seeds are dispersed by birds

Welwitschia mirabilis

This strange plant grows in the desert of Namibia. It has two large leaves that grow from a **basal meristem**. As the plant gets older the leaves split and start to look like numerous long tentacles (Figure 2.6.2.2.15). The tips of the leaves are ragged, as these are the oldest parts. The leaves are shiny and the setting is dry, indicating their xerophytic nature. In the center, where the two leaves meet, plants will produce either megastrobili or microstrobili (Figure 2.6.2.2.16).



Figure 2.6.2.2.15: A *Welwitschia* at the petrified forest, west of the town of Khorixas, Namibia. Photo by Nanosanchez, CC BY-SA 3.0, via Wikimedia Commons.



Figure 2.6.2.2.16: Strobili of *Welwitschia mirabilis*. Megastrobili (first photo) are larger and rounder, composed of tightly overlapping megasporophylls. Microstrobili (second photo) are smaller and thinner than the megastrobili. First image by C T Johansson, CC BY-SA 3.0, via Wikimedia Commons. Second image by Krzysztof Ziarnek, Kenraiz, CC BY-SA 4.0, via Wikimedia Commons.

Ephedra

Ephedra spp. have scale-like, opposite leaves produced on tough, photosynthetic stems. They produce swollen megastrobili that look like fruits (Figure 2.6.2.2.17), and microstrobili have extruded microsporangia, making them look like catkins (a type of inflorescence produced by some angiosperms, (Figure 2.6.2.2.18). Some *Ephedra* species produce alkaloids that have been extracted for stimulant use, including ephedrine and pseudoephedrine.



Figure 2.6.2.2.17: A thin stem of *Ephedra* showing opposite leaf arrangement of two scale-like leaves. Megasporophylls are swollen and red, making the megastrobilus appear fruit-like. Seeds are produced within these structures. Descriptive text: Thin green stems end in swollen red structures that appear to be separated into a few different segments. Two tiny, scale-like leaves emerging from either side of a node. Photo by Germán Escorza, CC BY-SA 4.0, via Wikimedia Commons.



Figure 2.6.2.2.18: Microstrobili of a male *Ephedra viridis*. These small structures look like inflorescenses with anthers emerging. From between the microsporophylls, branching structures emerge, topped with microsporangia releasing pollen. Photo by Stan Shebs, CC BY-SA 2.5, via Wikimedia Commons.

Gnetum

Gnetum spp. could easily be mistaken for flowering plants. They produce leaves with netted venation and fruit-like megastrobili. These plants are restricted to tropical areas and generally take on a tree-like habit.



Figure 2.6.2.2.19: *Gnetum* strobili. The leaves have a larger central vein with smaller, branching side veins (netted venation). In the first photo, a "female" plant has megastrobilus is covered with swollen structures that look like berries. These will eventually redden, increasing the berry similarity. In the second photo, a thin microstrobilus is shown on a "male" plant. These plants look very much like angiosperms and very little like gymnosperms. First photo by BotBln, CC BY-SA 3.0, via Wikimedia Commons. Second photo by Kembangraps, CC BY-SA 3.0, via Wikimedia Commons.

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2.6.3: ANGIOSPERMS

Learning Objectives

- Describe the shared derived characteristics of angiosperms.
- Connect these characteristics to the stressors these plants would have faced.

At the end of the Permian period, there was the largest mass extinction this planet has ever experienced. It is estimated that 96% of species that lived at that time went extinct. This event signaled the downturn for some groups and opened up space for others to emerge. The exact timing of the emergence of angiosperms is unknown, so it is difficult to relate their evolution to specific climatic conditions. However, there is relatively new fossil evidence that may place flowering plants as early as the Jurassic period, 174 mya. This was the age of the dinosaurs and coincides with the emergence of the first feathered dinosaurs -- birds! Much like the insects, birds would present interesting opportunities for this new group of plants, working as both pollinators and seed dispersers.

Angiosperms can be distinguished from other plants by a set of specialized characteristics that allowed them to compete in an already full world. The (usually) easiest thing to identify about an angiosperm are its **flowers**. These collections of modified leaves allowed this group of plants to attract pollinators and increase the chances of successful fertilization. Once pollinated, the fertilized seeds are encased in a protective ovary whose structure can be specialized for different methods of dispersal, such as animal ingestion, animal attachment, flotation, or wind dispersal. This protective ovary and the encased seed(s) are more commonly called a **fruit**. Inside the developing seeds, angiosperms provide an additional food source to the developing zygote, the **endosperm**.

Competing with the gymnosperms for access to sunlight was perhaps hopeless, so the angiosperms adapted ways to work smarter, not harder. In the xylem, they evolved large diameter conducting cells for rapid water uptake called **vessel elements**, though this made them vulnerable to freezing conditions. In the phloem, sieve cells evolved into **sieve tube elements**, increasingly specialized for transportation of photosynthates.

As you might have guessed from the vast number of species, angiosperms occupy incredibly diverse habitats and span a range of morphologies, from tiny plants floating as a film on the surface of a pond (Figure 2.6.3.1) to towering Eucalyptus trees dominating the forests of Tasmania, rivaling redwoods in height.



Figure 2.6.3.1: The world's smallest flowering plants belong to the genus *Wolffia*. Flowers are produced in a cavity within the plant, the top of which is visible here as a small depression in the larger compartment. Photo by Stefan.lefnaer, CC BY-SA 4.0, via Wikimedia Commons.

Selection Pressures and Drivers

1. **Competition for space**. Present day gymnosperms include the tallest, most massive, and some of the oldest organisms on the planet. With this in mind, you can imagine that they would be difficult to compete with. Angiosperms needed to evolve more efficient methods of transporting water and photosynthates, fertilization, and survival of offspring.
2. **Animals**. The primary response to animals that we see in gymnosperms is prevention of herbivory, though there is some insect pollination and animal seed dispersal. While herbivory is still a driver of selection for angiosperms, animals also served as a more efficient method of pollen delivery. Insects and birds could be lured in with sugary nectar or scents and colors that mimicked other resources, then dusted with pollen as they investigated. If the lures were specialized enough, they would continue seeking the same resource, leading them to another plant of the same species. These scents, colors, and nectar resources were produced by structures that also produced pollen and ovules -- the flower. Similarly, fruits allowed for the dual purpose of protecting seeds and co-opting animals as dispersal agents, whether by ingestion or attachment. Some fruits evolved production of sugary tissues and bright colors to attract animals, while others evolved hairs or spines to latch onto their bodies.

2.6.3.1: Flowers

2.6.3.2: Angiosperm Life Cycle

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2.6.3.1: Flowers

Learning Objectives

- Identify the components of a flower and to which whorl each belongs.
- Write and interpret floral formulas.
- Differentiate between flowers and inflorescences.
- Explain the difference between raceme-based and cymose inflorescences.

Flowers are sets of highly modified leaves that function to attract a pollinator or, if no animal pollinator is used, to optimize spore dispersal in some way. Over the course of evolutionary history and coevolution, this has lead to an incredible diversity of shape, size, color, smell, and just about any other characteristic you can think of. Because most plants are angiosperms and because flowers are often so diverse, learning the terminology to describe flowers is a major step in learning to identify plants.

The modified leaves in flowers are called **sepals**, **petals**, **stamens**, and **carpels** (Figure 2.6.3.1.1). These components are arranged in whorls and attach to an area called the **receptacle**, which is at the end of the stem that leads to the flower. This stem is called the **peduncle**. In the case of an inflorescence, where multiple florets are produced in place of a single flower, the stems leading to the florets are called pedicels (Figure 2.6.3.1.2).

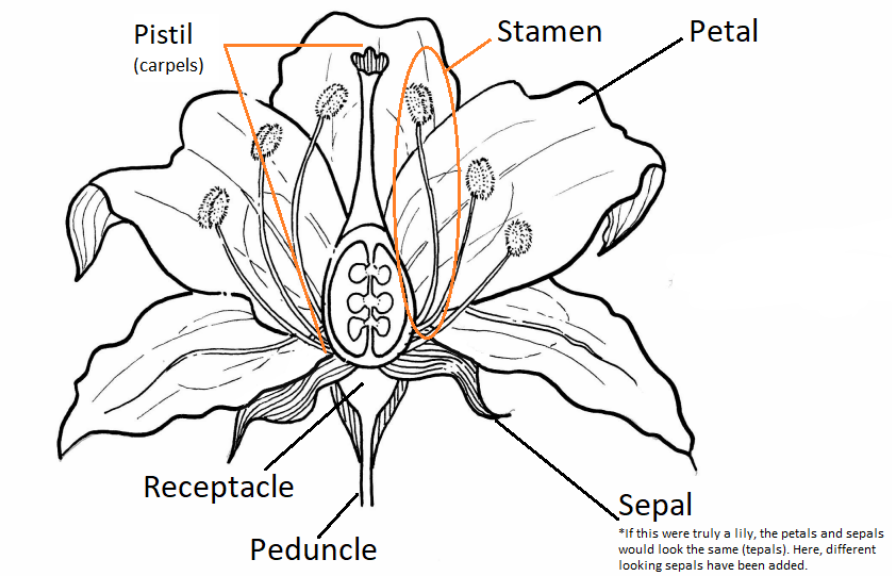


Figure 2.6.3.1.1: This diagram shows a long section through a flower. Starting from the bottom, there is a stem called the peduncle. The peduncle terminates in a region called the receptacle, where all of the parts of the flower are attached. Sepals are found on the outside of the flower, two are visible here, with petals located just within the ring of sepals. There are five petals visible. Inside the petals, six stamens encircle a central pistil (composed of fused carpels). Diagram by Nikki Harris CC BY-NC with labels added.



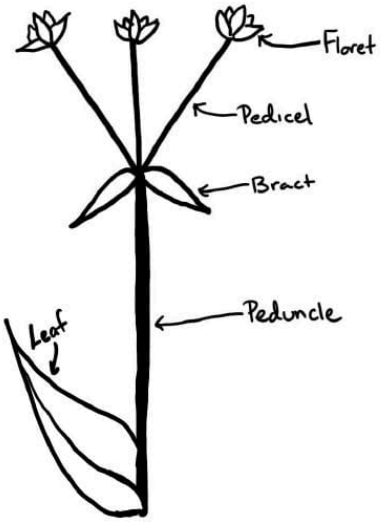


Figure 2.6.3.1.2: An image of an *Allium* inflorescence. Many small florets on stalks (pedicels) emerge from a central point at the tip of the peduncle. At this junction, papery leaves (bracts) can be seen. These features are labeled in a sketch (second image). Photo by ramazan_murtazaliev, CC-BY-NC. Sketch by Maria Morrow, Public Domain.

The general characters that a flower has are whorl morphology, sex, merosity, symmetry, and the position of the gynoecium. **Merosity** is simply the number of parts in each whorl of a plant structure, whether it is the number of sepals, petals in a corolla, or the number of stamens. Each of these characters will be discussed below.

Whorls

The outermost whorl of a flower is called the **calyx** and is composed of **sepals**. Inside the calyx is the **corolla**, which is composed of **petals**. The sepals are often smaller and less colorful than the petals, but this general rule can be misleading. For example, lilies and tulips have identical sepals and petals (called **tepals**, these can be seen in the florets in Figure 2.6.3.1.2). The only way you can distinguish between them is by location: Which whorl is on the outside?

The Perianth: Calyx and Corolla

Together, the calyx and corolla are called the **perianth** (peri- meaning around, anth- meaning flower; Figure 2.6.3.1.3). The calyx is the outermost whorl of the flower. In most coses, the sepals are not showy--lacking bright colors and typically smaller--and instead serve a protective function in the developing flower. The corolla is the whorl just within the calyx. Petals tend to be the showy part of the flower, specialized for attracting animal pollinators.

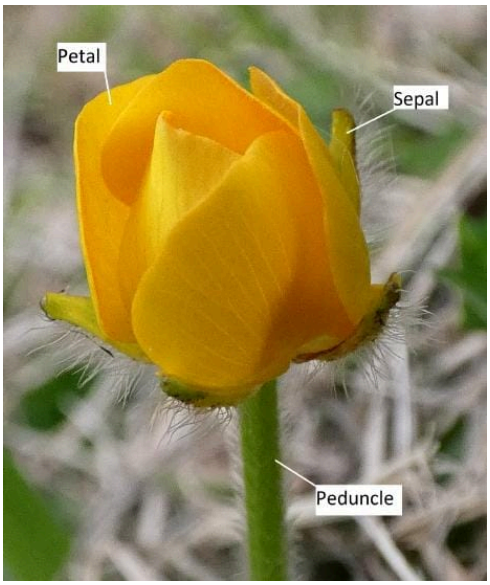


Figure 2.6.3.1.3: A closed buttercup (*Ranunculus* sp.) flower shows the entire perianth. The sepals are smaller and covered in long trichomes. There are four sepals visible, though a fifth hides on the other side. Inside the sepal whorl (calyx), there are five overlapping, yellow petals. These petals form the corolla. Photo by Maria Morrow, CC BY-NC.

Reproductive Whorls: Androecium and Gynoecium

Inside the perianth is the **androecium** (house of man), a whorl composed of **stamens**. Each stamen has a long **filament** holding up pollen sacs called **anthers** (Figure 2.6.3.1.4 – 5). Each lobed anther contains microsporangia, within which meiosis of the diploid microspore mother cells in the anther produces four haploid microspores. Each of these develops into a pollen grain consisting of two cells: a larger vegetative cell (the tube cell), inside of which is a a smaller germ cell (also called the generative cell). At some point, depending on the species, the germ cell divides by mitosis to produce 2 spermatia.

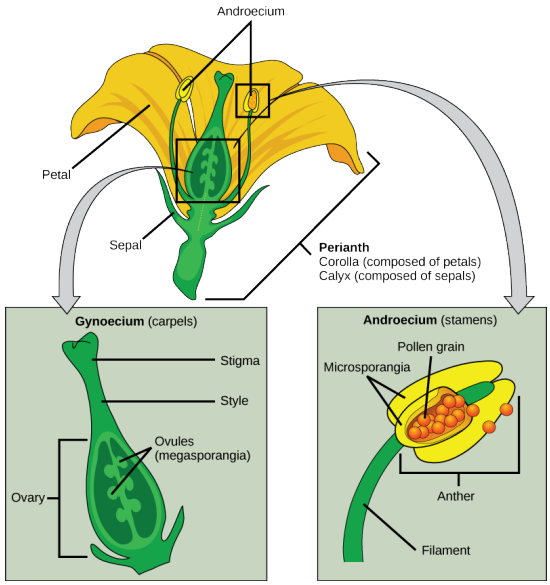


Figure 2.6.3.1.4: The four main parts of the flower are the calyx, corolla, androecium, and gynoecium. The androecium is the sum of all the male reproductive organs, and the gynoecium is the sum of the female reproductive organs. Descriptive text: The calyx (outermost whorl) is composed of sepals and the corolla (inside the calyx) is composed of petals. These two whorls form the perianth. At the center of the perianth is a vase-like structure called the carpel. A flower may have one or more carpels, but the example shown has only one. The narrow neck of the carpel, called the style, widens into a flat stigma at the top. The ovary is the wide part of the carpel. Ovules, or megasporangia, are clusters of pods in the middle of the ovary. The androecium is composed of stamens which cluster around the carpel. The stamen consists a long, stalk-like filament with an anther at the end. The anther shown is tri-lobed. Each lobe, called a microsporangium, is filled with pollen. (credit: modification of work by Mariana Ruiz Villareal)

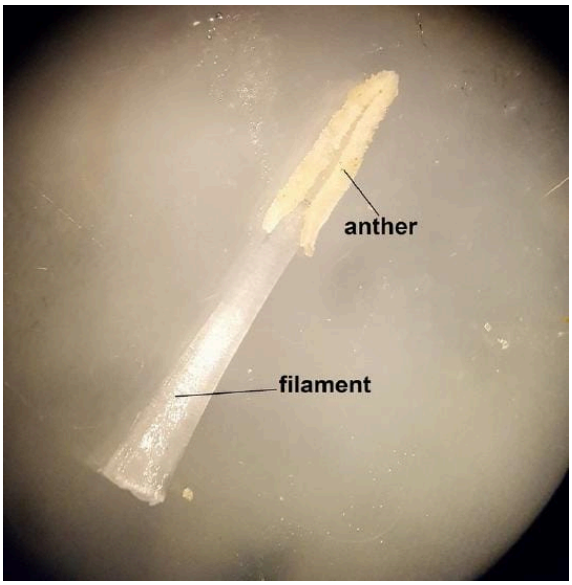


Figure 2.6.3.1.5: A single stamen that has been removed from a flower. The filament is long and flattened. At the end of the filament, there is an anther that has split partially open, releasing pollen grains. Photo by Melissa Ha, CC BY-NC .

Inside the androecium is the **gynoecium** (house of woman), which is composed of **carpels**. Each carpel has an **ovary** at the base where **ovules** are housed. A **style** emerges from the ovary and is topped by the **stigma** (Figure 2.6.3.1.6), where pollen is deposited. A carpel consists of a single ovary, style and stigma. Often several carpels are fused into a single structure, referred to as a **pistil**.

Within the ovule, a megasporangium produces a megaspore mother cell. Meiosis of the megaspore mother cell in each ovule produces 4 haploid cells, a large megaspore and 3 smaller cells that disintegrate. This megaspore develops into the megagametophyte, all within the ovule. Pollen grains land on the stigma and must grow a tube down the style to reach the ovule and complete fertilization.

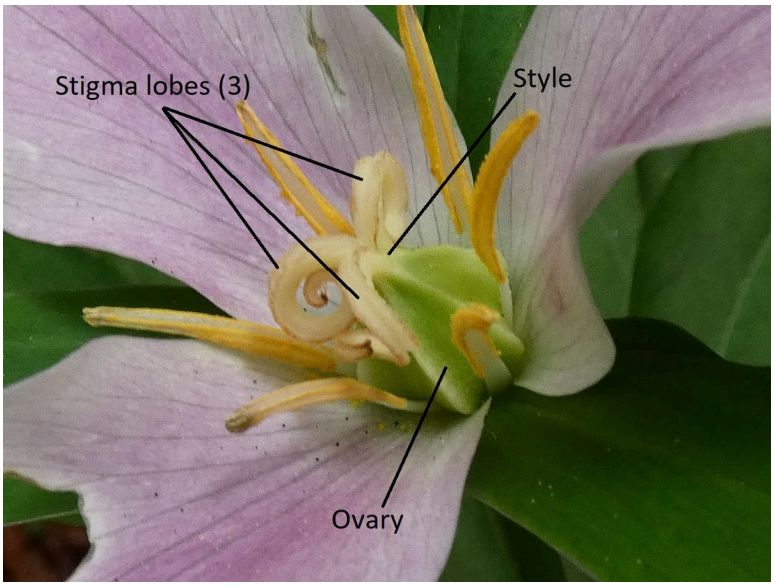


Figure 2.6.3.1.6: All of the whorls of this Trillium flower are visible in this picture. The sepals are on the exterior and green. The three petals are a light pink. There are six stamens, each with much longer anthers than filaments. The stamens encircle the enlarged ovary of this fertilized flower, which is grooved and beaked into an odd shape. A short style connects the ovary to three long, curling stigma lobes. Is this flower a monocot or eudicot? Photo by Maria Morrow, CC BY-NC.

Incomplete Flowers

Most flowers are composed of four whorls. If all whorls are present, a flower is said to be both **complete** and **perfect**. If any whorl is missing, the flower is **incomplete** (Figure 2.6.3.1.7). If one of those missing whorls is either the androecium (pollen-producing) or gynoecium (seed-producing), the flower is also **imperfect** (Figure 2.6.3.1.8).



Figure 2.6.3.1.7: This wild ginger flower (*Asarum caudatum*) has no corolla. It is incomplete, but it is still perfect. The hairy sepals are fused together at the base, then split into long, pointed tips that extend out like tendrils. These flowers are normally a deep wine red. Photo by mhays, CC-BY-NC.

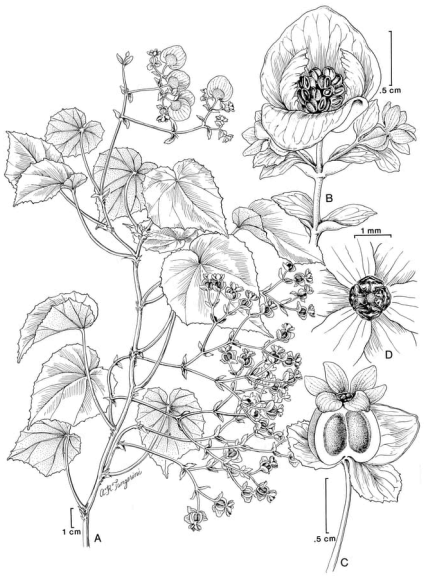


Figure 2.6.3.1.8: Drawing of *Begonia ynesiae*, which has imperfect flowers. Flowers either have an androecium or gynoecium but not both. A shows the overall palnt struture, B shows staminate flower (which has an androecium but no gynoecium), C and D show pistillate flowers (which has a gynoecium but no androecium). This species is named after Ynés Mexía, the first female Mexican-American botanist. She collected over 145,000 specimens and discovered more than 500 new species. You can learn more about her life and work here. Image by Ynés E. J. Mexía (public domain).

Evolution seems to favor (and be favored by) genetic variability. Genetic variability is promoted by **outbreeding -** sexual reproduction between genetically dissimilar parents. Just why sexual reproduction is so popular throughout the world of living things is still a hotly-debated question, but the fact remains.

Plants, being anchored in position, have a special problem in this regard. Many employ the services of animals (e.g., insects, birds, bats) to transfer pollen from plant to plant. But if the flowers have both sex organs, what is to prevent the pollen from fertilizing

its own eggs? Plants have evolved a variety of solutions. One of these is to produce imperfect flowers.

There are two types of imperfect flowers: staminate flowers contain only an androecium (Figure 2.6.3.1.9), and carpellate (or pistillate) flowers have only a gynoecium. **Monoecious** plants have both types of imperfect flower on the same plant. **Dioecious** plants have imperfect flowers on separate plants; that is, some plants are male, some female. Examples include willows, poplars, and the date palm. Most dioecious plants use an X-Y system of of sex determination like that in mammals. However, a few species use an X-to-autosome ratio system like that of *Drosophila*, and a very few use a ZW system like that of birds and lepidopterans.



Figure 2.6.3.1.9: This *Sirdavidia solannona* flower has no gynoecium, only tightly packed stamens at the center (a staminate flower). This flower is both imperfect and incomplete. Photo by Thomas L.P. Couvreur (Institut de Recherche pour le Développement , Montpellier, France), CC BY 4.0, via Wikimedia Commons.

But the vast majority of angiosperms have **perfect flowers**; that is containing both male and female sex organs. So how do they avoid self-fertilization? Many plants have self-incompatibility genes to prevent successful pollination between two of their own gametes. However, there is also a morphological solution: **heteromorphic flowers**. The flowers are perfect but come in two structural types; for example

- long stamens with a short style
- short stamens with a long style

A single plant has one type or the other. If the pollinator has a short tongue, pollination is favored from the first type to the second - but not the reverse. Heteromorphic flowers are not common, and even in the angiosperm families that favor them (e.g., primroses, flax), the same biochemical mechanisms of self-incompatibility that we will find in homomorphic flowers are usually present as well.

Fusion Within and Between Whorls

Determining the merosity of flowers is complicated by floral fusion. In many flowers, parts of a single floral whorl will be partially or completely fused together. When the fusion is between parts of the same whorl, such as the petals fusing together to form a tubular structure (a sympetalous flower), it is called **connation**. When there is fusion of parts between whorls, such as the stamen fusing the the petals, it is called **adnation**.

A frequent form of connation occurs within the gynoecium. In an apocarpous gynoecium, the carpels are free. In a syncarpous gynoecium, some or all parts of the carpels are fused (see Figure 2.6.3.1.10)

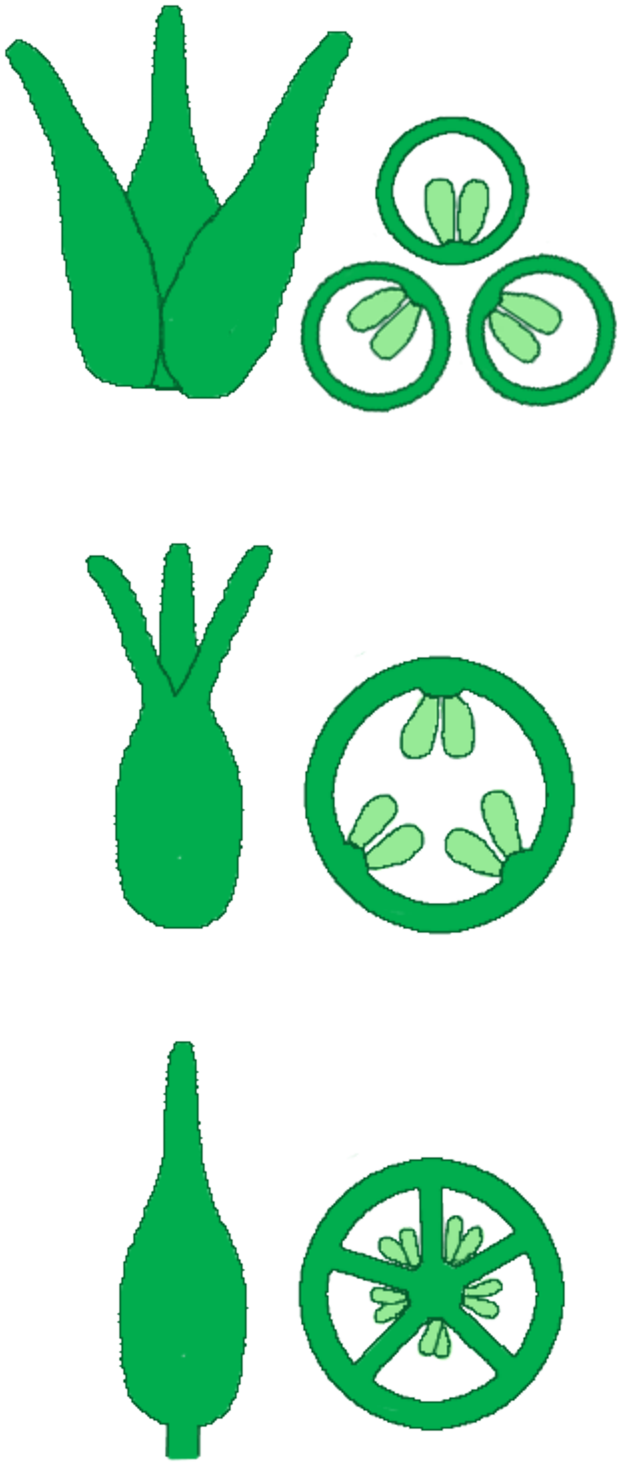


Figure 2.6.3.1.10: In an apocarpous gynoecium, the carpels are not fused together. The illustrated gynoecium on the left has three free carpels. A cross section of the ovaries shows the ovules inside. The gynoecium shown in the center is syncarpous, with fusion of the ovaries. A cross section of the ovary shows three sets of ovules. The gynoecium on the right is fully syncarpous with fusion of all parts (stigma, style, and ovary). The ovary cross section is divided into five distinct locules. Images by Michael G. Simpson. Redrawn and color: User:RoRo, Public domain, via Wikimedia Commons.

Floral Symmetry

Flowers that have multiple lines of symmetry (like a starfish) are **radially symmetrical**, also called actinomorphic or regular. Flowers with only a single line of symmetry (like you) are **bilaterally symmetrical**, also called zygomorphic or irregular (Figure 2.6.3.1.11).

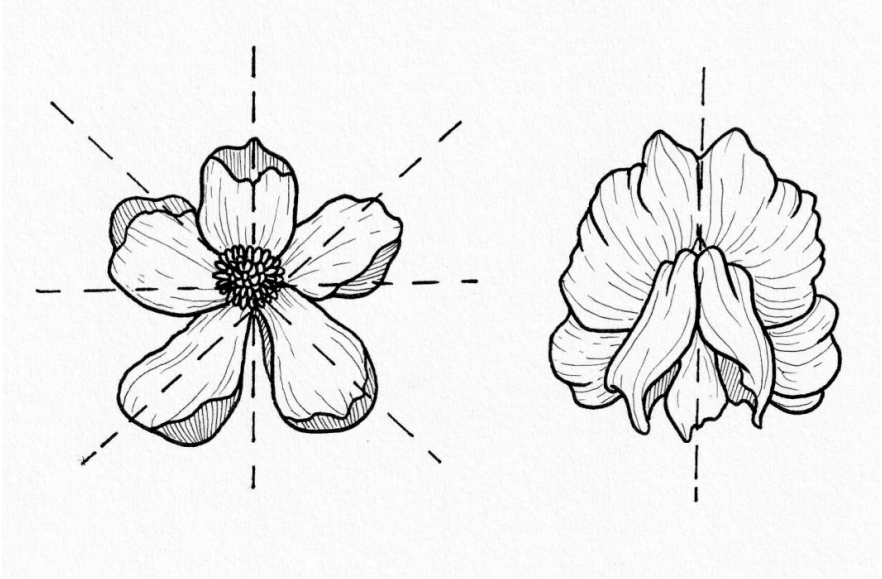


Figure 2.6.3.1.11: On the left is a picture of a radially symmetrical flower. It has five petals that all radiate out from a central point, like a star. We can draw many lines of symmetry through this flower, where if we folded the flower along that line, the two sides would line up with each other. (Note: There may be a line out of place here. Can you find it?) On the right is a bilaterally symmetrical flower. Only one line of symmetry can be drawn through this flower. Much like for humans, this flower is mirrored from side to side, but not top to bottom or any other direction. Diagram by Nikki Harris, CC BY-NC.

Ovary Position

We can use the location of the ovary to further distinguish between flowers (Figure 2.6.3.1.12). If the other whorls of the flower meet below the ovary (the ovary or ovaries look a bit like an egg or eggs in a nest; Figure 2.6.3.1.13), the ovary is **superior** (on top of the rest of the flower). This means that the rest of the flower parts are below the gynoecium, so we can also call this flower **hypogynous** (below the gynoecium). The two terms both describe the same situation, but superior refers only to the ovary while hypogynous refers to the flower, in general.

In the opposite situation, the other floral whorls join at a point above the ovary. In this case, the ovary is **inferior** and the flower is **epigynous** (on top of the gynoecium). As always, there are less clear situations. In some flowers, as in the rose family, the floral whorls join together and fuse at a point above the ovary, then travel down, around, and below the ovary as a fused unit. This fused unit is called a **hypanthium**. The ovary is termed **semi-inferior**, as it is located below the unfused parts of the floral whorls. Because the floral whorls travel around the ovary as the hypanthium, the flower is **perigynous** (peri- meaning around).



Figure 2.6.3.1.12: The first flower (a) is a drawing of a hypogynous flower. The calyx, corolla, and androecium fuse to the receptacle below the gynoecium. The ovary sits on top of these other whorls, a superior ovary. The central flower (b) is a perigynous flower. The calyx, corolla, and androecium fuse together to form a layer of tissue (hypanthium) that surrounds and fuses with the ovary. The ovary appears to sit below the other whorls, but is surrounded by the hypanthium (fused or not), a semi-inferior ovary. The last flower (c) is an epiogynous flower. The calyx, corolla, and androecium fuse together above the gynoecium. The ovary sits below these other whorls, an inferior ovary. Images by Gustav Hegi (1876–1932), Gustav Dunzinger, Public domain, via Wikimedia Commons.

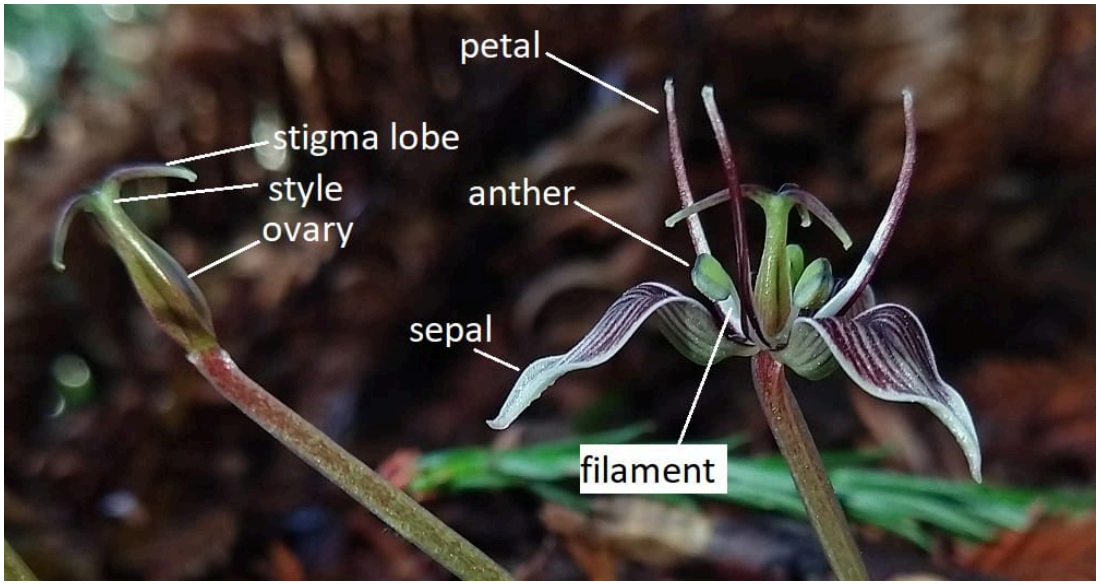


Figure 2.6.3.1.13: This flower has a superior ovary and is considered hypogynous. In the image above, we see two flowers (actually two florets of an underground umbel!) of a fetid adderstongue, *Scoliopus bigelovii*. The one on the left has shed all whorls except the gynoecium. This allows you to see what the gynoecium looks like and where it is positioned in the one on the right. In the complete flower, the sepals, petals, and stamens all meet below the ovary, which sits in the middle like one giant egg in an alien nest. Photo by Maria Morrow, CC BY-NC.

Inflorescences

An **inflorescence** is when, in the place of a single flower, multiple **florets** are formed. Florets can be sessile or attached by a stem called a **pedicel**. When leaf-like structures are found within the inflorescence, they are called **bracts**. There are a wide range of possibilities for the structure and development of inflorescences, though most can be split into four models: raceme-based, cymose, panicle, and intercalate (Figure 2.6.3.1.14). Two models are most widespread.

Raceme-based inflorescences are mostly monopodial, having **indeterminate growth**. This means that the terminal bud continues producing lateral florets, never truly forming a terminal floret. The inflorescence can be simple or compound (Figure 2.6.3.1.15).

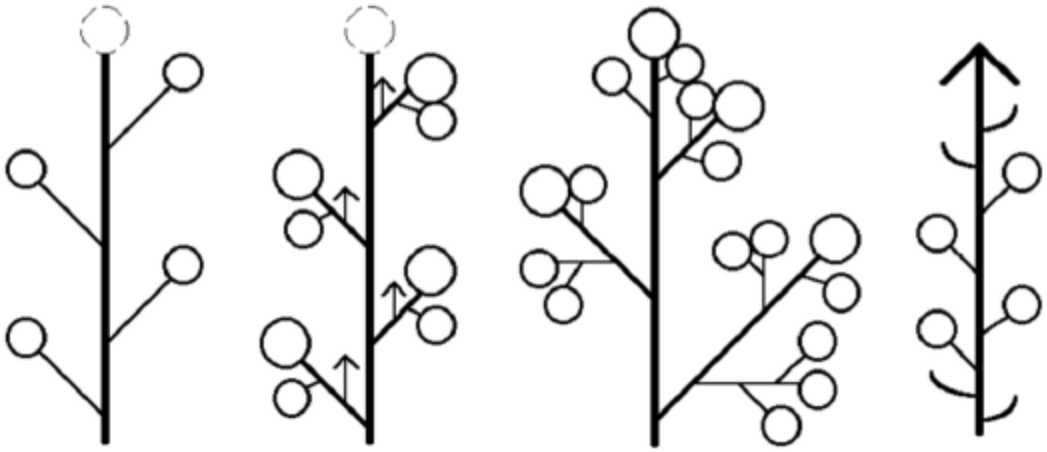


Figure 2.6.3.1.14: Four kinds of inflorescences (left to right): Model I (raceme-based) has single florets emerging on pedicels from the main peduncle. Model II (thyrsoid or cymose) has racemes emerging alternately from the main pedicel; the terminal florets are the oldest. Model III (panicle) has branched racemes emerging from the main peduncle, but unlike model II, the peduncle terminates in a floret. and Model IV (intercalate) produces lateral florets along the peduncle, separated by bracts, and continues to grow.

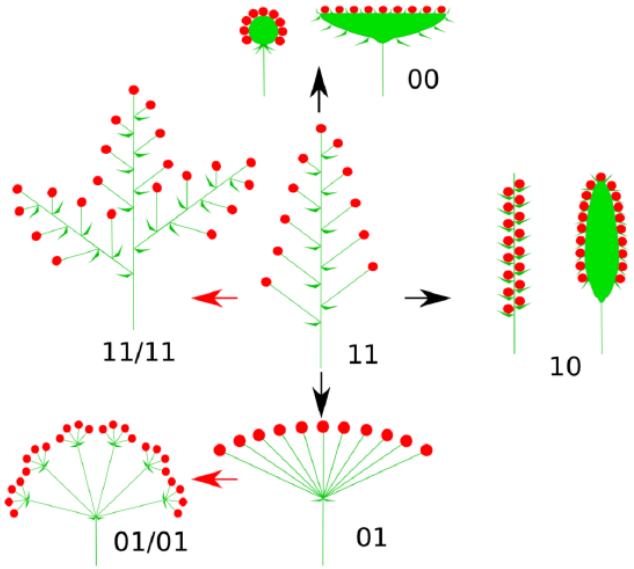


Figure 2.6.3.1.15: Different Model I inflorescences and their evolutionary connections. Circles represent florets, larger circles are older. Digits represent the simple encoding system: first position is main axis, second position are secondary axes (flower pedicels), 1 means developed, 0 reduced. Compound inflorescences have four digit positions, for the first and second orders of branching. Some names for these inflorescences: 11 raceme, 11/11 compound raceme, 10 spike (left) and spadix (right), 01 umbel, 01/01 compound umbel, 00 head. All of these models are shown diverging from a central 11 raceme model.

Cymose inflorescences are sympodial, having **determinate growth**. This means there is a terminal floret that forms first, then other florets are produced laterally (Figure 2.6.3.1.16). The order of lateral floret maturation can be a useful identification feature.

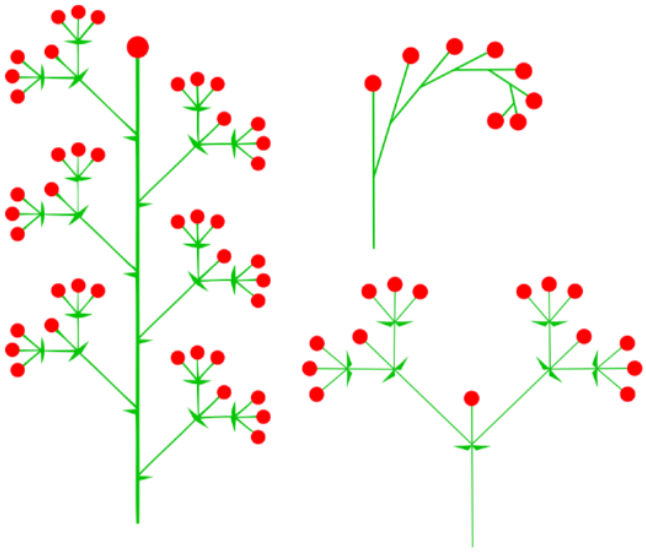


Figure 2.6.3.1.16: Model II inflorescences. Circles represent florets, larger circles are older. Thyrse (left), cyme (top right), and dichasium (bottom right). The dichasium has a stunted central flower flanked by two long pedicels that each have a compound inflorescence with a stunted central floret flanked by two longer pedicels that end in a cluster of florets. It is fractal. The thyrse has a large terminal floret; each lateral floret has the same structure as the lateral florets in the dichasium. The cyme has a terminal flower that opens first, then a later floret that produces another later floret, which produces another lateral floret, and so on, forming a spiral.

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2.6.3.2: Angiosperm Life Cycle

Learning Objectives

- Identify structures and phases in the angiosperm life cycle; know their ploidy.
- Explain how fertilization occurs within a flower.
- Label a developing ovary cross section.

Angiosperms have a complex life cycle. The gametophytes have been further reduced: antheridia were lost in the gymnosperms and archegonia were lost in the angiosperms. Both gametophytes are now housed within the flower, a structure composed of highly modified leaves specialized for pollination. From flowers, fruits are produced, a protective structure that (usually) develops from the ovary wall and is specialized for seed dispersal.

The Microgametophyte (AKA the Pollen Grain)

The microgametophyte develops and reaches maturity within the microsporangia (Figure 2.6.3.2.1). The microsporangia, which are usually bi-lobed, are also called **pollen sacs**. These pollen sacs are found in the anther of the stamen, which is at the end of the filament.

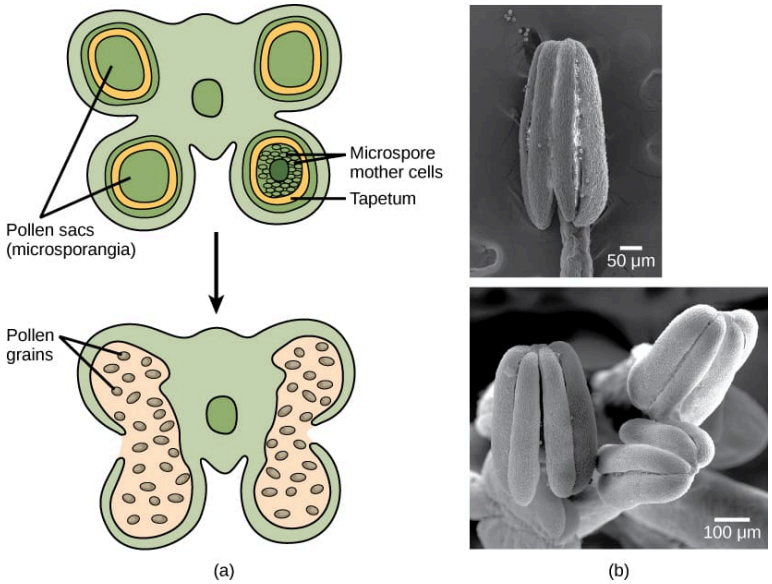


Figure 2.6.3.2.1: Shown is (a) a cross section of an anther at two developmental stages. The immature anther (top) contains four microsporangia, or pollen sacs. Each microsporangium contains hundreds of microspore mother cells that will each give rise to four pollen grains. The tapetum supports the development and maturation of the pollen grains. Upon maturation of the pollen (bottom), the pollen sac walls split open and the pollen grains (male gametophytes) are released. (b) In these scanning electron micrographs, pollen sacs are ready to burst, releasing their grains. (credit b: modification of work by Robert R. Wise; scale-bar data from Matt Russell)

Within the microsporangium (pollen sac), many microspore mother cells divide by meiosis to each give rise to four haploid microspores, each of which will ultimately form a pollen grain (Figure 2.6.3.2.2). An inner layer of cells in the microsporangium, known as the tapetum, provides nutrition to the developing microspores and contributes key components to the pollen wall. Upon maturity, the microsporangia burst, releasing the pollen grains from the anther.

Each pollen grain has two coverings: the exine (thicker, outer layer) and the intine (Figure 2.6.3.2.2). The exine contains sporopollenin, a complex waterproofing substance supplied by the tapetal cells. Sporopollenin allows the pollen to survive under unfavorable conditions and to be carried by wind, water, or biological agents without undergoing damage.

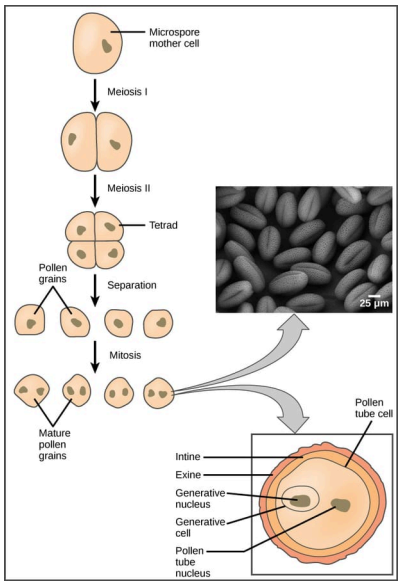


Figure 2.6.3.2.2: Pollen develops from the microspore mother cells. The mature pollen grain is composed of two cells: the pollen tube cell and the generative cell, which is inside the tube cell. The pollen grain has two coverings: an inner layer (intine) and an outer layer (exine). The inset scanning electron micrograph shows Arabidopsis lyrata pollen grains. Descriptive text: The mother cell undergoes meiosis to form a tetrad of cells, which separate to form the pollen grains. The pollen grains undergo mitosis without cytokinesis, resulting in four mature pollen grains with two nuclei each. One is called the generative nucleus, and the other is called the pollen tube nucleus. Two projective layers form around the mature pollen grain, the inner intine and the outer exine. Micrograph shows a pollen grain, which looks like puffed wheat. (credit "pollen micrograph": modification of work by Robert R. Wise; scale-bar data from Matt Russell)

Mature pollen grains contain two cells: a generative cell and a pollen tube cell. The generative cell is contained within the larger pollen tube cell. When a pollen grain reaches the stigma, it germinates into a **pollen tube**. The generative cell migrates with the pollen tube to enter the ovary. During its transit inside the pollen tube, the generative cell divides to form two gametes (spermatia). These, along with the tube nucleus (also known as the vegetative nucleus), migrate down the pollen tube as it grows through the style, the micropyle, and into the ovule chamber.

In *Arabidopsis*, the pollen tube follows a gradient of increasing concentration of a small defensin-like protein secreted by the synergids (see The Megagametophyte).

The Megagametophyte

Within the ovary of the gynoecium, ovules are produced. Ovules consist of a double-layered integument with a small opening called the micropyle. The integument surrounds the megasporangium. Both the micropyle and megasporangium are diploid tissue of the sporophyte and are connected to the ovary wall by a region of tissue called the funiculus. The funiculus connects to a region of the ovary called the placenta, where nutritive support is provided the ovary wall and supplied to the developing ovule.

Within the megasporangium a single diploid megaspore mother cell divides by meiosis to produce four haploid megaspores. One of these will survive and three will disintegrate. The nucleus of the surviving megaspore undergoes 3 successive mitotic divisions. The 8 nuclei that result are distributed and partitioned off by cell walls to form the **embryo sac** (Figure 2.6.3.2.3). The embryo sac is composed of 7 cells. The **egg cell**, located near the micropylar end, is flanked by 2 **synergid** cells. The large **central cell** contains 2 **polar nuclei** (a dikaryotic cell). The final three cells are the **antipodal** cells, located on the opposite side as the egg and synergids (Figure 2.6.3.2.4).

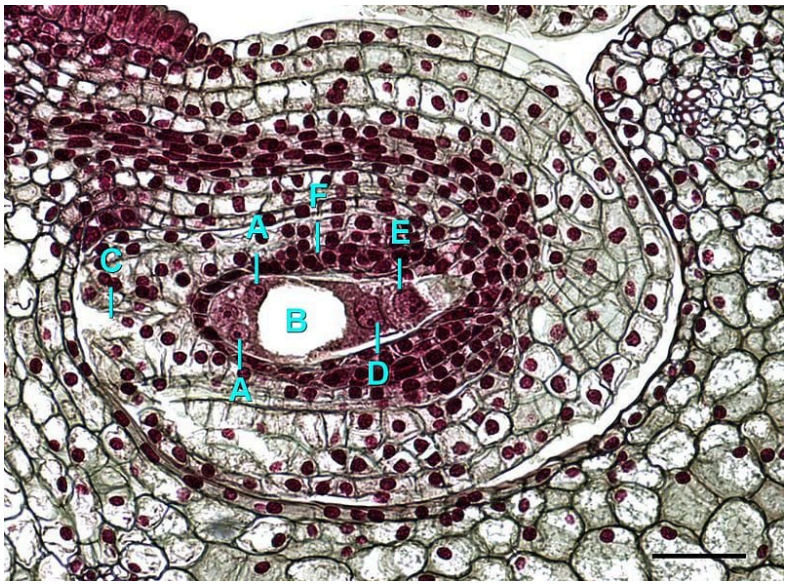


Figure 2.6.3.2.3: Photomicrograph of a *Lilium* ovary at the eight nucleate stage. The integument surrounds the megasporangium, with a gap on one side (the micropyle). Inside the megasporangium, the megagametophyte is developing. It is composed of synergid cells (on the micropylar end) flanking an egg. There is a vacuole (space) in the center of the megagametophyte. The polar nuclei and antipodal cells are on the opposite side. A-Synergid cells, B-Vacuole, C-Micropyle, D-Polar nucleus, E-Antipodal cell, F-Integument. Scale=0.1mm. Jon Houseman, CC BY-NC, via Wikimedia Commons.

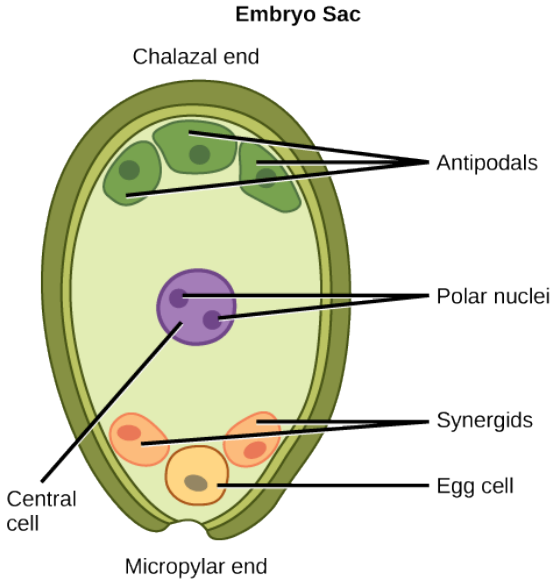


Figure 2.6.3.2.4: As shown in this diagram of the embryo sac in angiosperms, the ovule is covered by integuments and has an opening called a micropyle. Inside the embryo sac are three antipodal cells, two synergids, a central cell, and the egg cell. Descriptive text: Illustration shows the embryo sac, which is egg-shaped. The narrow end, called the micropylar end, has an opening that allows pollen to enter. The other end is called the chalazal end. Three cells called antipodals are at the chalazal end. The egg cell and two other cells called synergids are at the micropylar end. Two polar nuclei are inside the central cell in the middle of the embryo sac.

The synergids help guide the pollen tube for successful fertilization, after which they disintegrate. One of the spermatia produced by the pollen's generative cell fuses with the egg to form a diploid zygote. This zygote will grow into the sporophyte. The second spermatium fuses with the polar nuclei to produce a triploid **endosperm** (Figure 2.6.3.2.5). This event is called **double fertilization.** The endosperm will provide additional nutritive tissue for the growing embryo.

After fertilization, the integument will close the micropyle and develop into the **seed coat**, protecting the seed. The ovary wall will develop into the **pericarp** of the fruit.

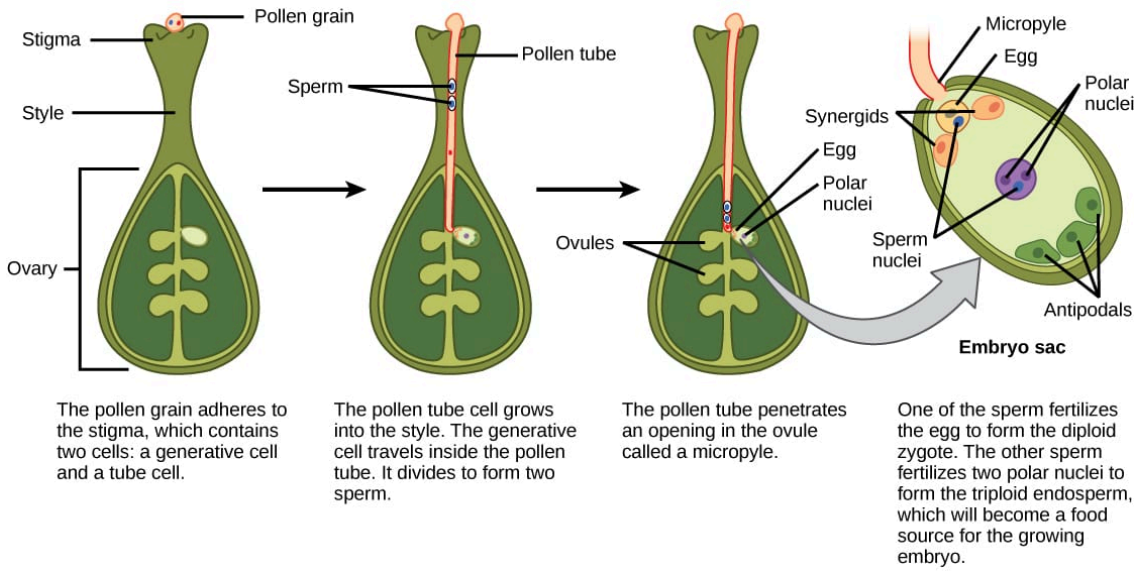


Figure 2.6.3.2.5: In angiosperms, one sperm fertilizes the egg to form the 2n zygote, and the other sperm fertilizes the central cell to form the 3n endosperm. This is called a double fertilization. Descriptive text: Illustration shows a vase-like gynoecium composed of a swollen ovary at the base and a long style (forming the neck of the vase) ending in a stigma. A pollen grain adheres to the stigma. The pollen contains two cells: a generative cell and a tube cell. The pollen tube cell grows through the stigma and into the style. The generative cell travels inside the pollen tube. It divides to form two sperm. The pollen tube penetrates an opening in the ovule called a micropyle. One of the sperm fertilizes the egg (between the two synergids) to form the zygote. The other sperm fertilizes two polar nuclei to form a triploid endosperm, which becomes a food source for the growing embryo. Three antipodal cells remain on the other side of the embryo sac.

Fruits

An unfertilized ovary, as shown in Figure 2.6.3.2.6, contains one or more developing ovules produced in compartments called **locules**. Each ovule is attached to a nutritional region of the ovary called the **placenta** by a strand of tissue called the **funiculus**. The sporophyte supports the developing ovule through this tissue pathway. Prior to fertilization, there is a small gap in the integument called the **micropyle**.

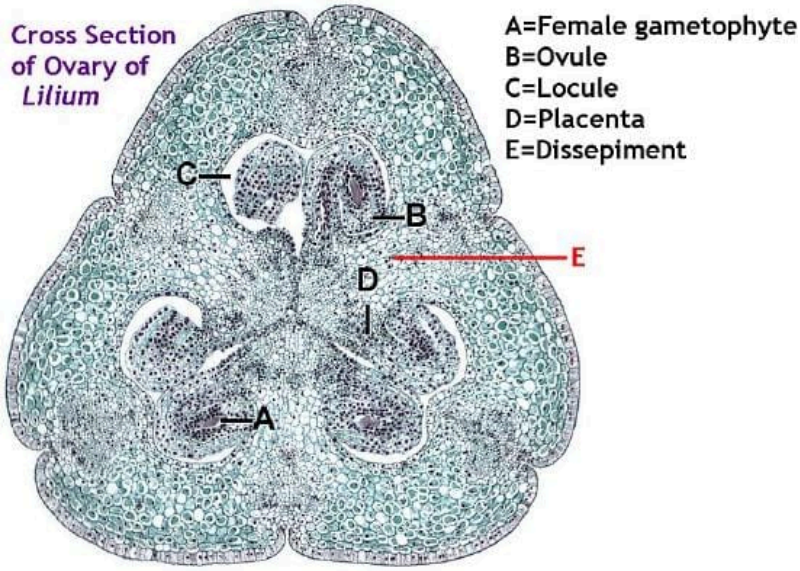


Figure 2.6.3.2.6: Cross section of *Lilium* ovary, showing A=Female gametophyte, B=Ovule, C=Locule, D=Placenta, E=Dissepiment. The ovary has three locules, each with two developing ovules. Each ovule attached to the ovary by a region of tissue called the placenta. The label in red added to original contribution of File:Lilium ovary L.jpg provided by Jon Houseman and Matthew Ford. JonRichfield, CC BY-NC, via Wikimedia Commons.

After fertilization, the ovary wall develops into the fruit, surrounding the seeds. In fleshy fruits that use animals for dispersal,

like the pears shown in Figure 2.6.3.2.7, this might include a swelling of the cells, increased sugar production, and a change in pigmentation. These are the type of fruits we are familiar with. However, all flowers turn into fruits. The fruits might be dry, spiky, or in other ways completely unappetizing, and this is become many fruits do not use animal ingestion as their method of dispersal (more on this in Chapter 8.3 Fruits and Dispersal).



Figure 2.6.3.2.7: These two images show clusters of pear blossoms from the same tree. The cluster on the left is in an earlier stage of development. The corolla is still attached and the stamens are radiating outward to disperse pollen. In the image on the right, the corolla has fallen off and the anthers have shriveled. The calyx is still visible and, just below it, the semi-inferior ovary and hypanthium are beginning to swell. Eventually, these will swell to many times their current size and form the fruits we know as pears. Photos by Maria Morrow, CC BY-NC.

The Full Life Cycle

The angiosperm life cycle is shown in Figure 2.6.3.2.12 and Video 2.6.3.2.1.

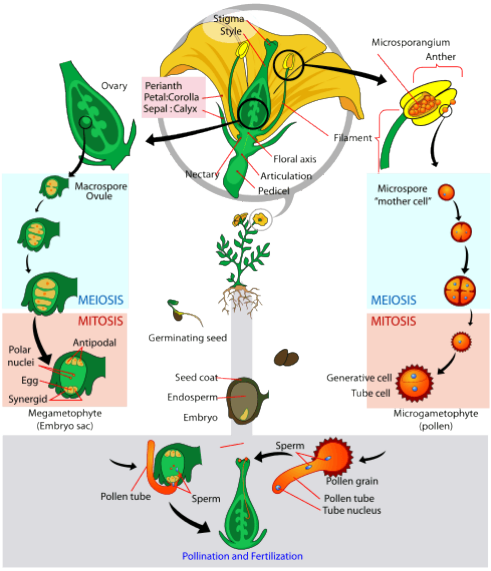


Figure 2.6.3.2.12: A diagram of the angiosperm life cycle. Pollination and fertilization take place within the ovary. The formation of the ovule takes place on the left hand side, moving from top to bottom. A macrospore ovule within the ovary undergoes meiosis, forming 4 nuclei, then mitosis, forming 8 nuclei but only 7 cells: 3 antipodals, two polar nuclei in the central cell, two synergids and an egg. This is the mature megagametophyte (embryo sac). The formation of the pollen grain takes place on the right hand side, again moving from top to bottom. Within one of the microsporangia, a microspore "mother cell" undergoes meiosis to form a pollen tetrad. Mitosis occurs within each pollen grain to produce a generative cell and a tube cell. This is the mature microgametophyte (pollen). At the center bottom of the image, pollination and double fertilization occurs, where the sperm cells fuse with the egg (forming a zygote) and polar nuclei (forming the triploid endosperm). The seed (composed of an external seed coat, small embryo, and large endosperm) develops through the center of the image, transitioning into a mature sporophyte at the top. Diagram by LadyofHats, Public domain, via Wikimedia Commons.

Watch Video 2.6.3.2.1 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 2.6.3.2.1: A digital, narrated rendition of the angiosperm life cycle. Sourced from YouTube.

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2.6.4: Chapter Summary

Seeds represent one of the most important innovations in plant evolution: a protected, nutrient-supplied embryo with the ability to await appropriate conditions for germination. Seeds and pollen allowed plants to limit their reliance on water for completion of their life cycle. The first plants to evolve seeds were the gymnosperms. Angiosperms then improved upon seed dispersal and pollination strategies with the evolution of fruits and flowers.

In gymnosperms, protective seeds filled with nutritive tissue (including the megagametophtye) replace spores as the dispersal mechanism. Antheridia are lost in the microgametophyte, which is reduced to four cells and is dispersed as a whole (pollen). The evolution of secondary growth allows for the lateral deposition of woody tissues. This latter development, along with xerophytic leaves, allows gymnosperms to tolerate a wide variety of new environmental stressors.

Cycads and ginkgos are more ancestral lineages of gymnosperms. Ginkgos are represented by a single surviving species: *Ginkgo biloba*. Cycads are primarily tropical and usually have large pinnately compound leaves. Like the Ginkgos, seeds and pollen are produced in strobili produced on separate plants. Gnetophytes are a group of gymnosperms that have convergently evolved several characteristics with angiosperms: fruit-like cones, vessel elements, and double fertilization. However, it is likely that they are a highly-derived group within the conifers, sister to the pine family! Most extant gymnosperms are conifers; this group includes some of Earth's oldest, largest, and longest lived organisms.

The majority of plant species are angiosperms. This is the most recent lineage of plants and, though its origins are murky, its members appear to form a monophyletic clade. Within the angiosperms, there are two major groups: monocots and dicots (the latter of which can be further divided into some early diverging angiosperm lineages and the eudicots). Angiosperms have the most reduced gametophytes of all plant lineages: the mature microgametophyte is composed of just 2 cells, while the megagametophyte has 7 cells (with 8 nuclei!). These gametophytes are housed within flowers, structures composed of highly modified leaves specialized for pollination.

Flowers are composed of a series of concentric whorls. The outermost whorl is the calyx, composed of sepals. Inside the calyx is the corolla, which is composed of petals. Together, the calyx and corolla comprise the perianth, which is usually the showy part of the flower in animal-pollinated species. The internal whorls are the fertile whorls. The androecium is composed of stamens, formed from a filament and anther (microsporangia are produced within the anthers). The gynoecium is composed of carpels, formed from an ovary, style, and stigma. The stigma is where pollen is received. The pollen must grow a pollen tube from the stigma to the ovary, traveling down the style to get there. Within the ovary, ovules are housed (megasporangia are produced within the ovules).

During pollination, the generative cell of the pollen produces two spermatia. One spermatium fertilizes the zygote, as in most plants, but the second spermatium fertilizes a dikaryotic cell called the central cell, forming a triploid endosperm. This event is called double fertilization. After fertilization, the ovule becomes a seed and the ovary begins to develop into a fruit.

Other adaptations within this group include specialized vascular cells: vessel elements in the xylem and sieve tube elements with companion cells in the xylem.

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

- Explain how heterospory led to the evolution of seeds.
- Connect r- and k-strategies to propagules produced by plants (e.g. spores, gametes, pollen, and seeds).
- List a few ways gymnosperms and angiosperms differ in life history traits.
- Describe the shared derived characteristics of gymnosperms.
- Connect these adaptations to the stressors this group of plants would have faced.
- Use morphological characteristics and life history traits to distinguish between ginkgos and flowering plants.
- Explain why *Ginkgo biloba* is called a living fossil.
- Use morphological characteristics and life history traits to distinguish between cycads and ferns.
- Define the term dioecious and provide an example.
- Use morphological features and life history traits to distinguish conifers from other plants.
- Connect the adaptations of conifers to dry and/or cold environments.

- Identify structures and phases in the *Pinus* life cycle; know their ploidy.
- Use morphological features and life history traits to distinguish gnetophytes from other plants.
- Describe the traits gnetophytes share with angiosperms.
- Describe the shared derived characteristics of angiosperms.
- Connect these characteristics to the stressors these plants would have faced.
- Identify the components of a flower and to which whorl each belongs.
- Write and interpret floral formulas.
- Differentiate between flowers and inflorescences.
- Explain the difference between raceme-based and cymose inflorescences.
- Identify the components of a flower and to which whorl each belongs.
- Write and interpret floral formulas.
- Differentiate between flowers and inflorescences.
- Explain the difference between raceme-based and cymose inflorescences.

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2.7: ANGIOSPERM DIVERSITY

It is likely that most plants you see are angiosperms. Of the nearly 400,000 species of land plants described, almost 90% are angiosperms. With the production of flowers specialized for pollination and fruits specialized for dispersal, angiosperms formed complex, interconnected relationships with a wide variety of other organisms. These close coevolutionary relationships may have increased speciation within this group. Regardless, the radiation of angiosperms is unprecedented among plants.

2.7.1: Monocots and Eudicots

2.7.2: Pollination Syndromes

2.7.3: Fruits and Dispersal

2.7.4: Angiosperm Families

2.7.5: Chapter Summary

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2.7.1: Monocots and Eudicots

Learning Objectives

- Compare and contrast monocots and eudicots.
- Differentiate between monocot and eudicot flowers and leaves.

Of over 400 families of angiosperms, some 80 of them fall into a single clade, called **monocots** because their seeds have only a single cotyledon. The remainder have seeds that produce two cotyledons (Figure 2.7.1.1). This group includes some early diverging angiosperms (ANA grade families and magnoliids), but the large majority of these occupy a single clade called the **eudicots**. In addition to developmental features, there are a few morphological and anatomical traits you can use to distinguish between these two major groups.



Figure 2.7.1.1: Monocots like the grass shown on the left produce only one cotyledon (mono- for one, -cot for cotyledons). Eudicots (on right), also sometimes called dicots, get their name from having two cotyledons (eu- for true, di- for two). Cotyledons are the first, fleshy leaves that enveloped the embryo as it grew. Image from Pengo, CC BY-SA 2.5, via Wikimedia Commons.

Monocots

Monocots have a single cotyledon in their seed, parallel venation in their leaves (Figure 2.7.1.2), flower parts in multiples of three (3-merous, see Figure 2.7.1.3), and vascular bundles dispersed throughout the stem in concentric circles. Monocots do not have true secondary growth, though some (such as bamboo) form tough, woody stems.



Figure 2.7.1.2: These two monocot leaves both have parallel venation. It is more obvious in the second leaf. However, if you look closely at the first leaf, you'll see that those veins do not cross each other. Instead, they travel in the same direction without overlapping, just as in the leaf on the right. Photos by Maria Morrow, CC-BY 4.0.

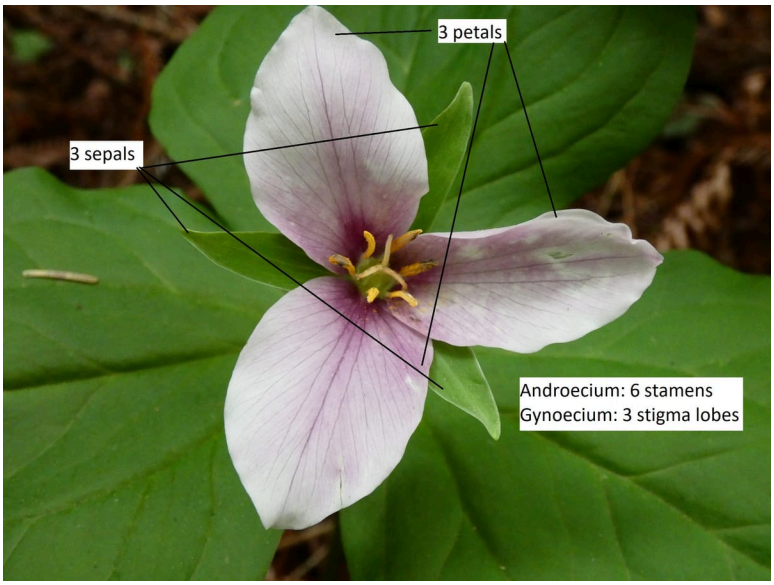


Figure 2.7.1.3: This *Trillium* is a monocot, which you can tell because it is 3-merous. There are three sepals, three petals, six stamens, and three stigma lobes visible in the gynoecium. Monocots have floral parts in sets of three (3-merous). Photo by Maria Morrow, CC-BY 4.0.

Some major groups of monocots are:

- palms (Arecaceae)
- orchids (Orchidaceae)
- yams, sweet potatoes (Dioscoreaceae)
- lilies, onion, asparagus (Liliaceae)
- bananas (Musaceae)
- all the **grasses** (Poaceae), which include many of our most important plants such as
  - corn (maize)
  - wheat
  - rice
  - and all the other cereal grains upon which we depend so heavily for food as well as
  - sugar cane and bamboo

Eudicots

Eudicots have two cotyledons in their seeds, netted venation in their leaves (Figure 2.7.1.4), flower parts in multiples of 4 or 5 (4-merous or 5-merous, see Figure 2.7.1.5), and vascular bundles in the stem arranged in a radial pattern like spokes of a wheel.



Figure 2.7.1.4: A skeletal holly leaf shows the network of vascular tissue. The lignified xylem and phloem fibers break down far more slowly than the parenchyma cells of the leaf. As the rest of the leaf tissues decompose, the lignified vascular tissue is left behind. This reveals the netted pattern of increasingly smaller side branches found in eudicot leaves. Photo by Maria Morrow, CC-BY 4.0.



Figure 2.7.1.5: Eudicot flowers tend to be 4-merous or 5-merous. The *Clarkia* flower (first image) is 4-merous. We cannot see the calyx, but there are four petals, 8 stamens, and 4 stigma lobes. The flax flower (second image) is 5-merous. There are five sepals poking out between the five petals and 5 stamens (with blue anthers!). The number of stigma lobes is not distinguishable in this image. Photos by Maria Morrow, CC-BY 4.0.

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2.7.2: Pollination Syndromes

Learning Objectives

- Explain pollination strategies with regard to genetic diversity.
- Explain what is meant by the term pollination syndrome.
- Use floral characteristics to predict a plants pollinator(s).

In angiosperms, **pollination** is defined as the placement or transfer of pollen from the anther to the stigma of the same flower or another flower. In gymnosperms, pollination involves pollen transfer from the male cone to the female cone. Upon transfer, the pollen germinates to form the pollen tube and the sperm for fertilizing the egg.

Pollination has been well studied since the time of Gregor Mendel. Mendel successfully carried out self- as well as cross-pollination in garden peas while studying how characteristics were passed on from one generation to the next. Today's crops are a result of plant breeding, which employs **artificial selection** to produce the present-day **cultivars** (a term that refers to cultivated varieties). A case in point is today's corn, which is a result of years of breeding that started with its ancestor, a grass called teosinte (see Figure 2.7.2.1). The teosinte that the ancient Mayans originally began cultivating had small seeds—vastly different from today's relatively giant ears of corn and plump kernels. Interestingly, though these two plants appear to be entirely different, the genetic difference between them is miniscule.



Figure 2.7.2.1: The first image shows the inflorescence and developing fruits produced by teosinte, while the second image shows a comparison between teosinte fruits (left) and the fruits produce by modern corn (right). In the second image, the fruits are compared to a quarter, as well as their approximate size on the plant. Note the difference in overall plant structure between the two. How might this relate to the size of the ears produced in modern corn? First image Matt Lavin from Bozeman, Montana, USA, CC BY-SA 2.0, via Wikimedia Commons. Second image by National Science Foundation, Public domain, via Wikimedia Commons. Descriptive text for second image: A diagram of a teosinte plant next to a modern corn plant. The teosinte plant has a central stem with many side branches; the fruits are produced on the side branches and the main stem; the fruits are shown next to a quarter and the line of fruits is about twice as high and much thinner. The modern corn plan has only a central stem with ears produced there; shown next to a quarter, the ear is perhaps 10 times as high and 3-4 times as wide.

Pollination and Genetic Diversity

Pollination takes two forms: self-pollination and cross-pollination. **Self-pollination** occurs when the pollen from the anther is deposited on the stigma of the same flower, or another flower on the same plant. Self-pollination occurs in flowers where the

stamen and carpel mature at the same time, and are positioned so that the pollen can land on the flower's stigma. This method of pollination does not require an investment from the plant to provide nectar and pollen as food for pollinators, but results in lower genetic diversity within the population. Self-pollination often exists like a "plan B", in case cross-pollination is, for some reason, impossible. Sometimes, self-pollinated flowers even do not open; these flowers are called **cleistogamous**.

Cross-pollination is the transfer of pollen from the anther of one flower to the stigma of another flower on a different individuals of the same species. This method relies on a pollen vector but results in higher genetic diversity.

Living species have adapted to ensure survival of their progeny; those that fail become extinct. Genetic diversity is therefore required so that in changing environmental or stress conditions, some of the progeny can survive. Self-pollination leads to the production of plants with less genetic diversity, since genetic material from the same plant is used to form gametes, and eventually, the zygote. In contrast, cross-pollination—or out-crossing—leads to greater genetic diversity because the microgametophyte and megagametophyte are derived from different plants.

Because cross-pollination allows for more genetic diversity, plants have developed many ways to avoid self-pollination. In some species, the pollen and the ovary mature at different times. These flowers make self-pollination nearly impossible. By the time pollen matures and has been shed, the stigma of this flower is mature and can only be pollinated by pollen from another flower. Some flowers have developed physical features that prevent self-pollination. The primrose is one such flower. Primroses have evolved two flower types with differences in anther and stigma length: the pin-eyed flower has anthers positioned at the pollen tube's halfway point, and the thrum-eyed flower's stigma is likewise located at the halfway point. Insects easily cross-pollinate while seeking the nectar at the bottom of the pollen tube. This phenomenon is also known as heterostyly. Many plants, such as cucumber, have male and female flowers located on different parts of the plant, thus making self-pollination difficult. In yet other species, the male and female flowers are borne on different plants (dioecious). All of these are barriers to self-pollination; therefore, the plants depend on pollinators to transfer pollen. The majority of pollinators are biotic agents such as insects (like bees, flies, and butterflies), bats, birds, and other animals. Other plant species are pollinated by abiotic agents, such as wind and water.

In summary, self-incompatibility is a mechanism that prevents self-fertilization in many flowering plant species to increase genetic diversity at the population level. The working of this self-incompatibility mechanism has important consequences for plant breeders because it inhibits the production of inbred and hybrid plants.

Incompatibility Genes in Flowers

In recent decades, *incompatibility genes*—which prevent pollen from germinating or growing into the stigma of a flower—have been discovered in many angiosperm species. If plants do not have compatible genes, the pollen tube stops growing. Self-incompatibility is controlled by the S (sterility) locus. Pollen tubes have to grow through the tissue of the stigma and style before they can enter the ovule. The carpel is selective in the type of pollen it allows to grow inside. The interaction is primarily between the pollen and the stigma epidermal cells. In some plants, like cabbage, the pollen is rejected at the surface of the stigma, and the unwanted pollen does not germinate. In other plants, pollen tube germination is arrested after growing one-third the length of the style, leading to pollen tube death. Pollen tube death is due either to apoptosis (programmed cell death) or to degradation of pollen tube RNA. The degradation results from the activity of a ribonuclease encoded by the S locus. The ribonuclease is secreted from the cells of the style in the extracellular matrix, which lies alongside the growing pollen tube.

Pollination Syndromes

Over time, angiosperms evolved different flower morphologies, smells, and colors that corresponded to their particular pollen vector. These sets of characteristics, called **pollination syndromes**, allow scientists to predict the pollinators for different plants. For example, cup-shaped flowers are usually pollinated with massive animals like beetles and even bats. Funnel-shaped flowers as well as labiate flowers (with lips), are adapted to flies and bees. Flowers with long spurs attract butterflies and birds (like hummingbirds or sugarbirds). Likewise, many of the organismal vectors evolved features or behaviors to specialize in pollination of particular plants. This tandem evolution toward increasing specificity is called **coevolution**. Interestingly, flower phenotypes can also correlate to other environmental factors (e.g. Peach et al. 2020). For more images of pollination syndromes, see Chapter 14.1 Pollination Syndromes in the Photographic Atlas.

Pollination by Deception

Orchids are highly valued flowers, with many rare varieties (Figure 2.7.2.2). They grow in a range of specific habitats, mainly in the tropics of Asia, South America, and Central America. At least 25,000 species of orchids have been identified.



Figure 2.7.2.2: Certain orchids use food deception or sexual deception to attract pollinators. Shown here is a bee orchid (*Ophrys apifera*) that mimics the appearance of a *Eucera longicornis* female bee. Male *E. longicornis* bees try to mate with the petal, covering themselves in pollen from the overhanging anthers and depositing any pollen they may have from prior bee orchids onto the stigma. (credit: David Evans)

Flowers often attract pollinators with food rewards, in the form of nectar. However, some species of orchid are an exception to this standard: they have evolved different ways to attract the desired pollinators. They use a method known as food deception, in which bright colors and perfumes are offered, but no food. *Anacamptis morio*, commonly known as the green-winged orchid, bears bright purple flowers and emits a strong scent. The bumblebee, its main pollinator, is attracted to the flower because of the strong scent—which usually indicates food for a bee—and in the process, picks up the pollen to be transported to another flower.

Other orchids use sexual deception. *Chiloglottis trapeziformis* emits a compound that smells the same as the pheromone emitted by a female wasp to attract male wasps. The male wasp is attracted to the scent, lands on the orchid flower, and in the process, transfers pollen. Some orchids, like the Australian hammer orchid, use scent as well as visual trickery in yet another sexual deception strategy to attract wasps. The flower of this orchid mimics the appearance of a female wasp and emits a pheromone. The male wasp tries to mate with what appears to be a female wasp, and in the process, picks up pollen, which it then transfers to the next counterfeit mate.

Bees

Bees are perhaps the most important pollinator of many garden plants and most commercial fruit trees (Figure 2.7.2.3). Most bees that people notice are the social bees, bumblebees and honeybees, though there are thousands of species of solitary bees that have essential pollination roles. Bees have branched hairs covering their bodies, making them excellent pollinators as more pollen grains are likely to be caught upon their external surfaces and transferred onto other plants.

Bees collect energy-rich pollen and nectar for their survival and energy needs, so flowers that have coevolved with bees contain both nectar and pollen. Since bees cannot see the color red, bee-pollinated flowers usually have shades of blue, yellow, violet or other colors. They visit flowers that are open during the day, are brightly colored, have a strong aroma or scent, with a landing area of some kind, typically with the presence of a nectar guide. A **nectar guide** can include regions on the flower with pigments that are visible only to bees, and not to humans (such as UV); it helps to guide bees to the center of the flower, thus making the pollination process more efficient. The pollen sticks to the bees' fuzzy hair, and when the bee visits another flower, some of the

pollen is transferred to the second flower.

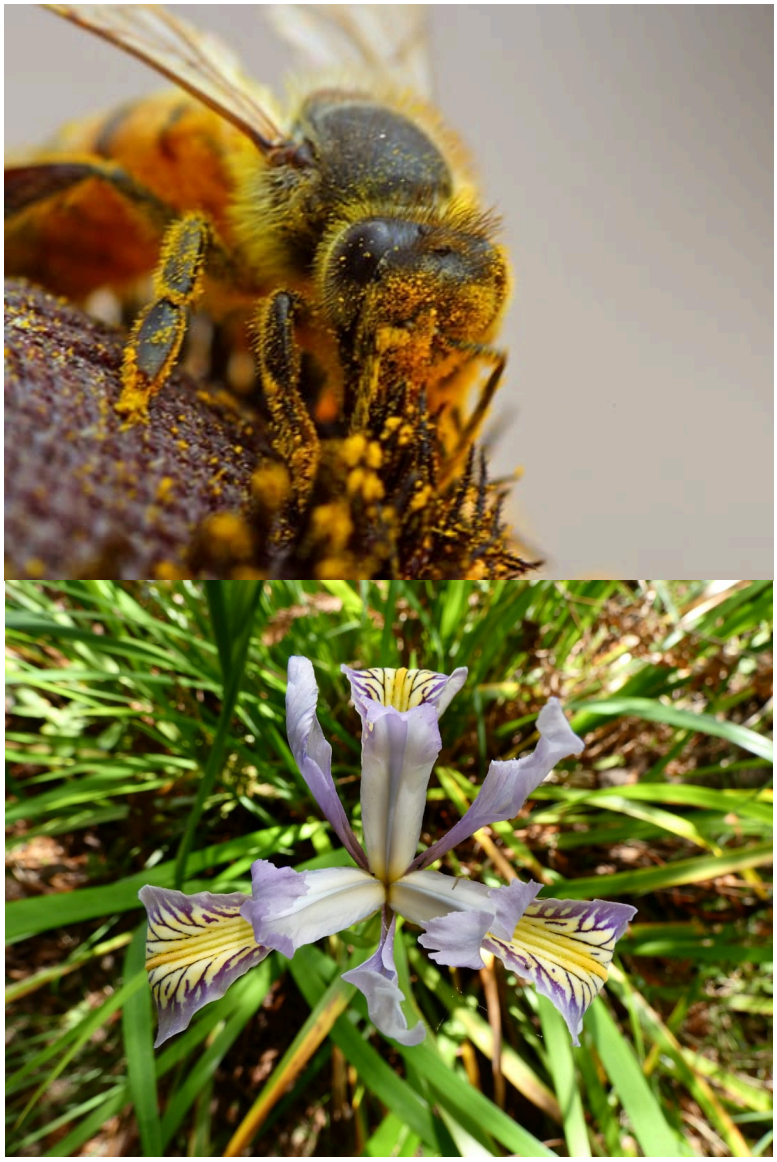


Figure 2.7.2.3: Insects, such as bees, are important agents of pollination. The first image shows a bee covered in pollen. Bees are covered in branched hairs (unlike flies, which have unbranched hairs), specialized for pollen collection. The second image shows an *Iris*. This *Iris* flower has a bee pollination syndrome. The primary colors are purple and yellow. There are nectar guides (lines on the petals) leading the bee to the center of the flower. To get there, the bee must crawl under the stigma first, then under the anthers. This flower has a pleasant, sweet smell. First image: modification of work by Jon Sullivan. Second image: Photo by Maria Morrow, CC-BY 4.0.

Recently, populations of honeybees (an introduced European species) have been in decline due to a variety of factors, including pesticides (like neonicotinoids) and parasitic mites. Because solitary bees are not operated by commercial industry, impacts on these populations have been less well-documented. However, declines in bee populations will have extremely important impacts on our food security, as bees are used to pollinate many food crops.

Wasps are also important insect pollinators, and pollinate many species of figs.

Flies

Many fly species are important pollinators. These flies often look and behave much like bees, performing important roles in pollination. However, since these flowers would generally be classified under a bee pollination syndrome, we will instead discuss a

second category of fly for the fly pollination syndrome. These insects (flies and sometimes carrion beetles) are typically not looking for a flower, but for a corpse or some dung to feed on or lay eggs in. Some flowers have evolved to trick flies into pollination by emitting a decaying smell or an odor of rotting flesh. These flowers, which produce nectar, usually have dull colors, such as brown or purple. They often feature some kind of trap-like feature so when a fly visits, it has to bounce around inside the flower a bit before leaving (this increases the chance of pollen deposition, both on the flower and on the fly). Examples include the corpse flowers (*Amorphophallus* and *Rafflesia*) and dragon arum (*Dracunculus*).



Figure 2.7.2.4: Rafflesia arnoldii makes the world's largest known flowers. They can be over a meter across and are adapted to mimic rotting meat in smell and appearance. The rest of the plant lives parasitically inside the vines of *Tetrastigma*--it doesn't make any stems, roots, or leaves! Photo by User:Rendra Regen Rais, CC BY-SA 3.0, via Wikimedia Commons.

Butterflies and Moths

Butterflies, such as the monarch, pollinate many garden flowers and wildflowers, which usually occur in clusters. These flowers are brightly colored, have a strong fragrance, are open during the day, and have nectar guides to make access to nectar easier. The pollen is picked up and carried on the butterfly's limbs.

Moths, on the other hand, pollinate flowers during the late afternoon and night. The flowers pollinated by moths are pale or white and are flat, enabling the moths to land. One well-studied example of a moth-pollinated plant is the yucca plant, which is pollinated by the yucca moth. The shape of the flower and moth have adapted in such a way as to allow successful pollination. The moth deposits pollen on the sticky stigma for fertilization to occur later. The female moth also deposits eggs into the ovary. As the eggs develop into larvae, they obtain food from the flower and developing seeds. Thus, both the insect and flower benefit from each other in this symbiotic relationship. The corn earworm moth and Gaura plant have a similar relationship (Figure 2.7.2.5).



Figure 2.7.2.5: A corn earworm moth sips nectar from a night-blooming *Gaura* plant. (credit: Juan Lopez, USDA ARS)

Bats

In the tropics and deserts, bats are often the pollinators of nocturnal flowers such as agave, guava, and morning glory. The flowers are usually large and white or pale-colored; thus, they can be distinguished from the dark surroundings at night. The flowers have a strong, fruity, or musky fragrance and produce large amounts of nectar. They are naturally large and wide-mouthed to accommodate the head of the bat (Figure 2.7.2.6). As the bats seek the nectar, their faces and heads become covered with pollen, which is then transferred to the next flower.



Figure 2.7.2.6: Bat pollinated flowers, like those shown here on *Cresentia alata*, are open at night and tend to be large, white, and have lots of pollen. They usually emit a strong fruity or musky smell. Photo by शैलजा देशपांडे, CC BY-SA 4.0, via Wikimedia Commons.

Birds

Many species of small birds, such as the hummingbird (Figure 2.7.2.7) and sun birds, are pollinators for plants such as orchids and other wildflowers. Flowers visited by birds are usually sturdy and are oriented in such a way as to allow the birds to stay near the flower without getting their wings entangled in the nearby flowers, such as dangling (pendant). The flower typically has a curved, tubular shape, which allows access for the bird's beak. Brightly colored, odorless flowers that are open during the day are

pollinated by birds. As a bird seeks energy-rich nectar, pollen is deposited on the bird's head and neck and is then transferred to the next flower it visits. Botanists have been known to determine the range of extinct plants by collecting and identifying pollen from 200-year-old bird specimens from the same site.



Figure 2.7.2.7: Hummingbirds have adaptations that allow them to reach the nectar of certain tubular flowers. These flowers have narrow tubes perfect for a hummingbird's long bill and tongue. There is not a great landing pad for insects, so the ability to hover makes it easier to gather the nectar. (Photo credit: Lori Branham)

Wind

Most species of conifers, and many angiosperms, such as grasses, maples and oaks, are pollinated by wind. Pine cones are brown and unscented, while the flowers of wind-pollinated angiosperm species are usually green, small, may have small or no petals, and produce large amounts of pollen. Unlike the typical insect-pollinated flowers, flowers adapted to pollination by wind do not produce nectar or scent. In wind-pollinated angiosperm species, the anthers are often large and hang out of the flower, and, as the wind blows, the lightweight pollen is carried with it (Figure 2.7.2.8). The flowers usually emerge early in the spring, before the leaves, so that the leaves do not block the movement of the wind. The pollen is deposited on the exposed feathery stigma of the flower (Figure 2.7.2.9).



Figure 2.7.2.8: A person knocks pollen from a pine tree. The clusters of pollen cones release clouds of pollen grains. Mass production of pollen is part of the wind pollination strategy.



Figure 2.7.2.9: These male (a) and female (b) catkins are from the goat willow tree (Salix caprea). Note how both structures are light and feathery to better disperse and catch the wind-blown pollen. Descriptive text: Photo A shows the long, thin flower male of the white willow, which has long, hair-like appendages jutting out all along its length. Photo B shows the female flower from the same plant. The shape is similar, but the hair-like appendages are missing.

Water

Some plants, such as Australian sea grass and pond weeds, are pollinated by water. The pollen floats on water, and when it comes into contact with the flower, it is deposited inside the flower.

Summary Table of Pollination Syndromes

Table 2.7.2.1 summarizes the pollination syndromes described in the categories above.

Table 2.7.2.1: Pollination Syndromes (adapted from the US Forest Service).

Pollination Syndrome	Color	Structure	Scent	Nectar or Pollen
Wind	Dull, perianth often absent or reduced	Large feathery stigmas, large anthers	None	No nectar, large amounts of pollen
Birds	Reds and pinks	Often tubular or cupped	None	Lots of hidden nectar, moderate pollen
Bees	Purples, blues, yellows, white, UV	Flat and shallow or tubular, with landing area	Sweet, fresh, mild	Pollen often sticky and scented, nectar usually present
Bats	White, dull green, or purple	Often bowl-shaped or pendant, anthers protruding	Musty or fruity, strong, emitted at night	Lots of hidden nectar
Moths	White, pale pink or purple	Often tubular or cupped, no landing pad	Strong and sweet, emitted at night	Lots of hidden nectar, limited pollen
Butterflies	Bright colors	Tubular, with wide landing pad	Faint, fresh	Lots of hidden nectar, limited pollen
Flies	Dark red, purple, brown	Shallow, funnel, or trap-like	Putrid, rotting	No nectar, moderate pollen

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2.7.3: Fruits and Dispersal

Learning Objectives

- Describe the transition from ovary and ovule to fruit and seed.
- Use characteristics of fruits, including pericarp morphology, to identify fruit type.
- Use characteristics of fruits to predict the dispersal agent for a plant's seeds.

All flowers become fruits (Figure 2.7.3.1). This may be surprising at first, as what we culturally refer to as a fruit is a bit different than the botanical definition. Many of the "vegetables" and other plant products (e.g. grains, legumes, and nuts) that you get from the store are actually fruits! The term angiosperm refers to the fruit: angio- means vessel and sperm refers to the seed; fruits are the vessel that houses the seed or seeds. Fruits are a development of the **ovary wall** and sometimes other flower parts. As seeds mature, they release the hormone auxin, which stimulates the wall of the ovary to develop into the fruit. In fact, commercial fruit growers may stimulate fruit development in unpollinated flowers by applying synthetic auxin to the flower. This chapter section will cover the anatomy of a fruit, including the ovary, different fruit types, and finally, how these fruits are specialized for different dispersal mechanisms.



Figure 2.7.3.1: These two images show clusters of pear blossoms from the same tree. The cluster on the left is in an earlier stage of development. The corolla is still attached and the stamens are radiating outward to disperse pollen. In the image on the right, the corolla has fallen off and the anthers have shriveled. The calyx is still visible and, just below it, the semi-inferior ovary and hypanthium are beginning to swell. Eventually, these will swell to many times their current size and form the fruits we know as pears. Photos by Maria Morrow, CC-BY 4.0.

A fruit is defined as ripened ovary, flower, or whole inflorescence. Depending on how these parts interact to form the fruit, we can classify them into different fruit types. The **pericarp** (Figure 2.7.3.2), which is comprised of the **exocarp**, **mesocarp**, and **endocarp**, is derived from the ovary wall.

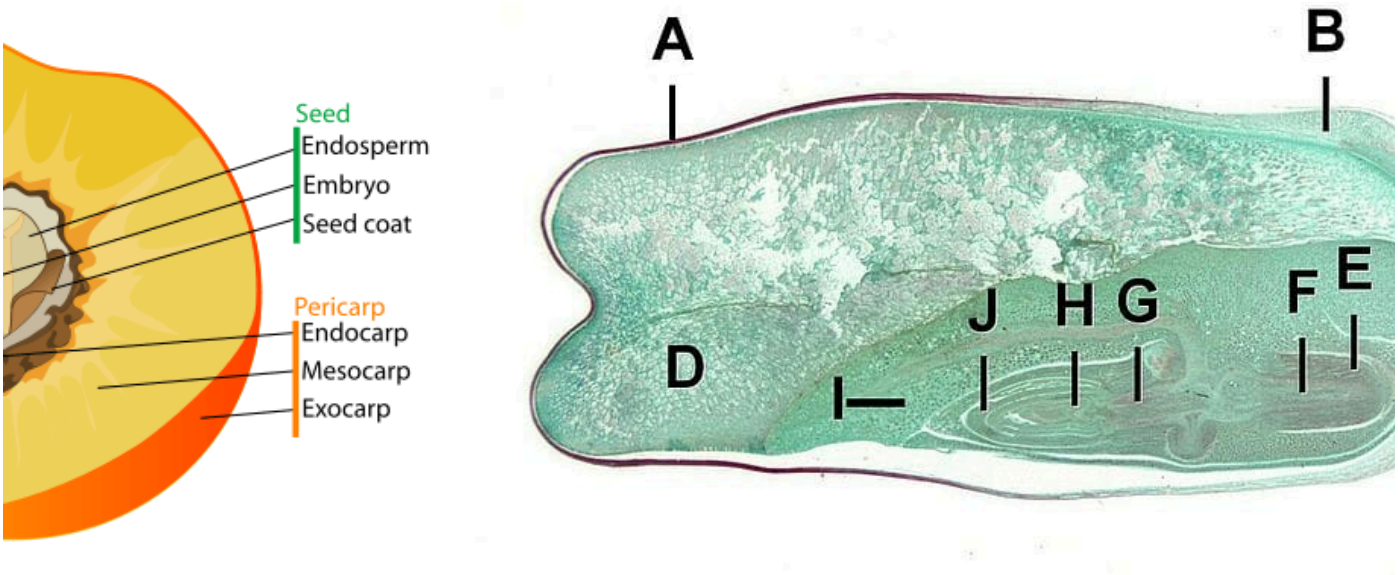


Figure 2.7.3.2: Two fruits with different pericarp morphology. The pericarp of a fruit can be separated into distinct layers, as in the first photo, or completely fused together, as in the second photo. The first photo shows a peach, which is a type of fruit called a drupe. It has a stony endocarp enclosing a single seed, a fleshy mesocarp, and a thin exocarp. The second photo shows a corn kernel, which is a type of fruit called a caryopsis. In this fruit type, the pericarp (A) is thin, layers are indistinguishable, and it is completely fused to the seed coat. First mage by LadyofHats, Public domain, via Wikimedia Commons. Second image by Jon Houseman, CC BY-SA 4.0, via Wikimedia Commons. Labels are as follows: A=Pericarp, B=Aleurone, C=Tip cap, D=Endosperm, E=Coleorhiza, F=Radicle, G=Hypocotyl, H=Plumule, I=Scutellum, J=Coleoptile. Scale=1.4mm.

Ovary Anatomy

An unfertilized ovary, as shown in Figure 2.7.3.3, contains one or more developing **ovules** produced in compartments called **locules**. Within the ovule, the megasporangium is surrounded by tissue within the called the integument. Both of these are diploid tissues of the sporophyte. A diploid megaspore mother cell is produced within the megasporangium, which will divide by meiosis to produce the haploid megagametophyte (see Chapter 7.3.2: Angiosperm Life Cycle for a refresher). Each ovule is attached to a nutritional region of the ovary called the **placenta** by a strand of tissue called the **funiculus**. The sporophyte supports the developing ovule through this tissue pathway. Prior to fertilization, there is a small gap in the integument called the **micropyle**.

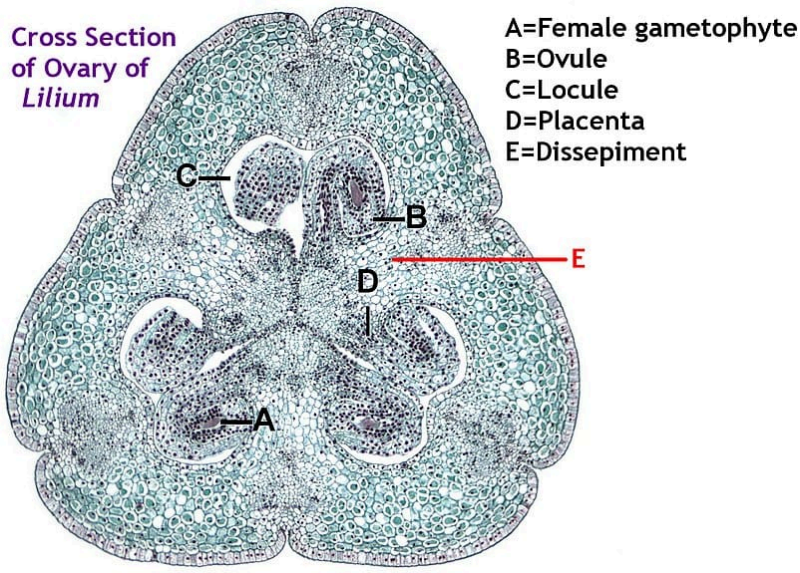


Figure 2.7.3.3: Cross section of *Lilium* ovary, showing A=Female gametophyte, B=Ovule, C=Locule, D=Placenta, E=Dissepiment. The ovary has three locules, each with two developing ovules. Each ovule attached to the ovary by a region of tissue called the placenta. The ovary wall will develop into the fruit and the ovules will develop into seeds, if fertilized. The label in red added to original contribution of File:Lilium ovary L.jpg provided by Jon Houseman and Matthew Ford. JonRichfield, CC BY-SA 4.0, via Wikimedia Commons.

After fertilization, ovules become **seeds**. The micropyle closes and the integument becomes the **seed coat**. The megasporangium, called the **nucellus**, serves as nutritive tissue for the developing embryo. Angiosperms provide an additional food source to the developing zygote, the **endosperm**. The ovary wall develops into the pericarp.

Fruit Types

Fruits may be classified as simple, aggregate, multiple, or accessory, depending on their origin (Figure 2.7.3.11). If the fruit develops from a single carpel or fused carpels of a single ovary, it is known as a **simple fruit**, as seen in nuts and beans. An **aggregate fruit** is one that develops from more than one carpel, but all are in the same flower: the mature carpels fuse together to form the entire fruit, as seen in the raspberry. A **multiple fruit** develops from an inflorescence or a cluster of flowers. An example is the pineapple, where the flowers fuse together to form the fruit.

Fruits can be **dry** or **fleshy**. An example of dry fruit is a peanut (*Arachis*), the shell of the peanut is the pericarp, which is dry at maturity. Examples of fleshy fruits include apples (*Malus*) or oranges (*Citrus*), where the pericarp or some other part of the floral structure becomes swollen with liquid.

Dry fruits can be further classified into **dehiscent** fruits, which open at maturity, or **indehiscent** fruits, which do not open independently. **Schizocarp** fruits are in between: they do not open but break into several parts (usually the distinct locules), and each part contains one seed inside. For example, maple fruit consists of two “wings”, each of them contains part of the full fruit and one seed.

In addition, fruits can be monomerous (1-seeded) like a nut or an achene, or bear multiple seeds (like the follicle in a tulip, *Tulipa*).

Accessory Fruits

Accessory fruits (sometimes called false fruits) are not derived from the ovary, but from another part of the flower, such as the receptacle (Figure 2.7.3.4) or the hypanthium (Figure 2.7.3.5).

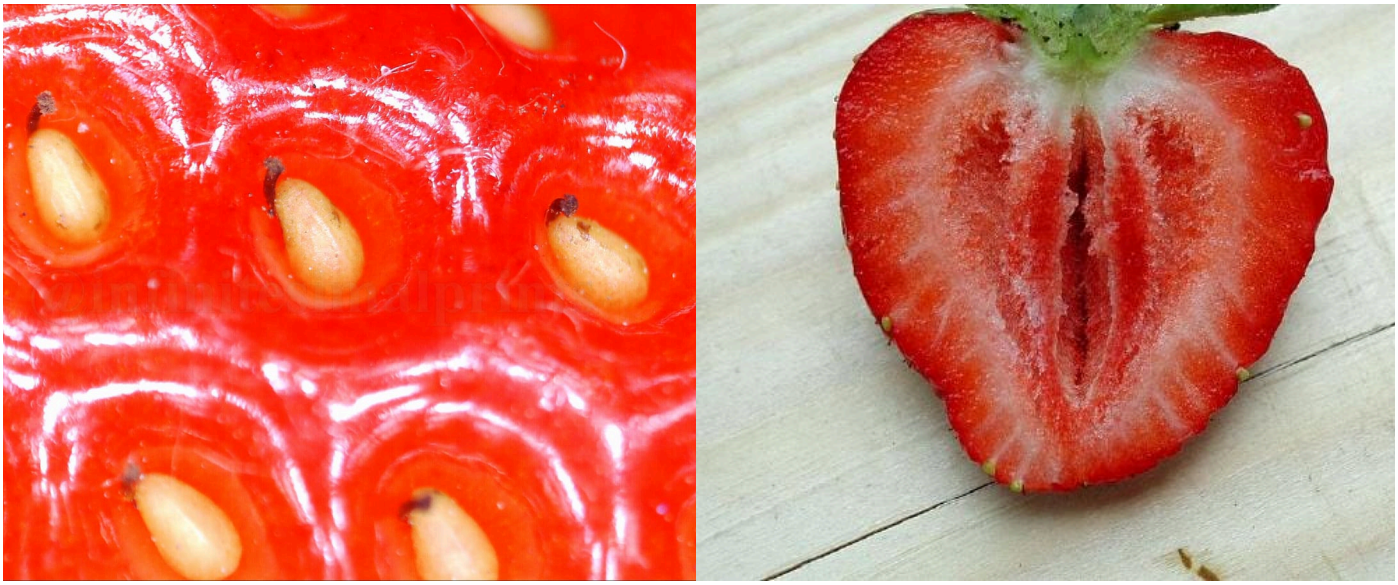


Figure 2.7.3.4: Strawberries are accessory fruits formed from a swollen receptacle. The receptacle reddens and swells, pushing the developing fruits outward. The fruits are achenes that look like seeds, stuck to the outside of the receptacle. If you look closely, you can see the styles attached to the narrow end of each achene, each with a stigma at the end. Because strawberries are formed from multiple free carpels, they are also an aggregate fruit. In the second image, the green layer is the calyx. First strawberry photo by Troy Pemberton (found on Instagram as Infinitesimal Prints), used with permission. Sliced strawberry photo by Paolo Neo, Public domain, via Wikimedia Commons.

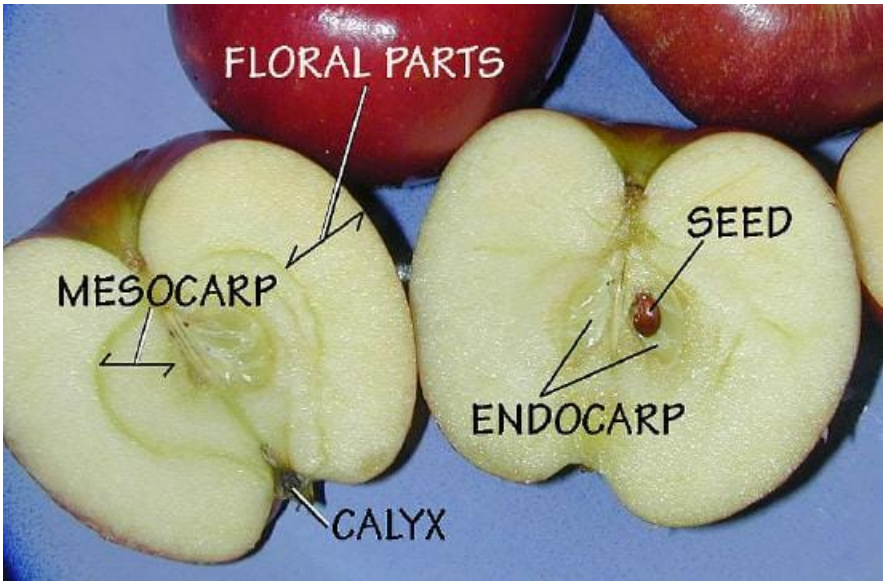


Figure 2.7.3.5: A pome is an accessory fruit made from a fleshy hypanthium. The papery core is the pericarp, which contains the seeds. Eric Guinther, CC BY-SA 3.0, via Wikimedia Commons.

Dichotomous Key to Common Fruits

Use the following dichotomous key to identify fruit types! Note: If the fleshy part of the fruit is composed of something other than the ovary, it is an **accessory fruit**.

1. Fruit from one carpel of one flower .....[Simple Fruit].... 2

1. Fruit from more than one carpel or from an inflorescence 16

    2. Fleshy at maturity 3

    2. Dry at maturity 8

3. Thin exocarp, fleshy mesocarp, stony endocarp surrounding single, large seed ..... **Drupe**

3. Fruit not as described above..... 4

4. Seeds in a linear order, separate from ovary wall, pericarp splits on two seams ...Legume (immature)

4. Fruit not as described above..... 5

5. Papery endocarp forms a core. Derived from a perigynous flower.....**Pome**

5. Endocarp fleshy (not a papery core) 6

6. Thin exocarp, fleshy mesocarp, one to many seeds ..... **Berry**

6. Exocarp thickened and leathery (modified berries) 7

7. Exocarp and mesocarp form leathery rind, locules filled with juice-filled trichomes .....**Hesperidium**

7. Exocarp forms tough skin/rind, thick mesocarp, not divided into separate locules ..... **Pepo**

8. Dehiscent (splits open at maturity), usually many seeds 9

8. Indehiscent (does not split open), usually one seeded 12

9. Derived from a carpel with one locule 10

9. Derived from a carpel with more than one locule 11

10. Dehiscent along one seam ..... **Follicle**

10. Dehiscent along two seams ..... **Legume**

11. From two locules with a central partition ..... Silique (elongate) or silicle (round)

11. From more than two locules..... **Capsule**

12. Ovary wall extends to form a wing ..... **Samara**

12. Fruit not winged 13

13. Outer wall not especially thick or hard, seed small ... 14

13. Outer wall hardened, seed relatively large 15

14. Seed not tightly attached to pericarp ..... **Achene**

14. Seed fused to pericarp, grains ..... **Caryopsis**

15. Stony pericarp surrounds one large seed ..... **Nut**

15. Relatively thin exocarp, fibrous mesocarp, single large seed ..... (dry) Drupe

16. Derived from one flower with many free carpels ..... **Aggregate Fruit**

16. Derived from an inflorescence (many florets) ..... **Multiple Fruit**

Fruit and Seed Dispersal

The fruit has a single purpose: seed dispersal. Seeds contained within fruits need to be dispersed far from the mother plant, so they may find favorable and less competitive conditions in which to germinate and grow. Fruits promote the dispersal of their

content of seeds in a variety of ways:

- **Ballistic.** Some fruits, as they dry, open explosively expelling their seeds. The pods of many legumes (e.g., wisteria) do this.
- **Wind.** Wind-dispersed fruit are lightweight and may have wing-like appendages that allow them to be carried by the wind. Some have a parachute-like structure to keep them afloat.
- **Water.** Many aquatic angiosperms and shore dwellers (e.g., the coconut palm) have floating fruits that are carried by water currents to new locations.
- **Animal attachment.** The cocklebur and sticktights achieve dispersal of their seeds by sticking to the coat (or clothing) of a passing animal.
- **Animal ingestion.** Nuts and berries entice animals to eat them. Buried and forgotten (nuts) or passing through their g.i. tract unharmed (berries), the seeds may end up some distance away from the parent plant.

All of the above mechanisms allow for seeds to be dispersed through space, much like an animal's offspring can move to a new location. Seed dormancy allows plants to disperse their progeny through time: something animals cannot do. Dormant seeds can wait months, years, or even decades for the proper conditions for germination and propagation of the species. These dormant seeds can accumulate in the soil, forming a **seed bank**. Areas prone to disturbances, like fire, often rely on the seed bank to regenerate plant communities post-disturbance.

Ballistic

In ballistic dispersal, seeds are shot from the fruit. This can be accomplished via a build up of turgor pressure within the fruit (as in dwarf mistletoe and wild cucumber), a twisting action, or some other method. Watch Video 2.7.3.1 to see ballistic seed dispersal in action!

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 2.7.3.1: Watch this fun video of different plants utilizing ballistic seed dispersal. Sourced from YouTube.

Wind

Fruits dispersed by wind, like samaras or the achenes of a dandelion, are generally winged (Figure 2.7.3.6). In the case of a dandelion, each achene is attached to a modified calyx that forms an umbrella-like structure to catch on the wind.



Figure 2.7.3.6: Samaras are winged achenes adapted to wind dispersal. The maple samaras on the left are also schizocarps, breaking apart at maturity into two separate fruits. Left image by Gmihail at Serbian Wikipedia, CC BY-SA 3.0 RS, via Wikimedia Commons. Right image by Marco Schmidt [1], CC BY-SA 3.0 via Wikimedia Commons.

Water

Some fruits, such as those of some aquatic plants like lotus or plants adapted to island living, are specialized for water dispersal. This usually involves a buoyant pericarp, as in the fibrous husk of the water-dispersed coconut. Similarly, willow and silver birches produce lightweight fruit that can float on water. Watch Video 2.7.3.2 to see the journey of a water-dispersed sea bean.

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 2.7.3.2: Watch this clip to see the aquatic journey of the sea bean. Toward the end of the video, be on the lookout for mangrove pneumatophores. Sourced from YouTube.

Animal Vectors

Many fruits have evolved to use animals for dispersal. Fruits with velcro-like projections or sticky pericarps latch onto mammal fur or bird feet and are transported to a new locale without needing to survive a journey through the digestive tract (Figure 2.7.3.7). Other fruits have specialized for animal ingestion. Among these are the fruits we typically consider fruits, those that are typically sweet, fleshy, often brightly colored and intended for consumption. The seeds must either survive the digestive tract, deposited later in nutrient-rich substrate, or depend on animals who are sloppy eaters, dispersing some of the seeds as they eat others.

Some of these are highly specialized, with a single species or group of animals as the intended dispersal vector. For example, hot peppers like habañero chiles are hot because they contain a compound called capsaicin (see Figure 2.7.3.8). They also tend to be red. This is because these peppers have specialized for bird dispersal vectors. Both birds and mammals are attracted to the color red. However, mammals often have a more thorough digestive tract, meaning seeds need more investment in protection to survive the journey. However, mammals like you and I interpret capsaicin as spicy, perhaps painful, and are often deterred by it (though many exceptions apply among humans), while birds are immune to these effects. Because of this interesting difference

in physiology, some people add cayenne pepper to their suet bird feeders to keep the squirrels away.

Some animals, like squirrels, bury seed-containing fruits for later use; if the squirrel does not find its stash of fruit, and if conditions are favorable, the seeds germinate. Some birds are also known to cache nuts for later. Plants that produce nuts generally rely on this storage behavior in their animal dispersers.



Figure 2.7.3.7: Animal attachment. Fruits of *Xanthium*, cockleburrs, have hooked spikes that allow them to attach to passing animals. Photo by Muséum de Toulouse, CC BY-SA 3.0 via Wikimedia Commons.



Figure 2.7.3.8: Habañero chiles (and other spicy peppers) have specially adapted for bird dispersal. They contain a compound called capsaicin that is incredibly spicy to most mammals but does not bother birds. Photo from The original uploader was Fir0002 at English Wikipedia., CC BY 2.5 via Wikimedia Commons.

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2.7.4: Angiosperm Families

Learning Objectives

- Interpret a floral formula.
- Describe the characteristics used to identify each of the four largest angiosperm families.

Knowing who is related to whom in the plant world can provide important information. Often, closely related organisms will have similar life history traits, such as defense compounds or other secondary metabolites. Identifying which family an unknown plant belongs to might provide insight into potential interactions with other organisms (see Orchidaceae below), its capability to resist particular environmental conditions or stressors, its edibility or toxicity, or whether it produces compounds that might be used medicinally.

For example, plants like poison oak (*Toxicodendron diversilobum*) and poison ivy (*Toxicodendron radicans*) are in the family Anacardiaceae and produce an oil called urushiol. This oil causes a (sometimes severe) allergic reaction in many people, resulting in an itchy, blistering rash. Mango (*Mangifera indica*) and cashew (*Anacardium occidentale*). also belong to this family, but these are not known for giving itchy rashes. However, as someone who is quite allergic to poison oak, I unknowingly ate a mango with the skin on and broke out in a rash all around my mouth and lower face, just like how I react to touching poison oak. Indeed, cashews are just the seed of the cashew fruit. The rest of the fruit and seed coat are removed due to the urushiol content.

Additionally, while there are over 350,000 species of flowering plants, there are only around 400 families. Being able to quickly narrow an unknown plant to family is an essential skill in plant identification. So how can we tell who belongs to the same family among plants? For flowering plants, we can use **floral formulas.**

Floral Formulas

Since there are so many terms about flowers, and at the same time, flower structure and diversity always were of immense importance in botany, two specific ways were developed to make flower description more compact. First is a flower formula. This is an approach where every part of flower is designated with a specific letter, numbers of parts with digits, and some other features (whorls, fusion, position) with other signs.

- Symmetry: ***** means radial symmetry, while **X** means bilateral symmetry.
- Whorls: **K** is the calyx, **C** is the corolla, **A** is the androecium, and **G** is the gynoecium. The number that follows each letter represents the number of parts in that whorl. For the gynoecium, a line under the number indicates an inferior ovary, while a line above the number indicates a superior ovary.
- Fusion: In most representations, connation is indicated by circling the number, while adnation is indicated by drawing a line connecting the numbers of the fused whorls.

Here are a few examples of floral formulas, followed by their interpretation:

$*K_4C_4A_{2+4}\underline{G_{(2)}}$: flower actinomorphic, with four sepals, four petals and six stamens in two whorls, ovary superior, with two fused carpels

$\uparrow K_{(5)}[C_{(1,2,2)}A_{2,2}]\underline{G_{(2\times2)}}$: flower zygomorphic, with five fused sepals, five unequal fused petals, two-paired stamens attached to petals, superior ovary with two subdivided carpels

$*K_{(5)}C_{(5)}[A_5\underline{G_{(3)}}]$: actinomorphic flower with five fused sepals and five fused petals, five stamens attached to pistil, ovary inferior, with three fused carpels

The following signs are used to enrich formulas:

PLUS "+" is used to show different whorls; *minus* "−" shows variation; "∨" = "*or*"

BRACKETS "[]" and "()" show fusion. In most representations, connation is indicated by circling the fused whorl, while adnation is indicated by drawing a line underneath the formula connecting those whorls.

COMMA "," shows inequality of flower parts in one whorl

MULTIPLICATION "$\times$" shows splitting

INFINITY "∞" shows indefinite number of more than 12 parts

Flower diagram is a graphical way of flower description. This diagram is a kind of cross-section of the flower. Frequently, the structure of pistil is not shown on the diagram. Also, diagrams sometimes contain signs for the description of main stem (axis) and flower-related leaf (bract). The best way to show how to draw diagram is also graphical (Figure $2.7.4.1$); formula of the flower shown there is $*K_5C_5A_5\underline{G_{(5)}}$.

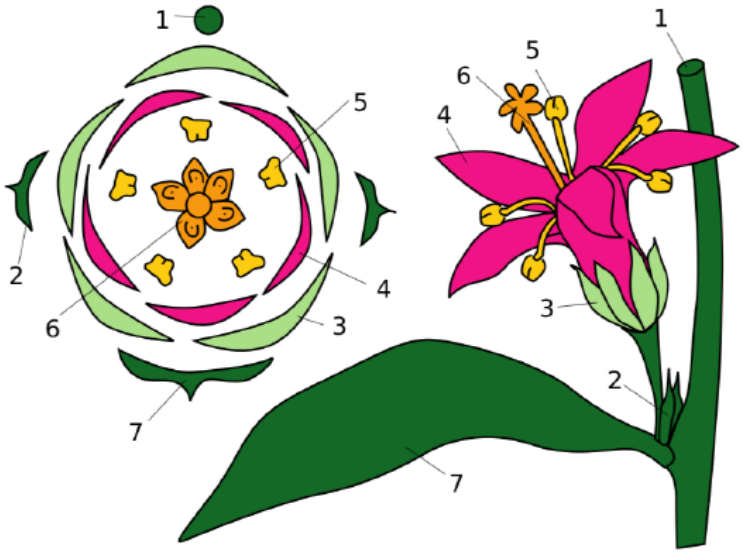


Figure $2.7.4.1$: How to draw a diagram (graphical explanation): compare numbers on plant and on diagram. On the left of the image, a simplified aerial view of the flower represents the floral diagram. In the center is a star-like 5-lobed stigma surrounded by 5 4-lobed anthers. There are 5 pink crescent shapes that form a circle around this (the petals) and 5 pale green crescents that form a circle around these (the calyx). Three darker green, bracket like shapes represent leaves and a single dark green circle represents the peduncle.

Review of Terms and Formula Designations

FLOWER PARTS occur in whorls in the following order—sepals, petals, stamens, pistils.

> (The only exceptions are flowers of *Eupomatia* with stamens then perianth, *Lacandonia* with pistils then stamens, and some monocots like *Triglochin*, where stamens in several whorls connect with tepals.)

PEDICEL flower stem

RECEPTACLE base of flower where other parts attach

HYPANTHIUM cup-shaped receptacle (Figure $2.7.4.2$)

PERIANTH = CALYX + COROLLA

> **SEPALS** small and green, collectively called the CALYX, **formula**: K
>
> **PETALS** often large and showy, collectively called the COROLLA, **formula**: C
>
> **TEPALS** used when sepals and petals are not distinguishable, they form SIMPLE PERIANTH, **formula**: P

ANDROECIUM collective term for stamens: **formula**: A

STAMEN = FILAMENT + ANTHER

ANTHER structure containing pollen grains

FILAMENT structure connecting anther to receptacle

GYNOECIUM collective term for pistils/carpels, **formula**: G. Gynoecium can be composed of:

1. A single CARPEL = simple PISTIL, this is MONOMERY
2. Two or more fused CARPELS = compound PISTIL, this is SYNCARPY
3. Two or more unfused CARPELS = two or more simple PISTILS, this is APOCARPY

(Note that variant #4, several compound pistils, does not exist in nature.)

To determine the number of CARPELS in a compound PISTIL, count LOCULES, points of placentation, number of STYLES, STIGMA and OVARY lobes.**PISTIL** Collective term for carpel(s). The terms CARPEL and PISTIL are equivalent when there is no fusion, if fusion occurs then you have 2 or more CARPELS united into one PISTIL.

CARPEL structure enclosing ovules, may correspond with locules or placentas

OVARY basal position of pistil where OVULES are located. The ovary develops into the fruit; OVULES develop into seeds after fertilization.

LOCULE chamber containg OVULES

PLACENTA place of attachment of OVULE(S) within ovary

STIGMA receptive surface for pollen

STYLE structure connecting ovary and stigma

FLOWER Floral unit with sterile, male and female zones

ACTINOMORPHIC FLOWER A flower having multiple planes of symmetry, also called radially symmetrical, **formula**: $*$

ZYGOMORPHIC FLOWER A flower having only one plane of symmetry, also called bilaterally symmetrical, **formula**: ↑

PERFECT FLOWER A flower having both sexes

MALE / FEMALE FLOWER A flower having one sex, **formula**: ♂ / ♀

MONOECIOUS PLANTS A plant with unisexual flowers with both sexes on the same plant

DIOECIOUS PLANTS A plant with unisexual flowers with one sex on each plant, in effect, male and female plants

SUPERIOR OVARY most of the flower is attached below the ovary, **formula**: $\underline{G}_{...}$

INFERIOR OVARY most of the flower is attached on the top of ovary, **formula**: $\overline{G}_{...}$

(Inferior ovary only corresponds with monomeric or syncarpous flowers.)

WHORL flower parts attached to one node

Major Families

This section will cover some of the largest families of angiosperms, including their floral formula and general characteristics.

Orchidaceae, the Orchid Family

Orchids are one of the most species-rich group of plants, containing over 28,000 species (Figure 2.7.4.1). These plants tend to be tropical and epiphytic (growing on other plants). However, as can be assumed from their vast diversity, orchids can be found in many ecosystems and growing on a variety of substrates, including rocks! Their flowers are often highly modified, including long nectar spurs, hairy petals, and strange morphologies. Many orchids are fly pollinated. Follow this link to see observations of orchids from across the globe and in your region!

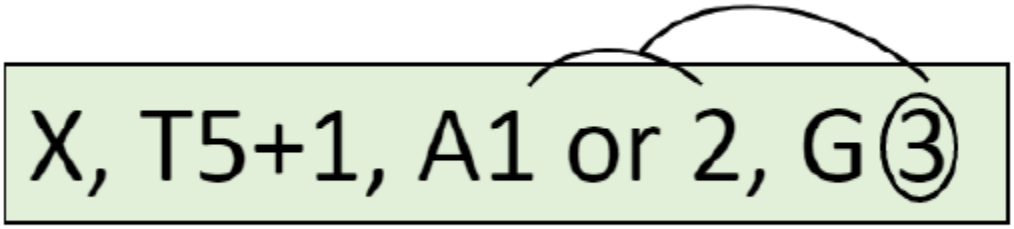


Figure 2.7.4.1: Floral formula of the Orchidaceae. Flowers are bilaterally symmetrical. These flowers have tepals, so the K and C have been replaced by a T. There are 5 tepals that are similar in appearance and one that is different. The androecium contains one or two stamens that are fused to the gynoecium, which contains three fused carpels. Diagram by Melissa Ha, CC-BY-NC.

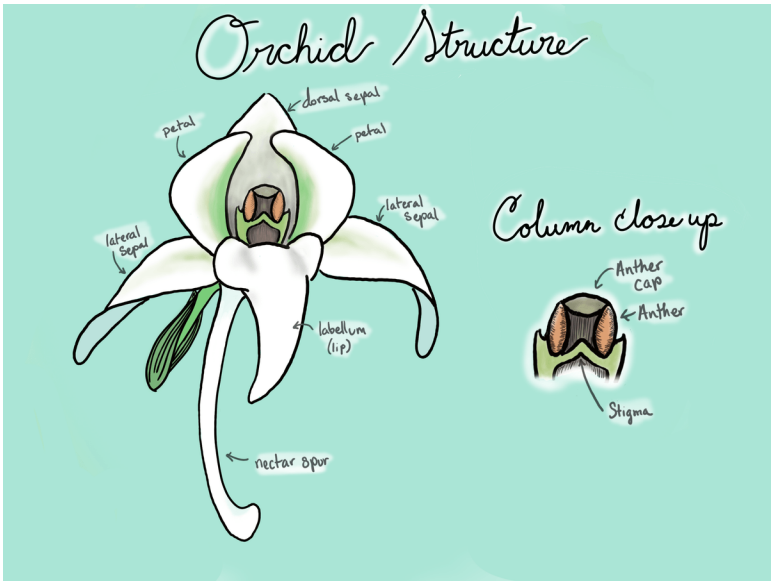


Figure 2.7.4.2: A diagram of general orchid flower structure, with a close up on the column. The column is a structure formed from the fusion of the androecium and gynoecium. This flower has two lateral sepals emerging from the sides and one vertically oriented dorsal sepal. There are two petals vertically oriented on either side of a the central column. In front of the column, a forward-extending petal is labeled as the labellum (or lip). A nectar spur (a tubular structure formed from the perianth) extends below the flower. Within the column, anthers flank a central stigma. Diagram by Maria Morrow, CC-BY-NC.



Figure 2.7.4.3: Orchids produce a spectacular diversity of floral morphologies. The first image is *Anoectochilus albolineatus,* an orchid whose labellum forms tendrils like spider legs. The second image is *Caleana major*, also called the large flying duck orchid for its uncanny similarity to a cartoon duck. First image by Safwanah Safwan, CC-BY-NC. Second image by Ambikab, CC-BY-NC.

Orchids make a large number of tiny seeds, i.e. the tiny black specks in vanilla bean ice cream are the seeds of the orchid *Vanilla plantifolia*. An interesting, r-selected strategy with a twist: the seeds parasitize mycorrhizal fungi. Orchid seeds will not germinate if they do not have a fungal partner. As the fungal hyphae penetrate into the orchid cells, they formed coiled structures. The orchid feeds on the fungal hyphae until it has produced its first leaves and can photosynthesize on its own. At this point, the relationship can be shifted toward mutualism, with sugars transfered from plant to fungus. However, some orchids have lost the ability to make chlorophyll and instead, continue to feed from their fungal partner. These plants are referred to as **mycoheterotrophs**. The mycoheterotrophic orchid *Rhizanthella gardneri* undergoes its entire life cycle underground!

Asteraceae, the Aster Family or Composite Family

There are more than 32,000 accepted species in Asteraceae—a recent and dramatic increase in described species has sent them soaring past the orchids (for the time being). They have a cosmopolitan distribution, but are better represented in temperate and subtropical regions. This family is primarily herbaceous but does contain some woody species. Members of this family produce head inflorescences with one or two different types of florets that all attach to a common receptacle (Figure 2.7.4.4). Disc florets have radial symmetry, while ligulate florets have bilateral symmetry (Figure 2.7.4.5). Some inflorescences contain only disc florets (e.g. thistle), some only ligulate florets (e.g. dandelions), and others contain a combination of the two (e.g. daisy). The inflorescence is subtended by layers of bracts called phyllaries, forming an involucre.

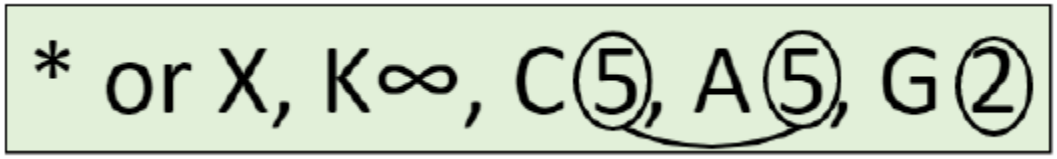


Figure 2.7.4.4: Floral formula of the Asteraceae. Disc florets are radially symmetrical, while ray florets are bilaterally symmetrical. There are many unfused sepals. There are 5 fused petals. The androecium contains 5 fused stamens that are also fused to the petals. The gynoecium contains 2 fused carpels. Diagram by Melissa Ha, CC-BY-NC.



Figure 2.7.4.5: A long section through a head inflorescence and and one ligulate (ray) floret. The cone (center) of the head inflorescence is composed of radially symmetrical disc florets that have fused yellow petals. These are encircled by a ring of ray florets with white, fused petals and bilateral symmetry. All florets are attached to an enlarged receptacle area. A single ray floret is shown on the right. This one has 5 fused yellow petals. The calyx is reduced to a ring of fuzz called a pappus. The stigma is two-lobed.

The calyx is reduced to hairs or bristles (**pappus**, see Figure 2.7.4.6 – 7), petals are fused into a tube or ligula (with 5 or 3 teeth). The pollen is lifted up and distributed by the outer sides of the stigmas, called secondary pollen presentation (Figure 2.7.4.6). Florets have inferior ovaries. The fruit is an achene and the mature seed has almost no endosperm.

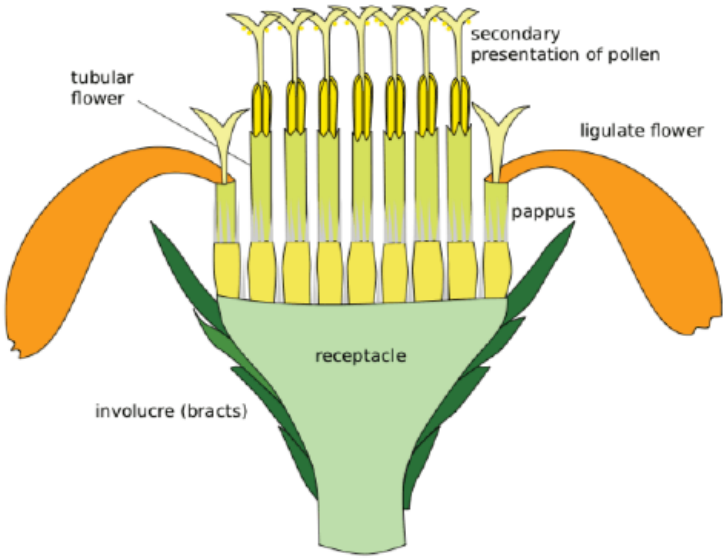


Figure 2.7.4.6: Disc florets showing secondary pollen presentation by the stigmas, with anthers forming a tight ring around the styles. The modified calyx (pappus) is shown at the base of the florets. Ligulate florets are shown on each side; these lack anthers. All florets are attached to a common, swollen receptacle which is lined with bracts, forming an involucre.



Figure 2.7.4.7: Pappus of *Cirsium vulgare* florets. These bull thistle florets have shed their corollas, revealing the modified, bristle-like calyx, the pappus. Photo by Tatyana Zarubo, CC-BY-NC.

Many plants withing the Asteraceae are used for oils, vegetables, ornamentals and medicinal plants are distributed in multiple subfamilies. The most commercially important of these are:

- Carduoideae: mostly tubular flowers

  -*Centaurea*—knapweed

  -*Cynara*—artichoke

  -*Carthamus*–safflower

- Cichorioideae: mostly 5-toothed ligulate (pseudo-ligulate) flowers + lacticifers with latex

  -*Taraxacum*—dandelion

  -*Lactuca*—lettuce

- Asteroideae: tubular + 3-toothed ligulate flowers

  -*Helianthus*—sunflower (BTW, “canola”, or Brassica napus from Cruciferae is the second main source of vegetable oil)

  -*Artemisia*—sagebrush

  -*Tagetes*—marigold and lots of other ornamentals

Fabaceae, the Legume Family

With around 19,000 species, Fabaceae (Figure 2.7.4.8) is the third largest angiosperm family after orchids and asters. This family is widely distributed throughout the world, but does particularly well in the tropics. These plants form root nodules with nitrogen-fixing bacteria. Leaves are alternate, pinnately compound (once or twice), with stipules. Plants in this family have legumes as fruits (one locule dehiscent along a single suture).



Figure 2.7.4.8: Floral formula of the Fabaceae. Because of the differences between the three subfamilies, a single floral formula becomes complex. Most flowers are bilaterally symmetrical, though they are radially symmetrical in Mimosoideae. There are 5 sepals and 5 petals with varying degrees of fuision. In most cases, there are 10 stamens, but Mimosoideae has many. There is a single carpel with an inferior ovary. Diagram by Melissa Ha, CC-BY-NC.

There are three subfamilies (Caesalpinioideae, Mimosoideae, Papilionoideae) with distinct characteristics. In Papilionoideae the petals are mostly free, unequal and have special names: *banner*, *keel* and *wing* (Figure 2.7.4.9). In Mimosoideae, they fuse and form a tube with radial symmetry. There are usually 10 stamens with 9 fused and one free; in Mimosoideae, stamens are numerous. There is a single carpel in the gynoecium, meaning the ovary will have a single locule.

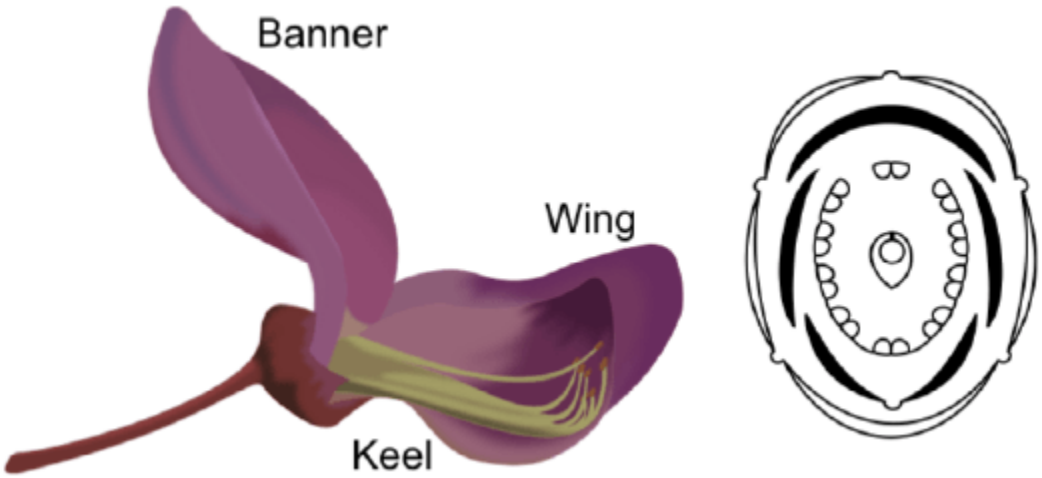


Figure 2.7.4.9: Flowers of Papilionoideae subfamily. The large, upright petal in the back is the banner. Two wings extend out to the sides. A keel, composed of two fused petals, houses the reproductive whorls. The floral diagram shows that there are 9+1 stamens (one of the stamens is separate from the others.

Some representatives of Fabaceae include:

- Mimosoideae: stamens numerous, petals connected

  -*Acacia*—dominant tree of African and Australian savannas, often with phyllodes

  -*Mimosa*—sensitive plant

- Papilionoideae: stamens 9+1, petals mostly free; this subfamily contains many extremely important food plants with high protein value

  -*Glycine*—soybean

  -*Arachis*—peanut with self-buried fruits

  -*Phaseolus*—bean

  -*Pisum*—pea

Poaceae, the Grass Family

Grasses are monocots. There are approximately 12,000 species of grasses widely distributed throughout the world, but most

genera concentrate in the tropics. Grasses tend to be wind dispersed and prefer dry, sunny places. They often form turf (tussocks)—compact structures where old grass stems, rhizomes, roots, and soil parts are intermixed. Grasses form grasslands—specific ecological communities widely represented on Earth (for example, North American prairies are grasslands). Grasses are also important components of other ecosystems (e.g. wetlands). Stems of grasses are usually hollow and round. The leaves have sheathing bases.

Grass florets are reduced, wind-pollinated, usually bisexual (Figure 2.7.4.10), and form complicated spikelets. Each spikelet bears two *glumes*; each flower has *lemma* and *palea* scales (Figure 2.7.4.11). The perianth is reduced to lodicules. Stamens from 6 to 1 (most often 3), with large anthers. The fruit of grasses is a **caryopsis,** what we commonly refer to as a grain. Grasses are incredibly important commercially as food sources, construction, biofuels, and components of many products: rice, corn, wheat, sugarcane, barley, rye, sorghum, and bamboo are all grasses. The study of grasses is called agrostology--it can be both aggravating and glumey.

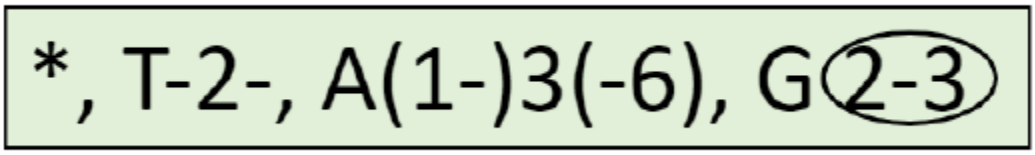


Figure 2.7.4.10: Floral formula of the Poaceae. Grass florets are strange, indeed! They have a reduced perianth with two lodicules (T) due to their wind pollination syndrome. The androecium usually contains 3 stamens, but there may be 1 or 6. The gynoecium contains 2-3 fused carpels. Diagram by Melissa Ha, CC-BY-NC.

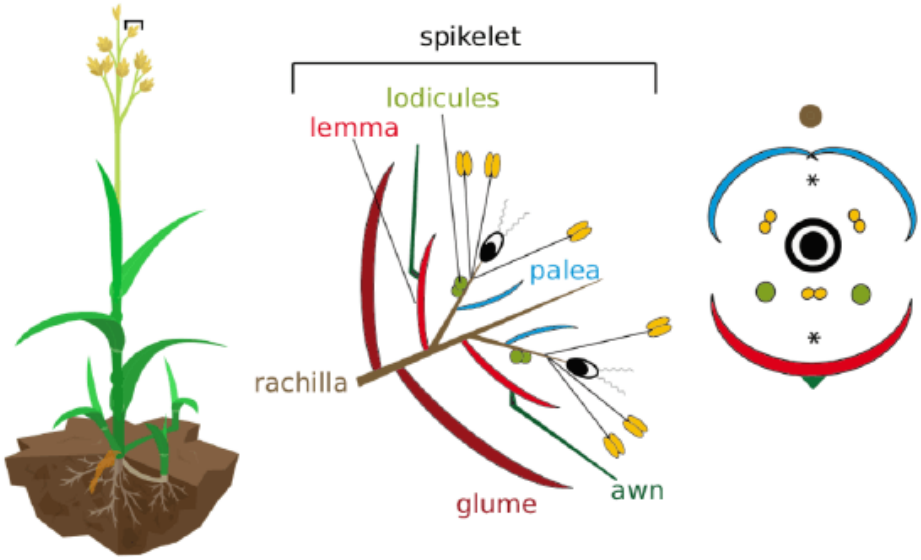


Figure 2.7.4.11: Floral structures in the Poaceae. On the left is a grass plant with sheathing leaves around a single stem topped by an inflorescence composed of florets. In the center is a diagram of a spikelet. Each spikelet is composed of a central rachilla, two glumes on the outside that enclose a lemma and an awn, and two florets composed of lodicules, palea, stamens, and carpels. On the right is a flower diagram of a grass floret. The diagram shows a circle for the rachilla next to two palea. On the other side, the floret is enclosed by an awn or lemma. In the center, there are two lodicules, three anthers, and a single carpel with two feathery stigmas (each shown as asterix).

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2.7.5: Chapter Summary

Angiosperms are an incredibly diverse group of plants. They have many avenues in which to specialize and speciate. Lineages of flowering plants have evolved in tandem with their pollinators by forming increasingly specialized flowers. These sets of specialized floral characteristics--including morphology, color, smell, and the presence of nectar or pollen--are considered together as the plant's pollination syndrome. Wind pollinated flowers are reduced and lack strong odors or nectar, though they contain large amounts of pollen. Bird pollinated flowers contain lots of nectar that they hide in tubular structures, often pigmented red or pink (colors that birds see well, but bees can't distinguish from greens), and lacking strong scents. Bee pollinated flowers can be a variety of colors, but tend toward blues, purples, and yellows. They tend to have sweet, fresh scents and a place for the bee to land. Moth and bat pollinated flowers are white and open at night. Some flowers have even evolved to trick flies into accidental pollination by mimicking a corpse.

They have also evolved fruits specialized for their particular seed dispersal agent. Some fruits release seeds on their own through a variety of explosive mechanisms. Others rely on wind (using wing-like structures) or water (using floats) for dispersal. Still others have coevolved with animals. Some have evolved velcro-like spines or sticky substances to attach to passing animals. Others have evolved to be eaten, some only by specific animals, and hope to survive the digestive tract or have at least some seeds escape the process.

These opportunities for specialization, as well as perhaps the influence of self-incompatibility genes and other factors, has resulted in over 350,000 species of angiosperms classified into over 400 families. However, much of angiosperm diversity can be found in a few major families. Among these are the asters (32,000), orchids (28,000), legumes (19,000), and grasses (12,000).

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

- Compare and contrast monocots and eudicots.
- Differentiate between monocot and eudicot flowers and leaves.
- Explain pollination strategies with regard to genetic diversity.
- Explain what is meant by the term pollination syndrome.
- Use floral characteristics to predict a plants pollinator(s).
- Describe the transition from ovary and ovule to fruit and seed.
- Use characteristics of fruits, including pericarp morphology, to identify fruit type.
- Use characteristics of fruits to predict the dispersal agent for a plant's seeds.
- Interpret a floral formula.
- Describe the characteristics used to identify each of the four largest angiosperm families.

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3: PLANT STRUCTURE

Plants cells are complex structures with several organelles lacking in animal cells. Among these are the cell wall, central vacuole, and plastids (the most familiar of which are chloroplasts). There are three main tissue types, called epidermal, ground, and vascular tissue. Each tissue type consists of specialized cells adapted for unique functions. Plants have two organ systems: the root system and the shoot system (figure $3.a$). The root system is typically belowground and consists of roots, which specialized in water and nutrient absorption. The shoot system consists of stems and leaves and is typically aboveground. Stems function in supporting the plant and transporting materials (conduction), and leaves function in photosynthesis. This unit will explore these structure at the macroscopic and microscopic level.



Figure 3.1: The shoot system consists of the stems and leaves, and the root system is the fibrous mat embedded in the soil. Image by Maria Morrow (CC-BY-NC).

3.1: Cells and Tissues

3.1.1: Introduction to Cells

3.1.2: Plant Cell Structure

3.1.3: Plant Tissues

3.1.4: Chapter Summary

3.2: Roots

3.2.1: Organs and Organ Systems

3.2.2: External Root Structure

3.2.3: Internal Root Structure

3.2.4: Root Modifications

3.2.5: Chapter Summary

3.3: Stems

3.3.1: Stem Morphology (External Structure)

3.3.2: Internal Anatomy of the Primary Stem

3.3.3: Secondary Stem

3.3.4: Stem Modifications

3.3.5: Chapter Summary

3.4: Leaves

3.4.1: External Structure of Leaves

3.4.2: Internal Leaf Structure

3.4.3: Leaf Modifications

3.4.4: Chapter Summary

Thumbnail Image: Cross section of a beach grass leaf from Berkshire Community College Bioscience Image Library (public domain).

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3.1: CELLS AND TISSUES

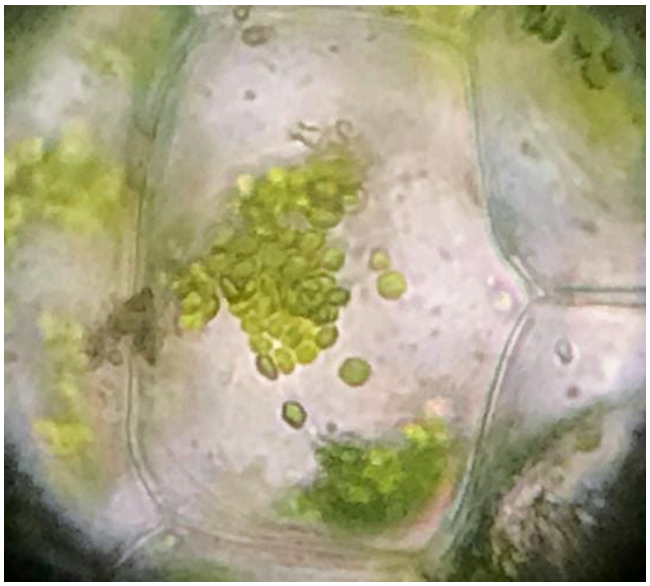


Figure 3.1.1: An *Elodea* cell and green chloroplasts, Credit: Kammy Algiers (CC-BY)

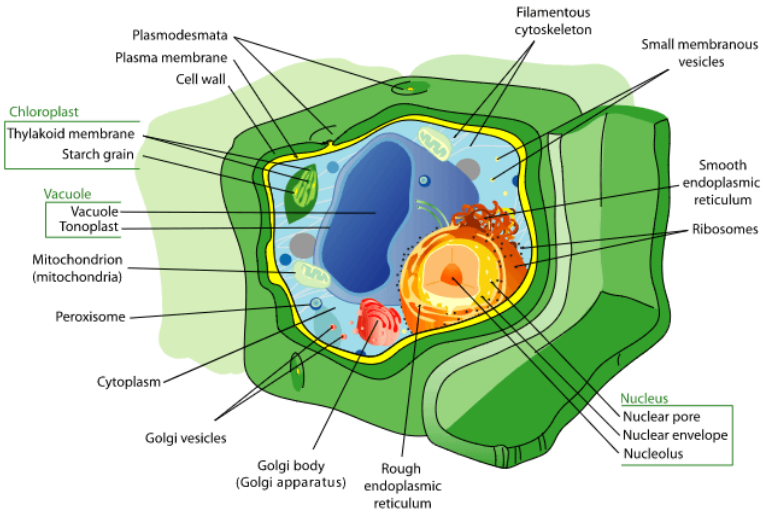


Figure 3.1.2: A typical plant cell Credit: Mariana Ruiz Villarreal (public domain).

Plants are multicellular organisms composed of eukaryotic cells. Cells are the basic building blocks of the organism. Plants are autotrophic and thus many of their cells contain large amounts of chloroplast, the organelle for photosynthesis (Figure 3.1.1). The green color of leaves are due to the large amounts of chloroplast within the cells. Plant cells obtain many other organelles, which we will study in this chapter (Figure 3.1.2). Cells with similar functions are arranged in tissues, which are arranged into plant organs such as roots, stems, and leaves. Together, these organs and their associated organ systems form the plant organism.

3.1.1: Introduction to Cells
3.1.2: Plant Cell Structure
3.1.3: Plant Tissues
3.1.4: Chapter Summary

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3.1.1: Introduction to Cells

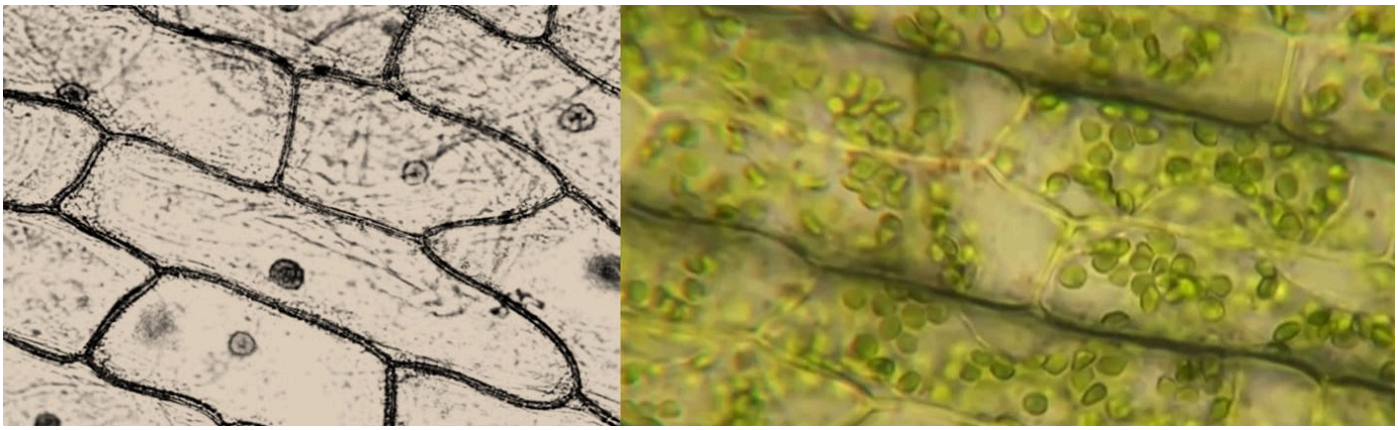


Figure 3.1.1.1:(a) onion cells, and (b) *Elodea* cells, both viewed with a light microscope. Credit: Kammy Algiers (CC-BY).

Learning Objectives

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

A cell is the smallest unit of a living thing. Whether comprised of one cell (like bacteria) or many cells (like a plant, Figure 3.1.1.1), we call it an organism. Thus, cells are the basic building blocks of all organisms.

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

Cell Theory

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

Cell Size

At 0.1 to 5.0 µm in diameter, prokaryotic cells are significantly smaller than eukaryotic cells, which have diameters ranging from 10 to 100 µm (Figure 3.1.1.2. The prokaryotes' small size allows ions and organic molecules that enter them to quickly diffuse to other parts of the cell. Similarly, any wastes produced within a prokaryotic cell can quickly diffuse. This is not the case in eukaryotic cells, which have developed different structural adaptations to enhance intracellular transport.

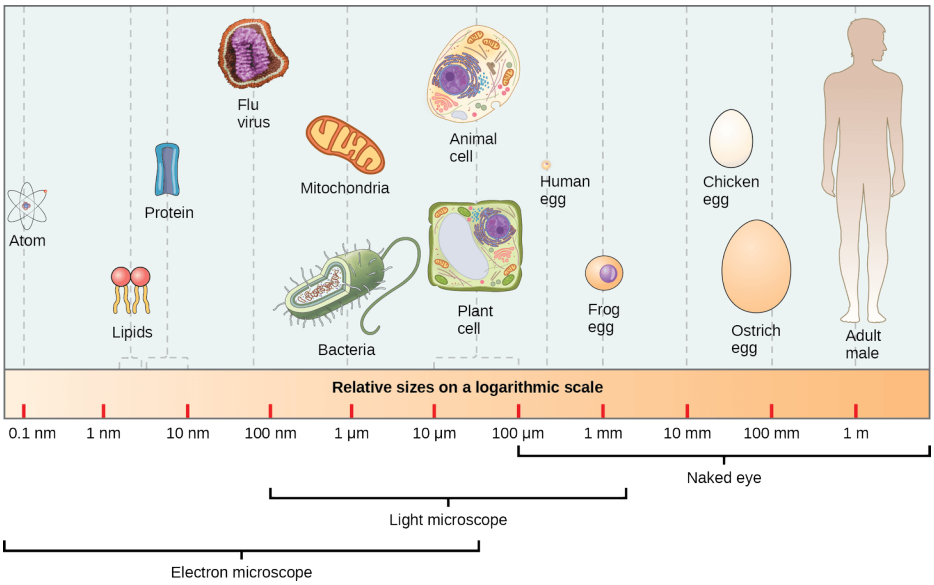
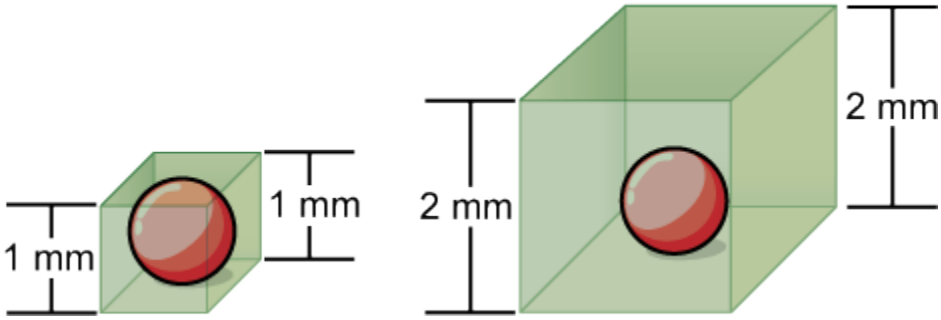


Figure 3.1.1.2): This figure shows relative sizes of microbes on a logarithmic scale (recall that each unit of increase in a logarithmic scale represents a 10-fold increase in the quantity measured). Note that the smallest object is an atom, about 1 nm in size while the largest is a human, at approximately 1m tall.

Small size, in general, is necessary for all cells, whether prokaryotic or eukaryotic. Let's examine why that is so. First, we'll consider the area and volume of a typical cell. Not all cells are spherical in shape, but most tend to approximate a sphere. You may remember from your high school geometry course that the formula for the surface area of a sphere is $4\pi r^2$, while the formula for its volume is $4\pi r^3/3$. Thus, as the radius of a cell increases, its surface area increases as the square of its radius, but its volume increases as the cube of its radius (much more rapidly). Therefore, as a cell increases in size, its surface area-to-volume ratio decreases. This same principle would apply if the cell had a cube shape (Figure 3.1.1.3). If the cell grows too large, the plasma membrane will not have sufficient surface area to support the rate of diffusion required for the increased volume. In other words, as a cell grows, it becomes less efficient. One way to become more efficient is to divide. Other ways are to increase surface area by foldings of the cell membrane, become flat or thin and elongated, or develop organelles that perform specific tasks. These adaptations lead to developing more sophisticated cells, which we call eukaryotic cells.

Visual connection



(Figure 3.1.1.3**)**: Notice that as a cell increases in size, its surface area-to-volume ratio decreases. When there is insufficient surface area to support a cell's increasing volume, a cell will either divide or die. The cell on the left has a volume of 1 mm^3 and a surface area of 6 mm^2, with a surface area-to-volume ratio of 6 to 1; whereas, the cell on the right has a volume of 8 mm^3 and a surface area of 24 mm^2, with a surface area-to-volume ratio of 3 to 1.

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3.1.2: Plant Cell Structure

Learning Objectives

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

Components of All Cells

All cells contain these same four components: 1. **plasma** (**cell**) **membrane**, a phospholipid bilayer with a mosaic of proteins, which functions as a barrier between the cell and its environment. 2. **cytoplasm**, the region between the region of DNA and plasma membrane, and the **cytosol**, a fluid, jelly-like region inside the cell where chemical reactions take place. 3. **DNA**, the heredity information of cells, which can be found in a nucleus of eukaryotic cells and the a nucleoid region of prokaryotic cell. 4. **ribosomes**, or protein-synthesizing structures composed of ribosomes and proteins. These structures can be found on the image of the plant cell (Figure 3.1.2.1).

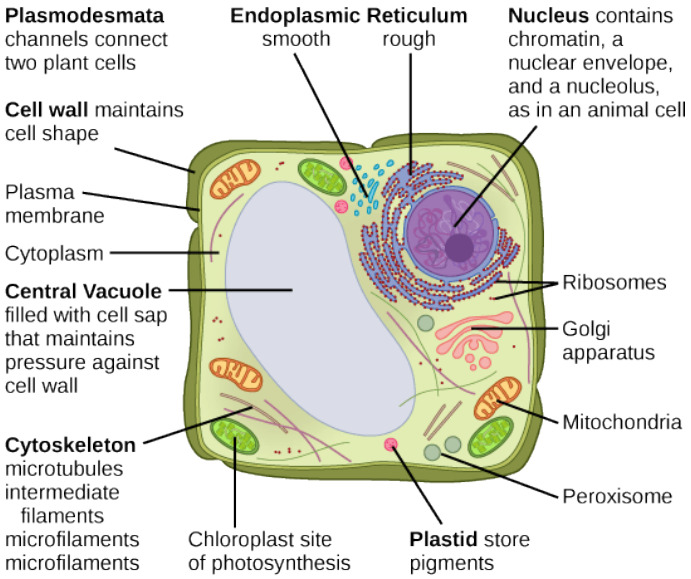
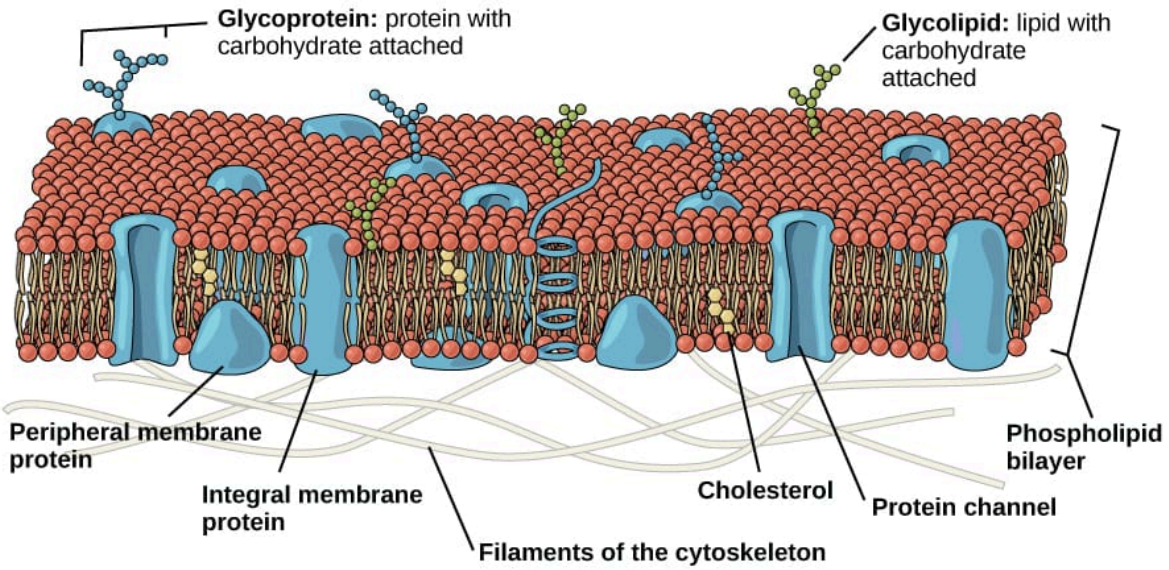


Figure 3.1.2.1): This figure show the major organelles and other cell components of a typical eukaryotic plant cell. The plant cell has a cell wall, chloroplasts, plastids, and a central vacuole—structures not in animal cells. Most cells do not have lysosomes or centrosomes.

The Plasma Membrane

Both prokaryotic and eukaryotic cells have a plasma membrane (Figure 3.1.2.2), a phospholipid bilayer with embedded proteins that separates the internal contents of the cell from its surrounding environment. A phospholipid is a lipid molecule with two fatty acid chains and a phosphate-containing group. The plasma membrane controls the passage of organic molecules, ions, water, and oxygen into and out of the cell. Wastes (such as carbon dioxide and ammonia) also leave the cell by passing through the plasma membrane. The plasma membrane are semi-permeable and allow small and/or non-polar molecules to pass through. Water, being small, can pass through the membrane and will move from an area of low solute concentration to an area of high solute concentration by the process of **osmosis**.



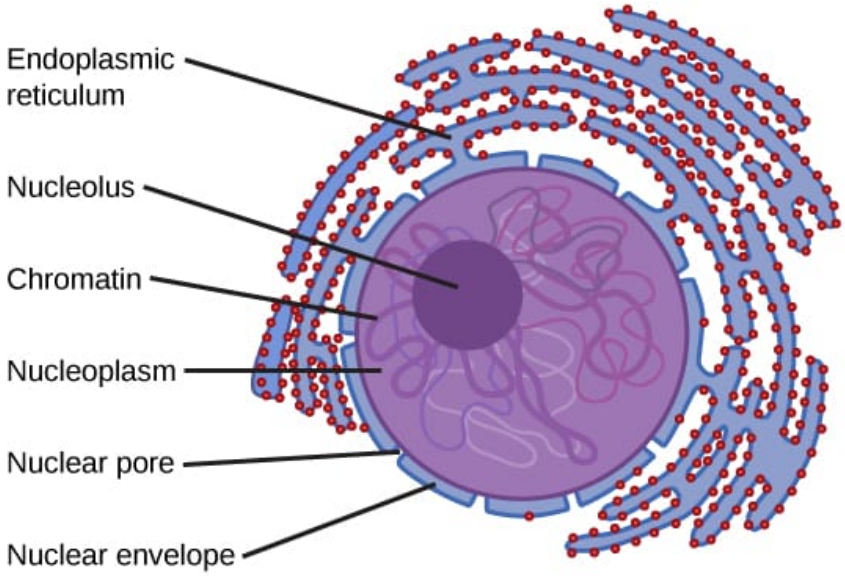
(Figure 3.1.2.2): The eukaryotic plasma membrane is a phospholipid bilayer with proteins and cholesterol embedded in it.

The Cytoplasm

The cytoplasm is the cell's entire region between the plasma membrane and the nuclear envelope (a structure we will discuss shortly). It is comprised of organelles suspended in the gel-like cytosol, the cytoskeleton, and various chemicals (Figure 3.1.2.1). Even though the cytoplasm consists of 70 to 80 percent water, it has a semi-solid consistency, which comes from the proteins within it. However, proteins are not the only organic molecules in the cytoplasm. Glucose and other simple sugars, polysaccharides, amino acids, nucleic acids, fatty acids, and derivatives of glycerol are also there. Ions of sodium, potassium, calcium, and many other elements also dissolve in the cytoplasm. Many metabolic reactions, including protein synthesis, take place in the cytoplasm.

DNA

In eukaryotic cells, the DNA is typically housed in a nucleus (plural = nuclei), the most prominent organelle in a cell (Figure 3.1.2.1 . This organelle directs the synthesis of ribosomes and proteins. Let's look at it in more detail (Figure 3.1.2.3).



(Figure 3.1.2.3): The nucleus stores chromatin (DNA plus proteins) in a gel-like substance called the nucleoplasm. The nucleolus is a condensed chromatin region where ribosome synthesis occurs. We call the nucleus' boundary the nuclear envelope. It consists of two phospholipid bilayers: an outer and an inner membrane. The nuclear membrane is continuous with the endoplasmic reticulum. Nuclear pores allow substances to enter and exit the nucleus.

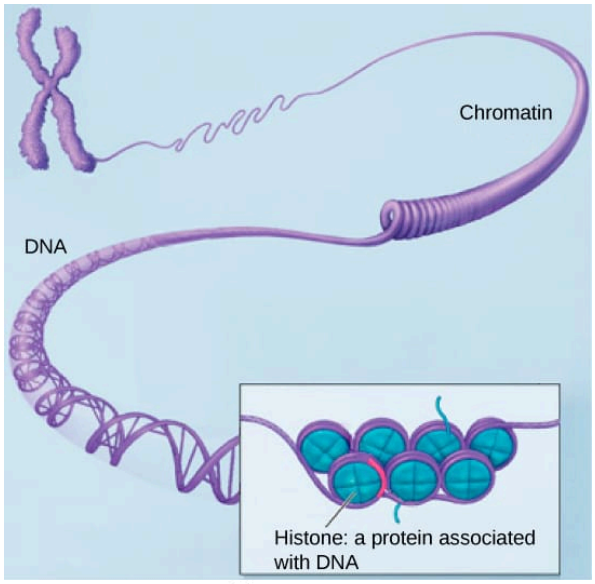
The Nuclear Envelope

The **nuclear envelope** is a double-membrane structure that constitutes the nucleus' outermost portion (Figure 3.1.2.3. Both the nuclear envelope's inner and outer membranes are phospholipid bilayers.

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

Chromatin and Chromosomes

To understand chromatin, it is helpful to first explore **chromosomes**, structures within the nucleus that are made up of DNA, the hereditary material. You may remember that in prokaryotes, DNA is organized into a single circular chromosome. In eukaryotes, chromosomes are linear structures. Every eukaryotic species has a specific number of chromosomes in the nucleus of each cell. For example, in humans, the chromosome number is 46, while in fruit flies, it is eight. Chromosomes are only visible and distinguishable from one another when the cell is getting ready to divide. When the cell is in the growth and maintenance phases of its life cycle, proteins attach to chromosomes, and they resemble an unwound, jumbled bunch of threads. We call these unwound protein-chromosome complexes **chromatin** (Figure 3.1.2.4. Chromatin describes the material that makes up the chromosomes both when condensed and decondensed.



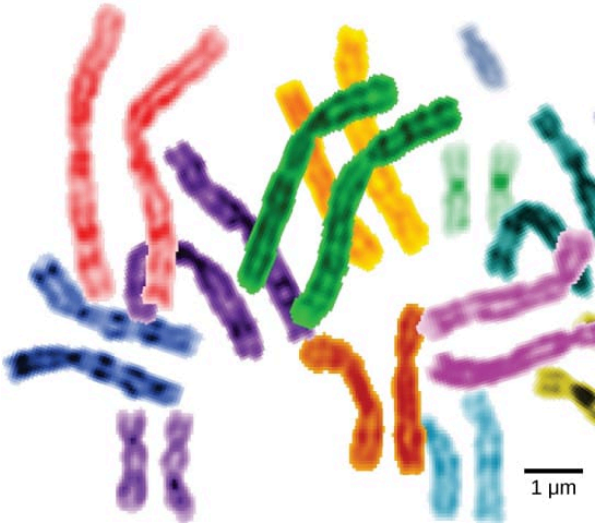


Figure 3.1.2.4: (a) This image shows various levels of chromatin's organization, DNA tightly coiled into two thick cylinders and DNA coiled around proteins called histones. (b) Paired chromosomes, colored as pairs. Notice individuals of each pair are the same size to one another. (credit b: modification of work by NIH; scale-bar data from Matt Russell)

The Nucleolus

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

Ribosomes

Ribosomes are the cellular structures responsible for protein synthesis. They are not organelles. They can be small dot-like structures that float freely in the cytoplasm (known as free ribosomes) or they may be attached to the plasma membrane's cytoplasmic side or the endoplasmic reticulum's cytoplasmic side and the nuclear envelope's outer membrane, and called attached ribosomes (Figure 3.1.2.1). Ribosomes are large protein and RNA complexes consisting of two subunits, a large and a small (Figure 3.1.2.5. Ribosomes receive their “orders” for protein synthesis from the nucleus where the DNA transcribes into messenger RNA (mRNA). The mRNA travels to the ribosomes, which translate the code provided by the sequence of the

nitrogenous bases in the mRNA into a specific order of amino acids in a protein. Amino acids are the building blocks of proteins.

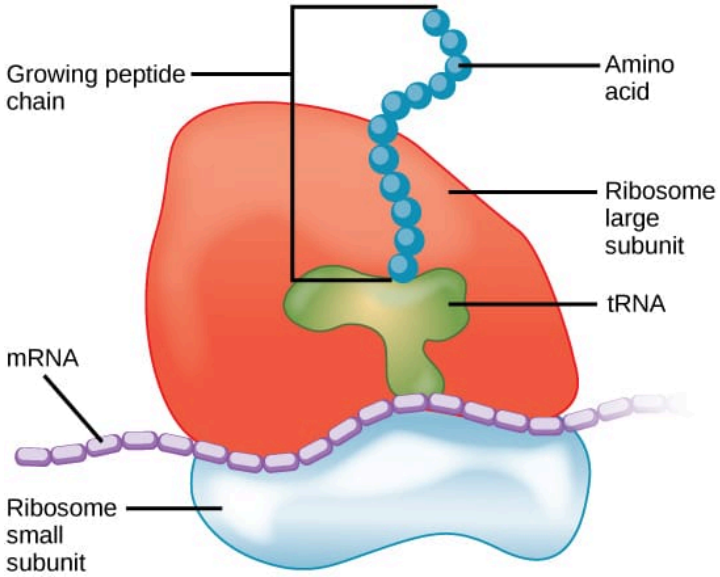


Figure 3.1.2.5: A large subunit (top) and a small subunit (bottom) comprise ribosomes. Note that the large subunit sits on top of the small subunit. During protein synthesis, ribosomes assemble amino acids into proteins using information from a chain of mRNA. The tRNA carries amino acids to the ribosome, where the arrangement is made.

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

Components Unique to Eukaryotic Cells

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

Endomembrane System

The endomembrane system (endo = “within”) is a group of membranes and organelles (Figure 3.1.2.6) in eukaryotic cells that works together to modify, package, and transport lipids and proteins. It includes the nuclear envelope, lysosomes, and vesicles, the tonoplast (see below), and the endoplasmic reticulum and Golgi apparatus. Although not technically *within* the cell, the plasma membrane is included in the endomembrane system because, as you will see, it interacts with the other endomembranous organelles. The endomembrane system does not include either mitochondria or chloroplast membranes.

Visual Connection

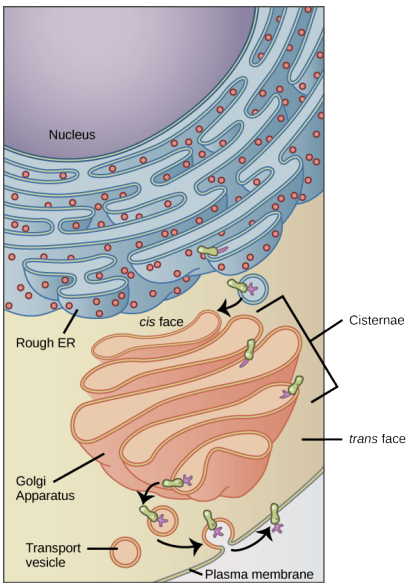


Figure 3.1.2.6Membrane and secretory proteins are synthesized in the rough endoplasmic reticulum (RER). The RER also sometimes modifies proteins. In this illustration, an attachment of a (purple) carbohydrate modifies a (green) integral membrane protein in the ER. Vesicles with the integral protein bud from the ER and fuse with the Golgi apparatus' cis face. As the protein passes along the Golgi's cisternae, the addition of more carbohydrates further modifies it. After its synthesis is complete, it exits as an integral membrane protein of the vesicle that buds from the Golgi's **trans** face. When the vesicle fuses with the cell membrane, the protein becomes an integral portion of that cell membrane. (credit: modification of work by Magnus Manske)

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

The Endoplasmic Reticulum

The **endoplasmic reticulum (ER)** (Figure 3.1.2.6) is a series of interconnected membranous sacs and tubules that collectively modifies proteins and synthesizes lipids. They are formed as an extension of the nuclear membrane and fold out towards the cytoplasm. The two functions of the ER take place in separate areas: the rough ER and the smooth ER, respectively.

The **rough endoplasmic reticulum** (RER) can be found has ribosomes along its surface, and the proteins they create are either secreted or incorporated into membranes in the cell. The **smooth endoplasmic reticulum (SER)** is continuous with the RER but has few or no ribosomes on its cytoplasmic surface (Figure 3.1.2.6). SER functions include synthesis of carbohydrates, lipids, and steroid hormones; detoxification of medications and poisons; and storing calcium ions.

Vesicles

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

Golgi Apparatus

The lipids or proteins within the transport vesicles still need sorting, packaging, and tagging so that they end up in the right place. Sorting, tagging, packaging, and distributing lipids and proteins takes place in the **Golgi apparatus** (also called the Golgi body), a series of flattened membranes (Figure 3.1.2.6).

We call the side of the Golgi apparatus that is closer to the ER the *cis* face. The opposite side. closer to the plasma membrane,

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

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

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

Cytoskeleton

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

Mitochondria

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

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

Mitochondria are oval-shaped, double membrane organelles (Figure 3.1.2.7) that have their own ribosomes and DNA. Each membrane is a phospholipid bilayer embedded with proteins. The inner layer has folds called cristae. The area surrounded by the folds is called the mitochondrial matrix. The cristae and the matrix have different roles in cellular respiration.

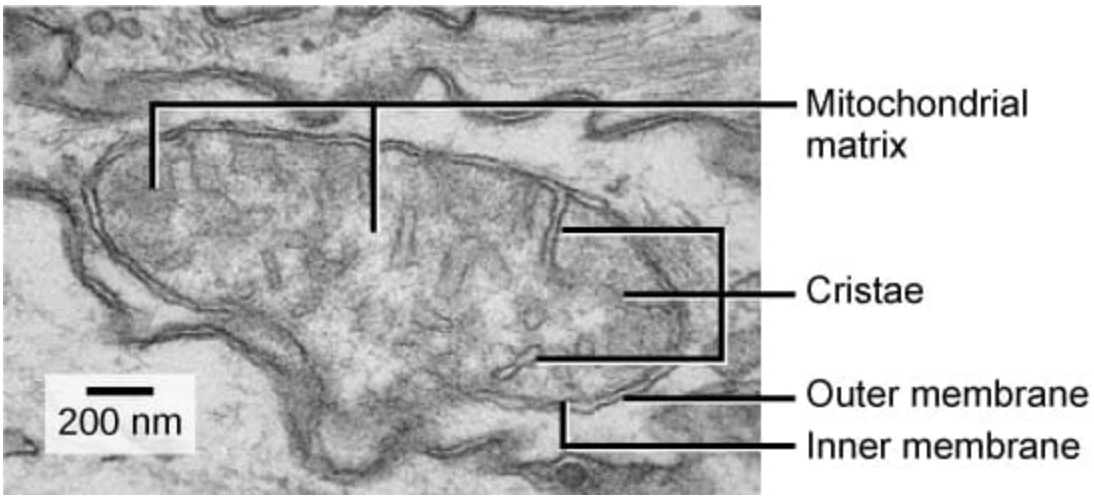


Figure 3.1.2.7: This electron micrograph shows a mitochondrion as viewed with a transmission electron microscope. This organelle has an outer membrane and an inner membrane. The inner membrane contains folds, called cristae, which increase its surface area. The space between the two membranes is called the intermembrane space, and the space inside the inner membrane is called the mitochondrial matrix. ATP synthesis takes place on the inner membrane. (credit: modification of work by Matthew Britton; scale-bar data from Matt Russell)

Peroxisomes

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

Components Unique to Plant Cells

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

Cell wall

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

Central Vacuole

The **central vacuole** is a large, membrane-bound structure that fills much of the plant cell. The membrane surrounding the central vacuole is called the **tonoplast**. The central vacuole plays a key role in regulating the cell's concentration of water in changing environmental conditions. Have you ever noticed that if you forget to water a plant for a few days, it wilts? That's because as the water concentration in the soil becomes lower than the water concentration in the plant, water moves out of the central vacuoles and cytoplasm (Figure 3.1.2.8). As the central vacuole shrinks, it leaves the cell wall unsupported. This loss of support to the plant's cell walls results in the wilted appearance. The central vacuole also supports the cell's expansion. When the central vacuole holds more water, the cell becomes larger without having to invest considerable energy in synthesizing new cytoplasm. Lastly, central vacuoles store nutrients, accumulate ions, or become a place to store wastes.



Figure 3.1.2.8 Osmosis (from left to right) in a hypertonic environment (high salt), an isotonic environment, and a hypotonic (low salt) environment. Blue color is for the vacuole. Red arrows on the right image show turgor—combined pressure of the vacuole and the cell wall.

Plastids

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

Chloroplasts store their pigments in interconnected sacs called **thylakoids** (Figure 3.1.2.9). These sacs are often found in stacks called **grana** (singular **granum**). The fluid portion of the double membraned chloroplast is called the **stroma**. Because the thylakoid stores chlorophyll a, b, and accessory pigments, it is the main region for the first reaction of photosynthesis, where sunlight is used to create molecular energy. In the stroma, the products of the first reaction are used to produce organic molecules such as glucose. The combination of these reactions allow these autotrophic organisms to produce their own organic food.

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

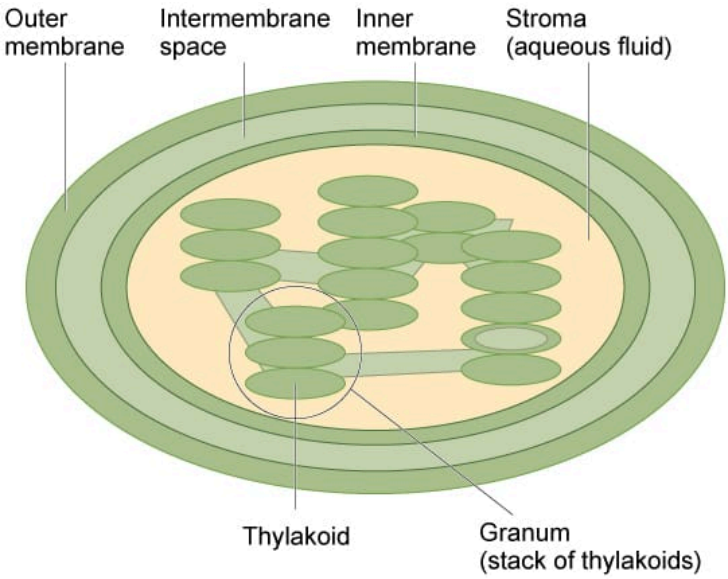


Figure 3.1.2.9: The chloroplast has an outer membrane, an inner membrane, and membrane structures called thylakoids that are stacked into grana. The space inside the thylakoid membranes is called the thylakoid space. The light harvesting reactions take place in the thylakoid membranes, and the synthesis of sugar takes place in the fluid inside the inner membrane, which is called the stroma. Chloroplasts also have their own genome, which is contained on a single circular chromosome.

Evolution Connection- Endosymbiosis

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

The Endosymbiosis Theory explains:

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

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

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3.1.3: Plant Tissues

Learning Objectives

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

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

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

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

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

Dermal Tissue

Dermal tissue covers the plant and can be found on the outer layer of roots, stems and leaves. Its main functions are *transpiration, gas exchange and defense*. The epidermis is an example of dermal tissue (Figure 3.1.3.1). It is composed of a single layer of epidermis cells. It may contains stomata and guard cells that allow gas exchange. It may contain root hairs that increase surface area or or trichomes used in transpiration or defense. It may contain a waxy cuticle if found on the upper surface of leaves, to aid with lowering transpiration.

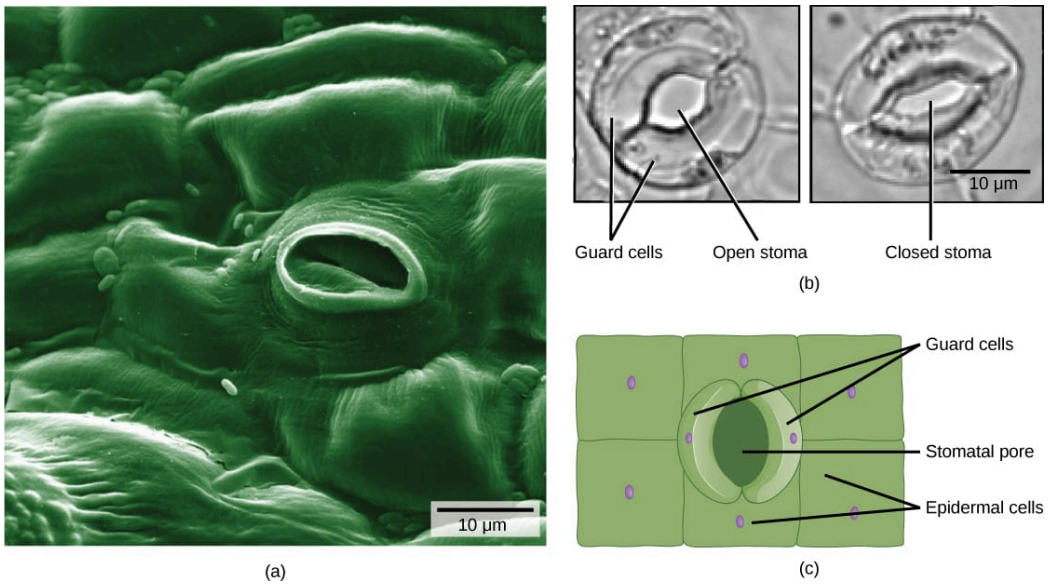


Figure 3.1.3.1: Openings called stomata (singular: stoma) allow a plant to take up carbon dioxide and release oxygen and water vapor. The (a) colorized scanning-electron micrograph shows a closed stoma of a eudicot. Each stoma is flanked by two guard cells that regulate its (b) opening and closing. The guard cells are more curved when the stoma is open compared to when it is closed. The (c) guard cells sit within the layer of epidermal cells (credit a: modification of work by Louisa Howard, Rippel Electron Microscope Facility, Dartmouth College; credit b: modification of work by June Kwak, University of Maryland; scale-bar data from Matt Russell)

In woody plants, the epidermis breaks apart into a thick **periderm** as secondary growth allows the plant to grow in girth. The cork cambium, which makes cork cells, the cork cells (which are dead at maturity), and the phelloderm (parenchyma cells on the inside of the cork cambium) together make up the periderm (Figure 3.1.3.2). The periderm functions as the first line of defense for the plant, protecting it from fire or heat injury, dehydration, freezing conditions, and/or disease.

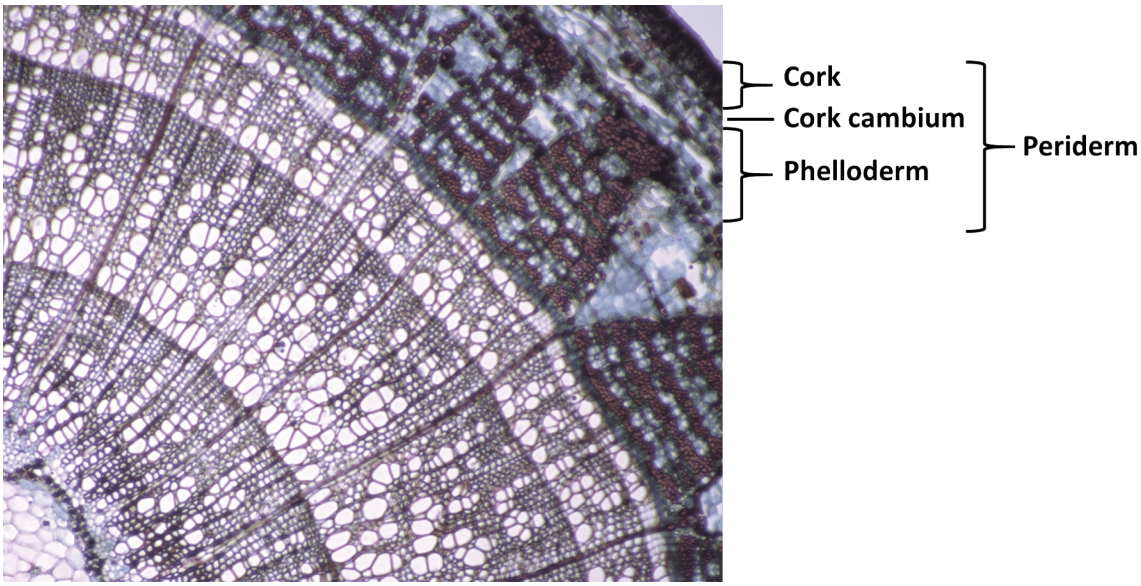


Figure 3.1.3.2: Cross section of a woody stem. The periderm is composed of the cork cambium, cork cells, and phelloderm. Credit: Kammy Algiers (CC-BY).

Ground Tissue

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

Collenchyma (Figures 3.1.3.3 – 4) is living supportive tissue that has elongated cells and an unevenly thickened primary cell wall. Its main function is the mechanical support of young stems and leaves via turgor.

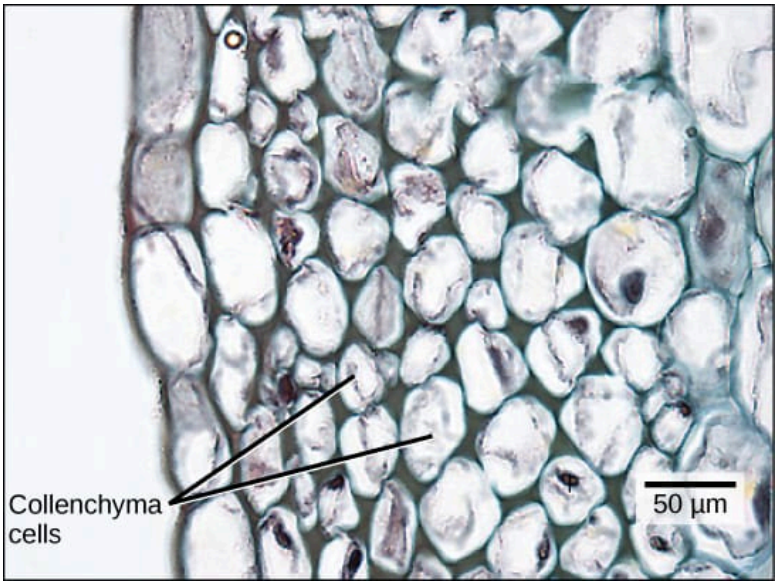


Figure 3.1.3.3: Collenchyma cell walls are uneven in thickness, as seen in this light micrograph. They provide support to plant structures. (credit: modification of work by Carl Szczerski; scale-bar data from Matt Russell)

Sclerenchyma is a dead supportive tissue that consists of long **sclerenchyma fibers** (Figure 3.1.3.4) or short, crystal-like cells (**sclereids**; Figure 3.1.3.5). Sclerenchyma fibers occur in groups (bundles). Sclereids may be branched or not and occur individually or in small clusters. Each cell has a uniformly thick *secondary wall* that is rich in lignin. Its main function is a support of older plant organs, and also hardening different parts of plants (for example, make fruit inedible before ripeness so no one will take the fruit before seeds are ready to be distributed). Without sclerenchyma, if a plant isn't watered, the leaves will droop because the vacuoles will decrease in size which lowers the turgor. Fibers inside phloem (see below) are sometimes regarded as a separate sclerenchyma.

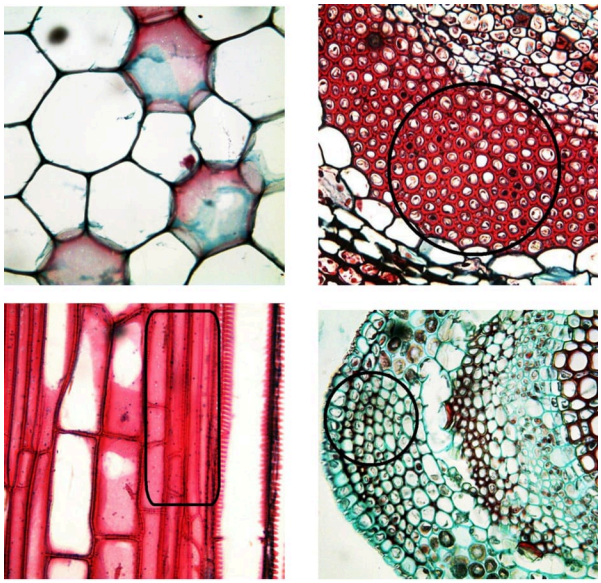


Figure 3.1.3.4: Left to right, top to bottom: parenchyma, sclerenchyma (cross- and longitudinal sections) and collenchyma. First three photos from the stem of *Helianthus*, fourth from *Medicago* stem. Magnification ×400.

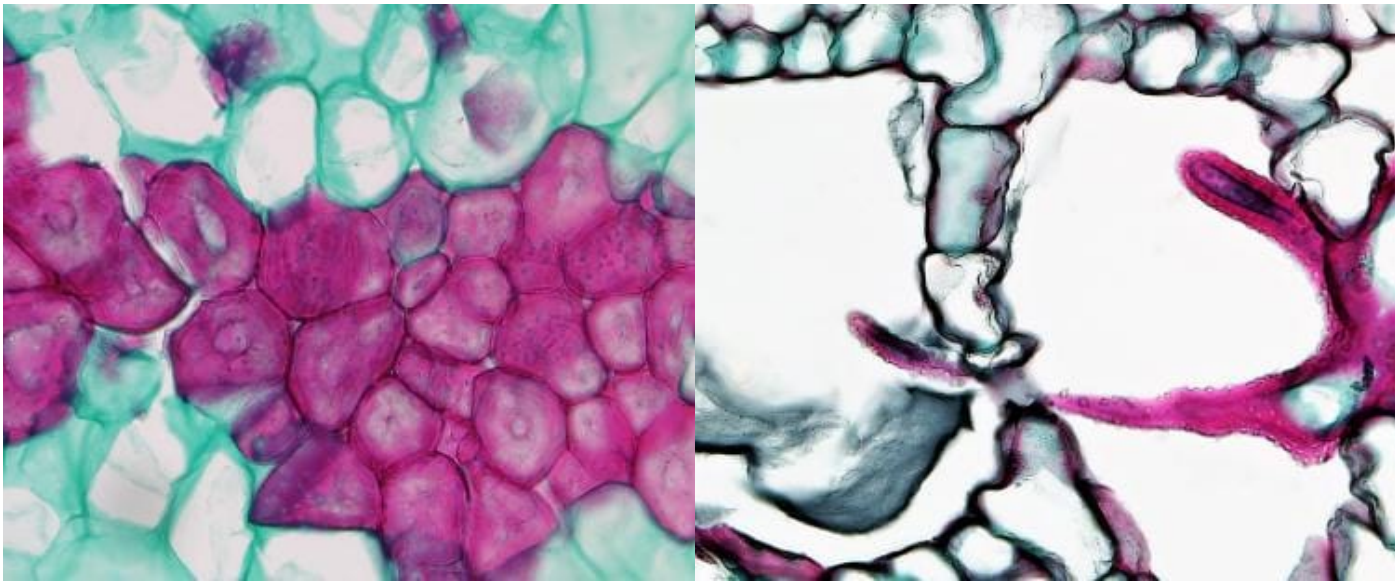


Figure 3.1.3.5: The grainy texture of pears (*Pyrus*) is due to clusters of stone cells (sclereids), the thick-walled cells that stained pink (left, magnification = 400X). Water lily (*Nymphea*) leaves contains single, branched sclereids (right, magnification = 400X). Left and right image by Berkshire Community College Bioscience Image Library (public domain).

Parenchyma (Figure 3.1.3.4) are spherical, elongated cells with a thin primary cell wall. It is a main component of young plant organs. The basic functions of parenchyma are *photosynthesis and storage*. They are also important in regeneration because they are **totipotent** (capable of differentiating into any cell type). Parenchyma cells are widespread in plant body. They fill the leaf, frequent in stem cortex and pith and is a component of complex vascular tissues (see below).

Vascular Tissue

Vascular tissue is the plumbing system of the plant. It allows water, minerals, and dissolved sugars from photosynthesis to pass through roots, stems, leaves, and other parts of the plant. It is primary composed of two types of conducting tissue: xylem and phloem. The veins on leaves are an example of vascular tissue, moving material through the plant in the same manner that our blood vessels carry nutrients through our body. The xylem and phloem always lie adjacent to each other (Figure 3.1.3.6). In stems, the xylem and the phloem form a structure called a vascular bundle; in roots, this is termed the vascular stele or vascular cylinder.

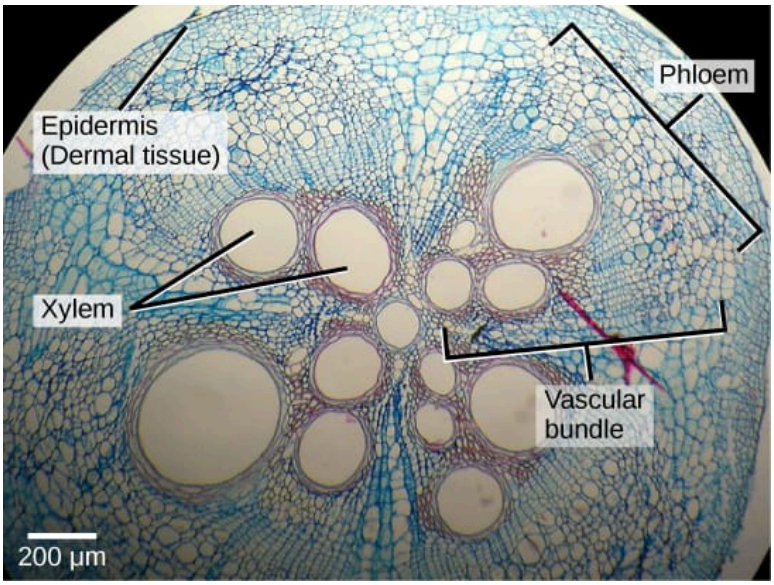


Figure 3.1.3.6: This light micrograph shows a cross section of a squash (*Curcurbita maxima*) stem. Each teardrop-shaped vascular bundle consists of large xylem vessels toward the inside and smaller phloem cells toward the outside. Xylem cells, which transport water and nutrients from the roots to the rest of the plant, are dead at functional maturity. Phloem cells, which transport sugars and other organic compounds from photosynthetic tissue to the rest of the plant, are living. The vascular bundles are encased in ground tissue and surrounded by dermal tissue. (credit: modification of work by "(biophotos)"/Flickr; scale-bar data from Matt Russell)

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

There are two type of tracheary elements: **vessel elements** and **tracheids** (Figure 3.1.3.7). Both cell types that are dead at maturity and have thickened secondary cell walls. These cells connect to one another and allow water to be transported through them. Structurally, the vessel elements are wider than tracheids and contain **perforation plates** between adjacent vessel elements (Figure $3.1.3.7 - 8$). Wide openings (slits or pores) in perforation plates allow water to flow vertically between vessel elements, forming a continuous tube. Both types of tracheary elements contain **pits**, gaps in their secondary cell walls. Adjacent cells have pits in the same locations, forming **pit pairs**, which allow water and minerals to flow between adjacent cells through the **pit membrane** (the remaining, thin primary cell walls in these regions; Figure $3.1.3.9 - 10$). Therefore, water flows through both perforation plates and pit pairs in vessel elements but only through pit pairs in tracheids. While water can move more quickly through vessel elements, they are more susceptible to air bubbles. An air bubble disrupts cohesion in the column of water moving up the tube of vessel elements preventing use of that particular pathway. In tracheids, an air bubble would only decommission a single tracheid rather than an entire column of vessel elements. Vessel elements are found only in angiosperms, but tracheids are found in both angiosperms and gymnosperms.

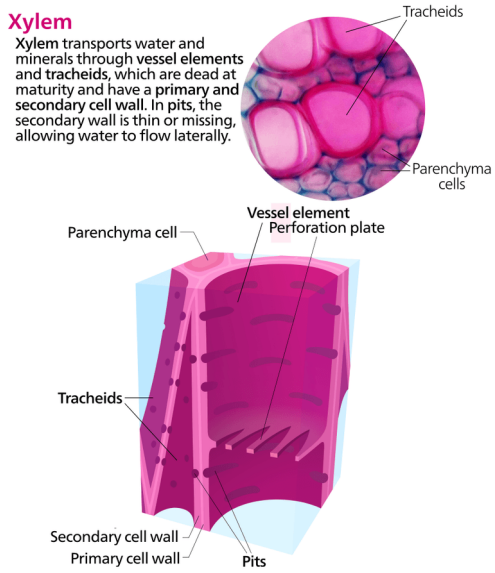


Figure 3.1.3.7: Xylem transports water and minerals through vessel elements and tracheids, which are dead at maturity and have a thin primary and thick secondary cell wall internal to the primary cell wall. In pits, the secondary wall is thin or missing, allowing water to flow laterally. The xylem of angiosperms contains both types of tracheary elements: vessel elements, and tracheids. Vessel elements are stacked up top of each other and contain perforation plates in between cells. Tracheids are thinner and lack performation plates. Pits are thinned regions in the cell wall that allow movement of water between adjacent tracheary elements. Image modified from Kelvinsong (CC-BY-SA).

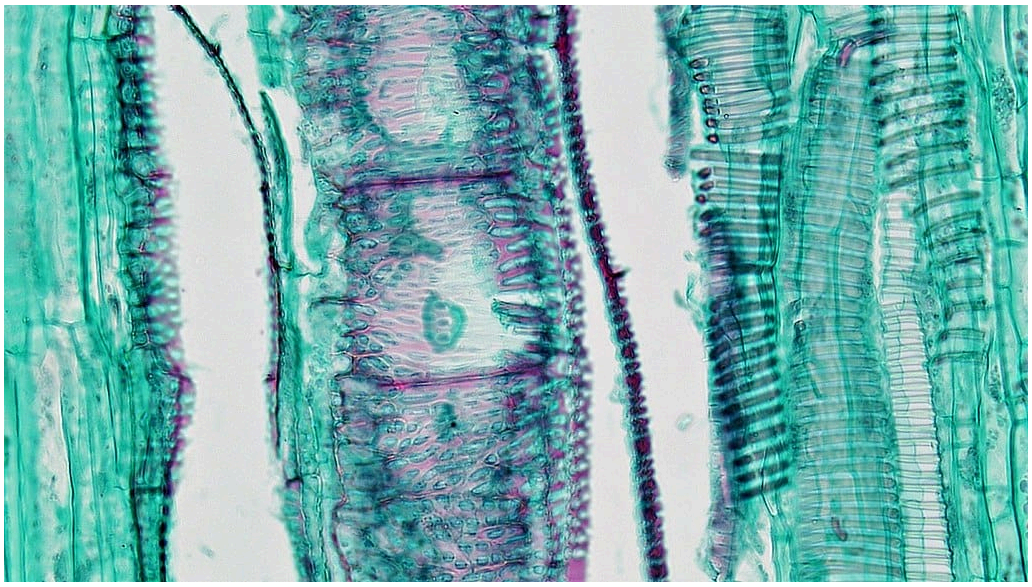


Figure 3.1.3.8: Longitudinal section of vessel elements in a *Cucurbita* (squash) stem (magnification = 400X). Horizontal purple lines represent perforation plates between cells in a column. The rings around the cells are annular cell wall thickenings. Image by Berkshire Community College Bioscience Image Library (public domain).

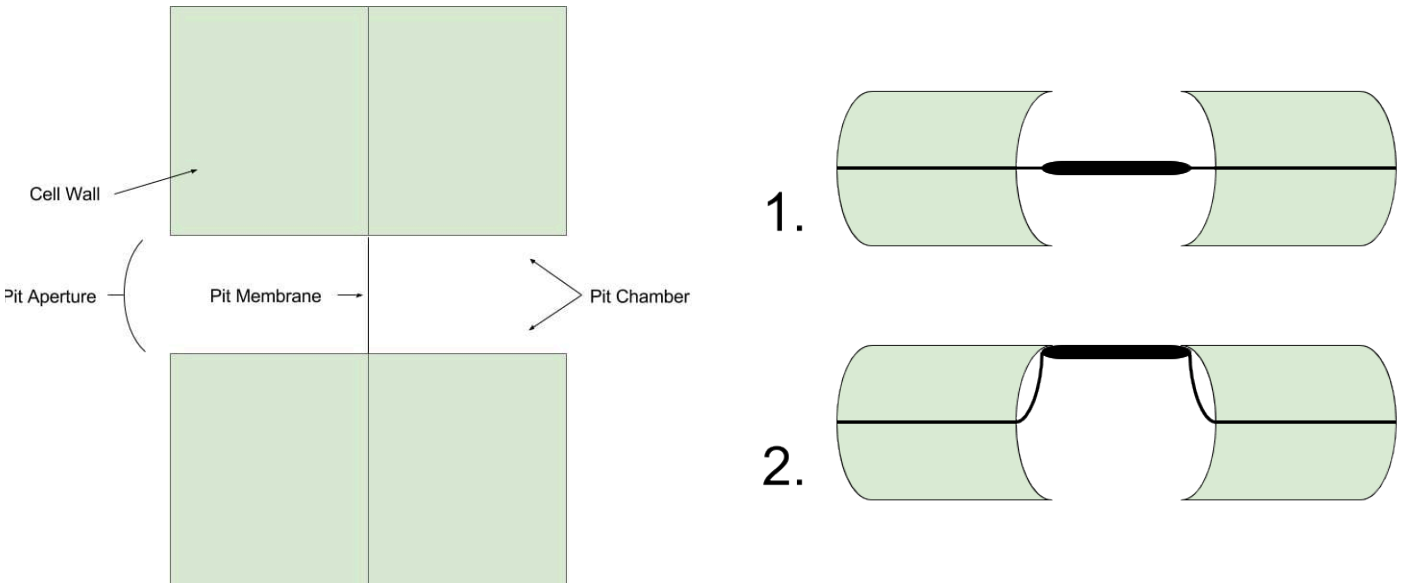


Figure 3.1.3.9: Pits are thinned regions of the cell wall (left). Pits of adjacent cells together form pit pairs separated by a pit membrane. On either side of the pit membrane is a pit chamber. The pit aperature is the opening to the pit chamber. The pit membranes of gymnosperms have a thickened central region called the torus (right). 1: The margo is the part of the membrane surrounding the torus. 2: The torus can block the pit opening (aperture) as needed to prevent air bubbles from spreading throughout the xylem. Left and right image by Pagliaccious (CC-BY-SA).

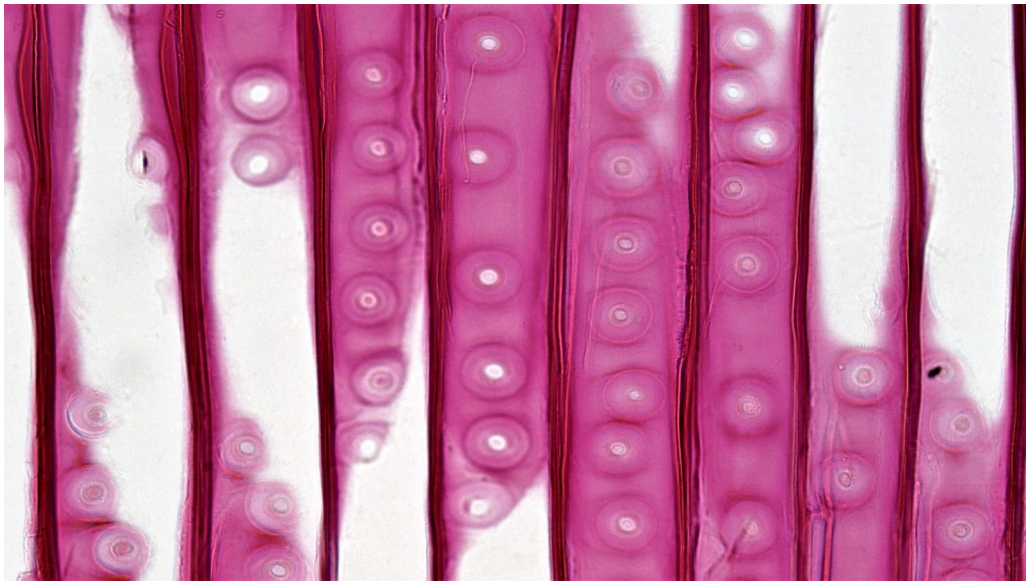


Figure 3.1.3.10: Bordered pits in tracheids of pine (*Pinus*) wood appear as bulls eyes. Pit pairs of some species have thickened outer regions (borders). Inside of this is a thinned membrane (margo) and a thickened central portion (torus). Image by Berkshire Community College Bioscience Image Library (public domain).

Phloem tissue transports organic compounds such as sugars from the site of photosynthesis to rest of the plant (Figure 3.1.3.11 – 12). The conducting cells of the phloem are called **sieve elements**. In comparison to tracheary elements, sieve elements have only primary cell walls (and thus thinner cell walls overall) and are alive at maturity; however, they lack certain organelles, including a nucleus. **Sieve-tube elements** are the sieve elements found only in angiosperms while **sieve cells** are found only in gymnosperms while. Both types of sieve elements have pores in their cell walls (**sieve areas**) that allow transfer of materials between adjacent cells, but these are concentrated at **sieve plates** in sieve-tube elements and evenly distributed in sieve cells. Because they lack essential organelles, sieve elements rely on specialized parenchyma cells to support them. **Companion cells** support sieve-tube elements in angiosperms, and **albuminous cells** support sieve cells in gymnosperms. Additionally parenchyma cells and sclerenchyma cells (phloem fibers) are also found in the phloem.

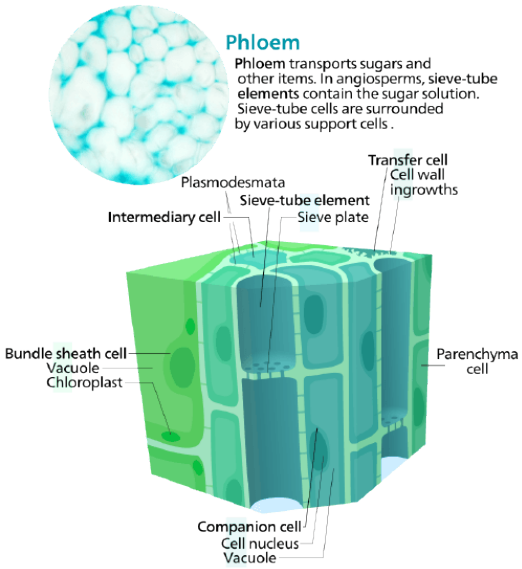


Figure 3.1.3.11: Phloem transports sugars and other items. In angiosperms, sieve-tube elements contain the sugar solution. Sieve-tube elements are the conducting cells of the phloem in angiosperms. Sieve plates allow sieve-tube elements stacked on top of each other to connect. Sieve-tube cells are surrounded by various support cells. Companion cells are narrower than sieve-tube elements and each contain a nucleus. They are connected to sieve-tube elements via plasmodesmata and provide them with the molecules they need to function (energy molecules, proteins, etc.) Some companion cells are specialized as intermediary cells, which are between the bundle sheath (see below) and sieve-tube element. Transfer cells are parenchyma cells with cell wall ingrowths, which increase surface area for transport. The bundle sheath cells form the bundle sheath, which surrounds vascular bundles (where the xylem and phloem are located). Within the bundle sheath cell are oval chloroplasts, a nucleus (not labeled), and the central vacuole, which fills most of the cell. Image by Kelvinsong (CC-BY-SA).

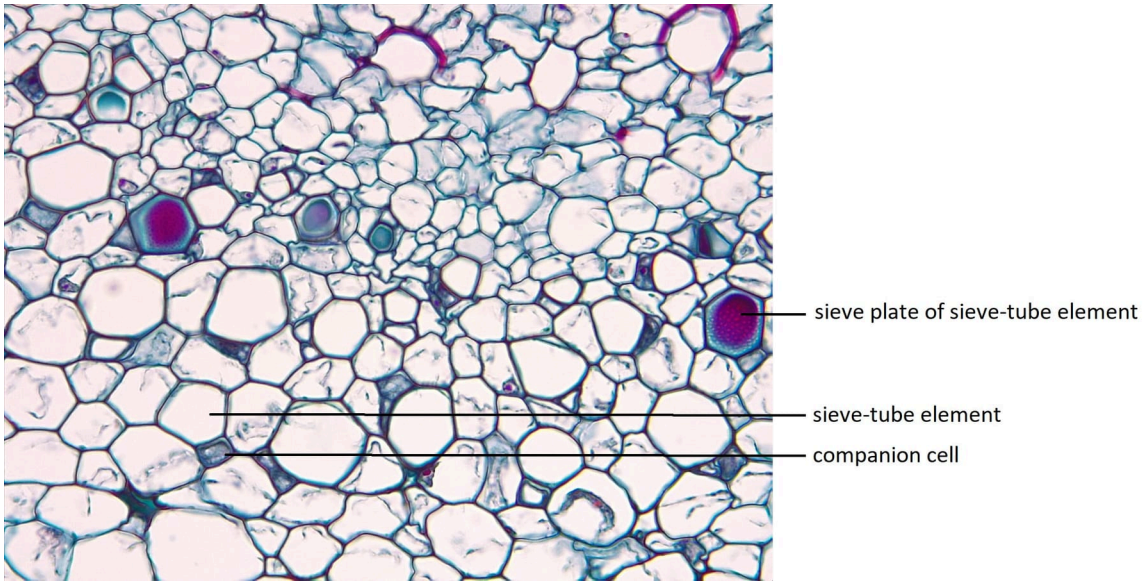


Figure 3.1.3.12: Phloem in a cross section of a *Cucurbita* (squash) stem, magnified at 400X. Each wide sieve-tube cell has a small, dark companion cell associated with it. (The companion cells are dark because each contains a nucleus.) The cross section cut exactly in between two sieve tube elements in some cases, revealing the sieve plate. Image by Melissa Ha (CC-BY).

The table below summarizes differences between xylem and phloem:

	Xylem	Phloem
Contains mostly	Dead cells	Living cells
Transports	Water & Minerals	Sugar
Direction	Up	Up and Down

	Xylem	Phloem
Biomass	Big	Small

Meristematic Tissue

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

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3.1.4: Chapter Summary

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

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

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

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

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3.2: ROOTS



Figure 3.2.1: Based on the type of substrate, roots can sometimes become visible on the ground. Credit: SKsiddhartthan (CC-BY-SA-4.0)

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

- Roots

3.2.1: Organs and Organ Systems

3.2.2: External Root Structure

3.2.3: Internal Root Structure

3.2.4: Root Modifications

3.2.5: Chapter Summary

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3.2.1: Organs and Organ Systems

Learning Objectives

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

Plant tissues form **organs** (such as leaves, stems, or roots), each of which perform a specific set of functions. Together, organs often work to form organ systems. Vascular plants have two distinct organ systems: a shoot system, and a root system. The **shoot system** consists of two portions: the vegetative (non-reproductive) parts of the plant, such as the leaves and the stems, and the reproductive parts of the plant, which include flowers and fruits. The shoot system generally grows above ground, where it absorbs the light needed for photosynthesis. The **root system**, which anchors the plant into the ground, absorbs water and minerals, and serves as a storage site for food is usually underground. (Figure 3.2.1.1) shows the organ systems of a typical plant.

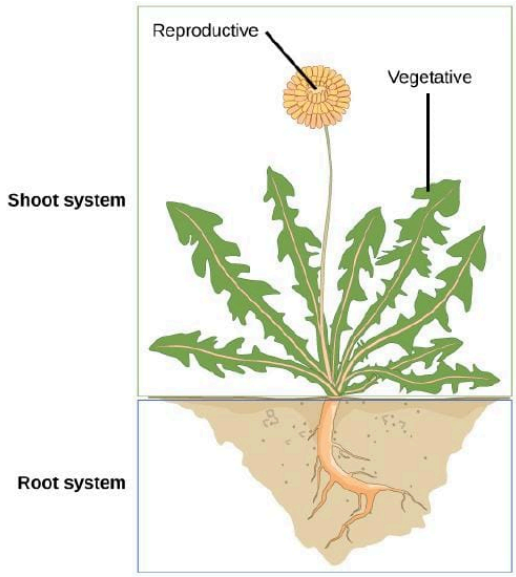


Figure 3.2.1.1: The shoot system of a plant consists of leaves, stems, flowers, and fruits. The root system anchors the plant while absorbing water and minerals from the soil. The dandelion root system consists of a single, thick root that branches into smaller roots.

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3.2.2: External Root Structure

Learning Objective

Identify the types of root systems found in plants.

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

Root systems are mainly of two types (Figure $3.2.2.1$). Eudicots have a tap root system, while monocots have a fibrous root system. A tap root system has a main root that grows down vertically, and from which many smaller lateral roots arise. Dandelions are a good example; their tap roots usually break off when trying to pull these weeds, and they can regrow another shoot from the remaining root). A tap root system penetrates deep into the soil. In contrast, a fibrous root system is located closer to the soil surface, and forms a dense network of roots that also helps prevent soil erosion (lawn grasses are a good example, as are wheat, rice, and corn). Some plants have a combination of tap roots and fibrous roots. Plants that grow in dry areas often have deep root systems, whereas plants growing in areas with abundant water are likely to have shallower root systems.



Figure $3.2.2.1$: (a) Tap root systems have a main root that grows down, while (b) fibrous root systems consist of many small roots. (credit b: modification of work by “Austen Squarepants”/Flickr)

Along with having different systems, there are **primary root** that originated from the root of the seedling (Figure $3.2.2.2a$) and **secondary (lateral) roots** originate from the primary roots, and **adventitious roots** originate on stems or leaves, rather than from the base of the embryo. Adventitious roots can grow if plant cuttings are placed in water (Figure $3.2.2.2b$).



Figure 3.2.2.2: a) Mung bean tap root (eudicot) and wheat bean fibrous root (monocot) from sprouts. b) Jade plant cutting, showing adventitious roots growing from stem after being placed in water. Credit: Kammy Algiers (CC-BY).

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3.2.3: Internal Root Structure

Learning Objectives

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

Root Anatomy

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

Longitudinal Section

If you were to cut a root down longitudinally, you would see the various layers inside. The tip of the root is protected by the **root cap**, a structure exclusive to roots and unlike any other plant structure. The root cap is continuously replaced because it gets damaged easily as the root pushes through soil. The root tip can be divided into three zones: a **zone of cell division**, a **zone of elongation**, and a **zone of maturation and differentiation** (Figure 3.2.3.1). The zone of cell division is a continuation of the root cap; it is made up of the actively dividing cells of the root meristem. The zone of elongation is where the newly formed cells begin to increase in length, thereby lengthening the root. They are older than cells at the zone of cell division. Beginning at the first root hair is the zone of cell maturation where the root cells begin to differentiate into special cell types. The root has an outer layer of cells called the epidermis, which surrounds areas of ground tissue and vascular tissue. The epidermis provides protection and helps in absorption. **Root hairs**, which are extensions of root epidermal cells, increase the surface area of the root, greatly contributing to the absorption of water and minerals. All three zones are in the first centimeter or so of the root tip.

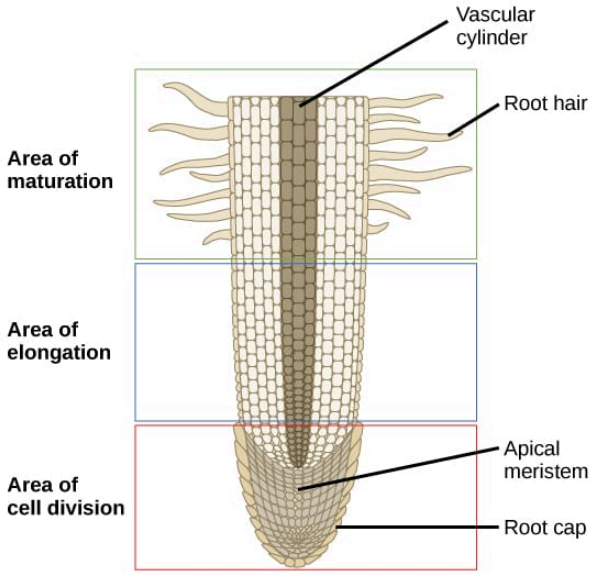
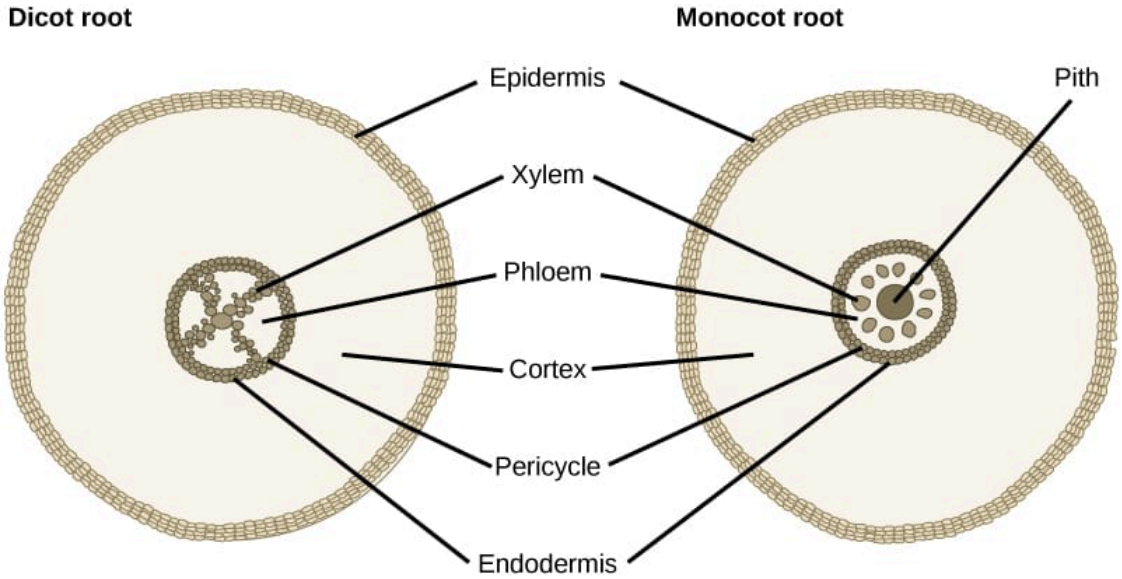


Figure 3.2.3.1: A longitudinal view of the root reveals the zones of cell division, elongation, and maturation. Cell division occurs in the apical meristem.

Cross Section

If you were to cut a cross section of the leaf, you could see other features that are not as obvious in the longitudinal section. Inside the root, the ground tissue may form two regions: the **cortex** and the **pith** (Figure 3.2.3.2). When comparing roots to stems, roots have much more cortex and very little pith. Whereas eudicot roots have no central pith, monocots have a small pith. Both cortex and pith include cells that store photosynthetic products. The cortex is between the epidermis and the vascular tissue, whereas the pith lies between the vascular tissue and the center of the root.

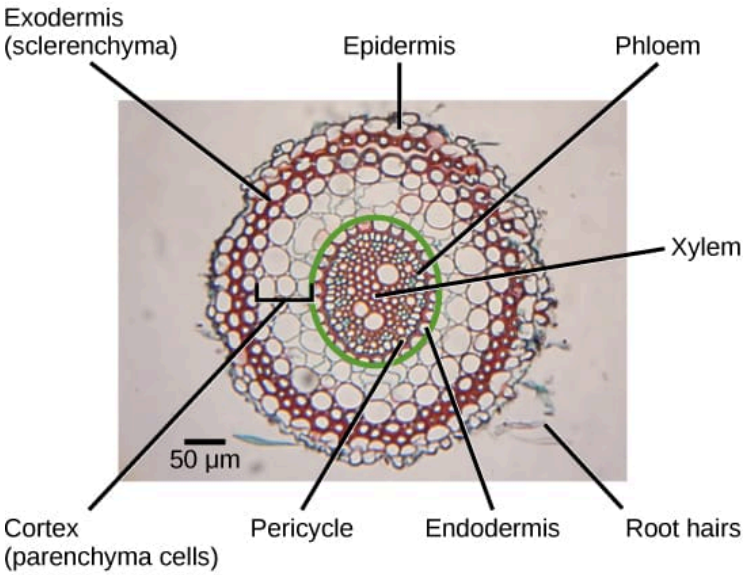
The inner portion of the root contains the vascular tissue (xylem and phloem). This area is called the **stele**. A layer of cells known as the **endodermis** borders the stele (Figure 3.2.3.2) and is considered the innermost layer of the cortex. The endodermis is exclusive to roots, and serves as a checkpoint for materials entering the root's vascular system. A waxy substance called suberin is present on the walls of the endodermal cells. This waxy region, known as the **Casparian strip**, forces water and solutes to cross the plasma membranes of endodermal cells instead of slipping between the cells. This ensures that only materials required by the root pass through the endodermis, while toxic substances and pathogens are generally excluded. The outermost cell layer of the root's vascular tissue is the **pericycle**, an area that can give rise to lateral roots.



(Figure 3.2.3.2): In (left) typical eudicots, the vascular tissue forms an X shape in the center of the root. In (right) typical monocots, the phloem cells and the larger xylem cells form a characteristic ring around the central pith.

Monocots

Note that the size of the stele in the monocot cross section is large (everything inside the green ring (Figure 3.2.3.3). The vascular tissue is arranged in a ring around the pith. This arrangement is called a **siphonostele**. The cortex surrounds the stele. The **endodermis** is the innermost layer of the cortex, and the **exodermis** is the outermost layer of the cortex. The exodermis controls the flow of water, ions, and nutrients. The outermost layer of the root (external to the cortex) is the epidermis, which covers the root and aids in absorption.



(Figure 3.2.3.3): Staining reveals different cell types in this light micrograph of a wheat (*Triticum*) root cross section. Sclerenchyma cells of the exodermis and xylem cells stain red, and phloem cells stain blue. Other cell types stain black. The stele, or vascular tissue, is the area inside endodermis (indicated by a green ring). Root hairs are visible outside the epidermis. (credit: scale-bar data from Matt Russell)

Eudicots

In eudicot roots, the vascular tissue fills the center of the root, and there is no pith. This arrangment is called a **protostele**. The xylem and phloem of the stele are arranged alternately in an X shape (Figure 3.2.3.4). Most of the root is composed of cortex tissue, and the **endodermis**, the innermost layer of the cortex, borders the stele. The outer layer of the root (external to the cortex) is the epidermis.



Figure 3.2.3.4: Eudicot root cross section. From center out, the xylem (in red) make an X, and the side tissues (green) make up the phloem.. The endodermis separates the stele from the cortex, which is the largest tissue. The last layer of cells on the edge is the epidermis layer. (Credit: Wikimedia)

Secondary Root Growth

Many roots have secondary growth as well as primary growth (figures 3.2.3.5 – 6). This occurs by the production of two types of meristemic tissue, the **vascular cambium** and the **cork cambium**. The cork cambium is responsible for the girth or growth in the diameter of the root. This occurs by the cork cambium adding vascular tissue to the root. Cells of the pericycle and procambium

(the meristematic tissue between the primary phloem and xylem) begin division, and form a vascular cambium around the primary xylem. The vascular cambium then divides to form secondary xylem on the inside and secondary phloem on the outside.

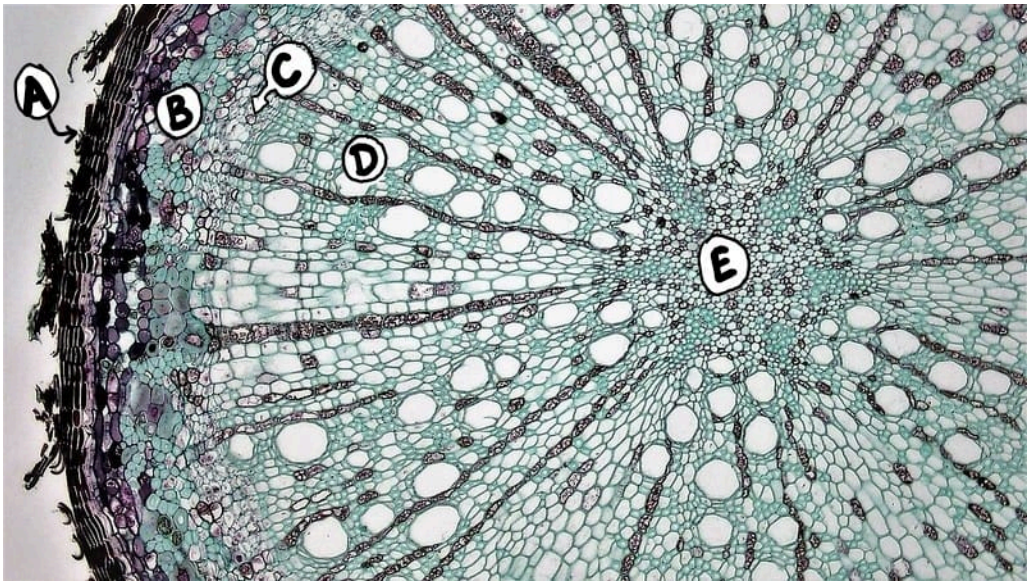


Figure 3.2.3.5: A labeled cross section through an older *Quercus* root, 100x. A=Periderms, B=Seconary Phloem, C=Vascular Cambium, D=Secondary Xylem, E=Primary xylem. Image from Berkshire Community College Bioscience Image Library (public domain). Labels added by Maria Morrow.

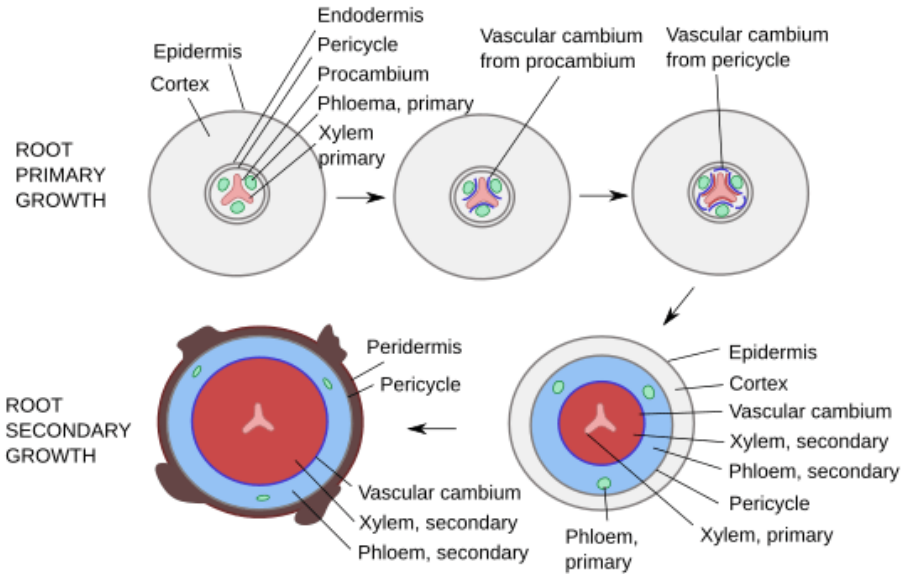


Figure 3.2.3.6: The process of secondary growth in roots begins when the vascular cambium (dark blue ring) arises from the pericycle and embryonic tissue called the procambium. The vascular cambium produces secondary xylem (dark red) internally and secondary phloem (light blue) externally. Additionally, the cork cambium arises from the pericycle and produces cork and phelloderm, forming the periderm (dark brown outer layer). Image from Atlas of Plant and Animal Histology (CC-BY-NC-SA)

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

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3.2.4: Root Modifications

Learning Objective

Describe the types of modified roots and their functions.

Root structures may be modified for specific purposes. For example, some roots are bulbous and store starch. Tap roots in plants such as carrots, turnips, and beets, are examples of roots that are modified for food storage (Figure 3.2.4.1).



Figure 3.2.4.1: Many vegetables are modified roots.

Aerial roots are forms of aboveground roots that provide additional support to anchor the plant. **Epiphytic roots** are a type of aerial root that enable a plant to grow on another plant. For example, the epiphytic roots of orchids develop a spongy tissue to absorb moisture. The banyan tree (*Ficus* sp.) begins as an epiphyte, germinating in the branches of a host tree. The plant's aerial roots develop from the branches and eventually reach the ground, providing additional support (Figure 3.2.4.2). In screwpine (*Pandanus* sp.), a palm-like tree that grows in sandy tropical soils. Plants which grow on sand have another problem: their substrate constantly disappears. To avoid this, plants developed **contractile roots** which may shorten and pull plant body deeper into the sand.



(a) (b)

Figure 3.2.4.2: The (a) banyan tree, also known as the strangler fig, begins life as an epiphyte in a host tree. Aerial roots extend to the ground and support the growing plant, which eventually strangles the host tree. The (b) screwpine develops aboveground roots that help support the plant in sandy soils. (credit a: modification of work by "psyberartist"/Flickr; credit b: modification of work by David Eikhoff)

Plants growing in ocean coastal swamps need additional specializations. Roots of mangroves are frequently modified into supportive aerial roots called **stilt roots.** Stilt roots are adventitious and grow from lateral branches. Swamp plants are often flooded and need additional adaptations for respiration. **Pneumatophores** are specialized roots that grow upward and allow oxygen and carbon dioxide exchange from the plant's root system. They passively catch the air via multiple pores (Figure 3.2.4.3).



Figure 3.2.4.3: Mangrove pneumatophores in Sulawesi. (Credit: Wikimedia CC BY_SA 3.0)

Some aerial roots will function as photosynthetic organs as well. Though rare, you can see green photosynthetic roots in some plants such as epiphytic orchids (Figure 3.2.4.4). In some cases, the plant is leaf-less so all the photosynthesis is done by the aerial roots. In other plants, the aerial roots aid in photosynthesis.



Figure 3.2.4.4: Photosynthetic roots of leafless orchid *Chiloschista segawai*.

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

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

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3.2.5: Chapter Summary

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

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

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

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

Glossary

adventitious root
Casparian strip
endodermis
fibrous root system
pericycle
root cap
root hair
stele
tap root system

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3.3: STEMS

The shoot system of a plant consists of stems and leaves (Figure 3.3.1). Stems may range in length from a few millimeters to hundreds of meters, and also vary in diameter, depending on the plant type. Stems are usually aboveground, although the modified stems of some plants, such as the potato, also grow underground. Stems may be herbaceous (soft) or woody in nature. A stem may be unbranched, like that of a palm tree, or it may be highly branched, like that of a magnolia tree.



Figure 3.3.1: The shoot system of bamboo plants. Image by RanaAnees (CC-BY-SA).

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

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- Stems

3.3.1: Stem Morphology (External Structure)

3.3.2: Internal Anatomy of the Primary Stem

3.3.3: Secondary Stem

3.3.4: Stem Modifications

3.3.5: Chapter Summary

Thumbnail image: Cross section of the woody stem of *Aristolochia*. Image by Berkshire Community College Bioscience Image

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3.3.1: Stem Morphology (External Structure)

Learning Objective

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

Plant stems, whether above or below ground, are characterized by the presence of nodes and internodes (Figure 3.3.1.1). **Nodes** are points of attachment for leaves. Leaves often consist of a thin region that attaches to the stem (the **petiole**) and a broader **blade** (see Leaves). The stem region between two nodes is called an **internode**. An **axillary bud** is usually found in the **axil**—the area between the base of a leaf and the stem—where it can give rise to a branch called an **axillary shoot** (Figure 3.3.1.2). The **shoot apex** at the tip shoot contains the **shoot apical meristem** surrounded by developing leaves called **leaf primordia** (see Meristems).

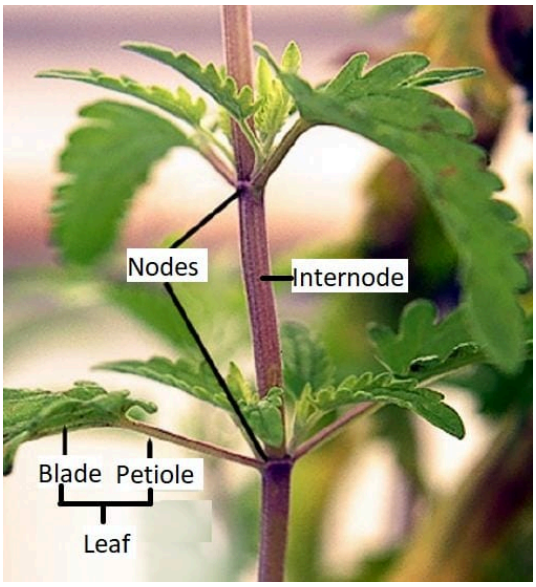


Figure 3.3.1.1: Leaves are attached to the plant stem at areas called nodes. An internode is the stem region between two nodes. The smaller leaves just above the nodes are the beginning of axillary shoots, which arose from axillary buds. Image modified from OpenStax (CC-BY)



Figure 3.3.1.2: Axillary buds of sweet granadilla (*Passiflora ligularis*). One of the axillary buds is labeled with an arrow. Image modified from Eiku (CC-BY-SA).

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3.3.2: Internal Anatomy of the Primary Stem

Learning Objectives

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

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

All three tissue types are represented in the primary stem. The **epidermis** is the dermal tissue that surrounds and protects the stem. The epidermis typically consists of one layer of cells. A waxy cuticle on the outside of these cells limits water loss. Epidermal cells are the most numerous and least differentiated of the cells in the epidermis. Pores in the epidermis called **stomata** (singular: stoma) allow for gas exchange. Each stoma is bordered by a pair of **guard cells**, which regulate stomatal opening. While stomata are present in stems, they occur at higher densities in leaves. Trichomes are hair-like structures on the epidermal surface. They help to reduce transpiration (the loss of water by aboveground plant parts), increase solar reflectance, and store compounds that defend the leaves against predation by herbivores (Figure 3.3.2.1).



Figure 3.3.2.1: Trichomes extend from the epidermis of this *Datrua inoxia* stem. Image by Silk666 (CC-BY-SA).

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

Cross sections reveal three possible arrangements of vascular tissue (**steles**) in the stem. The first arrangement (**solenostele**) is present in a few eudicots, such as basswood (*Tilia*). In the solenostele, the vascular tissue appears as a continuous ring (**vascular cylinder**; Figure 3.3.2.2). The **interfascicular regions** (pith rays) of parenchyma cells that separate vascular tissue are thus extremely narrow. The second arrangement (**eustele**) is present in most eudicots such as sunflower (*Helianthus*) and buttercup (*Ranunculus*). In the eustele, vascular tissue is clustered into distinct **vascular bundles** arranged in a ring, allowing for thicker interfascicular regions in between them (Figure 3.3.2.3 – 4). In these solenosteles and eusteles, the vascular tissue separates ground tissue into an outer cortex and central pith. The third arrangement (**atactostele**) is present in most monocots, such as

corn (*Zea mays*) and a few eudicots. In the atactostele, vascular bundles are scattered throughout the stem (Figure 3.3.2.3, 5). While vascular bundles near the outside of the stem are packed more densely in this third arrangement, their distribution is somewhat disorderly. There is no distinction between the cortex and pith in the third arrangement.

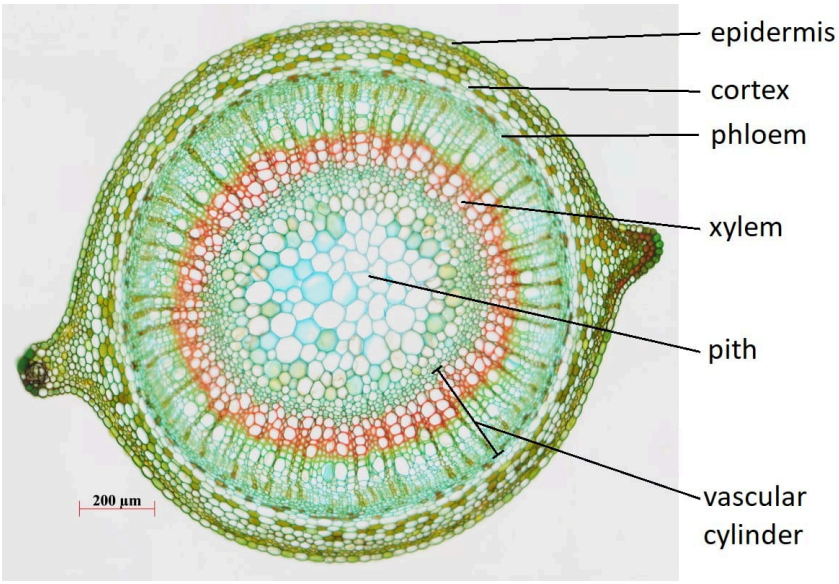


Figure 3.3.2.2: Cross section of a common St. John's Wort (*Hypericum perforatum*) stem, illustrating a solenostele. The epidermis borders the entire root. The central pith (greenish-blue, in the center) and peripheral cortex (narrow zone 3–5 cells thick just inside the epidermis) are composed of parenchyma cells. Vascular tissue, forming the vascular cylinder, is composed of xylem (red) and phloem tissue (green, between the xylem and cortex) surrounds the pith. Image by RolfDieterMueller (CC-BY)

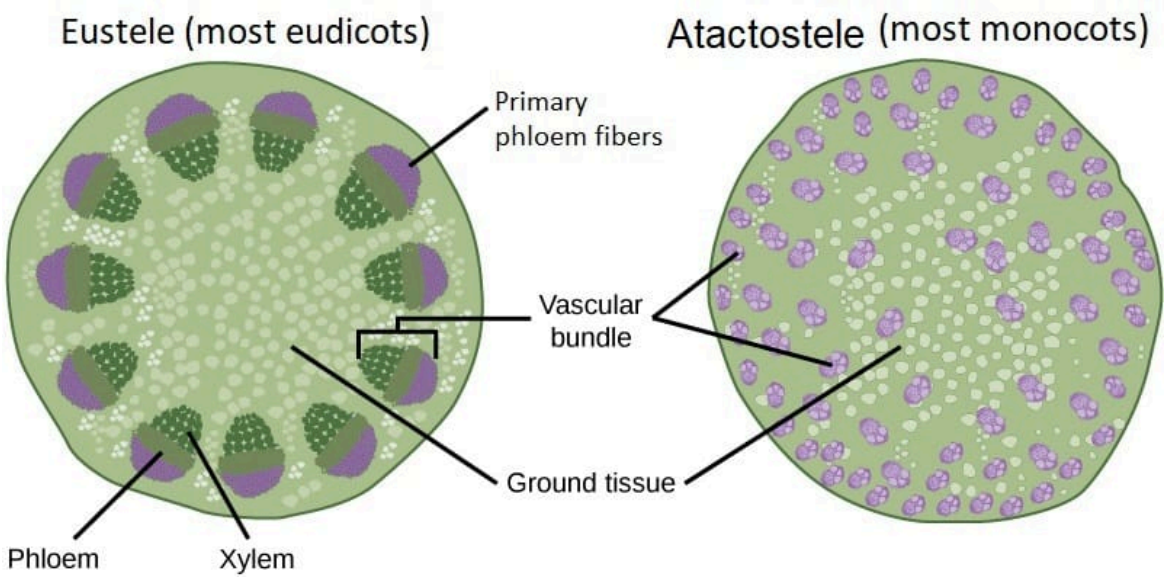


Figure 3.3.2.3: In eusteles (left), vascular bundles are arranged around the periphery of the ground tissue. The xylem tissue is located toward the interior of the vascular bundle, and phloem is located toward the exterior. Primary phloem fibers cap the vascular bundles. In atactosteles (right), vascular bundles composed of xylem and phloem tissues are scattered throughout the ground tissue.

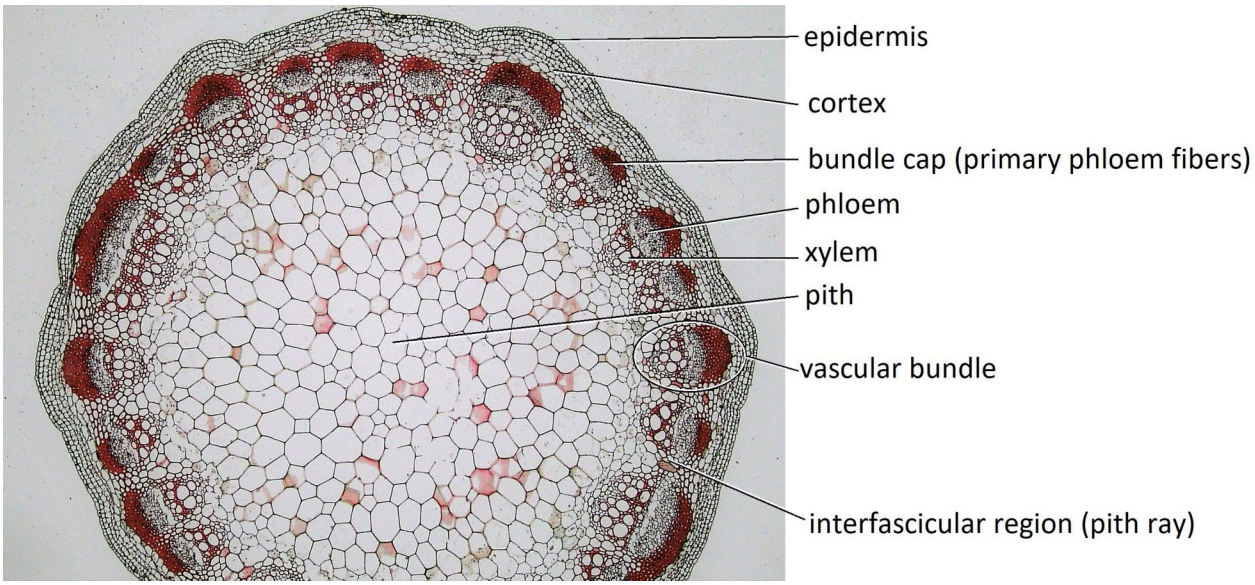


Figure 3.3.2.4: Cross section of a sunflower (*Helianthus*) stem, illustrating a eustele. Vascular bundles are arranged in a ring. The interfascicular regions between the vascular bundles are thick compared to the solenostele, where they were too thin to be visible. The ground tissue is separated into an outer cortex and a central pith. The epidermis borders the entire stem. Image labeled from Berkshire Community College Bioscience Image Library (public domain)

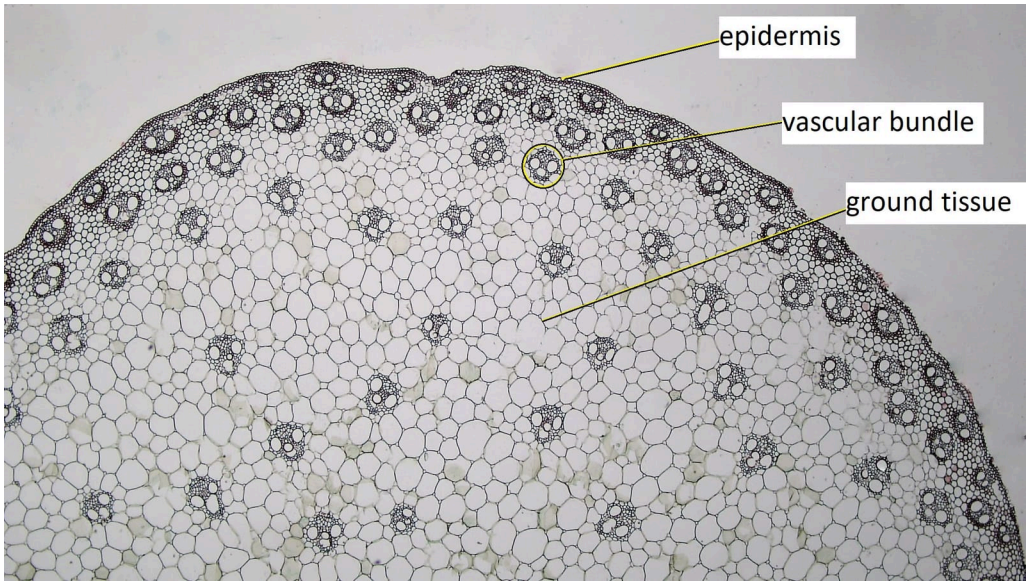


Figure 3.3.2.5: Cross section of a corn (*Zea mays*) stem, an example of an atactostele, at 40X magnification. Vascular bundles are scattered but are at a higher density near the outside of the stem. In contrast to solenosteles and eusteles, the ground tissue is not separated into a pith and cortex. The epidermis borders the entire stem. Image labeled from Berkshire Community College Bioscience Image Library (public domain)

The cells of embryonic tissue called the **procambium** (see Meristems) divides to produce primary xylem internally and primary phloem externally. In some vascular bundles, some procambial cells remain and form the **fascicular cambium** in the center of the vascular bundle. Once the stem has finished lengthening, sclerenchyma fibers called **primary phloem fibers** are produced just outside of the primary phloem. The primary phloem fibers of each vascular bundle are sometimes called phloem caps (bundle caps). If primary phloem fibers surrounded the entire vascular bundle, they form a **bundle sheath** (Figure 3.3.2.6).

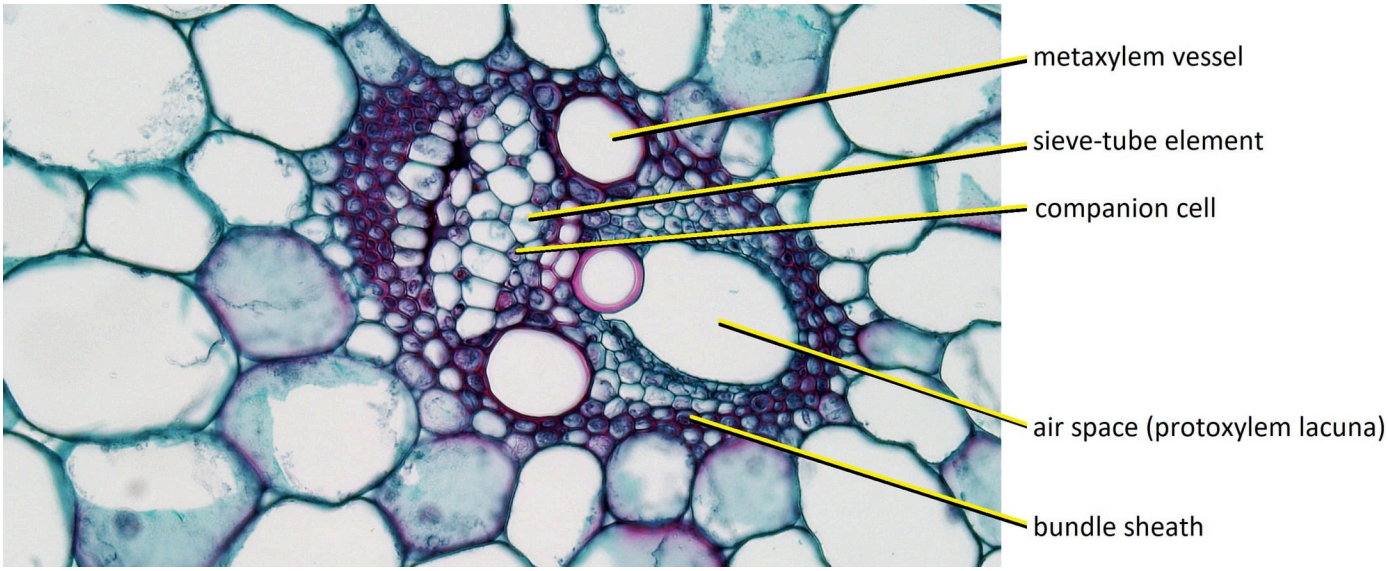


Figure 3.3.2.6: A vascular bundle in the stem of corn (*Zea mays*) at 400X magnification. The protoxylem vessel element matured prior to the metaxylem vessel elements of the xylem. At maturity, the protoxylem vessel breaks, leaving an air space. The sieve-tube elements and companion cells form the phloem. The **bundle sheath** consists of primary phloem fibers (sclerenchyma fibers) that surround the vascular bundle. Image labeled from Berkshire Community College Bioscience Image Library (public domain)

Vascular bundles connect leaves and stems. The strands of vascular tissue that connect the leaves to the stem are called **leaf traces**. Just above leaf traces are portions of stem without vascular tissue called **leaf trace gaps**. Similarly, **branch traces** connect axillary shoots to the main stem, leaving **branch trace gaps** just above them (Figure 3.3.2.7 – 8).

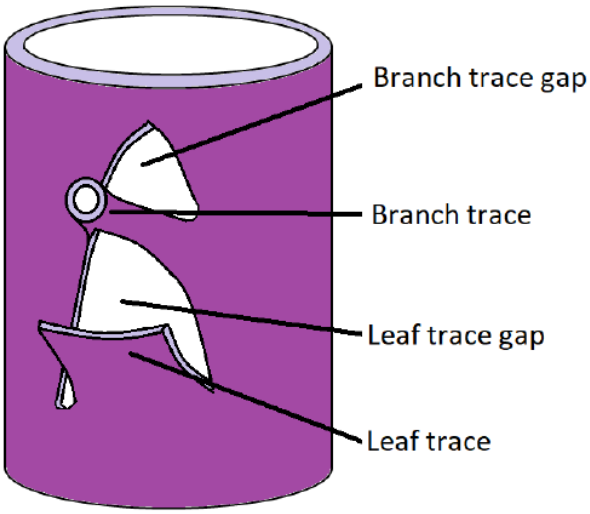


Figure 3.3.2.7: The purple cylinder represents the vascular tissue in a stem. Vascular tissue leaves the stem to enter the leaf, forming a **leaf trace**. The space without vascular tissue just above the leaf trace is the **leaf trace gap**. The **branch trace** likewise produces a **branch trace gap**. Image by Melissa Ha (CC-BY).

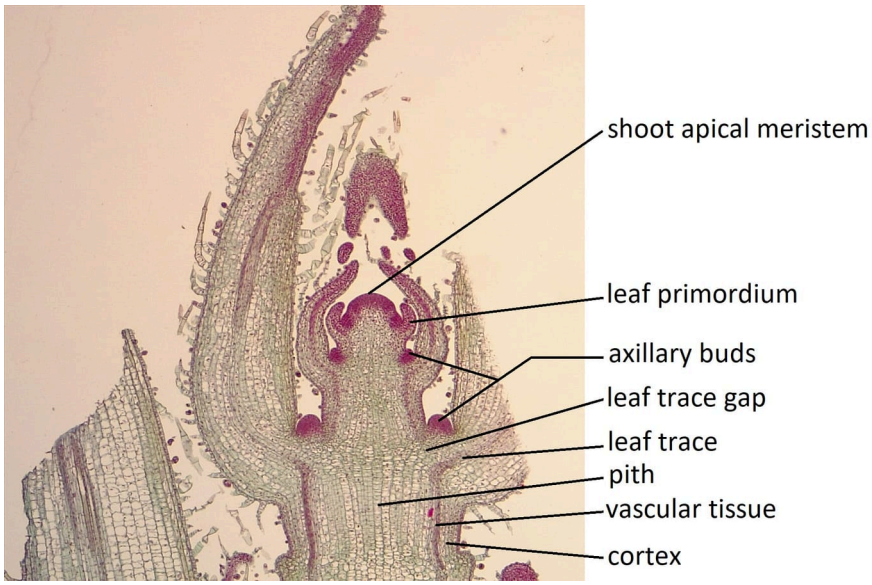


Figure 3.3.2.8: A longitudinal section of a *Coleus* shoot tip. The **leaf trace gaps** are spaces without vascular tissue just above the **leaf traces**, which are strands of vascular tissue moving from the stem to the leaf. The three tissue system in this stem are represented by the epidermis (outer layer of dermal tissue, not labeled), pith and cortex (ground tissue), and vascular tissue between the pith and cortex. At the upper tip is the shoot apical meristem. Youong leaves (leaf primordia) emerge from either side. Axillary buds emerge just above where each leaf or leaf primordium meets the stem. Image by Melissa Ha (CC-BY).

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3.3.3: Secondary Stem

Learning Objectives

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

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

Secondary Meristems (Lateral Meristems)

Two **secondary meristems** (**lateral meristems**) are responsible for secondary growth: the vascular cambium and cork cambium (Figure 3.3.3.1).

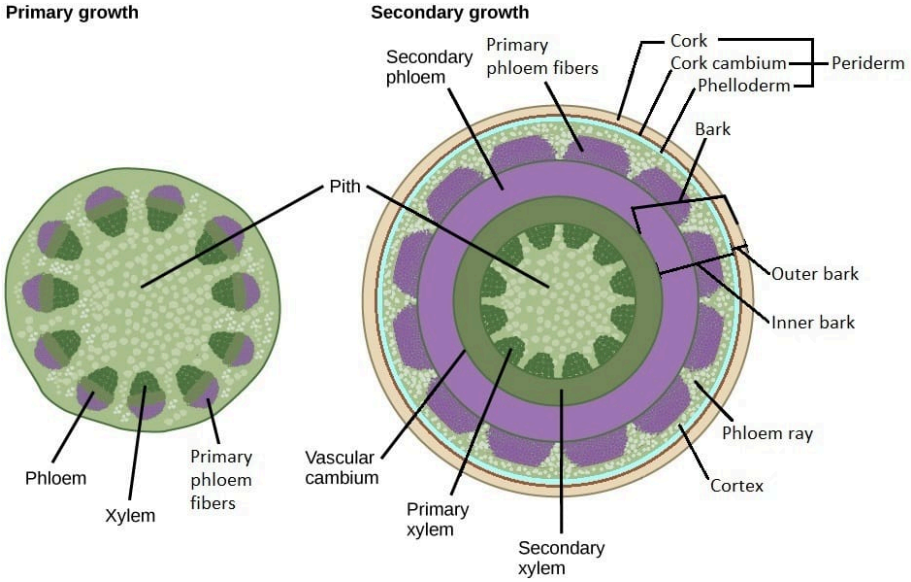


Figure 3.3.3.1: In woody plants, primary growth (left) is followed by secondary growth (right), which allows the plant stem to increase in thickness or girth. Secondary vascular tissue is added by the vascular cambium, and the cork cambium generates the periderm. In the primary stem, vascular bundles surround a central pith. Each vascular bundle has xylem on the inside, phloem on the outside, and primary phloem fibers external to the phloem. In the secondary stem, the pith, primary xylem, primary phloem fibers, and cortex remain. The vascular cambium, which is between the primary xylem and primary phloem fibers, has deposited secondary xylem internally and secondary phloem externally. The periderm is external to the cortex and consists of the phelloderm, cork cambium, and cork (from inside to outside). All tissue layers external to the vascular cambium form the bark. The cork cambium and cork form the outer bark, and the inner bark is everything between the vascular cambium and cork cambium.

The **vascular cambium** produces secondary vascular tissue. The **fusiform initials** are the cells of the vascular cambium that divide to produce secondary xylem internally and secondary phloem externally. The **ray initials** are the cells of the vascular cambium that produce **vascular rays** (xylem rays and phloem rays). These are bands of parenchyma that are perpendicular to the concentric layers of xylem and phloem (Figure 3.3.3.2). They function in storage, producing secondary compounds (molecules used by the plant that are not essential parts of metabolism), and transporting materials between the xylem and phloem. As the

secondary stem thickens, the phloem rays thicken externally (becoming wedge-shaped) to accommodate the increasing diameter. While the vascular cambium is technically only a single layer cell layer, it looks similar to the layers of cells that surround it (that it recently divided to produce), and this entire region is sometimes called the vascular cambium as a result.

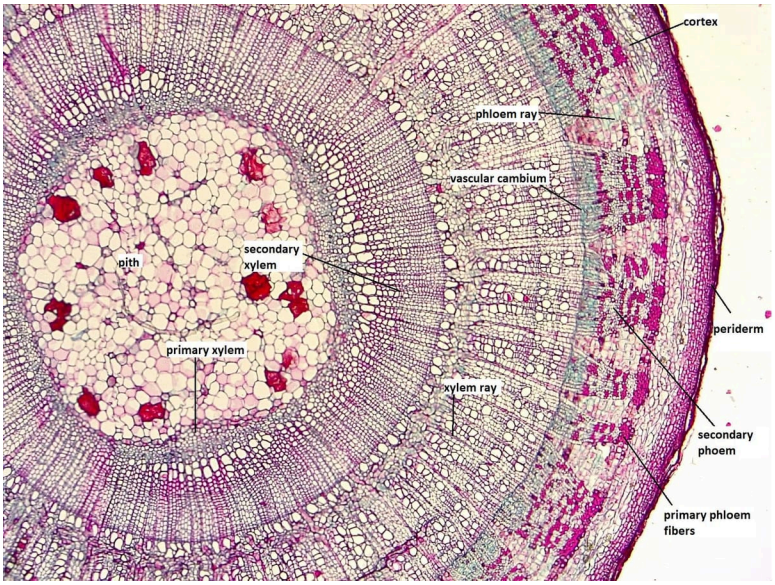


Figure 3.3.3.2: Cross section of a basswood (*Tilia*) stem magnified at 400X. The periderm is the outermost layer and has thin, dark layers. Some appear to be peeling. Within this is the cortex. Next, is are clusters of primary phloem fibers, narrow, thick-walled sclerenchyma cells, which stained bright pink. Within this is the secondary phloem. It alternates with wedge-shaped phloem rays. The phloem rays consist of plump, thin-walled parenchyma cells. Within the secondary phloem is the thin vascular cambium, which divides to produce secondary phloem externally and secondary xylem internally. Next are several thick layers of secondary xylem, which contain wide, thick-walled vessel elements. There are five concentric layers in the secondary xylem, and each is annual ring. The inner portion of each annual ring has the widest vessel elements. This is the spring (early) wood. The outer portion of each annual ring has narrower conducting cells of the summer (late wood). Thin, xylem rays pass through the secondary xylem like spokes of a wheel. Some align with the phloem rays. Within the secondary xylem is the primary xylem. In the center is the pith, which contains plump, thin-walled, white parenchyma cells. Image by Melissa Ha (CC-BY-NC).

The vascular cambium arises from stem cells within and between the vascular bundles in some silenosteles and eusteles. Within vascular bundles, such stem cells (specifically, procambial cells) form the **fascicular cambium**. In the interfascicular regions between vascular bundles is **interfascicular cambium** (Figure 3.3.3.3). The fascicular cambium and interfascicular cambium ultimately form the vascular cambium. In contrast, the vascular cambium in roots arises from the procambium and pericycle.

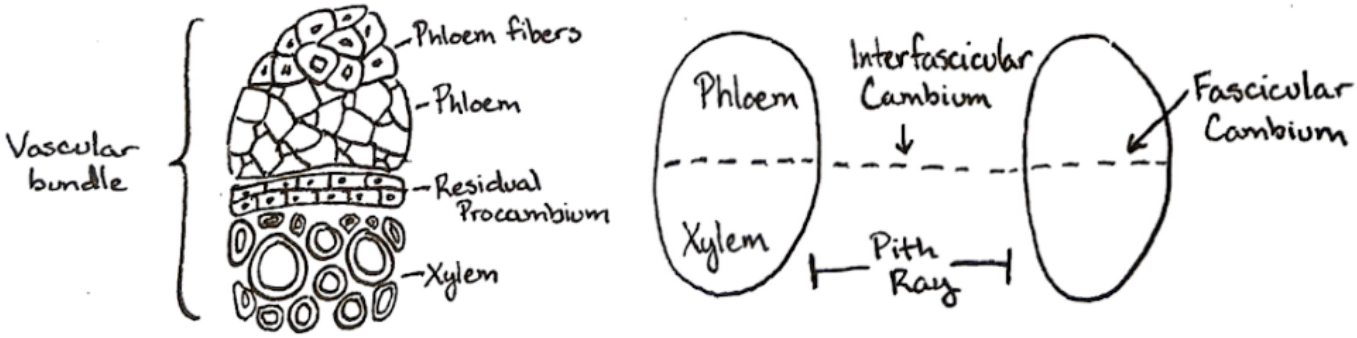


Figure 3.3.3.3: The vascular bundle of a eustele (left) and two vascular bundles with the interfascicular region (pith ray) between them. The vascular bundle consists of narrow, thick-walled phloem fibers, phloem, residual procambium, and thick-walled xylem. The interfascicular cambium and fascicular cambium (from the residual procambium) form the vascular cambium. Image by Maria Morrow (CC-BY).

The **cork cambium** divides to produce phelloderm internally and cork externally. Together, the phelloderm, cork cambium, and cork form the **periderm**, the dermal tissue of the secondary plant body (figure 3.3.3.4). The first cork cambium produced by a stem arises from the cortex, but subsequent cork cambia are produced by the parenchyma cells of the secondary phloem. (In contrast, the cork cambium arises from the pericycle in roots.)

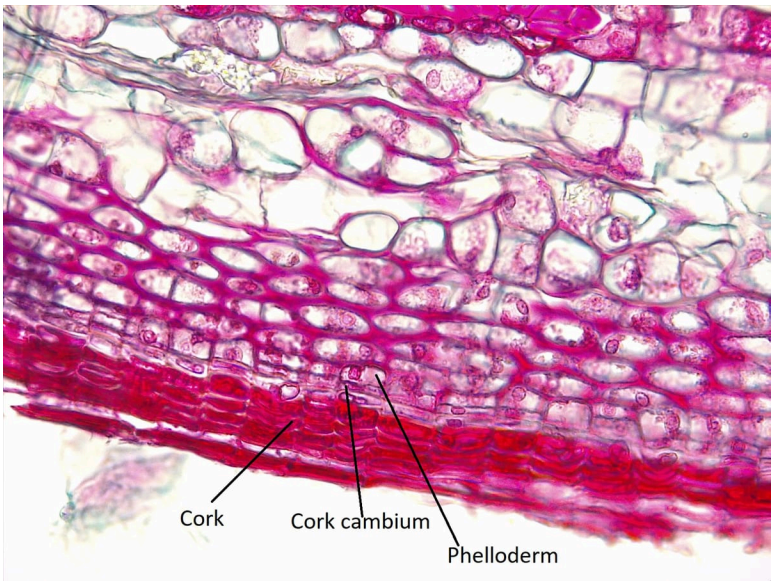


Figure 3.3.3.4: Cross section of a basswood (*Tilia*) stem magnified at 400X. The three layers of the periderm are labeled. From outside to inside they are the cork, cork cambium, and phelloderm. Image by Melissa Ha (CC-BY-NC).

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

Periderm and Bark

At the end of the secondary stem's first year of growth, the periderm replaces the epidermis, but the cortex and pith are retained. In contrast, roots that undergo secondary growth do not have piths to begin with, and the cortex is lost during secondary growth. Like the epidermis, most of the periderm is not permeable to water vapor, carbon dioxide, and gaseous oxygen. This is due to the waxy suberin that fills the cork cells, which are dead at maturity. However, gas exchange with the environment is possible at **lenticels**, elevated regions of the periderm with many intercellular air spaces (Figure 3.3.3.5 – 6). To produce lenticels, some cork cambium cells divide and grow much faster, which will finally break the periderm open. Woody stems do not do regular gas exchange as primary stems do by opening and closing stomata, but woody plants still have leaves with high densities of stomata to regulate gas exchange.



Figure 3.3.3.5: Lenticels on the bark of this cherry tree enable the woody stem to exchange gases with the surrounding atmosphere. (credit: Roger Griffith)



Figure 3.3.3.6: A cross section of an elderberry (*Sambucus*) secondary stem showing a lenticel. (Magnification = 100X). Image by Berkshire Community College Bioscience Image Library (public domain).

Bark consists of all of the tissue layers external to the vascular cambium. It protects the plant against physical damage and helps reduce water loss. In a one-year stem from inside to outside, this would be the secondary phloem, primary phloem fibers, cortex, phelloderm, cork cambium, and cork. The cork cambium divides the inner and outer bark. The **inner bark** is everything within the cork cambium. The **outer bark** is the cork cambium and everything external to it (Figure 3.3.3.7).

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

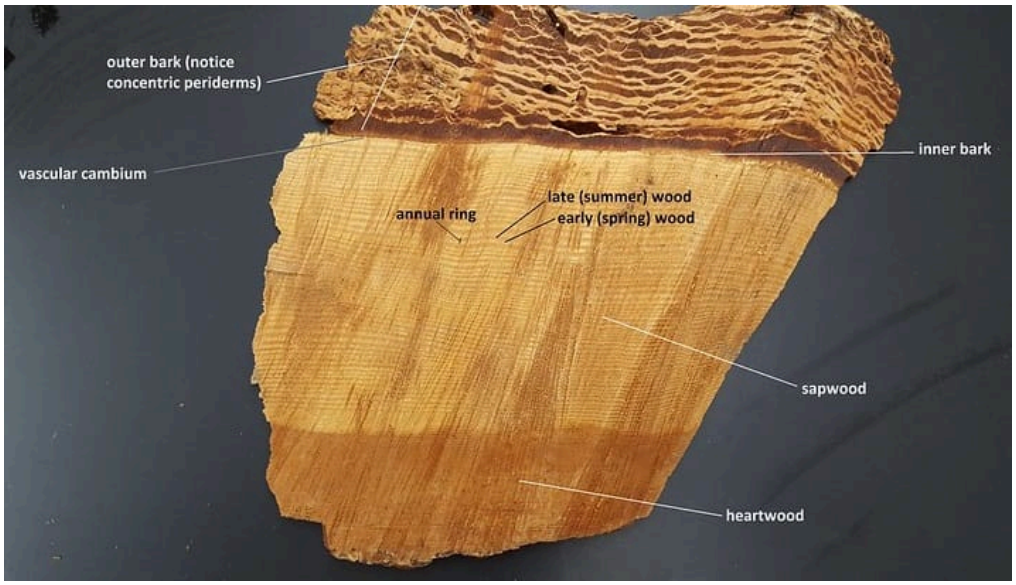


Figure 3.3.3.7: A cross section of a Douglas fir trunk reveals outer bark and a thin layer of inner bark. The outer bark has distinct, wavy stripes, representing concentric periderms. Everything external to the vascular cambium (both the inner and outer bark) form the bark. The sapwood is the conducting (living) portion of the xylem and is lighter than the heartwood. Each annual ring contains a band of light early wood and an outer band of dark late wood. Image by Melissa Ha (CC-BY-NC).

Wood (Secondary Xylem)

Wood consists of the secondary xylem produce by the vascular cambium (Figure 3.3.3.8). In contrast to the phloem, old layers of secondary xylem are retained and are not easily crushed. However, the oldest secondary xylem (close to the center of the secondary stem) no longer conducts water. This is the **heartwood**, which stores various compounds and appears darker than the surrounding wood. To block the flow of water in the heartwood, plants use tylosesvessel element “stoppers”, which also help control winter functioning of vessels. A tylose forms when a cell wall of parenchyma grows into the tracheary element; they look like bubbles. The **sapwood** surrounds the heartwood, is lighter in color, and consists of the conducting xylem, which was more recently produced (Figure 3.3.3.7).

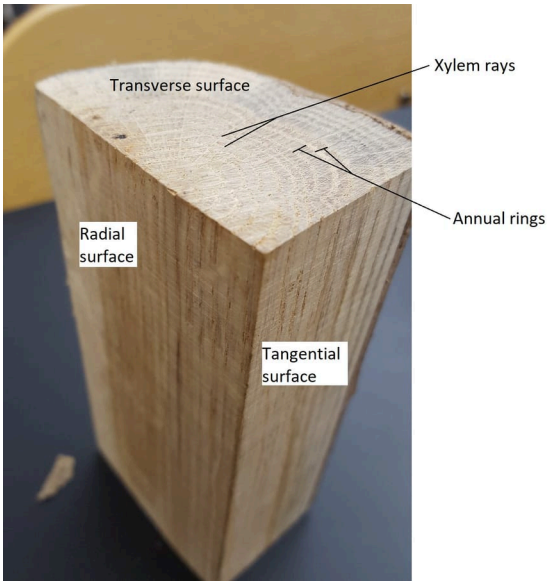


Figure 3.3.3.8: Wood can be examined through three different sections. A cross section reveals the **transverse surface**. In this view, annual rings are concentric circles, and xylem rays intersect them like the spokes of a wheel. Cutting from the periphery to the center (like cutting a slice of pie) reveals the **radial surface**. In this view, the annual rings appear as vertical lines. Cutting along the outside of the stem (tangential to it) reveals the **tangential surface** (oblique surface). In this view, annual rings more spaced apart and unevenly so. Image by Melissa Ha (CC-BY-NC).

In the spring of temperate regions, the vascular cambium produces wide tracheary elements (the conducting cells of the xylem, either vessel elements or tracheids). These transport large volumes of water, which is abundant due to spring rains. During the summer, the vascular cambium produces narrow tracheary elements as a result of lower water availability. In the winter, the vascular cambium's activity is low. It resumes the next spring by again producing the wide tracheary elements of **early wood** (spring wood), which distinctly contrast with the adjacent **late wood** (summer wood) from the previous year. Early wood appears lighter and is less dense than late wood. Each year of wood production is thus visible in a cross section of a woody stem because it consists of a light layer and a dark layer. These are called **annual rings** (tree rings; Figure $3.3.3.9-10$) and can be used to determine the age of a tree or branch through the study of **dendrochronology**. Furthermore, thick annual rings indicate wet years, and thin annual rings indicate dry years.

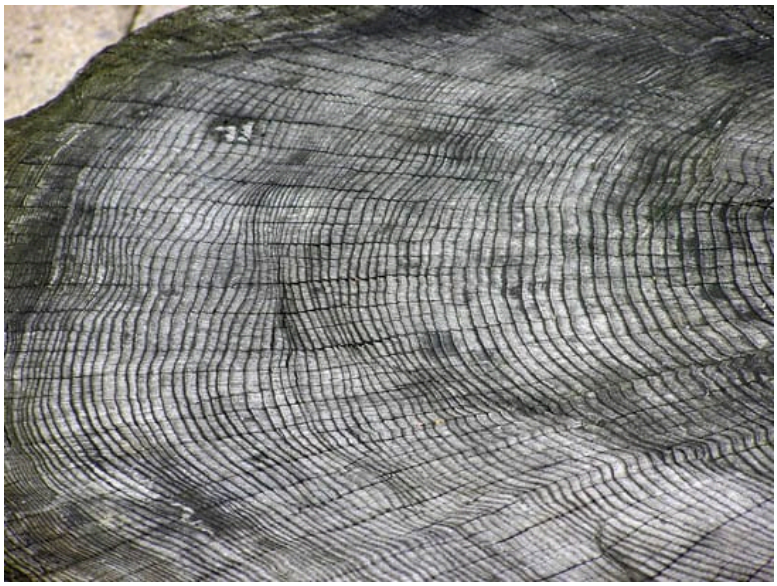


Figure $3.3.3.9$: The rate of wood growth increases in summer and decreases in winter, producing a characteristic ring for each year of growth. Seasonal changes in weather patterns can also affect the growth rate—note how the rings vary in thickness. (credit: Adrian Pingstone)

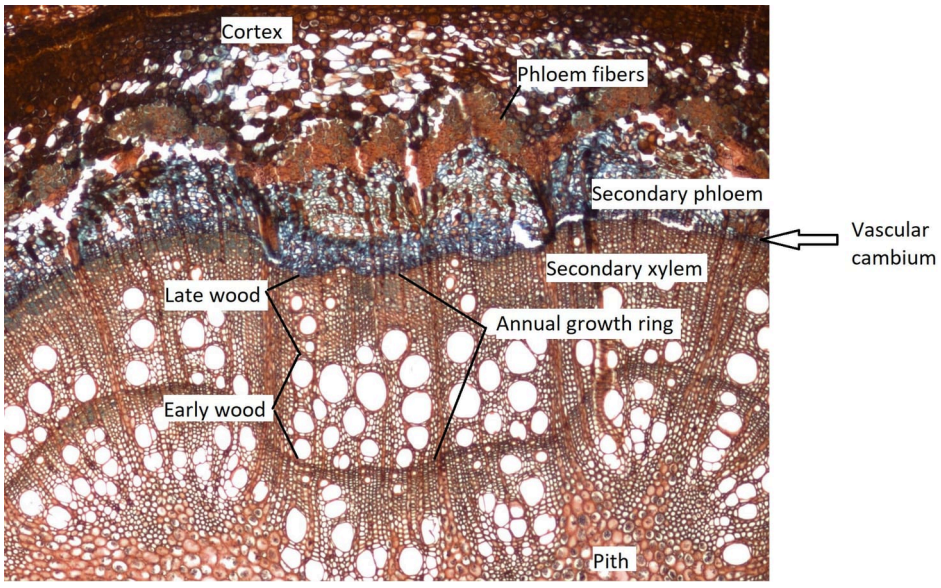


Figure $3.3.3.10$: In this cross section of a two-year-old oak stem, the inner portion of each annual ring contains early wood, which consists of wide tracheary elements. The outer part of each annual ring contains of late wood, which consists of narrow tracheary elements. The pith is inside the wood. The vascular cambium is just outside the wood. Next, is the secondary phloem, the phloem fibers (which consist of narrow, thick-walled cells), and the cortex. Image by Maria Morrow (CC-BY-NC).

Some trees (like oaks, *Quercus*) have large vessel elements are found primarily in early wood; this pattern is known as **ring porous** (Figure $3.3.3.10$). Large vessel elements of other trees (like elm, *Ulmus*) occur more evenly in both early and late wood. This pattern is known as **diffuse porous** wood: with large vessel elements in both early and late wood. (Diffuse porous species still produce annual rings due to differences in tracheid size.) Trees growing in climates without well-expressed seasons, such as

the tropical rainforest, will not make annual rings at all.

Hardwoods are produced by angiosperms and contain both vessel elements and tracheids (figure 3.3.3.10). **Softwoods** are produced by conifer trees (in the gymnosperm phylum Coniferophyta) and contain only tracheids (Figure 3.3.3.11). These terms are misnomers to an extent, however, because hardwoods are not always denser than softwoods. Xylem rays tend to occupy a greater volume in hardwoods relative to softwoods. Additionally, the arrangement of cells appears more disorderly in hardwoods due to the large size of vessel elements. Finally, softwoods contain **resin ducts** (Figure 3.3.3.11), which contain a thick substance (resin) important in defense and response to injury.

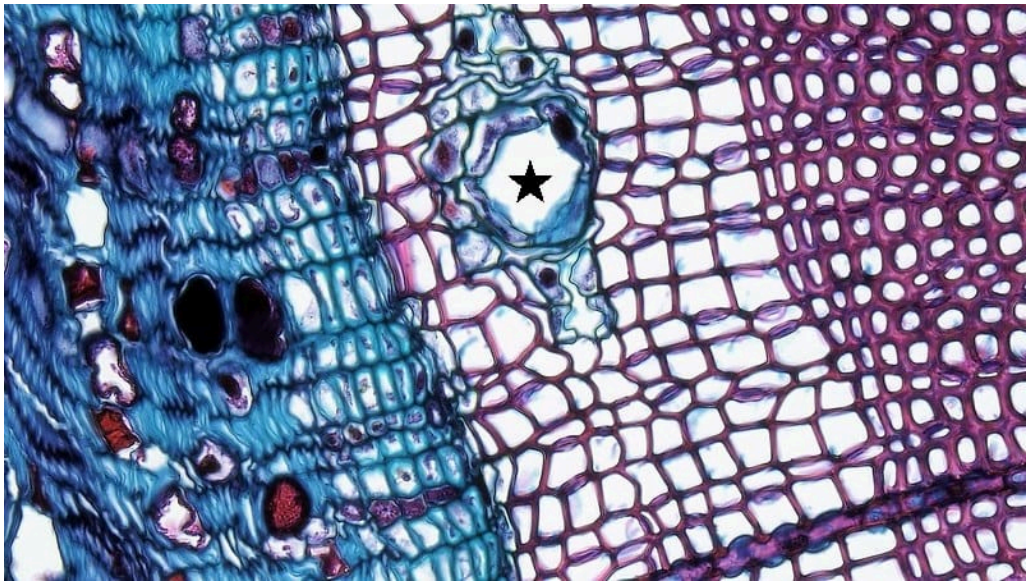


Figure 3.3.3.11: A cross section of a five-year-old pine (*Pinus*) stem magnified at 400X. The black star marks a resin duct. It is surrounded by the parenchyma cells that produce resin. Image by Berkshire Community College Bioscience Image Library (public domain).

Winter Twigs

Winter deciduous trees and shrubs in temperate regions become dormant in winter. The twigs of these species have the basic external features of a stem (axillary buds, nodes, etc.), but they are modified to facilitate dormancy in the winter and resumption of growth in the spring. At the end of a winter twig is the **terminal bud**, which contains a shoot apex surrounded by protective structures called **bud scales**. When the terminal bud resumes growth, the bud scales fall off and leave marks called terminal bud-scale scars. These form a ring around the twig, marking the winter of each year. **Lateral buds** are similar in structure to terminal buds, but they are found at each node. Just below the lateral buds are **leaf scars**, where the leaves were formerly attached. Within the leaf scars are **bundle scars**, marking leaf traces (consisting of vascular bundles) that moved from the stem to the leaf (Figure 3.3.3.12).

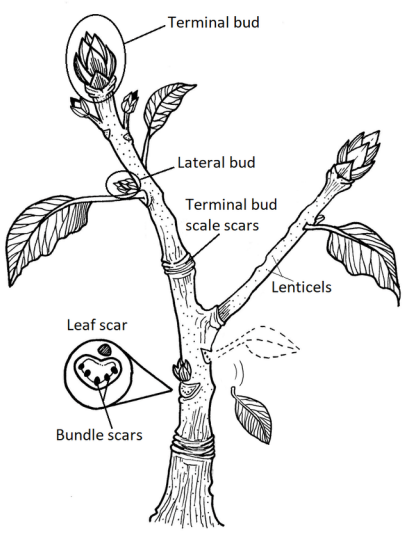


Figure 3.3.3.12: Winter twigs contain terminal buds at the ends and lateral buds at each node. Below each lateral bud is a leaf scar containing bundle scars. Lenticels are raised portions in the periderm and appear as dots in the bark from a distance. Terminal bud scale scars resemble rings of indentations around the twig and are formed after a terminal bud resumes growth. Image labeled from Nikki Harris (CC-BY-NC).

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3.3.4: Stem Modifications

Learning Objective

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

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

Rhizomes and stolons are horizontal stems that function in propagation (Figure 3.3.4.1). **Rhizomes** are belowground stems that burrow into the ground just below the soil surface. They have short internodes and usually have small, scale-like leaves that are not photosynthetic. Buds from the axils of the leaves make new branches that will grow to become aboveground shoots. Ginger (*Zingiber*) and Johnson grass (*Sorghum halepense*) form rhizomes. **Stolons** (runners) are aboveground horizontal shoots, which sprout and produce a new plants. Compared to rhizomes, stolons have long internodes. Examples include strawberry (*Fragaria*), spider plants (*Chlorophytum*), and Bermuda grass (*Cynodon dactylon*).



Figure 3.3.4.1: Examples of horizontal stems. Ginger rhizomes are thick and belowground (top), and stolons of this spider plant are aboveground with long internodes (bottom). Leaves and roots emerge from the end of a stolon, forming a smaller plant. Top image by Sengai Podhuvan (CC-BY-SA), and bottom image by Eptalon (CC-BY-SA).

Tubers, corms, and bulbs are modified for starch storage. **Tubers**, such as potatoes, are thick, belowground stems found at the tips of rhizomes or stolons (figure 3.3.4.2). The “eyes” of potato are actually lateral buds, and the tuber body is comprised of many parenchyma cells that contain amyloplasts with starch. Corms and bulbs are modified shoots. A **corm** is a short, thick underground storage stem with thin scaly leaves (for example, *Gladiolus* and *Crocus*; Figure 3.3.4.3; Video 3.3.4.1). A **bulb**, such as an onion, differs from a corm in the fact that it stores its nutrients in its fleshy leaves (Figure 3.3.4.3). Lilies and tulips also form bulbs.



Figure 3.3.4.2: Potato tubers are expanded, belowground stems modified for starch storage. Image by pxhere (public domain).

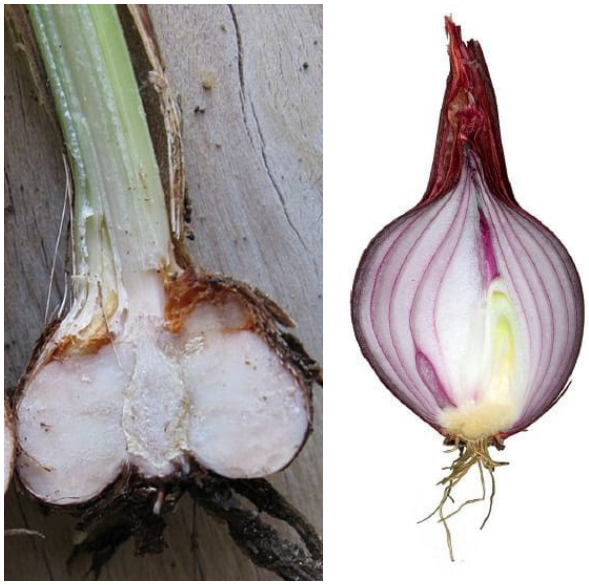


Figure 3.3.4.3: Both corms (left) and bulbs (right) are shoots modified for starch storage. The *Crocosmia* corm has a thick, expanded stem stores starch, and the leaves that surround it are non-photosynthetic and papery. The onion bulb has a relatively small stem surrounded by thick, fleshy leaves. Left image by JonRichfield (CC-BY-SA), and right image by Amada44 (CC-BY-SA).

Some plants have sharp, generally narrow projections that function in defense against herbivores. Such structures are called **thorns** when they arise from an entire stem. Hawthorn (*Crataegus*) and *Bougainvillea* produce thorns. In contrast, **prickles** form from the surface tissues (epidermis and cortex) of the stem rather than the whole organ (figure 3.3.4.4). Rose (*Rosa*) and blackberry (*Rubus*) produce prickles. **Spines** are similar structures derived from leaves (see Leaf Modifications).

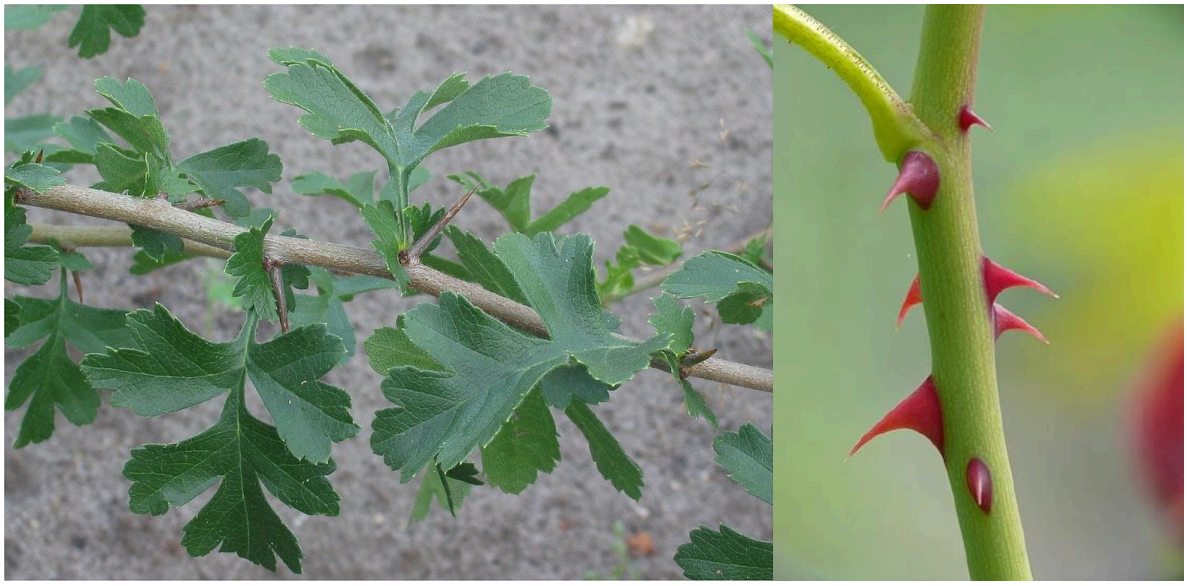


Figure 3.3.4.4: Thorns (left) and prickles (right). The thorns of the hawthorn are derived from the whole stem. They arise from axillary buds in the axils just above the leaves. The sharp projections on the rose stem are technically classified as prickles because they are derived from only the surface tissues of the stem. Left image by Rasbak (CC-BY-SA), and right image by Ingrid Taylar (CC-BY).

Tendrils are thin, string-like structures that allow the shoot to attach to other surfaces to access light. Tendrils can be derived from stems, leaves, or leaflets, and they are common in vines. Morning glory and sweet potato (*Ipomoea*), grapes (*Vitis*), and many members of the cucumber family (Cucurbitaceae) such as cucumbers, pumpkin, and squash have tendrils that arise from stems (Figure 3.3.4.5).



Figure 3.3.4.5: The thin, pale tendrils of the wild cucumber plant arise from stems and coil around surrounding structures. Image by erwin66as (public domain)

Cladophylls (cladodes) are stems that resemble leaves in function and appearance, arise from the axils of a shoot, and have determinate growth (stop growth after reaching a certain size). They may be cylindrical (*Asparagus;* Figure 3.3.4.6) or flattened (butcher's broom, *Ruscus;* figure 3.3.4.7). **Phylloclades** are flattened stems that resemble leaves that can continue growing indeterminately (Figure 3.3.4.8). They are subtended by reduced, scale-like leaves. Examples include prickly pear cactus (*Opuntia*), Christmas cactus (*Schlumbergera*), and ribbon plant, *Homalocladium*. **Phyllodes** are similar are similar to cladophylls and phylloclades, but they are modified petioles (see Leaf Modifications).



Figure 3.3.4.6: Cladophylls in *Asparagus* (left) and actual leaves of young asparagus marked by arrows (right). Left image by DenesFeri (CC-BY-SA), and right image by Sam Saunders (CC-BY-SA).



Figure 3.3.4.7: Cladophylls in butchers broom (*Ruscus*) are flattened like leaves. A flower arises from a node within the cladophyll. Image by Rosser1954 (CC-BY-SA).



Figure 3.3.4.8: Phylloclades in Christmas cactus. Image by Mokkie (CC-BY-SA).

Some shoots are modified as **insect traps** are used by some carnivorous plants, such as bladderwort (*Utricularia*; Video 3.3.4.1).

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

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3.3.5: Chapter Summary

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

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

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

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

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

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

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3.4: LEAVES

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

Usually, true leaves are easily distinguishable, but in some species, modified stems (cladophylls and phyloclades) or leaflets (parts of leaves) superficially appear like whole leaves. True leaves subtend an axillary bud in the axil and are lateral (rather than at the tip, or apex of the shoot; Figure 3.4.1). New shoots and leaves do not arise from true leaves.

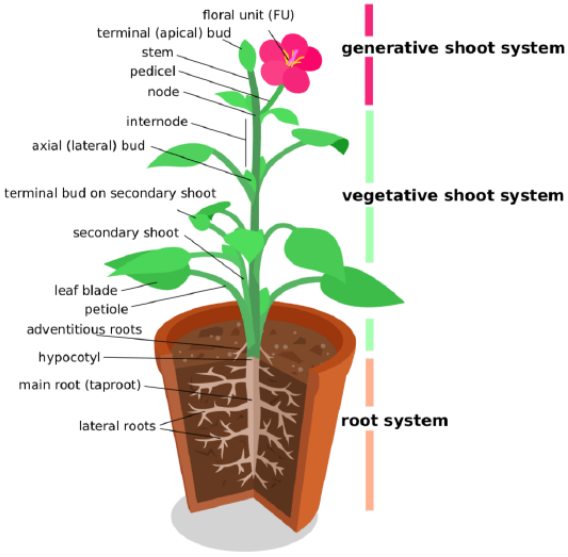


Figure 3.4.1: Leaves are lateral structures of the shoot system. The plant here is divided into a generative shoot system, vegetative shoot system, and root system. The generative shoot system consists of the floral unit, which is supported by the pedicel. The vegetative shoot system consists of stems and leaves. Leaves attach at nodes on the main stem. Stem segments between nodes are internodes. Leaves consist of a flattened blade and stalklike petiole, and they subtend axillary buds (labeled axial bud here). Some axillary buds have developed into secondary shoots. Terminal (apical) buds are found at the end of stems. In the root system, lateral roots arise from the main root (taproot). Adventitious roots arise from the stem. At the base of the main stem, just before it transitions to the main root is the hypocotyl.

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

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- Leaves

3.4.1: External Structure of Leaves
3.4.2: Internal Leaf Structure
3.4.3: Leaf Modifications
3.4.4: Chapter Summary

Thumbnail image: The red petal-like structures of the poinsettia plant are actually modified leaves called bracts, which are adapted to attract pollinators. The true flowers tiny structures where the bracts meet. Image by Scott Bauer (public domain).

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3.4.1: External Structure of Leaves

Learning Objectives

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

Each leaf typically has a flat, wide portion called the **blade** (lamina), which is also the widest part of the leaf (Figure 3.4.1.1). Some leaves are attached to the plant stem by a stalklike petiole and are called **petiolate leaves** (Figure 3.4.1.2). Although petioles are narrow and often resemble stems, they are considered part of the leaf. A petiolate leaf thus consists of the blade and the petiole. Petioles usually attach at to the **margin** (edge) of the blade along the base, but in **peltate** leaves, the petiole is attached underneath the blade (Figure 3.4.1.3). Leaves that do not have a petiole and are directly attached to the plant stem are called **sessile** (apetiolate) leaves (Figure 3.4.1.4). In a special type of sessile leaves called **perfoliate** leaves, the stem passes through the center of the blade (Figure 3.4.1.4). Many leaves have a **midrib**, which travels the length along the center of the leaf. The midrib contains the **main vein** (primary vein) of the leaf as well as supportive ground tissue (collenchyma or sclerenchyma).

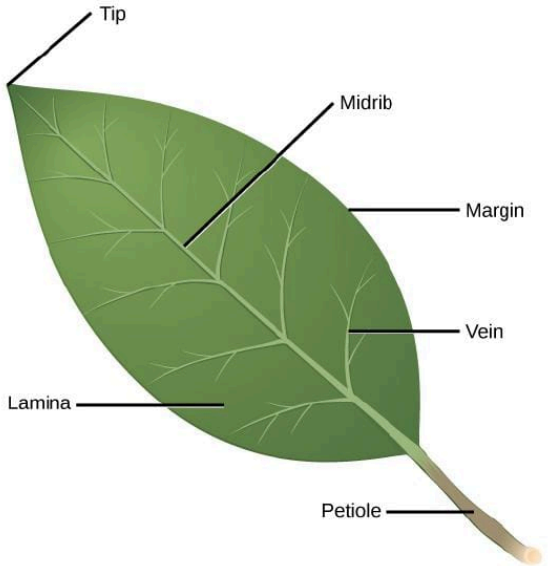


Figure 3.4.1.1: A typical eudicot leaf. Many leaves consist of a stalk-like petiole and a wide, flat blade (lamina). The midrib extends from the petiole to the leaf tip and contains the main vein. Additional veins branch from the midvein. The margin is the edge of the leaf.



Figure 3.4.1.2: The petiolate leaves of the geranium consist of a petiole and blade (lamina). The wide lamina is attached to the stalk-like petiole. In the sessile leaves of *Aster amellus*, the blade is attached directly to the stem. Left image by Melissa Ha (CC-BY), and right image by Enrico Blasutto (CC-BY-SA).



Figure 3.4.1.3: In the peltate leaves of nasturtium, petioles attach underneath the leaf blade, similar to an umbrella. Image by Melissa Ha (CC-BY).



Figure 3.4.1.4: The stem runs through the center of the blade in the perfoliate leaves of miner's lettuce. Image by Wikimediaimages/Pixabay (Pixabay license).

Small, green appendages usually found at the base of the petiole are known as **stipules** (Figure 3.4.1.5). Other structures located near leaf base **sheath** (typical for grasses, lilies, and related species) and **ocrea** (typical for buckwheat family, Polygonaceae).

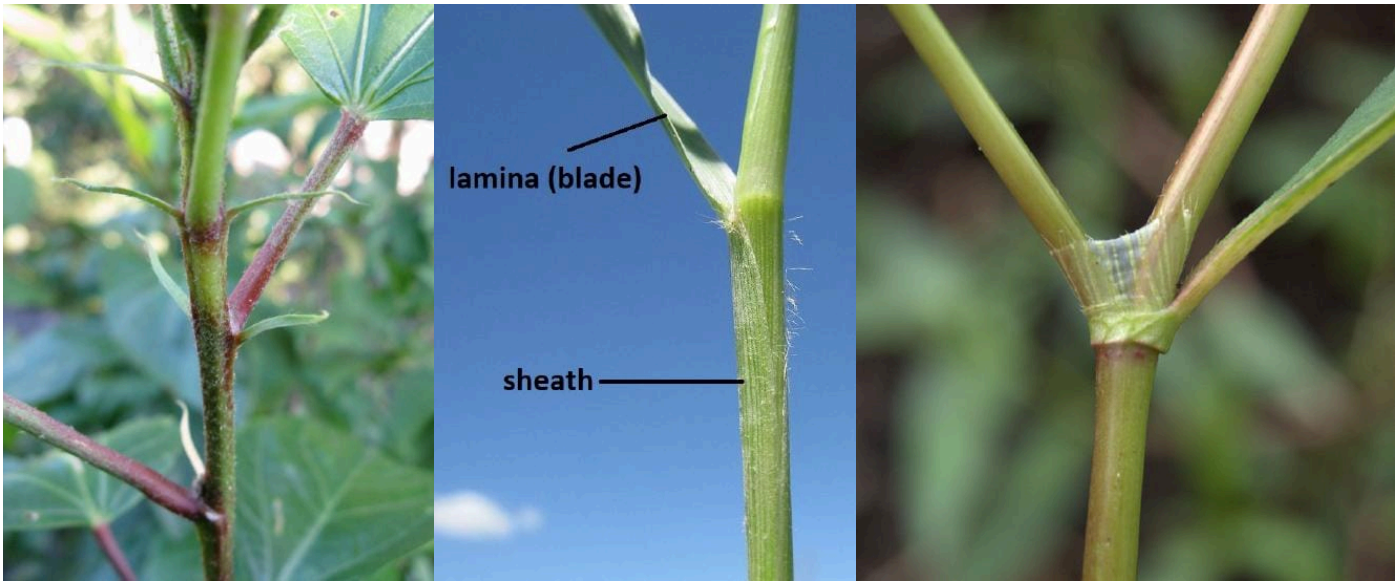


Figure 3.4.1.5: Left: In *Hibiscus*, two small, narrow, green stipules emerge at the base of each petiole. Middle: This grass blade (lamina) is attached to a sheath, which wraps around the stem. Right: The ocrea of *Persicaria maculosa* from the buckwheat family is constructed of fused stipules. Left image by Nadiatalent (CC-BY-SA), middle image by Harry Rose (CC-BY), and right image by Martin Olsson (CC-BY-SA).

Phyllotaxy

The arrangement of leaves on a stem is known as **phyllotaxy**. The number and placement of a plant's leaves will vary depending on the species, with each species exhibiting a characteristic leaf arrangement. Leaves arrangements are classified as either alternate, opposite, or whorled (Figure 3.4.1.6). Plants that have only one leaf per node have leaves that are said to be **alternate**, and alternate leaves often spiral up the stem. In an **opposite** leaf arrangement, two leaves arise at the node (with the leaves usually connecting opposite each other along the branch). Pairs of opposite leaves may face all in the same direction, or each pair can rotate at 90° (**decussate**). If there are three or more leaves connected at a node, the leaf arrangement is classified as **whorled,** and each whorl can also rotate. Each type of spiral phyllotaxis has its own angle of divergence.

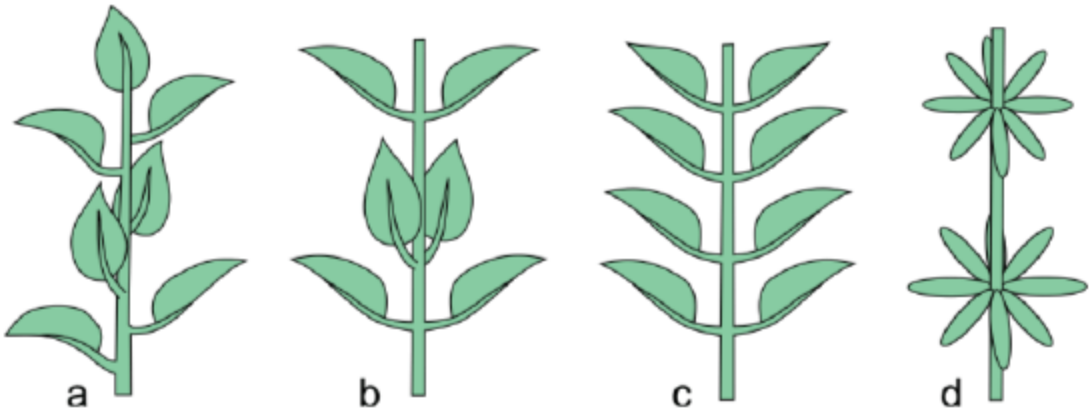


Figure 3.4.1.6: Types of phyllotaxis (leaf arrangement): (a) alternate— with only one leaf attaching to each node, (b) and (c) opposite— with two leaves attaching at each node, and (d) whorled— with more than two leaves attached at each node. While both (b) and (c) illustrate opposite arrangements, leaf pairs are perpendicular to each other in (b) and aligned in (c).

Simple and Compound Leaves

Leaves may be simple or compound (Figure 3.4.1.7). In a **simple** leaf, the blade is either completely undivided (Figures 3.4.1.8, 12, 13)—or it has lobes, but the separation does not reach the midrib, as in the maple leaf. In a **compound** leaf, the leaf blade is completely divided, forming **leaflets**, as in the locust tree. Each leaflet may have its own stalk but is attached to the rachis. A **palmately compound** leaf resembles the palm of a hand, with leaflets radiating outwards from one point (Figure 3.4.1.8). Examples include the leaves of poison ivy, the buckeye tree, or the familiar houseplant *Schefflera* sp. (common name "umbrella plant"). **Pinnately compound** leaves take their name from their feather-like appearance; the leaflets are arranged along the midrib, as in rose leaves (*Rosa* sp.), or the leaves of hickory, pecan, ash, or walnut trees (Figure 3.4.1.8). **Trifoliate** leaves, such as in clover or strawberry, have only three leaflets (Figure 3.4.1.9)

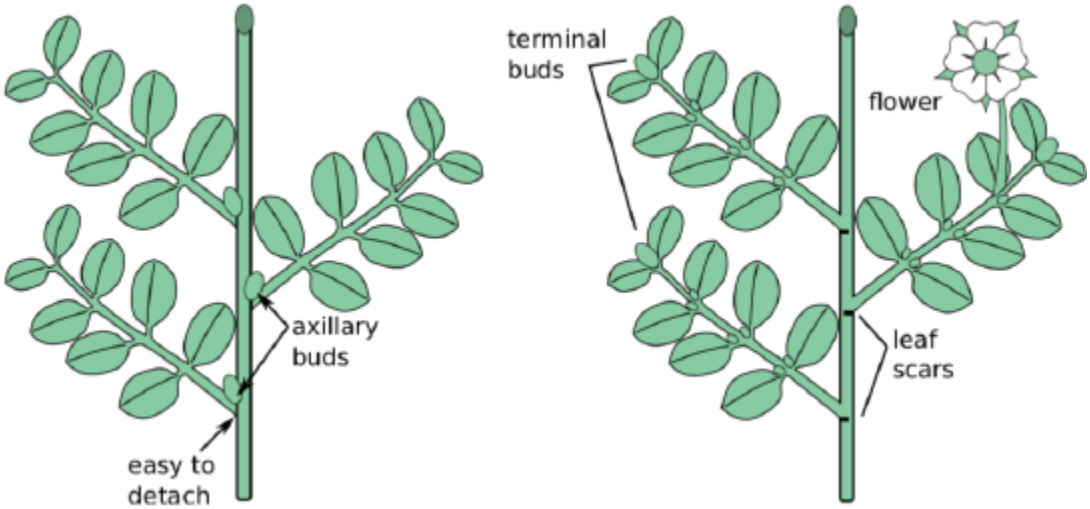


Figure 3.4.1.7: Compound leaves (left) and simple leaves (right). While these plants appear similar, each true leaf has an axillary bud above. On the left, the axillary bud is above each compound leaf (but not each leaflet). On the right, each leaf has a bud above it, identifying them as leaves rather than leaflets. Leaflets are always on the same plane with in a leaf (such that the leaf is flat), but this is not the case for multiple simple leaves on the same branch.

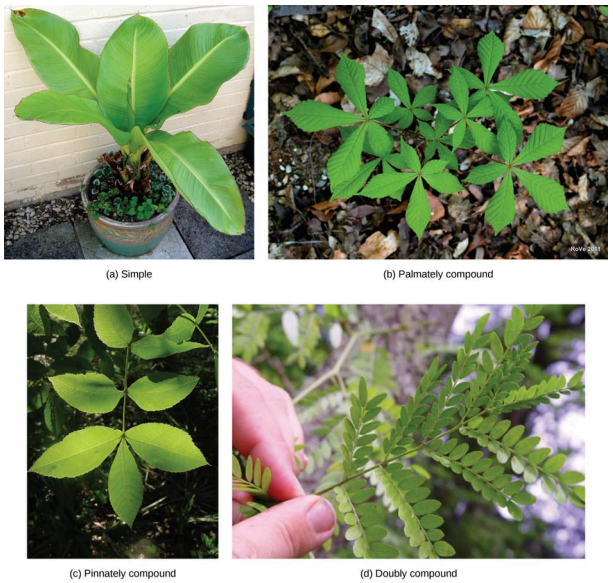


Figure 3.4.1.8: Leaves may be simple or compound. In simple leaves, the blade is continuous. The (a) banana plant (*Musa* sp.) has simple leaves. In compound leaves, the blade is separated into leaflets. Compound leaves may be palmate or pinnate. In (b) palmately compound leaves, such as those of the horse chestnut (*Aesculus hippocastanum*), the leaflets branch from the petiole. In (c) pinnately compound leaves, the leaflets branch from the midrib (rachis), as on a scrub hickory (*Carya floridana*). The (d) honey locust has double compound leaves, in which leaflets branch from the veins. (credit a: modification of work by "BazzaDaRambler"/Flickr; credit b: modification of work by Roberto Verzo; credit c: modification of work by Eric Dion; credit d: modification of work by Valerie Lykes)



Figure 3.4.1.9: The trifoliate leaves of strawberry each consist of three leaflets. Each leaflet has a dentate margin, consisting of symmetrical teeth. Image by Melissa Ha (CC-BY).

Simple leaves have just one level of hierarchy whereas compound leaves have two or more levels of hierarchy (Figure 3.4.1.10). Pinnately compound leaves with two levels of hierarchy are **unipinnate**. Those with three levels of hierarchy are called **bipinnate** (twice pinnate; doubly compound), and those with four levels of hierarchy are **tripinnate**. For compound leaves, a botanist could describe characteristics of the leaf overall as well as the shape, margin, and venation (see below) of the leaflets.

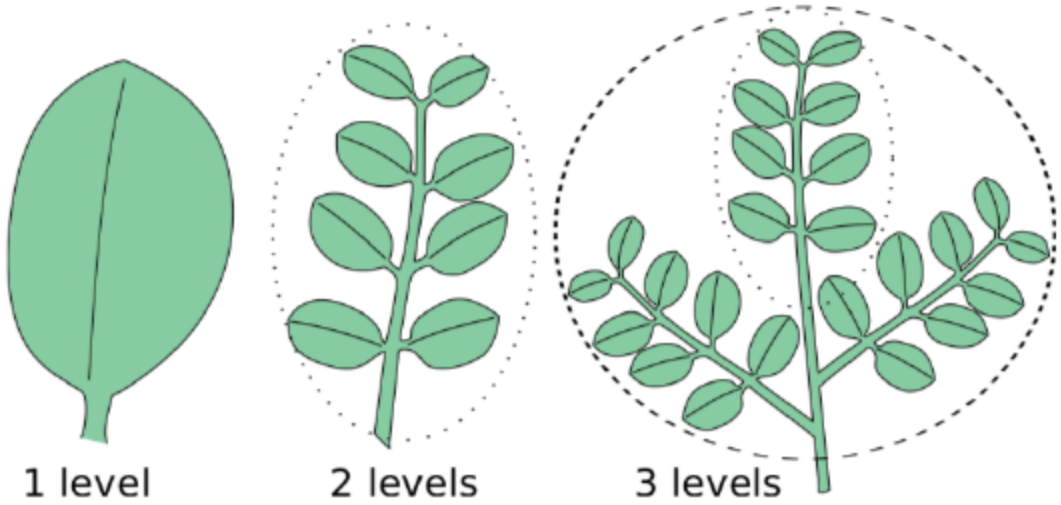


Figure 3.4.1.10: Leaves with one (simple), two (unipinnate), and three (bipinnate) levels of hierarchy. The blade of the simple leaf is continuous. In the unipinnate leaf, the blade is divided into leaflets, which attach on either side of the midrib (rachis). In the bipinnate leaf, each leaflet is further subdivided. The dotted lines indicate the shape of each level, which is not necessarily the same for each level.

Venation

Leaf veins are vascular bundles coming to the leaf from stem. The arrangement of veins in a leaf is called the venation pattern. Frequently, there is one or more **main vein** (primary vein) and **secondary veins** that branch from it. **Tertiary veins** branch from secondary veins (Figure 3.4.1.11).

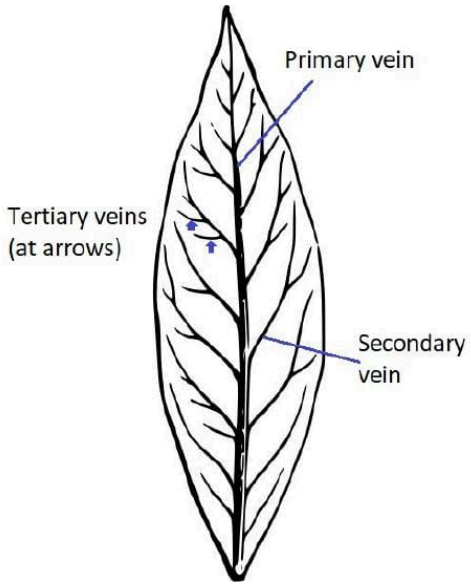


Figure 3.4.1.11: The main (primary) vein of this leaf is the largest, central vein. Secondary veins emerge from the primary vein. Tertiary veins (at arrows) emerge from the secondary veins. Image modified from freesvg (public domain).

There are three main arrangements of the most prominent (major) of the leaf. They may all run longitudinally (**parallel venation**, Figure 3.4.1.12), they may branch from a single midvein (**pinnate venation**, Figure 3.4.1.8a, 12), or they may arise from a single point at the base of the leaf (**palmate venation**; Figure 3.4.1.13). Parallel venation is found in monocots, and pinnate and palmate venation is common in eudicots. The maidenhair tree, ginkgo (*Ginkgo biloba*), has a unique venation pattern in which each vein divides into two similar parts. This is known as **dichotomous venation** (Figure 3.4.1.12).

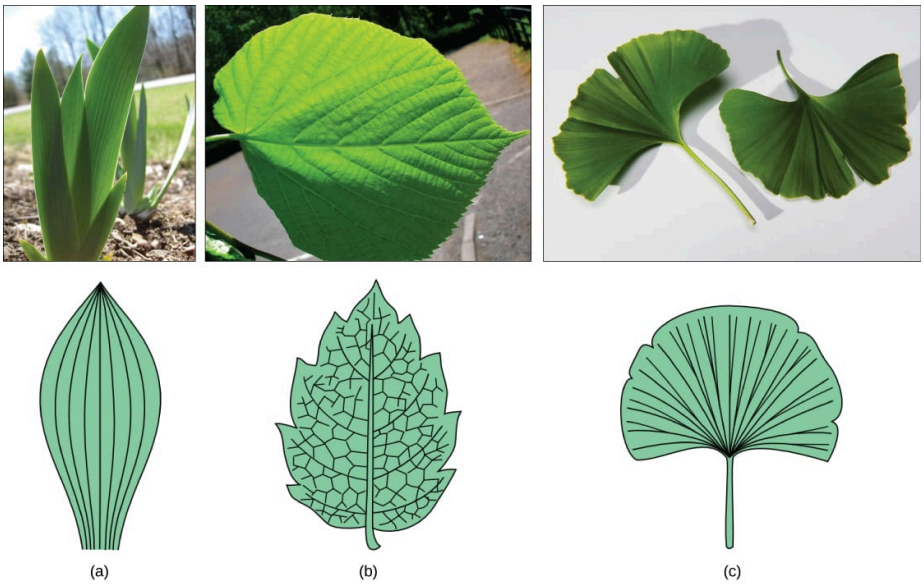


Figure 3.4.1.12: (a) Tulip (*Tulipa*), a monocot, has leaves with parallel venation, with veins running up the leaves in the same direction. They do not intersect. (b) Linden (*Tilia cordata*) is a eudicot with pinnate and reticulate venation. Veins radiate out from the midrib, and smaller veins radiate out from these.The (c) *Ginkgo biloba* tree has dichotomous venation with veins radiating out from the petiole. Each of these veins branches into two veins. (credit a photo: modification of work by “Drewboy64”/Wikimedia Commons; credit b photo: modification of work by Roger Griffith; credit c photo: modification of work by "geishaboy500"/Flickr; credit abc illustrations: modification of work by Agnieszka Kwiecień)

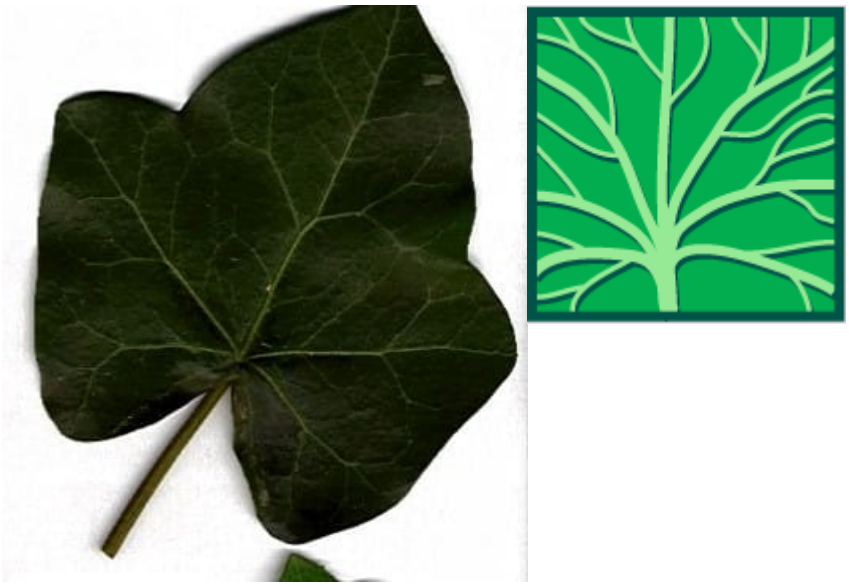


Figure 3.4.1.13: In leaves with palmate venation, multiple main veins branch from a central point, which is near the base of the leaf, similarly to how the fingers radiate from the palm of a hand. Left image cropped from Maksim (CC-BY-SA), and right image by Maksim (CC-BY-SA).

The less prominent (minor) veins of a leaf may form a branching, netlike pattern, which is called **reticulate venation** (Figure 3.4.1.14). In contrast, the minor veins are arranged neatly, forming a ladderlike structure in **percurrent venation**.

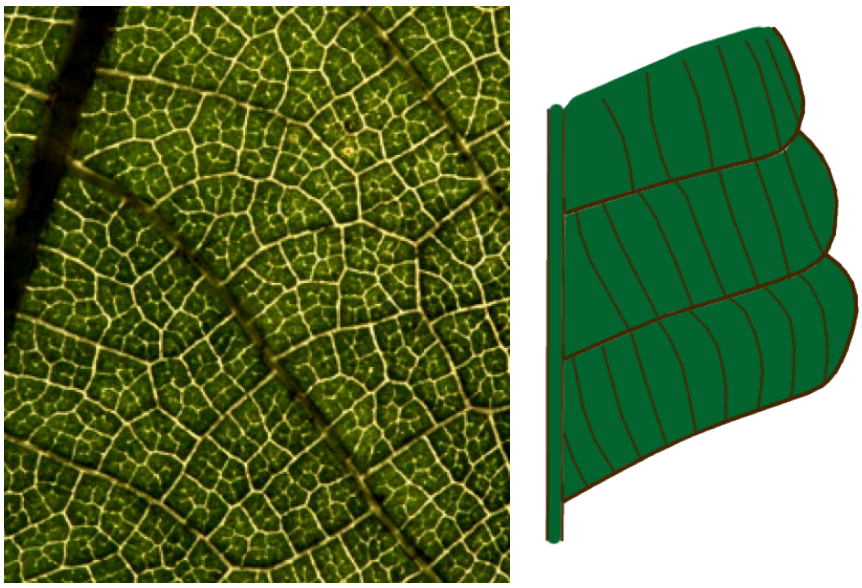


Figure 3.4.1.14: Minor veins may demonstrate reticulate venation (left) or percurrent (right). Left image cropped from Katifori E, Magnasco MO (2012) Quantifying Loopy Network Architectures. PLoS ONE 7(6): e37994 (CC-BY), and right image by RoRo (public domain).

Margins

The margin describes the outline of a simple leaf or leaflet (Figure 3.4.1.15). Leaves with smooth margins are called **entire**. Those with irregularly wavy margins are **undulate**. **Lobate** (lobed) leaves may be **palmately lobate** (with lobes outlining the palmate venation pattern of veins arising from a single point at the base of the leaf) or **pinnately lobate** (with lobes outlining the pinnate venation pattern of secondary veins branching from a midvein; Figure 3.4.1.16). Toothed leaves have small projections (teeth) and indentations that do not align with the venation. For **serrate** leaves, the sharp teeth point forward, like a serrated knife. For **dentate** leaves, sharp teeth are symmetrical, like equilateral triangles. For **crennate** leaves, the teeth are rounded rather than sharp.

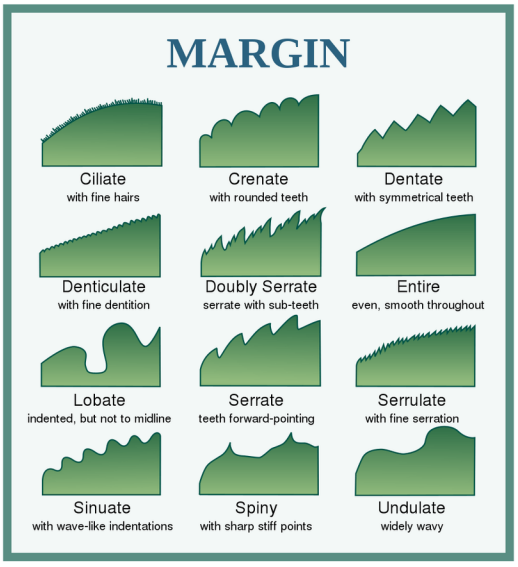


Figure 3.4.1.15: Examples of leaf margins. Ciliate margins have fine hairs. Crenate margins have rounded teeth, dentate margins have symmetrical teeth, and denticulate margins have fine dentition (small teeth). Serrate margins have forward-facing teeth, like a serrated knife. Doubly serrate margins are serrate with sub-teeth. Entire margins are smooth. Lobate margins are indented, but not to the midline. Serrulate margins have fine serration. Sinuate margins have wave-like indentations. Spiny margins have sharp, stiff points, and undulate leaf margins are widely, irregularly wavy. Image cropped from McSush/Debivort (CC-BY-SA).



Figure 3.4.1.16: Lobed leaves have indentations that match the venation pattern. Oak leaves (left) are pinnately lobate. The leaves on the right are palmately lobate. Images by Melissa Ha (CC-BY).

Shape

There are several general leaf shapes (Figure 3.4.1.17). The widest part of **ovate** leaves is near the based whereas the widest portion of **obovate** leaves is near the apex (tip). If the widest portion of the leaves is equidistant form the apex and base, the leaf may be elliptic or oblong. In **elliptic** leaves, a single wide middle portion tapers as it approaches the apex or base. **Oblong** leaves are similarly, but there is a longer section in the middle of these leaves that is uniformly wide. **Linear** leaves are long and thin. **Lanceolate** leaves are lance-shaped and somewhat intermediate between ovate and linear.

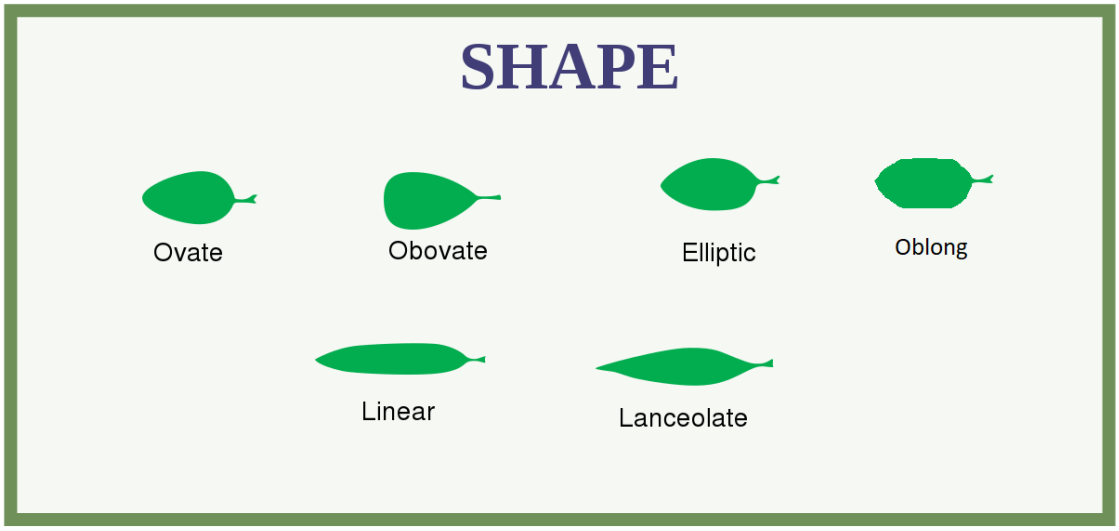


Figure 3.4.1.17: Six main leaf shapes. Ovate leaves are egg-shaped, but the base is the widest portion. Obovate are egg-shaped, but the base is the narrowest portion. Elliptic leaves have a wide center and taper at the base and tip. Oblong leaves are elongated. Linear leaves are long, and lanceolate leaves are lance-shaped. Image modified from McSush/Debivort (CC-BY-SA).

The leaf shape can be described in further detail using specific terminology that applies to the leaf apex (Figure 3.4.1.18) and leaf base (Figure 3.4.1.19). The leaf apex could be **rounded**, **acute** (forming an angle less than 90°), **obtuse** (forming an angle greater than 90°), **attenuate** (tapering to a point), or **acuminate** (dramatically curving inward to a narrow point). The base of the leaf blade could be **rounded**, **acute**, **obtuse**, **truncate** (straight), **cuneate** (wedge-shaped or triangular), or **cordate** (indented in

the center, like an upside-down heart).

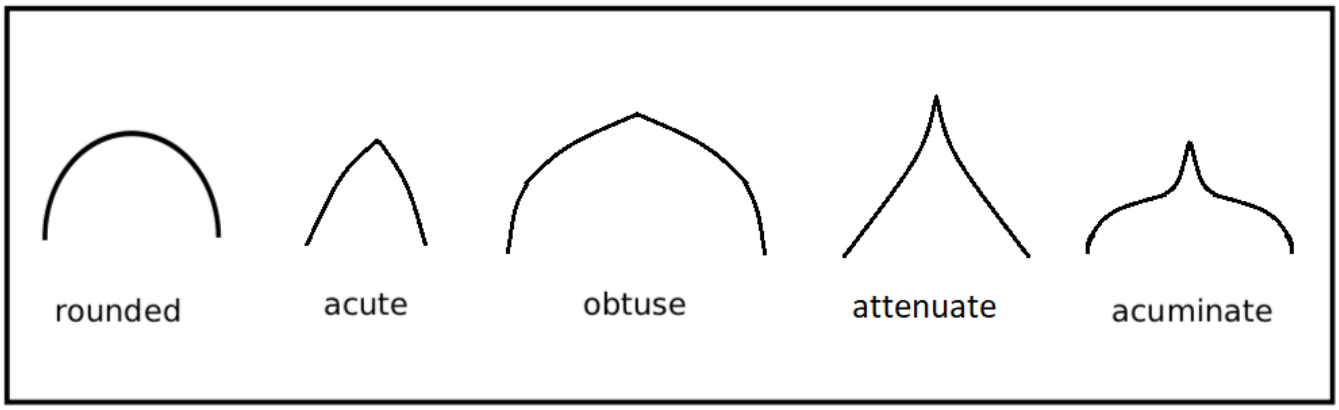


Figure 3.4.1.18: Five leaf apex shapes. The leaf apex could be rounded, acute (forming an angle less than 90°), obtuse (forming an angle greater than 90°), attenuate (tapering to a point), or acuminate (dramatically curving inward to a narrow point). Image modified by Melissa Ha (CC-BY) from Shipunov (public domain).

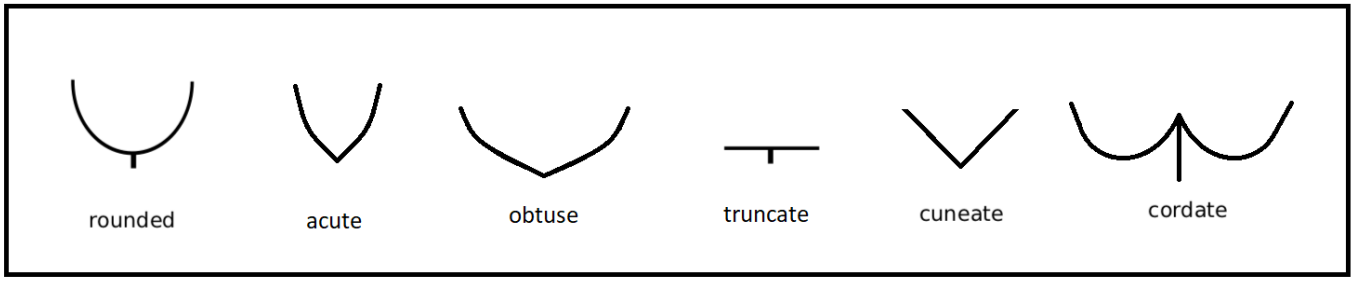


Figure 3.4.1.19: Six leaf base shapes. The base of the leaf blade could be rounded, acute (forming an angle less than 90°), obtuse (forming an angle greater than 90°), truncate (straight), cuneate (wedge-shaped or triangular), or cordate (indented in the center, like an upside-down heart). Image modified by Melissa Ha (CC-BY) from Shipunov (public domain).

Hetrophylly

Heterophylly refers to a plant having more than one kind of leaf. A plant can have both juvenile leaves and adult leaves, water leaves and air leaves, or sun leaves and shade leaves. In California live oak, leaves growing closely to the ground have sharp teeth, presumably to deter herbivores such as deer. Leaves at the top of the plant are too high for herbivores to reach and have entire margins. California sycamore has both palmately lobed leaves and small, perfoliate leaves (Figure 3.4.1.20).



Figure 3.4.1.20: The California sycamore exhibits heterophylly because it has two different leaf types. The stem pierces a small, circular perfoliate leaf in the center of the image. The other larger leaves are palmately lobate. Image by Melissa Ha (CC-BY).

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3.4.2: Internal Leaf Structure

Learning Objectives

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

Tissue Organization in Leaves

All three tissue types are represented in leaves. The epidermis represents the dermal tissue, the mesophyll that fills the leaf is ground tissue, and the vascular bundles that form the leaf veins represent vascular tissue (Figure 3.4.2.1). These three tissues will be discussed using a eudicot leaf that is adapted to a moderate amount of water (mesophytic leaf). Variations in leaf structure are discussed later on this page.

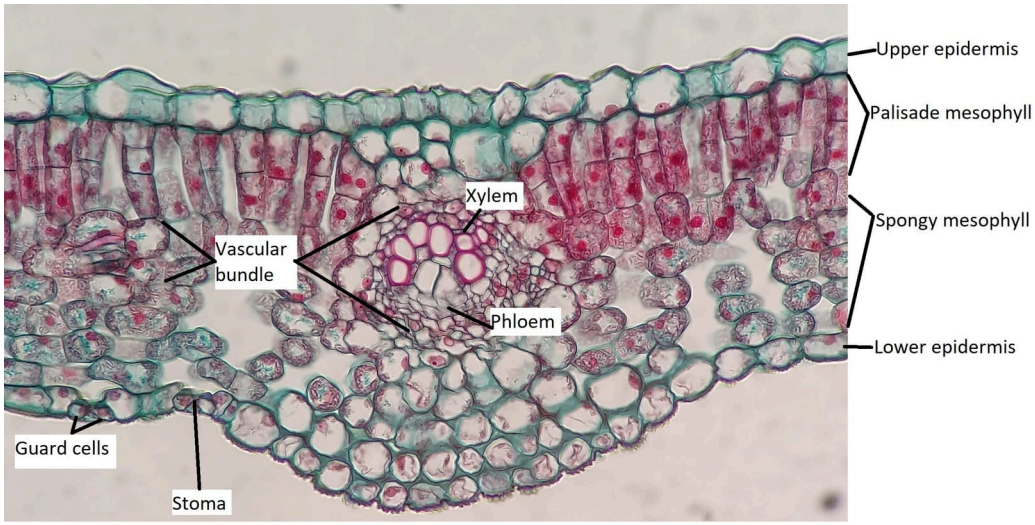


Figure 3.4.2.1: A cross section through a eudicot leaf. The upper epidermis is a single layer of parenchyma cells. There are no stomata present in the upper epidermis of this leaf. Below the epidermis, cells (appearing pink due to staining of the nuclei and chloroplasts) are arranged in columns, forming the palisade mesophyll. Beneath the palisade mesophyll is the spongy mesophyll. The cells are approximately the same size as the palisade mesophyll, but there are large intercellular spaces between them. The lower epidermis is another single layer of parenchyma cells, but several stomata (flanked by guard cells) are visible in this epidermal layer. A large vascular bundle is in the center of the leaf. The xylem (stained pink) is on the top and the phloem is on the bottom. Image by Maria Morrow (CC-BY-NC).

Epidermis

The outermost layer of the leaf is the **epidermis**; it is present on both sides of the leaf and is called the upper and lower epidermis, respectively. Botanists call the upper side the adaxial surface (or adaxis) and the lower side the abaxial surface (or abaxis). The epidermis helps in the regulation of gas exchange. It contains **stomata** (singular = stoma; Figure 3.4.2.2), openings through which the exchange of gases takes place. Two **guard cells** surround each stoma, regulating its opening and closing, and the guard cells are sometimes flanked by **subsidiary cells**. Guard cells are the only epidermal cells to contain chloroplasts. In most cases, the lower epidermis contains more stomata than the upper epidermis because the bottom of the leaf is cooler and less prone to water loss.

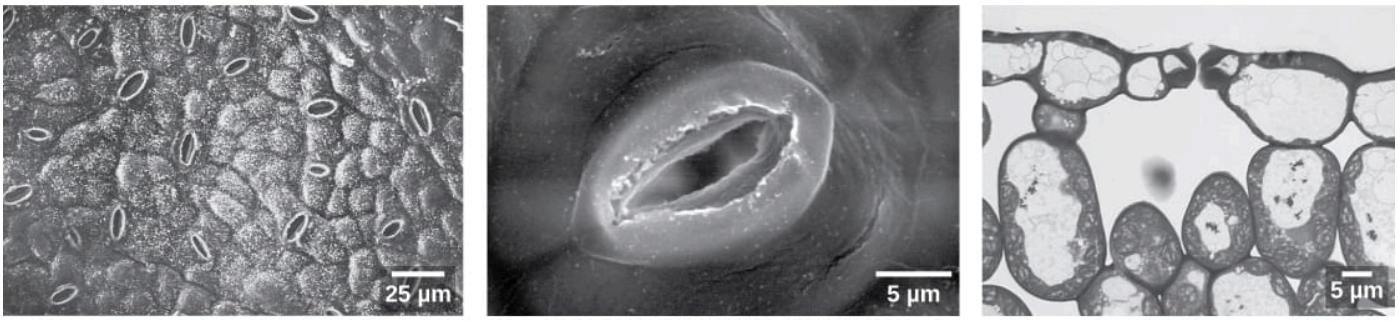


Figure 3.4.2.2: Visualized at 500x with a scanning electron microscope, several stomata are clearly visible on (a) the surface of this sumac (*Rhus glabra*) leaf. The small, oval-like stomata are scattered on the bumpy surface of the leaf. At 5,000x magnification, the thick lip-like guard cells of (b) a single stoma from lyre-leaved sand cress (*Arabidopsis lyrata*) have the appearance of lips that surround the opening. In this (c) light micrograph cross-section of an *A. lyrata* leaf, the guard cell pair is visible along with the large, substomatal air space in the leaf. The other cells in the leaf (mesophyll cells) are egg-shaped. (credit: modification of work by Robert R. Wise; part c scale-bar data from Matt Russell)

The epidermis is usually one cell layer thick; however, in plants that grow in very hot or very cold conditions, the epidermis may be several layers thick to protect against excessive water loss from transpiration. A protective layer called the **cuticle** covers surface of the epidermal cells (Figure 3.4.2.3). The cuticle is rich in lignin (which lends some rigidity) and waxes (which function in waterproofing). The cuticle reduces the rate of water loss from the leaf surface. Other leaves may have small hairs (**trichomes**) on the leaf surface. Trichomes help to deter herbivory by restricting insect movements, or by storing toxic or bad-tasting compounds; they can also reduce water loss by blocking air flow across the leaf surface (Figure 3.4.2.4). For this reason, trichomes (like stomata) are frequently denser on the lower side of the leaf.

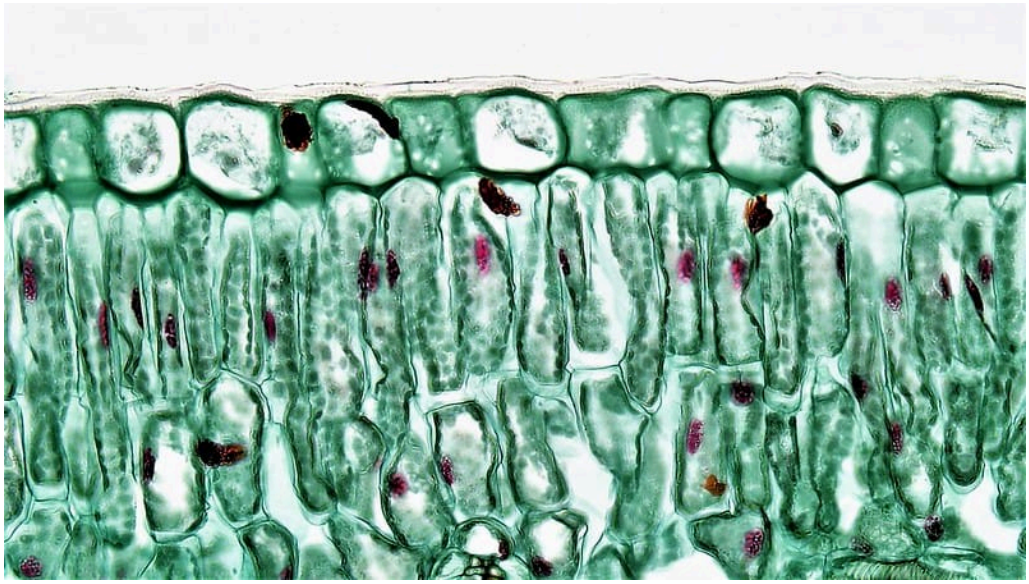


Figure 3.4.2.3: A cross section through the upper epidermis and the upper portion of the mesophyll (palisade mesophyll). On top of the upper epidermis of this leaf, a transparent layer of cuticle is visible, sealing the top of the leaf. Image by Berkshire Community College Bioscience Image Library (public domain).

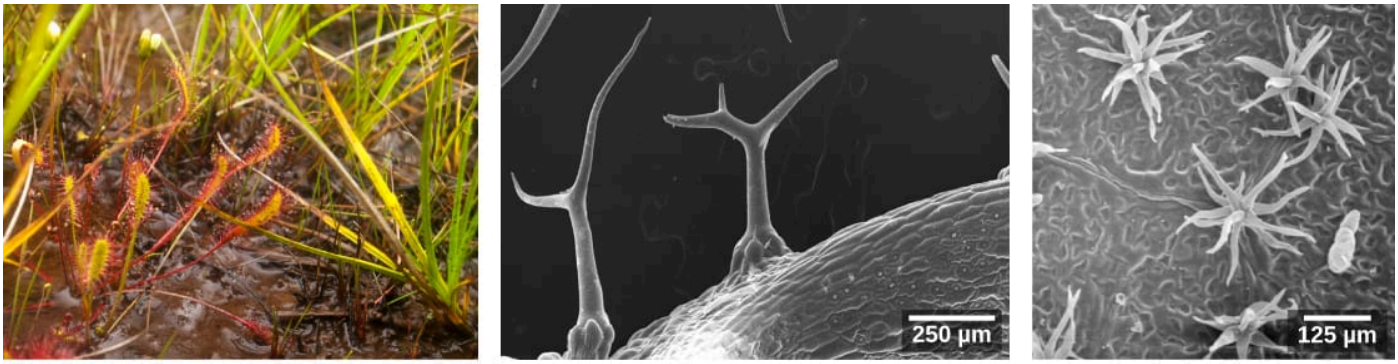


Figure 3.4.2.4: Trichomes give leaves a fuzzy appearance as in this (a) sundew (Drosera sp.). Scanning electron micrographs of (b) branched, tree-like trichomes on the leaf of *Arabidopsis lyrata* and (c) multibranched trichomes, which resemble sea anenomes, on a mature *Quercus marilandica* leaf. (credit a: John Freeland; credit b, c: modification of work by Robert R. Wise; scale-bar data from Matt Russell)

Mesophyll

Below the epidermis are layers of cells known as the **mesophyll**, or "middle leaf." Mesophyll cells contain many chloroplasts and specialize in photosynthesis. The mesophyll of most leaves typically contains two arrangements of parenchyma cells: the **palisade parenchyma** and **spongy parenchyma** (Figure 3.4.2.5). The palisade parenchyma (also called the palisade mesophyll) has column-shaped and may be present in one, two, or three layers. The palisade cells specialize in capturing incoming sunlight (including slanted sun rays), rotating chloroplasts to the top of the leaf and then allowing them to regenerate by cycling them toward the leaf's center. They also decrease the intensity of sunlight for the spongy mesophyll. Although palisade cells may appear tightly packed in a cross section because there are many rows of cells behind those in the foreground, there is actually ample space (**intercellular air spaces**) between them. Below the palisade parenchyma are seemingly loosely arranged cells of an irregular shape. These are the cells of the **spongy parenchyma** (or spongy mesophyll). The intercellular air spaces found between mesophyll cells facilitate gaseous exchange.

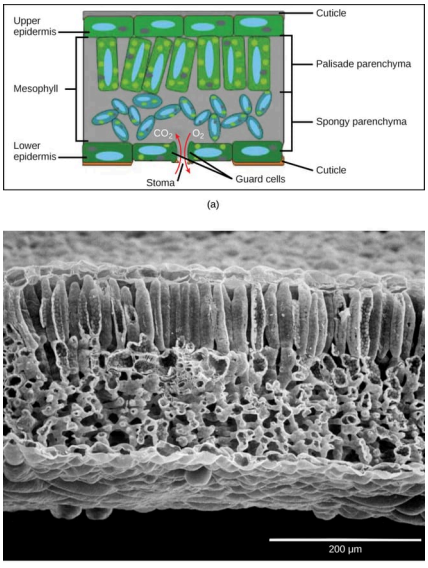


Figure 3.4.2.5: The meosphyll often consists of palisade and spongy parenchyma. Part A is a leaf cross section illustration. A flat layer of rectangular cells make up the upper and lower epidermis. A cuticle layer protects the outside of both epidermal layers. A stoma in the lower epidermis allows carbon dioxide to enter and oxygen to leave. Oval guard cells surround the pore. Sandwiched between the upper and lower epidermis is the mesophyll. The upper part of the mesophyll is comprised of columnar cells called palisade parenchyma. The lower part of the mesophyll is made up of loosely packed spongy parenchyma. Part B is a scanning electron micrograph of a leaf in which all the layers described above are visible. Palisade cells are about 50 microns tall and 10 microns wide and contain tiny bumps, which are the chloroplasts. Spongy cells smaller and irregularly shaped. (credit b: modification of work by Robert R. Wise)

Vascular Bundles (Veins)

Like the stem, the leaf contains vascular bundles composed of xylem and phloem (Figure $3.4.2.6 - 7$). When a typical stem vascular bundle (which has xylem internal to the phloem) enters the leaf, xylem usually faces upwards, whereas phloem faces downwards. The conducting cells of the xylem (tracheids and vessel elements) transport water and minerals to the leaves. The sieve-tube elements of the phloem transports the photosynthetic products from the leaf to the other parts of the plant. The phloem is typically supported by a cluster of fibers (sclerenchyma) that increase structural support for the veins. A single vascular bundle, no matter how large or small, always contains both xylem and phloem tissues.

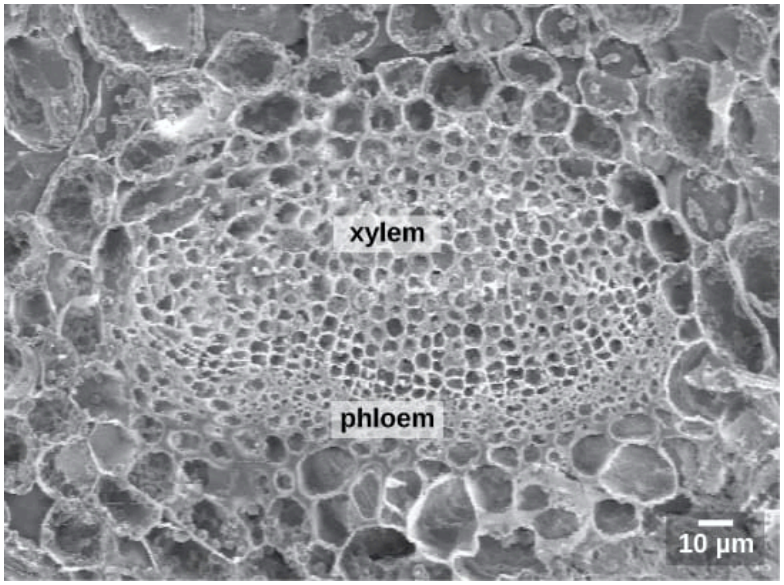


Figure $3.4.2.6$: This scanning electron micrograph shows xylem (larger cells on top) and phloem (smaller cells on bottom) in the leaf vascular bundle from the lyre-leaved sand cress (*Arabidopsis lyrata*). (credit: modification of work by Robert R. Wise; scale-bar data from Matt Russell)

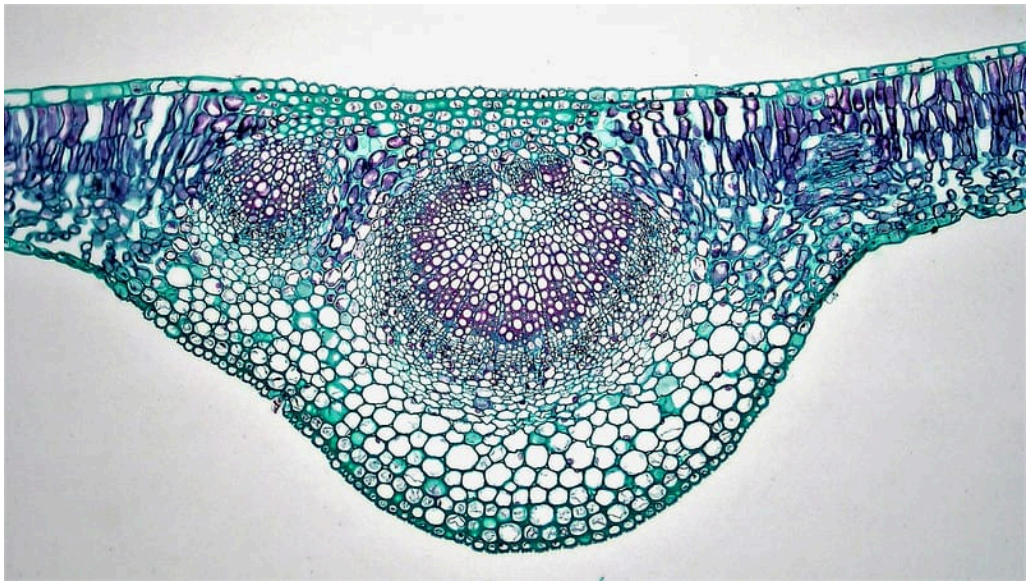


Figure $3.4.2.7$: A cross section through the midvein of a eudicot leaf. The xylem tissue within the large vascular bundle is arranged in an arcing semi-circle, with phloem tissue in an arc traveling just below it. The thick cell walls of the large xylem vessels stain reddish, while the cells of the phloem are smaller with thin cell walls and stain blue. There are layers of collenchyma cells under the epidermis both above and below the midvein. The vascular bundle just to the left of the midrib is coming more or less straight at us, so it is easy to distinguish the tissues. In contrast, the vascular bundle to the right of the midrib was moving diagonally and so was caught in an oblique section and looks more like a smear. Image by Berkshire Community College Bioscience Image Library (public domain).

Leaf Adaptations

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

In regards to water, there are three main types of plants: mesophytes, hydrophytes, and xerophytes. **Mesophytes** are typical plants which adapt to moderate amounts of water ("meso" means middle, and "phyte" means plant). Many familiar plants are mesophytes, such as lilac, *Ranunculus* (buttercup), roses, etc. **Hydrophytes** grow in water ("hydro" refers to water). Their leaf blades are frequently highly dissected (deeply lobed) to access gases dissolved in water, and their petioles and stems have air canals to supply underwater organs with gases. Hygrophytes (not discussed further) live in constantly wet environment, their leaves adapted to rapidly release water through the stomata. They sometimes even excrete of water drops through the leaf margins (guttation). **Xerophytes** are adapted to the scarce water ("xero" refers to dryness). Xerophytes are found in deserts and Mediterranean climates (such as in much of California), where summers are hot and dry. The leaves of mesophytes are called mesophytic, hydrophyte leaves are called hydrophytic, and so on. The structure of mesophytic leaves was already described (Figure 3.4.2.1). Adaptaions in hydrophytic and xerophytic leaves and discussed below in more detail.

Hydrophytic Leaves

The structure of a hydrophytic leaf differs from a mesophytic leaf due to selective pressures in the environment -- water is plentiful, so the plant is more concerned with staying afloat and preventing herbivory. Hydrophytic leaves have a thin epidermal layer and the absence of stomata in the lower epidermis (Figure 3.4.2.8). In the spongy mesophyll, there are large pockets where air can be trapped, helping the leaf float. This type of parenchyma tissue, specialized for trapping gases, is called **aerenchyma**. Sharp, branched sclereids (astrosclereids) traverse the mesophyll of a hydrophytic leaf. These provide the leaf structural support, as well as prevention of herbivory. Vascular tissue is somewhat reduced in hydrophytic leaves.

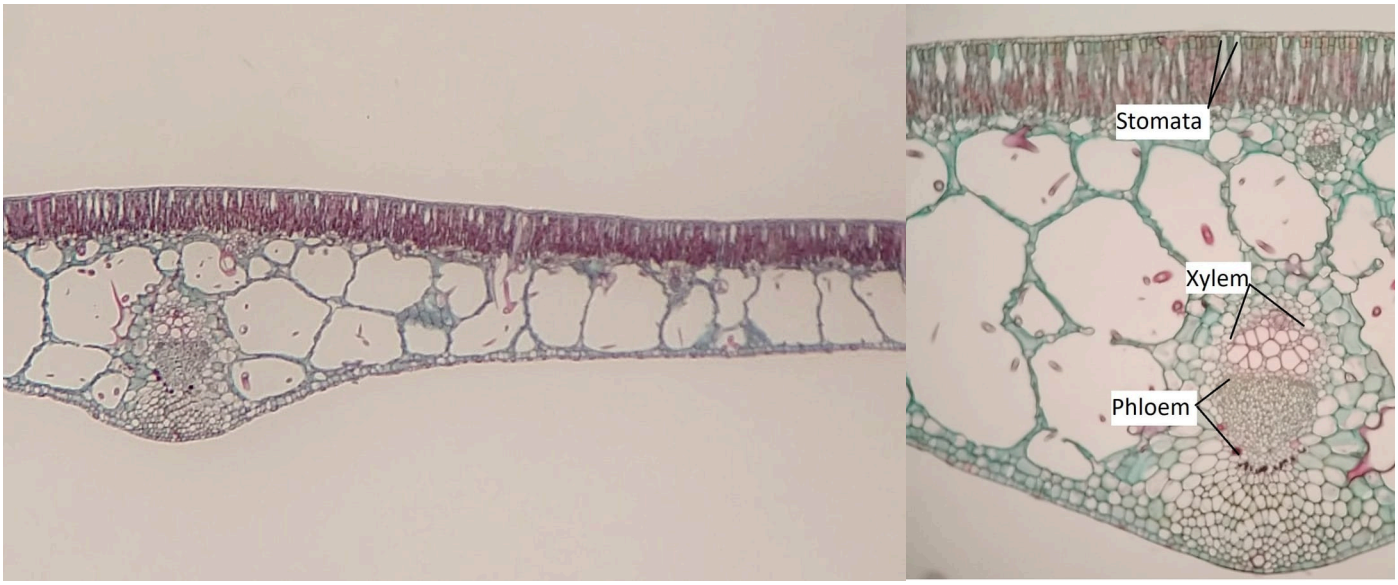


Figure 3.4.2.8: Cross sections through a hydrophytic leaf from *Nymphaea* (water lily) at two magnifications. The upper epidermis is a thin layer of parenchyma with many stomata. Below each stoma, there is a chamber of air located within the palisade mesophyll (this makes them easier to find). Under the palisade mesophyll is a much larger region of spongy mesophyll than in the mesophytic leaf. Most of the space is taken up by large air pockets, making this tissue aerenchyma. The lower epidermis has no stomata. Within the mesophyll, there are spiky, pink-stained astrosclereids that have been sectioned at different angles during slide preparation. These stain pink due to the lignin in their thick secondary cell walls. Images by Maria Morrow (CC-BY-NC).

Xerophytic Leaves

Xerophytic leaves (Figure 3.4.2.9) have thick cuticles to limit water loss, especially on the upper epidermis (Figure 3.4.2.10). Both the upper and lower epidermis consists of several layers (multiple epidermis). Sometimes the additional layers are called the **hypodermis** ("hypo" meaning under; "dermis" meaning skin). Depressions in the lower epidermis creates a pockets that are lined with trichomes, and the stomata are located at the base of these pockets (called **stomatal crypts;** figure 3.4.2.10). The trichomes help capture evaporating moisture and maintain a relatively humid environment around the stomata. These stomatal crypts are located only on the underside of the leaves, where they experience less sun exposure and therefore less water loss. The upper epidermis is free from stomata.

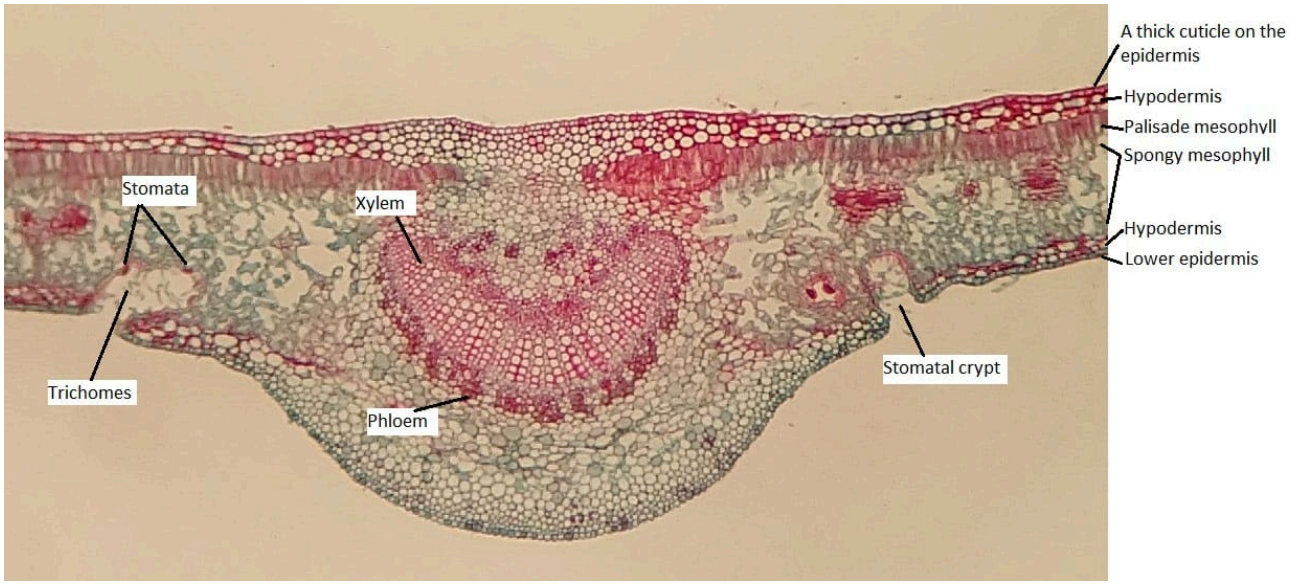


Figure 3.4.2.9: Tissue organization through the xerophytic leaf of oleander (*Nerium*). On the right side of the image, the layers of tissue are labeled from the upper surface of the leaf to the lower. The upper epidermis of the leaf is sealed by a thick, waxy cuticle. There are no stomata present in the upper epidermis. Just below the epidermis are several layers of tightly packed cells called the hypodermis. Beneath the hypodermis, the palisade and spongy mesophylls are arranged as in a mesophytic leaf. There are more layers of hypodermis between the spongy mesophyll and the lower epidermis. There are invaginations in the lower epidermis called stomatal crypts. Stomata are located within these, surrounded by trichomes. Image by Maria Morrow (CC-BY-NC).

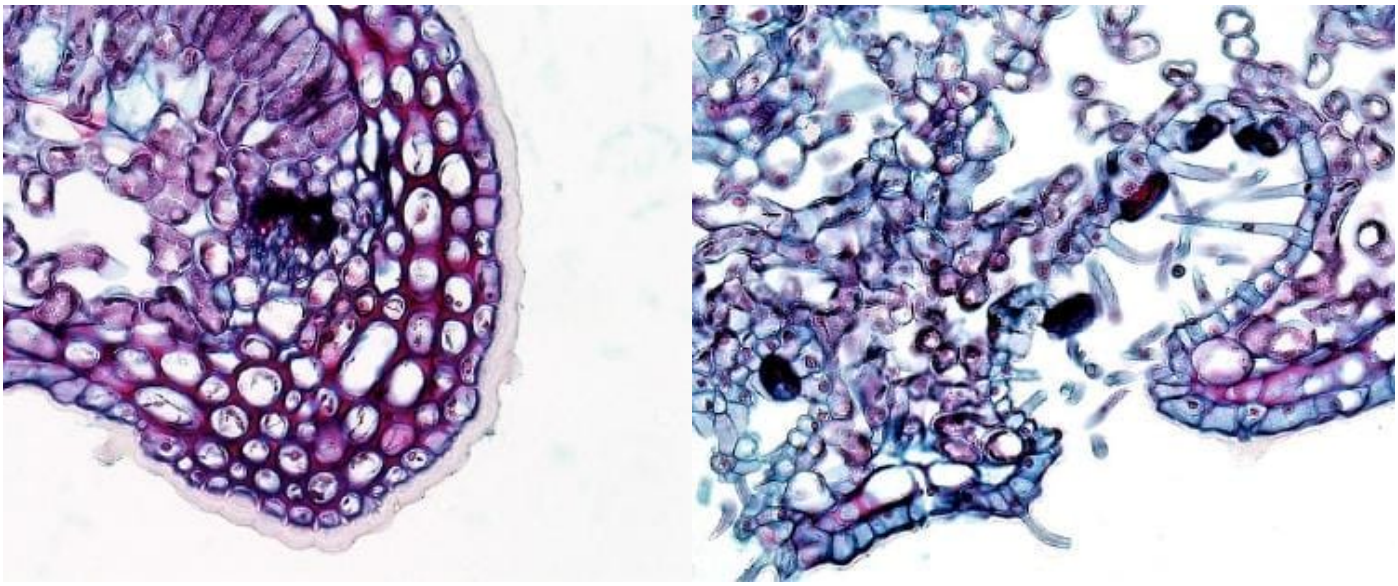


Figure 3.4.2.10: The margin of the xerophytic leaf of oleander (*Nerium*). Left: There is a thick cuticle on the upper epidermis (it looks like a transparent skin). The cuticle gets thinner as it transitions to the lower epidermis. Right: A stomatal crypt on the lower epidermis is filled with trichomes. Several closed stomata are visible; they are bordered by dark guard cells. Images from Berkshire Community College Bioscience Image Library (public domain).

Pine Leaves

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

The epidermis of the leaf seems to be more than one cell layer thick (figure 3.4.2.11). These subsequent layers of epidermis-like tissue under the single, outer layer of true epidermis are called the **hypodermis** , which offers a thicker barrier and helps prevent water loss. The epidermis itself is coated on the outside by a thick layer of wax called the **cuticle**. Because waxes are hydrophobic, this also helps prevent water loss through the epidermis. The stomata are typically sunken, occurring within the hypodermis instead of the epidermis. **Sunken stomata** create a pocket of air that is protected from the airflow across the leaf and can aid in maintaining a higher moisture content (figure 3.4.2.12).

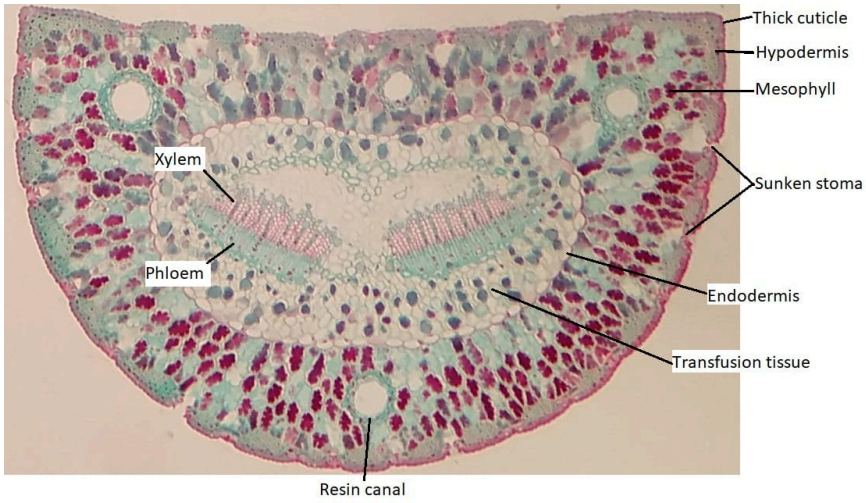


Figure 3.4.2.11: Cross section of a pine leaf (needle). Much like the *Nerium* leaf, this leaf is coated in a thick cuticle and there is a hypodermis below the epidermis (because this leaf is so round, there is not really a distinct 'upper' and 'lower'). There are no stomatal crypts, but the stomata are sunken, located in the hypodermis. The leaf has a low surface area to volume ratio (more volume, less surface area), which decreases water loss. In the center of the leaf, There is a large region surrounded by an suberized endodermis (much look in a root). There are two vascular bundles within this region, surrounded by transfusion tissue. Image and caption (modifed) by Maria Morrow (CC-BY-NC).

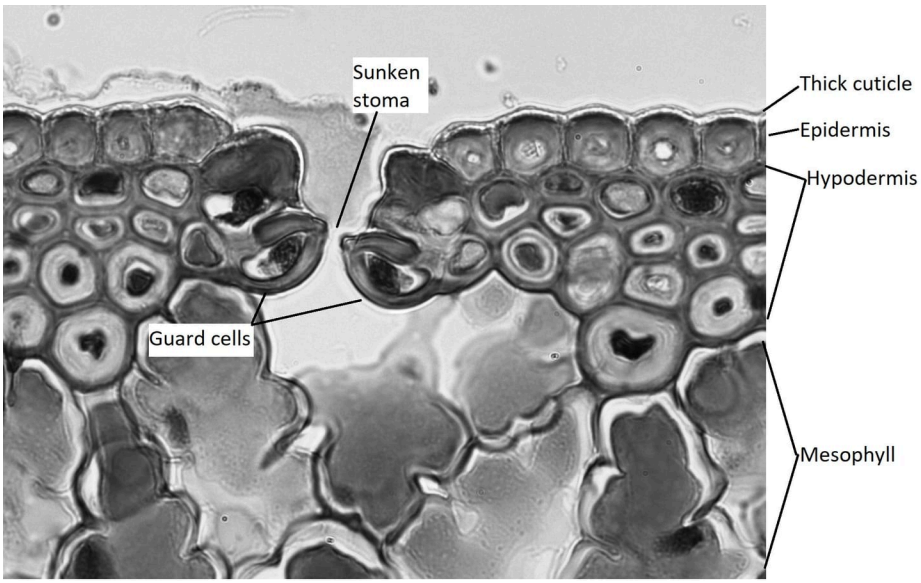


Figure 3.4.2.12: A closer view of a sunken stoma and the outermost layers of the pine needle. The thick cuticle is visible as a transparent layer coating the small epidermal cells. Each of the epidermal cells has a thick cell wall. The hypodermis is composed of 3-4 layers of small, tightly packed cells that also have thick walls (sclerenchyma). The guard cells of the stoma are located about three layers below the epidermis, and the cuticle can be seen extending down over them. The stoma is open in this image. Below the stoma, there is a gap of air space, then highly invaginated mesophyll cells. Image by Maria Morrow (CC-BY-NC).

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

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

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

Corn Leaves

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

Corn is not necessarily a xerophyte, but it is adapted to deal with high temperatures. One of these adaptations, C_4 type photosynthesis is discussed in Photorespiration and Photosynthetic Pathways and results in a cell arrangement called **Kranz anatomy**. The vascular bundles are surrounded by obviously inflated parenchyma cells that form a structure called a **bundle sheath**, and these are packed with chloroplasts (Figure 3.4.2.13). (Bundle sheaths surround vascular bundles of other types of leaves as well, but the bundle sheath cells are much smaller). Mesophyll cells encircle the bundle sheath cells. In C_4 photosynthesis, carbon dioxide is first gathered by the mesophyll cells and temporarily stored as a four-carbon sugar. This four-carbon sugar is transferred to the bundle sheath cells, where it is broken down to release carbon dioxide. It is in the bundle sheath cells where a process called the Calvin cycle, and glucose is ultimately produced. C_4 photosynthesis concentrates carbon dioxide inside the bundle sheath cells, reducing the need to frequently open stomata for gas exchange. This helps conserve water.

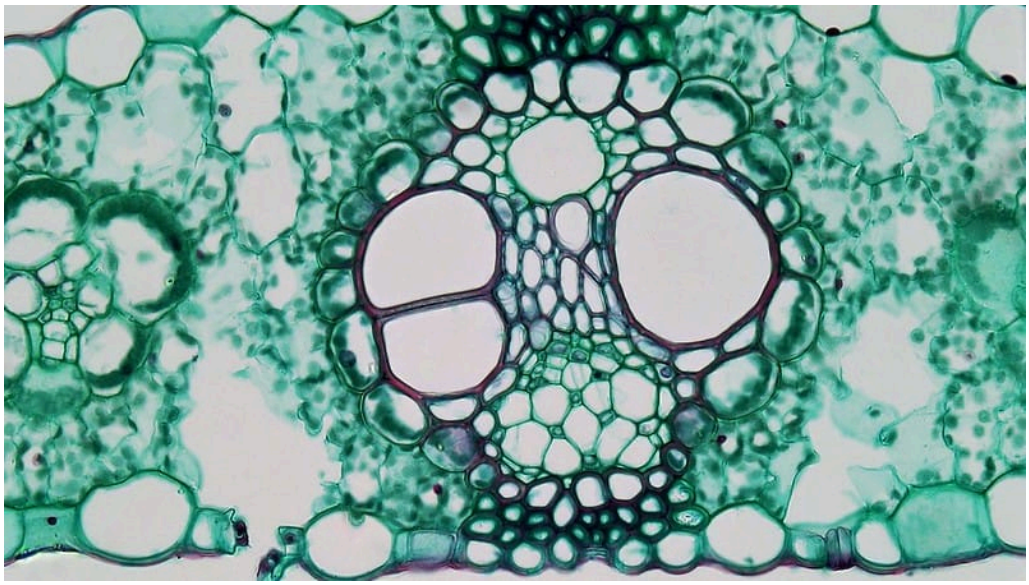


Figure 3.4.2.13: A vascular bundle of a corn (*Zea mays*) leaf. There are two vascular bundles in this image. The one on the left is difficult to distinguish and most of what you see are the enlarged bundle sheath cells. The larger vascular bundle on the right has less prominent bundle sheath cells, though they still form a distinct border between the vascular tissue and the mesophyll. The xylem tissue is located closer to the upper epidermis. You can locate it by searching for the large, open cells (vessel elements) with red-stained secondary walls. Below the xylem is the phloem tissue, which encompasses a smaller area. The larger cells in the phloem are sieve-tube elements, and the smaller ones are companion cells. Images from Berkshire Community College Bioscience Image Library (public domain).

When moisture is plentiful, the corn leaves are fully expanded and able to maximize photosynthesis. When moisture is limited, the leaves roll inward, limiting both moisture loss and photosynthetic capacity. This is accomplished by the presence of **bulliform cells** in the upper epidermis (Figure 3.4.2.14). These clusters of enlarged cells are swollen with water when there is abundant water available. As the water content in the plant decreases, these cells shrivel, causing the upper epidermis to curl or fold inward at these points. This adaptation to sun exposure can be found in many other grasses, as well (corn is a member of the Poaceae, the grass family).

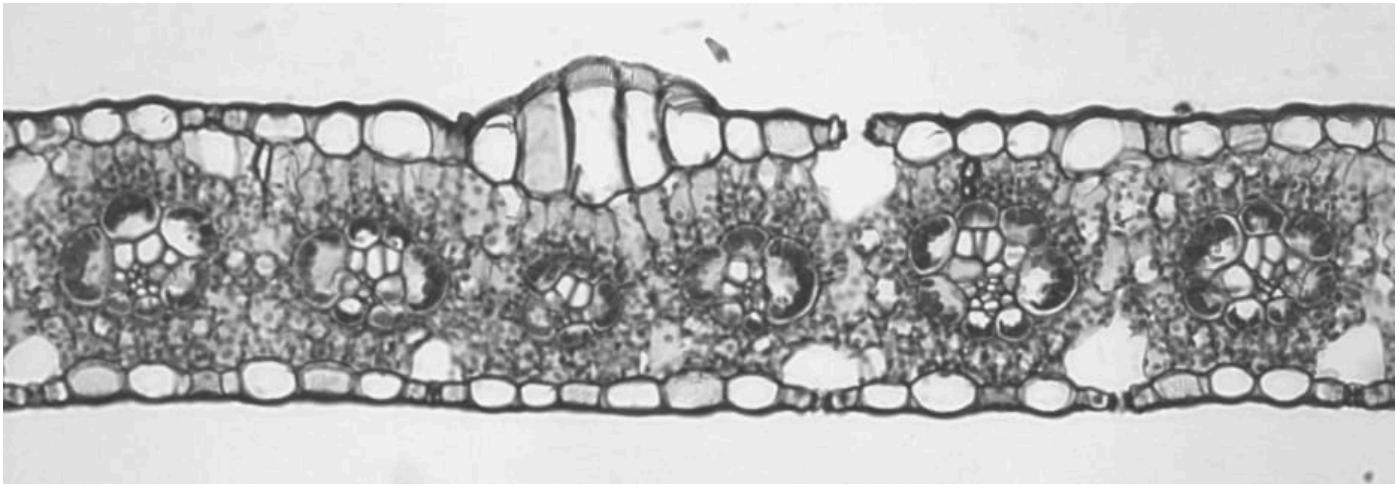


Figure 3.4.2.14: Cross section of *Zea mays* (corn). The bulliform cells of are the group of tall cells along the upper epidermis, just to the left of the opening (stoma).

Sun and Shade Leaves

The light intensity experienced by a developing leaf influences its structure. Leaves that develop when consistently exposed to direct sunlight (sun leaves) thus differ from leaves exposed to low light intensities (shade leaves) in several ways (Figure 3.4.2.15). Relative to shade leaves, sun leaves are smaller and thicker. This reduces surface area relative to volume, conserving water, which would otherwise be easily lost under bright sunlight and resultantly warmer temperatures. In contrast, the broad, thin shape

of shade leaves helps capture sufficient light when light intensity is low. The thicker cuticle of sun leaves also limits water loss. They have more palisade parenchyma and more vascular tissue. Sun leaves can maintain a high photosynthetic rate at high light intensities, but shade leaves cannot.

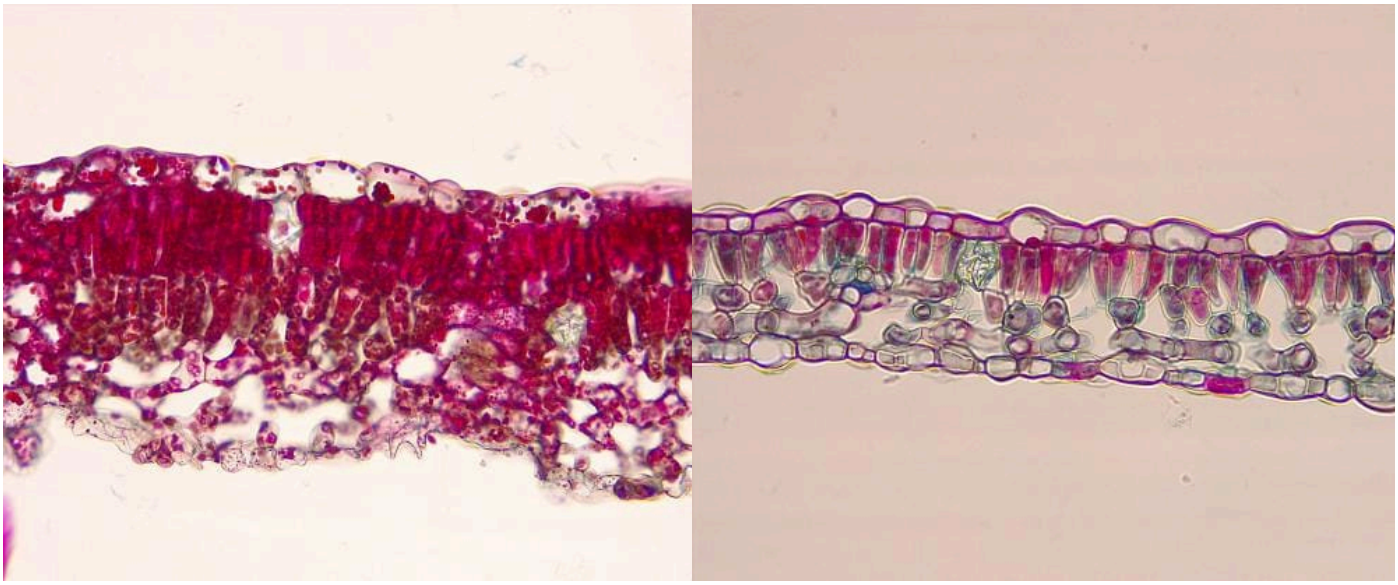


Figure 3.4.2.15: Cross sections of a sun leaf (left) and shade leaf (right). The palisade parenchyma of the sun leaf consists of several layers, but there is only a single layer in the shade leaf. The chloroplasts (red dots) are also packed more densely in both the palisade and spongy mesophyll cells of the sun leaf compared to the shade leaf. The sun leaf is overall thicker. Images by Melissa Ha (CC-BY).

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3.4.3: Leaf Modifications

Learning Objective

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

The structure and function of a leaf can be modified over the course of evolution as a plant adapts to a particular environment (Figure 3.4.3.1). When function of the leaf blade is no longer primarily photosynthesis, some other plant part is usually modified to take its place. **Storage leaves** are thick leaves underground that store starch (as with a bulb; see Stem Modifications). **Succulent leaves** are also thickened leaves, but they are found above ground, still conduct photosynthesis, and function primarily in water storage (Figure 3.4.3.2).

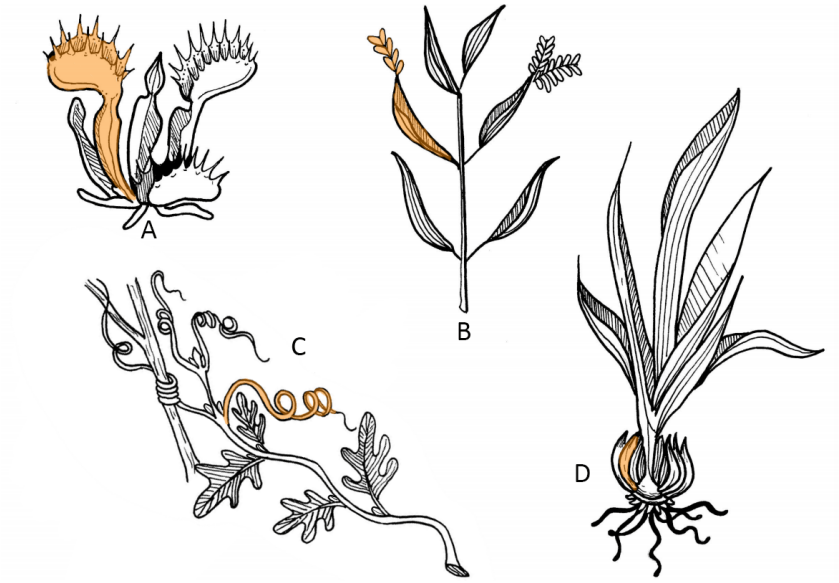


Figure 3.4.3.1: A diagram of leaf modifications. In each plant (A-D), one leaf has been shaded with orange. In A, the blade has been modified for a trap, the petiole is flattened into a phyllode. In B, the blade is a compound leaf and the petiole is flattened into a phyllode. In C, some of the leaves are thin, coiling tendrils (emerging below axillary buds). In D, the basal leaves are thick and fleshy with a short stem (a bulb). Diagram by Nikki Harris (CC-BY) with labels and color added by Maria Morrow.



Figure 3.4.3.2: Succulent leaves are thickened for water storage. Left photo by Simon Burchell (CC-BY-SA), and right image by Melissa Ha (CC-BY).

Spines are sharp projections derived from leaves that function in plant defense. Almost all cacti (in the plant family Cactaceae) have spines (Figure 3.4.3.3). Other examples include barberry and some *Acacia* species, in which large spines house mutualist ants. Spines can also be formed from stipules (stipular spines) or bud scales. Recall from Stem Modifications that thorns and prickles have the same function, but they are derived from whole stems or the outer tissue layers of stems, respectively.



Figure 3.4.3.3: Cactus spines are not stems, but modified leaves. These spines have a thick cuticle and stomata can be seen as darker green areas within the pale white cuticle. Photo by André Karwath (CC-BY-SA).

Tendrils are another structure that can originate from multiple structures, including stems, leaves, or leaflets. These are narrow, coiling structures that climbing plants attach to nearby structures for support (Figure 3.4.3.4).



Figure 3.4.3.4: Left: The tips of the leaves of glory lily are modified as tendrils. Right: some of the leaflets in the compound leaves of pea plants are modified as tendrils. Left image by Krishna satya 333 (CC BY-SA), and right image by Melissa Ha (CC-BY).

A **phyllode** resembles cladodes and phylloclades but refers to a flattened petiole that resembles a leaf blade (rather than a narrow stalk). The Australian acacias (*Acacia*) have phyllodes (Figure 3.4.3.5).



Figure 3.4.3.5: Acacia koa with a flat phyllode between the branch and the pinnately compound leaf blades. Image and caption from Wmpearl (public domain).

Showy bracts are brightly colored leaves function in attracting pollinators. From a distance, showy bracts often appear like the petals of a flower. However, the actual flowers are typically small and in a cluster surrounded by the bracts (Figure 3.4.3.6).



Figure 3.4.3.6: Showy bracts are brightly colored leaves modified to attract pollinators in *Bougainvillea* (left) and dogwood (right). Although bracts superficially look like petals, the actual petals are part of tiny flowers at the central point where the bracts meet. Images by Melissa Ha (CC-BY).

Plantlets are mini plants that grow on the main plant and then fall off and grow into new plants. In *Kalanchoë* , mitosis at meristems along the leaf margins produce tiny plantlets that fall off and grow independently into mature plants. This is a form of asexual reproduction (Figure 3.4.3.7).



Figure 3.4.3.7: Plantlets on the leaf margins of *Kalanchoë.* Plantlets that fall and land on the soil can grow into full-sized plants. Note that this species is also an example of succulent leaves. Image by Melissa Ha (CC-BY).

Carnivorous plants grow in bogs where the soil is low in nitrogen, and their leaves are adapted to help them to survive this nutrient-poor environment. In these plants, leaves are modified as **traps** to capture insects. While they still conduct photosynthesis to capture energy and synthesize sugars (and are thus autotrophs), they rely on insect-capturing leaves as a supplementary source of much-needed nitrogen, similar to fertilizer. Several examples of carnivorous plants are the cobra lily (*Darlingtonia*), various pitcher plants (*Nepenthes* [Figure 3.4.3.8], *Cephalotus*, *Sarracenia*), the butterwort (*Utricularia*), the sundew (*Drosera*; Figure 3.4.3.9), and the best known, the Venus flytrap (*Dionaea;* Figure 3.4.3.h).

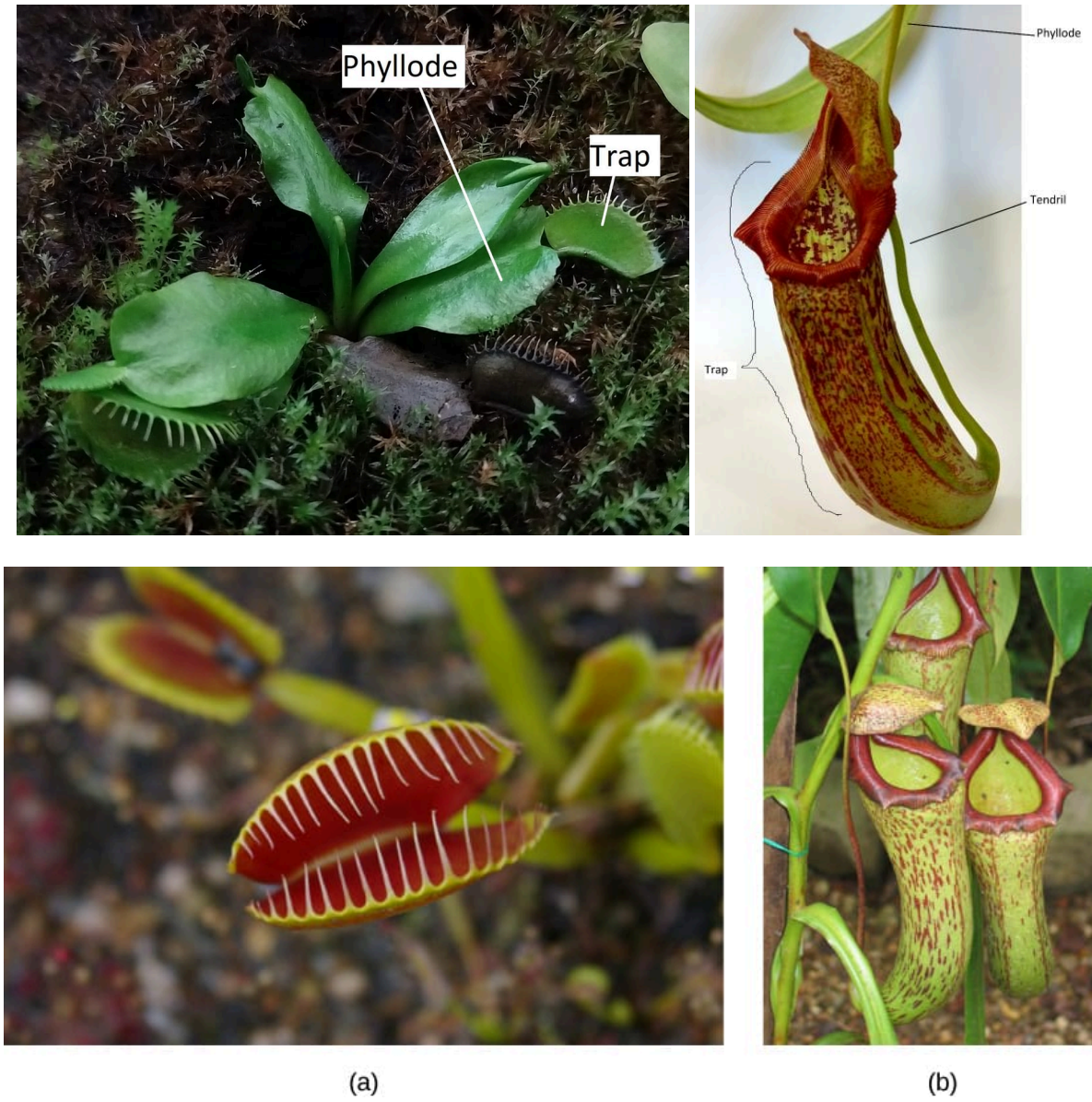


Figure 3.4.3.8: The (a) Venus flytrap has modified leaves that can capture insects. When an unlucky insect touches the trigger hairs inside the leaf, the trap suddenly closes. The opening of the (b) pitcher plant is lined with a slippery wax. Insects crawling on the lip slip and fall into a pool of water in the bottom of the pitcher, where they are digested by bacteria. The plant then absorbs the smaller molecules. Top two photos by Maria Morrow (CC-BY). Bottom photos are modification of work by Peter Shanks; credit b: modification of work by Tim Mansfield.

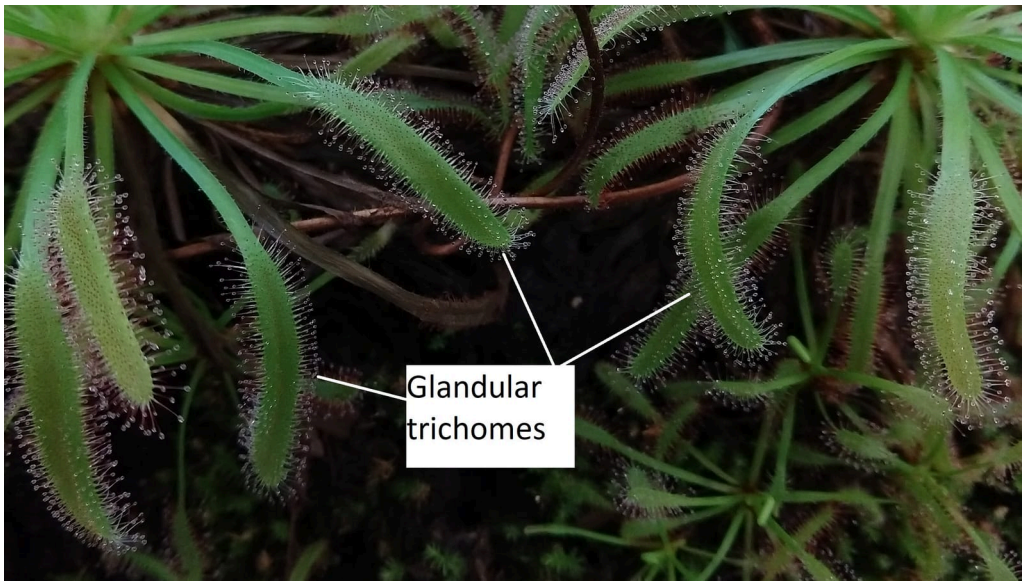


Figure 3.4.3.9: The ends of sundew (*Drosera* sp.) leaves are covered with glandular trichomes. Each trichome has a blob of sticky fluid at the tip. Insects are attracted to the fluid, becoming trapped in it, as the plant slowly digests their bodies for the mineral nutrients that are lacking in their environment. Image by Maria Morrow (CC-BY).

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3.4.4: Chapter Summary

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

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

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

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

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

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4: PLANT PHYSIOLOGY AND REGULATION

Plant physiology focuses on the chemistry and physics of how plants function. Plants capture light energy and produce sugars through photosynthesis and break down these sugars through aerobic cellular respiration. They respond to a variety of environmental conditions through growth changes, life events like germination or flowering, and even, in special cases, through movement. Plants rely on soils for mineral nutrients and water, and **biogeochemical cycles** replenish soils with these nutrients. Once water and minerals are absorbed, they must be transported through the xylem, and this movement is driven by the loss of water vapor from leaves (**transpiration**) and the cohesive and adhesive properties of water. Likewise, sugar-rich **assimilate** must be moved, or **translocated**, through the phloem. Five main types of **hormones** in plants are responsible for relaying messages throughout the plant body. Throughout this unit are examples of how plants **regulate** their internal conditions whether it the concentration of carbon dioxide in the leaves; the positioning of stems, roots, and leaves; or the movement and retention of water (Figure 4.1).



Figure 4.1: Plants balance water loss with their need for carbon dioxide through stomatal opening (top) and closure (bottom). Image by KuriPop (CC-BY-SA).

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4.1: Photosynthesis and Respiration

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Thumbnail image: A normal Arabidopsis plant (left) and a mutant that does not respond properly to the hormone auxin. Image by William M. Gray (CC-BY).

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4.1: PHOTOSYNTHESIS AND RESPIRATION

Photosynthesis and aerobic cellular respiration are key metabolic pathways. Photosynthesis is essential to all life on earth; both plants and animals depend on it (Figure 4.1.1). It is the only biological process that can capture energy that originates in outer space (sunlight) and convert it into chemical compounds (carbohydrates) that most organisms use to power their metabolism through aerobic cellular respiration or other pathways. In brief, the energy of sunlight is captured and used to energize electrons, which are then stored in the covalent bonds of sugar molecules. How long lasting and stable are those covalent bonds? The energy extracted today by the burning of coal and petroleum products represents sunlight energy captured and stored by photosynthesis almost 200 million years ago.



Figure 4.1.1: The leaves of this oak tree capture light energy from the sun through photosynthesis. (The dark spheres are oak apple galls, induced by the California gall wasp.) Image by Melissa Ha (CC-BY).

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4.1.1: Energy and ATP

4.1.2: Aerobic Cellular Respiration

4.1.3: Photosynthesis Overview and Equation

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4.1.5: The Light-dependent Reactions

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4.1.1: Energy and ATP

Learning Objectives

- Describe the different types of energy.
- Describe the structure and function of ATP.

Understanding photosynthesis and aerobic cellular respiration relies on the fundamentals of energy. **Energy** is defined as the ability to do work, and there are several types of energy (Figure 4.1.1.1). **Kinetic energy** is the energy of motion. Examples include a ball rolling down a hill, heat energy, and light energy. **Heat energy** is technically energy that is transferred between systems without doing work. The higher the temperature, the faster molecules in matter move. **Potential energy** is the energy that matter possesses but is not currently being used. For example, a ball sitting a the top of the hill that has not yet rolled down the hill possesses potential energy. **Chemical energy** is an example of potential energy that is stored in molecules. When molecules that are higher energy and less stable react to form products that are lower energy and more stable, this stored energy is released.



Figure 4.1.1.1: Water stored at the top of a dam has potential energy (left). Water rushing down an incline has kinetic energy (right). Image by OpenStax (CC-BY). Access for free at openstax.org.

Adenosine triphosphate (**ATP**) is considered the energy currency of the cell because it provides usable energy. Structurally, ATP resembles a modified nucleotide (the building blocks of DNA and RNA). Specifically, it consists of adenine, ribose, and three phosphate groups (Figure 4.1.1.2). The bonds between the phosphate groups are unstable. When these bonds are broken, more stable bonds are formed in their place, releasing energy. **Phosphorylation** refers to adding a phosphate group (PO_4^{3-}) to a molecule. However, it often refers specifically to synthesizing ATP by adding a phosphate group to **adenosine diphosphate** (**ADP**).

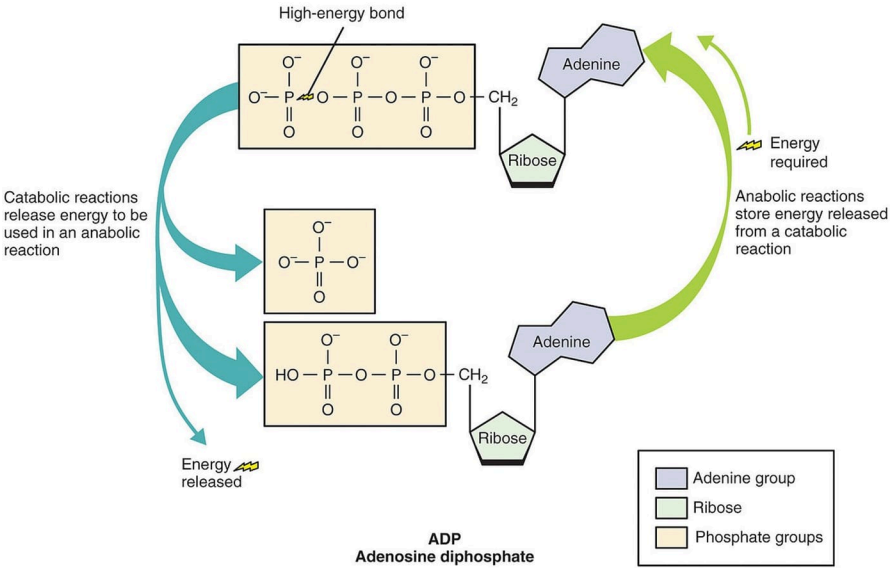


Figure 4.1.1.2: ATP consists of adenine, ribose, and three phosphate groups. ADP is similar but only has two phosphate groups. With energy input, adenosine triphoshate (ATP) can be synthesized from adenosine diphosphate (ADP) and a phosphate group. This occurs during anabolic reactions, which store energy. ATP can then be broken down to provide usable energy to the cell. This occurs during catabolic reactions, which release energy. Image by OpenStax (CC-BY). Access for free at openstax.org.

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4.1.2: Aerobic Cellular Respiration

Learning Objectives

- Identify the reactants and products of aerobic cellular respiration.
- Explain each step of aerobic cellular respiration and where in the cell it occurs.

Not only do plants produce sugars through photosynthesis, but they also break down these sugars to generate usable energy in the form of ATP through **aerobic cellular respiration**. Glucose begins its breakdown outside of the mitochondria in a metabolic pathway called glycolysis. However, the majority of the reactions that produce ATP happen within the mitochondria (in eukaryotic cells; Figure 4.1.2.1). During these reactions, electron carriers are created and oxygen pulls the electrons through an electron transport chain to create ATP, which powers cellular activity. The oxygen you breathe in combines with electrons to form water, which you breathe out. The carbon dioxide you breathe out comes from the carbon in glucose, which your body metabolized.

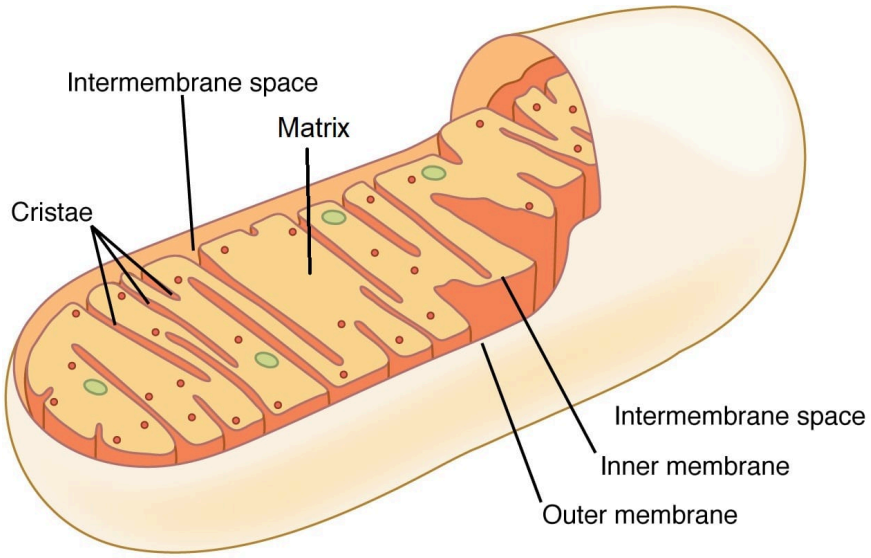


Figure 4.1.2.1: The mitochondria are the energy-conversion factories of the cell. A mitochondrion is composed of two separate lipid bilayer membranes. The folds of the inner membrane are called cristae, and the space between membranes is the intermembrane space. The matrix is in the center. Along the inner membrane are various molecules that work together to produce ATP, the cell's major energy currency. Image (relabeled) and caption (modified) by OpenStax (CC-BY). Access for free at openstax.org.

Here is a net reaction for cellular respiration:

$$C_6H_{12}O_6 + 6\,O_2 \rightarrow 6\,CO_2 + 6\,H_2O + ATP$$

glucose + oxygen $\rightarrow$ carbon dioxide + water + energy

Step 1: Glycolysis

When glucose is transported into the cytoplasm of cells, it is broken down into two molecules of **pyruvate** (Figure 4.1.2.2). This process is called **glycolysis** (glyco- for glucose and -lysis, meaning to break apart). Glycolysis involves the coordinated action of many different enzymes. As these enzymes start to break the glucose molecule apart, an initial input of energy is required. This initial energy is donated by molecules of ATP.

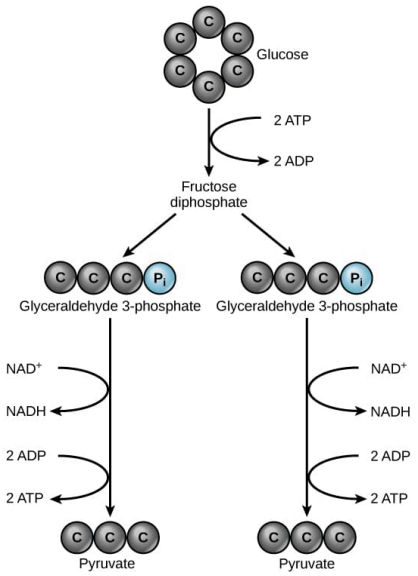


Figure 4.1.2.2: In glycolysis, glucose (represented by a ring of six carbons) is converted to fructose-1,6-bisphosphate (labeled fructose diphosphate). This consumes 2 ATP, releasing 2 ADP. Fructose-1,6-bisphosphate is broken into two glyceraldehyde-3-phosphate molecules. Each is represented by a chain of three carbons attached to a phosphate (P_i). The phosphate is removed from each of the two glyceraldehyde-3-phosphate molecules, producing 2 pyruvates, 2 NADH, and 4 ATP. Overall, glycolysis consumes 2 ATP, but it then generates 4 ATP and 2 NADH. Image by OpenStax (CC-BY). Access for free at openstax.org.

Though two molecules of ATP are used to get glycolysis going, four more molecules of ATP are produced during the reaction, resulting in the net production of two ATP per molecule of glucose. In addition to ATP, two molecules of **nicotinamide adenine dinucleotide** (**NAD^+**) are reduced to form NADH (Figure 4.1.2.3). When NAD^+ is reduced to NADH, two high energy electrons derived from breaking the bonds of glucose are added to it. One of those negatively charged electrons is balanced by the positive charge (+) on NAD^+. The other is balanced by adding a proton (H^+) to the molecule.

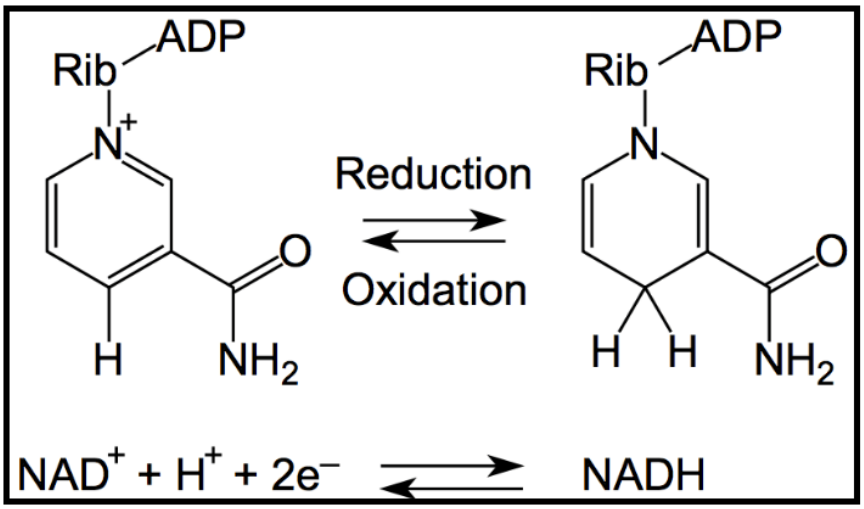


Figure 4.1.2.3: When NAD^+ is reduced to NADH, it gains one proton (H^+) and two electrons (e^-). The reverse reaction (oxidation) can also occur. The chemical structure of NAD^+ is a modified version of two nucleotides attached together. It is represented by ADP (adenosine diphosphate) attached to ribose (rib, a five-carbon sugar), attached to a ring of carbon and nitrogen.

Step 2: Pyruvate oxidation

If oxygen is present, aerobic cellular respiration can continue. The two molecules of pyruvate are transported into the matrix of

the mitochondrion. During transport, each pyruvate is converted into a 2-carbon molecule called acetyl-CoA. The other carbon atom from each pyruvate molecule exits the cell as $\mathrm{CO_2}$. The electrons from this broken bond are captured by another molecule of $\mathrm{NAD^+}$, reducing it to NADH. Because two molecules of pyruvate are produced from each glucose molecule during glycolysis, two acetyl CoA molecules are produced (one from each pyruvate) during pyruvate oxidation (Figure $4.1.2.4$).

Step 3: The Citric Acid (Krebs) Cycle

The two acetyl-CoA molecules enter a cycle which, much like glycolysis, involves the action of many different enzymes to release energy and transport it in energy-carrying molecules, including 2 ATP, 6 NADH, and 2 $\mathrm{FADH_2}$, another electron carrier (Figure $4.1.2.4$). This cycle takes place within the matrix of the mitochondrion.

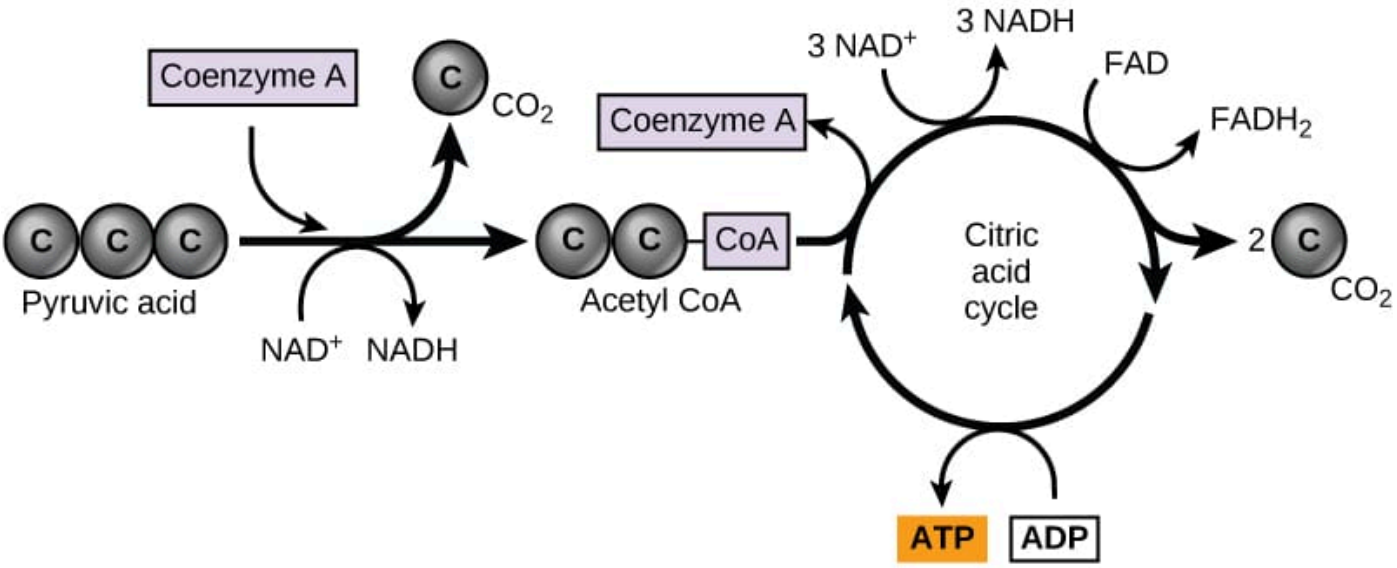


Figure $4.1.2.4$: Combined view of pyruvate oxidation and the citric acid cycle. During pyruvate oxidation, pyurvate/pyruvic acid (three carbons) is converted to acetyl CoA (two carbons). In this process, one carbon dioxide molecule is released and one molecule of $\mathrm{NAD^+}$ is reduced to NADH. In the citric acid cycle, acetyl CoA breaks into two carbon dioxide molecules. This process releases 2 NADH, 1 $\mathrm{FADH_2}$, and 1 ATP per pyruvate, and double that per glucose. Image by OpenStax (CC-BY). Access for free at openstax.org.

Step 4: Oxidative Phosphorylation

This stage of cellular respiration has two steps. During the **electron transport chain**, our electron carriers power a series of proton pumps that move $\mathrm{H^+}$ 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 (Figure $4.1.2.5$).

At the end of the electron transport chain, the low energy electrons need to be picked up to make space for more electrons. An oxygen atom picks up two electrons and, to balance the charge, two $\mathrm{H^+}$ 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.

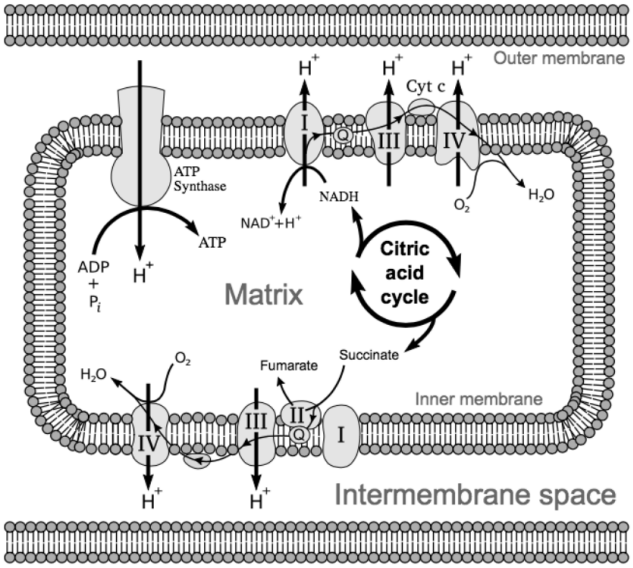


Figure 4.1.2.5: This view of the mitochondrion shows the outer membrane and inner membrane, which borders the matrix. The intermembrane space is between the outer and inner membranes. Pyruvate oxidation (not shown) and the citric acid cycle occur in the matrix. The citric acid cycle (along with glycolysis and pyruvate oxidation) supplies NADH to the electron transport chain of oxidative phosphorylation. ($FADH_2$ also provides electrons to the electron transport chain, but it is not shown here.) Electrons from NADH are passed from complex I to coenzyme Q to complex III to cytochrome c to complex IV to gaseous oxygen, which is reduced to form water. The three complexes, which are embedded in the inner membrane pump protons into the intermembrane space. Protons move down their proton gradient through ATP synthase, generating ATP.

Chemiosmosis

Why are the protein complexes pumping H^+ into the intermembrane space? The intermembrane space is relatively small. As more H^+ are added to this area, the intermembrane space becomes increasingly positively charged, while the matrix becomes increasingly negatively charged. This is similar to how a battery stores energy--by creating an electrochemical gradient. The positive charges repel each other and would “prefer” to be balanced across both sides of the membrane. However, they cannot directly pass through the membrane. Even though they are small, H^+ ions carry a full charge, making them too polar to pass through the nonpolar tails of the phospholipid bilayer that composes the mitochondrial membranes.

An enzyme called **ATP synthase** allows the H^+ to move back into the matrix. This enzyme is structured much like a waterwheel or turbine -- the flow of protons through the enzyme physically rotates it, converting the potential energy stored in the electrochemical gradient into kinetic energy (movement)! This kinetic energy is used to force another phosphate group onto ADP, converting the kinetic energy back into chemical energy, which is stored in the bonds of ATP

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4.1.3: Photosynthesis Overview and Equation

Learning Objectives

- Explain the relevance of photosynthesis to other living things.
- Identify the substrates and products of photosynthesis.
- Describe the main structures involved in photosynthesis.
- Relate the light-dependent and light-independent reactions.

Plants, algae, and certain bacteria (cyanobacteria and green and purple sulfur bacteria) are among the organisms capable of performing photosynthesis (Figure 4.1.3.1). Because they use light to manufacture their own food, they are called **photoautotrophs** (literally, "self-feeders using light"). Other organisms, such as animals, fungi, and most other bacteria, are termed **heterotrophs** ("other feeders"), because they must rely on the sugars produced by photosynthetic organisms for their energy needs. A third very interesting group of bacteria synthesize sugars, not by using sunlight's energy, but by extracting energy from inorganic chemical compounds; hence, they are referred to as **chemoautotrophs**.

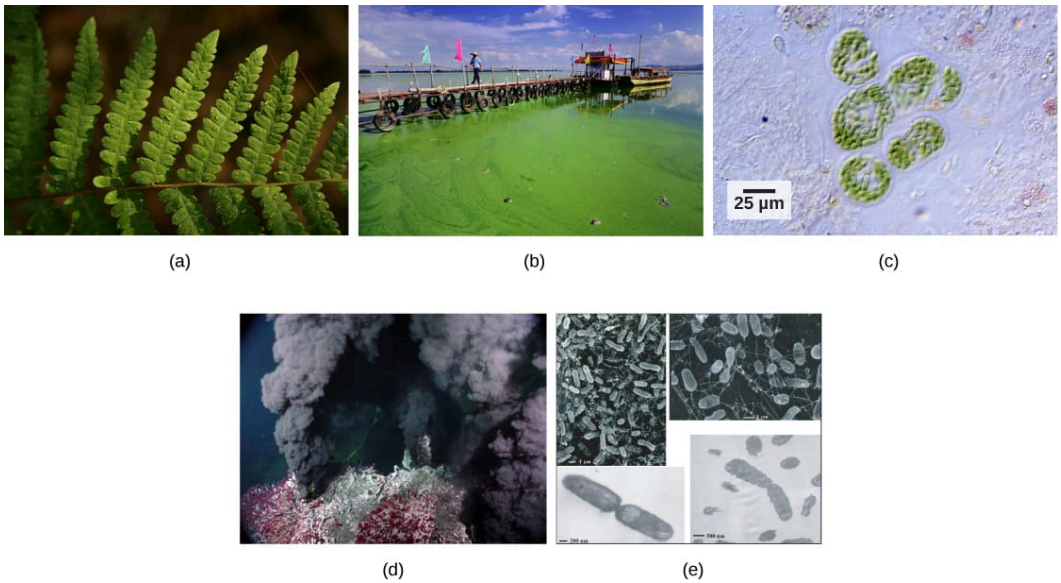


Figure 4.1.3.1: Photoautotrophs including (a) plants, (b) algae, and (c) cyanobacteria synthesize their organic compounds via photosynthesis using sunlight as an energy source. Cyanobacteria and planktonic algae can grow over enormous areas in water, at times completely covering the surface. In a (d) deep sea vent, chemoautotrophs, such as these (e) thermophilic bacteria, capture energy from inorganic compounds to produce organic compounds. The ecosystem surrounding the vents has a diverse array of animals, such as tubeworms, crustaceans, and octopi that derive energy from the bacteria. (credit a: modification of work by Steve Hillebrand, U.S. Fish and Wildlife Service; credit b: modification of work by "eutrophication&hypoxia"/Flickr; credit c: modification of work by NASA; credit d: University of Washington, NOAA; credit e: modification of work by Mark Amend, West Coast and Polar Regions Undersea Research Center, UAF, NOAA)

The importance of photosynthesis is not just that it can capture sunlight's energy. Photosynthesis is vital because it evolved as a way to store the energy in solar radiation (the "photo-" part) as high-energy electrons in the carbon-carbon bonds of carbohydrate molecules (the "-synthesis" part). Those carbohydrates are the energy source that heterotrophs use to power the synthesis of ATP via celluar respiration. Therefore, photosynthesis powers 99 percent of Earth's ecosystems.

Photosynthesis Equation

Photosynthesis is a multi-step process that requires sunlight, carbon dioxide (which is low in energy), and water as substrates (Figure 4.1.3.2). After the process is complete, it releases oxygen and produces glyceraldehyde-3-phosphate (GA3P), simple carbohydrate molecules (which are high in energy) that can subsequently be converted into glucose, sucrose, or any of dozens of other sugar molecules. These sugar molecules contain energy and the energized carbon that all living things need to survive.

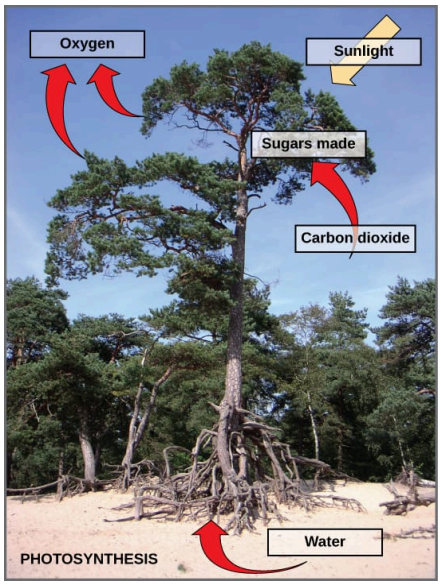


Figure 4.1.3.2: Photosynthesis uses solar energy, carbon dioxide, and water to produce energy-storing carbohydrates. Oxygen is generated as a waste product of photosynthesis.

The following is the chemical equation for photosynthesis (Figure 4.1.3.3). Although the equation looks simple, the many steps that take place during photosynthesis are actually quite complex.

Photosynthesis Equation

Carbon dioxide	+	Water	SUNLIGHT →	Sugar	+	Oxygen
$6CO_2$		$6H_2O$		$C_6H_{12}O_6$		$6O_2$

Figure 4.1.3.3: The basic equation for photosynthesis is deceptively simple. In reality, the process takes place in many steps involving intermediate reactants and products. Glucose, the primary energy source in cells, is made from two three-carbon GA3Ps. Technically, water is both reactant and product in photosynthesis, which is not reflected in the balanced chemical equation shown. Sunlight is used as an energy source.

Structures of Photosynthesis

Before learning the details of how photoautotrophs turn sunlight into food, it is important to review the structures involved. Recall from the Leaves chapter that leaves consist of several layers of cells, and the process of photosynthesis occurs in the **mesophyll** (middle layer). Note that other parts of the plant, such as the stems, are photosynthetic as well. The gas exchange of carbon dioxide and oxygen occurs through the **stomata** (singular: stoma), which also participate in water balance. The stomata are typically located on the underside of the leaf, which helps to minimize water loss. Each stoma is flanked by **guard cells** that regulate their opening and closing.

In all autotrophic eukaryotes, photosynthesis takes place inside the **chloroplast**. For plants, chloroplast-containing cells exist in the mesophyll. Chloroplasts have a double membrane envelope (composed of an outer membrane and an inner membrane). Within the chloroplast are stacked, disc-shaped structures called **thylakoids**. Embedded in the thylakoid membrane is **chlorophyll**, a **pigment** (molecule that absorbs light) responsible for the initial interaction between light and plant material, and numerous proteins that make up the **electron transport chain**. The thylakoid membrane encloses an internal space called the **thylakoid lumen**. As shown in Figure 4.1.3.4, a stack of thylakoids is called a **granum** (plural: grana), and the liquid-filled space surrounding the granum is called **stroma** or “bed” (not to be confused with stoma or “mouth,” an opening on the leaf epidermis).

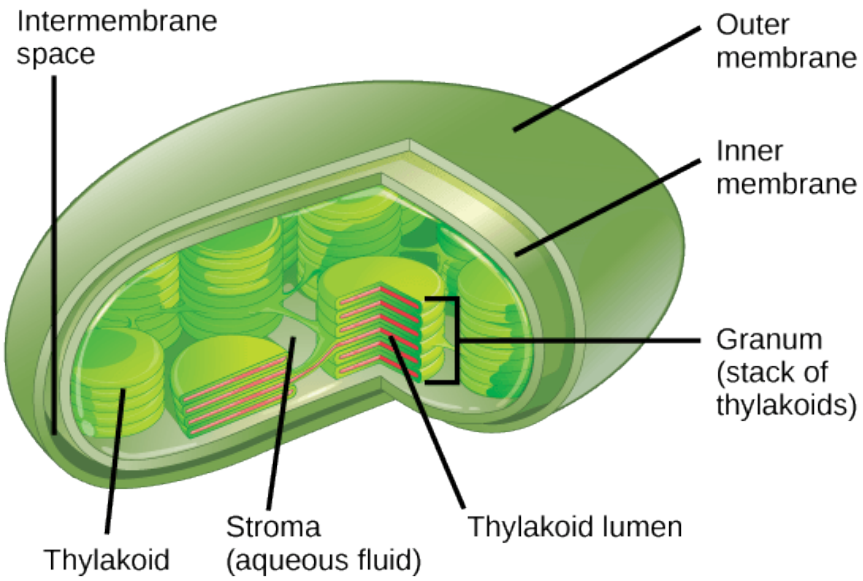


Figure 4.1.3.4: Photosynthesis takes place in chloroplasts, which have an outer membrane and an inner membrane. The space between the outer and inner membranes is called the intermembrane space. Stacks of thylakoids called grana form a third membrane layer. The thylakoids form stacks called grana. The liquid inside the inner membrane is called the stroma, and the space inside the thylakoid is called the thylakoid lumen.

Steps of Photosynthesis

Photosynthesis takes place in two sequential stages: the **light-dependent reactions** and the **light independent-reactions** (Calvin cycle). In the light-dependent reactions, energy from sunlight is absorbed by chlorophyll and that energy is converted into stored chemical energy. Light-dependent reactions require water and produce oxygen and energy in the form of ATP. In the light-independent reactions, the chemical energy harvested during the light-dependent reactions drive the assembly of sugar molecules from carbon dioxide. Therefore, although the light-independent reactions do not use light as a reactant, they require the products of the light-dependent reactions to function. In addition, several enzymes of the light-independent reactions are activated by light.

The light-dependent reactions utilize ATP and **nicotinamide adenine dinucleotide phosphate** (**NADPH**) to temporarily store the energy. Because NADPH carries two high-energy electrons, it is often referred to as an **electron carrier**. It can be thought of as "full" because it is rich in energy in its reduced state. When a molecule is reduced, electrons have been added to it. Electrons have a negative charge, so this is termed "**reduction**". NAPDH move energy from light-dependent reactions to light-independent reactions. After the energy is released, the "empty" (**oxidized**) version, $NADP^+$, returns to the light-dependent reactions to obtain more high-energy electrons. Likewise, the ATP produced during the light-dependent reactions fuels the light-independent reactions. It then returns in a lower-energy form (ADP) to the light-dependent reactions to become phosphorylated again. Figure 4.1.3.5 illustrates the components inside the chloroplast where the light-dependent and light-independent reactions take place.

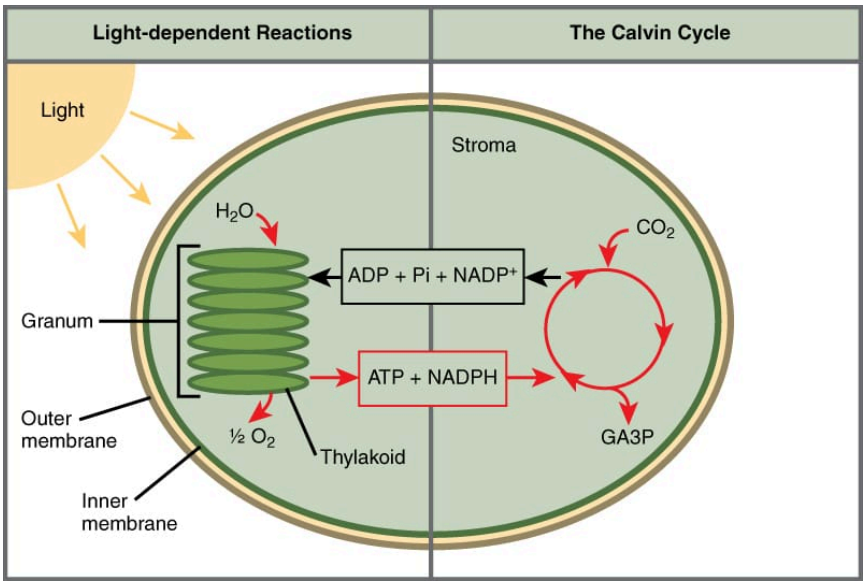


Figure 4.1.3.5: Photosynthesis takes place in two stages: light-dependent reactions and the light-independent reactions (Calvin cycle or Calvin-Benson cycle). Light-dependent reactions, which take place in the thylakoid membrane, use light energy to make ATP and NADPH. In the process, water is used and oxygen is produced. Energy from ATP and NADPH are used to power the Calvin cycle, which produces GA3P from carbon dioxide. ATP is broken down to ADP and Pi, and NADPH is oxidized to $NADP^+$. The cycle is completed when the light reactions convert these molecules back into ATP and NADPH.

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4.1.4: Discovery of Photosynthesis

Learning Objective

Summarize the experimental results that revealed details about the process of photosynthesis.

The history of the studies done on photosynthesis dates back into the 17th century with Jan Baptist van Helmont. He rejected the ancient idea that plants take most of their biomass from the soil. For the proof, he performed an experiment using a willow tree. He started with a willow tree with a mass of 2.27 kg. Over 5 years, it grew to 67.7 kg. However, the mass of the soil only decreased by 57 grams. Van Helmont came to the conclusion that plants must obtain most of their mass from water. He did not know about gases.

Joseph Priestley ran a series of experiments in 1772 (Figure 4.1.4.1). He tested a mouse, a candle, and a sprig of mint under hermetically sealed (no air can go in or out) jar. He first observed that a mouse and a candle behave very similarly when covered, in that they both "spend" the air. However, when a plant is placed with either the candle or mouse, the plant "revives" the air for both.

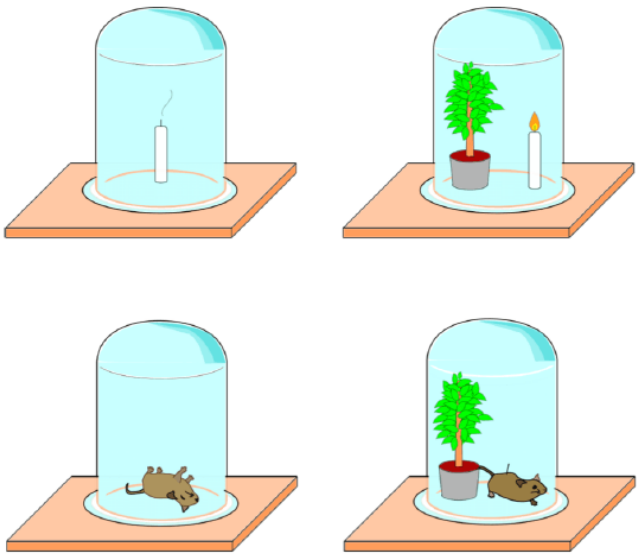


Figure 4.1.4.1: Experiments of J. Priestley (1772) demonstrating that plants provided "air" needed for a candle to burn or a mouse to breath.

Further ideas were brought about in the late 1700's. Jan Ingenhousz and Jean Senebier found that the air is only reviving in the day time and that CO_2 is assembled by plants. Antoin-Laurent Lavoiser found that "revived air" is a separate gas, oxygen.

But what is the oxygen "maker"? There are many pigments in plants, and all accept and reflect some parts of rainbow. To identify the culprit, Thomas Engelmann ran an experiment (Figure 4.1.4.2) using a crystal prism that shine different wavelengths (colors) of visible light on the algae *Spirogyra* algae. He then measured oxygen production with **aerotactic** bacteria, which move towards areas of high oxygen concentration. A high density of bacteria cells accumulated in the blue and red parts of the spectrum, indicating this was where the most oxygen was produced and the most photosynthesis was conducted. This was a huge find. It tells that the key photosynthetic pigment should accept blue and red rays, and thus reflect green rays. The photosynthetic pigment chlorophyll *a* best fits this description.

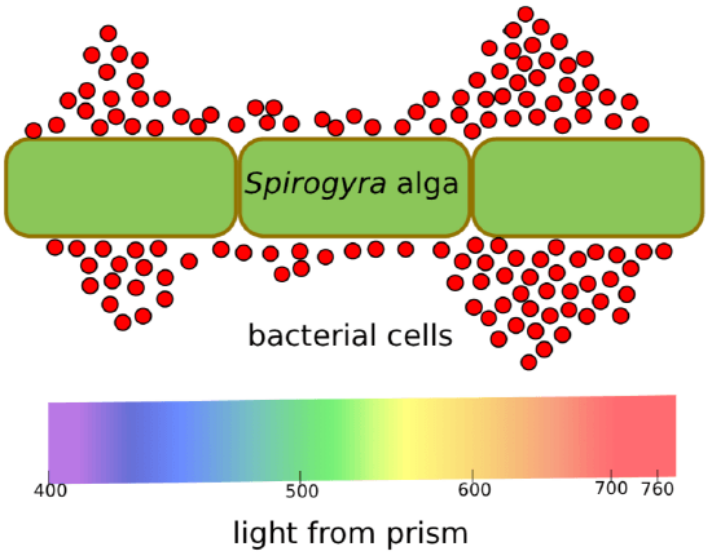


Figure 4.1.4.2: The experiment of Thomas Engelmann (1881) involved separating the wavelengths of visible light using a prism. The rainbow of visible light ranges from approximately 400 nm (violet) to 700 nm (red). The algae *Spirogyra* produced the most oxygen bubbles in blue and red parts of the visible light spectrum, and bacterial cells thus accumulated in these regions.

Another important fact was discovered by Frederick Blackman in 1905. He found that if light intensity is low, the increase of temperature actually has very little effect on the rate of photosynthesis. However, the reverse is not exactly true, and light is able to intensify photosynthesis even when it is cold.

This could not happen if light and temperature are absolutely independent factors. If temperature and light are components of the chain, light was first ("ignition") and temperature was second. This ultimately shows that photosynthesis has two stages (now called the light-dependent and light-independent stages). The light-dependent stage relates the to intensity of the light. The light-independent stage relates more with the temperature as it involves many enzymes.

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4.1.5: The Light-dependent Reactions

Learning Objectives

- Relate wavelength, energy, and the type of electromagnetic radiation (and the color of visible light).
- Explain how plants absorb energy from sunlight.
- Detail the steps of the light-dependent interactions.

How can light be used to make food? When a person turns on a lamp, electrical energy becomes light energy. Like all other forms of kinetic energy, light can travel, change form, and be harnessed to do work. In the case of photosynthesis, light energy is converted into chemical energy, which photoautotrophs use to build carbohydrate molecules (Figure 4.1.5.1). However, photoautotrophs only use a few specific components of sunlight.



Figure 4.1.5.1: Photoautotrophs can capture light energy from the sun, converting it into the chemical energy used to build food molecules. (credit: Gerry Atwell)

What Is Light Energy?

The sun emits an enormous amount of **electromagnetic radiation** (solar energy). Humans can see only a fraction of this energy, which portion is therefore referred to as “visible light”. The manner in which solar energy travels is described as waves. Scientists can determine the amount of energy of a wave by measuring its **wavelength**, the distance between consecutive points of a wave. A single wave is measured from two consecutive points, such as from crest to crest or from trough to trough (Figure 4.1.5.2). The difference between wavelengths relates to the amount of energy carried by them.

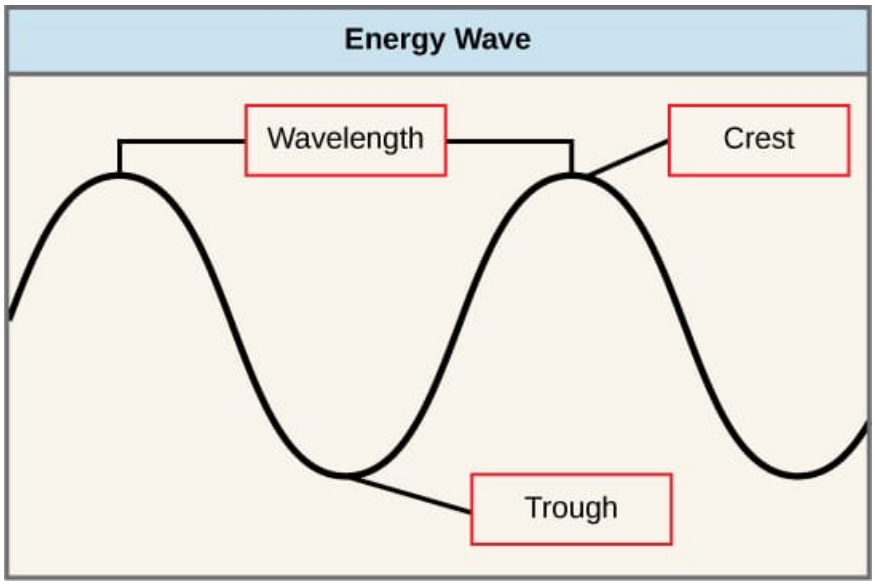


Figure 4.1.5.2: The wavelength of a single wave is the distance between two consecutive points of similar position (two crests or two troughs) along the wave.

Visible light constitutes only one of many types of electromagnetic radiation emitted from the sun and other stars. Scientists differentiate the various types of radiant energy from the sun within the electromagnetic spectrum. The electromagnetic spectrum is the range of all possible frequencies of radiation (Figure 4.1.5.3). Several types of electromagnetic radiation originate from the sun, including X-rays and ultraviolet (UV) rays. The higher-energy waves can penetrate tissues and damage cells and DNA, explaining why both X-rays and UV rays can be harmful to living organisms.

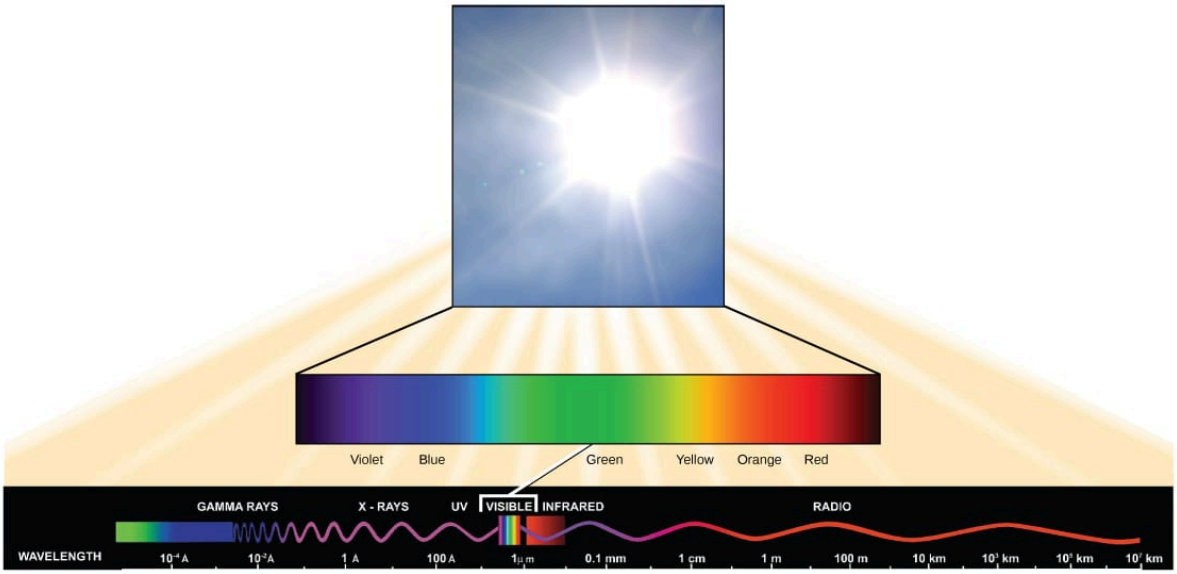


Figure 4.1.5.3: The sun emits energy in the form of electromagnetic radiation. This radiation exists at different wavelengths, each of which has its own characteristic energy. All electromagnetic radiation, including visible light, is characterized by its wavelength. Gamma rays have a very short wavelength, on the order of one thousandth of a nanometer (nm). Radio waves have a very long wavelength, on the order of one kilometer. Visible light ranges from violet (380 nm) to blue, green, yellow, orange, and finally red (750 nm) at the end of the spectrum.

Each type of electromagnetic radiation travels at a particular wavelength. The longer the wavelength (or the more stretched out it appears in the diagram), the less energy is carried. Short, tight waves carry the most energy. This may seem illogical, but think of it in terms of a piece of moving a heavy rope. It takes little effort by a person to move a rope in long, wide waves. To make a rope move in short, tight waves, a person would need to apply significantly more energy.

Absorption of Light

Light energy initiates the process of photosynthesis when pigments absorb the light. Organic pigments, whether in the human retina or the chloroplast thylakoid, have a narrow range of energy levels that they can absorb. Energy levels lower than those represented by red light are insufficient to excite electrons in the retinal pigments. Energy levels higher than those in blue light will physically tear these molecules apart, called bleaching. So retinal pigments can only "see" (absorb) 700 nm to 400 nm light, which is therefore called visible light. For the same reasons, plants pigment molecules absorb only light in the wavelength range of 700 nm to 400 nm; plant physiologists refer to this range for plants as photosynthetically active radiation.

The visible light seen by humans as white light actually exists in a rainbow of colors. Certain objects, such as a prism or a drop of water, disperse white light to reveal the colors to the human eye. The visible light portion of the electromagnetic spectrum shows the rainbow of colors, with violet and blue having shorter wavelengths, and therefore higher energy. At the other end of the spectrum toward red, the wavelengths are longer and have lower energy (Figure 4.1.5.4).

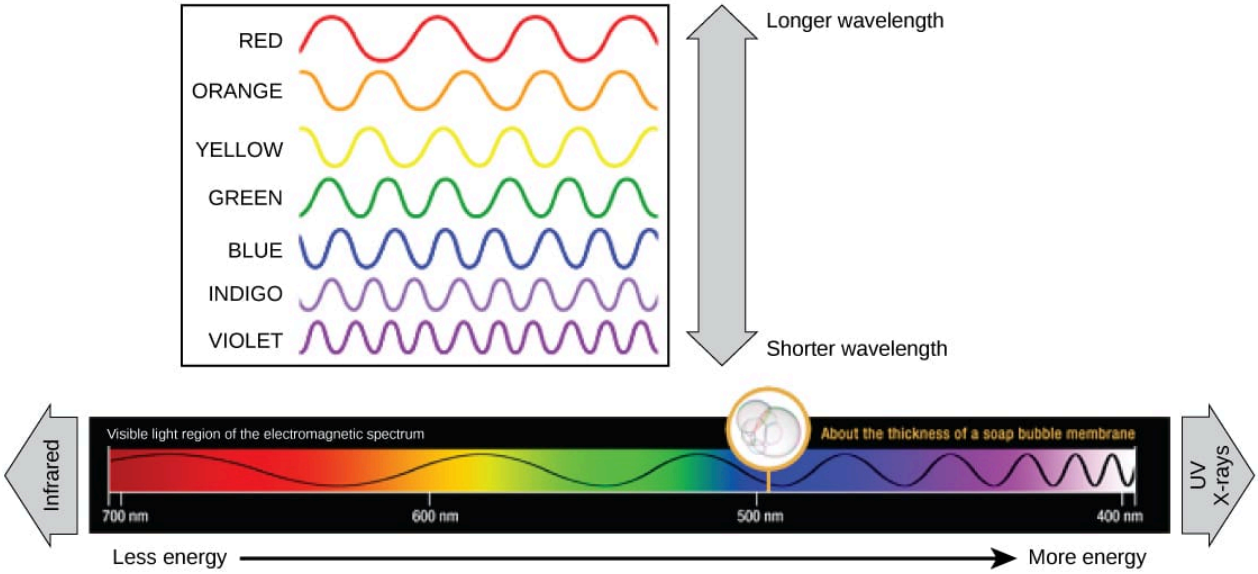


Figure 4.1.5.4: The colors of visible light do not carry the same amount of energy. Violet has the shortest wavelength (approximately 400 nm) and therefore carries the most energy. Next is indigo, blue, green, yellow, orange, and finally red, which has the longest wavelength (approximately 700 nm) and carries the least amount of energy. 500 nanometers is about the thickness of a soap bubble membrane. Infrared has longer wavelengths than red light, and UV and X-rays have shorter wavelengths than violet light. (credit: modification of work by NASA)

Understanding Pigments

Different kinds of pigments exist, and each has evolved to absorb only certain wavelengths (colors) of visible light. Pigments reflect or transmit the wavelengths they cannot absorb, making them appear in the corresponding color.

Chlorophylls and **carotenoids** are the two major classes of photosynthetic pigments found in plants and algae; each class has multiple types of pigment molecules. There are five major chlorophylls: *a*, *b*, *c* and *d* and a related molecule found in prokaryotes called bacteriochlorophyll. Chlorophyll *a* and chlorophyll *b* are found in plant chloroplasts and will be the focus of the following discussion.

With dozens of different forms, carotenoids are a much larger group of pigments. The carotenoids found in fruit—such as the red of tomato (lycopene), the yellow of corn seeds (zeaxanthin), or the orange of an orange peel (β-carotene)—are used as advertisements to attract seed dispersers. In photosynthesis, carotenoids function as photosynthetic pigments that are very efficient molecules for the disposal of excess energy. When a leaf is exposed to full sun, the light-dependent reactions are required to process an enormous amount of energy; if that energy is not handled properly, it can do significant damage. Therefore, many carotenoids reside in the thylakoid membrane, absorb excess energy, and safely dissipate that energy as heat.

Each type of pigment can be identified by the specific pattern of wavelengths it absorbs from visible light, which is the absorption spectrum. The graph in Figure 4.1.5.5 shows the absorption spectra for chlorophyll *a*, chlorophyll *b*, and a type of carotenoid pigment called β-carotene (which absorbs blue and green light). Notice how each pigment has a distinct set of peaks and troughs,

revealing a highly specific pattern of absorption. Chlorophyll *a* absorbs wavelengths from either end of the visible spectrum (blue and red), but not green. Because green is reflected or transmitted, chlorophyll appears green. Carotenoids absorb in the short-wavelength blue region, and reflect the longer yellow, red, and orange wavelengths.

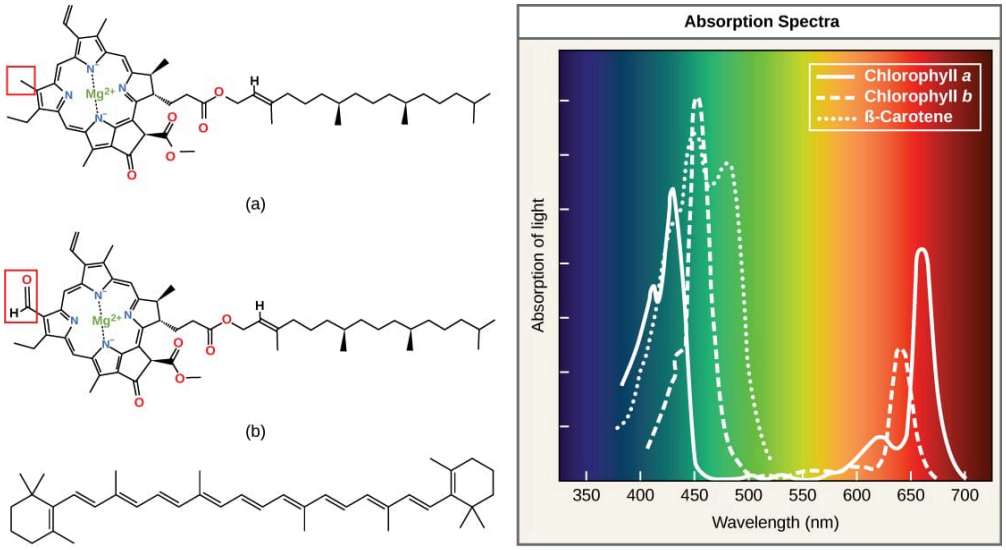


Figure 4.1.5.5: (a) Chlorophyll *a*, (b) chlorophyll *b*, and (c) *β*-carotene are hydrophobic organic pigments found in the thylakoid membrane. Chlorophyll a and chlorophyll b are made up of a long hydrocarbon chain attached to a large, complex ring made up of nitrogen and carbon. Magnesium is associated with the center of the ring. Chlorophyll b differs from chlorophyll a in that it has a CHO group instead of a CH_3 group associated with one part of the ring (indicated in the red box, are responsible for the green color of leaves). *β*-carotene is a branched hydrocarbon with a six-membered carbon ring at each end. β-carotene is responsible for the orange color in carrots. Each pigment has (d) a unique absorbance spectrum. Chlorophyll *a* peaks around 430 and 660 nm. Chlorophyll *b* peaks around 450 nm and 640 nm. *β*-carotene peaks around 450-500 nm and 640 nm.

Many photosynthetic organisms have a mixture of pigments; using them, the organism can absorb energy from a wider range of wavelengths. Not all photosynthetic organisms have full access to sunlight. Some organisms grow underwater where light intensity and quality decrease and change with depth (Figure 4.1.5.6). Other organisms grow in competition for light. Plants on the rainforest floor must be able to absorb any bit of light that comes through, because the taller trees absorb most of the sunlight and scatter the remaining solar radiation (Figure 4.1.5.7).

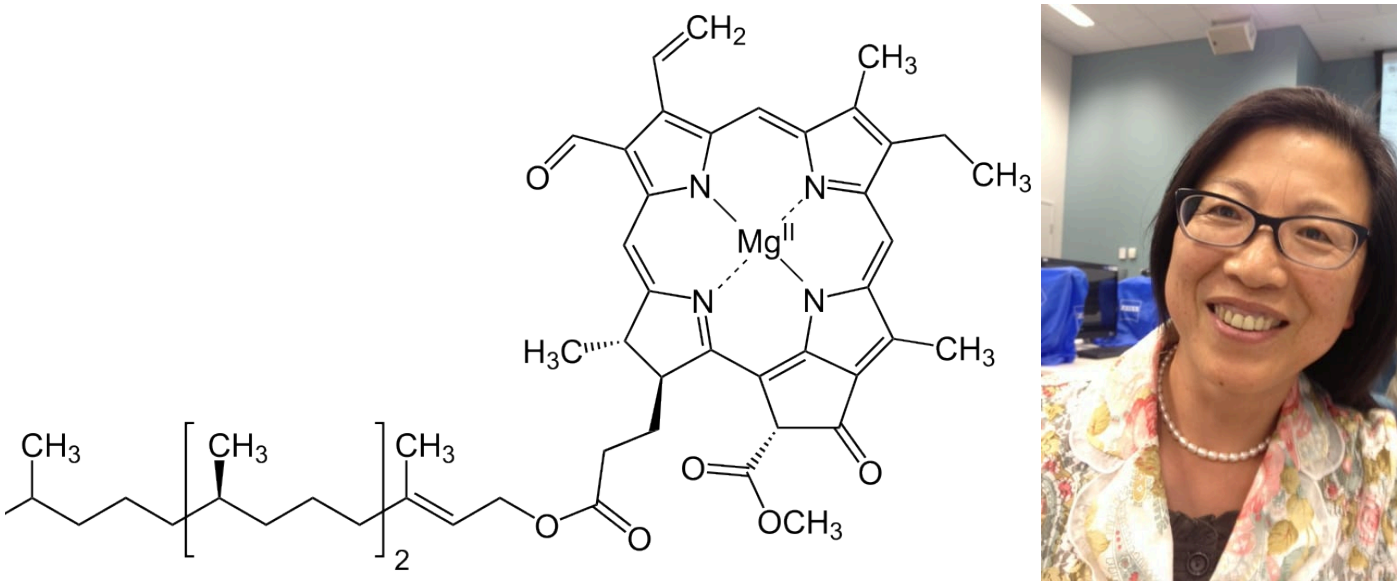


Figure 4.1.5.6: In 2010, a new type of chlorophyll, chlorophyll *f* (left), was discovered by Min Chen (right) and colleagues in 2010. It allows cyanobacteria to photosynthesize while deep inside of rocks and absorb infrared light (706 nm) for photosynthesis. Left image by Yikrazuul (public domain), and right image by Ariconte (CC-BY-SA).



Figure 4.1.5.7: Plants that commonly grow in the shade have adapted to low levels of light by changing the relative concentrations of their chlorophyll pigments. (credit: Jason Hollinger)

When studying a photosynthetic organism, scientists can determine the types of pigments present by generating absorption spectra. An instrument called a **spectrophotometer** can differentiate which wavelengths of light a substance can absorb. Spectrophotometers measure transmitted light and compute from it the absorption. By extracting pigments from leaves and placing these samples into a spectrophotometer, scientists can identify which wavelengths of light an organism can absorb. Additional methods for the identification of plant pigments include various types of **chromatography** that separate the pigments by their relative affinities to solid and mobile phases.

How Light-Dependent Reactions Work

The overall function of light-dependent reactions is to convert solar energy into chemical energy in the form of NADPH and ATP. This chemical energy supports the light-independent reactions and fuels the assembly of sugar molecules. In the light-dependent reactions protein complexes and pigment molecules work together to produce NADPH and ATP (Figure 4.1.5.8 and Video 4.1.5.1).

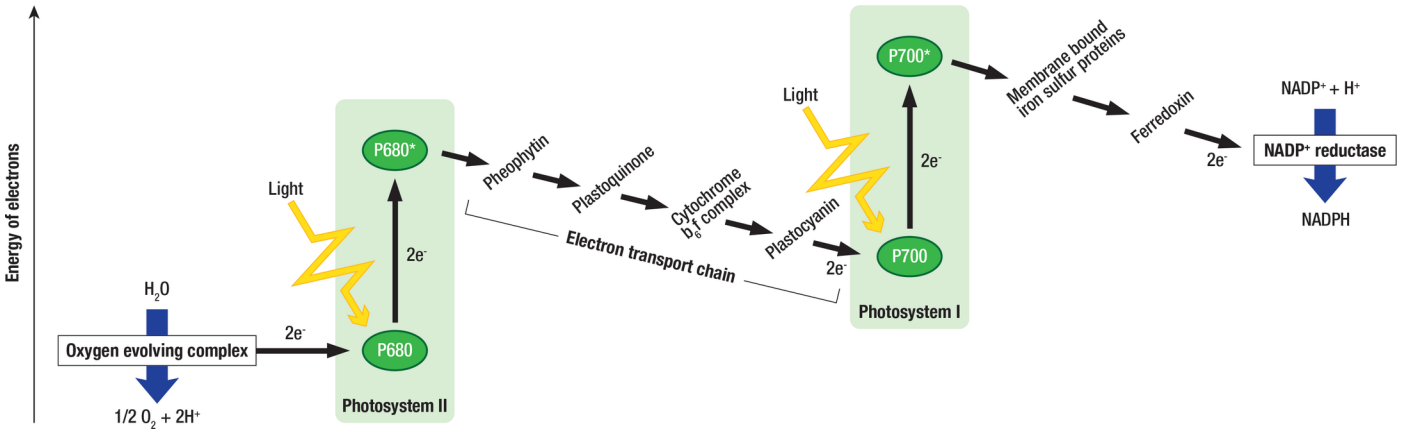


Figure 4.1.5.8: The photosynthesis Z-scheme shows the unidirectional flow of electrons from photosystem II ultimately to $NADP^+$. First, photosystem II absorbs light energy. Excited electrons ($2e^-$) are passed to pheophytin, plastoquinone, cytochrome b_6f complex, plastocyanin, and then to photosystem I. This provides energy for ATP synthesis via photophosphorylation (not shown). Photosystem I then absorbs light energy. Excited electrons are passed to membrane sulfur proteins, ferredoxin, and finally to NADP+ reductase, which reduces $NADP^+$ to NADPH. Electrons initially lost from photosystem II are replaced by oxidizing water, producing gaseous oxygen. Image by Jen Valenzuela (CC-BY).

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 4.1.5.1: Here is an animation of the light-dependent reactions.

Photosystems Absorb Light Energy

The actual step that converts light energy into chemical energy takes place in a multiprotein complex called a **photosystem**, two types of which are found embedded in the thylakoid membrane, **photosystem II** (PSII) and **photosystem I** (PSI) (Figure 4.1.5.9). The two complexes differ on the basis of what they oxidize (that is, the source of the low-energy electron supply) and what they reduce (the place to which they deliver their energized electrons).

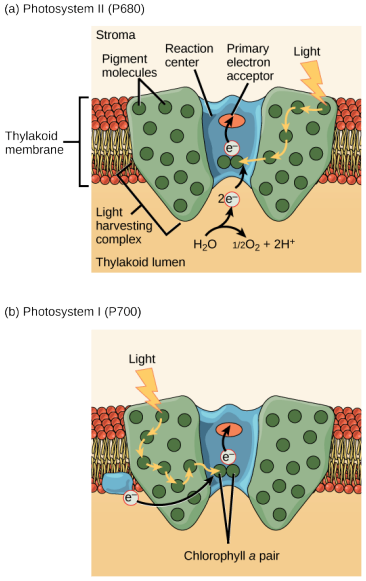


Figure 4.1.5.9: A photosystem consists of an antenna complex (labeled as light-harvesting complex) and a reaction center at the core. Pigments in the antenna complex pass light energy to two special chlorophyll a molecules in the reaction center. The light excites an electron from the chlorophyll a pair, which passes to the primary electron acceptor. The excited electron must then be replaced. In (a) photosystem II, the electron comes from the splitting of water, which releases oxygen as a waste product. In (b) photosystem I, the electron comes from the chloroplast electron transport chain discussed below.

Both photosystems have the same basic structure; a number of antenna proteins to which the chlorophyll molecules are bound surround the **reaction center**, where the photochemistry takes place. Each photosystem is serviced antenna complex, which passes energy from sunlight to the reaction center. The **antenna complex** consists of multiple antenna proteins that contain a mixture of 300–400 chlorophyll *a* and *b* molecules as well as other pigments like carotenoids. (Technically, photosystems consist of the reaction center and the antennae complex, and a photosytem plus light-harvesting complexes comprises a photosystem complex, but in Figure 4.1.5.9, the light-harvesting complex is labeled as the antennae complex.) The absorption of a single **photon**, or distinct quantity or "packet" of light, by any of the chlorophylls pushes that molecule into an excited state. In short, the light energy has now been captured by biological molecules but is not stored in any useful form yet. The energy is transferred from chlorophyll to chlorophyll until eventually (after about a millionth of a second), it is delivered to the reaction center. Up to this point, only energy has been transferred between molecules, not electrons.

The reaction center contains a pair of chlorophyll *a* molecules with a special property. Those two chlorophylls can undergo oxidation upon excitation; they can actually give up an electron. It is at this step in the reaction center, this step in photosynthesis, that light energy is converted into an excited electron.

Electrons Move Down the Electron Transport Chain, Providing Energy to Pump Protons into the Thylakoid Lumen

The reaction center of PSII (called P680) delivers its high-energy electrons, one at the time, to the primary electron acceptor, and through the **electron transport chain** (Pq to cytochrome b6f complex to plastocyanine) to PSI (Figure 4.1.5.10). The **cytochrome b6f complex**, an enzyme composed of two protein complexes, transfers the electrons from the carrier molecule **plastoquinone** (Pq) to the protein **plastocyanin** (Pc), ultimately facilitating the transfer of electrons from PSII to PSI. During this process, cytochrome b6f pumps protons from the stroma into the thylakoid lumen using the energy from electrons moving down the electron transport chain.

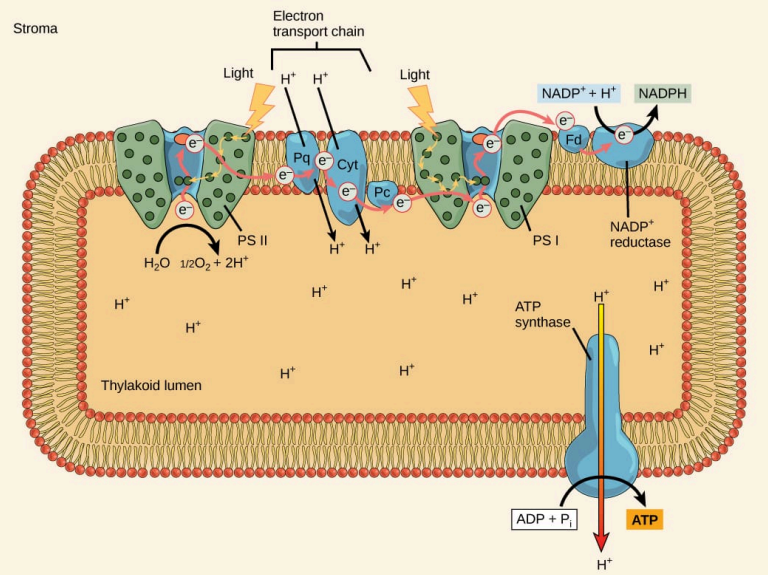


Figure 4.1.5.10: In the photosystem II (PSII) reaction center, energy from sunlight is used to extract electrons from water, producing half an oxygen molecule and two protons in the process. The electrons travel through the chloroplast electron transport chain to photosystem I (PSI), which passes the electron to NADP+ reductase, which uses it to convert NADP+ and a proton to NADPH. The electron transport chain moves protons (H^+) across the thylakoid membrane into the lumen. At the same time, splitting of water adds protons to the lumen, and reduction of NADPH removes protons from the stroma. The net result is a low pH in the thylakoid lumen, and a high pH in the stroma. ATP synthase moves protons down their electrochemical gradient, from the lumen to the stroma, and uses the energy from this gradient to make ATP.

Photophosphorylation

The synthesis of ATP in the light-dependent reactions is called **photophosphorylation**. The buildup of protons inside the thylakoid lumen creates a concentration gradient. The passive movement (facilitated diffusion) of protons from high concentration (in the thylakoid lumen) to low concentration (in the stroma) is harnessed to create ATP. The protons build up energy at high concentrations because they all have the same electrical charge, repelling each other.

To release this energy, protons will rush through any opening, similar to water jetting through a hole in a dam. In the thylakoid, that opening is a passage through a specialized protein channel called the **ATP synthase**. The energy released by the proton stream allows ATP synthase to attach a third phosphate group to ADP, which forms a molecule of ATP (Figures 4.1.5.10 – 11). The flow of protons through ATP synthase is called **chemiosmosis** because the ions move from an area of high to an area of low concentration through a semi-permeable structure.

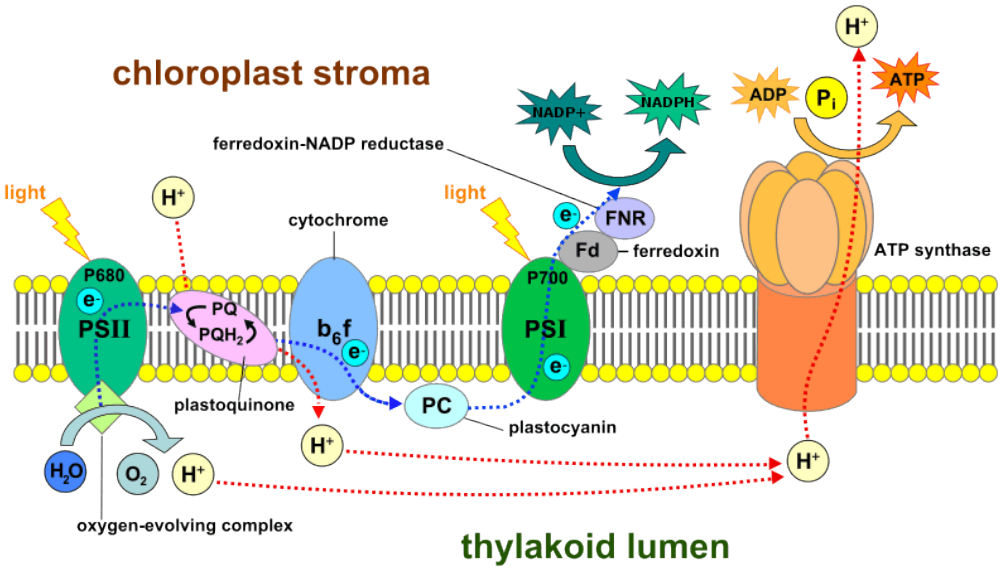


Figure 4.1.5.11: The electron transport chain, water photolysis, and photophosphorylation in the light-dependent reactions. Light is first absorbed by photosystem II (PS II) and high-energy electrons (e^-) are transferred to pheophytin (not shown), which pass electrons to plastoquinone (PQ) and then to cytochrome b_6/f complex, which pumps protons (H^+) into the thylakoid lumen. Electrons then are passed to plastocyanin (PC) and then photosystem I (PSI). PS I reabsorbs light energy, and high-energy electrons are passed to ferredoxin (Fd) and then to ferredoxin-$NADP^+$ reductase. Finally, the electrons reduce $NADP^+$ to NADPH. Protons move down their electrochemical gradients through ATP synthase into the stroma, generating ATP. Electrons lost from PS III are replaced by oxidizing water (H_2O), releaseing gaseous oxygen (O_2) and protons. Image by Somepics (CC-BY-SA).

Water Photolysis

P680's missing electron is replaced by extracting a low-energy electron from water; thus, water is split (**water photolysis**) and PSII is re-reduced. Splitting one H_2O molecule releases two electrons, two protons, and one atom of oxygen (Figures 4.1.5.10 – 11). Those protons, in addition to the ones transported by cytrochrome b6f, accumulate in the thylakoid lumen and fuel photophosphorylation. Splitting two molecules is required to form one molecule of diatomic O_2 gas. About 10 percent of the oxygen is used by mitochondria in the leaf to support aerobic cellular respiration, the process of breaking down glucose to generate ATP. The remainder escapes to the atmosphere where it is used by aerobic organisms to support respiration.

Reduction of $NADP^+$

Because the electrons have lost energy prior to their arrival at PSI, they must be re-energized by PSI, hence, another photon is absorbed by the PSI antenna. That energy is relayed to the PSI reaction center (called P700). P700 is oxidized and sends high-energy electrons to the electron carrier $NADP^+$ to form NADPH. Thus, PSII captures the energy to create proton gradients to make ATP, and PSI captures the energy to reduce $NADP^+$ into NADPH. The two photosystems work in concert, in part, to guarantee that the correct proportions of NADPH and ATP needed for the light-independent reactions are generated. Other mechanisms exist to fine tune that ratio to exactly match the chloroplast's constantly changing energy needs.

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4.1.6: Light-independent Reactions

Learning Objectives

- Detail the three steps of the light-independent reactions.
- Define carbon fixation.

After the energy from the sun is converted into chemical energy temporarily stored in the bonds of ATP and NADPH molecules, the cell has the fuel needed to build carbohydrate molecules for long-term energy storage. The products of the light-dependent reactions, ATP and NADPH, have lifespans in the range of millionths of seconds, whereas the products of the light-independent reactions (carbohydrates and other forms of reduced carbon) can survive for hundreds of millions of years. The carbohydrate molecules made will have a backbone of carbon atoms. Where does the carbon come from? It comes from carbon dioxide, the gas that is a waste product of respiration in microbes, fungi, plants, and animals.

In plants, carbon dioxide (CO_2) enters the leaves through stomata, where it diffuses over short distances through intercellular spaces until it reaches the mesophyll cells. Once in the mesophyll cells, CO_2 diffuses into the stroma of the chloroplast—the site of light-independent reactions of photosynthesis (Figure 4.1.6.1). The light-independent reactions (also known as the Calvin cycle) can be organized into three basic stages: fixation, reduction, and regeneration (Video 4.1.6.1).

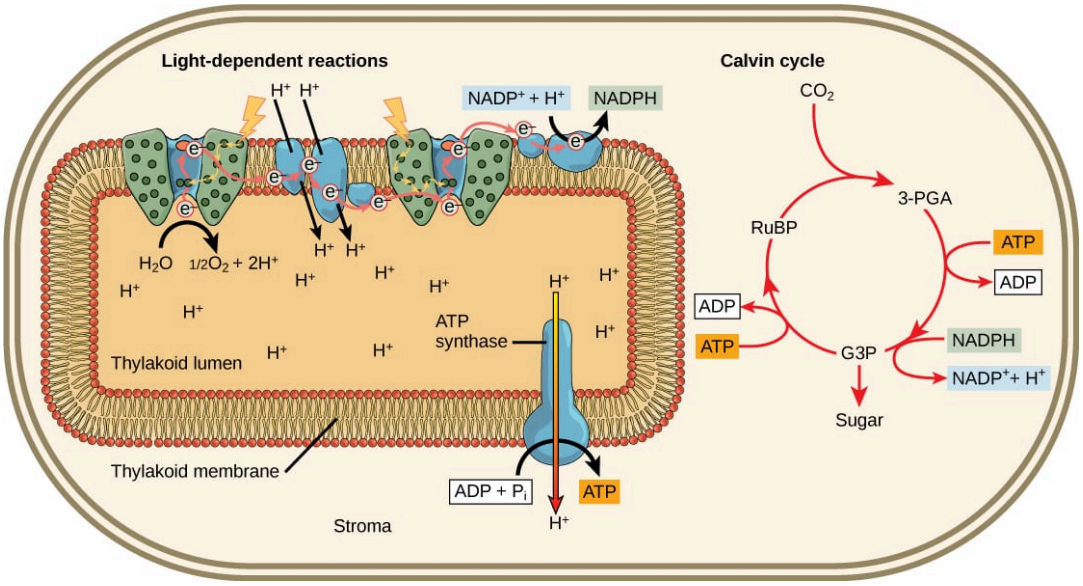


Figure 4.1.6.1: Light-dependent reactions harness energy from the sun to produce chemical bonds, ATP, and NADPH. These energy-carrying molecules are made in the stroma where carbon fixation takes place as part of the light-independent reactions (Calvin cycle). The entire image represents the chloroplasts, which is bound by a double membrane. The solution within the chloroplasts is the stroma. A portion of the thylakoid membrane is on the left, and it encloses the thylakoid lumen. Embedded in it are various photosystems (collections of pigments) and protein complexes, which form an electron transport chain. Excited electrons move along the electron transport chain and are ultimately used to reduce $NADP^+$, producing NADPH. The energy from the electrons is used to pump protons into the thylakoid lumen. Protons move down their concentration gradient through ATP synthase, generating ATP. Water is oxidized to replace lost electrons, releasing gaseous oxygen (O_2). The Calvin cycle on the right shows how carbon dioxide (CO_2) is added to rubulose-1,5,-bisphosphate (RuBP) to produce 3-phosphoglycerate (3-PGA). ATP and NADPH are consumed to reduce 3-PGA to glyceraldehyde-3-phosphate (G3P), which can be used to produce other sugars (glucose). Additional ATP is consumed to regenerate RuBP from G3P, completing the cycle.

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 4.1.6.1: Here is an animation of the light-independent reactions (Calvin cycle):

Stage 1: Fixation

In the stroma, in addition to CO_2, two other components are present to initiate the light-independent reactions: an enzyme called **ribulose-1,5-bisphosphate carboxylase/oxygenase** (**RuBisCO**), and three molecules of **ribulose-1,5-bisphosphate** (**RuBP**), as shown in Figure 4.1.6.2. RuBP has five atoms of carbon, flanked by two phosphates.

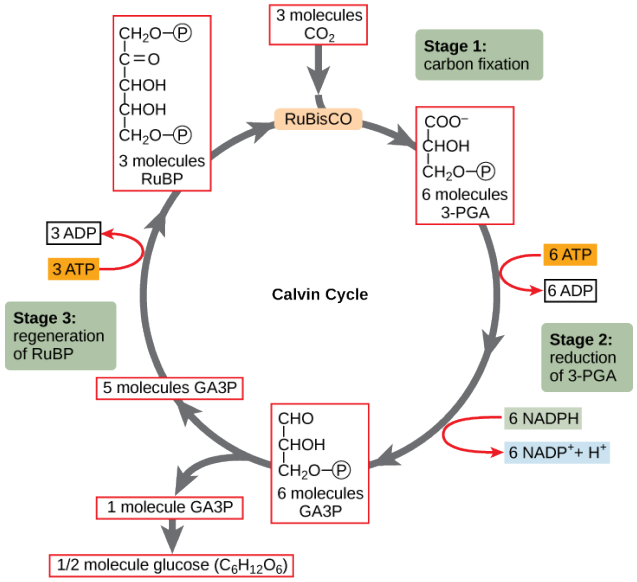


Figure 4.1.6.2: The light-independent reactions (Calvin cycle) has three stages. In stage 1, the enzyme RuBisCO adds carbon dioxide to RuBP, which immediately splits, producing two three-carbon 3-PGA molecules. In stage 2, two NADPH and two ATP are used to reduce 3-PGA to GA3P. In stage 3, RuBP, the molecule that starts the cycle, is regenerated so that the cycle can continue. One ATP is used in the process. Only one carbon dioxide molecule is incorporated at a time, so the cycle must be completed three times to produce a single three-carbon GA3P molecule, and six times to produce a six-carbon glucose molecule.

RuBisCO catalyzes a reaction between CO_2 and RuBP. For each CO_2 molecule that reacts with one RuBP, two molecules of another compound, **3-phosphoglycerate** (3-PGA), form. 3-PGA has three carbon atoms and one phosphate. Each turn of the cycle involves only one RuBP and one carbon dioxide and forms two molecules of 3-PGA. The number of carbon atoms remains the same, as the atoms move to form new bonds during the reactions (3 atoms from 3 CO_2 + 15 atoms from 3 RuBP = 18 atoms in 3 atoms of 3-PGA). This process is called **carbon fixation**, because CO_2 is "fixed" from an inorganic form into organic molecules.

Stage 2: Reduction

ATP and NADPH are used to convert the six molecules of 3-PGA into six molecules of a chemical called **glyceraldehyde 3-phosphate** (G3P). That is a reduction reaction because it involves the gain of electrons by 3-PGA. Recall that **reduction** is the gain of an electron by an atom or molecule. Six molecules of both ATP and NADPH are used. For ATP, energy is released with the loss of the terminal phosphate atom, converting it into ADP; for NADPH, both energy and a hydrogen atom are lost, converting it into $NADP^+$. Both of these molecules return to the nearby light-dependent reactions to be reused and re-energized.

Stage 3: Regeneration

Interestingly, at this point, only one of the G3P molecules leaves the light-independent reactions and is sent to the cytoplasm to contribute to the formation of other compounds needed by the plant. Because the G3P exported from the chloroplast has three carbon atoms, it takes three "turns" of the cycle to fix enough net carbon to export one G3P. But each turn makes two G3P, thus three turns make six G3P. One of these six is exported while the remaining five G3P molecules remain in the cycle and are used to regenerate RuBP, which enables the system to prepare for more CO_2 to be fixed. Three more molecules of ATP are used in these regeneration reactions.

Evolution Connection: Photosynthesis

During the evolution of photosynthesis, a major shift occurred from the bacterial type of photosynthesis that involves only one photosystem and is typically anoxygenic (does not generate oxygen) into modern oxygenic (does generate oxygen) photosynthesis, employing two photosystems. This modern oxygenic photosynthesis is used by many organisms—from giant tropical leaves in the rainforest to tiny cyanobacterial cells—and the process and components of this photosynthesis remain largely the same (Figure 4.1.6.3). Photosystems absorb light and use electron transport chains to convert energy into the chemical energy of ATP and NADPH. The subsequent light-independent reactions then assemble carbohydrate molecules with this energy.

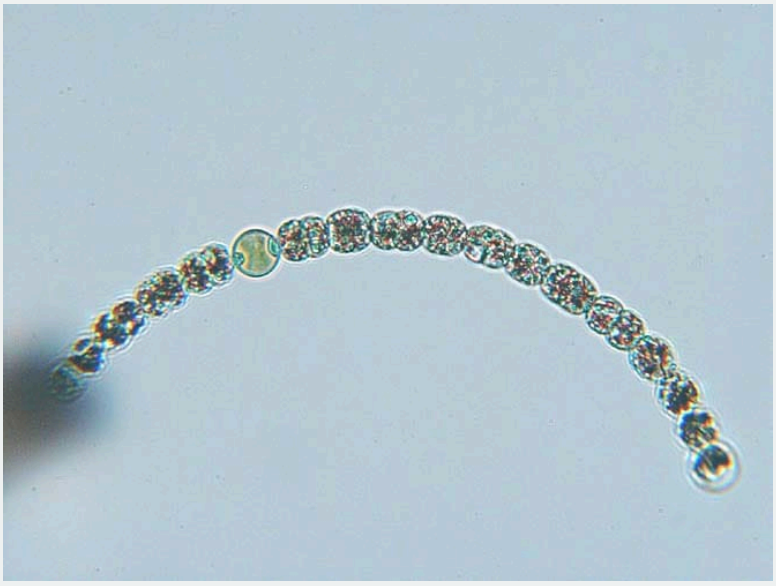


Figure 4.1.6.3: Cyanobacteria, like *Anabaena circinalis*, do essentially the same type of photosynthesis as plants and algae. Image by Bdcarl (CC-BY-SA).

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4.1.7: Photorespiration and Photosynthetic Pathways

Learning Objectives

- Define photorespiration.
- Explain how C3, C4, and CAM plants reduce photorespiration.
- Outline the C_4 pathway and compare its use by C_4 plants and CAM plants.

Different plant species have adaptations that allow them to do different variations of the light-independent reactions. These are called **photosynthetic pathways**. Plants are classified as C_3, C_4, or CAM depending on their use of these pathways, but note that some plants can switch photosynthetic pathways depending on environmental conditions. The process for light-independent reactions described in the previous section was the **C_3 pathway**: the compound formed during fixation (3-PGA) has three carbon atoms. Before discussing the details of the C_4 pathway, it is important to understand the circumstances that led to these adaptations.

Photorespiration

As its name suggests, **ribulose-1,5-bisphosphate carboxylase/oxygenase** (**RuBisCO**) catalyzes two different reactions. The first is adding CO_2 to ribulose-1,5- bisphosphate (RuBP) — the **carboxylase** activity. The second is adding O_2 to RuBP — the **oxygenase** activity.

The oxygenase activity of RuBisCO forms the three-carbon molecule 3-phosphoglycerate (3-PGA), just as in the light-independent reactions, and the two-carbon molecule glycolate. The glycolate enters peroxisomes, where it uses O_2 to form intermediates that enter mitochondria where they are broken down to CO_2. So this process uses O_2 and liberates CO_2 as aerobic cellular respiration does, which is why it is called **photorespiration**. It undoes the work of photosynthesis, which is to build sugars.

Which action of RuBisCO predominates depends on the relative concentrations of O_2 and CO_2 with high CO_2, low O_2 favoring the carboxylase action and high O_2, low CO_2 favoring the oxygenase action. The light reactions of photosynthesis liberate oxygen, and more oxygen dissolves in the cytosol of the cell at higher temperatures. Therefore, high light intensities and high temperatures (above ~ 30°C) favor the second reaction and result in photorespiration.

C_3 Plants

One solution to photorespiration is for plants to open their stomata to release O_2 and obtain CO_2. However, if conditions are hot or dry, this will result in too much water loss (**transpiration**). For this reason, C_3 plants, which only do the C_3 pathway and do not use the C_4 pathway to prevent photorespiration (see below), do best in cool, moist areas. Rice and potatoes are examples of C_3 plants.

C_4 Plants

Many angiosperms have developed adaptations which minimize the losses to photorespiration. They all use a supplementary method of CO_2 uptake which initially forms a four-carbon molecule compared to the two three-carbon molecules that are initially formed in the C_3 pathway. Hence, these plants are called **C_4 plants**. Note that C_4 plants will eventually conduct the light-independent reactions (C_3 pathway), but they form a four-carbon molecule first.

C_4 plants have structural changes in their leaf anatomy so that synthesizing the four-carbon sugar (the C_4 pathway) and resuming the light-independent reactions (C_3 pathways) are separated in different parts of the leaf with RuBisCO sequestered where the CO_2 level is high and the O_2 level low. After entering through stomata, CO_2 diffuses into a mesophyll cell (Figure 4.1.7.1). Being close to the leaf surface, these cells are exposed to high levels of O_2, but they have no RuBisCO so cannot start photorespiration

(nor the light-independent reactions).

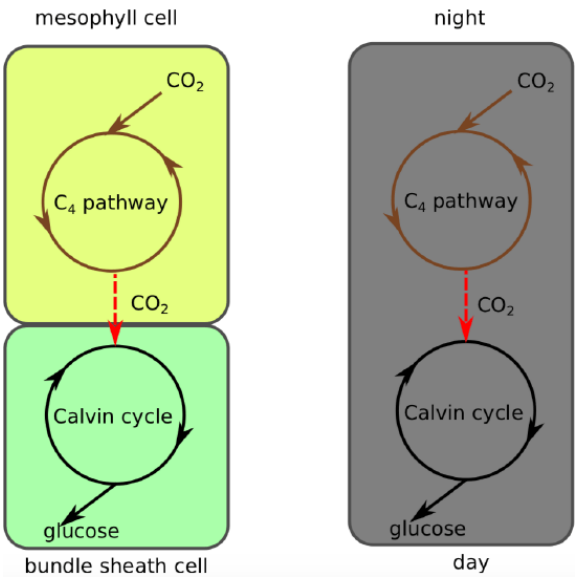


Figure 4.1.7.1: C_4 plants conduct the C4 pathway in the mesophyll cells and the Calvin cycle (C_3 pathway) in the bundle sheath cells, meaning they spatially separate the two (left). CAM plants (right) conduct the C4 pathway at night and the Calvin cycle (C_3 pathway) during the day, resulting an a temporal separation of the two.

Instead, the CO2 is inserted into a three-carbon compound called **phosphoenolpyruvic acid** (**PEP**) forming the four-carbon compound **oxaloacetic acid**. Oxaloacetic acid is converted into malic acid or aspartic acid (both have 4 carbons), which is transported through plasmodesmata into a **bundle sheath cell**. Bundle sheath cells are deep in the leaf, so atmospheric oxygen cannot diffuse easily to them (Figure 4.1.7.2). Additionally, they often have thylakoids with reduced photosystem II complexes (the one that produces O2). Both of these features keep oxygen levels low in bundle sheath cells, which is where the four-carbon compound is broken down into carbon dioxide, which enters the light-independent reactions (C_3 pathway) to form sugars and pyruvic acid, which is transported back to a mesophyll cell where it is converted back into **PEP**.

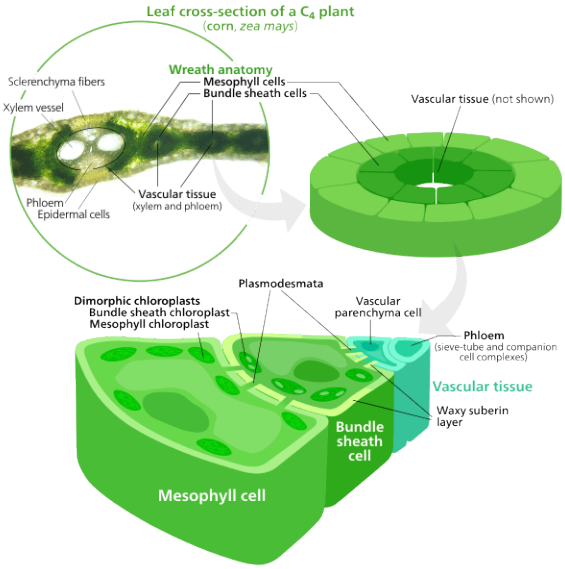


Figure 4.1.7.2: Cross section and diagram of a C4 plant, showing mesophyll cells surrounding bundle sheath cells in concentric circles. The bundle sheath cells are larger and have more chloroplasts than in other plants. This arrangement is called Kranz anatomy (wreath anatomy). Vascular bundles contain xylem (vessel elements and tracheids) and phloem (sieve-tube and companion cell complexes). A vascular parenchyma is also shown in the vascular bundle. Waxy suberin borders the bundle sheath cells. The chloroplasts in the mesophyll cells are distinct from those in the bundle sheath cells, and the chloroplasts are thus called dimorphic. Sclerenchyma fibers are just above and below the vascular bundle, and epidermal cells surround the entire leaf. Image by Kelvinsong (CC-BY-SA).

These C4 plants are well adapted to (and likely to be found in) habitats with high daytime temperatures and intense sunlight. Because they use the C4 pathway to prevent photorespiration, they do not have to open their stomata to the same extent as C3 plants and can thus conserve water. Some examples crabgrass, corn (maize), sugarcane, and sorghum. Although comprising only ~3% of the angiosperms by species, C4 plants are responsible for ~25% of all the photosynthesis on land.

CAM Plants

CAM stands for **c**rassulacean **a**cid **m**etabolism because it was first studied in members of the plant family Crassulaceae. **CAM plants** also do the C4 pathway. However, instead of segregating the C4 and C3 pathways in different parts of the leaf, CAM plants separate them in **time** instead (Table 4.1.7.1). As a result, CAM plants do not need to open their stomata in the daytime to reduce photorespiration because they have already formed a four-carbon molecule at night that can be broken down to release carbon dioxide during the day.

Table 4.1.7.1: Activities of CAM plants at night and in the morning.

Night	Morning
• CAM plants take in CO_2 through their open stomata (they tend to have reduced numbers of them). • The CO_2 joins with PEP to form the four-carbon oxaloacetic acid. • This is converted to four-carbon **malic acid** that accumulates during the night in the central vacuole of the cells.	• The stomata close (thus conserving moisture as well as reducing the inward diffusion of oxygen). • The accumulated malic acid leaves the vacuole and is broken down to release CO_2. • The CO_2 is taken up into the light-independent reactions (C3 pathway).

CAM plants thus thrive in conditions of high daytime temperatures, intense sunlight, and low soil moisture. Some examples of CAM plants include cacti (Figure 4.1.7.3), pineapples, all epiphytic bromeliads, sedums, and the "ice plant" that invade the California coast line.



Figure 4.1.7.3: Cultivated cacti in the Singapore Botanic Gardens. Image by Calvin Teo (CC-BY-SA).

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4.1.8: Chapter Summary

Photosynthesis and aerobic cellular respiration are two key metabolic pathways conducted by plants. The process of photosynthesis transformed life on Earth. By harnessing energy from the sun, photosynthesis evolved to allow living things access to enormous amounts of energy. Because of photosynthesis, living things gained access to sufficient energy that allowed them to build new structures and achieve the biodiversity evident today.

Only certain organisms, called **photoautotrophs**, can perform photosynthesis; they require the presence of chlorophyll, a specialized pigment that absorbs certain portions of the visible spectrum and can capture energy from sunlight. Photosynthesis uses carbon dioxide and water to assemble carbohydrate molecules and release oxygen as a waste product into the atmosphere. Eukaryotic autotrophs, such as plants and algae, have organelles called chloroplasts in which photosynthesis takes place, and starch accumulates. In prokaryotes, such as **cyanobacteria**, the process is less localized and occurs within folded membranes, extensions of the plasma membrane, and in the cytoplasm.

The **pigments** of the first part of photosynthesis, **the light-dependent reactions**, absorb energy from sunlight. A **photon** strikes the antenna pigments of **photosystem II** to initiate photosynthesis. The energy travels to the reaction center that contains chlorophyll *a* to the **electron transport chain**, which pumps protons into the thylakoid interior. This action builds up a high concentration of ions. The protons flow through **ATP synthase** via **chemiosmosis** to form molecules of **ATP**, which are used for the formation of sugar molecules in the second stage of photosynthesis. Photosystem I absorbs a second photon, which results in the formation of an **NADPH** molecule, another energy and reducing power carrier for the light-independent reactions.

Using the electron carriers formed in the first steps of photosynthesis, the **light-independent reactions**, or the Calvin cycle, take in CO_2 from the environment. An enzyme, **RuBisCO**, catalyzes a reaction with CO_2 and another molecule, RuBP. After three cycles, a three-carbon molecule of G3P leaves the cycle to become part of a carbohydrate molecule. The remaining G3P molecules stay in the cycle to be regenerated into RuBP, which is then ready to react with more CO_2.

Photorespiration is the process by which RuBisCO binds to O_2 instead of CO_2 and breaks down rather than builds sugars. **C_3, C_4**, and **CAM** plants have different strategies for reducing photorespiration.

Just like animals, plants must also break down sugars to produce usable energy in the form of ATP through the process of **aerobic cellular respiration**. The process begins with **glycolysis** in the cytoplasm, continues with **pyruvate oxidation** and the **citric acid cycle** in the mitochondrial **matrix**, and concludes with **oxidative phosphorylation** in the **cristae** of the mitochondria. Overall, it consumes glucose and gaseous oxygen and releases carbon dioxide and water.

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

- Describe the different types of energy.
- Describe the structure and function of ATP.
- Explain the relevance of photosynthesis to other living things.
- Identify the substrates and products of photosynthesis.
- Describe the main structures involved in photosynthesis.
- Relate the light-dependent and light-independent reactions.
- Summarize the experimental results that revealed details about the process of photosynthesis.
- Relate wavelength, energy, and the type of electromagnetic radiation (and the color of visible light).
- Explain how plants absorb energy from sunlight.
- Detail the steps of the light-dependent interactions.
- Detail the three steps of the light-independent reactions.
- Define carbon fixation.
- Define photorespiration.
- Explain how C3, C4, and CAM plants reduce photorespiration.
- Outline the C_4 pathway and compare its use by C_4 plants and CAM plants.
- Identify the reactants and products of aerobic cellular respiration.
- Explain each step of aerobic cellular respiration and where in the cell it occurs.

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4.2: ENVIRONMENTAL RESPONSES

Animals can respond to environmental factors by moving to a new location. Plants, however, are rooted in place and must respond to the surrounding environmental factors. Plants have sophisticated systems to detect and respond to light, gravity, temperature, and physical touch (Figure 4.2.1). Plants may grow towards or away from environmental stimuli, and these growth responses are called **tropisms**. Environmental factors, particularly temperature and the hours of light and dark each day, also control flowering in many species. Plants detect the latter through **photoperiodism**. In the absence of light, plants respond physiologically to increase the chance of accessing light. Finally, plants rely on environmental cues to break dormancy in seeds and buds on winter twigs.



Figure 4.2.1: The first flower to bloom in space. The International Space Station provides a unique opportunity to study the growth of plants under microgravity. Image by NASA (CC-BY-NC).

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4.2.1: Tropisms

4.2.2: Flowering

4.2.3: Photoperiodism

4.2.4: Etiolation and Shade Avoidance

4.2.5: Dormancy

4.2.6: Chapter Summary

Thumbnail image: Sensitive plant (*Mimosa pudica*) exhibits a thigmonastic movement. The leaflets and leaves retract when it is touched. Image by piqsels (public domain)

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4.2.1: Tropisms

Learning Objectives

- Distinguish among phototropism, gravitropism, hydrotropism, and thigmotropism.
- Discuss the adaptive value of tropisms.
- Describe the mechanism of phototropism in shoots.
- Describe the mechanism of gravitropism in shoots and roots.
- Distinguish among thigmotropism, thigmonastic movements, and thigmomorphogenesis.

A **tropism** is directional growth in response to a stimulus. A **positive tropism** occurs when a plant (or a part of the plant) grows towards the stimulus, and a **negative tropism** is growth away from the stimulus.

Phototropism is directional growth in response to light (Figure 4.2.1.1). (More generally, **photomorphogenesis** is the growth and development of plants in response to light.) Stems are positively phototropic, and roots are typically negatively phototropic. **Gravitropism** is directional growth in response to gravity. Stems are negatively gravitropic, and roots are positively gravitropic. The adaptive value of these tropisms is clear. Stems growing upward and/or toward the light will be able to expose their leaves so that photosynthesis can occur. Roots growing downward and/or away from light are more likely to find the soil, water, and minerals they need. Plants can also grow directionally in response to water (**hydrotropism**) and touch (**thigmotropism**).



Figure 4.2.1.1: Azure bluets (*Houstonia caerulea*) display a phototropic response by bending toward the light. Image by Cory Zanker.

Phototropism in Shoots

Plants can detect different characteristics of light, such as quantity, quality, duration, and direction. They can tell the time of day and time of year by sensing and using various wavelengths of sunlight. Plants are generally capable of detecting and responding to at least three wavelengths of light: **blue light, red light,** and **far-red light**. The different wavelengths are detected by different **photoreceptors** (Figure 4.2.1.2), an example of which are phototropins.

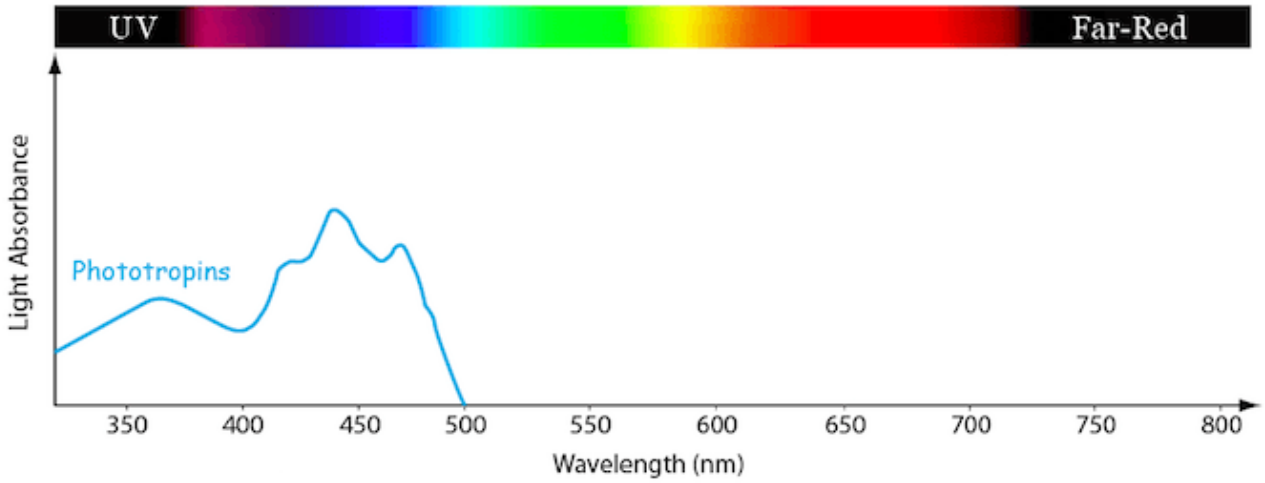


Figure 4.2.1.2: The absorption spectrum of phototropins, blue-light photoreceptors in plants. They absorb the most light between 400 and 500 nanometers (nm). Visible light ranges from violet (400 nm) to red (700 nm). Ultraviolet light has a shorter wavelength than visible light, and far red light has a longer wavelenth.

The Shoot Tip Detects Light and Induces Phototropism

In their 1880 treatise *The Power of Movements in Plants*, Charles Darwin and his son Francis first described phototropism as the bending of seedlings toward light. The Darwins used grass seedlings for some of their experiments. When grass seeds germinate, the primary leaf pierces the seed coverings and the soil while protected by the **coleoptile**, a hollow, cylindrical sheath that surrounds it (Figure 4.2.1.3).



Figure 4.2.1.3: The coleoptile is a sheath surrounding the young shoot of some seedlings, including corn (shown above) and grass (studied by the Darwins' phototropism experiment). Image by Melissa Ha (CC-BY)

Once the seedling has grown above the surface, the coleoptile stops growing and the primary leaf pierces it. If they placed an opaque cover over the tip, phototropism failed to occur even though the rest of the coleoptile was illuminated from one side. However, when they buried the plant in fine black sand so that only its tip was exposed, there was no interference with the tropism — the buried coleoptile bent in the direction of the light (Figure 4.2.1.4). In conclusion, light was perceived by the tip of the plant (the apical meristem), but that the response (bending) took place in a different part of the plant. The signal had to travel from the apical meristem to the base of the plant.

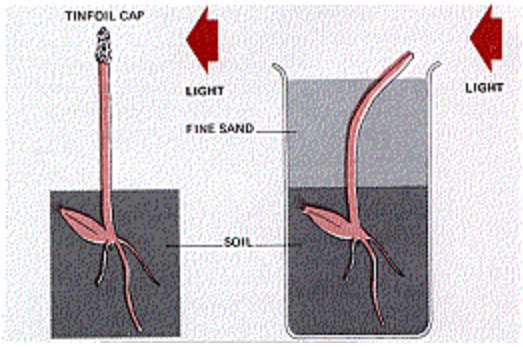


Figure 4.2.1.4: In the Darwins' experiment, there was not phototropism when the tip of the coleoptile was covered (left). When the tip was exposed, phototropism occured (right).

We now know that phototropism is a response to blue wavelengths of light. The detection of light in the apical meristem occurs via phototropins called **phot1** and **phot2**, which specifically detect **blue light** (Figure 4.2.1.5). The aptly-named **phototropins** are protein-based receptors responsible for mediating the phototropic response. Like all plant photoreceptors, phototropins consist of a protein portion and a light-absorbing portion, called the **chromophore**. Together, the two are called a chromoprotein. In phototropins, the chromophore is a covalently-bound molecule of flavin; hence, phototropins belong to a class of proteins called flavoproteins.

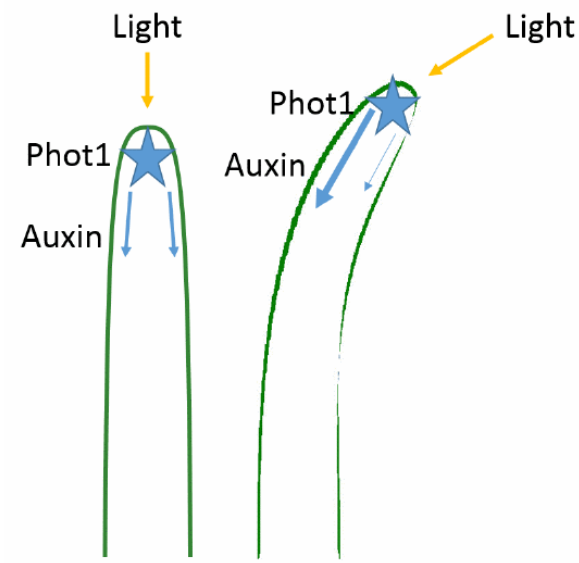


Figure 4.2.1.5: Blue light activates phot1 and phot2 (not shown). The hormone auxin (see Auxin section) then accumulates on the shaded side of the stem in response to phot1 and phot2 activation. Auxin promotes cell elongation, causing bending toward the light.

The Hormone Auxin from the Shoot Tip Stimulates Elongation on the Shaded Side of the Stem

In 1913, the Danish plant physiologist Peter Boysen-Jensen demonstrated that a chemical signal produced in the plant tip was responsible for the bending at the base. He cut off the tip of a seedling, covered the cut section with a layer of gelatin, and then replaced the tip. The seedling bent toward the light when illuminated. However, when impermeable mica flakes were inserted between the tip and the cut base, the seedling did not bend. A refinement of the experiment showed that the signal traveled on the shaded side of the seedling. When the mica plate was inserted on the illuminated side, the plant did bend towards the light. When a horizontal incision was made on the illuminated side and the mica inserted in it, phototropism was normal (Figure 4.2.1.6). Therefore, the chemical signal was a growth stimulant because the phototropic response involved faster cell elongation on the shaded side than on the illuminated side.

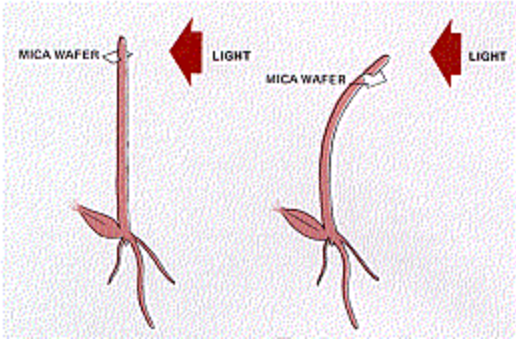


Figure 4.2.1.6: The Boysen-Jensen experiment showed that a chemical signal (now known to be auxin) passed from the shoot tip to the shaded side of the coleoptile, resulting in positive phototropism.

We now know that **auxin** is the chemical signal that accumulates and stimulates elongation on shaded side of coleoptile. H. W. Went placed a coleoptile that has previously been illuminated from one side on two separated agar blocks. The block on the side that had been shaded accumulated almost twice as much auxin as the block on the previously lighted side (Figure 4.2.1.7).

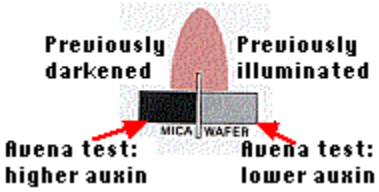


Figure 4.2.1.7: The Went experiment showed that auxin concentration was greater in the shaded side of the coleoptile.

Auxin stimulates cell elongation on the shady side of the stem through a process called the **acid growth hypothesis**: Auxin causes cells to activate proton pumps, which then pump protons out of the cells and into the space between the plasma membrane and the cell wall. The movement of protons into the extracellular space does two things:

- The lower pH activates **expansin**, which breaks the links between the cellulose fibers in the cell walls, making them more flexible.
- The high concentration of protons causes sugars to move into the cell, which then creates an osmotic gradient where water moves into cell causing the cell to expand.

Phototropism in Roots

Although roots are underground, they can be exposed to light directly as well. Not only can light penetrate up to a few centimeters in the upper layers of some soils, the plant itself can also guide light through the stem to the roots. Additionally, roots can also be exposed to light shortly after germination in the top layer of the soil or because cracks in the soil emerge that trigger a phototropic reaction. Negative phototropism in roots may be evolutionarily advantageous because it increases root efficiency and enhances seedling survival under dry conditions. As in shoots, phototropin 1 is involved in root phototropism. Directional auxin transport and an auxin gradient are associated with root phototropsim, but it is unclear whether they mediate the process.

Gravitropism

Whether or not they germinate in the light or in total darkness, shoots usually sprout up from the ground, and roots grow downward into the ground. A plant laid on its side in the dark will send shoots upward when given enough time. Gravitropism also involves the unequal distribution of auxin.

When an oat coleoptile tip is placed on two separated agar blocks, as shown here, there is no difference in the auxin activity picked up by the two blocks. When the preparation is placed on its side, however, the lower block accumulates twice as much auxin activity as the upper block. Under natural conditions, this would cause greater cell elongation on the underside of the coleoptile and the plant would bend upward (Figure 4.2.1.8).

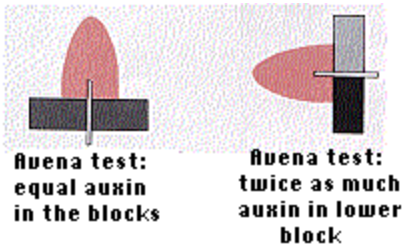


Figure 4.2.1.8: When a coleoptile is placed on its side, auxin accumulates in the lower side.

Specialized amyloplasts called **statoliths** settle downward in response to gravity. Statoliths are found in the inner part of a stem's cortex (the starch sheath) and in the the central column of the root cap (columella). When a plant is tilted, the statoliths drop to the new bottom cell wall. A few hours later, the shoot or root will show growth in the new vertical direction (Figure 4.2.1.9).

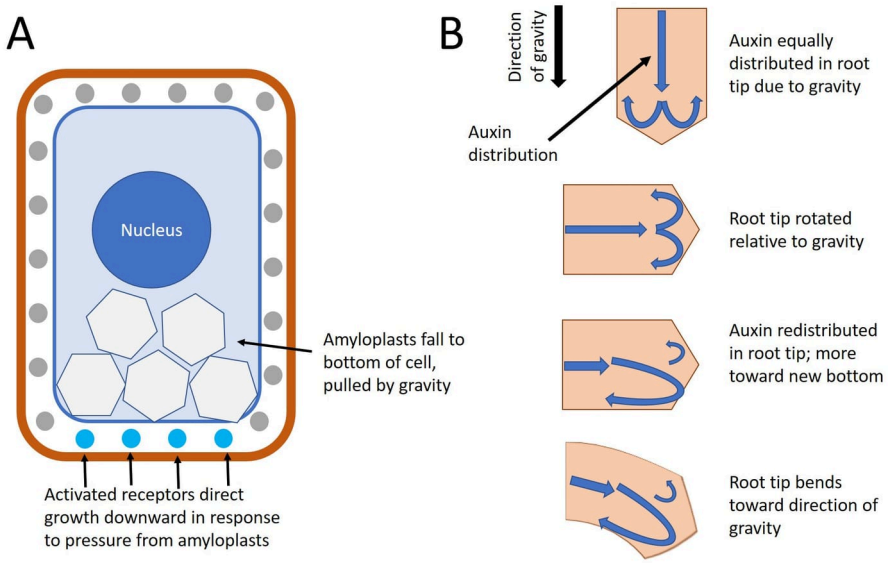


Figure 4.2.1.9: Auxin and specialized amyloplasts called statoliths together mediate gravitropism. **A** Statoliths (amyloplasts) fall to the bottom of cells and activate pressure-sensitive receptors which direct growth downward. **B** Auxin distribution in the root tip changes as a result of gravity, with auxin accumulating in the direction of gravity. Higher auxin distribution in roots inhibits cell elongation while lower auxin distribution promotes cell elongation. Image credit: A, modeled after Freeman Biological Sciences 5th edition Figure 40.12; B, modeled after Freeman Biological Sciences 5th edition Figure 40.13

The mechanism that mediates gravitropism is reasonably well understood. When amyloplasts settle to the bottom of the gravity-sensing cells in the root or shoot, they physically contact the endoplasmic reticulum (ER), causing the release of calcium ions from inside the ER. Calcium may be released by ion channels sensitive to mechanical stimulation. This calcium signaling in the cells causes auxin transport proteins (**PIN proteins**) to redistribute to the underside of the cell leading to the polar transport of auxin to the bottom of the cell. In roots, a high concentration of indoleacetic acid (IAA) inhibits cell elongation. The effect slows growth on the lower side of the root, while cells develop normally on the upper side. IAA has the opposite effect in shoots, where a higher concentration at the lower side of the shoot stimulates cell expansion, causing the shoot to grow up. After the shoot or root begin to grow vertically, the amyloplasts return to their normal position. Another hypotheses—involving the entire cell in the gravitropism effect—have been proposed to explain why some mutants that lack amyloplasts may still exhibit a weak gravitropic response.

Plant Tropisms in Space

Considering the fundamental role of plants in producing fresh food and recycling of air and water, plant tropism research is critical for advancing plant-based life support systems in space. Understanding of the relative strengths of the different root tropisms would be needed to properly guide root growth by technological means, as the gravity vector is absent in space. For example, by exposing roots in microgravity to blue light, they could be induced to develop away from light toward the

growth medium. Furthermore, the possibility of performing explorative experiments in the space environment, together with the development of new technologies, is crucial to pave the way toward the goal of deepening our fundamental understanding of plant tropisms and their underlying molecular networks on Earth.

Modified by Melissa Ha from Muthert, L., Izzo, L. G., van Zanten, M., & Aronne, G. (2020). Root Tropisms: Investigations on Earth and in Space to Unravel Plant Growth Direction. *Frontiers in plant science*, *10*, 1807. https://doi.org/10.3389/fpls.2019.01807. CC BY

Hydrotropism

Water acquisition is an important function of plant roots. Because water availability in the soil is often spatially and temporally patchy, roots of many species can exert directional root growth toward water; i.e., positive hydrotropism. The underlying mechanisms of hydrotropism are still being researched. Gravitropism is often dominant over hydrotropic responses, making it difficult to study hydrotropism in isolation. In contrast to phototropism and gravitropism, hydrotropism does not result from an auxin gradient resulting from directional auxin transport. However, auxin still appears to play a role in signaling hydrotropism.

Thigmotropism, Thigmomorphogensis, and Thigmonastic Movements

The shoot of a pea plant winds around a trellis while a tree grows on an angle in response to strong prevailing winds. These are examples of how plants respond to touch or wind.

The movement of a plant subjected to constant directional pressure is called thigmotropism, from the Greek words *thigma* meaning “touch,” and *tropism* implying “direction.” Tendrils are one example of plants displaying positive thigmotropism (Video 4.2.1.1). The meristematic region of tendrils is very touch sensitive; light touch will evoke a quick coiling response. Cells in contact with a support surface contract, whereas cells on the opposite side of the support expand. Application of jasmonic acid is sufficient to trigger tendril coiling without a mechanical stimulus.

Video 4.2.1.1: This video shows an example of positive thigmotropism in morning glory plants, which require a support structure of some type to grow optimally. The time lapse images were taken at 10 minute intervals. This video has no sound. Here is a description: The morning glory stems (which are modified as tendrils) grow in a counterclockwise pattern, widening their radius with each rotation. When they encounter one of the two wooden stakes on either side of the plant, grow in a tight coil around it.

Plant roots exhibit negative thigmotropism when contacting obstacles in the soil. When plant roots encounter an obstacle in their growth path, the root first continues growing in the same direction until it slips sideways. The root bends away from the stimulus and then bends again in the opposite direction, creating a step-like shape. Note that at this point the root "side stepped" the obstacle and is now continuing to grow in the original direction. If the root contacts another part of the obstacle, the same bending pattern will occur. Thigmotropism in roots may be mediated by calcium, but other signaling mechanisms have also been proposed. Following contact, the calcium concentration in the root cap is greater than that of surrounding regions. (Under regular conditions, calcium concentration in the root cap is lower.) Ultimately, the directional transport of auxin results in an auxin gradient. When touching an obstacle during downward growth, the root bends and auxin accumulates at the higher (concave) side of the root suppressing elongation. Greater elongation on the convex (lower) side of the root causes it to bend away from the obstacle.

Thigmomorphogenesis is a slow developmental change in the shape of a plant subjected to continuous mechanical stress. When trees bend in the wind, for example, growth is usually stunted and the trunk thickens. Strengthening tissue, especially xylem, is produced to add stiffness to resist the wind’s force. Researchers hypothesize that mechanical strain induces growth and differentiation to strengthen the tissues. Ethylene and jasmonate are likely involved in thigmomorphogenesis.

A **thigmonastic movement** is a touch response independent of the direction of stimulus. In the Venus flytrap, two modified leaves are joined at a hinge and lined with thin fork-like tines along the outer edges (Video 4.2.1.2). Tiny hairs are located inside the trap. When an insect brushes against these trigger hairs, touching two or more of them in succession, the leaves close quickly, trapping the prey. Glands on the leaf surface secrete enzymes that slowly digest the insect. The released nutrients are absorbed by the leaves, which reopen for the next meal.

Video 4.2.1.2: This video below shows an example of thigmonastic movements in a Venus flytrap. There is no only ambient sound in this video and no speaking. Here is a description. At 0:08, a fly enters the taco-shaped trap of the Venus flytrap. It escapes

before the tines (prongs) interlock, as shown in a slow-motion replay. At 0:42, another fly crawls into the trap. It crawls around a bit before the trap closes, locking it inside.

Another example of thigmonastic movement occurs in the sensitive plant (*Mimosa pudica*). Its leaflets and leaves retract in response to touch, and this is thought to be an adaptation that deters herbivores (Video 4.2.1.3).

Video 4.2.1.3: The leaflets of the sensitive plant retract when touched. This video has no speaking, but there are natural sounds (such as birds) in the background and laughing when the leaflets retract.

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4.2.2: Flowering

Learning Objective

Describe the environmental conditions that induce flowering.

The flowering plants (angiosperms) go through a phase of **vegetative growth** producing more stems and leaves and a flowering phase where they produce the organs for sexual reproduction. In **annuals** the vegetative phase begins with germination of the seed. Flowering follows and ends with the senescence and death of the plant. In **biennials**, the vegetative phase takes up the first year; flowering followed by death occurs the second year. In **perennials**, flowering typically occurs year after year when conditions are appropriate (Figure 4.2.2.1)



Figure 4.2.2.1: Annuals, like snapdragon (*Antirrhinum majus*), complete their life cycles in one year (or less), growing, flowering, and dying (left). Biennials, like mullein (*Verbascum*) form vegetative rosettes in the first year and flower and die the second year (middle). Perennials, like lavender (*Lavendula*), persist and flower each year (right). Images from left to right by Off2riorob (licensed under CC-BY), Dcrjsr (licensed under CC-BY), Lairich Rig (licensed under CC-BY), and Greyspshaw22 (licensed under CC-BY-SA).

Flowering involves the conversion of the apical meristem into a **floral meristem**, from which all the parts of the flower will be produced. Signals that change the fate of the apical meristem include the following:

- maturity of the plant
- temperature
- the plant hormone gibberellin
- for many plants, photoperiod (daylength; see Photoperiodism section)

Many annual plants (e.g., winter wheat) and biennial plants have their time of flowering delayed unless they have undergone a preceding period of wintertime cold. The change brought about by this prolonged exposure to the cold is called **vernalization**.

In *Arabidopsis*, vernalization involves a gene designated *Flowering Locus C* (*FLC*), which encodes a transcription factor that blocks the expression of the genes needed for flowering. Recall that one of the two DNA strands in a gene is called the sense (coding) strand and has the same sequence as the RNA transcript. The other DNA strand is called the antisense (non-coding) strand and has a sequence that is complementary to the RNA transcript. The antisense strand acts as a template during transcription. In the fall, the level of FLC mRNA is high. With the onset of cold temperatures, production of an antisense transcript of *FLC* (called *COOLAIR*) increases as does, later, a sense transcript of part of the *FLC* gene. Both of these transcripts are non-coding; that is, they are not translated into protein. Instead, they cooperate in suppressing the production of FLC mRNA and its

translation into FLC protein. With the arrival of spring, there is no FLC protein remaining to suppress flowering so flowering can begin.

The buds of many species of woody angiosperms found in temperate climates, such as apples and lilacs, also need a preceding period of cold weather before they can develop into flowers. So these plants cannot be grown successfully at lower latitudes because the winters never get cold enough (a few days at 0–10°C). This bud dormancy is localized. Prior chilling of one bud on a lilac stem enables it to flower while the other, nonchilled, buds on the stem remain dormant (Figure 4.2.2.2).

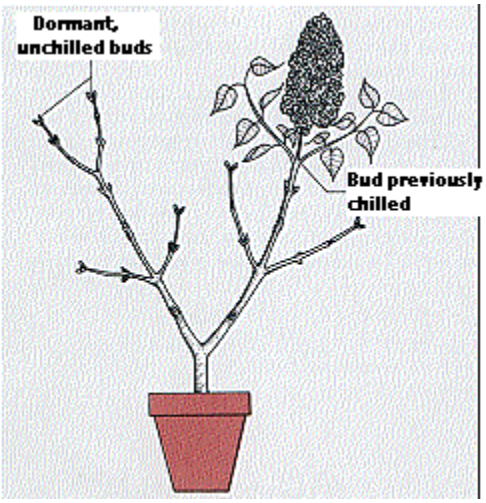


Figure 4.2.2.2: Vernalization (chilling) of lilac buds induces flowering, but the effect is localized. Unchilled buds on the same plant remain dormant.

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4.2.3: Photoperiodism

Learning Objectives

- Describe the mechanism of photoperiodism with respect to flowering.
- Distinguish among short-day, long-day, and day-neutral plants.
- Define circadian rhythms and provide examples in plants.

Detection of seasonal changes is crucial to plant survival. Although temperature and light intensity influence plant growth, they are not reliable indicators of season because they may vary from one year to the next. Day length is a better indicator of the time of year. Many angiosperms flower at about the same time every year. This occurs even though they may have started growing at different times. Their flowering is a response to the changing length of day and night as the season progresses. It helps promote cross pollination. The biological response to the timing and duration of day and night is called **photoperiodism**.

The Phytochrome System and the Red/Far-Red Response

Plants use the phytochrome system to sense the change of season, which can control flowering. The **phytochromes** are a family of photoreceptors. They are chromoproteins with a linear tetrapyrrole chromophore (a molecule that absorbs light), similar to the ringed tetrapyrrole light-absorbing head group of chlorophyll. A phytochrome is a homodimer: two identical protein molecules, each conjugated to a light-absorbing molecule (compare to rhodopsin). Plants make 5 phytochromes: **PhyA**, **PhyB**, as well as C, D, and E. There is some redundancy in function of the different phytochromes, but there also seem to be functions that are unique to one or another. The phytochromes also differ in their absorption spectrum; that is, which wavelengths (e.g., red vs. far-red) they absorb best. Phytochromes have two photo-interconvertible forms: Pr and Pfr. Pr absorbs red light (~667 nm) and is immediately converted to Pfr. Pfr absorbs far-red light (~730 nm) and is quickly converted back to Pr. Absorption of red or far-red light causes a massive change to the shape of the chromophore, altering the conformation and activity of the phytochrome protein to which it is bound. Pfr is the physiologically active form of the protein; therefore, exposure to red light yields physiological activity. Exposure to far-red light inhibits phytochrome activity. Together, the two forms represent the phytochrome system (Figure 4.2.3.1).

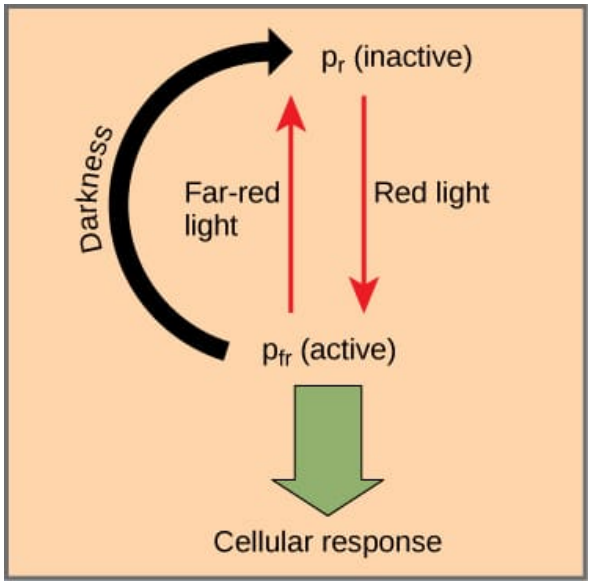


Figure 4.2.3.1: The biologically inactive form of phytochrome (Pr) is converted to the biologically active form Pfr under illumination with red light. Far-red light and darkness convert the molecule back to the inactive form.

The phytochrome system acts as a biological light switch. It monitors the level, intensity, duration, and color of environmental light. The effect of red light is reversible by immediately shining far-red light on the sample, which converts the chromoprotein to the inactive Pr form. Additionally, Pfr can slowly revert to Pr in the dark, or break down over time. In all instances, the physiological

response induced by red light is reversed. The active form of phytochrome (Pfr) can directly activate other molecules in the cytoplasm, or it can be transported to the nucleus, where it directly activates or represses specific gene expression.

Unfiltered sunlight is rich in red light but deficient in far-red light. Therefore, at dawn, all the phytochrome molecules in a leaf quickly convert to the active Pfr form, and remain in that form until sunset. In the dark, the Pfr form takes hours to slowly revert back to the Pr form. If the night is long (as in winter), all of the Pfr form reverts. If the night is short (as in summer), a considerable amount of Pfr may remain at sunrise. By sensing the Pr/Pfr ratio at dawn, a plant can determine the length of the day/night cycle. In addition, leaves retain that information for several days, allowing a comparison between the length of the previous night and the preceding several nights. Shorter nights indicate springtime to the plant; when the nights become longer, autumn is approaching. This information, along with sensing temperature and water availability, allows plants to determine the time of the year and adjust their physiology accordingly.

In 1920 two employees of the U. S. Department of Agriculture, W. W. Garner and H. A. Allard, discovered a mutation in tobacco - a variety called Maryland Mammoth - that prevented the plant from flowering in the summer as normal tobacco plants do. Maryland Mammoth would not bloom until late December. Experimenting with artificial lighting in winter and artificial darkening in summer, they found that Maryland Mammoth was affected by photoperiod. Because it would flower only when exposed to short periods of light, they called it a **short-day** plant. Examples of other short-day plants include chrysanthemums, rice (*Oryza sativa*), poinsettias, morning glory (*Pharbitis nil*), and cocklebur (*Xanthium*).

Experiments with the cocklebur have shown that the term short-day is something of a misnomer; what the cocklebur needs is a sufficiently **long night** (Figure 4.2.3.2). Short-day (long-night) plants flower in the late summer and early fall, when nights exceed a critical length (often eight or fewer hours). In short-day plants, the active form of phytochrome (Pfr) suppresses flowering. During long periods of darkness (long nights), Pfr is converted to Pr. With Pfr no longer present, flowering is not suppressed, and short-day plants flower. If a flash of light interrupts the dark period, Pr is converted back to Pfr, and flowering is suppressed.

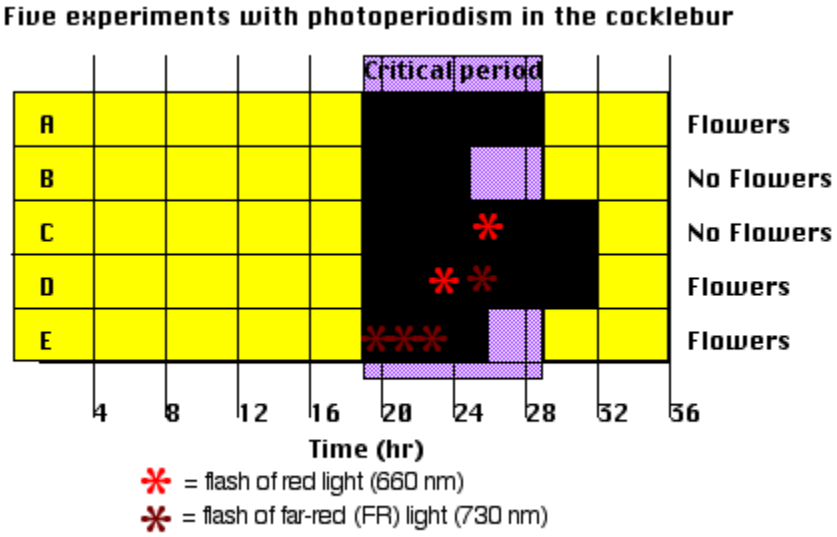


Figure 4.2.3.2: Cockleburs (adapted to the latitude of Michigan) will flower only if they have been kept in the dark for at least 8.5 hours — the **critical period** (**A** and **B**). Interruption of an otherwise long night by light — **red** (**660 nm**) rays are particularly effective — prevents flowering (**C**). Unless it is followed by irradiation with **far-red** (**730 nm**) light (**D**). An intense exposure to far-red light at the start of the night reduces the dark requirement by two hours (**E**).

Long-day (short-night) plants flower during the spring, when darkness is less than a critical length (often eight to 15 hours). Examples include spinach, *Arabidopsis,* sugar beet, and the radish flower.

Flowering in **day-neutral** plants, such as the tomato, is not regulated by photoperiod.

Photoperiodism also explains why some plant species can be grown only in a certain latitude. Spinach, a long-day plant, cannot flower in the tropics because the days never get long enough (14 hours). Ragweed, a short-day plant, fails to thrive in northern Maine because by the time the days become short enough to initiate flowering, a killing frost in apt to occur before reproduction and the formation of seeds is completed.

Some plants do not neatly fit into the categories of short day, long day, or day neutral. In 1941, Marie Taylor Clark found that flowering in scarlet sage did not flower under daylengths longer than 16 hours, suggesting it was a short-day plant; however, days that were too short (6 hours) slowed flower development. Flower development was optimal with daylengths of 10 hours.

The leaves produce a chemical signal called **florigen** that is transmitted to the apical meristems to start their conversion into floral meristems. The chemical nature of florigen has been sought for decades. The most recent evidence suggests that at least one component is the protein encoded by the gene *FLOWERING LOCUS T* (***FT***). Due to florigen signaling, the entire plant will bloom even if only a part of one leaf is exposed to the correct photoperiod (Figure 4.2.3.3).

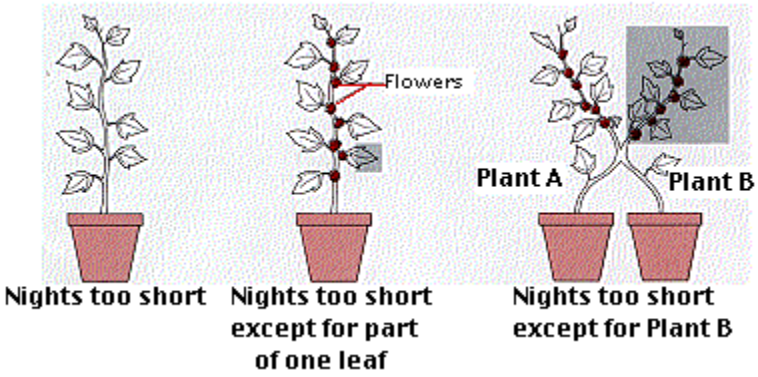


Figure 4.2.3.3: The cocklebur needs at least 8.5 hours of darkness in order to flower. Grafting a cocklebur (**B**) that receives the required period of darkness to one (**A**) that does not causes flowering in both. Evidently the florigen signal passes from **B** to **A** through their connected vascular systems.

Career Connection: Horticulturist

The word “horticulturist” comes from the Latin words for garden (hortus) and culture (cultura). This career has been revolutionized by progress made in the understanding of plant responses to environmental stimuli. Growers of crops, fruit, vegetables, and flowers were previously constrained by having to time their sowing and harvesting according to the season. Now, horticulturists can manipulate plants to increase leaf, flower, or fruit production by understanding how environmental factors affect plant growth and development.

Greenhouse management is an essential component of a horticulturist’s education. To lengthen the night, plants are covered with a blackout shade cloth. Long-day plants are irradiated with red light in winter to promote early flowering. For example, fluorescent (cool white) light high in blue wavelengths encourages leafy growth and is excellent for starting seedlings. Incandescent lamps (standard light bulbs) are rich in red light, and promote flowering in some plants. The timing of fruit ripening can be increased or delayed by applying plant hormones. Recently, considerable progress has been made in the development of plant breeds that are suited to different climates and resistant to pests and transportation damage. Both crop yield and quality have increased as a result of practical applications of the knowledge of plant responses to external stimuli and hormones.

Horticulturists find employment in private and governmental laboratories, greenhouses, botanical gardens, and in the production or research fields (Figure 4.2.3.4). They improve crops by applying their knowledge of genetics and plant physiology. To prepare for a horticulture career, students take classes in botany, plant physiology, plant pathology, landscape design, and plant breeding. To complement these traditional courses, horticulture majors add studies in economics, business, computer science, and communications.



Figure 4.2.3.4: Horticulturalist Anderson Ifui (left) with Jack McGilchrist, the technical adviser for the Australian Volunteer Initiative (right), at Honiara Botanic gardens in the Solomon Islands in 2004. Image by Peter Davis/AusAID (CC-BY).

Circadian Rhythms

Circadian rhythms are changes based on a 24-hour cycle. For example, flowers might open every morning and close every evening or vice versa. In *Oxalis* and silk tree (*Albizia julibrissin*), leaflets expand during the day and retract at night. Circadian rhythms may also involve physiological processes like photosynthetic rate or the the production of floral scent compounds.

Under constant conditions, circadian rhythms may drift out of phase with the environment (figure 4.2.3.5). However, when exposed to environmental changes (e.g., alternating day and night), the rhythms become **entrained**; that is, they now cycle synchronized with the cycle of day and night with a period of exactly 24 hours. Internal circadian clocks also adjust to changing photoperiods. Suppose a plant that flowers throughout the spring opens its flowers every morning. The sun rises earlier in the late spring compared to the early spring (photoperiod increases in late spring). As time passes and the plant detects the changing photoperiod (technically, plants measure the length of the night rather than daylength; see above), the circadian clock would adjust such that its flowers opened earlier. In *Arabidopsis*, the entrainment of circadian rhythms requires that light is detected by phytochromes (absorb red light) and cryptochromes (absorb blue light).



Figure 4.2.3.5: The leaves and leaflets of the silk tree (*Albizia julibrissin*) expand during the day (left) and retract and night (right). These diurnal (daily) movements are an example of circadian rhythms. Image is public domain.

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4.2.4: Etiolation and Shade Avoidance

Learning Objectives

- Contrast etiolated seedlings with those grown in light.
- Describe the adaptive value of etiolation.

Plants grown in the dark have elongated stems, are white or yellow (due to lack of chlorophyll), and have small leaves (Figures 4.2.4.1 and 2). This phenomenon is called **etiolation**, and it is a mechanism that increases the chance that the plant will access light.

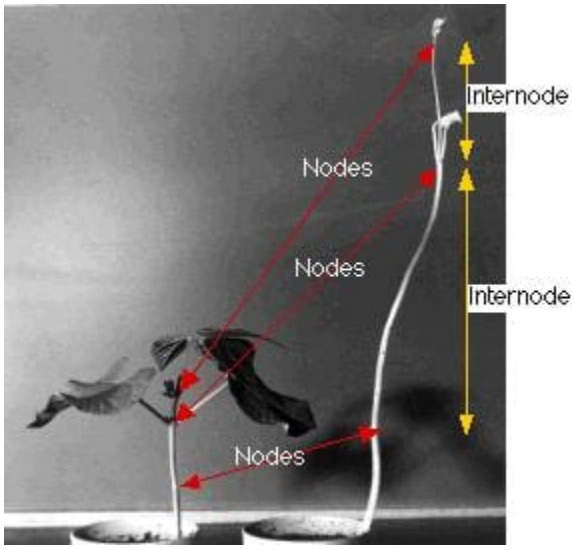


Figure 4.2.4.1: Common garden bean seedlings grown in the light (left) and in darkness (right). The dark-grown is etiolated, exhibiting elongated internodes, pale coloration, and small leaves. Each seedling has three nodes (the bottom ones where the cotyledons were attached), but the dark-grown seedling is taller because its internodes are greatly elongated. When the food reserves in its seed are exhausted, the dark-grown seedling will die (unless placed in the light).



Figure 4.2.4.2: Etiolated Spanish blue bells (*Hyacinthoides hispanica*) with elongated, yellow and white stems and leaves. Image by Chiswick Chap (licensed under CC-BY-SA)

The prevention of etiolation in *Arabidopsis* is mediated by **phytochrome B**. When sunlight (660 nm) converts Pr into Pfr, Pfr moves from the cytoplasm into the nucleus. There it stimulates the activity of DELLA proteins, which bind to and inhibit proteins called **PIFs** (phytochrome-interacting factors). PIFs are transcription factors that bind to and turn on promoters of genes that, among other effects, stimulate cell and thus stem elongation. DELLA proteins prevent PIFs from binding to the promoters of their target genes, resulting in reduced cell elongation (no etiolation) in the presence of light.

Gibberellins are plant hormones that promote stem elongation thus mimicking the etiolation response. They do this by triggering the degradation of DELLA proteins, which frees PIFS to bind to the promoters of genes needed for cell elongation.

The shade-avoidance response also involves phytochrome and and PIFs. This response helps ensure that the plant accesses enough sunlight to be able to conduct photosynthesis. Natural sunlight contains about the same amount of red (660 nm) as far-red (735 nm) light. However, chlorophyll absorbs 660 nm light strongly, so that the light that filters through a canopy of foliage is enriched in far-red light. This is absorbed by Pfr, converting it into inactive Pr such that PIFs are no longer inhibited. The now-active PIFs turn on the genes needed for auxin synthesis, and auxin stimulates stem elongation.

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4.2.5: Dormancy

Learning Objectives

- List the environmental factors that break seed dormancy (induce germination) and define the horticultural techniques based on these factors.
- Explain how phytochrome mediates light-induced germination in lettuce.

During certain time periods or environmental circumstances, active growth is not advantageous for a plant. For example, the embryos in seeds must stay dormant for long enough to disperse from the parent plant or until there are suitable conditions for growth (temperature, light availability, water, etc.). In seeds, the phytochrome system is not used to determine direction and quality of light (shaded versus unshaded). Instead, is it used merely to determine if there is any light at all. This is especially important in species with very small seeds, such as lettuce. Because of their size, lettuce seeds have few food reserves. Their seedlings cannot grow for long before they run out of fuel. If they germinated even a centimeter under the soil surface, the seedling would never make it into the sunlight and would die. In the dark, phytochrome is in the Pr (inactive form) and the seed will not germinate; it will only germinate if exposed to light at the surface of the soil. Upon exposure to light, Pr is converted to Pfr, which signals transcription of the gene that encodes **amylase**, an enzyme that breaks down starches stored in the seed into simple sugars. Germination then proceeds. Experimentally exposing lettuce seeds to red light induces germination because this converts Pr to Pfr. Exposure to far red light inhibits germination because this causes the active form of phtochrome (Pfr) to be converted to the inactive form (Pr; Figure 4.2.5.1).

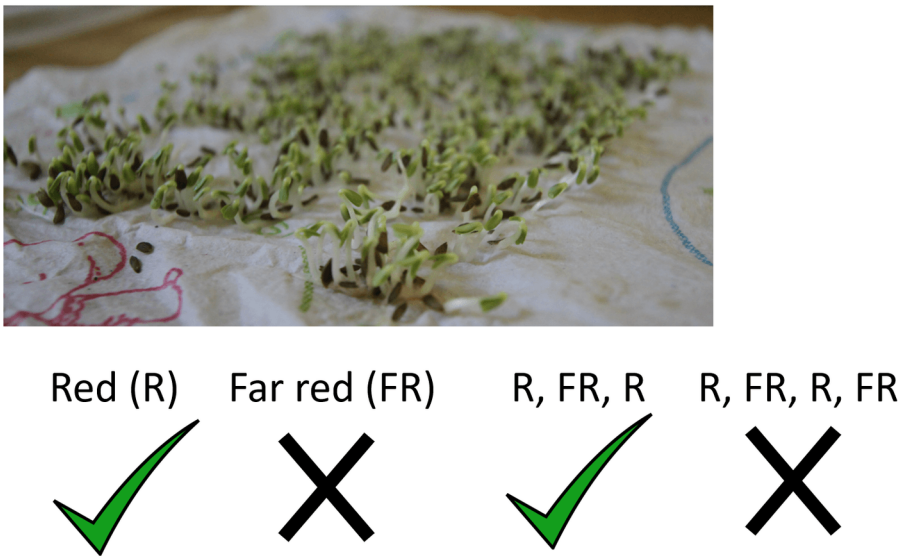


Figure 4.2.5.1: The germination of lettuce seeds (top) is controlled by light. From left to right: Lettuce seeds do not germinate in the dark, but they do germinate when exposed to red light. When exposed to far red light, lettuce seeds do not germinate. Alternating exposure to red light and far red light results in germination if red light is last in the sequence. If far red light ends the sequence, germination does not occur. Image prepared by Melissa Ha using checkmarks (public domain) and lettuce sprouts by Kanu Hawaii (licensed under CC-BY)

Several additional factors are involved in seed germination. Exposure to a cold period can also induce germination in seeds. Cold **stratification** is a horticultural technique that involves storing seeds in cold conditions to promote germination. Sometimes seeds require mechanical abrasion of the seed coat, facilitated by the soil. **Scarification** is a horticultural technique that simulates this abrasion by cutting the seed coat with a knife or other means. Seeds may also require exposure to water, which can wash chemicals from the seed coat that inhibit germination. Seeds that are dispersed by animals that eat the fruits are adapted to the acids in the digestive tract. To promote germination in these species, horticulturalists may need to bathe these seeds in acid.

Likewise, trees in certain climates become dormant in the winter (setting of winter buds; Figure 4.2.5.2). Similarly to how it

controls flowering, photoperiodism mediated by phytochrome stops vegetative growth and promotes the setting of winter buds. This occurs as the days grow shorter in the autumn. To break dormancy in the spring, the buds may need to first be exposed to cold winter temperatures. In other cases, a certain period of time just needs to pass.



Figure 4.2.5.2: Dormant bud on twig of Arizona walnut (*Juglans major*). Image by Whitney Cranshaw (licensed under CC-BY).

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4.2.6: Chapter Summary

Plants respond to light, gravity, water, physical contact, temperature, and other environmental factors. **Tropisms** are a response involve directional growth toward or away from a stimulus. **Positive phototropism** in stems is mediated by blue-light receptors called **photoreceptors** and an auxin gradient. **Positive gravitropism** in roots and **negative gravitropism** in shoots involves specialized amyloplasts called **statoliths** as well as an auxin gradient. Plants also change biological activities according to a 24-hour cycle maintained by an internal clock. These **circadian rhythms** can be **entrained** to the environment. Flowering is another response to environmental factors, such as temperature and photoperiod. **Photoperiodism** with respect to flowering involves two interconvertible forms of the red-light **phytochrome** with which plants can measure the length of the dark period (night). Seedlings respond to a lack of light by **etiolated** growth, which helps them access light. Light, temperature, rainfall, and other environmental factors can break seed dormancy (induce germination).

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

- Distinguish among phototropism, gravitropism, hydrotropism, and thigmotropism.
- Discuss the adaptive value of tropisms.
- Describe the mechanism of phototropism in shoots.
- Describe the mechanism of gravitropism in shoots and roots.
- Distinguish among thigmotropism, thigmonastic movements, and thigmomorphogenesis
- Define circadian rhythms and provide examples in plants.
- Describe the environmental conditions that induce flowering
- Describe the mechanism of photoperiodism with respect to flowering.
- Distinguish among short-day, long-day, and day-neutral plants.
- Contrast etiolated seedlings with those grown in light and describe the adaptive value of etiolation.
- List the environmental factors that break seed dormancy (induce germination) and define the horticultural techniques based on these factors.
- Explain how phytochrome mediates light-induced germination in lettuce.

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4.3: NUTRITION AND SOILS

Cucurbitaceae is a family of plants first cultivated in Mesoamerica, although several species are native to North America (Figure 4.3.1). The family includes many edible species, such as squash and pumpkin, as well as inedible gourds. In order to grow and develop into mature, fruit-bearing plants, many requirements must be met and events must be coordinated. Seeds must germinate under the right conditions in the soil; therefore, temperature, moisture, and soil quality are important factors that play a role in germination and seedling development. Soil quality and climate are significant to plant distribution and growth. The young seedling will eventually grow into a mature plant, and the roots will absorb nutrients and water from the soil. At the same time, the aboveground parts of the plant will absorb carbon dioxide from the atmosphere and use energy from sunlight to produce organic compounds through photosynthesis. This chapter will explore the complex dynamics between plants and soils.



(a) (b)

Figure 4.3.1: For this (a) squash seedling (Cucurbita maxima) to develop into a mature plant bearing its (b) fruit, numerous nutritional requirements must be met. (credit a: modification of work by Julian Colton; credit b: modification of work by "Wildfeuer"/Wikimedia Commons)

4.3.1: Essential Elements

4.3.2: Soils

4.3.3: Nutrient Cycles

4.3.4: Chapter Summary

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Thumbnail image: A root nodule of broad bean (*Vicia faba*), which hosts symbiotic nitrogen-fixing bacteria (*Rhizobium*). Nitrogen fixation converts gaseous nitrogen into ammonium, which is available in the soil to plants. Image by Whitney Cranshaw, Colorado State University, Bugwood.org (CC-BY).

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4.3.1: Essential Elements

Learning Objectives

- List the essential elements required by plants and summarize their functions.
- Describe how plants obtain nutrients, including the mechanism of cation exchange.
- Distinguish between macronutrients and micronutrients.

Plants are unique organisms that can absorb nutrients and water through their root system, as well as carbon dioxide from the atmosphere. Soil quality and climate are the major determinants of plant distribution and growth. The combination of soil nutrients, water, and carbon dioxide, along with sunlight, allows plants to grow.

The chemical composition of plants reflects the **essential elements**, which are necessary for plant growth and reproduction. For an element to be regarded as essential, three criteria are required: 1) a plant cannot complete its life cycle without the element; 2) no other element can perform the function of the element; and 3) the element is directly involved in plant nutrition. There is some disagreement of the number of essential elements for plants with experts listing as few as 15 or as many as 20. Nineteen essential elements are discussed here. While identifying essential elements may seem straightforward, the nutritional needs of plants somewhat depend on the species and environmental conditions. As a result, some may argue that certain elements, like cobalt (Co), are essential, but it is typically only considered a **beneficial element**.

Chemical Composition of Plants

The majority of the plant body consists of carbon (C), hydrogen (H), and oxygen (O). Plants obtain carbon from carbon dioxide in the atmosphere and hydrogen from the water absorbed by the roots. Oxygen atoms come from carbon dioxide and gaseous oxygen in the atmosphere, as well as from water. Water typically comprises 80 to 90 percent of the plant's total weight. However, carbon and oxygen constitute about 45% of dry plant tissue (biomass) each, and hydrogen makes up 6%. The remaining 4% of dry biomass consists of elements that are obtained from the soil. These **mineral nutrients** are categorized as macronutrients and micronutrients.

Macronutrients are required in relatively large quantities (more than 0.1% of dry biomass). The macronutrients in order of contribution to dry biomass are nitrogen (N), potassium (K), calcium (Ca), magnesium (Mg), phosphorus (P), sulfur (S), and silicon (Si). Nitrogen, potassium, and phosphorus are major components in fertilizer (figure 4.3.1.1). Silicon is only absolutely required by horsetails, but many other plant species contain silicon and benefit from its presence. Some sources consider carbon, oxygen, and hydrogen macronutrients. However, this text will not because they are obtained from the atmosphere and/or water rather than minerals in the soil.



Figure 4.3.1.1: Left: The nitrogen, potassium, and phosphorus are the primary nutrients in most fertilizers. Fertilizers feature NPK ratios, which detail the percentage of each of nutrient in the fertilizer. Right: Compost forms from decomposed vegetation and supplies plants with essential elements. Images by Kammy Algiers (CC-BY-NC).

Micronutrients are required in small quantities (less than 0.01% of dry biomass). Plant micronutrients are chlorine (Cl), iron (Fe), boron (B), manganese (Mn), sodium (Na), zinc (Zn), copper (Cu), nickel (Ni), and molybdenum (Mo). Sodium is primarily required by plants using certain photosynthetic pathways (C_4 and CAM), but like silicon, it benefits many plant species.

Absorption of Mineral Nutrients

Plants absorb most mineral nutrients from the soil as ions. Some of these essential elements are **cations**, including potassium (K^+), calcium (Ca^{2+}), magnesium (Mg^{2+}), iron (Fe^{3+} or Fe^{2+}), manganese (Mn^{2+}), sodium (Na^+), zinc (Zn^{2+}), copper (Cu^+ and Cu^{2+}), and nickel (Ni^{2+}). Other nutrients are found in the form of **anions**, including dihydrogen phosphate ($H_2PO_4^-$) or hydrogen phosphate (HPO_4^{2-}), sulfate (SO_4^{2-}), chloride (Cl^-), and molybdate (MoO_4^{2-}). Plants obtain nitrogen from the soil as nitrate (NO_3^-) or ammonium (NH_4^+). Boron is absorbed as boric acid (H_3BO_3) or its **conjugate base**, dihydrogenborate ($H_2BO_3^-$). Silicon is available as silicic acid (H_4SiO_4).

Cations in the soil are bound to negatively charged **clay** particles or the organic acids that form **humus** (see Soils), and this makes it difficult for plants to absorb them. Plants have a mechanism called **cation exchange**, which releases cations and frees them for absorption (figure 4.3.1.2). This occurs when the roots pump protons (H^+) into the soil. The protons bind to the clay and humus, taking the place of the cation nutrients, such as K^+ ,Ca^{2+}, and Mg^{2+}. These nutrients are then freely dissolved in the water in the soil and can enter the roots. Roots can also increase proton concentration (decrease pH) of the soil indirectly by releasing carbon dioxide, which reacts with water to form carbonic acid. Protons released when carbonic acid molecules disassociate can then contribute to cation exchange.

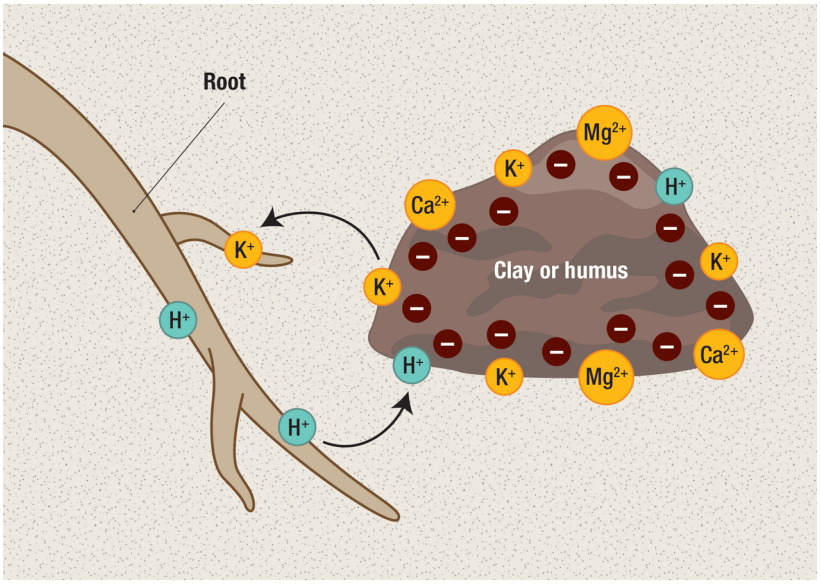


Figure 4.3.1.2: The process of **cation exchange** occurs when protons (H^+) are released from roots. Protons bind to negatively charged clay or humus, releasing other cations, including calcium (Ca^{2+}), potassium (K^+), and magnesium (Mg^{2+}). The root can then absorb the cation nutrients that were released. Image by Jen Valenzuela (CC-BY-NC).

To absorb iron, plants must either release protons creating acidic conditions, which promote the conversion (reduction) of Fe^{3+} to Fe^{2+}, or produce special compounds called **siderophores**. These bind to Fe^{3+} forming a complex, which can then be transported into the root.

Because anions are not attracted to clay and humus in the soil, it is easier for them to **leach** from the soil when it is irrigated or when it rains. For this reason, anions like nitrates and phosphates are common causes of **eutrophication** (see Threats to Biodiversity).

Mycorrhizae, the symbiotic fungi that grow around or inside of root cells, help plants absorb a variety of mineral nutrients, particularly phosphorus.

Functions of Essential Elements

Each essential element has multiple roles. For example, calcium acts a second messenger, transmitting signals within a cell, and as a cofactor, assisting enzyme function. While multiple functions for most of the essential elements are described below, they are organized based on one of their primary functions.

Elements in Biological Macromolecules

Carbon dioxide is a reactant in photosynthesis, and carbon is required to form biological macromolecules (carbohydrates, lipids, proteins, and nucleic acids). For example, the carbohydrate cellulose is the main structural component of the plant cell wall and makes up over thirty percent of plant matter (figure 4.3.1.3). Besides the biological macromolecules, plants contain many other organic molecules, such as the chlorophyll and plastoquinone, and all of these contain carbon. In fact, **organic molecules** are defined as those that contain carbon and hydrogen, typically have carbon-to-carbon bonds, and are often larger and more complex than inorganic molecules.

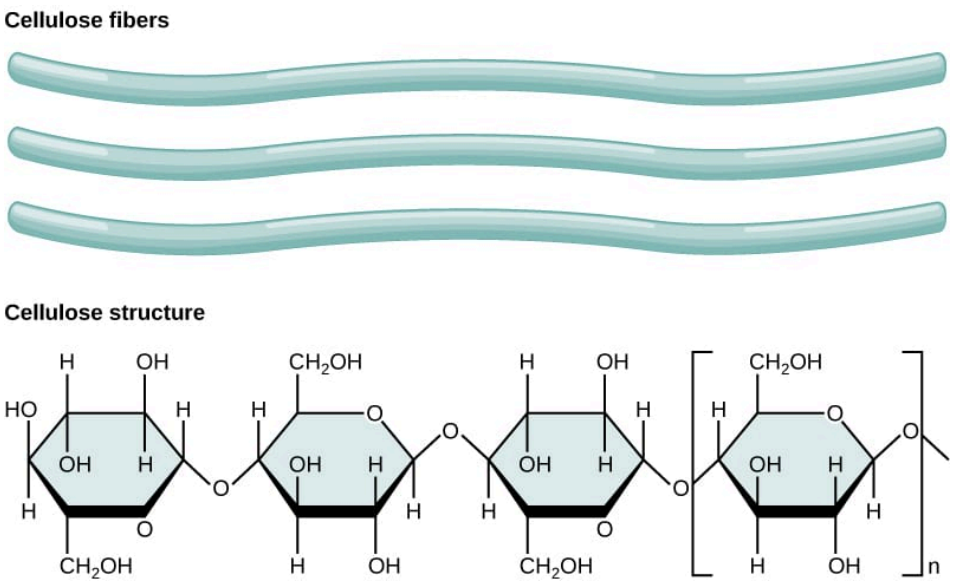


Figure 4.3.1.3: Cellulose is a polysaccharide found in plant cell walls. It is the most abundant organic compound on earth. Plants are able to make their own cellulose, and they ultimately obtain carbon dioxide from the atmosphere to do so.

Hydrogen and oxygen are components of water and all of the biological macromolecules. Hydrogen is found in all organic compounds, and oxygen is found in many, as well. Gaseous oxygen is also a reactant in aerobic cellular respiration.

Nitrogen is part of proteins, nucleic acids, and chlorophyll. Nitrogen is also used in the synthesis of some vitamins, such as vitamin B6, which serves as a coenzyme in protein synthesis.

Phosphorus is necessary to synthesize nucleic acids and **phospholipids**, which form the plasma membrane, chloroplasts, and many other plant cell structures. **Adenosine triphosphate (ATP)**, the primary form of ready-to-use energy in the cell, contains three phosphate groups, each with a phosphate in the center (figure 4.3.1.4). Plants generate ATP by binding a phosphate group with adenosine diphosphate (ADP) through **oxidative phosphorylation** during cellular respiration and during **photophosphorylation** in photosynthesis.

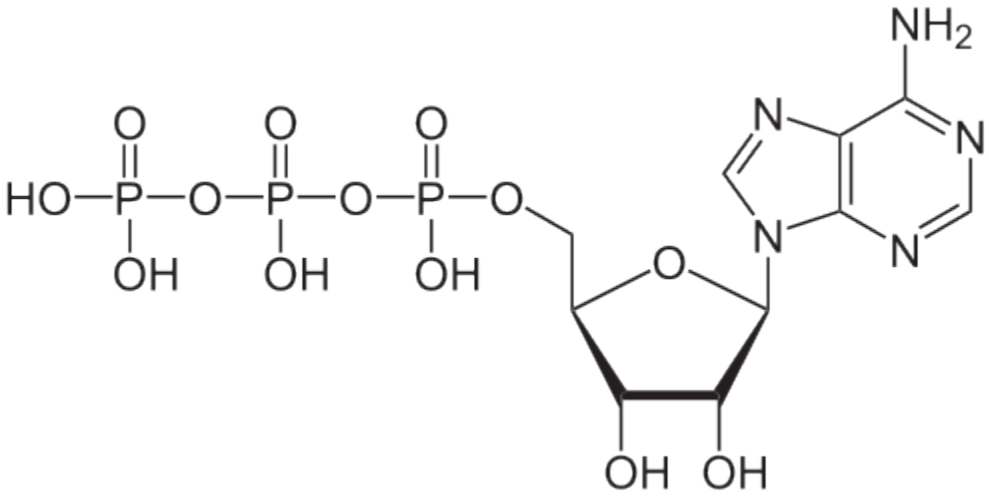


Figure 4.3.1.4: Chemical structure of adenosine triphosphate (ATP). Image by NEUROtiker (public domain).

Sulfur is part of certain amino acids, such as cysteine and methionine, and is present in several coenzymes. For example, it connects coenzyme A to acetyl groups, forming acetyl CoA, the starting molecule for the Krebs cycle (tricarboxylic acid cycle) of cellular respiration. Sulfur also plays a role in photosynthesis as a component of the iron sulfur proteins that transfer electrons from photosystem I to $NADP^+$.

Elements that Maintain Ion Balance

Potassium and chlorine play roles in regulating stomatal opening and closure. As the openings for gas exchange, stomata help maintain a healthy water balance. This process is supported by a potassium ion pump as well as the movement of chloride through symport and anion channels. Potassium is also a cofactor for many enzymes, including those involved in photosynthesis. Chlorine, along with calcium, is essential for **water photolysis**, which generates oxygen during photosynthesis. Calcium also transmits signals within the cell (including as a second messenger during stomatal closure), acts as a cofactor for many enzymes, and contributes to cell wall structure at the **middle lamellae** between adjacent cells.

Elements Involved in Enzyme Function

Magnesium, zinc, nickel, copper, and manganese all function as cofactors. Specifically, manganese assists with water photolysis. Zinc aids with the synthesis of chlorophyll. Nickel is involved breaking down urea. Copper can serve as a cofactor or a component of the enzyme itself. For example, the copper in plastocyanin allows it to transport electrons during photophosphorylation. In addition to aiding with enzyme function, magnesium is additionally important to the photosynthetic process because it is part of chlorophyll (figure 4.3.1.5).

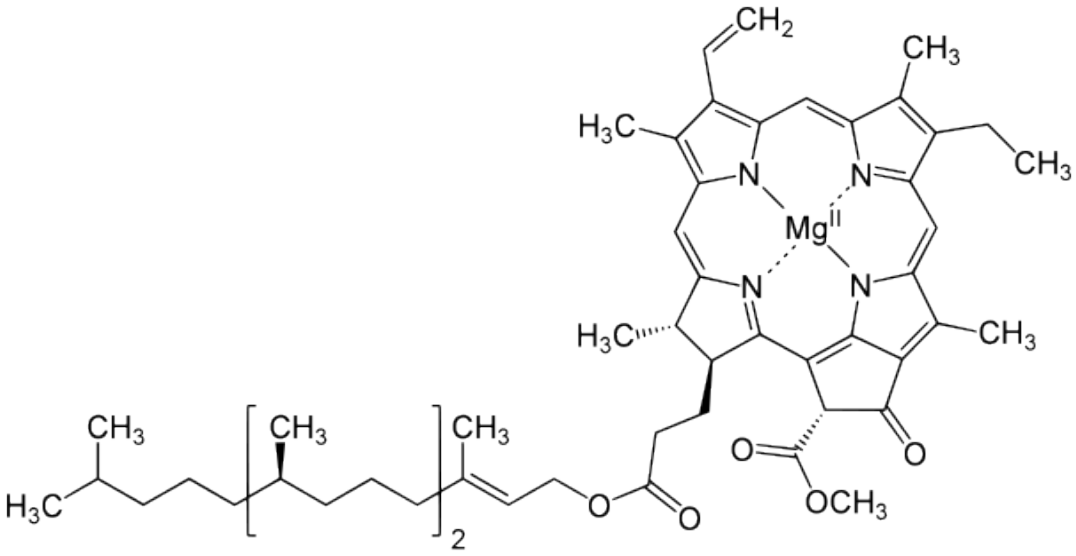


Figure 4.3.1.5: The chemical structure of chlorophyll a. Image by Yikrazuul (public domain).

Like copper, iron facilitates electron transport in enzymes. It is found in the cytochromes involved in oxidative phosphorylation and photophosphorylation. Iron is also plays a role in synthesizing chlorophyll. Molybdenum is a component of a few enzymes in plants, including one that helps plants use nitrate.

Sodium helps some plants synthesize phosphoenolpyruvate (PEP). Carbon dioxide is added to PEP to form oxaloacetate during C_4 and CAM photosynthesis.

Elements in Cell Walls

Of course, polysaccharides such as cellulose, which contain carbon, hydrogen, and oxygen, are the main components of plant cell walls. However, other elements play more minor roles. Calcium in the middle lamella was already mentioned. Additionally, silicon plays a role in cell wall structure in horsetails. Boron is involved in cell wall structure and elongation.

Nutrient Deficiencies

Deficiencies in any of these nutrients—particularly the macronutrients—can adversely affect plant growth (Figure 4.3.1.6). Depending on the specific nutrient, a lack can cause stunted growth, slow growth, or **chlorosis** (yellowing of the leaves). Extreme deficiencies may result in leaves showing signs of **necrosis** (death of the tissues). The location of the symptoms, such as in old

leaves versus young leaves, can also be telling. Some nutrients like iron are immobile, so an iron deficiency would cause chlorosis in young leaves. On the other hand, magnesium can be transported from old leaves to developing ones. As a result, a magnesium deficiency would be manifested as chlorsis in the old leaves.

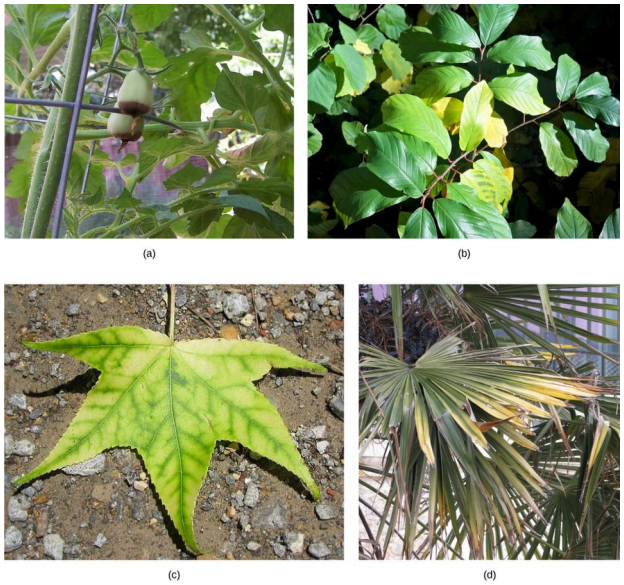


Figure 4.3.1.6: Nutrient deficiency is evident in the symptoms these plants show. This (a) grape tomato suffers from blossom end rot caused by calcium deficiency. The fruits have turned dark brown on the bottom. The yellowing in this (b) *Frangula alnus* results from magnesium deficiency. Inadequate magnesium also leads to (c) intervenal chlorosis, seen here in a sweetgum leaf. This (d) palm is affected by potassium deficiency. (credit c: modification of work by Jim Conrad; credit d: modification of work by Malcolm Manners)

Everyday Connection: Hydroponics

Hydroponics is a method of growing plants in a water-nutrient solution instead of soil (Figure 4.3.1.7). Since its advent, hydroponics has developed into a growing process that researchers often use. Scientists who are interested in studying plant nutrient deficiencies can use hydroponics to study the effects of different nutrient combinations under strictly controlled conditions. Hydroponics has also developed as a way to grow flowers, vegetables, and other crops in greenhouse environments. You might find hydroponically grown produce at your local grocery store. Today, many lettuces and tomatoes in your market have been hydroponically grown.



Figure 4.3.1.7: These plants are grown indoors and without soil using hydroponics and artificial lighting. Image by Satoshi KINOKUNI (CC-BY).

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4.3.2: Soils

Learning Objectives

- Identify and describe each component of soil.
- Distinguish among sand, silt, and clay and explain how particle size influences water holding capacity and soil texture.
- Describe each horizon in a typical soil profile.
- Explain how soils are formed, describing each of the five major factors that affects soil formation and composition.
- Explain what determines soil pH and how soil pH affects nutrient absorption by plants.

Plants obtain mineral nutrients from the soil, which serves as a natural medium for land plants. Soil is the outer loose layer that covers the surface of Earth. Soil quality is a major determinant, along with climate, of plant distribution and growth. Soil quality depends not only on the chemical composition of the soil, but also on climate, topography, and organisms living in the soil. In agriculture, the history of the soil, such as the cultivating practices and previous crops, modifies the characteristics and fertility of that soil.

Soil Composition

Soil consists of organic matter (about 5%), inorganic mineral matter (40-45% of soil volume), and water (about 25%) and air (about 25%). The amount of each of the four major components of soil depends on the amount of vegetation, soil compaction, and water present in the soil.

The organic material consists of dead organisms in various stages of decomposition. It is dark-colored because it contains **humus**, partially decayed matter containing organic acids. Humus enriches the soil with nutrients, gives the soil a loose texture that holds water, and allows air to diffuse through it. Oxygen is essential to permit cellular respiration in plant roots, decay organisms, and other inhabitants of the soil. The organic component of soil serves as a cementing agent, returns nutrients to the plant, allows soil to store moisture, makes soil tillable for farming, and provides energy for soil microorganisms. Most soil microorganisms—bacteria, algae, or fungi—are dormant in dry soil, but become active once moisture is available.

The inorganic material of soil consists of rock, slowly broken down into smaller particles that vary in size. Soil particles that are 100 µm to 2 mm in diameter are **sand**. (A **micrometer**, µm, 10^{-6} m, or a millionth of a meter.) Soil particles between 2 and 100 µm are called **silt**, and even smaller particles, less than 2 µm in diameter, are called **clay**.

Soil should ideally contain 50 percent solid material and 50 percent pore space (Figure 4.3.2.1). **Pore space** refers to the gaps in between soil particles. The larger the soil particles, the larger the pore spaces. Water can quickly pass through large pore spaces, so soils high in sand drain easily. Smaller soil particles have more surface area relative to volume and produce narrow pore spaces. Water clings to these surfaces, and soils high in clay thus retain water. (Clay is also negatively charged, which attracts water.) About one-half of the pore space should contain water, and the other half should contain air.

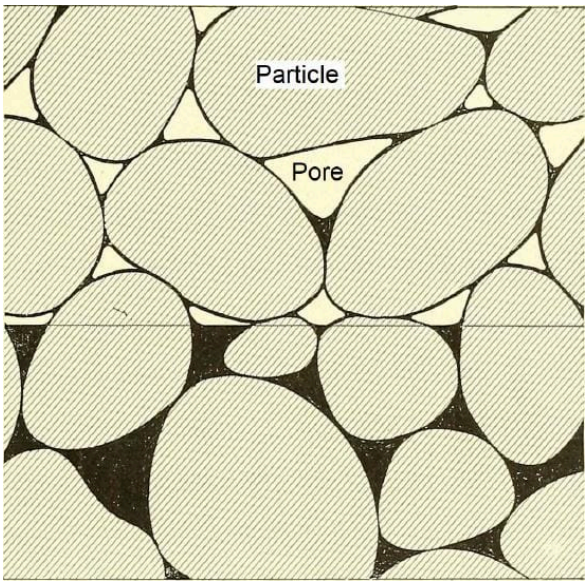


Figure 4.3.2.1: Soil particles and the pore spaces in between them. The black shading represents water, which fills the pore spaces in the lower portion of the soil and clings to narrow portions of pore space in the top portion of the soil. Image from "Forest physiography; physiography of the United States and principles of soils in relation to forestry" (public domain).

Water holding capacity is a measure of of the soils ability to retain water. Technically, it is the field capacity minus the permanent wilting percentage. The **field capacity** is the percentage of water retained by the soil after excess water is allowed the drain. The **permanent wilting percentage** (permanent wilting point) is the amount of water left in the soil once the plants have fatally wilted. This measures the amount of water stored in the soil that is actually available to plants.

Soils texture is based on percentages of sand, silt, and clay (Figure 4.3.2.2). Soils that have a high percentage of one particle size are named after that particle (a clay soil has a high percentage of clay). Other soils have a mixture of two particle sizes and very little of the third size. For example, silty clay has roughly 50% clay and 50% silt while sandy clay has 50-60% sand and 35-50% clay. Some soils have no dominant particle size and contain a mixture of sand, silt, and humus. These soils are called **loams**, and they are optimal for agriculture. A medium loam has roughly 40% sand, 40% silt, and 20% clay. Larger particles (sand) facilitate drainage, and small particles (clay) facilitate water retention, so loam soils both have good drainage and can remain moist. Medium loams have a water holding capacity of approximately 35%. Soils that deviate slightly from a medium loam include loamy sand, sandy loam, sandy clay loam, clay loam, silty clay loam, and silty loam.

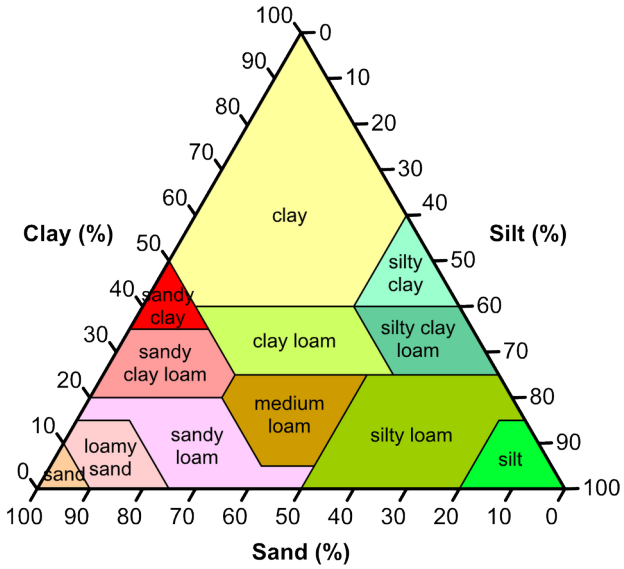


Figure 4.3.2.2: A soil composition pyramid (or soil triangle) is used to determine the soil texture based on the percentages of sand, silt, and clay. First, find the percentage of clay and trace a line horizontally to the right. At the same time, find the percentage of silt and trace a line diagonally (down and to the left, parallel to the clay axis). The two lines will meet at the correct soil type. For example, traced lines from 20% clay and 40% silt intersect at the medium loam category. To confirm, trace a diagonal line (down and to the right, parallel to the sit axis) from this point to the sand axis. This line cross the axis at 40%. In summary, a line can be traced from each axis that is parallel to axis that is counterclockwise of it. Most soils that contain more than 40% are classified as clays. Exceptions are silty clays, which contain 40-60% clay and 40-60% silt. Another exception are sandy clays, which contain 35-50% clay and 50-70% sand. Clay loams and silty clay loams contain 25-40% clay. Clay loams contain 20-60% silt, and silty clay loams contain 60-75% silt. Sandy clay loams contain 20-35% clay and 50-80% sand. Medium loams contain 5-25% clay, 20-50% silt, and 30-55% sand. Soils with more than 50% silt and no more than 25% clay are either silty loams or silts. Silts have 80-100% silt and no more than 15% clay. Sand have 90-100% sand. Loamy sands have 75-90% sand and no more than 15% clay. A soil with a composition that does not fit into the already described categories would be a sandy loam. Image by Richard Wheeler/Zephyris at English Wikipedia (CC-BY-SA).

Organic Versus Mineral Soils

Soils can be divided into two groups based on how they form. **Organic soils** are those that are formed from sedimentation and often contain more than 30% organic matter. They form when organic matter, such as leaf litter, is deposited more quickly than it can be decomposed (Figure 4.3.2.3). **Mineral soils** are formed from the weathering of rocks, typically contain no more than 30% organic matter, and are primarily composed of inorganic material. **Weathering** occurs when biological, physical, and chemical processes, such as erosion, leaching, or high temperatures, break down rocks.



Figure 4.3.2.3): Decomposition of organic material occurs very slowly in this acidic bog. The organic material accumulates, which is characteristic of organic soils. Image by William L. Farr (CC-BY-SA).

Soil Horizons

Soil distribution is not homogenous because its formation results in the production of layers; together, the vertical section of a soil is called the **soil profile**. Within the soil profile, soil scientists define zones called horizons. A **horizon** is a soil layer with distinct physical and chemical properties that differ from those of other layers.

The typical soil profile has four distinct layers: 1) O horizon; 2) A horizon; 3) B horizon and 4) C horizon (Figure 4.3.2.4). Some soils may have additional layers or lack one of these layers. The thickness of the layers is also variable, and depends on the factors that influence soil formation. In general, immature soils may have O, A, and C horizons, whereas mature soils may display all of these, plus additional layers.

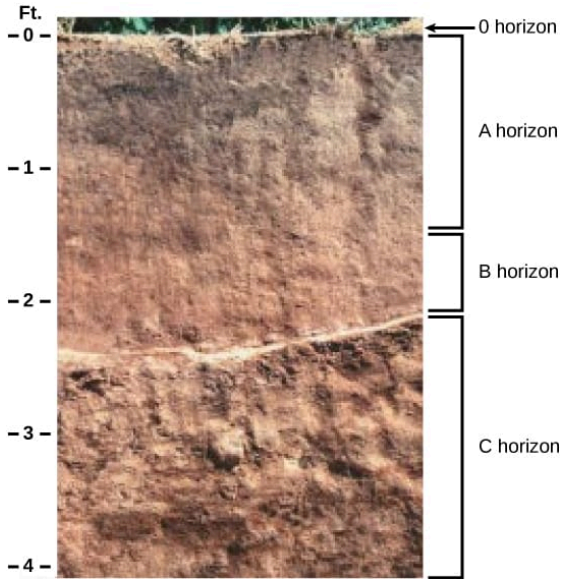


Figure 4.3.2.4: The San Joaquin soil profile has an O horizon, A horizon, B horizon, and C horizon. The numbers to the left of the soil profile represent depth in feet. The O horizon is at the soil surface and is a rich black color. The brown A horizon starts beneath the O horizon and extends to about two-and-a-half feet beneath the surface. The B horizon is reddish brown and extends from the bottom of the A horizon to about two feet deep. The C horizon extends from the bottom of the B horizon to the bottom of the photo at a depth of four feet. The C horizon is light brown and has a coarser consistency than the A or B horizons. (credit: modification of work by USDA)

O horizon

The very top of the **O horizon** (organic layer) consists of partially decayed organic debris like leaves. This horizon is usually dark in color because of humus.

A horizon

The **A horizon** (topsoil) consists of a mixture of organic material with inorganic products of weathering, and it is therefore the beginning of true mineral soil. In this area, rainwater percolates through the soil and carries materials from the surface. The A horizon may be only 5 cm (2 in.), or it may over a meter. For instance, river deltas like the Mississippi River delta have deep layers of topsoil. Microbial processes occur in the top soil, and this horizon supports plant growth. Many organisms, such as earthworms and insects, live among the plant roots in this horizon.

B horizon

The **B horizon** (subsoil) consists of small particles that have moved downward, resulting in a dense layer in the soil. In some soils, the B horizon contains nodules or a layer of calcium carbonate. The subsoil is usually lighter in color that topsoil and often contains an accumulation of minerals.

C horizon

The **C horizon** (soil base), includes the **parent material**, the organic and inorganic substances from which soils form. Weathering parent material represents the first steps in the chemical breakdown of rock into soil. Often the weathered parent material is underlain by the parent material itself, although in some places it has been carried from another location by wind, water, or glaciers. Beneath the C horizon lies bedrock. The chemical nature of the parent material, whether granite, limestone, or sandstone, for example, has a great influence on the fertility of the soil derived from it.

Factors Affecting Soil Formation and Composition

The fundamental factors that affect soil genesis can be categorized into five elements: climate, organisms, topography (or relief), parent material, and time. One could say that the relief, climate, and organisms dictate the local soil environment and act together to cause weathering and mixing of the soil parent material over time.

Climate

The role of climate in soil development includes aspects of temperature and precipitation. Soils in very cold areas with permafrost conditions (such as the Arctic tundra) tend to be shallow and weakly developed due to the short growing season. In warm, tropical climates, soils tend to be thicker (but lacking in organic matter), with extensive leaching and mineral alteration due to heavy precipitation. In such climates, organic matter decomposition and chemical weathering occur at an accelerated rate. The presence of moisture and nutrients from weathering will also promote biological activity: a key component of a quality soil. The soils of four biomes are described below as examples of the effects of climate on soil composition.

Tropical Rainforests

The lushness of the jungle biome is somewhat illusory. While productivity is high, the soils themselves tend to be of very poor quality (Figure $4.3.2.5$). Because of the high rainfall, nutrients are quickly washed out of the topsoil unless they are incorporated in the forest plants. As plant and animal debris falls to the ground, it is quickly decomposed because of the warmth and moisture there. Thus minerals are found mainly in the forest plants, not in the soil. When the plants are removed and cultivation attempted, the soils quickly lose fertility. The situation is made worse by the lack of humus. Additionally, the topsoil may be no thicker than 5 cm (~2 inches), and most of these soils have high iron and aluminum content. Once exposed to the sun, these soils quickly bake into a brick-like material that cannot be cultivated.



Figure 4.3.2.5: Soil profile from tropical rainforest in Loreto, Peru. The yellow tape indicates depth in ft on the left and in cm on the right. The brown A horizon is approximately 20 cm deep. Two distinct layers of soil are found in the subsoil (B horizon), an orange-brown upper layer and a lighter bottom layer. Image by Soil Science (CC-BY).

Temperate Forests

These regions receive 75–100 cm (~30-39") or more of precipitation each year. Enough water falls on the soil so that much of it passes down to the water table. As it does so, it carries minerals with it. Such soils tend to be acidic and of low and (if unattended) diminishing fertility when used for agriculture. Only by regular fertilization and liming (to restore calcium and raise pH) can productive agriculture be carried out in them. In the U.S., the soils east of the Appalachian Mountains tend to be of this sort (Figure 4.3.2.6).



Figure 4.3.2.6: Soil profile from Pennsylvania temperate forest. Meter tape indicates depth in cm. Dark A horizon, which is approximately 30 cm deep, rests on top of the lighter subsoil (B horizon). Image by Soil Science (CC-BY).

Temperate Grasslands

In the plains of North America, the annual rainfall is sufficiently low (~50 cm, 20") that little or no rainfall percolates down to the water table. Calcium and other minerals are not carried below the reach of plant roots and so remain available for use. This keeps the pH and general fertility high (Figure 4.3.2.7). Except to the extent that minerals are lost when crops are removed, the minerals

simply recycle from subsoil to topsoil and back to the subsoil. The self-restoring fertility of the soils of the plains states accounts for this region being the "breadbasket" of the nation (and other countries as well).

The grasses in undisturbed prairie are perennial. Their extensive root systems help prevent soil erosion, and the return of the season's above-ground growth to the topsoil returns minerals and provides humus to it. These advantages are diminished when annual grasses such as wheat and corn are grown instead and removed in the harvest.



Figure 4.3.2.7: A temperate grassland soil profile. The A horizon (topsoil) is very dark brown, indicating much organic content. Underneath, the subsoil (B horizon) is a medium brown, still containing a fair amount of organic content. This soil has an additional layer, the E (eluviated) horizon, which is lighter and located between the A and B horizons. It consists of minerals leached from the top soil. Image by USDA NRCS (public domain).

Deserts

The rainfall here is so low, 25 cm (10") per year or less, that any water that does not immediately run off remains near the surface and is largely lost by evaporation. The **salts** it carries are left near the top of the soil. Their accumulation may make the soil so alkaline and so salty that most crops cannot be grown (Figure 4.3.2.8).

In the U. S., the situation is especially severe in the Great Basin because water flowing down from the mountains—bearing its load of dissolved salts—cannot flow on to the ocean but simply flows out onto the valley floors and evaporates. Large areas of formerly unproductive desert in the United States, Israel, and Egypt have been converted into fertile fields through irrigation. However, even the best irrigation water contains dissolved salts. If just enough water is applied to meet the needs of the crop, the salts are never carried deep in the soil. The high rate of evaporation found in these areas hastens the accumulation of salts in the upper layers of the soil. If uncorrected, the condition may become so severe that only salt-tolerant crops, like sugar beets, can be grown.



Figure 4.3.2.8: Salt formations at the Badwater Basin in Death Valley, California. Minerals accumulate when water pools in this low-lying area, making conditions impossible for agriculture. Some plants, like pickleweed and saltgrass, are adapted to grow around the edges of the salt flats. Image by "Mike" Michael L. Baird (CC-BY).

Organisms

The presence of living organisms in the soil (**soil biota**) greatly affects soil formation and structure. A diversity of animals found in the soil such as nematodes, spiders, insects, centipedes, millipedes, pillbugs, slugs, and earthworms (Figure 4.3.2.9). The soil also contains microorganisms like bacteria, archaea, fungi, and "protists". Animals and microorganisms can produce pores and crevices, and plant roots can penetrate into crevices to produce more fragmentation. Plant secretions promote the development of microorganisms around the root, in an area known as the **rhizosphere**. Through the process of **hydraulic redistribution**, plants can relocate water in the soil. For example, deep roots can pull water from the lower soil levels and release it at the upper levels. Additionally, leaves and other material that fall from plants decompose and contribute to soil composition. Microorganisms not only decompose organic matter, but contribute to other processes in nutrient cycles, such as nitrogen fixation.

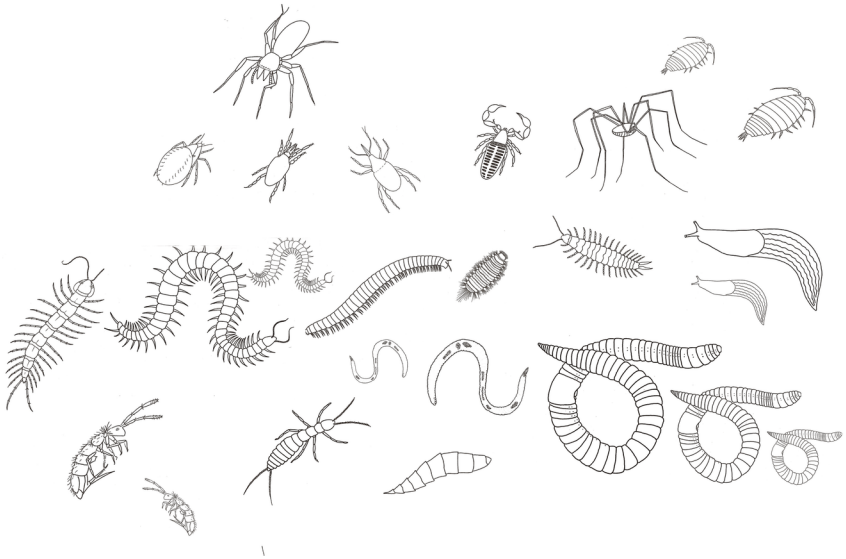


Figure 4.3.2.9: Illustration of animals commonly found in the soil. Image by Arne Hendriks (CC-BY)

Parent Material

Mineral soils form directly from the weathering of bedrock, the solid rock that lies beneath the soil, and therefore, they have a similar composition to the original rock. Other soils form in materials that came from elsewhere, such as sand and glacial drift. Materials located in the depth of the soil are relatively unchanged compared with the deposited material. Sediments in rivers may have different characteristics, depending on whether the stream moves quickly or slowly. A fast-moving river could have sediments of rocks and sand, whereas a slow-moving river could have fine-textured material, such as clay and silt.

The type of parent material may also affect the rapidity of soil development. Parent materials that are highly weatherable (such as volcanic ash) will transform more quickly into highly developed soils, whereas parent materials that are quartz-rich, for example, will take longer to develop. Parent material also provide nutrients to plants and can affect soil internal drainage.

Topography

Regional surface features (familiarly called “the lay of the land”) can have a major influence on the characteristics and fertility of a soil. Topography affects water runoff, which strips away parent material and affects plant growth. Steeps soils are more prone to erosion and may be thinner than soils that are relatively flat or level. **Infiltration**, the percolating of water through the soil, is limited in steep soils.

The local topography can have important microclimatic effects. In the northern hemisphere, south-facing slopes are exposed to more direct sunlight angles and are thus warmer and drier than north-facing slopes. The cooler, moister north-facing slopes have a more dynamic plant community due to less **evapotranspiration** (the combination of liquid water escaping as water vapor and water vapor exiting stomata in plants). They consequently have thicker soils because extensive root systems stabilize the soil and reduce erosion (Figure 4.3.2.10).



Figure 4.3.2.10: A north-facing slope (left) and south-facing slope (right) in the Mediterranean climate (chaparral) of the Santa Monica Mountains, California. Vegetation on the north-facing slope is denser due to cool, moist conditions relative to the south-facing slope. Iamge by Noah Elhardt (CC-BY).

Soil drainage affects mineral composition and organic matter accumulation. Well-drained soils, generally on hills or sideslopes, are more brownish or reddish due to conversion of ferrous iron (Fe^{2+}) to minerals with ferric (Fe^{3+}) iron. More poorly drained soils in flat areas tend more be more greyish, greenish-grey (gleyed), or dark colored, due to iron reduction (to Fe^{2+}) and accumulation and preservation of organic matter in areas tending towards anoxic. Areas with poor drainage also tend to be lowlands into which soil material may wash and accumulate from surrounding uplands, often resulting in overthickened A or O horizons. In contrast, steeply sloping areas in highlands may experience erosion and have thinner surface horizons

Time

Time is an important factor in soil formation because soils develop over long periods. Soil formation is a dynamic process. Materials are deposited over time, decompose, and transform into other materials that can be used by living organisms or deposited onto the surface of the soil.

In general, soil profiles tend to become thicker (deeper), more developed, and more altered over time. However, the rate of change is greater for soils in youthful stages of development. The degree of soil alteration and deepening slows with time and at some point, after tens or hundreds of thousands of years, may approach an equilibrium condition where erosion and deepening (removals and additions) become balanced. **Young soils** (< 10,000 years old) are strongly influenced by parent material and typically develop horizons and character rapidly. Over time, as weathering processes deepen, mix, and alter the soil, the parent material becomes less recognizable as chemical, physical, and biological processes take their effect. **Moderate age soils** (roughly 10,000 to 500,000 years old) are slowing in profile development and deepening, and may begin to approach equilibrium conditions. **Old soils** (>500,000 years old) have generally reached their limit as far as soil horizonation and physical structure, but may continue to alter chemically or mineralogically.

Soil development is not always continual. Geologic events such as landslides, glacier advance, or the rising of shorelines can rapidly bury soils. Erosions in rivers and shorelines can cause removal or truncation of soils, and wind or flooding slowly deposited sediment that add to the soil. Animals can mix the soil and sometimes cause **soil regression**, a reversal or "bump in the road" for the normal path of development, and this increases development over time.

Soil pH and Nutrient Availability

Most plants grow well in soils at a pH of 5.5-6.5. These acidic conditions mean that there is a greater proton concentration. Protons can bind to negative soil particles, freeing essential elements that occur as cations in the soil, similar to the mechanism of cation exchange. Additionally, acidic conditions help rocks break down, which adds mineral nutrients to the soil. Some nutrients also dissolve more easily at this pH, making it easier for roots to absorb them. Finally, some cations will precipitate, becoming unavailable to plants, if the soil is alkaline (basic).

Soil pH also indirectly affects nutrient availability by influencing decomposition rates by microorganisms. When conditions are extremely acidic or basic, decomposition is slowed. Even in the pH range that is suitable for decomposition, the microbial community differs depending on pH with fungi becoming more dominant in slightly acidic conditions.

Several factors determine soil pH. Organic material in soil decreases pH to an extent, but it also acts as a buffer, limiting changes in pH. Climate is also important, with high amounts of rainfall increasing leaching and lowering pH. Some types parent material, such as those high in silicon, decrease pH, while others, such as limestone increase pH.

Soil Taxonomy

Soils are classified into one of 12 soil orders based on soil horizons, how they form, and their chemical compositions. For example, Mollisols (Figure 4.3.2.7), which are found in temperate grasslands, have a thick topsoil rich in organic content. Aridisols, on the other hand, are dry soils that contain calcium carbonate and are found in deserts. Each soil order is further divided into suborders. See USDA's The Twelve Orders of Soil Taxonomy and The Twelve Soil Orders from the University of Idaho for more details.

Career Connections: Soil Scientist

A soil scientist studies the biological components, physical and chemical properties, distribution, formation, and morphology of soils (Figure 4.3.2.11). Soil scientists need to have a strong background in physical and life sciences, plus a foundation in mathematics. They may work for federal or state agencies, academia, or the private sector. Their work may involve collecting data, carrying out research, interpreting results, inspecting soils, conducting soil surveys, and recommending soil management programs.



Figure 4.3.2.11: This soil scientist is studying the horizons and composition of soil at a research site. Image by Norm Stephens (public domain).

Many soil scientists work both in an office and in the field. According to the United States Department of Agriculture (USDA), "A soil scientist needs good observation skills to be able to analyze and determine the characteristics of different types of soils. Soil types are complex and the geographical areas a soil scientist may survey are varied. Aerial photos or various satellite images are often used to research the areas. Computer skills and geographic information systems help the scientist to analyze the multiple facets of geomorphology, topography, vegetation, and climate to discover the patterns left on the landscape." Soil scientists play a key role in understanding the soil's past, analyzing present conditions, and making recommendations for future soil-related practices.

References

Careers in Soil Science. National Resources Conservation Service / United States Department of Agriculture. Accessed 2020-08-05.

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4.3.3: Nutrient Cycles

Learning Objectives

- Explain the processes of carbon, nitrogen, and phosphorus cycling.
- Explain the process by which rhizobia infect legumes and form root nodules.

Nutrient cycles, also known as **biogeochemical cycles**, describe the movement of chemical elements through different media, such as the atmosphere, soil, rocks, bodies of water, and organisms. Nutrient cycles keep essential elements available to plants and other organisms. The cycling of three macronutrients are discussed below. The first is the carbon cycle. Plants acquire carbon through photosynthesis. The nitrogen and phosphorus cycles are also discussed, and plant acquire nitrogen and phosphorus as mineral nutrients from the soil.

The Carbon Cycle

The carbon cycle is actually comprised of several interconnected cycles: one dealing with rapid carbon exchange among living organisms and the other dealing with the long-term cycling of carbon through geologic processes (Figure 4.3.3.1). The overall effect is that carbon is constantly recycled in the dynamic processes taking place in the atmosphere, at the surface and in the crust of the earth. The vast majority of carbon resides as inorganic minerals in crustal rocks. Other **reservoirs** of carbon, places where carbon accumulates, include the oceans and atmosphere. Some of the carbon atoms in your body today may long ago have resided in a dinosaur's body, or perhaps were once buried deep in the Earth's crust as carbonate rock minerals.

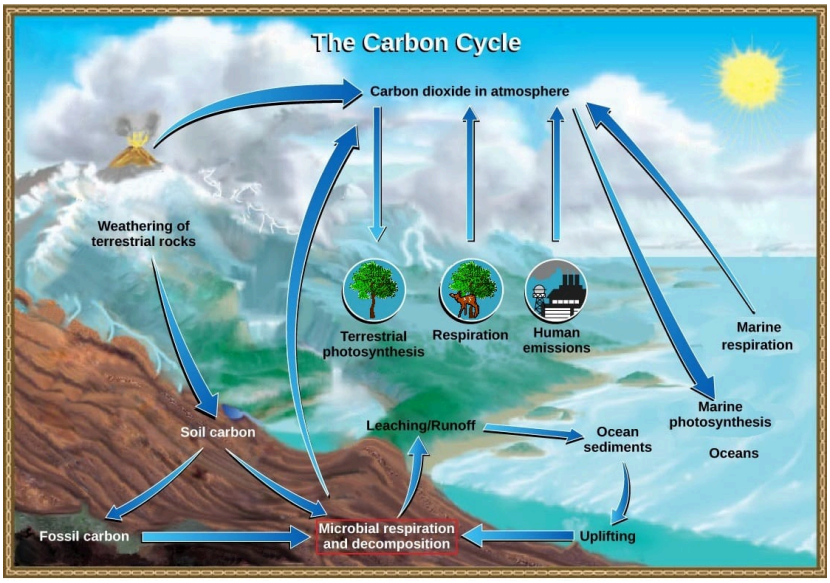


Figure 4.3.3.1: Carbon dioxide in the atmosphere is converted to organic carbon through photosynthesis by terrestrial organisms (like trees) and marine organisms (like algae). Respiration by terrestrial organisms (like trees and deer) and marine organisms (like algae and fish) release carbon dioxide back into the atmosphere. Additionally, microbes that decompose dead organisms release carbon dioxide through respiration. Weathering of terrestrial rocks also brings carbon into the soil. Carbon in the soil enters the water through leaching and runoff. It can accumulate into ocean sediments and reenter land through uplifting. Long-term storage of organic carbon occurs when matter from living organisms is buried deep underground and becomes fossilized. Volcanic activity and, more recently, human emissions stored carbon back into the carbon cycle. Modified from John M. Evans and Howard Perlman, USGS using tree and deer (both public domain).

Carbon Cycles Slowly between Land and the Ocean

On land, carbon is stored in soil as organic carbon in the form of decomposing organisms or terrestrial rocks. Decomposed plants and algae are sometimes buried and compressed between layers of sediments. After millions of years fossil fuels such as coal,

oil, and natural gas are formed. The **weathering** of terrestrial rock and minerals release carbon into the soil.

Carbon-containing compounds in the soil can be washed into bodies of water through **leaching.** This water eventually enters the ocean. Atmospheric carbon dioxide also dissolves in the ocean, reacting with water molecules to form **carbonate** ions (CO_3^{2-}). Some of these ions combine with calcium ions in the seawater to form **calcium carbonate** ($CaCO_3$), a major component of the shells of marine organisms. These organisms eventually die and their shells form sediments on the ocean floor. Over geologic time, the calcium carbonate forms limestone, which comprises the largest carbon reservoir on Earth.

Carbonate also precipitates in sediments, forming carbonate rocks, such as limestone. Carbon sediments from the ocean floor are taken deep within Earth by the process of **subduction**: the movement of one tectonic plate beneath another. The ocean sediments are subducted by the actions of **plate tectonics**, melted and then returned to the surface during volcanic activity. Plate tectonics can also cause **uplifting**, returning ocean sediments to land.

Carbon Cycles Quickly between Organisms and the Atmosphere

Carbon dioxide is converted into glucose, an energy-rich organic molecule through **photosynthesis** by plants, algae, and some bacteria. They can then produce other organic molecules like complex carbohydrates (such as starch), proteins and lipids, which animals can eat. Most terrestrial autotrophs obtain their carbon dioxide directly from the atmosphere, while marine autotrophs acquire it in the dissolved form (bicarbonate, HCO_3^-).

Plants, animals, and other organisms break down these organic molecules during the process of **aerobic cellular respiration**, which consumes oxygen and releases energy, water and carbon dioxide. Carbon dioxide is returned to the atmosphere during gaseous exchange. Another process by which organic material is recycled is the decomposition of dead organisms. During this process, bacteria and fungi break down the complex organic compounds. Decomposers may do respiration, releasing carbon dioxide, or other processes that release methane (CH_4). Photosynthesis and respiration are actually reciprocal to one another with regard to the cycling of carbon: photosynthesis removes carbon dioxide from the atmosphere and respiration returns it. A significant disruption of one process can therefore affect the amount of carbon dioxide in the atmosphere.

Cellular respiration is only one process that releases carbon dioxide. Physical processes, such as the eruption of volcanoes and release from **hydrothermal vents** (openings in the ocean floor) add carbon dioxide to the atmosphere. Additionally, the **combustion** of wood and fossil fuels releases carbon dioxide. The level of carbon dioxide in the atmosphere is greatly influenced by the reservoir of carbon in the oceans. The exchange of carbon between the atmosphere and water reservoirs influences how much carbon is found in each.

Nitrogen Cycle

Getting nitrogen into living organisms is difficult. Plants and algae are not equipped to incorporate nitrogen from the atmosphere (where it exists as tightly bonded, triple covalent N_2) although this molecule comprises approximately 78 percent of the atmosphere. Because most of the nitrogen is stored in the atmosphere, the atmosphere is considered a **reservoir** of nitrogen.

Nitrogen Fixation

The nitrogen molecule (N_2) is quite inert. To break it apart so that its atoms can combine with other atoms requires the input of substantial amounts of energy. **Nitrogen fixation** is the process of converting nitrogen gas into ammonia (NH_3), which spontaneously becomes ammonium (NH_4^+). Ammonium is found in bodies of water and in the soil (Figure $4.3.3.2$).

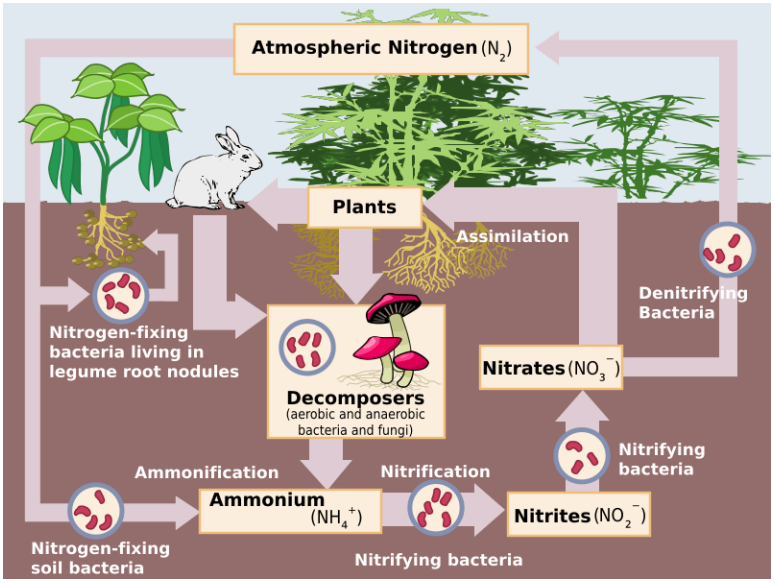


Figure 4.3.3.2: In the nitrogen cycle, nitrogen-fixing bacteria in the soil or legume root nodules convert nitrogen gas (N_2) from the atmosphere to ammonium (NH_4^+). Nitrification occurs when bacteria convert ammonium to nitrites (NO_2^-) and then to nitrates (NO_3^-). Nitrates re-enter the atmosphere as nitrogen gas through denitrification by bacteria. Plants assimilate ammonium and nitrates, producing organic nitrogen, which is available to consumers. (Only the assimilation of nitrates is shown in the diagram.) Decomposers, including aerobic and anaerobic bacteria and fungi) break down organic nitrogen and release ammonium through ammonification. (credit: "Nitrogen cycle" by Johann Dréo & Raeky is licensed under CC BY-SA 3.0)

Three processes are responsible for most of the nitrogen fixation in the biosphere. The first is **atmospheric fixation** by lightning. The enormous energy of lightning breaks nitrogen molecules and enables their atoms to combine with oxygen in the air forming nitrogen oxides. These dissolve in rain, forming nitrates, that are carried to the earth. Atmospheric nitrogen fixation probably contributes some 5-8% of the total nitrogen fixed. The second process is **industrial fixation.** Under great pressure, at a temperature of 600°C, and with the use of a catalyst, atmospheric nitrogen and hydrogen (usually derived from natural gas or petroleum) can be combined to form ammonia (NH3). Ammonia can be used directly as fertilizer, but most of it is further processed to urea and ammonium nitrate (NH4NO3).

The third process is **biological fixation**. Some nitrogen-fixing bacteria, like *Azotobacter*, are free-living. Others (*Rhizobium* and *Bradyrhizobium*) form a symbiotic relationship with plants in Fabaceae (bean or legume family), which includes beans, peas, soybeans, alfalfa, clovers, and many other species (Figure 4.3.3.3). Bacteria that form root nodules in legumes are informally called rhizobia. *Frankia* forms root nodules in alders, which are non-legume trees. Nitrogen-fixing cyanobacteria that are symbiotic with the water fern *Azolla* are essential to maintaining the fertility of semi-aquatic environments like rice paddies. Lichens that contain cyanobacteria can also fix nitrogen. Biological nitrogen fixation requires a complex set of enzymes and a huge expenditure of ATP. Although the first stable product of the process is ammonia, this is quickly incorporated into protein and other organic nitrogen compounds.



Figure 4.3.3.3: The root nodules of this soybean contain nitrogen-fixing bacteria. Image by United Soybean Board (CC-BY).

Rhizobia live freely in the soil, but they cannot fix atmospheric nitrogen until they have infected the roots of a legume. Legumes provide nitrogen-fixing bacteria with carbohydrates for energy and limit oxygen in the root nodule. **Nitrogenase**, the enzyme that fixes nitrogen, is inhibited by oxygen, but the bacteroids still need some oxygen to conduct cellular respiration to produce ATP. Legumes produce **leghemoglobin**, which binds oxygen like the hemoglobin of vertebrates. This reduces oxygen availability in the root nodule. Leghemoglobin contains iron and appears red when bound to oxygen; in fact, a freshly-cut nodule is red or pink (Figure 4.3.3.4).

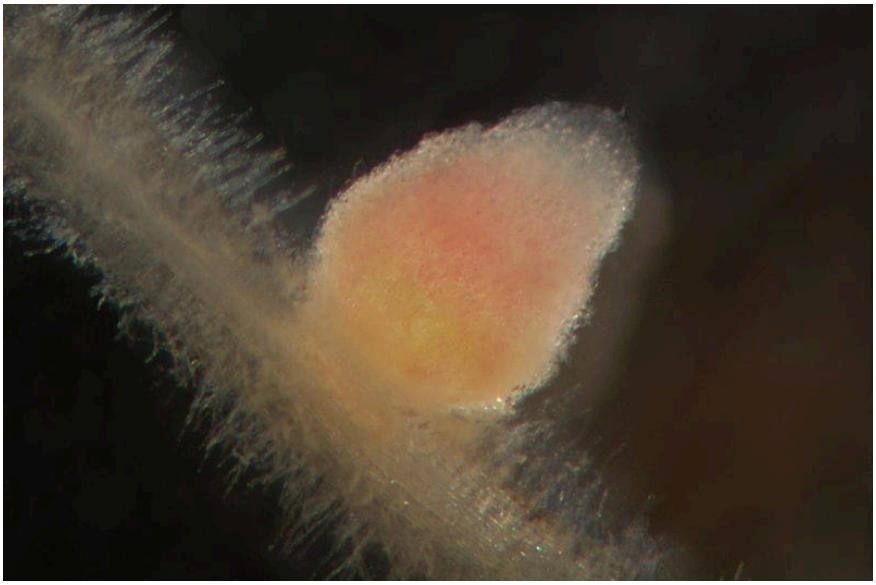


Figure 4.3.3.4: A dissected *Medicago* root nodule, which is cut in half. The pink coloration is due to leghemoglobin. Image by Ninjatacoshell (CC-BY-SA).

Root hairs release chemicals called **flavonoids**, which cause bacteria to synthesize **Nod factors**. These are chemical signals that bind to root epidermal cell receptors and induce the legume to produce nodules. Nod factors mediate interactions between specific strains of rhizobia and the associated legume species. Different strains of rhizobia produce different Nod factors, and different legumes produce receptors of different specificity. Because of the specificity of the interaction between the Nod factor and the receptor on the legume, some strains of rhizobia will infect only peas, some only clover, some only alfalfa, etc. The treating of legume seeds with the proper strain of rhizobia is a routine agricultural practice.

If the combination is correct, the bacteria enter an epidermal cell of the root and then migrate into the cortex. Their path runs within an intracellular channel that grows through one cortex cell after another. This **infection thread** is constructed by root hair,

not the bacteria, and is formed only in response to the infection. When the infection thread reaches a cell deep in the cortex, it bursts, and the rhizobia are engulfed by endocytosis into membrane-enclosed **symbiosomes** within the cytoplasm. At this time the cortical (cortex) cell goes through several rounds of mitosis—without cytokinesis —so the cell becomes **polyploid**. The cortical cells then begin to divide rapidly forming a **nodule**. This response is driven by the translocation of cytokinins from epidermal cells to the cells of the cortex. The rhizobia also go through a period of rapid multiplication within the nodule cells. Then they begin to change shape and lose their motility. The **bacteroids**, as they are now called, may almost fill the cell. Only now does nitrogen fixation begin.

Nitrification

Ammonium is converted by bacteria and archaea into nitrites (NO_2^-) and then nitrates (NO_3^-) through the process of **nitrification**. Like ammonium, nitrites and nitrates are found in water and the soil.

Denitrification

Some nitrates are converted back into nitrogen gas, which is released into the atmosphere. The process, called **denitrification**, is conducted by bacteria.

Assimilation

Ammonium and nitrates can be used directly by plants and other producers to make organic molecules such as DNA and proteins through the process of **assimilation**. This nitrogen is now available to consumers. Organic nitrogen is especially important to the study of ecosystem dynamics because many processes, such as primary production, are limited by the available supply of nitrogen.

Ammonification

Consumers excrete organic nitrogen compounds that return to the environment. Additionally dead organisms at each trophic level contain organic nitrogen. Microorganisms, such as bacteria and fungi, decompose these wastes and dead tissues, ultimately producing ammonium through the process of **ammonification.**

Phosphorus Cycle

Several forms of nitrogen (N_2, NH_4^+, NO_3^-, etc.) were involved in the nitrogen cycle, but phosphorus remains primarily in the form of the phosphate ion (PO_4^{3-}). Also in contrast to the nitrogen cycle, there is no form of phosphorus in the atmosphere.

Rocks are a reservoir for phosphorus, and these rocks have their origins in the ocean. Phosphate-containing ocean sediments form primarily from the bodies of marine organisms and from their excretions. However, volcanic ash, aerosols, and mineral dust may also be significant phosphate sources. This sediment is then moved to land over geologic time by the uplifting of Earth's surface (Figure 4.3.3.5). The movement of phosphate from the ocean to the land and through the soil is extremely slow, with the average phosphate ion having an oceanic residence time between 20,000 and 100,000 years.

Weathering of rocks releases phosphates into the soil and bodies of water. Plants can assimilate phosphates in the soil and incorporate it into organic molecules, making phosphorus available to consumers in terrestrial food webs. Waste and dead organisms are decomposed by fungi and bacteria, releasing phosphates back into the soil. Some phosphate is leached from the soil, entering into rivers, lakes, and the ocean. Primary producers in aquatic food webs, such as algae and photosynthetic bacteria, assimilate phosphate, and organic phosphate is thus available to consumers in aquatic food webs. Similar to terrestrial food webs, phosphorus is reciprocally exchanged between phosphate dissolved in the ocean and organic phosphorus in marine organisms.

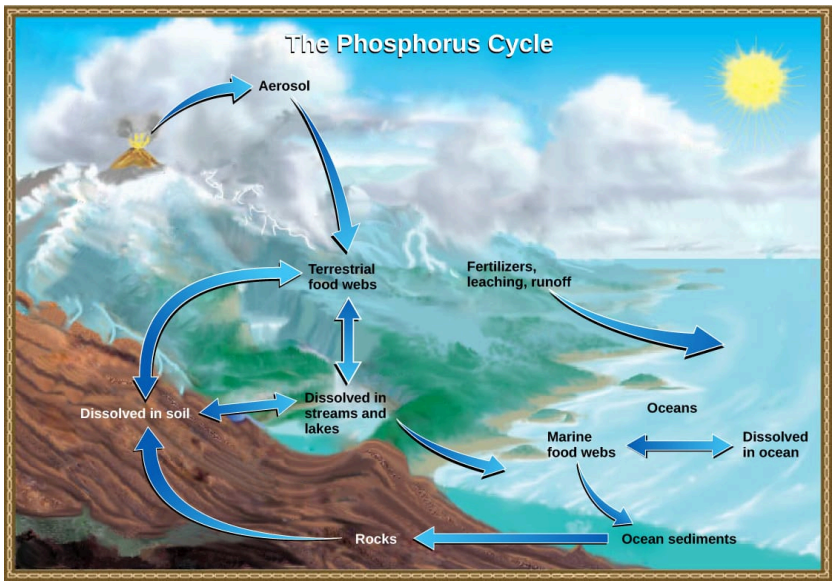


Figure 4.3.3.5: In nature, phosphorus exists as the phosphate ion (PO_4^{3-}). Phosphate enters the atmosphere from volcanic aerosols, which precipitate to Earth. Weathering of rocks also releases phosphate into the soil and water, where it becomes available to terrestrial food webs. Some of the phosphate from terrestrial food webs dissolves in streams and lakes, and the remainder enters the soil. Phosphate enters the ocean via surface runoff, groundwater flow, and river flow, where it becomes dissolved in ocean water or enters marine food webs. Some phosphate falls to the ocean floor where it becomes sediment. If uplifting occurs, this sediment can return to land. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

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4.3.4: Chapter Summary

Essential elements are indispensable elements for plant growth. Plants can absorb mineral nutrients and water through their root system, and carbon dioxide from the atmosphere. **Mineral nutrients** are divided into macronutrients and micronutrients. The **macronutrients** plants require are nitrogen, potassium, calcium, magnesium, phosphorus, sulfur, and silicon. Important **micronutrients** include chlorine, iron, boron, manganese, sodium, zinc, copper, nickel, and molybdenum.

Soil consists of organic and inorganic material as well as water and air. The organic material of soil is made of **humus**, which improves soil structure and provides nutrients. Soil inorganic material consists of rock slowly broken down into smaller particles that vary in size, such as sand, silt, and loam. Soils form slowly as a result of biological, physical, and chemical processes. Soil is not homogenous because its formation results in the production of layers called a **soil profile**. Most soils have four distinct **horizons,** or layers: O, A, B, and C. Their composition is influenced by the climate, presence of living organisms, topography, parent material, and time.

The chemical elements that organisms need continuously cycle through ecosystems. Cycles of matter are called **biogeochemical cycles,** or **nutrient cycles**, because they include both biotic and abiotic components and processes.

In the carbon cycle, carbon enters the soil through **weathering** of rocks and **leaches** into bodies of water. Aquatic organisms produce **calcium carbonate**, which ultimately forms ocean sediments. Through the process of **uplifting**, ocean sediments return to land. On shorter time scales, **photosynthesis** removes carbon dioxide from the atmosphere and converts it to organic carbon. Through **aerobic cellular respiration** by plants, animals, decomposers, and other organisms, organic carbon breaks down, releasing carbon dioxide back into the atmosphere.

Nitrogen gas in the atmosphere cannot be used by plants. Through **nitrogen fixation**, bacteria convert nitrogen into ammonium, which can then be converted to nitrites and nitrates through **nitrification**. Both free-living and symbiotic bacteria, some of which form **root nodules**, fix nitrogen. Plants can **asssimilate** ammonium and nitrates, making organic nitrogen available to consumers. Decomposition of organic matter releases ammonium back into the soil through the process of **ammonification**. **Denitrifying** bacteria release nitrogen gas from unused nitrates back into the atmosphere.

The phosphorus cycle is a simpler process than the nitrogen cycle. **Phosphates** enter the soil and water through **weathering** of rocks, where they can be assimilated. Assimilation and decomposition allow phosphates to cycle in terrestrial and marine ecosystems. Some phosphates are **leached** from the soil ultimately into the ocean, where the sediment, making ocean sediments a **reservoir** for phosphorus. Uplifting can move phosphorus-containing rocks to land.

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

- List the essential elements required by plants and summarize their functions.
- Describe how plants obtain nutrients, including the mechanism of cation exchange.
- Distinguish between macronutrients and micronutrients.
- Identify and describe each component of soil.
- Distinguish among sand, silt, and clay and explain how particle size influences water holding capacity and soil texture.
- Describe each horizon in a typical soil profile.
- Explain how soils are formed, describing each of the five major factors that affects soil formation and composition.
- Explain what determines soil pH and how soil pH affects nutrient absorption by plants.
- Explain the processes of carbon, nitrogen, and phosphorus cycling.
- Explain the process by which rhizobia infect legumes and form root nodules.

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4.4: HORMONES

Learning Objectives

- Explain the defining characteristics of a hormone.
- Name the five major plant hormones.

A plant's sensory response to external stimuli relies on chemical messengers (**hormones**). Plant hormones affect all aspects of plant life, from flowering to fruit setting and maturation (Figure $4.4.a$, and from phototropism to leaf fall. Just as in animals, hormones are signaling molecules which are present in very small amounts, transported throughout the plant body, and only elicit in responses in cells which have the appropriate hormone receptors. In plants, hormones travel large throughout the body such as through the vascular tissue (xylem and phloem) or cell-to-cell via plasmodesmata. Potentially every cell in a plant can produce plant hormones. In contrast, many animal hormones are produced only in specific glands. Plants do not have specialized hormone-producing glands.

Plant hormones are a group of unrelated chemical substances that affect plant growth, development, and other physiological processes. Five major plant hormones are traditionally described: **auxins** (particularly IAA), **cytokinins**, **gibberellins** (GAs), **abscisic acid** (ABA), and **ethylene**. Auxins, cytokinins, and gibberellins are groups of plant hormones whereas abscisic acid and ethylene are single compounds. Additional signaling molecules, such as jasmonates and salicylic acid are key in defense against pathogens and herbivores.



Figure $4.4.1$: Ripening of fruits such as bananas is mediated by plant hormones. Image by Forest Starr and Kim Starr (CC-BY).

- Hormones

4.4.1: Auxin
4.4.2: Cytokinins
4.4.3: Gibberellins
4.4.4: Abscisic Acid
4.4.5: Ethylene
4.4.6: Summary Table
4.4.7: Other Signaling Molecules
4.4.8: Chapter Summary

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Thumbnail image: A normal barley seedling (right) and a mutant deficient in the hormone gibberellic acid. The mutant produces less of the active hormone, and does not grow as rapidly. Image and description (modified) by CSIRO (CC-BY).

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4.4.1: Auxin

Learning Objectives

- Explain the mechanism of polar auxin transport.
- Identify locations of synthesis and actions of auxin.
- Define apical dominance and explain the role of auxin in maintaining it.
- Describe the commercial applications of auxin.
- Interpret and predict outcomes of experiments that demonstrate the action of auxin.

The term auxin is derived from the Greek word *auxein*, which means "to grow." While many synthetic auxins are used as herbicides, **indole-3-acetic acid** (**IAA**) is the only naturally occurring auxin that shows physiological activity (Figure 4.4.1.1). Auxin is synthesized in apical meristems, young leaves, and developing seeds.

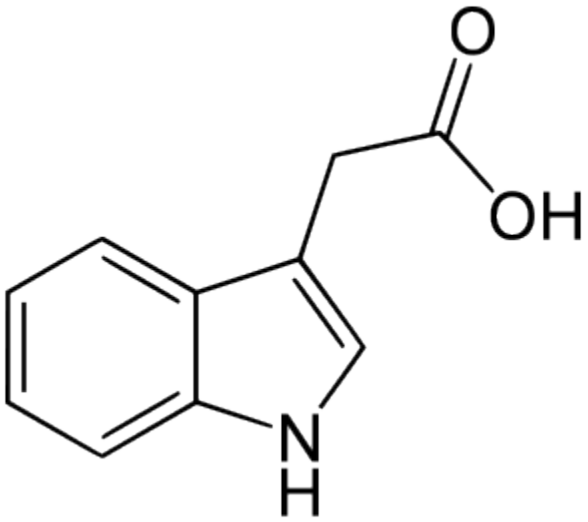


Figure 4.4.1.1: Chemical structure of indole-3-acetic acid (IAA)

The Discovery of Auxin

Recall from the Tropisms section that the Boysen-Jensen experiment showed a chemical signal must be downward from the tip of the coleoptile tip along the shaded side, resulting in phototropism. Went extracted the chemical signal involved in the Boysen-Jensen experiment. He removed the tips of several coleoptiles of oat, *Avena sativa*, seedlings. He placed these on a block of agar for several hours. At the end of this time, the agar block itself was able to initiate resumption of growth of the decapitated coleoptile. The growth was vertical because the agar block was placed completely across the stump of the coleoptile and no light reached the plant from the side (Figure 4.4.1.2). The unknown substance that had diffused from the agar block was named auxin. The amount of auxin in coleoptile tips was far too small to be purified and analyzed chemically. Therefore, a search was made for other sources of auxin activity.

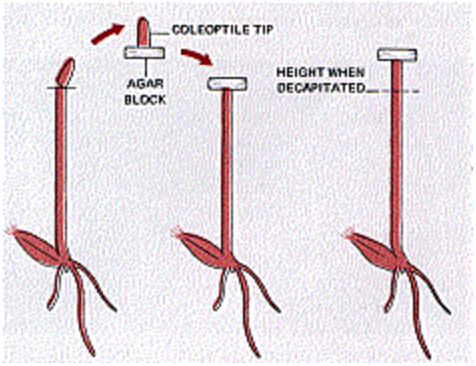


Figure 4.4.1.2: Went's experiment showing that the coleoptile transferred a chemical signal (now know to be auxin) into an agar block. The agar block could then stimulate cell elongation in the absence of the coleoptile tip.

This search was aided by a technique called the *Avena* test developed by Went for determining the relative amount of auxin activity in a preparation. The material to be assayed is incorporated into an agar block, and the block is placed on one edge of a decapitated *Avena* coleoptile. As the auxin diffuses into that side of the coleoptile, it stimulates cell elongation and the coleoptile bends away from the block (Figure 4.4.1.3). The degree of curvature, measured after 1.5 hours in the dark, is proportional to the amount of auxin activity (e.g., number of coleoptile tips used). The use of living tissue to determine the amount of a substance, such as in the *Avena* test, is called a **bioassay**.

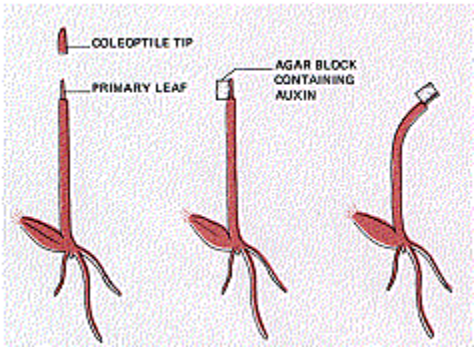


Figure 4.4.1.3: In the *Avena* test, the coleoptile tip is removed. (The primary leaf pierces the coleoptile.) Plant tissue is then allowed to transfer the chemical signal (now know to be auxin) into an agar block. The agar block is then placed on one side of the coleoptile, resulting in bending in the absence of the coleoptile tip.

The *Avena* test soon revealed that substances with auxin activity occur widely in nature. One of the most potent was first isolated from human urine. It was **indole-3-acetic acid** (**IAA**) and turned out to be the auxin actually used by plants.

Auxin Transport

Auxin moves through the plant by two mechanisms, called polar and nonpolar transport.

Polar Transport

In contrast to the other major plant hormones, auxins can be transported in a specific direction (**polar transport**) through parenchyma cells. The cytoplasms of parenchyma cells are neutral (pH = 7), but the region outside the plasma membranes of adjacent cells (the **apoplast**) is acidic (pH = 5). When auxin is in the cytoplasm, it releases a proton and becomes an anion (IAA-). It cannot pass through hydrophobic portion of the plasma membrane as an anion, but it does pass through special auxin efflux transporters called **PIN proteins.** Eight different types of these transmembrane proteins have been identified so far. When IAA- enters the acidic environment of the apoplast, it is protonated, becoming IAAH. This uncharged molecule can then pass through the plasma membrane of adjacent cells through diffusion or via **influx transporters**. Once it enters the cytoplasm, it loses its proton, becoming IAA^- again. PIN proteins can be unevenly distributed around the cell (for example, only occurring on the bottom of the cell), which directs the flow of auxin (Figure 4.4.1.4).

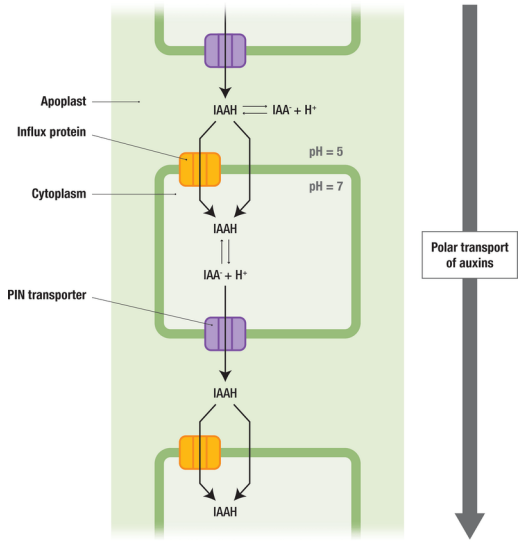


Figure 4.4.1.4: The polar transport of auxin. Auxin (IAAH) enters the cell through influx transporters (orange) or passes directly through the plasma membrane (not shown). In the cytoplasm (pH = 7), which has a higher pH than the apoplast (pH = 5), auxin dissociates to release a proton (H^+) and anion (IAA^-). It can no longer exit the cell through the way that it entered, but it can exit through PIN proteins (purple). In this example, PIN proteins are only on the lower side of the cell. Once IAA^- leaves the cell and enters the acidic apoplast, it binds to a proton becoming IAAH again. It then enters the next cells (below the first cell). This process continues, resulting in polar (unidirectional) transport. Image by Jen Valenzuela (CC-BY-NC).

Nonpolar Transport

Auxins can also be transported nondirectionally (**nonpolar transport**) through the phloem. It passes in the assimilate that translocates through the phloem from where it is synthesized (its "source", usually the shoot) to a "sink" (e.g., the root).

Actions of Auxin

Tropisms

Auxins are the main hormones responsible for phototropism and gravitropism. The auxin gradients that are required for these tropisms are facilitated by the movement of PIN proteins and the polar transport of auxin in response to environmental stimuli (light or gravity). Note that higher auxin concentration on one side of the stem typically causes that side of the stem to elongate; however, the effect is opposite in roots with higher auxin concentration inhibiting elongation (Figure 4.4.1.5).

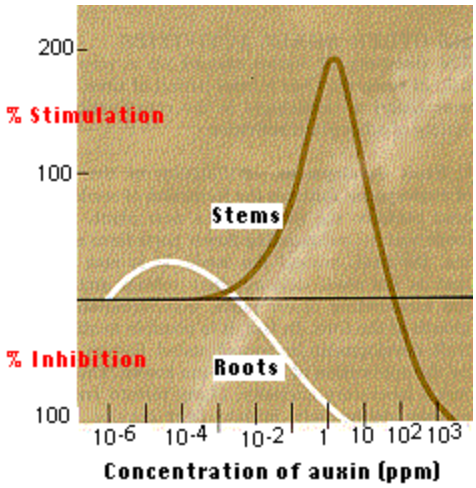


Figure 4.4.1.5: The graph (based on the work of K. V. Thimann) shows the effect of auxin concentration on root and stem growth. The x-axis shows the concentration of auxin in parts per million (ppm) on the log scale. The y-axis shows percent stimulation (positive) or inhibition (negative).The difference between the behavior of roots and stems lies in the difference in the sensitivity of their cells to auxin. Auxin concentrations high enough to stimulate stem growth (represented by a peak) inhibit root growth (represented by a dip).

Growth and Development

Embryo Development

Auxins play a role in embryo development. From the very first mitotic division of the zygote, gradients of auxin guide the patterning of the embryo into the parts that will become the organs of the plant, including the shoot apex, primary leaves, cotyledon(s), stem, and root.

Vascular Tissue Differentiation

They also control cell differentiation of vascular tissue.

Leaf Development and Arrangement

The formation of new leaves in the apical meristem is initiated by the accumulation of auxin. Already-developing leaves deplete the surrounding cells of auxin so that the new leaves do not form too close to them. In this way, the characteristic pattern of leaves in the plant is established. Auxin also controls the precise patterning of the epidermal cells of the developing leaf.

Root Initiation and Development

The localized accumulation of auxin in epidermal cells of the root initiates the formation of lateral or secondary roots. Auxin also stimulates the formation of **adventitious roots** in many species. Adventitious roots grow from stems or leaves rather than from the regular root system of the plant. Once a root is formed, a gradient of auxin concentration develops highest at the tip promoting the production of new cells at the meristem, and lowest in the region of differentiation, thus promoting the elongation and differentiation of root cells. The drop in auxin activity in the regions of elongation and differentiation is mediated by cytokinin — an auxin antagonist.

Shade Avoidance

Auxins stimulate cell elongation parts of the plants that have access to light as part of the shade-avoidance response (see Etiolation and Shade Avoidance).

Interactions with Other Growth-Regulating Hormones

Auxin is required for the function of other growth-regulating hormones such as **cytokinins**; cytokinins promote cell division, but only in the presence of auxin.

Apical Dominance

Apical dominance—the inhibition of **axillary bud** (lateral bud) formation—is triggered by downward transport of auxins produced in the apical meristem. Many plants grow primarily at a single apical meristem and have limited axillary branches (Figure 4.4.1.6). Growth of the shoot apical meristem (terminal shoot) usually inhibits the development of the lateral buds on the stem beneath. If the shoot apical meristem of a plant is removed, the inhibition is lifted, and axillary buds begin growth. However, if the apical meristem is removed and IAA applied to the stump, inhibition of the axillary buds is maintained (Figure 4.4.1.7). Gardeners exploit this principle by pruning the terminal shoot of ornamental shrubs, etc. The release of apical dominance enables lateral branches to develop and the plant becomes bushier. The process usually must be repeated because one or two laterals will eventually outstrip the others and reimpose apical dominance.

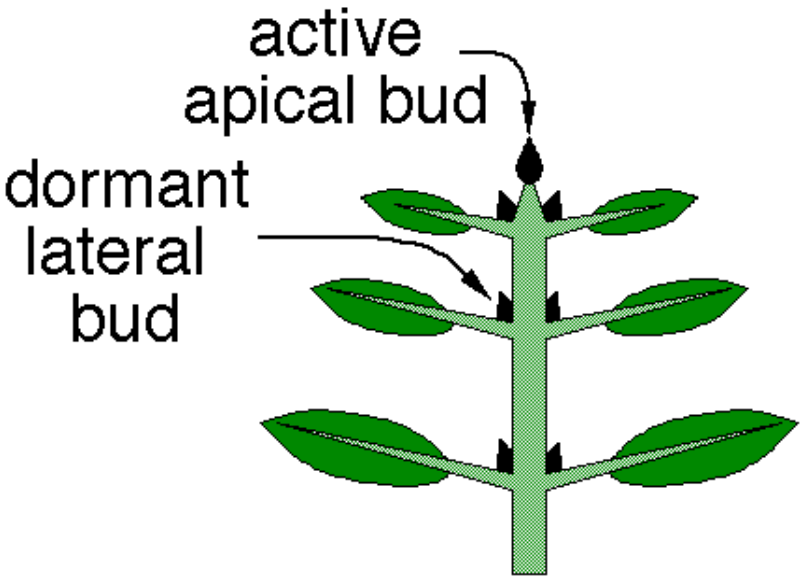


Figure 4.4.1.6: The auxin produced by the shoot apical meristem (apical bud) inhibits the growth of the axillary (lateral) buds, maintaining apical dominance. Image by Doctor Smart (CC BY-SA).

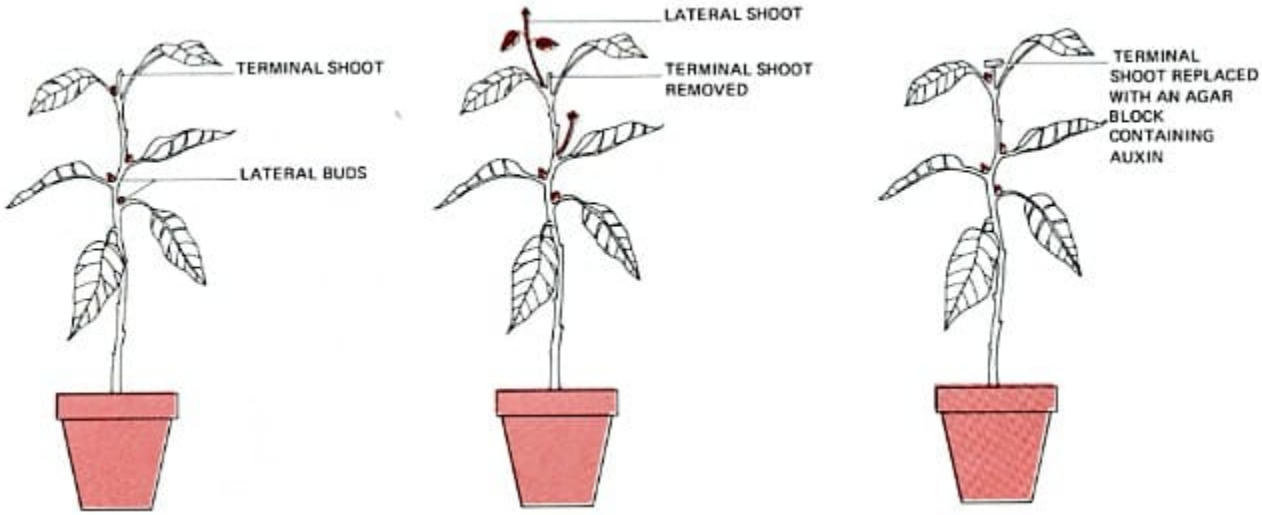


Figure 4.4.1.7: The shoot apical meristem (terminal shoot) produces auxin and inhibits the growth of the axillary (lateral) buds, maintaining apical dominance (left). If the shoot apical meristem is removed, the axillary buds will growth into axillary (lateral) shoots (middle). If the shoot apical meristem is removed and replaced with an agar block containing axuin, apical dominance is maintained (right).

The common white potato also illustrates the principle of apical dominance. Note that a potato is a tuber, which is an underground stem modified for starch storage. As with an ordinary shoot, the potato has a terminal bud (containing the shoot apical meristem) or "eye" and several axillary (lateral) buds. After a long period of storage, the terminal bud usually sprouts but the other buds do not. However, if the potato is sliced into sections, one bud to a section, the axillary buds develop just as quickly as the terminal bud (Figure 4.4.1.8).

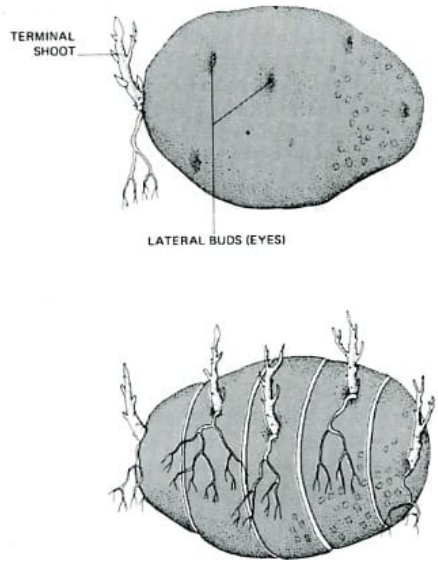


Figure 4.4.1.8: The eyes of the potato illustrate apical dominance. Each eye of the potato is a bud. In the top image, the shoot apical meristem of the terminal shoot produces auxin that inhibits the growth of axillary (lateral) buds. In the bottom image, the potato is sliced into sections, apical dominance does not occur, and each axillary bud (lateral bud/eye) grows.

As will be discussed in the Abscisic Acid section, abscisic acid in the lateral buds inhibits production of auxin, and removal of the apical bud will release this inhibition of auxin, allowing the lateral buds to begin growing.

Flowering and Fruit Development

Auxins promote flowering and fruit setting and ripening. Pollination of the flowers of angiosperms initiates the formation of seeds. As the seeds mature, they release auxin to the surrounding flower parts, which develop into the fruit that covers the seeds.

Prevention of Abscission

Some plants drop leaves and fruits in response to changing seasons (based on temperatures, photoperiod, water, or other environmental conditions). This process is called **abscission**, and is regulated by interactions between **auxin** and **ethylene**. During the growing season, the young leaves and fruits produce high levels of auxin, which blocks activity of ethylene; they thus remain attached to the stem. As the seasons change, auxin levels decline and permit ethylene to initiate **senescence**, or aging (see Ethylene).

Figure 4.4.1.9 demonstrates the role of auxin in abscission. If the blade of the leaf is removed, as shown in the figure, the petiole remains attached to the stem for a few more days. The removal of the blade seems to be the trigger as an undamaged leaf at the same node of the stem remains on the plant much longer, in fact, the normal length of time. If, however, auxin is applied to the cut end of the petiole, abscission of the petiole is greatly delayed.

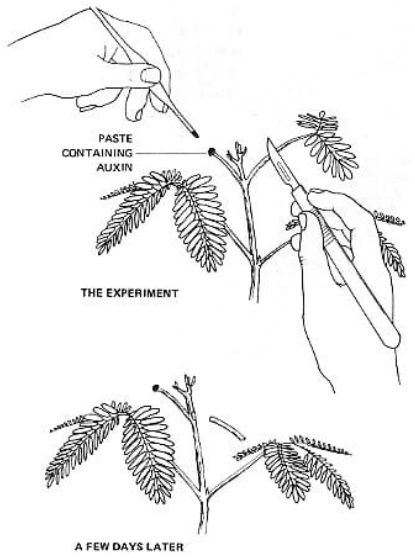


Figure 4.4.1.9: This experiment shows that removal of the leaf blades from a *Mimosa* plant results in abscission of the petiole. Leaf blades produce auxin, which prevents abscission. When an auxin paste is applied to the petiole, abscission does not occur.

Mechanisms of Auxin Action

Auxin effects are mediated by two different pathways: immediate, direct effects on the cell and turning on of new patterns of gene expression. The arrival of auxin in the cytosol initiates such immediate responses as changes in the concentration of and movement of ions in and out of the cell and reduction in the redistribution of PIN proteins. At the cellular level, auxin generally increases the rate of cell division and longitudinal cell expansion. Some of the direct effects of auxin may be mediated by its binding to a cell-surface receptor designated **ABP1** ("Auxin-binding protein 1").

Many auxin effects are mediated by changes in the transcription of genes. Auxin enters the nucleus and binds to its receptor, a protein called **TIR1** ("transport inhibitor response protein 1") which now can bind to proteins responsible for attaching ubiquitin to one or another of several **Aux/IAA proteins**. This triggers the destruction of the Aux/IAA proteins by proteasomes. Aux/IAA proteins normally bind transcription factors called auxin response factors (**ARF**) **preventing** them from activating the promoters and other control sequences of genes that are turned on (or off) by auxin. Destruction of the Aux/IAA proteins **relieves** this inhibition, and gene transcription begins.

This mechanism is another of the many cases in biology where a pathway is turned on by inhibiting the inhibitor of that pathway (a double-negative is a positive). The presence in the cell of many different Aux/IAA proteins (29 in *Arabidopsis*), many different ARFs (23 in *Arabidopsis*) and several (~4) TIR1-like proteins provides a logical basis for mediating the different auxin effects that are described here, but how this is done remains to be discovered.

Commercial Applications of Auxins

Commercial use of auxins is widespread in for propagation in nurseries, crop production, and killing weeds. Horticulturists may propagate desirable plants by cutting pieces of stem and placing them base down in moist soil. Eventually adventitious roots grow out at the base of the cutting. The process can often be hastened by treating the cuttings with a solution or powder containing a synthetic auxin.

Applying synthetic auxins to tomato plants in greenhouses promotes normal fruit development. Fruit growers often apply auxin sprays to cut down the loss of fruit from premature dropping. Additionally, outdoor application of auxin promotes synchronization of fruit setting and dropping to coordinate the harvesting season. Fruits such as seedless cucumbers can be induced to set fruit by treating unfertilized plant flowers with auxins.

Synthetic auxins are widely used as herbicides. Examples include **2,4-dichlorophenoxy acetic acid** (**2,4-D**) and **2,4,5-trichlorophenoxy acetic acid** (**2,4,5-T**), shown in Figure 4.4.1.10. 2,4-D and its many variants are popular because they are **selective herbicides**, killing broad-leaved eudicots but not narrow-leaved monocots. (No one knows the basis of this selectivity).

Why should a synthetic auxin kill the plant? It turns out that the auxin **influx transporter** works fine for 2,4-D, but that 2,4-D cannot leave the cell through the **efflux transporters**. Perhaps it is the resulting accumulation of 2,4-D within the cell that kills it. A mixture of 2,4,-D and 2,4,5-T was the "agent orange" used by the U.S. military to defoliate the forest in parts of South Vietnam. Because of health concerns, 2,4,5-T is no longer used in the U.S.

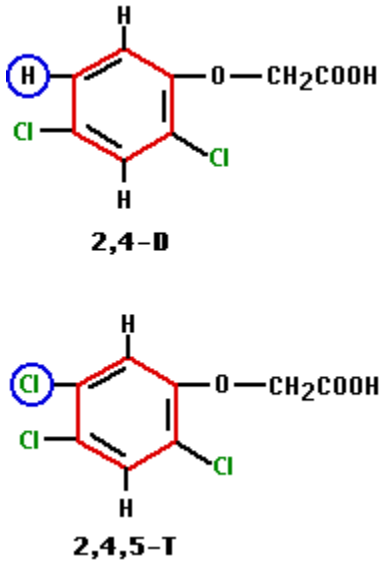


Figure 4.4.1.10: Chemical structures of the synthetic auxins 2,4-D (top) and 2,4,5-T (bottom). As the formulas show, 2,4,5-T is 2,4-D with a third chlorine atom, instead of a hydrogen atom, at the #5 position in the benzene ring (circled and in blue).

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4.4.2: Cytokinins

Learning Objective

Identify the locations of synthesis, transport, and actions of cytokinins.

Cytokinins are plant hormones that promote **cytokinesis** (cell division) are derivatives of the purine adenine. (They are not to be confused with cytokines.) The effect of cytokinins was first reported when it was found that adding the liquid endosperm of coconuts to developing plant embryos in culture stimulated their growth. Without the cytokinins from the endosperm, plant cells would not divide by mitosis. Almost 200 naturally occurring or synthetic cytokinins are known to date. **Zeatin** is an example of naturally occurring cytokinin (Figure 4.4.2.1), and kinetin is an example of a synthetic cytokinin.

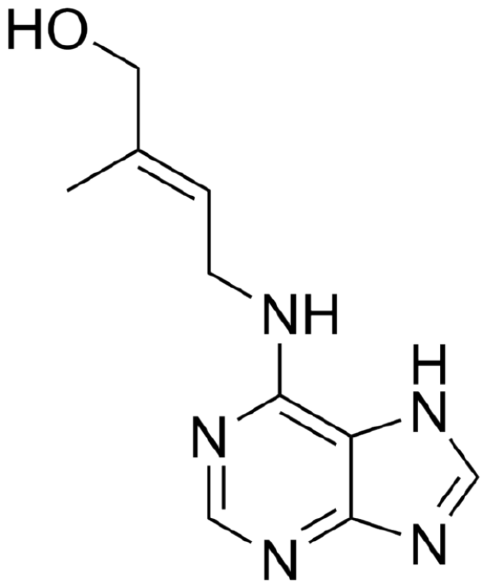


Figure 4.4.2.1: Zeatin, a naturally occurring cytokinin. Image by Edgar181 (public domain).

Cytokinins are synthesized in roots tips and other young structures where cell division is occurring such as embryos and fruits. They are also produced by wounded tissue. Cytokinins are transported through the xylem.

Actions of Cytokinins

One of the clearest examples of cytokinin stimulating cell division involves seed germination. The endosperm of monocot seeds, such as corn (maize), contains large stores of the precursor to the cytokinin zeatin. When the corn kernel germinates, zeatin moves from the endosperm to the root tip where it stimulates vigorous mitosis (Figure 4.4.2.2).



Figure 4.4.2.2: The root tips of these germinating wheat seedlings undergo rapid cell division induced by cytokinin. Image by Oksana Lastochkina (CC-BY).

Plant development is controlled by multiple hormones working together or balancing each other's effects. Cytokinins play an important role in plant development. They are involved in leaf formation, and they delay senescence in leaf tissues. Cytokinins also play a role in chloroplast development.

Cytokinins often counter the effects of auxin when regulating shoot and root development. Cytokinins inhibit apical dominance by stimulating axillary bud development, having the opposite effect as auxin. They inhibit the formation of lateral roots while auxin initiates lateral roots. When cytokinins are applied to a **callus** (mass of undifferentiated cells), shoots form. If auxin is applied, roots form. If the two hormones are applied in equal amounts, much the rate of cell division increases, but the callus does not produce distinct shoots and roots.

With respect to mediating roots gravitropism, however, the effect of cytokinin is similar to that of auxin. When a root is turned on its side, cytokinins accumulate on the lower side, inhibiting elongation there. As the upper surface of the root elongates, it bends downwards.

Mechanism of Cytokinin Action

Like auxins, cytokinin can cause changes in gene expression. To begin this process, a cytokinin binds to a receptor protein embedded in the plasma membrane of the cell. The internal portion of the receptor then attaches a phosphate group to a protein in the cytosol. This protein moves into the nucleus where it activates one or more nuclear transcription factors, which then bind to the promoters of genes. Transcription of these genes produces mRNAs that move out into the cytosol. Translation of these mRNAs produces the proteins that enable the cell to carry out its cytokine-induced function.

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4.4.3: Gibberellins

Learning Objectives

- Identify the locations of synthesis, transport, and actions of gibberellins.
- Interpret and predict the outcome of an experiment demonstrating the action of gibberellins.
- Describe the commercial applications of gibberellins.

During the 1930s Japanese scientists isolated a growth-promoting substance from cultures of a fungus that parasitizes rice plants. They called it gibberellin. **Gibberellins (GAs)** are a group of about 125 closely related plant hormones synthesized in the root and stem apical meristems, young leaves, and seed embryos. They are likely transported through the vascular tissue. One of the most active gibberellins - and one found as a natural hormone in the plants themselves - is **gibberellic acid** (**GA**; figure 4.4.3.1).

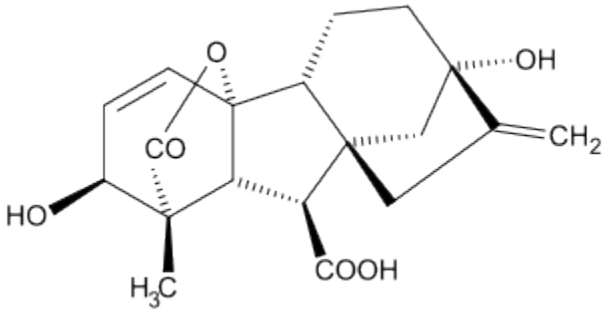


Figure 4.4.3.1: Chemical structure of the plant hormone gibberellic acid. Image by Minutemen (public domain).

Actions of Gibberellins

Several aspects of plant growth involve GAs, including stimulating shoot elongation, seed germination, and fruit and flower maturation. Other effects of GAs include gender expression (also see Ethylene) and the delay of senescence in leaves and fruit. Synthesis of gibberellins also helps grapevines climb up toward the light by causing meristems that would have developed into flowers to develop into **tendrils** instead.

Shoot elongation in this case results from both cell division and cell elongation. When applied in low concentrations to a bush or "dwarf" bean, the stem begins to grow rapidly. The length of the internodes becomes so great that the plant becomes indistinguishable from climbing or "pole" beans. GA seems to overcome the genetic limitations in many dwarf varieties.

Gibberellins break dormancy (a state of inhibited growth and development) in the seeds of plants that require exposure to cold or light to germinate. The seeds of some plant species rely on the imbibition (intake) of water to initiate germination. Intake of water activates gibberellins, which then signals to transcribe the gene encoding **amylase**, an enzyme that breaks down starches stored in the seed into simple sugars (note these final steps are identical to what occurs in phytochrome-regulated germination). Gibberellins also stimulate cell elongation of young roots during germination. When water is absent, germination in this pathway is blocked by a hormone called **abscisic acid,** which inhibits the activity of gibberellins. Thus gibberellins and abscisic acid act in opposition in regulating the the germination response.

Many plant species first produce a basal rosette of leaves. When daylength increase or the weather becomes cold, they **bolt,** producing a long stalk. Eventually, flowers and then fruits develop on this stalk. Gibberellins are responsible for inducing bolting (figure 4.4.3.2**.**



Figure 4.4.3.2: Arabidopsis thaliana plant as basal rosette (left). The plant on the right has bolted and started to flower. Gibberellins induce bolting. Left image by Quentin Groom (public domain), and right image by Frost Museum (CC-BY).

Mechanism of Gibberellin Action

Like auxins, gibberellins generally increase the rate of cell division and longitudinal cell expansion. Gibberellins also exert their effects by altering gene transcription through a mechanism similar to auxin in that a pathway is turned on by inhibiting the inhibitor of that pathway (a double-negative is a positive). First, Gibberellin enters the cell and binds to a soluble receptor protein called **GID1** ("gibberellin-insensitive dwarf mutant 1") which now can bind to a complex of proteins (**SCF**) responsible for attaching ubiquitin to one or another of several **DELLA proteins**. This triggers the destruction of the DELLA proteins by proteasomes. DELLA proteins normally bind gibberellin-dependent transcription factors, a prominent one is designated **PIF3/4**, **preventing** them from binding to the DNA of control sequences of genes that are turned on by gibberellin (also see Shade Avoidance and Etiolation).

The **dwarf** varieties of rice and wheat carry mutations related to GAs. In the case of rice, the mutation interfere with the synthesis of their gibberellins. The wheat mutation reduces is in the gene coding for a DELLA protein and reduce the plant's ability to respond to its own gibberellins. Dwarf varieties of sorghum and more recently maize (corn) also exist, but in these cases, the mutation interferes with auxin transport, not gibberellin activity.

Commercial Applications of Gibberellins

Gibberellin application assists with seedless grape production. Seedless grapes are obtained through standard breeding methods and contain inconspicuous seeds that fail to develop. Because GAs are produced by the seeds, and because fruit development and stem elongation are under GA control, these varieties of grapes would normally produce small fruit in compact clusters. Maturing grapes are routinely treated with GA to promote larger fruit size, as well as looser bunches (longer stems), which reduces the instance of mildew infection (Figure 4.4.3.3). Like auxins, GAs can be used commercially to induce fruit development in a variety of species.



Figure 4.4.3.3: In grapes, application of gibberellic acid increases the size of fruit and loosens clustering. (credit: Bob Nichols, USDA)

Gibberellins have a few other commercial applications. They can be applied to artificially induce bolting and flowering, such that plants produce seeds earlier. Addition of gibberellic acid to the winter buds of peach trees helps break dormancy. In urban areas, GA antagonists are sometimes applied to trees under power lines to control growth and reduce the frequency of pruning.

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4.4.4: Abscisic Acid

Learning Objectives

- Identify the locations of synthesis, transport, and actions of abscisic acid.
- Describe how ABA interacts with other plant hormones.

The plant hormone **abscisic acid** (ABA) was was once thought to be responsible for abscission; however, this is now known to be incorrect. Instead, ABA accumulates as a response to stressful environmental conditions, such as dehydration, cold temperatures, or shortened day lengths. Unlike animals, plants cannot flee from potentially harmful conditions like drought, freezing, exposure to salt water or salinated soil, and ABA plays in mediating adaptations of the plant to stress. Abscisic acid (Figure 4.4.4.1) resembles the carotenoid zeaxanthin (Figure 4.4.4.2), from which it is ultimately synthesized. It is produced in mature leaves and roots and transported through the vascular tissue.

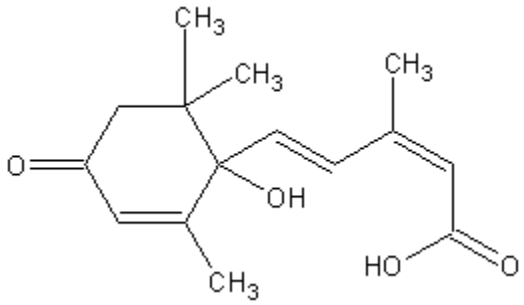


Figure 4.4.4.1: Chemical structure of the plant hormone abscisic acid (ABA). Image by Socrtwo (public domain).

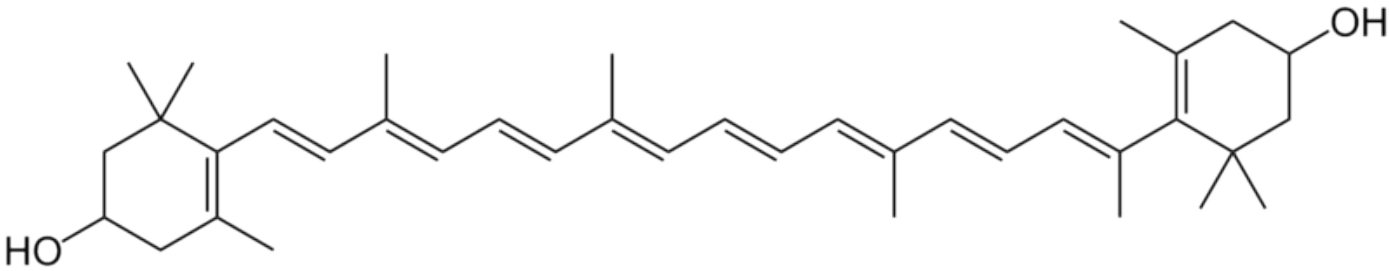


Figure 4.4.4.2: The carotenoid zeaxanthin absorbs blue light and reflecting orange and red light. It is a precursor to abscisic acid. Image by Shaddack (public domain).

Maintaining Dormancy

Seed Maturation and Inhibition of Germination

Seeds are not only important agents of reproduction and dispersal, but they are also essential to the survival of annual and biennial plants. These angiosperms die after flowering and seed formation is complete. Abscisic acid is essential for seed maturation and also enforces a period of seed dormancy, by blocking germination and promoting the synthesis of storage proteins. It is important the seeds not germinate prematurely during unseasonably mild conditions prior to the onset of winter or a dry season. As the hormone gradually breaks down over winter, the seed is released from dormancy and germinates when conditions are favorable in spring. As discussed in the Environmental Responses chapter, other environmental cues such as exposure to a cold period, light, or water are often also needed to for germination to occur.

Interestingly, mangrove species with **viviparous germination**, meaning that seeds germinate while still attached to the parent plant have reduced levels of ABA during embryo formation, providing further evidence of ABA's role in maintain seed dormancy (Farnsworth and Farrant 1998, *Am J. Bot.)*. These mangroves are adapted to drop germinated seeds into surrounding water to be dispersed (Figure 4.4.4.3).



Figure 4.4.4.3: The elongated seedlings of the red mangrove, *Rhizophora mangle*, are still attached to the parent plant, illustrating viviparous germination. Image by M.elle F. Legendre (public domain).

Bud Dormancy

Another effect of ABA is to promote the development of winter buds; it mediates the conversion of the apical meristem into a dormant bud. The newly developing leaves growing above the meristem become converted into stiff bud scales that wrap the meristem closely and will protect it from mechanical damage and drying out during the winter. Abscisic acid in the bud also acts to enforce dormancy so if an unseasonably warm spell occurs before winter is over, the buds will not sprout prematurely. Only after a prolonged period of cold or the lengthening days of spring (photoperiodism) will bud dormancy be lifted.

Response to Water Stress

Stomatal Closure

Abscisic acid also regulates the short-term drought response. Recall that stomata are pores in the leaf and are surrounded by a pair of **guard cells**. Much of the water taken up by a plant is lost as water vapor exists stomata. Low soil moisture causes an increase in ABA, which causes stomata to close, reducing water loss. Note that stomatal closure also prevents exchange of oxygen and carbon dioxide, which is necessary for efficient photosynthesis (see Photorespiration and Phytosynthetic Pathways). The response to abscisic acid occurs *even if blue light is present*; that is, signaling from drought via ABA overrides the signaling from blue light to open stomata. See Transport for more details about stomatal opening and closure.

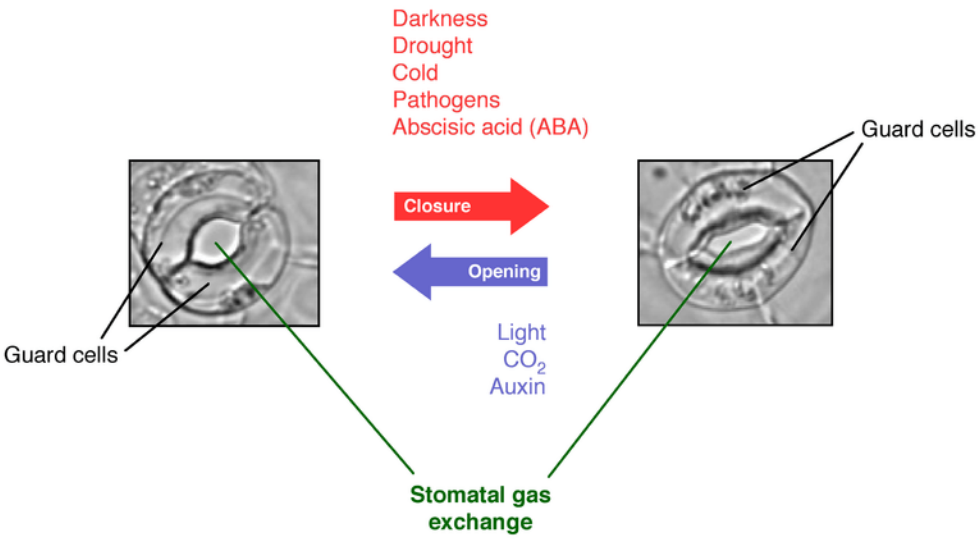


Figure 4.4.4.4: Several factors mediate the opening and closure of stomata, which are surrounded by kidney-shaped guard cells. Stomatal gas exchange occurs through the stomata. Darkness, drought, cold, pathogens, and abscisic acid (ABA) mediate stomatal closure. Specifically, drought causes the releases of ABA, which signals stomata closure. Stomatal opening is triggered by light, carbon dioxide (CO_2), and auxin. Image by June Kwak, Pascal Mäser (public domain).

Cellular Protection from Dehydration

Abscisic acid turns on the expression of genes encoding proteins that protect cells - in seeds as well as in vegetative tissues - from damage when they become dehydrated.

Interactions with Other Hormones

At a cellular level, abscisic acid inhibits both cell division and cell expansion. It often opposes the growth-inducing effects of auxin and gibberellic acid. For example, abscisic acid prevents stem elongation probably by its inhibitory effect on gibberellic acid. In maintaining apical dominance, however, ABA synergizes with auxin. Abscisic acid moves up from the roots to the stem (opposite the flow of auxin) and suppresses the development of axillary buds. The result is inhibition of branching (maintaining apical dominance).

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4.4.5: Ethylene

Learning Objectives

- Relate the chemical structure of ethylene to its mode of transport.
- Identify the locations of synthesis and actions of ethylene.
- Describe the commercial applications of ethylene.

Ethylene differs from other plant hormones in that it is a smaller and simpler molecule that is a volatile gas (Figure 4.4.5.1). Hundreds of years ago, when gas street lamps were installed in city streets, trees that grew close to lamp posts developed twisted, thickened trunks and shed their leaves earlier than expected. These effects were caused by ethylene volatilizing from the lamps. Aging tissues, such as those that are wilting or ripening, and nodes of stems produce ethylene.

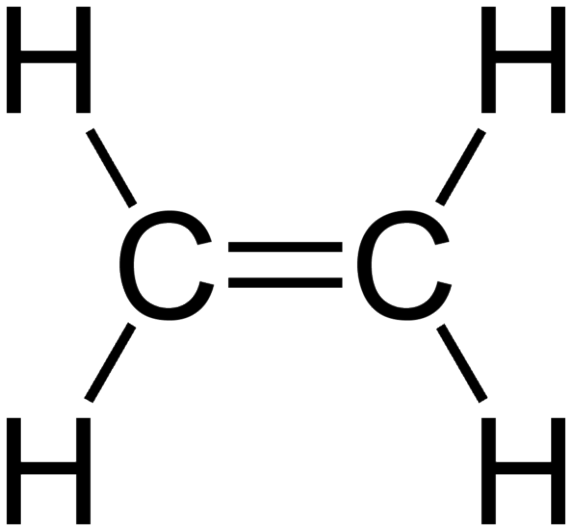


Figure 4.4.5.1: The chemical structure of ethylene. Image by Benjah-bmm27 (public domain).

Actions of Ethylene

Ethylene has many functions, and its major functions are associated with **senescence**, or aging. This includes fruit ripening, flower wilting, and leaf and fruit **abscission**. Ethylene also promotes germination in some cereals and sprouting of bulbs and potatoes. It is responsible for drooping of leaves and sprouting of potato buds. In **monoecious** plants, ethylene promotes the production of female flowers where as gibberellic acid promotes male flower production. Ethylene mediates the **triple response**, which makes the shoots of seedlings that are buried under debris grow short and wide as well as bend horizontally. This makes it possible for the shoot to push through the debris. Ethylene causes stem elongation in rice and other plants that are submerged in water. It promotes the breakdown of abscisic acid (ABA) and thus relieves ABA's inhibition of gibberellic acid.

Fruit Ripening

As they approach maturity, many fruits (e.g., apples, oranges, avocados) release ethylene. During fruit ripening, ethylene stimulates the conversion of starch and acids to sugars. Some people store unripe fruit, such as avocados, in a sealed paper bag to accelerate ripening; the gas released by the first fruit to mature will speed up the maturation of the remaining fruit.

Abscission

Ethylene induces the abscission of leaves, fruits, and flower petals. When auxin levels decline, ethylene triggers senescence and ultimately programmed cell death at the site of leaf attachment to the stem. A special layer of cells — the **abscission layer** (abscission zone) — forms at the base of the petiole or fruit stalk (Figure 4.4.5.2). In petioles of some plants, there are two parts of the abscission layer: the more distal separation layer and more proximal protective layer. Before abscission occurs, nutrients are absorbed into the stem so that they are not lost with the leaf. As the separation layer breaks down, the leaf breaks free at this point and leaf falls to the ground in a controlled manner without harming the rest of the plant. The protective layer, which was reinforced with suberin, serves as a seal.

Leaf abscission is particularly important for temperate deciduous trees in the autumn. This is a vital response to the onset of winter when ground water is frozen - and thus cannot support transpiration - and snow load would threaten to break any branches still in leaf.

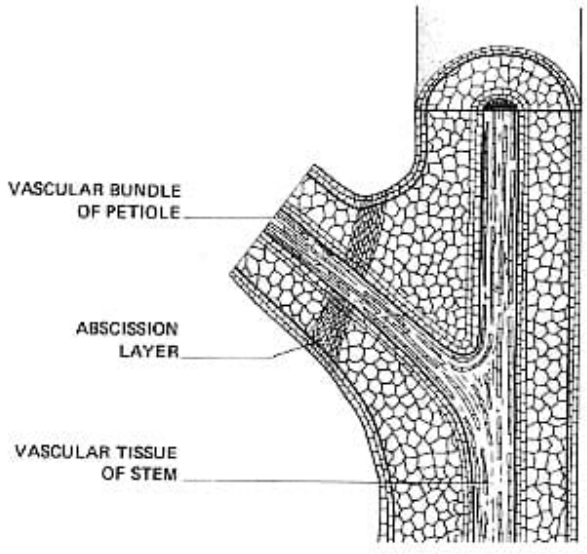


Figure 4.4.5.2: The abscission layer forms at the base of a petiole (as shown) or fruit stalk, ultimately allowing leaves or fruits to fall from the stem. Vascular tissue passes through the center of the stem and petiole. The abscission layer is a dark band of cells at the base of the petiole.

In drought conditions, the immediate response is closing stomata (see Abscisic Acid). However, because closed stomata prevent gas exchange, plants will die if the stomata remain closed for too long. Thus if a drought persists for too long, the plant will begin sacrificing certain areas by allowing the leaves or stems to die in localized regions. This process may be regulated by ethylene, which can induce localized cell death under certain conditions.

Mechanism of Ethylene Action

At a cellular level, ethylene can inhibit or promote cell division. It sometimes inhibits cell expansion. In other circumstances, it stimulates lateral cell expansion. The presence of ethylene is detected by transmembrane receptors in the endoplasmic reticulum (ER) of cells. Binding of ethylene to these receptors unleashes a signaling cascade that leads to activation of transcription factors and the turning on of gene transcription.

Commercial Applications of Ethylene

Ethylene is widely used in agriculture. Commercial fruit growers can buy equipment to generate ethylene so that their harvest ripens quickly and uniformly. Horticulturalists inhibit leaf dropping in ornamental plants by removing ethylene from greenhouses using fans and ventilation.

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4.4.6: Summary Table

Table 4.4.6.1: Summary of the sources, transport mechanism, and major actions of the five main plant hormones

Hormone	Source(s)	Transport mechanism	Major actions
Auxin	Apical meristems, young leaves, and developing seeds	Polar transport or nonpolar transport through the phloem	Tropisms, embryo and leaf development, root initiation, apical dominance, flowering and fruit development, prevention of abscission
Cytokinins	Root tips and other young tissues	Xylem	Gravitropism, cell division, germination, leaf formation, inhibition of apical dominance, inhibition of root initiation
Gibberellins	Young shoot tissues and seeds	Likely vascular tissue	Germination, shoot elongation, bolting, flowering, production of male flowers, fruit maturation
Ethylene	Stressed, wilting, or ripening tissues	Moves through the air as a gas	Abscission, senescence, fruit ripening, triple response, production of female flowers
Abscisic acid	Mature leaves and roots	Vascular tissue	Seed maturation and inhibition of germination, bud dormancy, stomatal closure

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4.4.7: Other Signaling Molecules

Learning Objectives

- Identify several signaling molecules beyond the five major plant hormones and describe their effects.
- Distinguish between the hypersensitive response and systemic acquired response.
- Explain the mechanisms by which signaling compounds aid in plant defense against pathogens and herbivores.

Recent research has discovered a number of compounds that also influence plant development. Their roles are less understood than the effects of the major hormones described so far.

Brassinosteroids

Brassinosteroids (Figure 4.4.7.1) are synthesized primarily in young tissues are important to many developmental and physiological processes. In fact, many sources considere them the sixth major plant hormones. Unlike the hormones discussed previously, brassinosteroids do not travel far from their site of synthesis. Signals between these compounds and other hormones, notably auxin and GAs, amplifies their physiological effect. Apical dominance, seed germination, gravitropism, lateral root formation, differentiation of cells in the vascular tissue, and resistance to freezing are all positively influenced by brassinosteroids. Root growth and fruit dropping are inhibited by steroids.

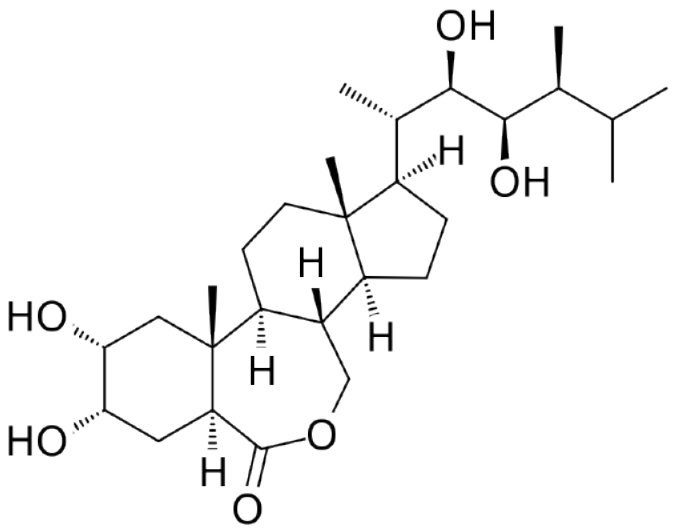


Figure 4.4.7.1: Brassinolide, an example of a brassinosteroid. Image by Wostr (public domain).

Systemin

Systemin, named for the fact that it is distributed systemically (everywhere) in the plant body upon production, is a short polypeptide that activates plant responses to wounds from **herbivores** (animals that feed on plant parts). It causes the plant to produce **jasmonic acid** (see below).

Jasmonates

Jasmonates play a major role in defense responses to herbivory (Figure 4.4.7.2). Their levels increase when a plant is wounded by an herbivore, resulting in an increase in toxic secondary metabolites. For example, **jasmonic acid** (Figure 4.4.7.3) also induces

transcription of protease inhibitors. Protease inhibitors both taste bad and prevent breakdown of proteins in the herbivore's gut, thus making the insect sick and deterring further herbivory. Jasmonates also contribute to the production of volatile compounds that attract natural enemies of herbivores. Chewing of tomato plants by caterpillars leads to an increase in jasmonic acid levels, which in turn triggers the release of volatile compounds that attract predators of the pest. Jasmonates also elicit the synthesis of volatile compounds that attract parasitoids, which are insects that spend their developing stages in or on another insect, and eventually kill their host.



Figure 4.4.7.2: Jasmonic acid mediates plant defense against herbivores such as this tobacco hornworm (*Manduca sexta*). Image by Scot Nelson (public domain).

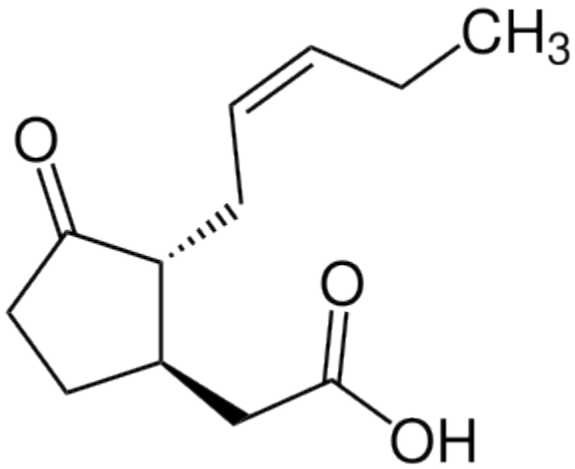


Figure 4.4.7.3: The chemical structure of jasmonic acid. Image by Minutemen (public domain).

Jasmonates also work with systemin to mediate responses to drought, damage by ground-level ozone, and ultraviolet light.

Salicylic Acid

Salicylic acid resembles aspirin (Figure 4.4.7.4) and is important for plant defense. It initiates the a systemic (whole body) response called the **systemic acquired response** (SAR) as a response to infection by parasites or pathogens. When a parasite or pathogen infects a cell, there is an specific, localized response called the **hypersensitive response** (HR). Following this very localized response, the plant initiates a systemic (whole body) response called the systemic acquired response (SAR). Salicylic acid is produced and converted to **methyl salicylate** (Figure 4.4.7.4) inducing the SAR in response to the HR. The SAR activates transcription of general "**pathogenesis-resistance**" genes, which are *not* pathogen-specific (unlike in the hypersensitive response), but serve as general defense against pathogenic infection. The SAR is slower than the hypersensitive response, and also differs in that it is systemic instead of localized to the site of the infection.

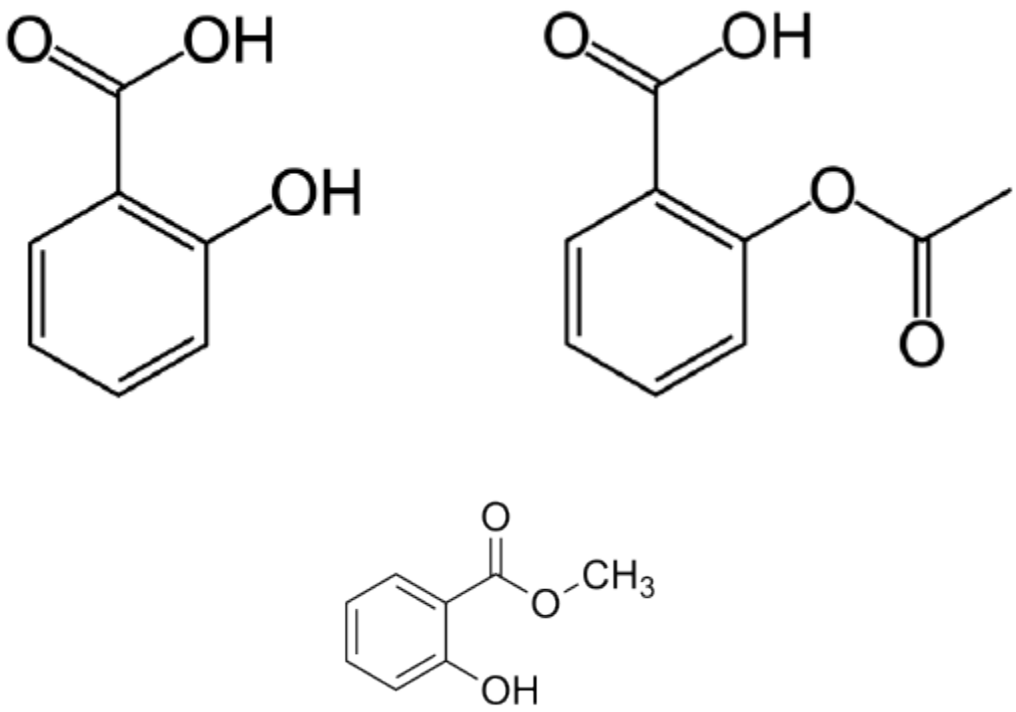


Figure 4.4.7.4: Salicylic acid (left) resembles aspirin, or acetylsalicylic acid (right). In acetylsalicylic acid, an acetyl group ($COCH_3$) has replaced the hydrogen in the hydroxyl group (OH) of salicylic acid. Methyl salicylate (bottom) has a similar structure to salicylic acid, but a methyl group (CH_3) has replaced the hydrogen in the carboxyl group (COOH). Left image by Fvasconcellos (public domain), right image by Benjah-bmm27 (public domain), and bottom image by Emeldir (public domain).

Similar to jasmonic acid, salicylic acid can mediates defense against insect herbivores. It is directly toxic to some herbivores. Additionally, in response to herbivory, salicylic acid can be converted to methyl salicylate, which is released as a gas. This volatile compound can attract natural predators and parasites of the herbivores.

Some plants, such as skunk cabbage (Figure 4.4.7.5) and elephant yam, are adapted to flower while snow still covers the ground. Salicylic acid mediates their ability to produce heat to melt the snow around them. Such plants are thus called **thermogenic** ("heat producing").



Figure 4.4.7.5: Skunk-cabbage (*Symplocarpus foetidus*) is a thermogenic plant, producing heat that melts the snow surrounding it. This process is mediated by salicylic acid. Image by John Winkelman (CC-BY).

Oligosaccharins

Oligosaccharins are short chains of simple sugars that play a role in plant defense against bacterial and fungal infections. They act locally at the site of injury, and can also be transported to other tissues.

Strigolactones

Strigolactones (Figure 4.4.7.6) promote seed germination in some species and inhibit lateral apical development in the absence of auxins. Strigolactones also play a role in the establishment of mycorrhizae, a mutualistic association of plant roots and fungi.

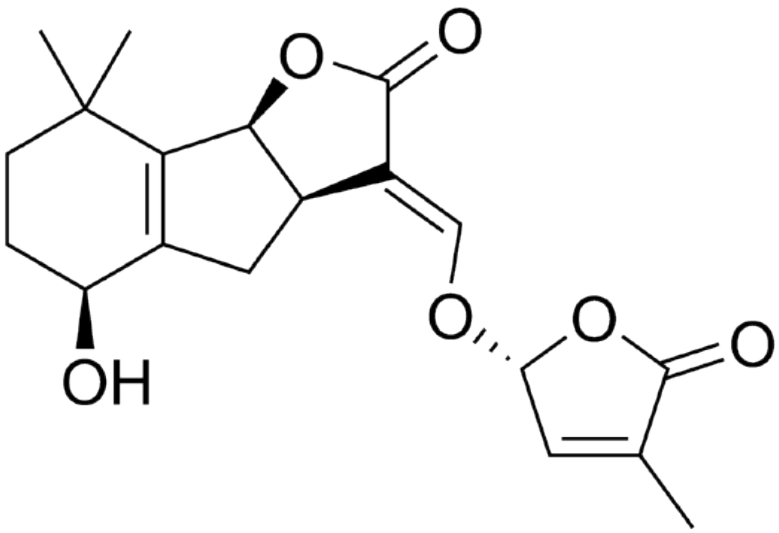


Figure 4.4.7.6: The chemical structure of (+)-strigol, a strigolactone.

Florigen

Florigen is a systemic signal that initiates flowering. It is also involved in the formation of storage organs and contributes to

plant architecture. It is synthesized in leaves and transported to the shoot apical meristem (SAM) where it promotes flowering in response to daylength cues. At the molecular level, florigen is represented as a protein product encoded by the *FLOWERING LOCUS T* (*FT*) gene, which is highly conserved (occurs/has a similar genetic sequence in) across flowering plants.

Florigen is considered one of the important targets for crop improvement. Regulation of flowering time is an important target for plant breeding because the control of flowering to a favorable time provides successful grain production in a given cropping area. Flowering at unfavorable seasons causes loss of yield due to insufficient growth of photosynthetic organs or poor fertility due to heat or cold stress during reproduction. Thus, understanding florigen function can contribute to novel breeding techniques in crops to produce cultivars that can start their reproductive stage at optimal seasons.

Supplemental Reading

Filgueiras, C. C., Martins, A. D., Pereira, R. V., & Willett, D. S. (2019). The Ecology of Salicylic Acid Signaling: Primary, Secondary and Tertiary Effects with Applications in Agriculture. *International journal of molecular sciences*, *20* (23), 5851. https://doi.org/10.3390/ijms20235851

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- Plant Hormones and Sensory Systems by Biology 1520 Introduction to Organismal Biology (licensed CC BY-NC-SA)
- Tsuji H. (2017). Molecular function of florigen. *Breeding science*, *67* (4), 327–332. https://doi.org/10.1270/jsbbs.17026 (licensed CC BY)

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4.4.8: Chapter Summary

Plant **hormones**—naturally occurring compounds synthesized in small amounts—can act both in the cells that produce them and in distant tissues and organs. **Auxins** are responsible for **apical dominance**, root growth, directional growth toward light, and many other growth responses. **Cytokinins** stimulate cell division and counter apical dominance in shoots. **Gibberellins** inhibit dormancy of seeds and promote stem growth. **Abscisic acid** induces dormancy in seeds and buds, and protects plants from excessive water loss by promoting stomatal closure. **Ethylene** gas speeds up fruit ripening and dropping of leaves. Other signaling molecules, such as **salicylic acid** and **jasmonates** are important to plant defense.

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

- Explain the defining characteristics of a hormone.
- Name the five major plant hormones and identify their locations of synthesis, transport, and actions.
- Describe interactions among the five major plant hormones.
- Explain the mechanism of polar auxin transport.
- Define apical dominance and explain the role of auxin in maintaining it.
- Interpret and predict the outcome of an experiments demonstrating the actions of auxin and gibberellic acid.
- Describe the commercial applications of auxin, ethylene, and gibberellins.
- Identify several signaling molecules beyond the five major plant hormones and describe their effects.
- Distinguish between the hypersensitive response and systemic acquired response.
- Explain the mechanisms by which signaling compounds aid in plant defense against pathogens and herbivores.

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4.5: TRANSPORT

The structure of plant roots, stems, and leaves facilitates the transport of water, nutrients, and photosynthates throughout the plant. The phloem and xylem are the main tissues responsible for this movement. Water and nutrients are absorbed from the soil by roots ands transported through the xylem. Much water is lost through the stomata in the leaves, and plants have a variety of adaptations to reduce water loss (Figure 4.5.1). The products of photosynthesis move through the phloem from sources to the tissues and organs that need them. These mechanisms of transport allow plant organs to specialize because they can export excess substances and import what they do not produce or collect locally.



Figure 4.5.1: The dragon's blood tree (*Dracaena cinnabari*) is adapted to the dry environment of Socotra Island in Yemen. The densely packed vegetation directs water towards the base of the tree and shades the soil below, allowing roots to absorb the water before it evaporates. Image by Rod Waddington (CC-BY-SA).

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- Transport

4.5.1: Water Transport

4.5.1.1: Water Potential

4.5.1.2: Transpiration

4.5.1.2.1: Adaptations to Reduce Transpiration

4.5.1.2.2: Stomatal Opening and Closure

4.5.1.3: Cohesion-Tension Theory

4.5.1.4: Water Absorption

4.5.2: Translocation (Assimilate Transport)

4.5.3: Chapter Summary

Thumbnail image: A potometer is used to measure transpiration rate, the loss of water through the stomata. Image by Theresa Knott and Rachel Knott (CC-BY-SA).

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4.5.1: WATER TRANSPORT

Water potential, transpiration, and stomatal regulation influence how water and nutrients are transported in plants. **Water potential** refers to the potential energy in water, and water moves towards the areas with the lowest water potential. Water is ultimately pulled to the top of the plant (**cohesion-tension theory**), and lost through **transpiration** through stomata. Complex mechanisms control stomatal opening and closure. Both adaptations that increase absorption of water through the roots (Figure 4.5.1.1) and those that limit transpiration ensure that plants collect and retain enough water.

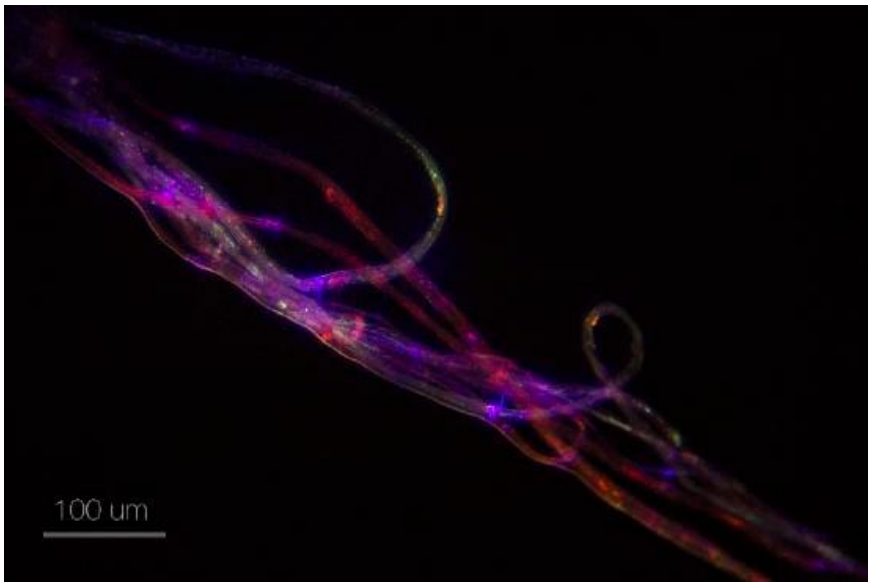


Figure 4.5.1.1: Microscope of stained root hairs of the soybean. Roots hairs are an example of an adaptation that increases water absorption. Image by Ihor Panas (CC-BY-SA).

- Topic hierarchy

4.5.1.1: Water Potential

4.5.1.2: Transpiration

4.5.1.2.1: Adaptations to Reduce Transpiration

4.5.1.2.2: Stomatal Opening and Closure

4.5.1.3: Cohesion-Tension Theory

4.5.1.4: Water Absorption

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4.5.1.1: Water Potential

Learning Objectives

- Define water potential and explain how it is influenced by solutes, pressure, gravity, and the matric potential.
- Explain which components of water potential plants can manipulate and describe how.

Plants are phenomenal hydraulic engineers. Using only the basic laws of physics and the simple manipulation of potential energy, plants can move water to the top of a tree approaching 116 m (~381 ft, see The Tallest Trees box). Plants can also use hydraulics to generate enough force to split rocks and buckle sidewalks (Figure 4.5.1.1.1). Plants achieve this because of water potential.



Figure 4.5.1.1.1: Plant roots can easily generate enough force to buckle and break concrete sidewalks, much to the dismay of homeowners and city maintenance departments. Image modified from Pedestrians Educating Drivers on Safety, Inc.

Water potential is a measure of the potential energy in water. Plant physiologists are not interested in the energy in any one particular aqueous system, but they are very interested in water movement between two systems. In practical terms, therefore, water potential is the difference in potential energy between a given water sample and pure water (at atmospheric pressure and ambient temperature). Water potential is denoted by the Greek letter ψ (*psi*) and is expressed in units of pressure (pressure is a form of energy) called megapascals (MPa). The potential of pure water ($\Psi_w^{\text{pure H2O}}$) is, by convenience of definition, designated a value of zero (although pure water contains plenty of potential energy, that energy is ignored). Water potential values for the water in a plant root, stem, or leaf are therefore expressed relative to $\Psi_w^{\text{pure H2O}}$.

The water potential in plant solutions is influenced by solute concentration, pressure, gravity, and factors called matrix effects. Water potential can be broken down into its individual components using the following equation:

$$\psi_{\text{system}} = \psi_{\text{total}} = \psi_s + \psi_p + \psi_g + \psi_m \tag{4.5.1.1.1}$$

where Ψ_s, Ψ_p, Ψ_g, and Ψ_m refer to the solute, pressure, gravity, and matric potentials, respectively. “System” can refer to the water potential of the soil water (Ψ^{soil}), root water (Ψ^{root}), stem water (Ψ^{stem}), leaf water (Ψ^{leaf}) or the water in the atmosphere ($\Psi^{\text{atmosphere}}$): whichever aqueous system is under consideration. As the individual components change, they raise or lower the total water potential of a system. When this happens, water moves to equilibrate, moving from the system or compartment with a higher water potential to the system or compartment with a lower water potential. This brings the difference in water potential between the two systems ($\Delta\Psi$) back to zero ($\Delta\Psi = 0$). Therefore, for water to move through the plant from the soil to the air (a process called transpiration), Ψ^{soil} must be > Ψ^{root} > Ψ^{stem} > Ψ^{leaf} > $\Psi^{\text{atmosphere}}$.

Water only moves in response to $\Delta\Psi$, not in response to the individual components. However, because the individual components influence the total Ψ_{system}, by manipulating the individual components (especially Ψ_s), a plant can control water movement. Solutes, pressure, gravity, and matric potential are all important for the transport of water in plants. Water moves from an area of higher total water potential to an area of lower total water potential.

Solute Potential

Solute potential (Ψ_s), also called osmotic potential, is negative in a plant cell and zero in distilled water. Typical values for cell cytoplasm are –0.5 to –1.0 MPa. Solutes reduce water potential (resulting in a negative Ψ_w) by consuming some of the potential energy available in the water. Solute molecules can dissolve in water because water molecules can bind to them via hydrogen bonds; a hydrophobic molecule like oil, which cannot bind to water, cannot go into solution. The energy in the hydrogen bonds between solute molecules and water is no longer available to do work in the system because it is tied up in the bond. In other words, the amount of available potential energy is reduced when solutes are added to an aqueous system. Thus, Ψ_s decreases with increasing solute concentration.

Because Ψ_s is one of the four components of Ψ_{system} or Ψ_{total}, a decrease in Ψ_s will cause a decrease in Ψ_{total}. Water moves towards areas of lower Ψ_s (and thus lower Ψ_{total}). In Figure 4.5.1.1.2, the semipermeable membrane that separates the two sides of the tube allows water but not solutes to pass. In the first tube, solute has been added to the right side. Adding solute to the right side lowers Ψ_s, causing water to move to the right side of the tube. As a result, the water level is higher on the right side.

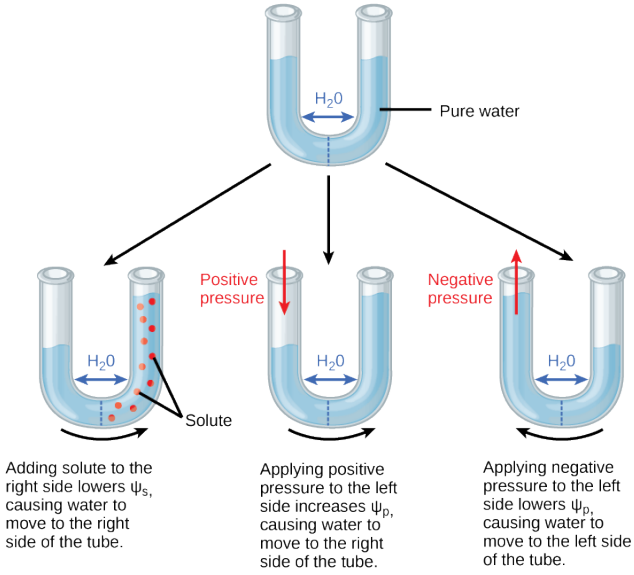


Figure 4.5.1.1.2: In this example with a semipermeable membrane between two aqueous systems, water will move from a region of higher to lower water potential until equilibrium is reached. Solutes (Ψ_s), pressure (Ψ_p), and gravity (Ψ_g) influence total water potential (Ψ_{total}) for each side of the tube, and therefore, the difference between Ψ_{total} on each side ($\Delta\Psi$). (Ψ_m , the potential due to interaction of water with solid substrates, is ignored in this example.). Water moves in response to the difference in water potential between the left and right sides of the tube. Top image: Pure water is on both sides of the tube. Bottom left image: Adding solute to the the right side lowers Ψ_s, causing water to move to the right side fo the tube. Bottom middle image: Applying positive pressure to the left side increases Ψ_p, causing water to move to the right side fo the tube. Bottom right image: Applying negative pressure to the left side lowers Ψ_p, causing water to move to the left side of the tube.

The internal water potential of a plant cell is more negative than pure water because of the cytoplasm's high solute content. Because of this difference in water potential water will move from the soil into a plant's root cells via the process of osmosis. This is why solute potential is sometimes called osmotic potential. Plant cells can metabolically manipulate Ψ_s (and by extension, Ψ_{total}) by adding or removing solute molecules. Therefore, plants have control over Ψ_{total} via their ability to exert metabolic control over Ψ_s.

Pressure Potential

Pressure potential (Ψ_p), also called turgor potential, may be positive or negative (Figure 4.5.1.1.*c*). Because pressure is an expression of energy, the higher the pressure, the more potential energy in a system, and vice versa. Therefore, a positive Ψ_p (compression) increases Ψ_{total}, and a negative Ψ_p (tension) decreases Ψ_{total}. The second tube in Figure 4.5.1.1.2) has pure water on both sides of the membrane. Positive pressure is applied to the left side. Applying positive pressure to the left side causes Ψ_p to increase. As a results, water moves to the right so that the water level is higher on the right than on the left. The third tube also has pure water, but this time negative pressure is applied to the left side. Applying negative pressure lowers Ψ_p, causing water to move to the left side of the tube. As a result, the water level is higher on the left.

Positive pressure inside cells is contained by the cell wall, producing turgor pressure. Pressure potentials are typically around 0.6–0.8 MPa, but can reach as high as 1.5 MPa in a well-watered plant. A Ψ_p of 1.5 MPa equates to 210 pounds per square inch (1.5 MPa x 140 lb in^{-2} MPa^{-1} = 210 lb/in^{-2}). As a comparison, most automobile tires are kept at a pressure of 30–34 psi. An example of the effect of turgor pressure is the wilting of leaves and their restoration after the plant has been watered (Figure 4.5.1.1.3). Water is lost from the leaves via transpiration (approaching Ψ_p = 0 MPa at the wilting point) and restored by uptake via the roots.



Figure 4.5.1.1.3: When (a) total water potential (Ψ_{total}) is lower outside the cells than inside, water moves out of the cells, and the plant wilts. When (b) the total water potential is higher outside the plant cells than inside, water moves into the cells, resulting in turgor pressure (Ψ_p) and keeping the plant erect. (credit: modification of work by Victor M. Vicente Selvas)

A plant can manipulate Ψ_p via its ability to manipulate Ψ_s and by the process of osmosis. If a plant cell increases the cytoplasmic solute concentration, Ψ_s will decline, Ψ_{total} will decline, the $\Delta\Psi$ between the cell and the surrounding tissue will decline, water will move into the cell by osmosis, and Ψ_p will increase. Ψ_p is also under indirect plant control via the opening and closing of stomata. Stomatal openings allow water to evaporate from the leaf, reducing Ψ_p and Ψ_{total} of the leaf and increasing it between the water in the leaf and the petiole, thereby allowing water to flow from the petiole into the leaf.

Gravitational Potential

Gravitational potential (Ψ_g) is always negative to zero in a plant with no height. The force of gravity pulls water downwards to the soil, reducing the difference in water potential between the leaves at the top of the plant and the roots. The taller the plant, the taller the water column, and the more influential Ψ_g becomes. On a cellular scale and in short plants, this effect is negligible and easily ignored. However, over the height of a tall tree like a giant coastal redwood, the gravitational pull of –0.1 MPa m^{-1} is equivalent to an extra 1 MPa of resistance that must be overcome for water to reach the leaves of the tallest trees. Plants are unable to manipulate Ψ_g.

Matric Potential

Matric potential (Ψ_m) is always negative to zero. In a dry system, it can be as low as –2 MPa in a dry seed, and it is zero in a water-saturated system. The binding of water to a matrix always removes or consumes potential energy from the system. Ψ_m is similar to solute potential because it involves tying up the energy in an aqueous system by forming hydrogen bonds between the water and some other component. However, in solute potential, the other components are soluble, hydrophilic solute molecules, whereas in Ψ_m, the other components are insoluble, hydrophilic molecules of the plant cell wall. Every plant cell has a cellulosic cell wall and the cellulose in the cell walls is hydrophilic, producing a matrix for adhesion of water: hence the name matric potential. Ψ_m is very large (negative) in dry tissues such as seeds or drought-affected soils. However, it quickly goes to zero as the seed takes up water or the soil hydrates. Ψ_m cannot be manipulated by the plant and is typically ignored in well-watered roots, stems, and leaves.

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4.5.1.2: TRANSPIRATION

Learning Objective

Define transpiration and identify how environmental factors affect transpiration rate.

Less than 1% of the water reaching the leaves is used in photosynthesis and plant growth. Most of it is lost in **transpiration**, the loss of water vapor to the atmosphere through stomata. It is a passive process, meaning that metabolic energy in the form of ATP is not required for water movement. The energy driving transpiration is the difference in water potential between the soil and the atmosphere. Transpiration serve two functions- it provides the force for lifting the water up the stems and it cools the leaves. However, the volume of water lost in transpiration can be very high. It has been estimated that over the growing season, one acre of corn (maize) plants may transpire 400,000 gallons (1.5 million liters) of water. As liquid water, this would cover the field with a lake 15 inches (38 cm) deep.

Transpiration involves several cellular structures in the leaf (Figure 4.5.1.2.1). Water on the surface of mesophyll cells saturates the cellulose microfibrils of the primary cell wall. The leaf contains many large intercellular air spaces for the exchange of oxygen for carbon dioxide, which is required for photosynthesis. The wet cell wall is exposed to this leaf internal air space, and the water on the surface of the cells evaporates into the air spaces, decreasing the thin film on the surface of the mesophyll cells.

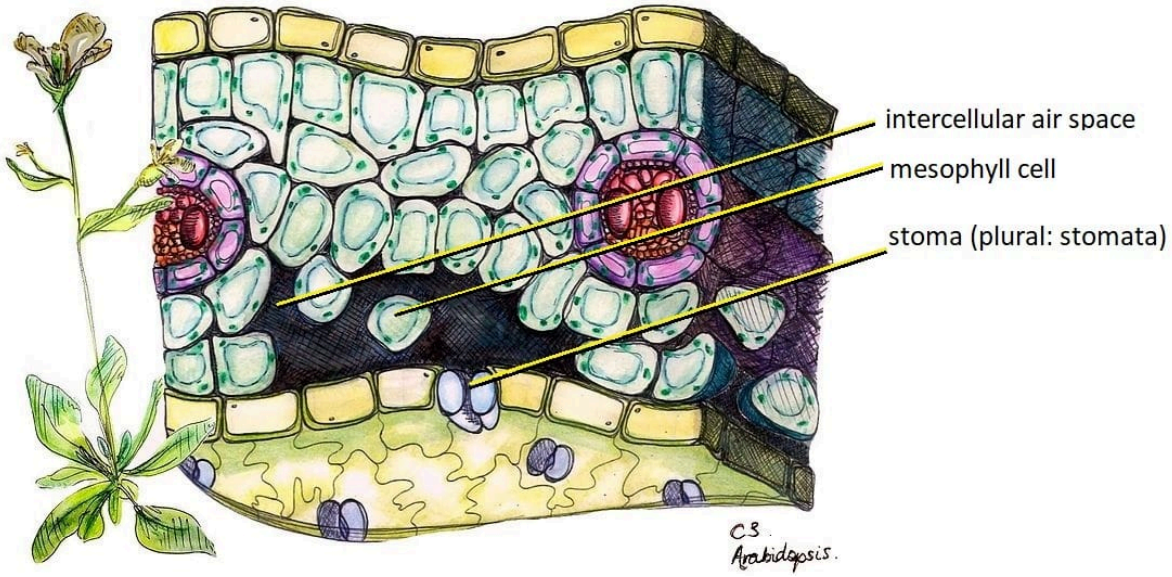


Figure 4.5.1.2.1: Intercellular air spaces are found between mesophyll cells in this illustration of an *Arabidopsis thaliana* leaf cross section. During transpiration, water evaporates from mesophyll cells and exits through stomata, the pores in the epidermis, which surrounds the leaf. Image modified from Ninghui Shi (CC-BY-SA).

Several environmental factors influence transpiration rate, which can be measured with a **potometer** (Figure 4.5.1.2.2). Light, high temperatures, and wind increase transpiration rate while humidity reduces it. Light stimulates stomatal opening (see Stomatal Opening and Closure), allowing water vapor to easily leave the leaf. Light also speeds up transpiration by warming the leaf. Plants transpire more rapidly at higher temperatures because water evaporates more rapidly as the temperature rises. At 30°C, a leaf may transpire three times as fast as it does at 20°C. Humidity decreases transpiration rate by reducing the difference in water potential between the air and intercellular air spaces. The rate of diffusion of any substance increases as the difference in concentration of the substances in the two regions increases. When the surrounding air is dry, diffusion of water out of the leaf goes on more rapidly. As transpiration occurs, the air surrounding a leaf becomes increasingly humid, reducing the difference in water potential between the intercellular air spaces and the atmosphere and slowing transpiration. When a breeze is present, however, the humid air is carried away and replaced by drier air. Plants can regulate transpiration through opening and closing stomata, and plants that live in especially hot or dry regions have special adaptations to reduce water loss.

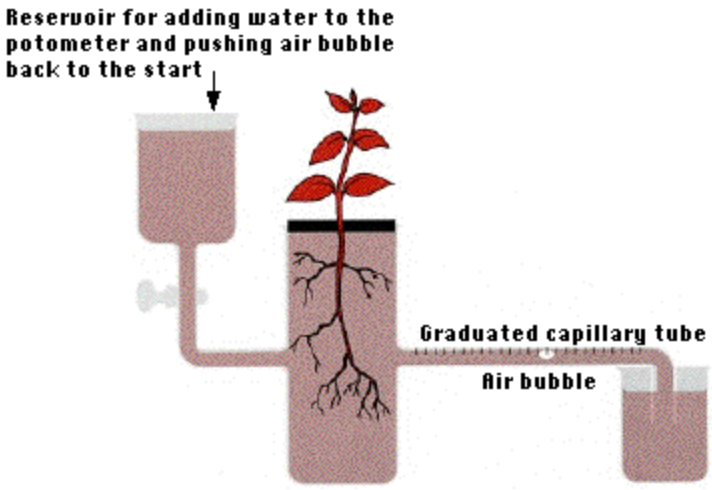


Figure 4.5.1.2.2: This potometer can measure transpiration rate. As water is transpired or otherwise used by the plant, it is replaced from the reservoir on the right. This pushes the air bubble to the left in the graduated capillary tube, providing a precise measure of the volume of water used.

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- Transpiration

4.5.1.2.1: Adaptations to Reduce Transpiration

4.5.1.2.2: Stomatal Opening and Closure

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4.5.1.2.1: Adaptations to Reduce Transpiration

Learning Objective

Describe the various adaptations that help plants reduce transpiration rate.

Plants have evolved over time to adapt to their local environment and reduce transpiration. Leaves are covered by a waxy cuticle on the outer surface that prevents the loss of water. Plants that grow in dry environments and plants that grow on other plants (**epiphytes**) have a much thicker waxy cuticle than those growing in more moderate, well-watered environments (Figure 4.5.1.2.1.1). Additionally, they often have a thick covering of **trichomes** or of stomata that are sunken below the leaf's surface (Figure 4.5.1.2.1.2). These adaptations impede air flow across the stomatal pore and reduce transpiration. Multiple epidermal layers are also commonly found in these types of plants .



Figure 4.5.1.2.1.1: Plants are suited to their local environment. Plants adapted to dry conditions such as the prickly pear cactus (*Opuntia* sp., left) and epiphytes like this tropical *Aeschynanthus perrottetii* (right) have adapted to very limited water resources. The leaves of a prickly pear are modified into spines, which lowers the surface area-to-volume ratio and reduces water loss. Photosynthesis takes place in the stem, which also stores water. *A. perottetii* leaves have a waxy cuticle that prevents water loss. The left image is a modification of work by Jon Sullivan, and the right image is a modification of work by L. Shyamal/Wikimedia Commons.

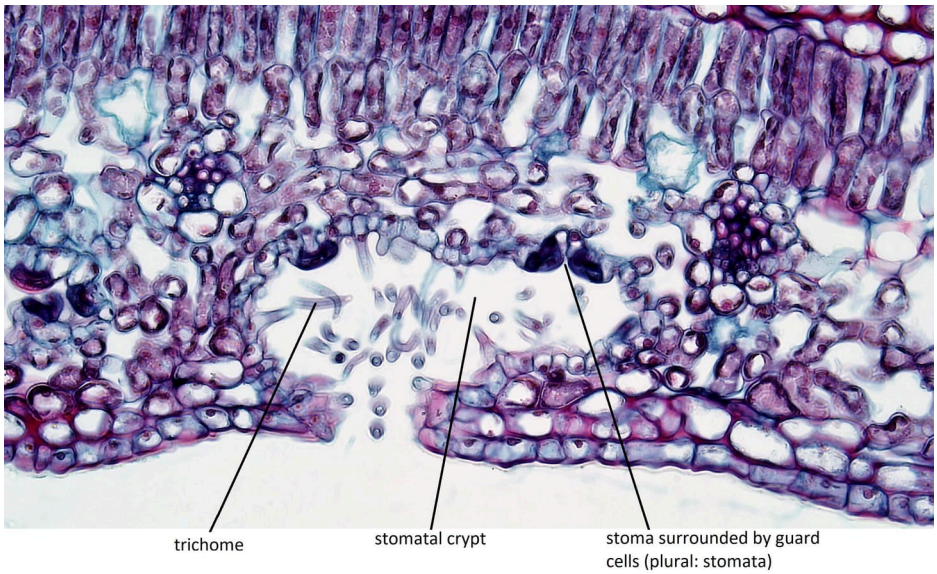


Figure 4.5.1.2.1.2: Cross section of an oleander (*Nerium* sp.) leaf. Oleander is adapted to dry conditions. Stomata are sunken into stomatal crypts and bordered by trichomes, reducing transpiration. Magnified at 400x. Image modified from Berkshire Community College Bioscience Image Library (public domain).

The size and shape of photosynthetic structures also influences transpiration rate. **Succulent** plants, common in deserts, have thick, fleshy leaves or stems (Figure 4.5.1.2.1.1, left). Other plants, such as the evergreen shrubs of the chaparral, have small, thick, tough leaves (Figure 4.5.1.2.1.3). Compared to thin, broad leaves, these shapes reduce surface area-to-volume ratio and decreases the opportunity for water loss. Plants with thin, broad leaves that live in climates with hot, dry seasons (such as chaparral or tropical forests that have a wet and dry season) may be **deciduous**, losing their leaves during these seasons to limit transpiration (Figure 4.5.1.2.1.4).



Figure 4.5.1.2.1.3: (left) The thick, tough leaves of chamise (*Adenostoma fasciculatum*) limit transpiration during dry, hot summers. Image by Tom Hilton (CC-BY). (right) Sal tree (*Shorea robusta*) is a tropical deciduous tree, losing its leaves during the dry season. Image by J.M.Garg (CC-BY-SA).

As discussed in 13.7: Photorespiration and Photosynthetic Pathways, CAM plants close their stomata during the day when light and high temperatures would otherwise increase transpiration rate. C_4 plants reduce the need to frequently open stomata by creating a high carbon dioxide concentration in the bundle sheath cells, which conduct the Calvin cycle. Regardless of photosynthetic pathway, plants can open and close stomata to regulate transpiration rate based on environmental conditions.

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4.5.1.2.2: Stomatal Opening and Closure

Learning Objectives

- Relate the pattern of cell wall thickening in guard cells to their function.
- Explain the mechanism by which blue light triggers stomatal opening.
- Explain the mechanism by which water stress, signaled by abscisic acid, triggers stomatal closure.

Regulation of transpiration is achieved primarily through the opening and closing of stomata on the leaf surface. Stomata are surrounded by two specialized cells called guard cells (Figure 4.5.1.2.2.1). Stomata must open to allow the gas exchange of carbon dioxide and oxygen for efficient photosynthesis (see Photorespiration), and light thus typically triggers stomatal opening. When stomata are open, however, water vapor is lost to the external environment, increasing the rate of transpiration. Therefore, plants must maintain a balance between gas exchange and water loss. Water stress, high temperatures, and high carbon dioxide concentration causes stomata to close.

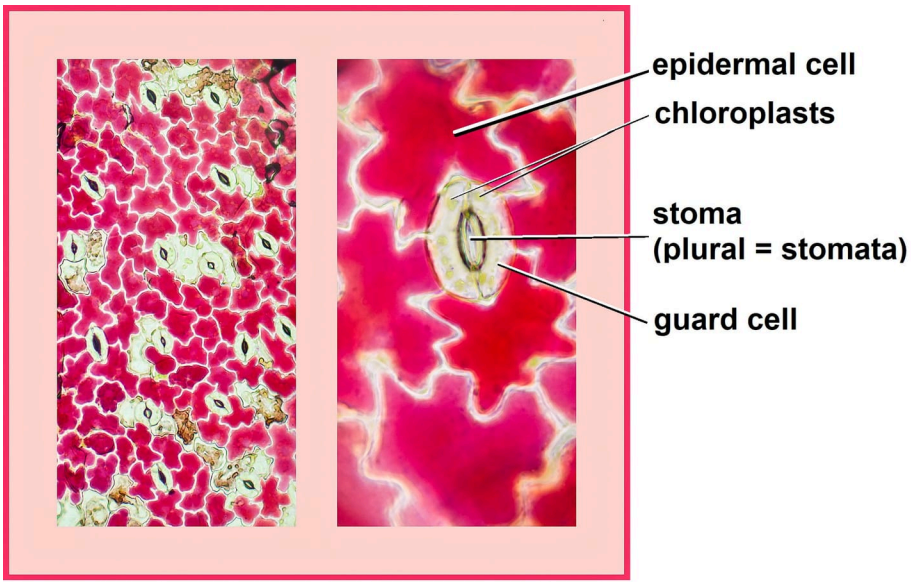


Figure 4.5.1.2.2.1: Italian chicory leaf epidermis showing stomata. The epidermal cells are shaped like puzzle pieces. The stomata (singular = stoma) are pores in the epidermis. Each is bordered by two guard cells, which are filled with oval, green chloroplasts. Image by Umberto Salvagnin (CC-BY).

Stomatal Opening

Guard cell walls are radially thickened such that the thickenings are concentrated around the stoma (plural: stomata; Figure 4.5.1.2.2.2). When turgor pressure increases in guard cells, the cells swell. However, the thickened inner walls near the stoma cannot expand, so they curve to accommodate the expanding outer walls. The curving of the guard cells opens the stoma.

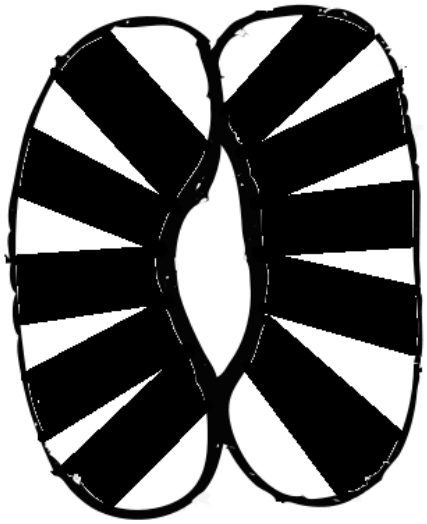


Figure 4.5.1.2.2.2: The guard cells that surround the stoma have radial cell wall thickenings (represented by solid black lines). The portion of the guard cell adjacent to the stoma (ventral side) has a fully thickened cell wall. The outer portion (dorsal side) has alternating bands of thick and thin cell wall. Image modified from Vojtech.dostal (public domain).

How does light cause stomata to open? Phototropins detect blue light, causing a proton pumps to export protons (H^+). ATP, generated by the light reactions of photosynthesis, drives the pump. The cytosol usually more negative than the extracellular solution, and this difference in charge (**membrane potential**) increases as protons leave the cell. This increase in membrane potential is called **hyperpolarization**, and it causes potassium (K^+) to move down its electrochemical gradient into the cytosol. Protons also move down their electrochemical gradient back into the cytosol, bringing chloride (Cl^-) with them through **symport** channels. Meanwhile, starch is broken down, producing sucrose and malate. Nitrate (NO_3^-) also enters the cell. The solute potential resulting high concentrations of potassium, chloride, sucrose, malate, and nitrate in the cytosol drives the osmosis of water into the the guard cells. This increases turgor pressure, and the guard cells expand and bend, opening the stoma (Figure 4.5.1.2.2.3).

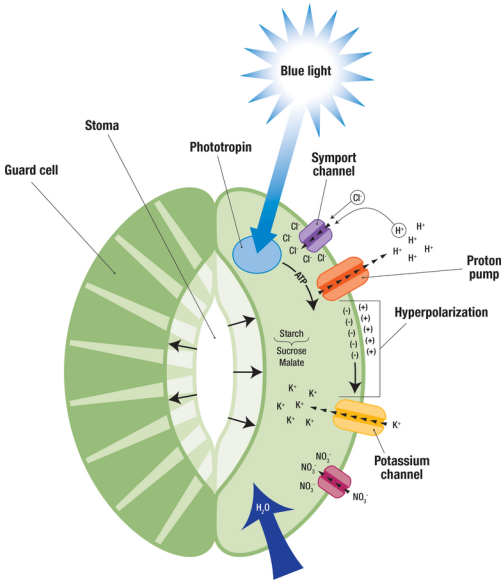


Figure 4.5.1.2.2.3: Phototropins respond to blue light and signal to the proton pump to export protons. This active transport is fueled by the ATP produced in the light-dependent reactions of photosynthesis. This causes the cell to become hyperpolarized, stimulating an influx of potassium ions. At the same time, chloride is symported into the guard cell with protons as they reenter the cell. Nitrate (NO_3^-) also enters the cell. Starch breaks down, producing sucrose and malate. These, along with the influx of ions, increases the solute concentration inside of the guard cells, driving water into the cells. This increases turgor pressure and causes the guard cells to expand. Due to their radial cell wall thickenings, the guard cells curve when they expand, opening the stoma (plural: stomata). Image by Jen Valenzuela (CC-BY-NC).

Table 4.5.1.2.2.1 illustrates how osmotic pressure (which results in turgor pressure) increases with light availability during the day. When the osmotic pressure of the guard cells became greater than that of the surrounding cells, the stomata opened. In the evening, when the osmotic pressure of the guard cells dropped to nearly that of the surrounding cells, the stomata closed.

Table 4.5.1.2.2.1: Osmotic pressure measured at different times of day in typical guard cells. The osmotic pressure within the other cells of the lower epidermis remained constant at ~1 MPa.

Time	Osmotic Pressure (MPa)
7 A.M.	1.46
11 A.M.	3.14
5 P.M.	1.88
12 Midnight	1.32

Stomatal Closure

When water is low, roots synthesize **abscisic acid** (ABA), which is transported through the xylem to the leaves. There, abscisic acid causes calcium channels to open. Calcium (Ca^{2+}) opens anion channels, and malate, chloride, and nitrate exit the cell. The membrane potential decreases (the difference in charge across the membrane becomes less pronounced) as anions leave the cell. Potassium exits the cell in response to this decrease in membrane potential (called **depolarization**). The loss of these solutes in the cytosol results in water leaving the cell and a decrease in turgor pressure. The guard cells regain their original shape, and the stoma closes (Figure 4.5.1.2.2.4).

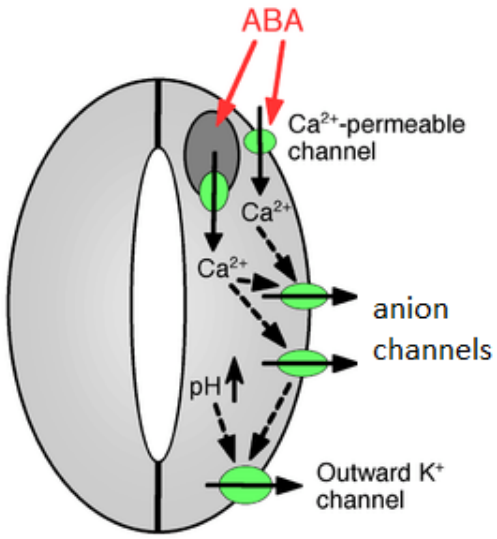


Figure 4.5.1.2.2.4: Stomatal closure is triggered by abscisic acid (ABA), which causes calcium (Ca^{2+}) ions to enter the cell. These open anion channels. At this point, the cytoplasm is not as negatively charged as it was before. The change in charge opens potassium (K^+) channels, and potassium leaves the cell as well. Water leaves the cells, causing them to loose turgor pressure. The stoma then closes. Image modified from June Kwak (public domain).

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4.5.1.3: Cohesion-Tension Theory

Learning Objectives

- Explain how water moves upward through a plant according to the cohesion-tension theory.
- Provide experimental evidence for the cohesion-tension theory.

In 1895, the Irish plant physiologists H. H. Dixon and J. Joly proposed that water is pulled up the plant by **tension** (negative pressure) from above. As we have seen, water is continually being lost from leaves by transpiration. Dixon and Joly believed that the loss of water in the leaves exerts a pull on the water in the xylem ducts and draws more water into the leaf. But even the best vacuum pump can pull water up to a height of only 10.4 m (34 ft) or so. This is because a column of water that high exerts a pressure of 1.03 MPa just counterbalanced by the pressure of the atmosphere. How can water be drawn to the top of a sequoia, the tallest is 113 m (370 ft) high? Taking all factors into account, a pull of at least ~1.9 MPa is probably needed.

The answer to the dilemma lies the **cohesion** of water molecules; that is the property of water molecules to cling to each through the hydrogen bonds they form (Figure 4.5.1.3.1). When ultrapure water is confined to tubes of very small bore, the force of cohesion between water molecules imparts great strength to the column of water. It has been reported that tensions as great as 21 MPa are needed to break the column, about the value needed to break steel wires of the same diameter. In a sense, the cohesion of water molecules gives them the physical properties of solid wires.

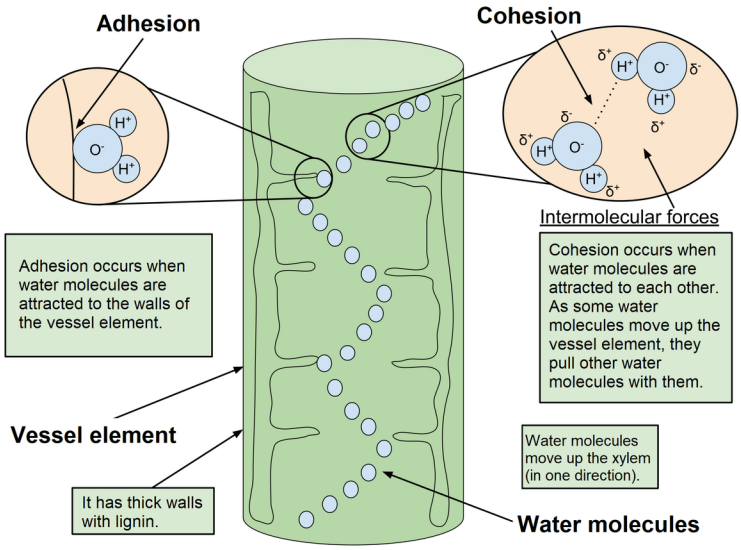


Figure 4.5.1.3.1: The cohesion and adhesion of water in the vessel element helps water move up the vessel without breaking under tension. Adhesion occurs when water molecules are attracted to the walls of the vessel element, which has thick walls with lignin, a stiff substance. Cohesion occurs when water molecules are attracted to each other. This is due to hydrogen bonds, which form between the partially negative oxygen of one molecule and the partially positive hydrogen of another molecule. Hydrogen bonds are a strong intermolecular force. As some water molecules move up the vessel element, they pull other water molecules with them. Water molecules move up the xylem (in one direction). Image modified from FeltyRacketeer6 (CC-BY-SA).

According to the **cohesion-tension theory**, transpiration is the main driver of water movement in the xylem. It creates negative pressure (tension) equivalent to –2 MPa at the leaf surface. Water from the roots is ultimately pulled up by this tension. Negative water potential draws water from the soil into the root hairs, then into the root xylem. Cohesion and adhesion draw water up the xylem. Transpiration draws water from the leaf through the stoma. Water potential becomes increasingly negative from the root cells to the stem to the highest leaves, and finally to the atmosphere (Figure 4.5.1.3.2).

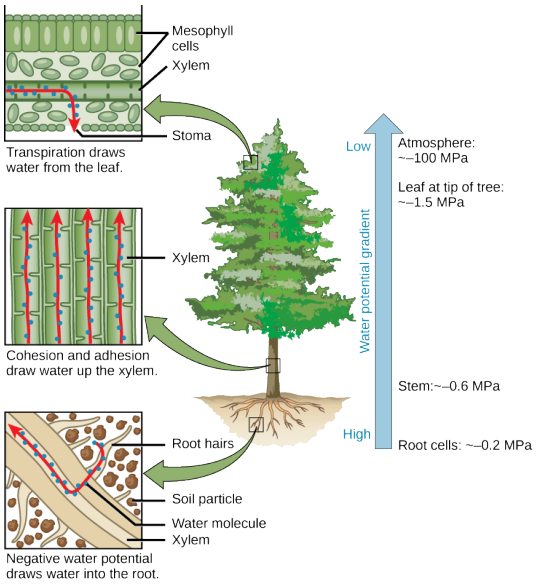


Figure 4.5.1.3.2: The cohesion–tension theory is shown. Evaporation from the mesophyll cells produces a negative water potential gradient that causes water to move upwards from the roots through the xylem. Water potential is measured in megapascals (MPa), which is a measure of pressure. Water potential decreases from the root cells (-0.2 MPa) to the stem (-0.6 MPa) to the leaf at the tip of a tree (-1.5 MPa) to the atmosphere (-100 MPa). Transpiration draws water from the leaf. The water leaves the tube-shaped xylem and enters the air space between mesophyll cells. Finally, it exits through the stoma. Cohesion and adhesion draw water up the xylem. Negative water potential draws water into the root. Water moves from the spaces between soil particles into the root hairs, and into the xylem of the root.

The water potential at the leaf surface varies greatly depending on the **vapor pressure deficit**, which can be negligible at high **relative humidity** (RH) and substantial at low RH. At night, when stomata typically shut and transpiration stops, the water is held in the stem and leaf by the adhesion of water to the cell walls of the xylem vessels and tracheids, and the cohesion of water molecules to each other.

The mechanism of the cohesion-tension theory is based on purely physical forces because the xylem vessels and tracheids are not living at maturity. Evaporation of water into the intercellular air spaces creates a greater tension on the water in the mesophyll cells , thereby increasing the pull on the water in the xylem vessels. The xylem vessels and tracheids are structurally adapted to cope with large changes in pressure. Rings in the vessels maintain their tubular shape, much like the rings on a vacuum cleaner hose keep the hose open while it is under pressure. Small perforations between vessel elements reduce the number and size of gas bubbles that can form via a process called **cavitation**. The formation of gas bubbles in xylem interrupts the continuous stream of water from the base to the top of the plant, causing a break termed an embolism in the flow of xylem sap. The taller the tree, the greater the tension forces needed to pull water, and the more cavitation events. In larger trees, the resulting embolisms can plug xylem vessels, making them non-functional.

The pulling force due to transpiration is so powerful that it enables some trees and shrubs to live in seawater. Seawater is markedly hypertonic to the cytoplasm in the roots of the red mangrove (*Rhizophora mangle*), and we might expect water to leave the cells resulting in a loss in turgor and wilting. However, the remarkably high tensions in the xylem (~3 to 5 MPa) can pull water into the plant against this osmotic gradient. Mangroves literally desalt seawater to meet their needs.

Experimental evidence supports the cohesion-tension theory. Over a century ago, a German botanist who sawed down a 21-m (70-ft) oak tree and placed the base of the trunk in a barrel of picric acid solution. The solution was drawn up the trunk, killing nearby tissues as it went. If the roots were the driving force, upward water movement would have stopped as soon as the acid killed the roots. However, the solution reached the top of the tree. When the acid reached the leaves and killed them, the water movement ceased, demonstrating that the transpiration in leaves was causing the water the upward movement of water.

According to the cohesion-tension theory, the water in the xylem is under tension due to transpiration. Consistent with this prediction, the diameter of Monterey pines decreases during the day, when transpiration rates are greatest (Figure 4.5.1.3.3). Because the water column is under tension, the xylem walls are pulled in due to adhesion.

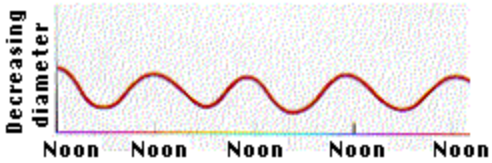


Figure 4.5.1.3.3: This graph shows the diameter of a Monterey pine over time. The diameter fluctuates on a daily basis reaching its minimum when the rate of transpiration reaches its maximum (around noon). Results obtained by D. T. MacDougall.

The Tallest Trees

By spinning branches in a centrifuge, it has been shown that water in the xylem avoids cavitation at negative pressures exceeding ~1.6 MPa. And the fact that giant redwoods (*Sequoia sempervirens*, Figure 4.5.1.3.4) can successfully lift water 109 m (358 ft), which would require a tension of ~1.9 MPa, indicating that cavitation is avoided even at that value. However, such heights may be approaching the limit for xylem transport. Measurements close to the top of one of the tallest living giant redwood trees, 112.7 m (~370 ft), show that the high tensions needed to transport water have resulted in smaller stomata, causing lower concentrations of CO_2 in the needles, reduced photosynthesis, and reduced growth (smaller cells and much smaller needles; Koch et al. 2004). The limits on water transport thus limit the ultimate height which trees can reach. The tallest living tree is a 115.9-m giant redwood, and the tallest tree ever measured, a Douglas fir, was 125.9 m.



Figure 4.5.1.3.4: A giant redwood tree (*Sequoia sempervirens*) 'Sherman' in the Sequoia National Park, California, USA. (Note that this is the same species but a different individual than the trees described in this box.) Image by Nagytibi and Revolus (CC-BY-SA).

Reference: Koch, G., Sillett, S., Jennings, G. *et al.* The limits to tree height. *Nature* **428,** 851–854 (2004). https://doi.org/10.1038/nature02417

Supplemental Reading

Woodward, I. Tall storeys. *Nature* **428,** 807–808 (2004). https://doi.org/10.1038/428807a

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4.5.1.4: Water Absorption

Learning Objectives

- Explain the function of root hairs.
- Define root pressure and explain its mechanism.
- Contrast the three pathways of water movement through the roots and identify each cell type or tissue involved.

Most plants secure the water and minerals they need from their roots. Water moves from the soil to the roots, stems, and ultimately the leaves, where transpiration occurs. The roots absorb enough water to compensate for water lost to transpiration. Rapid absorption is aided by **root hairs**, which extend from epidermal cells, increasing surface area (Figure 4.5.1.4.1). As discussed earlier in this chapter, roots draw water from the soil because they have lower water potential than the soil. Much of this difference in water potential is an indirect result of transpiration, but roots can also water potential by decreasing solute potential.



Figure 4.5.1.4.1: The young roots (radicles) of these radish seedlings are covered with fuzzy, white root hairs, which aid with water absorption. Image by Melissa Ha (CC-BY).

Root Pressure

When a tomato plant is carefully severed close to the base of the stem, sap oozes from the stump (Figure 4.5.1.4.2). The fluid comes out because roots are constantly absorbing water, drawing it into the vascular cylinder, and pushing it up the xylem. This is called **root pressure**, and it is created by the osmotic pressure of solutes trapped in the vascular cylinder by the **Casparian strip**.

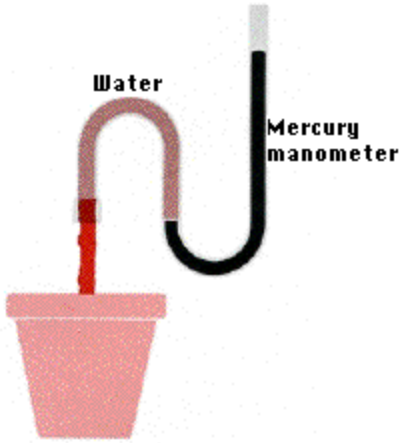


Figure 4.5.1.4.2: An experiment illustrating root pressure. The stem of a plant is severed and attached to a tube containing water. Mercury lies on top of the water. Root pressure pushes water out of the stem, moving the mercury up the tube.

Although root pressure plays a small role in the transport of water in the xylem in some plants and in some seasons, it does not account for most water transport. As evidence, few plants develop root pressures greater than ~0.2 kPa, and some develop no root pressure at all. Additionally, the volume of fluid transported by root pressure is not enough to account for the measured movement of water in the xylem of most trees and vines. Furthermore, the highest root pressures occur in the spring, but water moves through the xylem most rapidly in the summer (when transpiration is high).

As discussed in the Cohesion-Tension Theory section, transpiration, rather than root pressure, is typically the driving force for upward water movement in a plant. However, when transpiration rates are very low, such as in cool and humid weather, root pressure pushes water up the xylem faster than water is lost through the stomata. As a result water droplets are forced out of openings on the leaf margin, a phenomenon called **guttation** (Figure 4.5.1.4.3). Droplets resulting from guttation are not to be confused with dew droplets, which result from the condensation of water vapor when the air becomes colder and has less capacity to hold water. In other words, guttation results from water that was inside of the plant, but dew droplets form from water vapor that was in the surrounding air.



Figure 4.5.1.4.3: Guttation of a strawberry leaf. Image by Noah Elhardt (public domain).

Pathways of Water Movement

Water can move through the roots by three separate pathways: apoplast, symplast, and transmembrane (transcellular). In the **apoplast pathway** (apoplastic route), water moves through the spaces between the cells and in the cells walls themselves. In the **symplast pathway** (symplastic route), water passes from cytoplasm to cytoplasm through **plasmodesmata** (Figure 4.5.1.4.4

). In the **transmembrane pathway**, water crosses plasma membranes, entering and exiting each cell. Water moving through the transmembrane pathway thus moves through both the symplast (interconnected cytoplasms) and apoplast (cell walls and spaces in between cells). Water may also cross the tonoplast, entering the central vacuole as part of the transmembrane pathway.

Water from the soil is absorbed by the root hairs of the epidermis and then moves through the cortex through one of the three pathways. However, the inner boundary of the cortex, the **endodermis**, is impervious to water due to the Casparian strip. Regardless of how the water moved up to this point (apoplast, symplast, transmembrane), it must enter the cytoplasms of the endodermal cells. From here it can pass via plasmodesmata into the cells of the vascular cylinder (stele). Once inside, water is again free to move through the apolast, the symplast, or both (transmembrane).

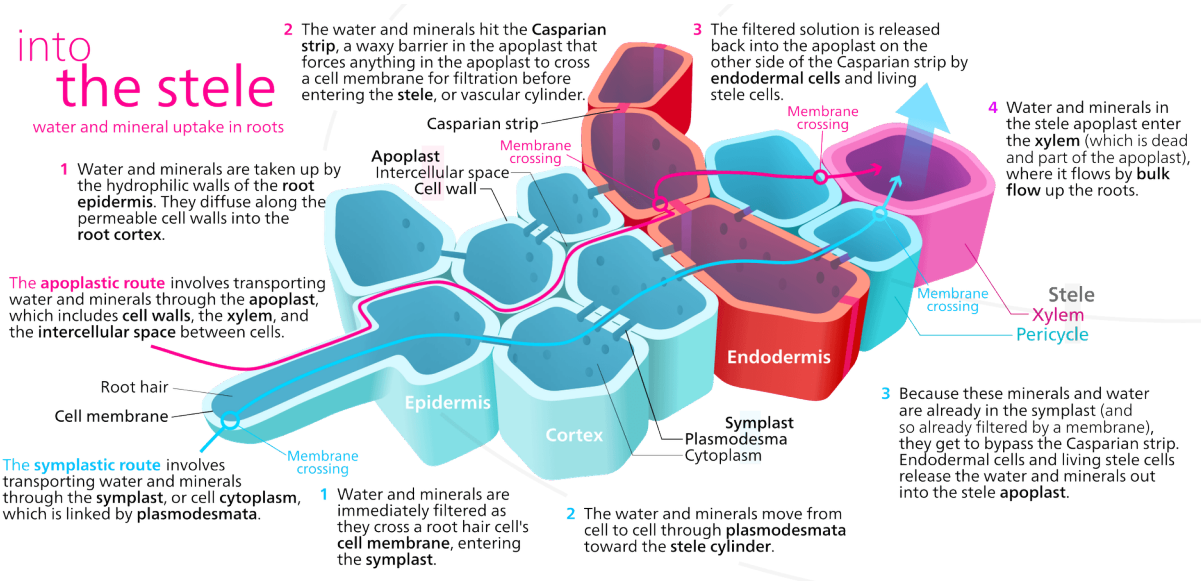


Figure 4.5.1.4.4: Movement of water and minerals through the roots. Water moves through the root hairs of the epidermal cells through the cortex, including the endodermis, before entering the outermost layer of the vascular cylinder, the pericycle. the vascular cylinder (stele). Water ultimately enters the conducting cells of the xylem. Water can move between cells and through the cell walls and intercellular spaces in the apoplast pathway (apoplastic route) or between adjacent cytoplasms through plasmodesmata in the symplast pathway (symplastic route). In both pathways, all water must move through the cytoplasm of the endodermal cells because the Casparian strip blocks apoplastic movement across the Casparian strip. The steps of the apoplastic pathway are as follows: (1) Water and minerals are taken up by the hydrophilic walls of the root epidermis. They diffuse along the permeable cell walls into the root cortex. (2) The water and minerals hit the Casparian strip, a waxy barrier in the apoplast that forces anything in the apoplast to cross a cell membrane for filtration before entering the stele, or vascular cylinder. (3) The filtered solution is released back into the apoplast on the other side of the Casparian strip by endodermal cells and living stele cells. (4) Water and minerals in the stele apoplast enter the xylem (which is dead and part of the apoplast), where it flows by bulk flow up the roots. The steps of the symplastic pathway are as follows: (1) Water and minerals are immediately filtered as they cross a root hair cell's cell membrane, entering the symplast. (2) The water and minerals move from cell to cell through plasmodesmata toward the stele cylinder. (3) Because these minerals and water are already in the symplast (and so already filtered by a membrane), they get to bypass the Casparian strip. Endodermal cells and living stele cells release the water and minerals out into the stele apoplast (the xylem). The transmembrane pathway is not shown. Image by Kelvinsong (CC-BY-SA).

Once in the xylem, water with the minerals that have been deposited in it (as well as occasional organic molecules supplied by the root tissue) move up in the vessel elements and tracheids. At any level, the water can leave the xylem and pass laterally to supply the needs of other tissues. At the leaves, the xylem passes into the petiole and then into the veins of the leaf. Water leaves the finest veins and enters the cells of the spongy and palisade layers. Here some of the water may be used in metabolism, but most is lost in transpiration.

Figure 4.5.1.4.4 illustrates minerals moving through the apoplast or symplast, but minerals typically move through the symplast. Minerals enter the root by active transport into the symplast of epidermal cells and move toward and into the vascular cylinder through the plasmodesmata connecting the cells. They enter the conducting cells of the xylem from the pericycle and other parenchyma cells via active transport through specialized transmembrane channels.

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4.5.2: Translocation (Assimilate Transport)

Learning Objectives

- Distinguish between sources and sinks and provide examples of each.
- Explain the process of phloem loading, distinguishing between apoplastic and symplastic pathways.
- Explain how assimilate translocations through the phloem according to the pressure-flow hypothesis.

Plants need an energy source to grow. In seeds and bulbs, food is stored in polymers (such as starch) that are converted by metabolic processes into sucrose for newly developing plants. Once green shoots and leaves are growing, plants are able to produce their own food through photosynthesis. The products of photosynthesis (mainly the sugar sucrose) are a major component of the substance found in the phloem, called **assimilate**. Ions, amino acids, certain hormones, and other molecules are also found in assimilate. The movement of assimilate is called **translocation**, or assimilate transport.

Sources and Sinks

Structures that produce or release sugars for the growing plant are referred to as **sources**. Examples include mature leaves, which produce sugar through photosynthesis, and storage organs, such bulbs, tubers, or storage roots. Sources produce or store more sugars than they need themselves and can thus export sugars. The points of sugar delivery, such as most roots, young shoots, and developing fruits and seeds, are called **sinks** (Figure 4.5.2.1). Because sinks do not produce enough sugars to meet their energy needs, they must import sugars from sources.



Figure 4.5.2.1: The mature leaves of this tree are sources, and the apples are sinks. Image by W.carter (public domain).

The pattern of assimilate flow changes as the plant grows and develops. Sugars are directed primarily to the roots early on, to shoots and leaves during vegetative growth, and to seeds and fruits during reproductive development. They are also directed to storage structures. Thus, the same organ may function as a source or a sink depending on the stage of development. For example, a young leaf may initially be a sink, but it will eventually grow and conduct enough photosynthesis to become a source. Similarly, a developing seed is a sink as the embryo develops. Once the seed germinates, however, starches stored in the seed break down, act as a source for the growing seedling structures.

The products from the source are usually translocated to the nearest sink through the phloem. For example, the highest leaves will send sugars upward to the growing shoot tip, whereas lower leaves will direct sugars downward to the roots. Intermediate leaves will send products in both directions, unlike the flow in the xylem, which is always unidirectional (soil to leaf to atmosphere).

Phloem Loading

Before discussing how sources transport sugars into the phloem (**phloem loading**), let's first review the conducting cells of the phloem. Stacks of these cylindrical cells called **sieve-tube elements** form column-like structures. Each cell is separated by a sieve plate (sieve-tube plate). The sieve plate has holes in it, like a slice of Swiss cheese, allowing for translocation. Lateral sieve areas on the side of the column allow different phloem tubes to interact. Sieve-tube elements have reduced cytoplasmic contents and rely on special parenchyma cells called companion cells, which assist with metabolic activities and provide energy (Figure 4.5.2.2). In addition to sieve-tube elements and companion cells, the phloem contains other parenchyma cells and may contain sclerenchyma fibers. In leaves, the phloem is found in vascular bundles (leaf veins), which are surrounded by a bundle sheath. Sugars are produced through photosynthesis in the mesophyll cells that fill most of the leaf (see diagram in Transpiration section).

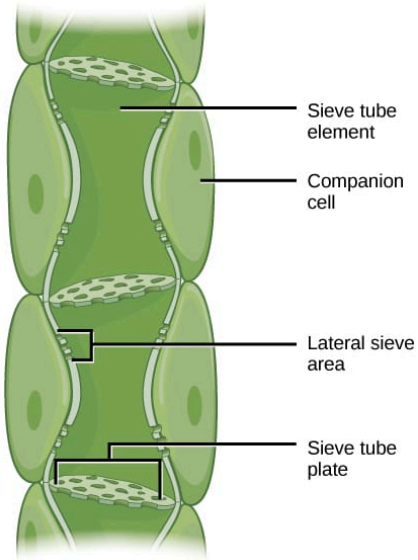


Figure 4.5.2.2: Sieve-tube elements are the conducting cells of the phloem in angiosperms. Assimilate travels through perforations in sieve plates (labeled sieve-tube plates), which connect stacked sieve-tube elements. Neighboring companion cells carry out metabolic functions for the sieve-tube elements and provide them with energy. Lateral sieve areas connect the sieve-tube elements to the companion cells.

There are two pathways of **phloem loading** (Figure 4.5.2.3). Both pathways begin the same way. The cytoplasms of most plant cells are interconnected via plasmodesmata.Augars through plasmodesmata from mesophyll cells to bundle sheath cells to the parenchyma cells of the phloem. From there, the pathways differ. The first pathway called **apoplastic phloem loading**, occurs when the regular parenchyma cells of phloem are not connected to the companion cells. In this case, sucrose must exist the regular parenchyma cells and enter the apoplast. It enters the companion cell cytoplasm as well as the inside of the sieve tube through **secondary active transport**. Protons are pumped into the apoplast (outside of the cells), when the protons re-enter the cells (move down their concentration gradient), they bring sucrose with them by flowing through carrier proteins called **sucrose-proton symporters**. In this way, sucrose is actively transported against its concentration gradient, and high sucrose concentrations accumulate in the assimilate of the phloem. The second pathway is **symplastic phloem loading**. When the regular parenchyma cells of the phloem are connected to companion cells via plamodesmata, sucrose can flow through the symplast all the way to the sieve-tube elements. There is no need for sucrose to leave the cytoplasm (enter the apoplast) and re-enter cells via sucrose-proton symport.

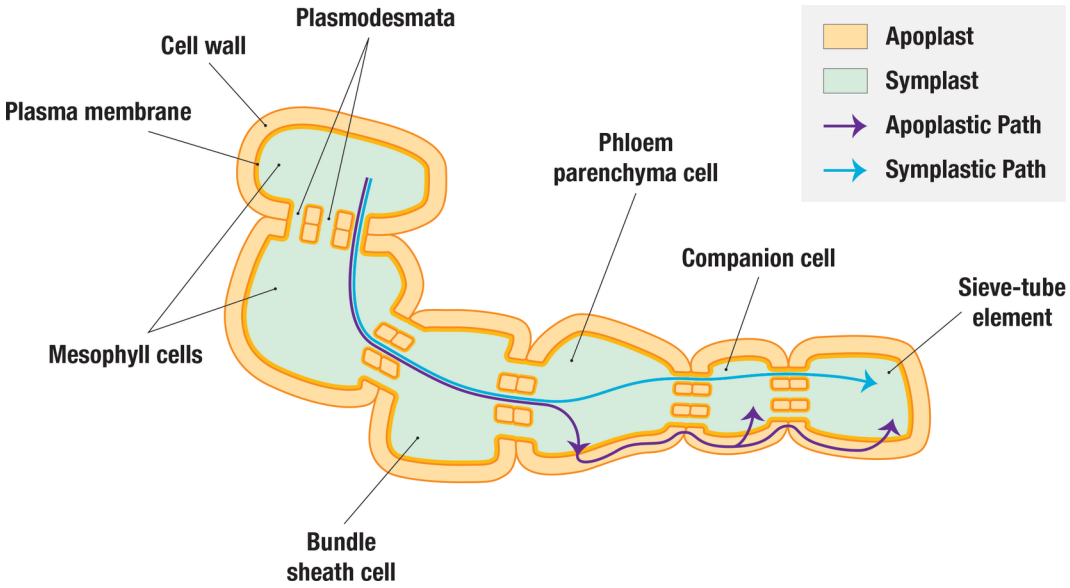


Figure 4.5.2.3: Apoplastic and symplastic phloem loading. The apoplast (yellow) consists of the cell wall and spaces between cells. The symplast (green) consists of cytoplasms interconnected via plasmodesmata. Both the apoplastic and symplastic pathways of phloem loading begin the same way, with sugars moving through the plasmodesmata that connect mesophyll cells with each other and bundle sheath cells. In symplastic phloem loading (top line, blue), sugars continue through plasmodesmata (remain in the symplast) to the companion cell and then to the sieve-tube element. In apoplastic phloem loading (bottom line, purple), sugars exit phloem parenchyma cells into the apoplast. They then reenter the symplast when they are actively transported into companion cells and sieve-tube elements. Image by Jen Valenzuela (CC-BY).

Pressure-Flow Hypothesis

What drives the movement of assimilate in the phloem? According to the **pressure-flow hypothesis**, assimilate moves due to osmosis of water to and from the xylem. While this is a passive process, it ultimately results from the active transport of sugars during phloem loading and unloading. In contrast with transpiration, an entirely passive process, translocation as a passive process that is indirectly driven by active processes.

Assimilate contains up to 30 percent sugar, and this high solute concentration decreases Ψ_s, which decreases the total water potential. The sugar concentration of the assimilate near sinks, where phloem loading occurs, is highest. This causes water to move by osmosis from the adjacent xylem into sieve tubes, thereby increasing pressure. The increase in pressure increases in total water potential causes the bulk flow of phloem from source to sink (Figure 4.5.2.4). Sugar concentration in the sink cells is lower than in the sieve-tube elements because the sink sucrose has been metabolized for growth, or converted to starch for storage or other polymers, such as cellulose, for structural integrity. Unloading at the sink end of the phloem tube occurs by either diffusion or active transport of sucrose molecules from an area of high concentration to one of low concentration. Unloading reduces the sugar concentration of assimilate near sinks, increasing water potential. As a result, water moves from the phloem by osmosis and is then transpired or recycled via the xylem back into the phloem sap.

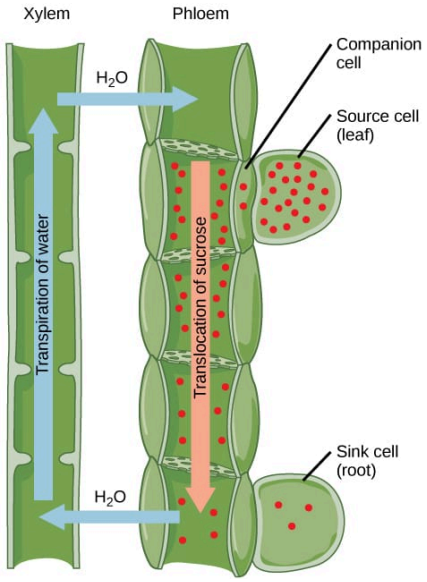


Figure 4.5.2.4: The pressure-flow hypothesis of assimilate transport. The assimilate, which is rich in sucrose, is actively transported from source cells into companion cells and then into the sieve-tube elements. This reduces the water potential, which causes water to enter the phloem from the xylem. The resulting positive pressure forces the assimilate down toward the sink cells, where sucrose is unloaded. At this point, there is no longer a high concentration of sucrose, and water returns to the xylem. The leaf is an example of a source, and the root is an example of a sink.

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4.5.3: Chapter Summary

Water and minerals move through the xylem, and sugars move through the phloem. Water potential and transpiration influence how water is transported through the xylem in plants as described by the **cohesion-tension theory**. **Water potential** (Ψ) is a measure of the difference in potential energy between a water sample and pure water and is influenced by solute concentration, pressure, gravity, and matric potential. **Transpiration** is primarily regulated by stomatal opening and closure. Roots must absorb water to replace the water lost through transpiration, and the high solute concentrations in the vascular cylinder results in **root pressure. Assimilate** containing sucrose move from sources to sinks through the plant's phloem. **Phloem loading** increases solute concentration and causes water to move by osmosis from the xylem into the phloem. The positive pressure that is produced pushes water and solutes down the pressure gradient. The sucrose is unloaded into the sink, and the water returns to the xylem vessels.

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

- Define water potential and explain how it is influenced by solutes, pressure, gravity, and the matric potential.
- Explain which components of water potential plants can manipulate and describe how.
- Define transpiration and identify how environmental factors affect transpiration rate.
- Describe the various adaptations that help plants reduce transpiration rate.
- Relate the pattern of cell wall thickening in guard cells to their function.
- Explain the mechanism by which blue light triggers stomatal opening.
- Explain the mechanism by which water stress, signaled by abscisic acid, triggers stomatal closure.
- Explain how water moves upward through a plant according to the cohesion-tension theory.
- Provide experimental evidence for the cohesion-tension theory.
- Explain the function of root hairs.
- Define root pressure and explain its mechanism.
- Contrast the three pathways of water movement through the roots and identify each cell type or tissue involved.
- Distinguish between sources and sinks and provide examples of each.
- Explain the process of phloem loading, distinguishing between apoplastic and symplastic pathways.
- Explain how assimilate translocations through the phloem according to the pressure-flow hypothesis.

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4.6: DEVELOPMENT

Development is the process by which an organism changes over its life. In angiosperms, development after sperm from the pollen tube fertilizes the egg in the ovule, forming the diploid **zygote**. Through cell division and differentiation, the zygote forms a mature embryo, which lies dormant within the seed until **germination** (Figure 4.6.1). A seedling emerges and continues to develop into mature plant, which will ultimately flower and undergo pollination, completing the life cycle.



Figure 4.6.1: These corn seedlings germinated prematurely (while still attached to the cob) due to poor soil conditions. Image by Alandmanson (CC-BY-SA)

The variety of tissues and organs in the plant body result from differences in gene expression. While all the diploid cells in a plant have the same genetic information, which genes are active in each structure varies, resulting in a complex, multicellular organism.

- Development

4.6.1: Embryogenesis

4.6.2: Meristems

4.6.3: Mature Embryos and Seed Structure

4.6.4: Germination

4.6.5: Shoot Development

4.6.6: Chapter Summary

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Thumbnail image: Different stages of germination in *Arabidopsis*. Image by Alena Kravchenko (CC-BY-SA)

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4.6.1: Embryogenesis

Learning Objectives

- Explain the steps of embryogensis in eudicots.
- Compare embryogenesis in eudicots versus monocots.

The Seed Plants chapter discussed the fertilization of the egg within the ovule. The zygote ultimately divides to produce the mature embryo, the ovule develops into a seed, and the ovary that contained one or more ovules develops into a fruit. A typical seed contains a seed coat, cotyledons, endosperm, and a single embryo. The development of the embryo occurs through a process called **embryogenesis**.

Embryogenesis in Eudicots

After fertilization in eudicots, the zygote (Figure $4.6.1.1-I$) divides to form two cells: the upper **apical cell** and the lower **basal cell** . The division of the basal cell gives rise to the suspensor, which attaches the embryo to the **micropyle** (the pore through which the pollen tube original entered). The suspensor provides a route for nutrition to be transported from the mother plant to the growing embryo. The apical cell also divides, initially producing a **proembryo** (figure $4.6.1.1-II$).

As the proembryo continues to divide, it takes a spherical form, called the **globular stage** (Figures $4.6.1.1-III$ and $4.6.1.2a$). The globular is the first stage that is considered the **embryo proper**. Next, cotyledons arise from the embryo proper, forming the **heart stage** (Figures $4.6.1.1-IV$ and $4.6.1.2-4$). **Cotyledons** are embryonic leaf-life structures that function in food storage, food absorption and/or photosynthesis. As the cotyledons elongate, and the base of the embryo thickens, it results a torpedo. (This stage is called the **torpedo stage;** Figures $4.6.1.1-V$ and $4.6.1.2c$). Cell division is concentrated at the **shoot apical meristem**, located at the shoot tip in between the cotyledons, and the **root apical meristem** at the most basal (bottom) part of the embryo. Most of the suspensor deteriorates during the torpedo stage.

The final stage of embryogenesis results in the **mature embryo** (Figures $4.6.1.1-VI$ and $4.6.1.2d$). The mature embryo includes an embryonic root called the **radicle**. The embryo becomes dormant at this point, halting metabolic activity and cell division. At this point, the seed is ready for dispersal. Growth resumes when the seed germinates and the embryo develops into a seedling.

In some eudicots, the **endosperm** (triploid tissue that was formed when a sperm fertilized the two polar nuclei) cells divide, and endosperm fills a substantial portion of the mature seed. The endosperm stores nutrients. In other (non-endospermic) eudicots, such as *Capsella bursa-pastoris*, the endosperm develops initially, but is then digested, and the nutrients are moved into the two cotyledons (Figure $4.6.1.2$). After germination, the developing seedling relies on these food reserves stored in the endosperm or cotyledons until the first set of leaves begin photosynthesis.

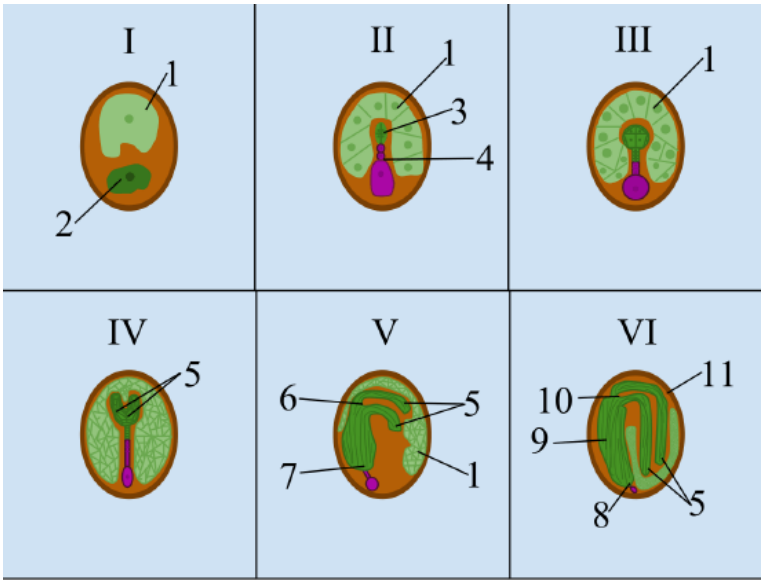


Figure 4.6.1.1: The stages of embryogenesis in eudicots. I. The developing seed contains the triploid endosperm (1) and the diploid zygote (2). II. The zygote divides, forming the proembryo (3), which is anchored to the micropyle by suspensor (4), which has a large basal cell. The endosperm has also divided. III. The embryo proper is in the globular stage, now a spherical mass of cells. IV. The embryo proper is heart stage. The heart shape results from the two cotyledons (5). V. The embryo proper is in the torpedo stage, which is cylindrical with a rounded base. The shoot apical meristem (6) is between the cotyledons, and the root apical meristem (7) is on the opposite end, anchored to the suspensor. VI. The mature embryo includes the radicle (8), the **hypocotyl** (9) is the stem-like axis below the cotyledons. The **epicotyl** (10) is the stem-like axis above the cotyledons. The integument of the ovule has developed into the seed coat (11), which surrounds the seed. Image by TheLAW14 (CC-BY-SA).

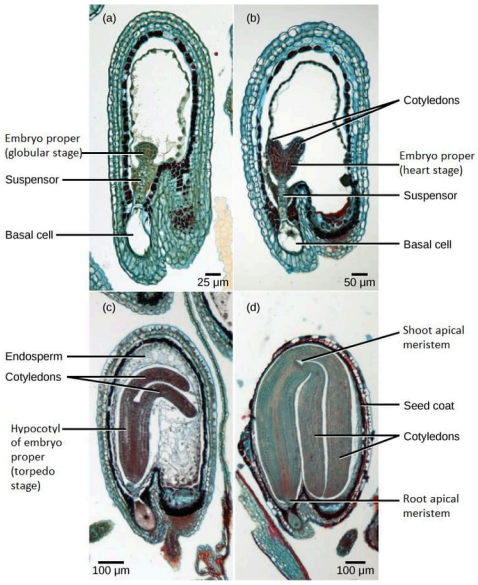


Figure 4.6.1.2: Selected stages of embryogenesis in the ovule of shepherd's purse (*Capsella bursa-pastoris*). After fertilization, the zygote divides to form an apical cell and basal cell. The apical cell divides to first produce a proembryo, and then form the embryo proper. The basal cell also divides, giving rise to the suspensor. The embryo proper is initially in the globular stage (a), which is a spherical mass of cells seen growing inside the oval-shaped ovule. As the cotyledons emerge the embryo proper enters the heart stage (b), which resembles a heart due to the two cotyledons. The base of the embryo widens to form a cylindrical hypocotyl, and the cotyledons start to bend in the torpedo stage (c). Cells inside the embryo grow in vertical columns. Finally, the mature embryo fills the seed and becomes dormant (d). The seed coat now surrounds the ovule. (credit: modification of work by Robert R. Wise; scale-bar data from Matt Russell; labels modified by Melissa Ha)

Embryogenesis in Monocots

The process of embryogenesis in monocots is similar to that of eudicots, but as there is only a single cotyledon, no heart stage occurs. Instead, the embryo proper of the monocot becomes cylindrical at this point in development. The shoot apical meristem, while still present at the shoot tip, is not in between cotyledons in the monocot (because there is only a single cotyledon).

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4.6.2: Meristems

Learning Objective

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

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

Apical meristems are located on the very ends of shoots (**shoot apical meristem**; SAM; Figure 4.6.2.1) and roots (**root apical meristem**; RAM; Figure 4.6.2.2). They produce three types **primary meristems**: the protoderm, ground meristem, and procambium. The **protoderm** gives rise to epidermis, which surrounds the plant. The **ground meristem** gives rise to ground tissue, a group of tissues with generalized functions such as photosynthesis, storage, and support. Finally, the **procambium** gives rise to the vascular tissue, which functions in transport. The three primary meristems first appear in the embryo proper, with the protoderm on the outside, the procambium in the center, and the ground meristem in between them.

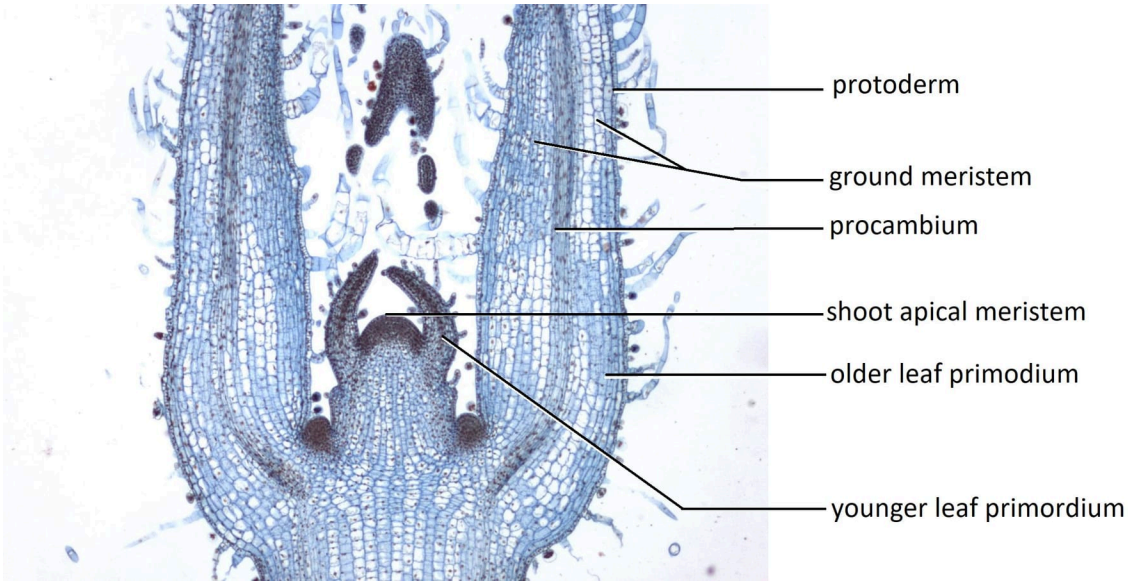


Figure 4.6.2.1: A longitudinal section of the shoot apex of *Coleus* includes the **shoot apical meristem** and the developing leaves (leaf primoridia) that surround it. The three **primary meristems** are visible in the leaf primordia. The **protoderm** surrounds the leaf primoridum, the **procambium** appears as a line running through the center, and the ground meristem fills the rest of the leaf primodium. Smaller, younger leaf primordia are closer to the shoot apical meristem than older leaf primordia are. Image labeled from Maria Morrow (CC-BY-NC).

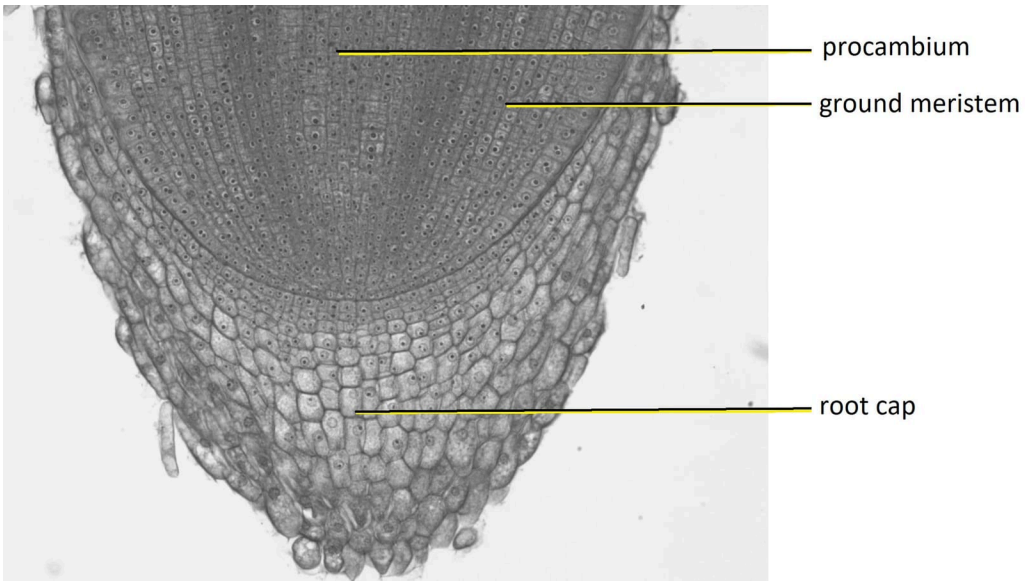


Figure 4.6.2.2: A longitudinal section of the root tip of corn (*Zea mays*). The large, lighter cells at the bottom form the protective root cap. The remaining visible portion of the root tip (above the root cap) is the **root apical meristem** (zone of cell division). It gives rise to the central **procambium** and the **ground meristem**, which is external to the procambium. The third primary meristem (**protoderm**) is not visible here. It would be the outer layer of the root tip, just above the current view. Image labeled from Maria Morrow (CC-BY-NC).

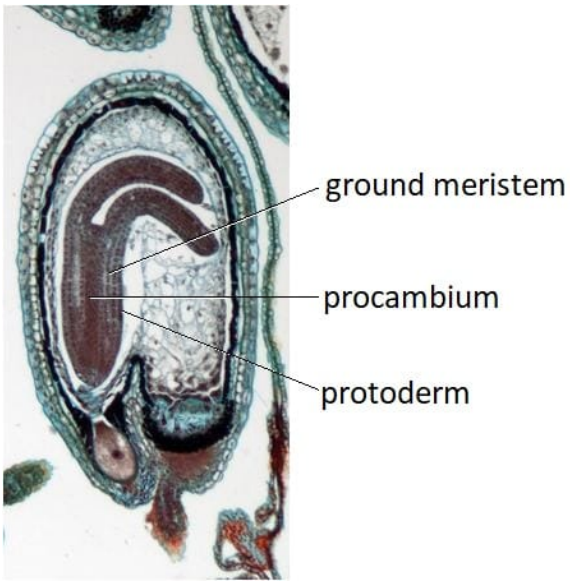


Figure 4.6.2.3: The torpedo stage of the *Capsella busra-pastoris* embryo proper showing the three primary meristems. Image labeled from Wisewire (CC-BY).

Secondary meristems (lateral meristems) result in secondary growth, a woody increase in girth. These include the vascular cambium and cork cambium. The **vascular cambium** arises from from the procambium and pericycle in roots. In stems, it arises from procambium cells of the vascular bundles (fascicular cambium) and parenchyma cells between vascular bundles (interfascicular cambium). The vascular cambium gives rise to secondary phloem (part of the bark) and secondary xylem (wood; Figures 4.6.2.4 – 5).

The **cork cambium** arises from the pericycle in roots and the parenchyma cells of the cortex in stems, both of which arise from the ground meristem. The cork cambium produces periderm, secondary dermal tissue that is also a component of bark. (See Roots and Secondary Stem for more details; Figures 4.6.2.4 – 5).)

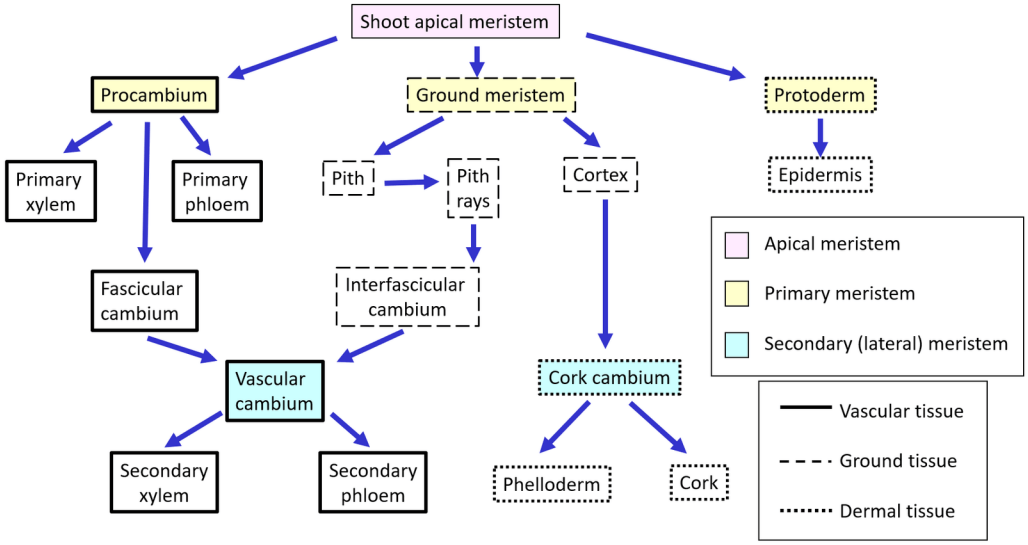


Figure 4.6.2.4: Tissue development in stems. The **shoot apical meristem** produces the three **primary meristems**: **procambium**, **ground meristem**, and **protoderm**. The procambium produces vascular tissues. The primary xylem, fascicular cambium, and primary phloem arise from the procambium. The ground meristem produces the pith and cortex, which are ground tissues. The pith generates pith rays, which give rise to the interfascicular cambium.The protoderm produces the epidermis, a dermal tissue. The **secondary meristems** (lateral meristems) are the **vascular cambium** and **cork cambium**. The vascular cambium arises from the procambial cells of the fascicular cambium and the interfascicular cambium. The secondary xylem and secondary phloem arise from the vascular cambium. The cortex gives rise to the cork cambium. The cork cambium and tissues it produces (phelloderm and cork) are dermal tissues. Image by Melissa Ha based on diagram from Maria Morrow (CC-BY).

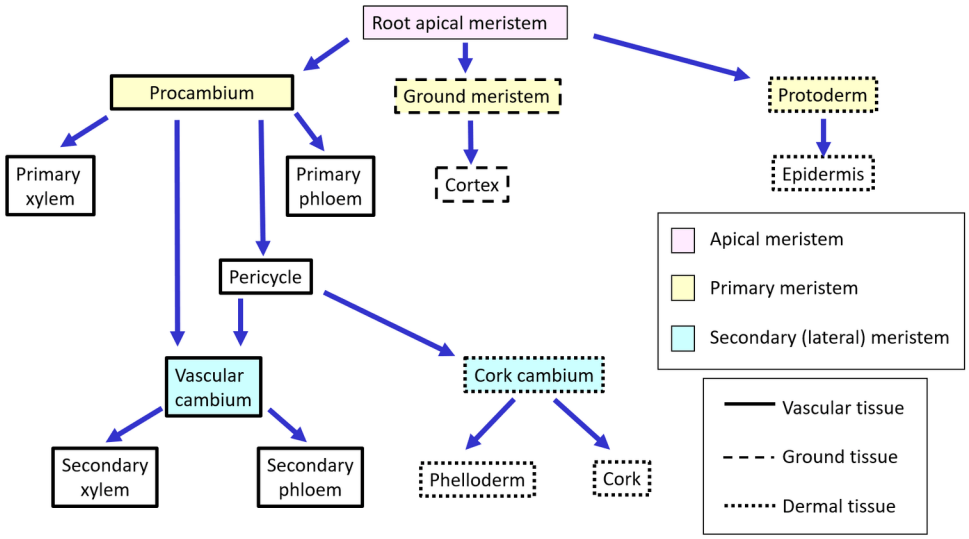


Figure 4.6.2.5: Tissue development in roots. The **root apical meristem** produces the three primary meristems: **procambium**, **ground meristem**, and **protoderm**. The procambium gives rise to vascular tissues, including the primary xylem and primary phloem. The ground meristem produces the cortex, a ground tissue. The protoderm produces the epidermis, a dermal tissue. The **secondary meristems** (lateral meristems) are the **vascular cambium** and **cork cambium**. The vascular cambium arises from the procambium and pericycle (which arose from the procambium). The vascular cambium produces secondary xylem and secondary phloem (both vascular tissues). The pericycle also produces the cork cambium, which gives rise to the phelloderm and cork (all dermal tissues). Image by Melissa Ha (CC-BY-NC).

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

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4.6.3: Mature Embryos and Seed Structure

Learning Objectives

- Locate the major seed structures and identify the function of each.
- Compare eudicot and monocot seeds.

Eudicot Seeds

The seed is protected by a **seed coat** that is formed from the integument of the ovule (Figure 4.6.3.1). The seed coat is further divided into an outer coat known as the **testa** and inner coat known as the **tegmen**. The **hilum** is a scar on the outside of the seed where it was attached to the endocarp (inner layer of the fruit wall). The **micropyle** is a small round structure next to the hilum where the pollen tube entered.

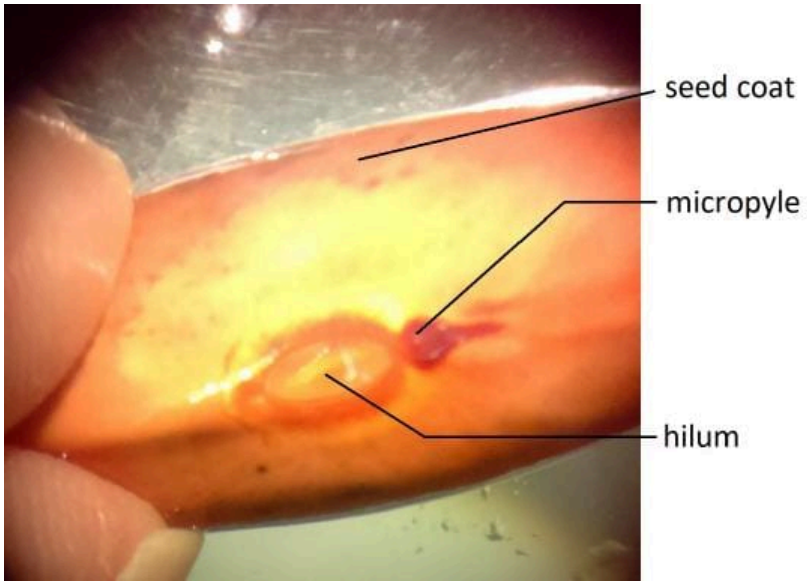


Figure 4.6.3.1: The external structures of a bean seed, an example of a eudicot (7X). The seed coat surrounds the seed. There is a round micropyle, where the pollen tube originally entered the ovule. The oval hilum is a scar from where the ovule was attached to the ovary. Image by Melissa Ha (CC-BY).

The **embryonic axis** (root-shoot axis) runs the length of the embryo. On end of the embryonic axis is the **plumule**, the young shoot apex, which includes the shoot apical meristem and developing leaves (**leaf primordia**). At the other end of the embryonic axis is the **radicle** (embryonic root). In some species, the radicle is not apparent in the embryo (in which case the distal end of the root is simply the root tip). The embryonic axis does not include the **cotyledons**. The portion of the embryo between the cotyledon attachment point and the radicle is known as the **hypocotyl** (hypocotyl means “below the cotyledons”). The portion of the embryonic axis between the cotyledon attachment and the shoot tip is the **epicotyl** (epicotyl means "above the cotyledons; Figures 4.6.3.2 – 3)). Some embryos lack a visible epicotyl because the cotyledons are attached to the embryonic axis at the shoot tip.

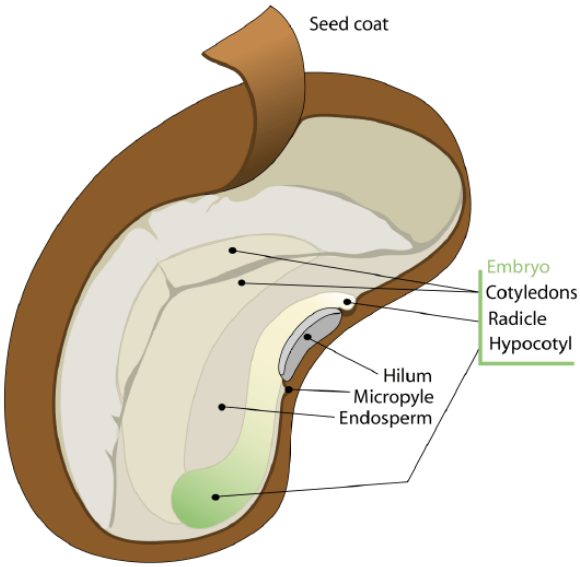


Figure 4.6.3.2: Diagram of a mature embryo from a bean seed, an example of a eudicot. The **seed coat** is a protective layer surrounding the seed. The two **cotyledons** form the bulk of the embryo. The stem-like axis below the cotyledons in the **hypocotyl**. At the tip of the hypocotyl is the **radicle** (the embryonic root). The **hilum** is an oval scar on the outside of the seed, and the **micropyle** is the small round structure adjacent to it. Image by LadyofHats (public domain).

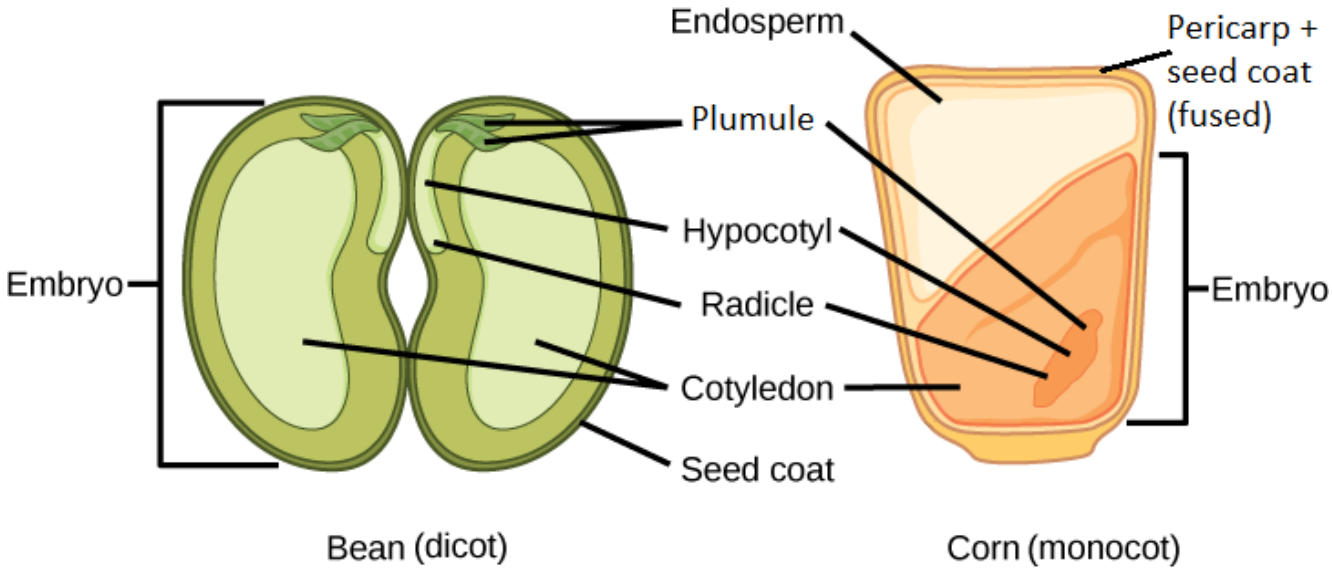


Figure 4.6.3.3: The structures of bean (eudicot) and corn (monocot) seeds. Eudicots (left) have two cotyledons. Monocots (right) have one cotyledon, called the **scutellum**, which channels nutrition to the growing embryo. Both monocot and eudicot embryos have a **plumule** (which contains developing leaves and the shoot apical meristem), a **hypocotyl** (embryonic stem below the cotyledons), and a **radicle** that forms the root. The embryonic axis comprises everything between the plumule and the radicle, not including the cotyledon(s). The corn "seed" is technically a caryopsis, a one-seeded fruit in which the pericarp (fruit wall) is fused with the seed coat.

The two cotyledons in the eudicot seed are connected to the rest of the embryo via vascular tissue (xylem and phloem). In **endospermic dicots**, the food reserves are stored in the endosperm. During germination, the two cotyledons therefore act as absorptive organs to take up the enzymatically released food reserves. Tobacco (*Nicotiana tabaccum*), tomato (*Solanum lycopersicum*), and pepper (*Capsicum annuum*) are examples of endospermic dicots. In **non-endospermic dicots**, the triploid endosperm develops normally following double fertilization, but the endosperm food reserves are quickly remobilized and moved into the developing cotyledon for storage. The two halves of a peanut seed (*Arachis hypogaea*; Figure 4.6.3.4) or a bean (*Phaseolus*; Figures 4.6.3.2 – 3) and the split peas (*Pisum sativum*; Figure 4.6.3.5) of split pea soup are individual cotyledons loaded with food reserves.

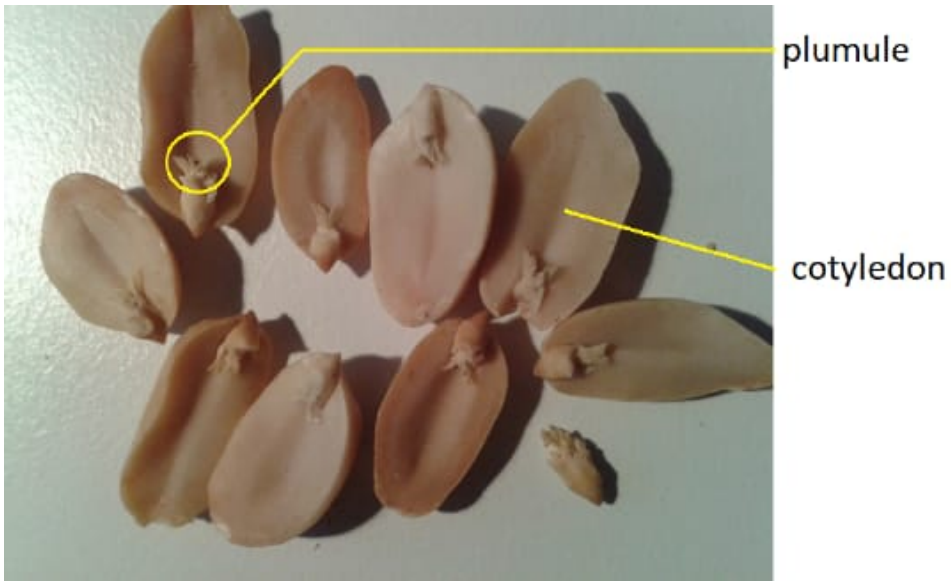


Figure 4.6.3.4: Each half of a peanut represents a cotyledon, which is rich with nutrients. The plumule, which contains tiny embryonic leaves, is found between the cotyledons. Image labeled from Jesusorizales (CC-BY-SA).

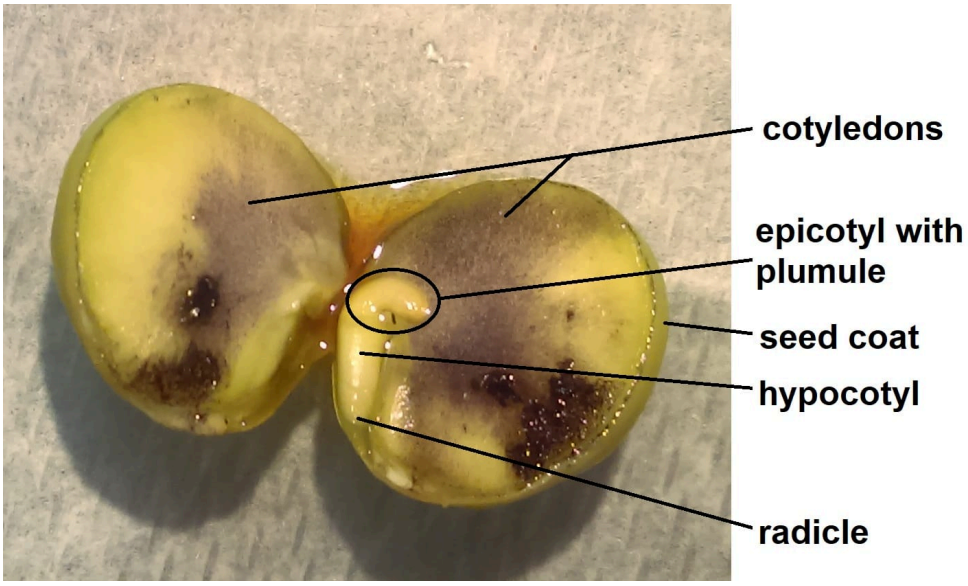


Figure 4.6.3.5: Like the peanut, each half of a pea represents a nutrient-filled cotyledon. The black coloration in the cotyledon is due to iodine staining the starch in the cotyledons. Most of the pea seed is filled with two cotyledons. The tiny embryonic axis consists of the plumule at the top and the descending hypocotyl. The radicle is at the tip of the hypocotyl. The seed coat surrounds the entire seed. Image by Melissa Ha (CC-BY).

Because seeds have food reserves to fuel germination, they also are a nutritious food source for people. Studying the nutrient content of seed crops such as beans can be used to increase the nutritive value of the plant using biotechnology. Maria Elena Zavala (Figure 4.6.3.6) is working to combat world hunger by manipulating plants to improve their nutritional qualities. For example, her research with beans is looking at how genetic engineering can be used to make the bean proteins more digestible and nutritious.



Figure 4.6.3.6: Maria Elena Zavala was the first Mexican-American woman to earn a PhD in botany in the United States. Her research includes manipulating plant genes as a way to improve plant productivity and address world hunger. Image by Lee Choo (CC BY-SA 4.0)

Monocot Seeds

The seeds of the most complex monocot family, Poaceae (the grass family), which includes corn and wheat, are highly specialized. The testa and tegmen of the seed coat are fused. The fruit is a **caryopsis** (grain), a one-seeded fruit in which the fruit wall (**pericarp**) is fused to the seed coat. Thus, not only are the two layers of the seed coat fused, but the seed coat is fused to the pericarp.

The single cotyledon is called a **scutellum**; the scutellum also has vascular connections to the rest of the embryo. The large inner layer of the endosperm that stores nutrients is called the **starchy endosperm**. The thin outer layer of the endosperm, which is a single layer of cells, is called the **aleurone**. Upon germination, enzymes are secreted by the aleurone. The enzymes degrade the stored carbohydrates, proteins and lipids, the products of which are absorbed by the scutellum and transported via a vasculature strand to the developing embryo. Therefore, the scutellum can be seen to be an absorptive organ, not a storage organ.

The root tip is protected by a sheath-like structure called the **coleorhiza**. Similarly, the **coleoptile** ensheaths the plumule at the shoot tip (Figure $4.6.3.7 - 10$).

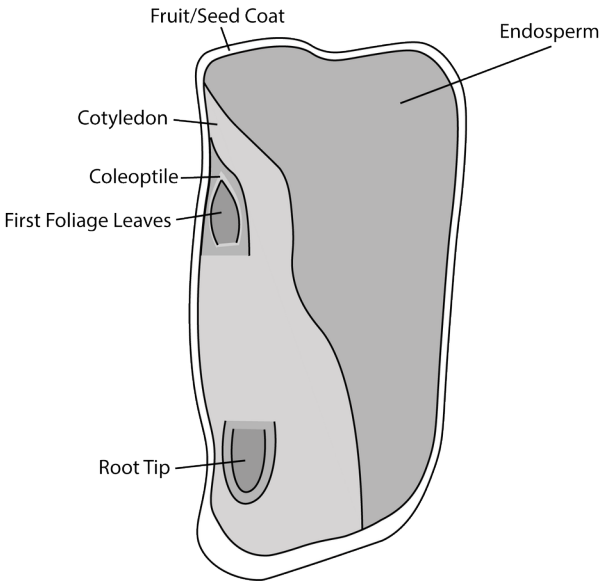


Figure 4.6.3.7: Diagram of a corn kernel, an example of a "complex" monocot. The single cotyledon is called the scutellum. The outer layer is the pericarp (fruit wall) fused with the seed coat. The endosperm fills much of the seed and stores starch. It actually consists of a thin outer layer (aleurone) and a thick inner layer (starchy endosperm). The young shoot (plumule) consists of the shoot apical meristem surrounded by young leaves (first foliage leaves). It is surrounded by a sheath called the coleoptile. The young root (radicle) is surrounded by a sheath called the coleorhiza (not labeled). Image by Sarah Greenwood (CC-BY-SA).

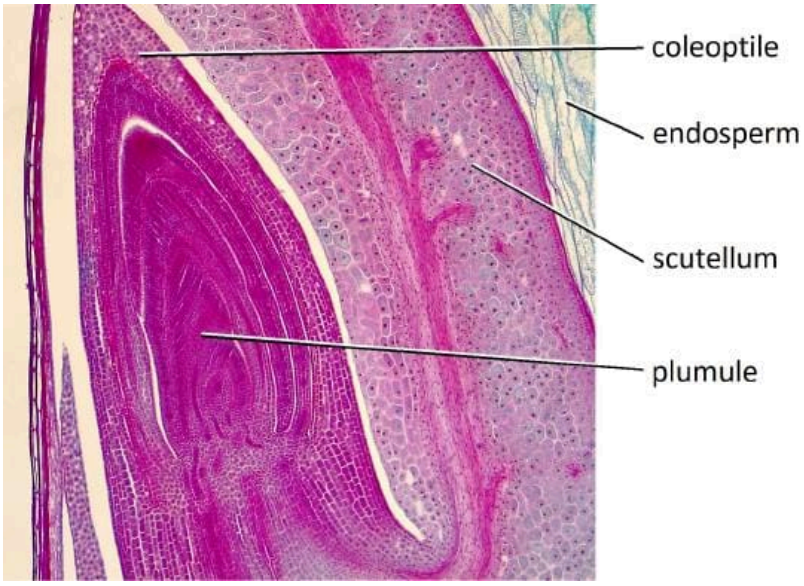


Figure 4.6.3.8: Longitudinal section of a the upper portion of a corn embryo, a monocot (40X). The **coleoptile** is the sheath that surrounds the **plumule**, which consists of the shoot apical meristem and layers of developing leaves. The **scutellum** is the single cotyledon. A small portion of the **endosperm** is visible in this view. Image by Melissa Ha (CC-BY).

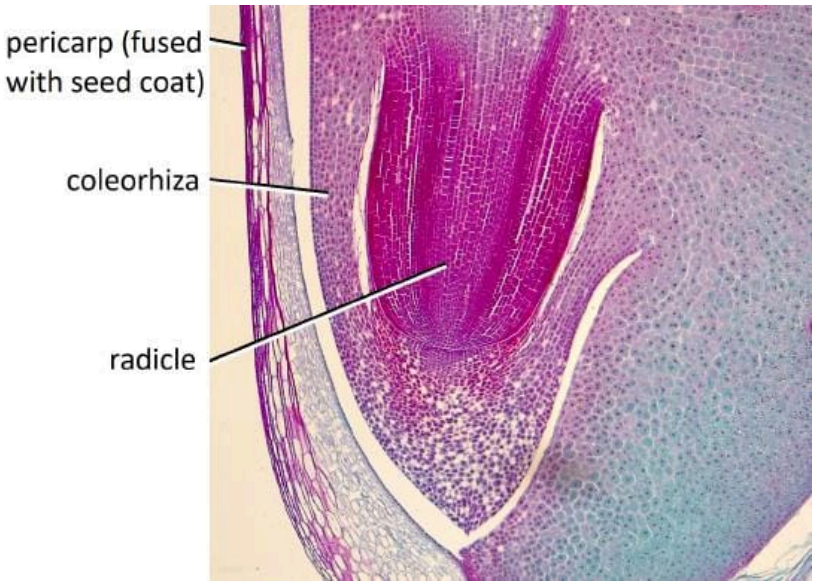


Figure 4.6.3.9: Longitudinal section of a the lower portion of a corn embryo, a monocot (40X). The outer layer is the **pericarp** fused with the **seed coat**. The **coleorhiza** surrounds the **radicle**, which is the embryonic root. Image by Melissa Ha (CC-BY).

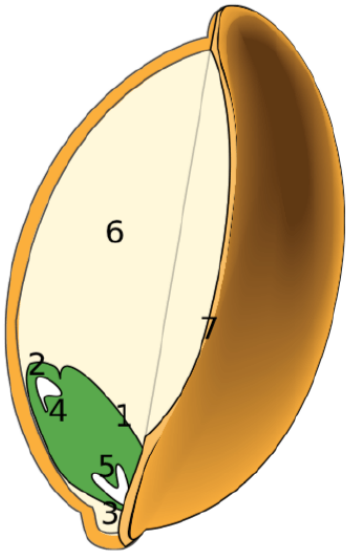


Figure 4.6.3.10: A grass seed (monocot). The scutellum (1) is the modified cotyledon of complex monocots such as grass. The coleoptile (2) is the sheath covering the young shoot tip (plumule, 4). The coleorhiza (3) is the sheath covering the young root (radicle, 5). The endosperm (6) fills much of the seed and nourishes the seedling upon germination. The seed coat (7) surrounds the seed and protects it.

Other Variations

Seeds are diverse. Pine (*Pinus*, a gymnosperm and thus neither a monocot nor eudicot) has multiple (five or more) cotyledons. Some plants like orchids (Orchidaceae, a monocot) do not have developed embryo and even endosperm in seeds; their germination depends on a presence of symbiotic (mycorrhizal) fungus.

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4.6.4: Germination

Learning Objectives

- Identify the environmental factors that stimulate germination.
- Distinguish between epigeous and hypogeous germination.
- Compare germination in eudicots versus monocots.

Many mature seeds enter a period of inactivity, or extremely low metabolic activity: a process known as dormancy, which may last for months, years or even centuries. Dormancy helps keep seeds viable during unfavorable conditions. **Germination** occurs when the embryo, which is dormant within a mature seed, resumes growth upon a return to favorable conditions. The embryo becomes a young seedling that is no longer confined within the seed coat.

In many seeds, the presence of a thick seed coat can inhibit germination through several mechanisms: (1) the embryo may not be able to break through the thick seed coat; (2) the seed coat may contain chemicals inhibitors; and (3) the seed coat prevents the embryo from accessing water and oxygen. Dormancy is also maintained by the relative hormone concentrations in the embryo itself.

Environmental Requirements for Germination

The requirements for germination depend on the species. Common environmental requirements include light, the proper temperature, presence of oxygen, and presence of water. Seeds of small-seeded species usually require light as a germination cue. This ensures the seeds only germinate at or near the soil surface (where the light is greatest). If they were to germinate too far underneath the surface, the developing seedling would not have enough food reserves to reach the sunlight. (Recall from 14.5 Dormancy that red light induces germination by converting the inactive form of phytochrome (Pr) to the active form (Pfr), which leads to the production of amylase. This enzyme breaks down the limited food reserves in the seed, facilitating germination.)

Not only do some species require a specific temperature to germinate, but they may also require a prolonged cold period prior to germination. In this case, cold conditions gradually break down a chemical germination inhibitor. This mechanism prevents seeds from germinating during an unseasonably warm spell in the autumn or winter in temperate climates. Similarly, plants growing in hot climates may have seeds that need a hot period in order to germinate, an adaptation to avoid germination in the hot, dry summers.

Water is always needed to allow vigorous metabolism to begin. Additionally, water can leach away inhibitors in the seed coat. This is especially common among desert annuals. Seeds that are dispersed by animals may need to pass through an animal digestive tract to remove inhibitors prior to germination. Similarly, some species require mechanical abrasion of the seed coat, which could be achieved by water dispersal. Other species are fire adapted, requiring fire to break dormancy (Figure 4.6.4.1).



Figure 4.6.4.1: Coffeeberry (*Frangula californica*) at the Regional Park Botanic Garden in Berkeley Hills, California. This species naturally occurs in the chaparral where wildfires trigger germination of its seeds. Image by Daderot (public domain).

The Mechanism of Germination

The first step in germination and starts with the uptake of water, also known as **imbibition**. After imbibition, 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.

Depending on seed size, the time taken for a seedling to emerge may vary. Species with large seeds have enough food reserves to germinate deep below ground, and still extend their epicotyl all the way to the soil surface while the seedlings of small-seeded species emerge more quickly (and can only germinate close to the surface of the soil).

During **epigeous germination**, the hypocotyl elongates, and the cotyledons extend above ground. During **hypogeous germination**, the epicotyl elongates, and the cotyledon(s) remain belowground (Figure 4.6.4.2). Some species (like beans and onions) have epigeous germination while others (like peas and corn) have hypogeous germination. In many epigeous species, the cotyledons not only transfer their food stores to the developing plant but also turn green and make more food by photosynthesis until they drop off.

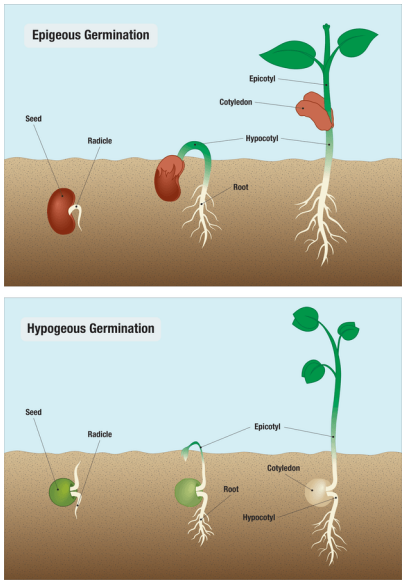


Figure 4.6.4.2: Epigeous germination in bean (top) and hypogeous germination in pea (bottom). For the bean, the radicle emerges from the seed. Next, the hypocotyl elongates, and the cotyledons are pushed aboveground. The epicotyl is just above the cotyledon. For the pea, the radicle also emerges from the seed. The epicotyl elongates, and the cotyledons remain below the ground. The hypocotyl remains short and lies between the root and cotyledon. Image by Jen Valenzuela (CC-BY).

Germination in Eudicots

Upon germination in eudicot seeds, the radicle emerges from the seed coat while the seed is still buried in the soil.

For epigeous eudicots (like beans), the hypocotyl is shaped like a hook with the plumule pointing downwards. This shape is called the plumule hook, and it persists as long as germination proceeds in the dark. Therefore, as the hypocotyl pushes through the tough and abrasive soil, the plumule is protected from damage. Additionally, the two cotyledons additionally protect the from mechanical damage. Upon exposure to light, the hypocotyl hook straightens out, the young foliage leaves face the sun and expand, and the epicotyl elongates (Figure 4.6.4.3).

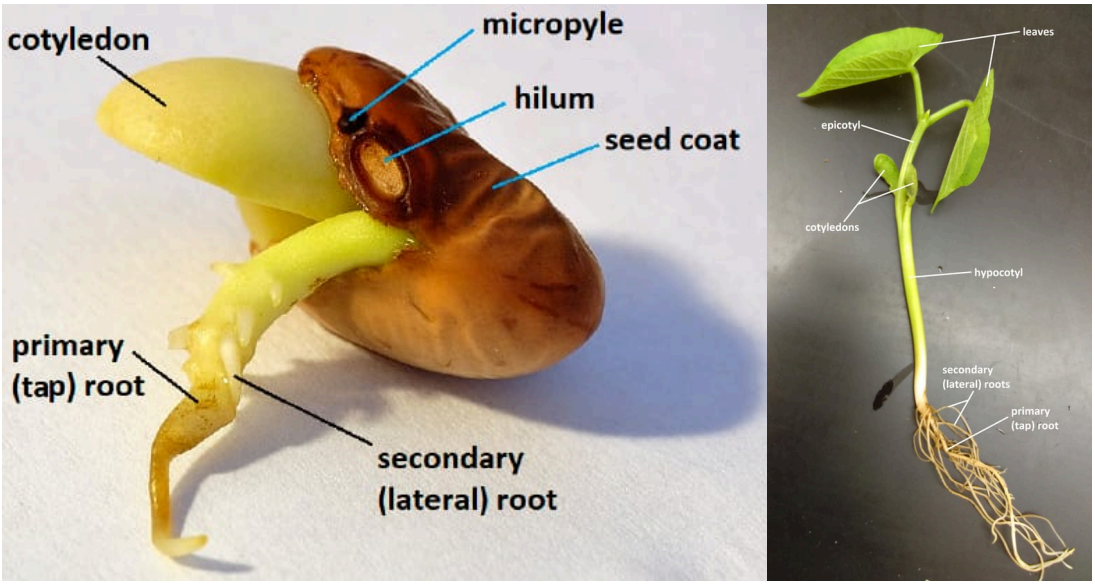


Figure 4.6.4.3: A bean seed begins to germinate (left) and a germinated bean seedling (right). Beans are epigeous eudicots, meaning that the hypocotyl elongates, pushing the cotyledons above the ground. On the right, the large cotyledons have just emerged from the seed coat. The oval hilum is next to a tiny, round micropyle on the seed coat. The primary (tap) root has emerged, and secondary (lateral) roots begin to branch from the primary root. On the left, the green hypocotyl has elongated, pushing the cotyledons aboveground. The cotyledons are green and still have the shape of the bean seed. The epicotyl is the part of the stem above the cotyledons. Broad, heart-shaped leaves branch from it. Unlike the cotyledons, these are true leaves. At the tip of the stem, between the leaves is the shoot apical meristem. There is a central, thick root called the primary (tap) root. The roots that branch form it are secondary (lateral) roots. Left image by Doronenko (CC-BY-SA). Right image by Melissa Ha (CC-BY).

In hypogeous eudicots (like peas), the epicotyl rather than the hypocotyl forms a hook, and the cotyledons and hypocotyl thus remain underground. When the epicotyl emerges from the soil, the young foliage leaves expand. The epicotyl continues to elongate (Figure 4.6.4.4).

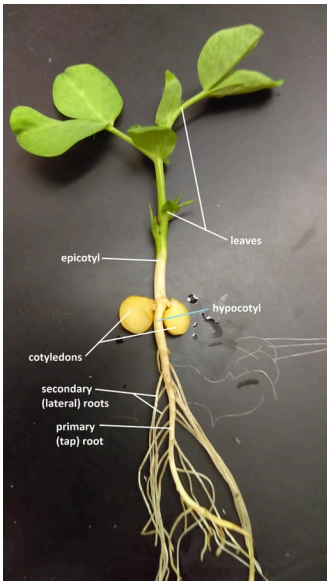


Figure 4.6.4.4: A germinated pea seedling. Peas a hypogeous eudicots. The hypocotyl never elongates, and the cotyledons remain below ground. The green and white epicotyl has elongated, giving rise to true leaves, and the cotyledons remain belowground. These true leaves are compound (are composed of smaller leaflets). This seedling has been uprooted and washed, but everything below the epicotyl was belowground. The hypocotyl is the short segment of stem between the cotyledons and roots. It never elongated enough to push the cotyledons above the ground. There is a central, thick root called the primary (tap) root. The roots that branch form it are secondary (lateral) roots. Image by Melissa Ha (CC-BY).

The radicle continues to grown downwards and ultimately produces the tap root. Lateral roots then branch off to all sides,

producing the typical eudicot tap root system.

Germination in Monocots

As the seed germinates, the radicle emerges and forms the first root. In epigeous monocots (such as onion), the single cotyledon will bend, forming a hook and emerge before the coleoptile (Figure 4.6.4.5). In hypogeous monocots (such as corn), the cotyledon remains belowground, and the coleoptile emerges first. In either case, once the coleoptile has exited the soil and is exposed to light, it stops growing. The first leaf of the plumule then pieces the coleoptile (Figure 4.6.4.6), and additional leaves expand and unfold. At the other end of the embryonic axis, the first root soon dies while adventitious roots (roots that arise directly from the shoot system) emerge from the base of the stem (Figure 4.6.4.7). This gives the monocot a fibrous root system.



Figure 4.6.4.5: The scallion (spring onion) is an epigeous monocot. The curved structure emerging from the ground is the single cotyledon. Later in the process, the coleoptile will emerge, and be pierced by the first leaf of the plumule. Image by Dennis Brown (CC-BY-SA)

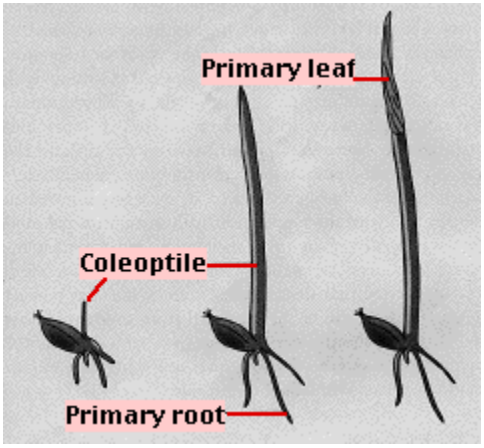


Figure 4.6.4.6: Germination of an oat seed, a hypogeous monocot. Here the first root formed by the radicle is labeled "primary root", but note that this differs from the primary (main) root of a eudicot tap root system. Note that several adventitious roots have also formed and will ultimately produce a fibrous root system. The coleoptile is the first component of the shoot system to emerge in hypogeous monocots, but it is ultimately pieced by the first (primary) leaf of the plumule.

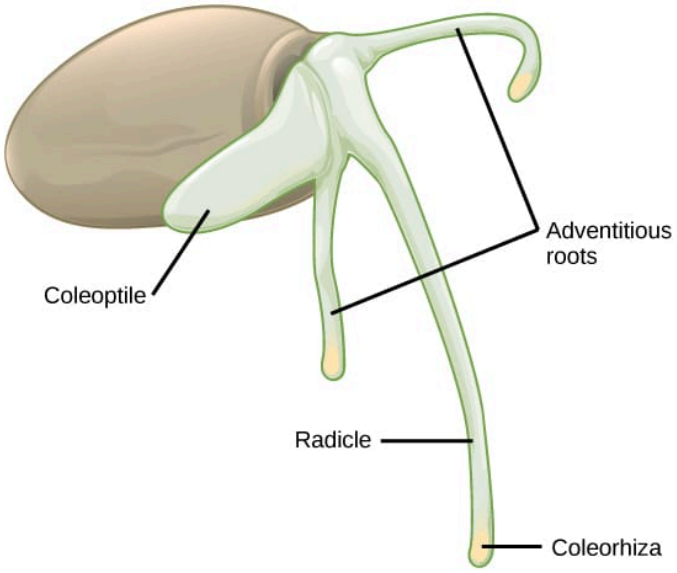


Figure 4.6.4.7: As this monocot grass seed germinates, the radicle, emerges first, followed by the coleoptile, and the adventitious roots. The coleorhiza, a protective sheath that surrounded the radicle in the dormant seed, is now at the tip of the radicle.

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4.6.5: Shoot Development

Learning Objective

- Define the roles of the shoot apical meristem, leaf primordia, intercalary meristems, and axillary buds in shoot development.
- Explain the mechanism of the ABCDE model of floral development.

Some plant parts, such as stems and roots, continue to grow throughout a plant's life: a phenomenon called **indeterminate growth**. Other plant parts, such as leaves and flowers, exhibit determinate growth, which ceases when a plant part reaches a particular size.

Stem and Leaf Development

In comparison to roots, in which cell division, elongation, and maturation occur in distinct regions (see Internal Root Structure), growth in stems occurs in several regions. Rapid cell division occurs at the shoot apical meristem of the shoot tip. Some of the cells produced from these divisions give rise to **leaf primordia**, which ultimately develop into leaves. Division, elongation, and cell differentiation (maturation) also occurs at the intercalary meristems of **internodes**, the stem segments between **nodes**, the points where leaves attach. As a result, multiple internodes can lengthen simultaneously. Under certain circumstances, the axillary buds at each node can become active and produce axillary shoots, which branch from the main stem.

Flower Development

Changes in gene expression can cause a shoot apical meristem to develop into a floral meristem, which leads to flowering. The **ABCDE model** (ABC model) of floral development directs the formation of each of the four whorls of a complete flower. From outside to inside, these whorls are the calyx (sepals), corolla (petals), androecium (stamens), and gynoecium (carpels). (See Angiosperms for more details; Figure 4.6.5.1.) Each unit of these whorls (sepal, petal, etc.) developmentally and evolutionarily originated from the leaf.

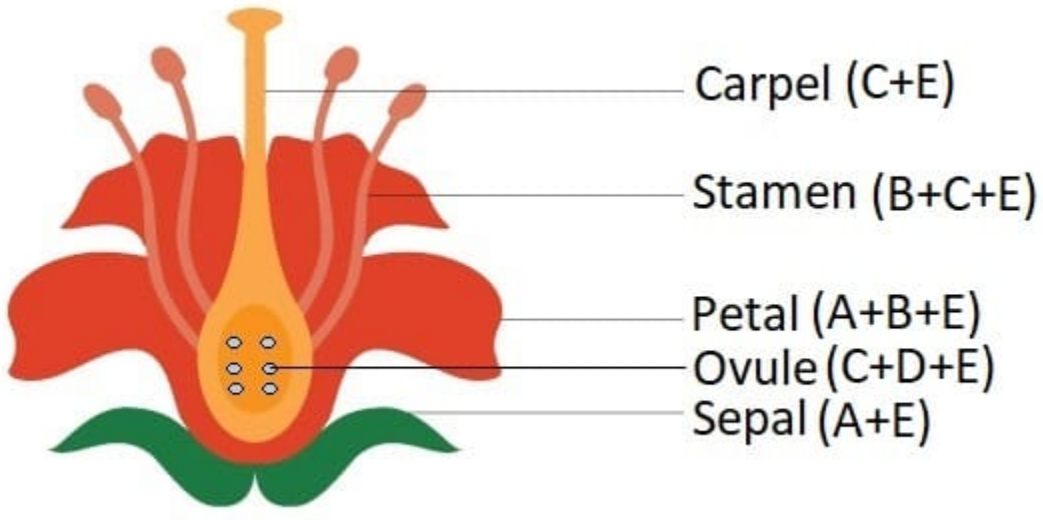


Figure 4.6.5.1: The four whorls of a flower are the calyx (sepals), corolla (petals), androecium (stamens), and gynoecium (carpels). The ovules are considered part of the carpels. Each structure results from expression of a different combination of genes, which are identified in parentheses: carpel (C+E), stamen (B+C+E), petal (A+B+E), ovule (C+D+E), and sepal (A+E). Image modified from Laura Aškelovičiūtė (CC-BY-SA).

The ABCDE model refers to five groups of homeotic genes, each represented by one letter. **Homeotic genes** are those that

control the development and organization of body parts (body plan). Each of the five groups of genes that encode the transcription factors (proteins required for gene expression), which turn on the genes for development of each whorl. Genetic analysis of mutants especially those found in the *Arabidopsis thaliana* and in the snapdragon (*Antirrhinum*) support the ABCDE model of flowering. Each group of genes has a distinct role as follows (Figure 4.6.5.2):

- A genes are needed for sepal and petal development
- B genes are needed for petal and stamen development.
- C gene are needed for stamen and carpel (including ovules) development.
- D genes are need for ovule development (part of the carpels).
- E genes are needed to produce any of the floral whorls.

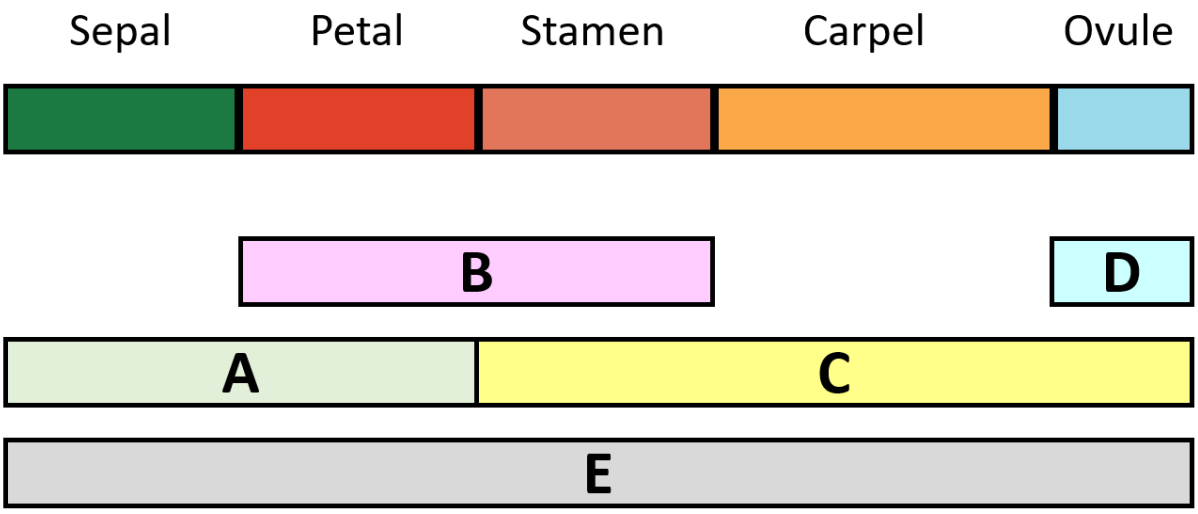


Figure 4.6.5.2: The ABCDE model of floral development. Different floral structures are represented by the top row of bars. (Note that each of the first four segments of this bar represents a whorl. Ovules are considered part of carpels, which make up the innermost whorl, the gynoecium.) The remaining bars each represent a different group of homeotic gene. Expression of these genes in different combinations produces each structure. See Figure 4.6.5.1 for a text description of which gene combinations produce each structure. Image by Melissa Ha (CC-BY).

Thus, each whorl results from the expression of a different gene combination as follows:

- Expression of A and E genes produce sepals.
- Expression of A, B, and E genes produce petals.
- Expression of B, C, and E genes produce stamens.
- Expression of C and E genes produce carpels. To produce ovules, which are considered part of the carpels, D genes must also be expressed (C+D+E = ovules).

In summary, the formation of a flower requires a cascade of sequential gene activity that gradually converts a mass of undifferentiated cells (the shoot apical meristem) into the parts of a flower. The genes encode transcription factors that act as master switches, turning on (or off) downstream genes that ultimately make each part of the flower in its appropriate location.

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4.6.6: Chapter Summary

During **embryogenesis** (the development of the embryo), the **proembryo** develops into the **embryo proper** and finally into the **mature embryo**. The mature embryo is surrounded by the **seed coat**. Depending on the species, nutrient-rich **endosperm** may remain in the mature seed between the embryo and seed coat. The embryo consists of the **cotyledon**(s) and **embryonic axis**, consisting of the **epicotyl** and **hypocotyl**. The young root is called the **radicle**. Monocot seeds differ from eudicot seeds in that they contain a single cotyledon (**scutellum**) and protective sheaths surrounding the young shoot and root, the **coleoptile** and **coleorrhiza**, respectively.

Cell division and growth are concentrated at meristems. The **shoot apical meristem** and **root apical meristem** produce three primary meristems: the **protoderm**, **ground meristem**, and **procambium**. The **cork cambium** and **vascular cambium** are secondary meristems, which allow woody plants to increase in girth.

The embryo then remains dormant until **germination**. Various environmental conditions such as proper temperature, light, and water may be required for germination depending on the species. Germination may be **epigeous**, in which cotyledon(s) rise above the ground, or **hypogeous**, in which cotyledon(s) remain belowground.

Rapid cell division at the shoot apical meristem initiates shoot development, but growth also occurs in the internodes throughout the shoot. Floral meristems develop from shoot apical meristems, and floral structure is controlled by the **ABCDE model**.

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

- Explain the steps of embryogensis in eudicots.
- Compare embryogenesis in eudicots versus monocots.
- Define and locate the two apical meristems and the three primary meristems.
- Locate the major seed structures and identify the function of each.
- Compare eudicot and monocot seeds.
- Identify the environmental factors that stimulate germination.
- Distinguish between epigeous and hypogeous germination.
- Compare germination in eudicots versus monocots.
- Define the roles of the shoot apical meristem, leaf primordia, intercalary meristems, and axillary buds in shoot development.
- Explain the mechanism of the ABCDE model of floral development.

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5: ECOLOGY AND CONSERVATION



Figure 4.1: A skipper caught by a crab spider, camouflaged in a sunflower. Image by Kammy Algiers (CC-BY)

Ecology is the study of the interaction of organisms with their biotic (living) and abiotic (non-living) environment. Plant ecologists study plants across many different biomes, both terrestrial and aqautic. They may be interested in studying plants at different levels of organization, such as the population level, the community level, or the ecosystem level. Many plant ecologists are interested in conservation biology, protecting the diversity of plants from human impacts. Understanding the connections between plants and other organisms helps us solve scientific problems and understand our world better.

5.1: Population Ecology

5.1.1: Population Size and Density

5.1.2: Life Histories and Natural Selection

5.1.3: Environmental Limits to Population Growth

5.1.4: Population Dynamics and Regulation

5.1.5: Chapter Summary

5.2: Communities and Ecosystems

5.2.1: Communities

5.2.2: Community Interactions

5.2.3: Symbiosis

5.2.4: Biodiversity in Ecosystems

5.2.5: Succession

5.2.6: Ecosystem

5.2.7: Energy and Energy Flow

5.2.8: Food Chains and Food Webs

5.2.9: Chapter Summary

5.3: Conservation

5.3.1: The Value of Biodiversity

5.3.2: Threats to Biodiversity
5.3.3: Preserving Biodiversity
5.3.4: Chapter Summary

5.4: Terrestrial Biomes

5.4.1: Introduction
5.4.2: Climate and Biomes
5.4.3: Tropical Rainforest
5.4.4: Tropical Deciduous Forest
5.4.5: Savannas
5.4.6: Desert
5.4.7: Mediterranean (Chaparral)
5.4.8: Temperate Grasslands (Prairie)
5.4.9: Temperate Deciduous Forests
5.4.10: 22.10 Temperate Rainforest
5.4.11: Boreal (Coniferous) Forests
5.4.12: Arctic Tundra
5.4.13: Chapter Summary

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5.1: POPULATION ECOLOGY



Figure 5.1.1: Individuals from a population of ground pink (*Linanthus dianthiflorus*). This flowering plant is an herbaceous species that is endemic to California. Image by Kammy Algiers (CC-BY)

Researchers study ecology at various levels. For example, at the organismal level, a scientist might be interested in the adaptations that enable individuals to live in specific habitats. These adaptations could be morphological (pertaining to the study of form or structure), physiological, or behavioral. In this chapter, we will focus on population ecology. A **population** is a group of interbreeding organisms that are members of the same species living in the same area at the same time. Organisms that are all members of the same species, a population, are called conspecifics (Figure 5.1.1). A population is identified, in part, by where it lives; its area of population may have natural or artificial boundaries. Natural boundaries might be rivers, mountains, or deserts, while examples of artificial boundaries include mowed grass or manmade structures such as roads. The study of population ecology focuses on the number of individuals in an area and how and why population size changes over time. Population ecologists are particularly interested in counting the Karner blue butterfly, for example, because it is classified as federally endangered.

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5.1.1: Population Size and Density

5.1.2: Life Histories and Natural Selection

5.1.3: Environmental Limits to Population Growth

5.1.4: Population Dynamics and Regulation

5.1.5: Chapter Summary

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5.1.1: Population Size and Density

Learning Objectives

- Describe how ecologists measure population size and density.
- Describe three different patterns of population distribution.

Population Size and Density

Populations are characterized by their **population size** (total number of individuals) and their **population density** (number of individuals per unit area). A population may have a large number of individuals that are distributed densely, or sparsely. There are also populations with small numbers of individuals that may be dense or very sparsely distributed in a local area. Population size can affect potential for adaptation because it affects the amount of genetic variation present in the population. Density can have effects on interactions within a population such as competition for food and the ability of individuals to find a mate.

Population Research Methods

Counting all individuals in a population is the most accurate way to determine its size. However, this approach is not usually feasible, especially for large populations or extensive habitats. Instead, scientists study populations by sampling, which involves counting individuals within a certain area or volume that is part of the population's habitat. Analysis of sample data enables scientists to infer population size and population density about the entire population.

A variety of methods can be used to sample populations. Scientists usually estimate the populations of sessile or slow-moving organisms with the quadrat method. A quadrat is a square that encloses an area within a habitat. The area may be defined by staking it out with sticks and string, or using a square made of wood, plastic, or metal placed on the ground (Figure 5.1.1.1).

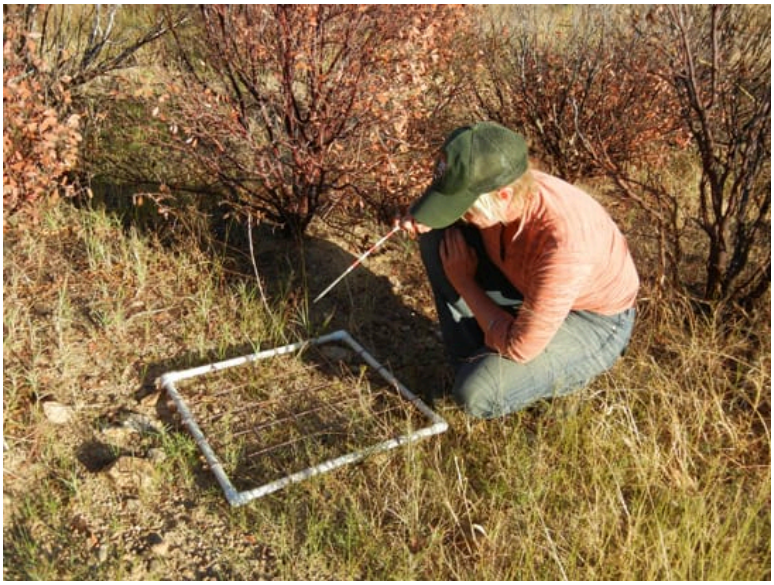


Figure 5.1.1.1: A scientist uses a quadrat to measure plant population size and density. A quadrat is a square frame of known area in which species of interest can be easily counted and measured.

A field study usually includes several quadrat samples at random locations or along a transect in representative habitat. After they place the quadrats, researchers count the number of individuals that lie within the quadrat boundaries. The researcher decides the quadrat size and number of samples from the type of organism, its spatial distribution, and other factors. For sampling daffodils, a 1 m^2 quadrat could be appropriate. Giant redwoods are larger and live further apart from each other, so a larger quadrat, such

as 100 m^2, would be necessary. The correct quadrat size ensures counts of enough individuals to get a sample representative of the entire habitat.

Species Distribution

In addition to measuring simple density, further information about a population can be obtained by looking at the distribution of the individuals. **Species dispersion patterns** (or distribution patterns) show the spatial relationship between members of a population within a habitat at a particular point in time. In other words, they show whether members of the species live close together or far apart, and what patterns are evident when they are spaced apart.

Individuals of a population can be distributed in one of three basic patterns: they can be more or less equally spaced apart (uniform dispersion), dispersed randomly with no predictable pattern (random dispersion), or clustered in groups (clumped dispersion). (Figure 5.1.1.2). Plants with wind-dispersed seeds disperse randomly, as they germinate wherever they happen to fall in a favorable environment. Uniform dispersion is observed in plants that secrete substances inhibiting the growth of nearby individuals (such as the release of toxic chemicals by the sage plant *Salvia leucophylla,* a phenomenon called allelopathy). A clumped dispersion may be seen in plants that drop their seeds straight to the ground, such as oak trees.

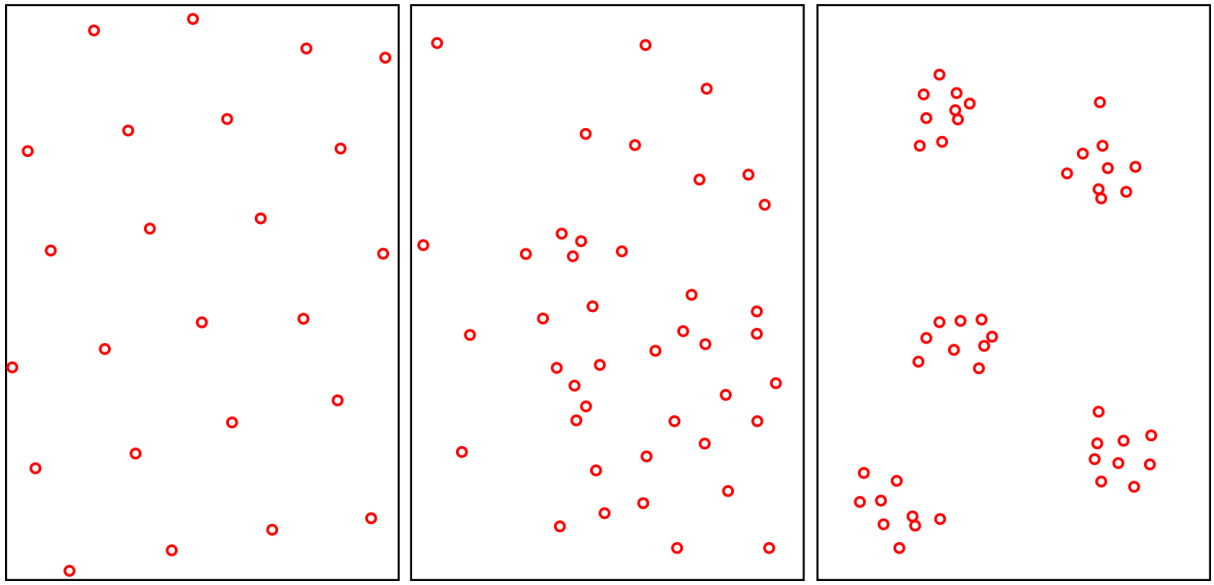


Figure 5.1.1.2: Species may have uniform, random, or clumped distribution. (Wikipedia; CC BY-SA 4.0).

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5.1.2: Life Histories and Natural Selection

Learning Objectives

- Describe how life history patterns are influenced by natural selection.
- Compare and contrast semelparity and iteroparity.

Life History Patterns

Energy is required by all living organisms for their growth, maintenance, and reproduction; at the same time, energy is often a major limiting factor in determining an organism's survival. Plants, for example, acquire energy from the sun via photosynthesis, but must expend this energy to grow, maintain health, and produce energy-rich seeds to produce the next generation. All species have an energy budget: they must balance energy intake with their use of energy for metabolism, reproduction, and energy storage.

Reproductives strategies

Population size can be influenced by the time reproduction begins, how often the organism reproduces, and how many offspring the organism produces in one reproductive period. The timing of reproduction in a life history also affects species survival. Organisms that reproduce early on have a greater chance of producing offspring, but this is usually at the expense of their growth and the maintenance of their health. Conversely, organisms that begin to reproduce later in life often have greater **fecundity** (ability to produce many offspring), but they risk that they will not survive to reproductive age.

These different energy strategies and tradeoffs are key to understanding the evolution of each species as it maximizes its fitness and fills its niche. In terms of energy budgeting, some species "blow it all" and use up most of their energy reserves to reproduce early before they die. Other species delay having reproduction to become stronger, more experienced individuals and to make sure that they are strong enough to provide parental care if necessary.

For example, an oak tree grows much slower than an annual grass. Though this is a high investment, oaks are well adapted to expected stressors such as fires or drought. On the other hand, alders and willows grow and colonize open riparian areas very quickly.

Single versus Multiple Reproductive Events

Some life history traits, such as fecundity, timing of reproduction, and parental care, can be grouped together into general strategies that are used by multiple species. **Semelparity** occurs when a species reproduces only once during its lifetime and then dies, as do annual plants. Such species use most of their resource budget during a single reproductive event, sacrificing their health to the point that they do not survive. Some bamboo exhibit a semelparity life strategy: they flower once and then die. The century plant, or agave, also exhibits this strategy, reproducing once towards the end of its life (Figure 5.1.2.1). **Iteroparity** describes a reproductive strategy where the species reproduces repeatedly during its life. Many plants reproduce using this strategy.



Figure 5.1.2.1: Left: Some bamboo produce large seed clusters (Credit: Vijayanrajapuram; CC BY-SA 4.0); Right: Agave (Century plant) lives for 10-30 years and reproduces only once before it dies (Credit: Alvesgaspar; CC BY-SA 4.0). Both are examples of semelparity.

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5.1.3: Environmental Limits to Population Growth

Learning Objectives

- Compare and contrast between exponential and logistic growth patterns.
- Give examples of exponential and logistic growth in natural populations.
- Describe the role of carrying capacity in population growth.
- Describe the influences of intraspecific competition in population size.

Although life histories describe the way many characteristics of a population (such as their age structure) change over time in a general way, population ecologists make use of a variety of methods to model population dynamics mathematically. These more precise models can then be used to accurately describe changes occurring in a population and better predict future changes. Certain models that have been accepted for decades are now being modified or even abandoned due to their lack of predictive ability, and scholars strive to create effective new models.

Exponential Growth

Charles Darwin, in his theory of natural selection, was greatly influenced by the English clergyman Thomas Malthus. Malthus published a book in 1798 stating that populations with unlimited natural resources grow very rapidly, and then population growth decreases as resources become depleted. This accelerating pattern of increasing population size is called **exponential growth**.

Though bacteria are often the noted examples of species that grow exponentially, we do see this in many photosynthetic species as well. For example, algae and cyanobacteria will often grow exponentially for a period of time with warmer temperatures, both in freshwater (ex: lakes) or salt water (ex: oceans). Exponential growth occurs when the **population growth rate**—the number of organisms added in each reproductive generation—is accelerating; that is, it is increasing at a greater and greater rate. For example, a population of 1000 can increase by 1000 in one hour, but then increase by 2000 the second hour, and to 4000 the third hour, and 8000 by the fourth hour. The number of organisms increases faster at every reproduction event. After 1 day and 24 of these cycles, a population could have increased from 1000 to more than 16 billion. When the population size is plotted over time, a J-shaped growth curve is produced (Figure 5.1.3.1, left graph).

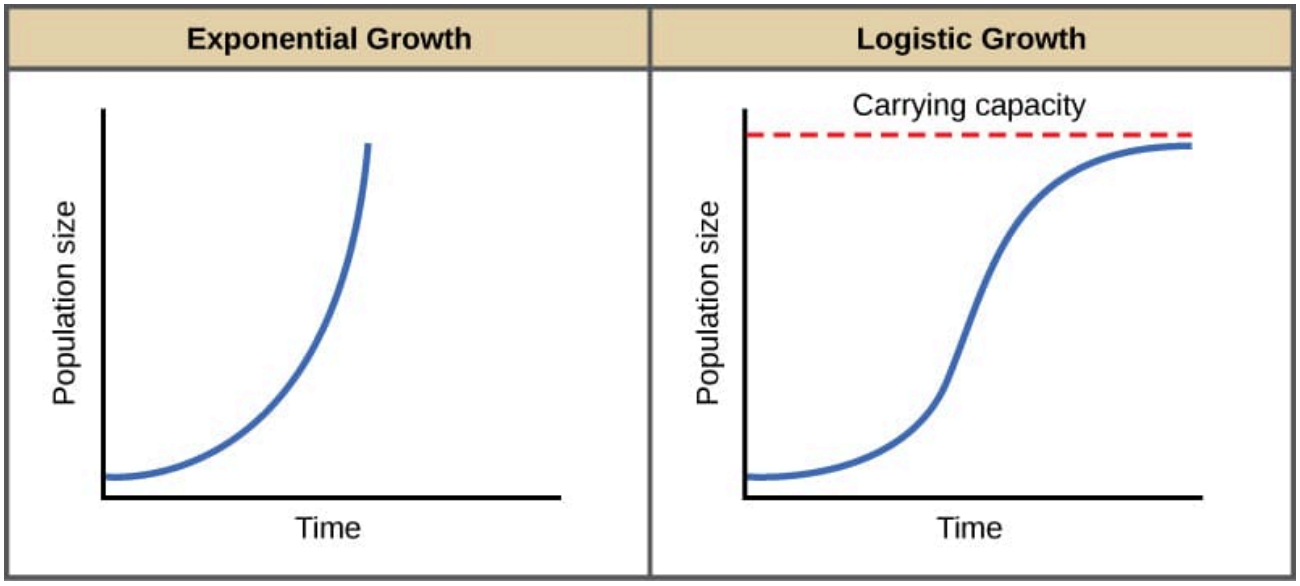


Figure 5.1.3.1: When resources are unlimited, populations exhibit exponential growth, resulting in a J-shaped curve. When resources are limited, populations exhibit logistic growth. In logistic growth, population expansion decreases as resources become scarce, and it levels off when the carrying capacity of the environment is reached, resulting in an S-shaped curve.

We often see examples of exponential growth for a period of time in nature. For example, after recovery, a plant species may exponentially grow for a period of time while establishing its previous niche. Non-native, **invasive species**, can often also grow exponentially, as they may not have the same environmental pressures (predators, parasites, competitors) in the introduced area and can increase dramatically once established.

Logistic Growth

In the real world, with its limited resources, exponential growth cannot continue indefinitely. Exponential growth may occur in environments where there are few individuals and plentiful resources, but when the number of individuals gets large enough, resources will be depleted, slowing the growth rate. Eventually, the growth rate will plateau or level off (Figure $5.1.3.1$, right graph). The pattern formed in this type of growth is called **logistic growth**, or S-curve. This population size, which represents the maximum population size that a particular environment can sustain, is called the **carrying capacity**.

There are three different sections to an S-shaped curve. Initially, growth is exponential because there are few individuals and ample resources available. Then, as resources begin to become limited, the growth rate decreases. Finally, growth levels off at the carrying capacity of the environment, with little change in population size over time.

Role of Intraspecific Competition

The logistic model assumes that every individual within a population will have equal access to resources and, thus, an equal chance for survival. For plants, the amount of water, sunlight, nutrients, and the space to grow are the important resources.

In the real world, phenotypic variation among individuals within a population means that some individuals will be better adapted to their environment than others. The resulting competition between population members of the same species for resources is termed **intraspecific competition** (intra- = “within”; -specific = “species”). Intraspecific competition for resources may not affect populations that are well below their carrying capacity—resources are plentiful and all individuals can obtain what they need. However, as population size increases, this competition intensifies. In addition, the accumulation of waste products can reduce an environment’s carrying capacity.

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5.1.4: Population Dynamics and Regulation

Learning Objectives

- Compare and contrast density-dependent growth regulation and density-independent growth regulation.
- Compare and contrast *K*-selected and *r*-selected species using examples of their life history traits.

The logistic model of population growth, while valid in many natural populations and a useful model, is a simplification of real-world population dynamics. Implicit in the model is that the carrying capacity of the environment does not change, which is not the case. The carrying capacity varies annually: for example, some summers are hot and dry whereas others are cold and wet. In many areas, the carrying capacity during the winter is much lower than it is during the summer. Also, natural events such as earthquakes, volcanoes, and fires can alter an environment and hence its carrying capacity. Additionally, populations do not usually exist in isolation. They engage in interspecific competition: that is, they share the environment with other species, competing with them for the same resources. These factors are also important to understanding how a specific population will grow.

Nature regulates population growth in a variety of ways. These are grouped into density-dependent factors, in which the density of the population at a given time affects growth rate and mortality, and density-independent factors, which influence mortality in a population regardless of population density. Note that in the former, the effect of the factor on the population depends on the density of the population at onset. Conservation biologists want to understand both types because this helps them manage populations and prevent extinction or overpopulation.

Density-dependent Regulation

Most **density-dependent factors** are biological in nature (biotic), and include predation, inter- and intraspecific competition, and diseases such as those caused by parasites. Usually, the denser a population is, the greater its mortality rate. For example, during intra- and interspecific competition, the reproductive rates of the individuals will usually be lower, reducing their population's rate of growth. In addition, low prey density increases the mortality of its predator because it has more difficulty locating its food source. High population density can also increase the transmission of parasites and prevalence of disease.

Density-independent Regulation

Many factors, typically physical or chemical in nature (abiotic), influence the mortality of a population regardless of its density, including weather, natural disasters, and pollution. A frosty night that emerging in early spring does not kill a higher or lower percentage of seedlings based on the density of the seedling population. Its chances of survival for the seedling are the same whether the population density is high or low.

In real-life situations, population regulation is very complicated and density-dependent and independent factors can interact. A dense population that is reduced in a density-independent manner by some environmental factor(s) will be able to recover differently than a sparse population.

Life Histories of *K*-selected and *r*-selected Species

While reproductive strategies play a key role in life histories, they do not account for important factors like limited resources and competition. The regulation of population growth by these factors can be used to introduce a classical concept in population biology, that of *K*-selected versus *r*-selected species.

***K*-selected species** are species selected by stable, predictable environments. Populations of *K*-selected species tend to exist close to their carrying capacity (hence the term *K*-selected) where intraspecific competition is high. These species have few, large offspring, have more parental care, and have a longer period of maturation development period. In plants, scientists think of parental care more broadly: how long fruit takes to develop or how long it remains on the plant are determining factors in the time

to the next reproductive event. Oak trees are great examples of *K*-selected species (Figure 5.1.4.1). Oak trees grow very slowly and take, on average, 20 years to produce their first seeds, known as acorns. As many as 50,000 acorns can be produced by an individual tree, but the germination rate is low as many of these rot or are eaten by animals such as squirrels. In some years, oaks may produce an exceptionally large number of acorns, and these years may be on a two- or three-year cycle depending on the species of oak (*r*-selection).

As oak trees grow to a large size and for many years before they begin to produce acorns, they devote a large percentage of their energy budget to growth and maintenance. The tree's height and size allow it to dominate other plants in the competition for sunlight, the oak's primary energy resource. Furthermore, when it does reproduce, the oak produces large, energy-rich seeds that use their energy reserve to become quickly established (*K*-selection).



Figure 5.1.4.1: Left: Oak trees produce many offspring that do not receive parental care, but are considered K-selected species based on longevity and late maturation (Credit Wikipedia; CC BY-SA 4.0). (b) Dandelions are considered r-selected species as they mature early, have short lifespans, and produce many offspring that receive no parental care (Credit Greg Hume; CC BY-SA 4.0).

In contrast, ***r*-selected species** have a large number of small offspring (hence their *r* designation (Table 5.1.4.1). This strategy is often employed in unpredictable or changing environments. Many weedy plants are considered r-selected. Dandelion are great examples of r-selected species, producing many small seeds on one flower head that are seed dispersed long distance (Figure 5.1.4.3). Many seeds are produced simultaneously to ensure that at least some of them reach a hospitable environment. Seeds that land in inhospitable environments have little chance for survival since their seeds are low in energy content. Note that survival is not necessarily a function of energy stored in the seed itself.

Table 5.1.4.1: Characteristics of K-selected and r-selected species

Characteristics of *K*-selected species	Characteristics of *r*-selected species
Mature late	Mature early
Greater longevity	Lower longevity
Increased parental care	Decreased parental care
Increased competition	Decreased competition
Fewer offspring	More offspring
Larger offspring	Smaller offspring

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5.1.5: Chapter Summary

Populations are characterized by their population size (total number of individuals) and their population density (number of individuals per unit area). Counting all individuals in a population is the most accurate way to determine its size. However, this approach is not usually feasible, especially for large populations or extensive habitats. Instead, scientists study populations by sampling, which involves counting individuals within a certain area or volume that is part of the population's habitat. Analysis of sample data enable scientists to infer population size and population density about the entire population. One method used the collect population size data in the field is using quadrat placed at random locations or along a transect in representative habitat. The size of the quadrat depends on the species monitoring. In addition to measuring simple density, further information about a population can be obtained by looking at the distribution of the individuals. Species may have uniform, random, or clumped distribution.

All species have evolved a pattern of living, called a life history strategy, in which they partition energy for growth, maintenance, and reproduction. These patterns evolve through natural selection; they allow species to adapt to their environment to obtain the resources they need to successfully reproduce. There are different life strategies that species may exhibit. A species may reproduce early in life to ensure surviving to a reproductive age or reproduce later in life to become larger and healthier. A species may reproduce once (semelparity) or many times (iteroparity) in its life.

Populations with unlimited resources grow exponentially, with an accelerating growth rate. When resources become limiting, populations follow a logistic growth curve. The population of a species will level off at the carrying capacity of its environment. Within populations, phenotypic variation among individuals means that some individuals will be better adapted to their environment than others. The resulting competition between population members of the same species for resources is termed intraspecific competition. Populations are regulated by a variety of density-dependent and density-independent factors. Species are divided into two categories based on a variety of features of their life history patterns: *r*-selected species, which have large numbers of offspring, and *K*-selected species, which have few offspring.

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

- Describe how ecologists measure population size and density.
- Describe three different patterns of population distribution.
- Describe how life history patterns are influenced by natural selection.
- Compare and contrast semelparity and iteroparity.
- Compare and contrast between exponential and logistic growth patterns.
- Give examples of exponential and logistic growth in natural populations.
- Describe the role of carrying capacity in population growth.
- Describe the influences of intraspecific competition in population size.
- Compare and contrast density-dependent growth regulation and density-independent growth regulation.
- Compare and contrast *K*-selected and *r*-selected species using examples of their life history traits.

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5.2: COMMUNITIES AND ECOSYSTEMS



Figure 5.2.1: Monarch butterflies cluster together on a eucalyptus branch in an overwinter site in Ventura, CA. Image by Kammy Algiers (CC-BY).

Populations typically do not live in isolation from other species. Populations that interact within a given area form a **community**. The organisms that form a community are found in **habitats**, physical environments where organisms live. However, only the **biotic** (living) components are considered part of a community. Scientists study ecology at the community level to understand how species interact with each other and compete for the same resources.

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- Communities and Ecosystems

5.2.1: Communities

5.2.2: Community Interactions

5.2.3: Symbiosis

5.2.4: Biodiversity in Ecosystems

5.2.5: Succession

5.2.6: Ecosystem

5.2.7: Energy and Energy Flow

5.2.8: Food Chains and Food Webs

5.2.9: Chapter Summary

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5.2.1: Communities

Learning Objective

- Describe the difference between intraspecific and interspecific interactions in reference to competition

Biotic Interactions

Biotic interactions refer to the relationships among organisms. They can be **intraspecific** (between members of the same species) or **interspecific** (between members of different species). When at least one of the interacting organisms is harmed, the relationship is called an **antagonism. Trophic interactions**, in which one species consumes another, are antagonisms. Competition, commensalism, and mutualism are some examples of biotic interaction we find in communities.

Competition

Competition occurs when organisms use the the same resources and one or both organisms is harmed. Plants often compete with one another for light (Figure 5.2.1.1). In the tropical rainforests, where water is not a limiting factor, and much of the carbon is aboveground, plants compete with one another intensely. Often times, this is an example of **interspecific** competition as various species of plants, with different adaptations, compete to get sunlight. However, many plants of the same species are competing for that limited space and sunlight as well. Thus, we also see **intraspecific** competition.



Figure 5.2.1.1: In the tropical rainforest, competition for light allows for various adaptations amongst plants. These trees in Costa Rica are covered with veins, moss, and lichens. The forest floor is covered with smaller shrubs and trees. Image by Kammy Algiers (CC-BY).

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5.2.2: Community Interactions

Learning Objectives

- Define herbivory
- Give examples of defenses against predation and herbivory

Herbivory

Herbivory describes the consumption of plants by animals, and it is another interspecific relationship that affects populations. Unlike animals, plants cannot outrun predators or use mimicry to hide from hungry animals (with a few exceptions). Some plants have developed mechanisms to defend against herbivory. Other species have developed strategies that rely on hungry animals; for example, herbivory provides a mechanism of seed distribution that aids in plant reproduction.

Defense Mechanisms against Predation and Herbivory

The study of communities must consider evolutionary forces that act on the members of the various populations contained within it. Species are not static, but slowly changing and adapting to their environment by natural selection and other evolutionary forces. Species have evolved numerous mechanisms to escape predation and herbivory. These defenses may be mechanical, chemical, physical, or behavioral.



Figure 5.2.2.1: (top) Galapagos Land Iguana eating cactus pad with spines from a prickly pear cactus. (bottom) a monarch caterpillar feeds on a milkweed plant. Images by Kammy Algiers (CC-BY).

Mechanical defenses, such as the presence of thorns on plants, may discourage herbivory by causing physical pain to the predator (Figure 5.2.2.1, top). Chemical defenses are also produced by many plants to discourage herbivory. Milkweed plants (*Asclepias* spp.) produce chemical defenses that protect them against most herbivores. However, as shown in Figure 5.2.2.1 (bottom), monarch caterpillars (*Danaus plexippus*) have evolved a way around these defenses. Monarch butterflies lay their eggs on milkweed plants, the preferred source of food for their developing larvae. If the caterpillars can survive the initial flood of sticky latex when they first bite into the leaf (a front line defense for the milkweed), they can continue to consume the tissues. These tissues contain toxins, but the caterpillar is able to store, rather than metabolize, these toxins and make its own body toxic to predators.

Plants can also be good sources of camouflage for animals. Often times, animals will blend in with the plants they sit on to avoid being detected by predators. The tropical walking stick is an insect with the coloration and body shape of a twig which makes it very hard to see when stationary against a background of real twigs (Figure 5.2.2.2). In another example, the chameleon can change its color to match its plant surroundings (Figure 5.2.2.2). Both of these are examples of camouflage, or avoiding detection by blending in with the background.



Figure 5.2.2.2: (top) The tropical walking stick and (bottom) the chameleon use body shape and/or coloration to prevent detection by predators. Credit top: modification of work by Linda Tanner; credit bottom: modification of work by Frank Vassen.

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5.2.3: Symbiosis

Learning Objectives

- Describe what is considered a symbiotic relationships between species
- Compare and contrast between commensalism, mutualism, and parasitism
- Describe symbiosis as it relates to nitrogen fixation
- Describe how saprophytes, epiphytes, and carnivorous plants depend on other orgnanisms

Symbiosis

Symbiotic relationships, or symbioses (plural), are close interactions between individuals of different species over an extended period of time which impact the abundance and distribution of the associating populations. Most scientists accept this definition, but some restrict the term to only those species that are mutualistic, where both individuals benefit from the interaction. In this discussion, the broader definition will be used.

Commensalism

A **commensal** relationship occurs when one species benefits from the close, prolonged interaction, while the other neither benefits nor is harmed. Birds nesting in trees provide an example of a commensal relationship (Figure 5.2.3.1). The tree is not harmed by the presence of the nest among its branches. The nests are light and produce little strain on the structural integrity of the branch, and most of the leaves, which the tree uses to get energy by photosynthesis, are above the nest so they are unaffected. The bird, on the other hand, benefits greatly. If the bird had to nest in the open, its eggs and young would be vulnerable to predators. Another example of a commensal relationship is the clown fish and the sea anemone. The sea anemone is not harmed by the fish, and the fish benefits with protection from predators who would be stung upon nearing the sea anemone.



Figure 5.2.3.1: The southern masked-weaver bird is starting to make a nest in a tree in Zambezi Valley, Zambia. This is an example of a commensal relationship, in which one species (the bird) benefits, while the other (the tree) neither benefits nor is harmed. (credit: "Hanay"/Wikimedia Commons)

Mutualism

A second type of symbiotic relationship is called **mutualism**, where two species benefit from their interaction. Some scientists

believe that these are the only true examples of symbiosis. Many animal pollinators have coevolved with plants, including many insects (bees, flies, butterflies, moths), birds (hummingbirds), and some mammals (bats). The pollinator usually receives a reward in the form of nectar or pollen, while the plant is able to distribute its pollen (which will produce the male gametes) to another plant. Flowers have evolved in response to natural selection to attract pollinators by scent, color, shape, phenology, and availability of the reward. Some plants are generalist and are pollinated by many different kinds of pollinators. Other plants are specialists and pollinated by only a few taxa, or perhaps even a single pollinator species (Figure 5.2.3.2).



Figure 5.2.3.2: a) Morning Glory being pollinated by a bee. Image by Kammy Algiers (CC-BY). b) a Mariposa Lily pollinated by a fly. Image by Kammy Algiers (CC-BY). c) A male Broad-Tailed Hummingbird visits a scarlet gilia flower at the Rocky Mountain Biological Laboratory. The hummingbird gains food (nectar) while aiding the gilia flower with reproduction. Image by David W. Inouye (CC-BY).

Mycorrhizae: A Plant-Fungal Mutualism

One of the most remarkable associations between fungi and plants is the establishment of mycorrhizae. **Mycorrhiza**, which is derived from the Greek words *myco* meaning fungus and *rhizo* meaning root, refers to the fungal partner of a mutualistic association between vascular plant roots and their symbiotic fungi. Nearly 90 percent of all vascular plant species (and many nonvascular plant species) have mycorrhizal partners. In a mycorrhizal association, the fungal mycelia use their extensive network of hyphae and large surface area in contact with the soil to channel water and minerals from the soil into the plant. In exchange, the plant supplies the products of photosynthesis to fuel the metabolism of the fungus.

There are several basic types of mycorrhizae. **Ectomycorrhizae** (“outside” mycorrhizae) depend on fungi enveloping the roots in a sheath (called a mantle). Hyphae grow from the mantle into the root and envelope the outer layers of the root cells in a network of hyphae called a *Hartig net* Figure 5.2.3.3. The fungal partner can belong to the Ascomycota, Basidiomycota or Zygomycota. **Endomycorrhizae** ("inside" mycorrhizae), also called *arbuscular mycorrhizae*, are produced when the fungi grow inside the root in a branched structure called an *arbuscule* (from the Latin for “little trees”). The fungal partners of endomycorrhizal associates all belong to the Glomeromycota. The fungal arbuscules penetrate root cells between the cell wall and the plasma membrane and are the site of the metabolic exchanges between the fungus and the host plant Figures 5.2.3.3*b* and 5.2.3.4*b*. Orchids rely on a third type of mycorrhiza. Orchids are epiphytes that typically produce very small airborne seeds without much storage to sustain germination and growth. Their seeds will not germinate without a mycorrhizal partner (usually a Basidiomycete). After nutrients in the seed are depleted, fungal symbionts support the growth of the orchid by providing necessary carbohydrates and minerals. Some orchids continue to be mycorrhizal throughout their life cycle.

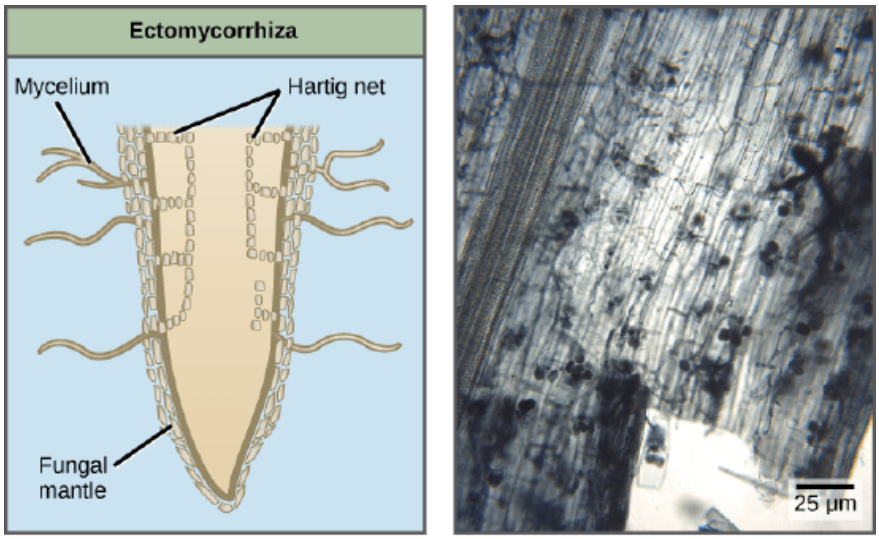


Figure 5.2.3.3 Two types of mycorrhizae. (a) Ectomycorrhizae and (b) arbuscular or endomycorrhizae have different mechanisms for interacting with the roots of plants. (credit b: MS Turmel, University of Manitoba, Plant Science Department)

If symbiotic fungi were absent from the soil, what impact do you think this would have on plant growth?

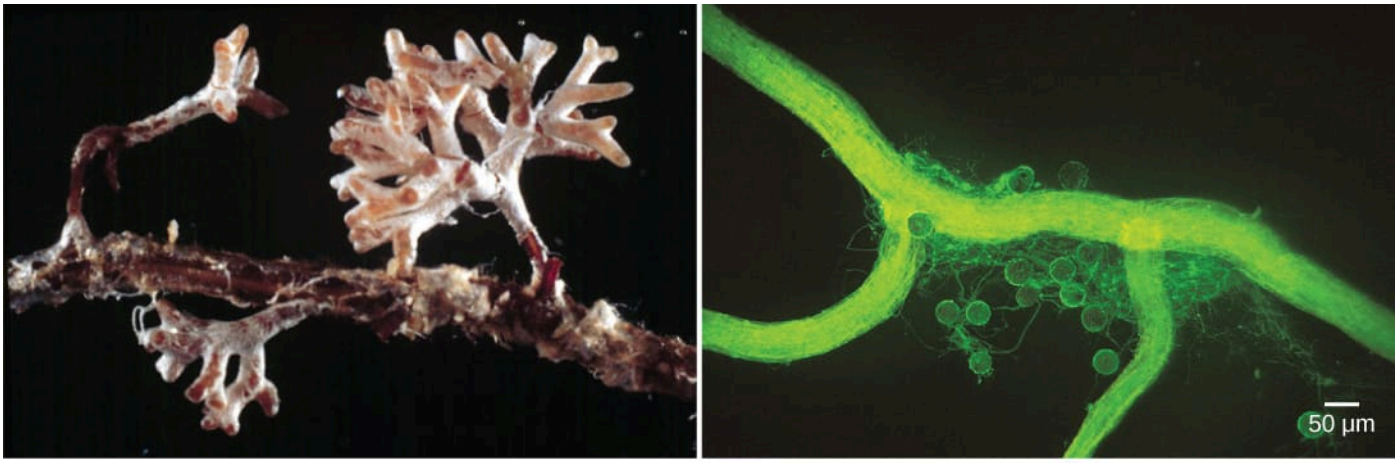


Figure 5.2.3.4 Mycorrhizae. The (a) infection of *Pinus radiata* (Monterey pine) roots by the hyphae of *Amanita muscaria* (fly amanita) causes the pine tree to produce many small, branched rootlets. The *Amanita* hyphae cover these small roots with a white mantle. (b) Spores (the round bodies) and hyphae (thread-like structures) are evident in this light micrograph of an arbuscular mycorrhiza by a fungus on the root of a corn plant. (credit a: modification of work by Randy Molina, USDA; credit b: modification of work by Sara Wright, USDA-ARS; scale-bar data from Matt Russell)

Other examples of fungus–plant **mutualism** include the endophytes: fungi that live inside tissue without damaging the host plant. Endophytes release toxins that repel herbivores, or confer resistance to environmental stress factors, such as infection by microorganisms, drought, or heavy metals in soil.

Nitrogen Fixation: Root and Bacteria Interactions

Nitrogen is an important macronutrient because it is part of nucleic acids and proteins. Atmospheric nitrogen, which is the diatomic molecule N_2, or dinitrogen, is the largest pool of nitrogen in terrestrial ecosystems. However, plants cannot take advantage of this nitrogen because they do not have the necessary enzymes to convert it into biologically useful forms. However, nitrogen can be "fixed," which means that it can be converted to ammonia (NH_3) through biological, physical, or chemical processes. As you have learned, biological nitrogen fixation (BNF) is the conversion of atmospheric nitrogen (N_2) into ammonia (NH_3), exclusively carried out by prokaryotes such as soil bacteria or cyanobacteria. Biological processes contribute 65 percent of

the nitrogen used in agriculture. The following equation represents the process:

$$N_2 + 16\,ATP + 8\,e^- + 8\,H^+ \rightarrow 2\,NH_3 + 16\,ADP + 16\,P_i + H_2 \quad (5.2.3.1)$$

The most important source of BNF is the symbiotic interaction between soil bacteria and legume plants, including many crops important to humans (Figure 5.2.3.5). The NH_3 resulting from fixation can be transported into plant tissue and incorporated into amino acids, which are then made into plant proteins. Some legume seeds, such as soybeans and peanuts, contain high levels of protein, and serve among the most important agricultural sources of protein in the world.



(a) (b) (c)

Figure 5.2.3.5: Some common edible legumes—like (a) peanuts, (b) beans, and (c) chickpeas—are able to interact symbiotically with soil bacteria that fix nitrogen. (credit a: modification of work by Jules Clancy; credit b: modification of work by USDA)

Farmers often rotate corn (a cereal crop) and soy beans (a legume), planting a field with each crop in alternate seasons. What advantage might this crop rotation confer?

Soil bacteria, collectively called rhizobia, symbiotically interact with legume roots to form specialized structures called nodules, in which nitrogen fixation takes place. This process entails the reduction of atmospheric nitrogen to ammonia, by means of the enzyme nitrogenase. Therefore, using rhizobia is a natural and environmentally friendly way to fertilize plants, as opposed to chemical fertilization that uses a nonrenewable resource, such as natural gas. Through symbiotic nitrogen fixation, the plant benefits from using an endless source of nitrogen from the atmosphere. The process simultaneously contributes to soil fertility because the plant root system leaves behind some of the biologically available nitrogen. As in any symbiosis, both organisms benefit from the interaction: the plant obtains ammonia, and bacteria obtain carbon compounds generated through photosynthesis, as well as a protected niche in which to grow (Figure 5.2.3.6).

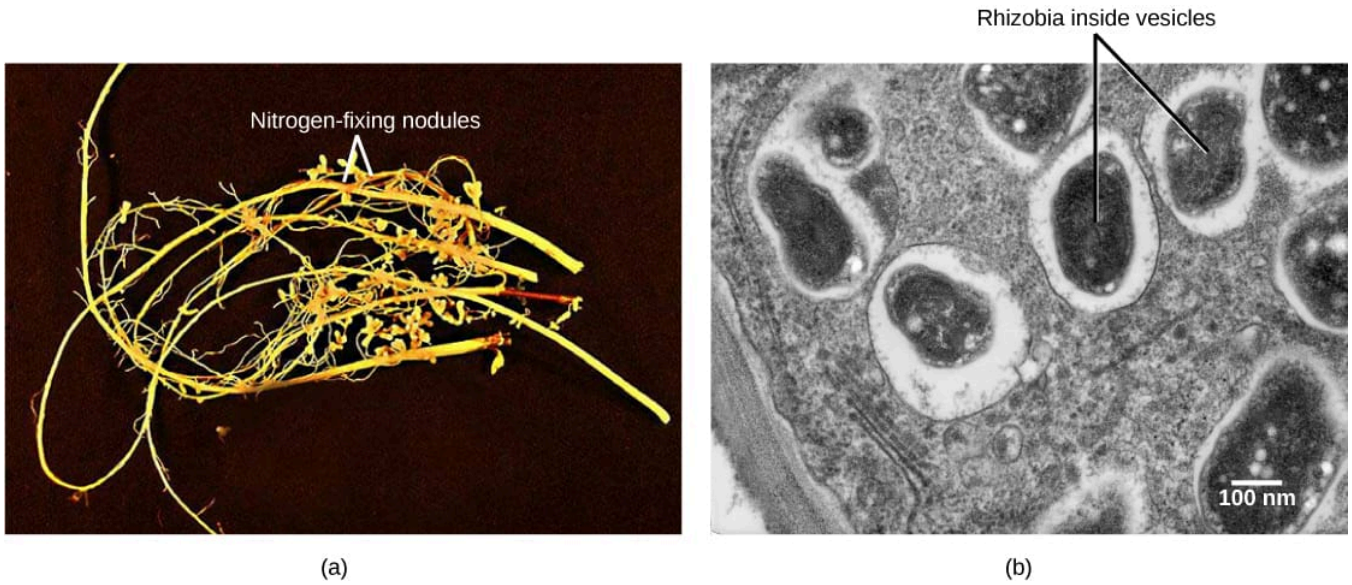


Figure 5.2.3.6: Soybean roots contain (a) nitrogen-fixing nodules. Cells within the nodules are infected with Bradyrhyzobium japonicum, a rhizobia or “root-loving” bacterium. The bacteria are encased in (b) vesicles inside the cell, as can be seen in this transmission electron micrograph. (credit a: modification of work by USDA; credit b: modification of work by Louisa Howard, Dartmouth Electron Microscope Facility; scale-bar data from Matt Russell)

Parasitism

A **parasite** is an organism that lives in or on another living organism and derives nutrients from it. In this relationship, the parasite benefits and the organism being fed upon (the host) is harmed. The host is usually weakened by the parasite as it siphons resources the host would normally use to maintain itself. The parasite, however, is unlikely to kill the host, especially not quickly, because this would not provide enough time for the organism to complete its reproductive cycle by spreading to another host. Dodder is an annual vine that grows parasitically on shrubs (Figure 5.2.3.7. Dodder has a weak, cylindrical stem that coils around the host and forms suckers. From these suckers, cells invade the host stem and grow to connect with the vascular bundles of the host. The parasitic plant obtains water and nutrients through these connections. The plant is a **holoparasite** because it is completely dependent on its host. Some parasitic plants, like leafy mistletoes, are fully photosynthetic and only use the host for water and minerals. These are considered **hemiparasites**. There are about 4,100 species of parasitic plants.



Figure 5.2.3.7: a. Dodder, in the genus *Cuscata* is a thin orange flowering plant that is a parasitizing on a shrub. Image by Kammy Algiers (CC-BY). b. The dodder is a holoparasite that penetrates the host’s vascular tissue and diverts nutrients for its own growth. Note that the vines of the dodder, which has white flowers, are beige. The dodder has no chlorophyll and cannot produce its own food. (credit: "Lalithamba"/Flickr)

Heterotrophic Plants

Heterotrophic plants not have chlorophyll (Figure 5.2.3.8). Instead, they steal sugars from other plants, sometimes through a mycorrhizal fungus. These latter plants are called mycoheterotrophs.



Figure 5.2.3.8: Mycoheterotrophic plants, like this Dutchmen's pipe (Monotropa hypopitys), obtain their food by parasitizing a mycorrhizal fungus. They do not have chlorophyll. (credit: modification of work by Iwona Erskine-Kellie)

Epiphytes

An **epiphyte** is a plant that grows on other plants, but is not dependent upon the other plant for nutrition (Figure 5.2.3.9). Epiphytes have two types of roots: clinging aerial roots, which absorb nutrients from humus that accumulates in the crevices of trees; and aerial roots, which absorb moisture from the atmosphere.



Figure 5.2.3.9: These epiphyte plants grow in the main greenhouse of the Jardin des Plantes in Paris.

Insectivorous Plants

An insectivorous plant has specialized leaves to attract and digest insects. The Venus flytrap is popularly known for its

insectivorous mode of nutrition, and has leaves that work as traps (Figure 5.2.3.10). The minerals it obtains from prey compensate for those lacking in the boggy (low pH) soil of its native North Carolina coastal plains. There are three sensitive hairs in the center of each half of each leaf. The edges of each leaf are covered with long spines. Nectar secreted by the plant attracts flies to the leaf. When a fly touches the sensory hairs, the leaf immediately closes. Next, fluids and enzymes break down the prey and minerals are absorbed by the leaf. Since this plant is popular in the horticultural trade, it is threatened in its original habitat.



Figure 5.2.3.10: A Venus flytrap has specialized leaves to trap insects. (credit: "Selena N. B. H."/Flickr)

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5.2.4: Biodiversity in Ecosystems

Learning Objectives

- Describe how species richness and relative abundance play a role on biodiversity
- Describe the role of keystone species in a community
- Descdribe the role of invasive species in a community

Biodiversity, Species Richness, and Relative Species Abundance

Biodiversity describes a community's biological complexity: it is usually measured by the number of different species, or **species richness,** in a particular area and their **relative abundance** (evenness). However, genetic diversity is increasingly considered as a component of biodiversity. The area in question could be a habitat, a biome, or the entire biosphere. Species richness is the term that is used to describe the number of species living in a habitat or biome. Species richness varies across the globe (Figure 5.2.4.1). One factor in determining species richness is latitude, with the greatest species richness occurring in ecosystems near the equator, which often have warmer temperatures, large amounts of rainfall, and low seasonality. The lowest species richness occurs near the poles, which are much colder, drier, and thus less conducive to life in Geologic time (time since glaciations). The predictability of climate or productivity is also an important factor. Other factors influence species richness as well. For example, the study of island biogeography attempts to explain the relatively high species richness found in certain isolated island chains, including the Galápagos Islands that inspired the young Darwin. Relative species abundance is the number of individuals in a species relative to the total number of individuals in all species within a habitat, ecosystem, or biome. Foundation species often have the highest relative abundance of species. For more on species richness, see The Value of Biodiversity.

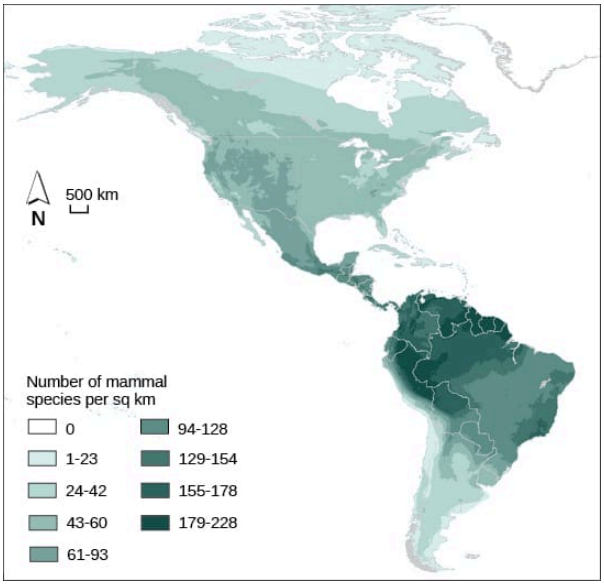


Figure 5.2.4.1: The greatest species richness for mammals in North and South America is associated with the equatorial latitudes. The highest number of mammal species, 179-228 per square kilometer, occurs in the Amazon region of South America. Species richness is generally highest in tropical latitudes, and then decreases to the north and south, with zero species in the Arctic regions. (credit: modification of work by NASA, CIESIN, Columbia University)

Keystone Species

A **keystone species** is one whose presence is key to maintaining biodiversity within an ecosystem and to upholding an ecological community's structure. A keystone species has a disproportionate impact on the overall ecosystem, meaning that even a small number of individuals can cause large scale changes. The intertidal sea star, *Pisaster ochraceus*, of the northwestern United States is a keystone species (Figure 5.2.4.2). Studies have shown that when this organism is removed from communities,

populations of their natural prey (mussels) increase. The increase in mussel results in a decrease in algae, wihch completely alters species composition and reduces biodiversity. Another keystone species is the banded tetra, a fish in tropical streams, which supplies nearly all of the phosphorus, a necessary inorganic nutrient, to the rest of the community. If these fish were to become extinct, the community would be greatly affected.



Figure 5.2.4.2: The Pisaster ochraceus sea star is a keystone species. (credit: Jerry Kirkhart)

Invasive Species

Invasive species are exotic or non-native organisms that, when introduced to an area out of their native range, threaten the ecosystem balance of that habitat. They often increase in numbers and decrease the native species composition. Thus, they have a significant impact on the community. For example, pampas grass (*Cortaderia selloana)*, a beloved ornamental found throughout the United States, is actually an invasive species native to South America. Pampas grass is fast growing and each plume produces up to 100,000 seeds. Seeds are wind dispersed and colonize quickly, particularly on disturbed ground. Leaves on this plant have sharp blades and can be harmful to birds. The native community in areas with invasive species often have less biodiversity because many native species in the area are eradicated by the presence of the invasive species. For more on invasive species, see 21.2: Threats to Biodiversity.



Figure 5.2.4.3: Pampas grass inflorescences. (credit: Jerry Kirkhart Wikipedia, licensed CC-BY-SA)

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5.2.5: Succession

Learning Objective

Describe community structure and succession

Community Dynamics

Community dynamics are the changes in community structure and composition over time, often following environmental disturbances such as volcanoes, earthquakes, storms, fires, and climate change. Communities with a relatively constant number of species are said to be at equilibrium. The equilibrium is dynamic with species identities and relationships changing over time, but maintaining relatively constant numbers. Following a disturbance, the community may or may not return to the equilibrium state.

Succession describes the sequential appearance and disappearance of species in a community over time after a severe disturbance. In primary succession, newly exposed or newly formed rock is colonized by living organisms. In **secondary succession**, a part of an ecosystem is disturbed and remnants of the previous community remain. In both cases, there is a sequential change in species until a more or less permanent community develops.

Primary Succession and Pioneer Species

Primary succession occurs when new land is formed, or when the soil and all life is removed from pre-existing land. An example of the former is the eruption of volcanoes on the Big Island of Hawaii, which results in lava that flows into the ocean and continually forms new land. From this process, approximately 32 acres of land are added to the Big Island each year. An example of pre-existing soil being removed is through the activity of glaciers. The massive weight of the glacier scours the landscape down to the bedrock as the glacier moves. This removes any original soil and leaves exposed rock once the glacier melts and retreats.

In both cases, the ecosystem starts with bare rock that is devoid of life. New soil is slowly formed as weathering and other natural forces break down the rock and lead to the establishment of hearty organisms, such as lichens and some plants, which are collectively known as **pioneer species** (Figure \(\PageIndex{1}\) because they are the first to appear. These species help to further break down the mineral-rich rock into soil where other, less hardy but more competitive species, such as grasses, shrubs, and trees, will grow and eventually replace the pioneer species. Over time the area will reach an equilibrium state, with a set of organisms quite different from the pioneer species.



Figure 5.2.5.1: During primary succession in lava on Maui, Hawaii, succulent plants are the pioneer species. (credit: Forest and Kim Starr)

Secondary Succession

A classic example of secondary succession occurs in forests cleared by wildfire, or by clearcut logging (figure 2.2.2.c2.2.2.c). Wildfires will burn most vegetation, and unless the animals can flee the area, they are killed. Their nutrients, however, are returned to the ground in the form of ash. Thus, although the community has been dramatically altered, there is a soil ecosystem present that provides a foundation for rapid recolonization.

Before the fire, the vegetation was dominated by tall trees with access to the major plant energy resource: sunlight. Their height gave them access to sunlight while also shading the ground and other low-lying species. After the fire, though, these trees are no longer dominant. Thus, the first plants to grow back are usually annual plants followed within a few years by quickly growing and spreading grasses and other pioneer species. Due, at least in part, to changes in the environment brought on by the growth of grasses and forbs, over many years, shrubs emerge along with small trees. These organisms are called intermediate species. Eventually, over 150 years or more, the forest will reach its equilibrium point and resemble the community before the fire. This equilibrium state is referred to as the **climax community**, which will remain until the next disturbance. The climax community is typically characteristic of a given climate and geology. Although the community in equilibrium looks the same once it is attained, the equilibrium is a dynamic one with constant changes in abundance and sometimes species identities.

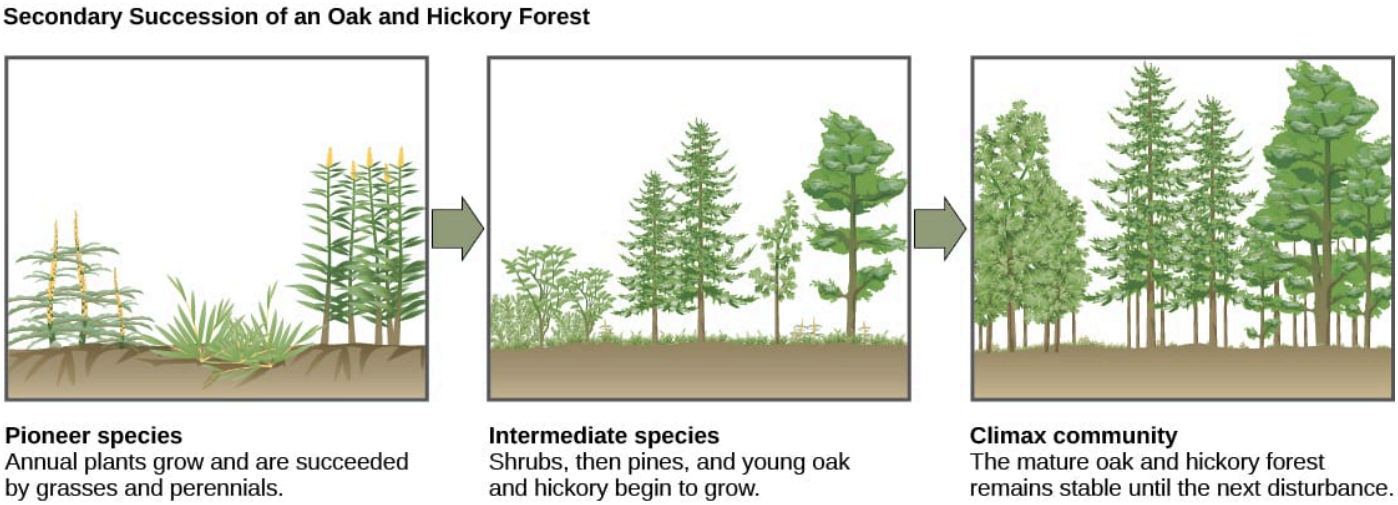


Figure 5.2.5.2: Secondary succession is shown in an oak and hickory forest after a forest fire. The first illustration shows a plot of land covered with pioneer species, including grasses and perennials. The second illustration shows the same plot of land later covered with intermediate species, including shrubs, pines, oak, and hickory. The third illustration shows the plot of land covered with a climax community of mature oak and hickory. This community remains stable until the next disturbance.

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5.2.6: Ecosystem

Learning Objective

Describe the difference between a community and an ecosystem

Communities are composed of living organisms and their interactions with one another and include **biotic** (living) components. **Ecosystems** are communities that include the **abiotic** (non-living) components of the environment as well (Video 5.2.6.1). These abiotic factors include temperature, amount of rainfall, sunlight, organic material and mineral nutrients, topography and attitude. Ecosystems can be small, such as the tide pools found near the rocky shores of many oceans, or large, such as the Amazon Rainforest in Brazil (Figure 5.2.6.1). Energy flow and nutrient cycling are some of topics central to the study of ecosystems.



(a) (b)

Figure 5.2.6.1: (a) tidal pool ecosystem in Matinicus Island in Maine is a small ecosystem, while the (b) Amazon Rainforest in Brazil is a large ecosystem. (credit a: modification of work by "takomabibelot"/Flickr; credit b: modification of work by Ivan Mlinaric)

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5.2.7: Energy and Energy Flow

Learning Objectives

- Describe how organisms acquire energy in a food web and in associated food chains
- Explain how the efficiency of energy transfers between trophic levels affects ecosystem structure and dynamics

Trophic interactions in a community can be represented by diagrams called **food chains** and **food webs**. Before discussing these representations in detail, we must first review the basics of energy. Energy flows through a community as a result of trophic interactions.

Energy

Virtually every task performed by living organisms requires energy. In general, **energy** is defined as the ability to do work, or to create some kind of change. Energy exists in different forms. Examples include light energy, kinetic energy, heat energy, potential energy, and chemical energy.

When an object is in motion, there is energy associated with that object. Think of a wrecking ball. Even a slow-moving wrecking ball can do a great deal of damage to other objects. Energy associated with objects in motion is called **kinetic energy**. **Heat energy** is the energy of motion in **matter** (anything that takes up space and has mass) and is considered a type of kinetic energy. The warmer the substance, the faster its molecules are moving. The rapid movement of molecules in the air, a speeding bullet, and a walking person all have kinetic energy. Now what if that same motionless wrecking ball is lifted two stories above ground with a crane? If the suspended wrecking ball is not moving, is there energy associated with it? The answer is yes. The energy that was required to lift the wrecking ball did not disappear, but is now stored in the wrecking ball by virtue of its position and the force of gravity acting on it. This type of energy is called **potential energy**. If the ball were to fall, the potential energy would be transformed into kinetic energy until all of the potential energy was exhausted when the ball rested on the ground. Wrecking balls also swing like a pendulum; through the swing, there is a constant change of potential energy (highest at the top of the swing) to kinetic energy (highest at the bottom of the swing). Other examples of potential energy include the energy of water held behind a dam or a person about to skydive out of an airplane (Figure 5.2.7.1.



Figure 5.2.7.1**:** Still water has potential energy; moving water, such as in a waterfall or a rapidly flowing river, has kinetic energy. (credit “dam”: modification of work by “Pascal”/Flickr; credit “waterfall”: modification of work by Frank Gualtieri)

Potential energy is not only associated with the location of matter, but also with the structure of matter. On a molecular level, there is potential energy stored within the bonds holding together the atoms in the food molecules we eat. The type of potential energy that exists within chemical bonds, and is released when those bonds are broken, is called **chemical energy**. Chemical energy is responsible for providing living cells with energy from food.

To appreciate the way energy flows into and out of biological systems, it is important to understand two of the physical laws

that govern energy. The **first law of thermodynamics** states that the total amount of energy in the universe is constant and conserved. In other words, there has always been, and always will be, exactly the same amount of energy in the universe. Energy exists in many different forms. According to the first law of thermodynamics, energy may be transferred from place to place or transformed into different forms, but it cannot be created or destroyed. The transfers and transformations of energy take place around us all the time. Light bulbs transform electrical energy into light and heat energy. Gas stoves transform chemical energy from natural gas into heat energy. Plants perform one of the most biologically useful energy transformations on earth: that of converting the energy of sunlight to chemical energy stored within biological molecules, such as sugars (Figure 5.2.7.2.

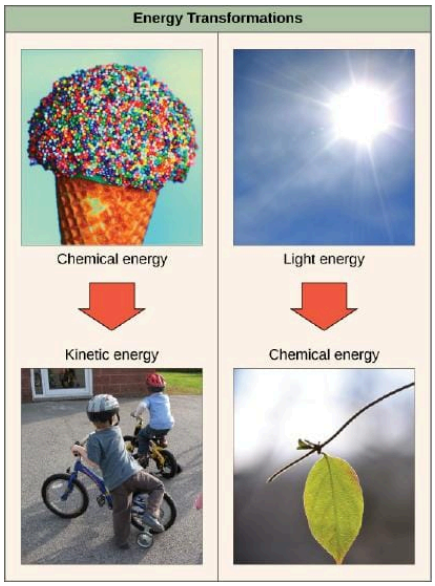


Figure 5.2.7.2: Shown are some examples of energy transferred and transformed from one system to another and from one form to another. The food we consume, represented by the ice cream cone, provides our cells with the chemical energy required to carry out bodily functions. This can be converted into kinetic energy (the energy of motion), which would be needed to ride a bike. Leaves conduct photosynthesis, converting light energy from the sun to chemical energy. (credit “ice cream”: modification of work by D. Sharon Pruitt; credit “kids”: modification of work by Max from Providence; credit “leaf”: modification of work by Cory Zanker)

The challenge for all living organisms is to obtain energy from their surroundings in forms that are usable to perform cellular work. A living cell’s primary tasks of obtaining, transforming, and using energy to do work may seem simple. However, the **second law of thermodynamics** explains why these tasks are harder than they appear. All energy transfers and transformations are never completely efficient. In every energy transfer, some amount of energy is lost in a form that is unusable. In most cases, this form is heat energy. For example, when a light bulb is turned on, some of the energy being converted from electrical energy into light energy is lost as heat energy. Likewise, some energy is lost as heat energy during the metabolic reactions that occur in organisms.

The concept of order and disorder relates to the second law of thermodynamics. The more energy that is lost by a system to its surroundings, the less ordered and more random the system is. Scientists refer to the measure of randomness or disorder within a system as **entropy**. High entropy means high disorder and low energy. Living things are highly ordered, requiring constant energy input to be maintained in a state of low entropy.

Energy Flow

Cells run on the chemical energy found mainly in carbohydrate molecules, and the majority of these molecules are produced by one process: **photosynthesis**. Through photosynthesis, certain organisms convert solar energy (sunlight) into chemical energy, which is then used to build carbohydrate molecules. The energy that is harnessed from photosynthesis enters the communities continuously and is transferred from one organism to another. Therefore, directly or indirectly, the process of photosynthesis provides most of the energy required by living things on Earth.

Organisms that conduct photosynthesis (such as plants, algae, and some bacteria), and organisms that synthesize sugars through other means are called **producers**. Without these organisms, energy would not be available to other living organisms, and life would not be possible. **Consumers**, like animals, fungi, and various microorganisms depend on producers, either directly or indirectly. For example, a deer obtains energy by eating plants. A wolf eating a deer obtains energy that originally came from the plants eaten by that deer (Figure 5.2.7.3. Using this reasoning, all food eaten by humans can be traced back to producers

that carry out photosynthesis (Figure 5.2.7.4). Dead producers and consumers are eaten by **detritivores** (which ingest on dead tissues) and **decomposers** (which further break down these tissues into simple molecules by secreting digestive enzymes). Invertebrate animals, such as worms and millipedes, are examples of detritivores, whereas fungi and certain bacteria are examples decomposers.



Figure 5.2.7.3**:** The energy stored in carbohydrate molecules from photosynthesis passes through the food chain. The predator that eats these deer is getting energy that originated in the photosynthetic vegetation that the deer consumed. (credit: Steve VanRiper, U.S. Fish and Wildlife Service)

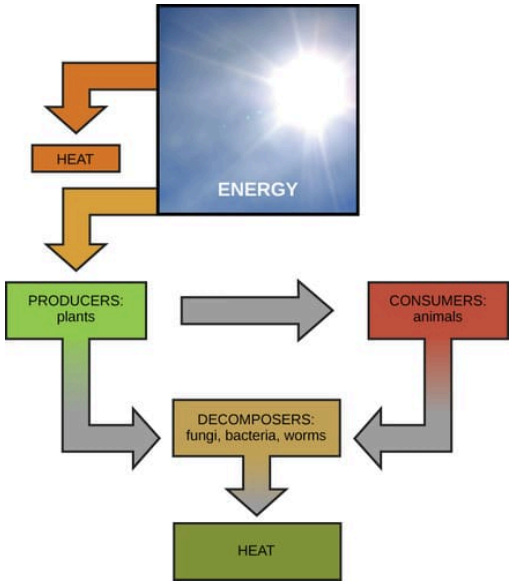


Figure 5.2.7.4: Ultimately, most life forms get their energy from the sun. This flow chart shows energy from the sun being captured by producers, such as plants, through photosynthesis. The energy is transferred to the consumers of the producers, such as animals. Energy can be obtained from producers directly (herbivores eat plants) or indirectly (carnivores eat herbivores). Decomposers eventually breakdown of dead organisms, including plant and animal material, and contribute to the nutrient pool. Fungi and bacteria are decomposers, and worms are detritivores (not shown).

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5.2.8: Food Chains and Food Webs

Learning Objectives

- Compare and contrast betrween a food chain and a food webs
- Describe energy transfer efficiency as it relates to trophic levels

Food Chains

A **food chain** is a linear sequence of organisms through which nutrients and energy pass as one organism eats another. Each organism in a food chain occupies a specific **trophic level** (energy level), its position in the food chain. The first trophic level in the food chain is the producers. The **primary consumers** (the herbivores the eat producers) are the second trophic level. Next are higher-level consumers. Higher-level consumers include **secondary consumers** (third trophic level), which are usually carnivores that eat the primary consumers, and **tertiary consumers** (fourth trophic level), which are carnivores that eat other carnivores. Higher-level consumers feed on the next lower tropic levels, and so on, up to the organisms at the top of the food chain: the **apex consumers**. In the Lake Ontario food chain shown in Figure 5.2.8.1, the Chinook salmon is the apex consumer at the top of this food chain.

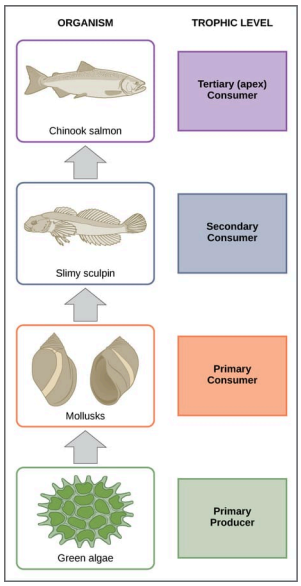


Figure 5.2.8.1: These are the trophic levels of a food chain in Lake Ontario at the United States-Canada border. Trophic levels with green algae as the primary producer, mollusks and snails are the primary consumers, and small fish (Slimy Sculpin) are the secondary consumers. The tertiary and apex consumer is Chinook salmon.

One major factor that limits the number of steps in a food chain is energy. Much of the energy from one tropic level to the next is lost as heat, due to the second law of thermodynamics. Only about 10% of the energy transfers from one trophic level to the next trophic level. Thus, after several transfers, the amount of energy remaining in the food chain may not be great enough to support viable populations at yet a higher trophic level.

Food Webs

While food chains are simple and easy to analyze, there is a one problem when using food chains to describe most communities. Even when all organisms are grouped into appropriate trophic levels, some of these organisms can feed at more than one trophic level. In addition, species feed on and are eaten by more than one species. In other words, the linear model of trophic interactions, the food chain, is a hypothetical and overly simplistic representation of community structure. A holistic model—which

includes all the interactions between different species and their complex interconnected relationships with each other and with the environment—is a more accurate and descriptive model. A **food web** is a concept that accounts for the multiple trophic interactions between each species (Figure 5.2.8.2).

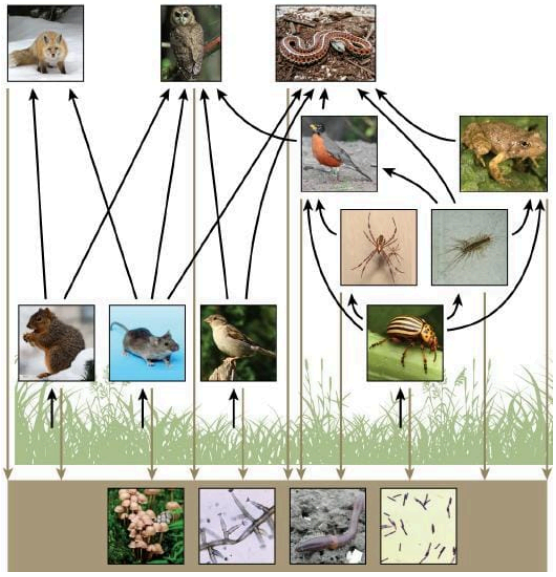


Figure 5.2.8.2 This food web shows the interactions between organisms across trophic levels. Arrows point from an organism that is consumed to the organism that consumes it. All the producers and consumers eventually become nourishment for the decomposers (fungi, mold, earthworms, and bacteria in the soil). (credit "fox": modification of work by Kevin Bacher, NPS; credit "owl": modification of work by John and Karen Hollingsworth, USFWS; credit "snake": modification of work by Steve Jurvetson; credit "robin": modification of work by Alan Vernon; credit "frog": modification of work by Alessandro Catenazzi; credit "spider": modification of work by "Sanba38"/Wikimedia Commons; credit "centipede": modification of work by “Bauerph”/Wikimedia Commons; credit "squirrel": modification of work by Dawn Huczek; credit "mouse": modification of work by NIGMS, NIH; credit "sparrow": modification of work by David Friel; credit "beetle": modification of work by Scott Bauer, USDA Agricultural Research Service; credit "mushrooms": modification of work by Chris Wee; credit "mold": modification of work by Dr. Lucille Georg, CDC; credit "earthworm": modification of work by Rob Hille; credit "bacteria": modification of work by Don Stalons, CDC)

Community Productivity and Transfer Efficiency

The rate at which photosynthetic producers incorporate energy from the sun is called **gross primary productivity**. In a cattail marsh, plants only trap 2.2% of the energy from the sun that reaches them. Three percent of the energy is reflected, and another 94.8% is used to heat and evaporate water within and surrounding the plant. However, not all of the energy incorporated by producers is available to the other organisms in the food web because producers must also grow and reproduce, which consumes energy. At least half of the 2.2% trapped by cattail marsh plants is used to meet the plants own energy needs.

Net primary productivity is the energy that remains in the producers after accounting for the metabolic needs of the producers and heat loss. The net productivity is then available to the primary consumers at the next trophic level. One way to measure net primary productivity is to collect and weigh the plant material produced on a m^2 (about 10.7 ft^2) of land over a given interval. One gram of plant material (e.g., stems and leaves), which is largely carbohydrate, yields about 4.25 kcal of energy when burned. Net primary productivity can range from 500 kcal/m^2/yr in the desert to 15,000 kcal/m^2/yr in a tropical rain forest.

In an aquatic community in Silver Springs, Florida, the gross primary productivity (total energy accumulated by the primary producers) was 20,810 kcal/m^2/yr (Figure 5.2.8.3). The net primary productivity (energy available to consumers) was only 7,632 kcal/m^2/yr after accounting for energy lost as heat and energy require to meet the producer's metabolic needs.

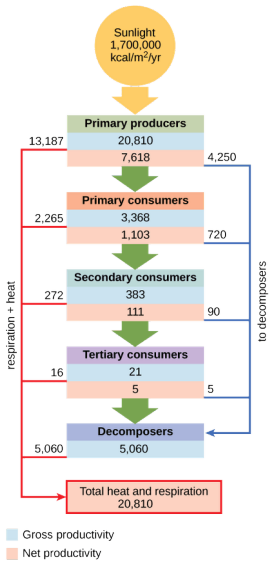


Figure 5.2.8.3**:** The flow of energy through a spring ecosystem in Silver Springs, Florida. Notice that the energy decreases with each increase in trophic level. The energy content of primary producers (gross productivity) is 20,810 kcal/m^2/yr. The gross productivity of primary consumers is much smaller, about 3,368 kcal/m^2/yr. The gross productivity of secondary consumers is 383 kcal/m^2/yr, and the gross productivity of tertiary consumers is only 21 kcal/m^2/yr. The net productivity of each trophic level is less than the gross productivity because some energy is used to meet metabolic needs (respiration), and some energy is lost as heat. For example, the net productivity of primary consumers was 1,103 kcal/m^2/yr, only about a third of the gross productivity.

Only a fraction of the energy captured by one trophic level is assimilated into biomass, which makes it available to the next trophic level. Assimilation is the biomass of the present trophic level after accounting for the energy lost due to incomplete ingestion of food, energy used to conduct work by that trophic level, and energy lost as waste. Incomplete ingestion refers to the fact that some consumers eat only a part of their food. For example, when a lion kills an antelope, it will eat everything except the hide and bones. The lion is missing the energy-rich bone marrow inside the bone, so the lion does not make use of all the calories its prey could provide. In Silver Springs, only 1103 kcal/m^2/yr from the 7618 kcal/m^2/yr of energy available to primary consumers was assimilated into their biomass. (The **trophic level transfer efficiency** between the first two trophic levels was approximately 14.8 percent.)

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5.2.9: Chapter Summary

Communities include all the different species living in a given area. Biotic interactions refer to the relationships among organisms. Competition occurs when organisms at the same trophic level use the the same resources, and one or both organisms is harmed. Many organisms have developed defenses against predation and herbivory, including mechanical defenses, warning coloration, and mimicry, as a result of evolution and the interaction with other members of the community. Two species cannot exist in the same habitat competing directly for the same resources. Species may form symbiotic relationships such as commensalism or mutualism. Community structure is described by its foundation and keystone species. Communities respond to environmental disturbances by succession (the predictable appearance of different types of plant species) until a stable community structure is established. The variety of these species is called species richness. Relative abundance is the number of individuals in a species relative to the total number of individuals in all species within a habitat, ecosystem, or biome. In communities, some species play a bigger role than others. keystone species impact the biodiversity within an ecosystem by upholding an ecological community's structure. Invasive species have an overall negative impact on the community. Community dynamics are the changes in community structure and composition over time. Succession describes the sequential appearance and disappearance of species in a community over time after a severe disturbance.

Ecosystems are communities that include the abiotic components of the environment as well. Energy is defined as the ability to do work, or to create some kind of change. Two of the physical laws that govern energy are the first and second law of thermodynamics. Energy flows from producers to consumers and recycled by detritivores and decomposers. Trophic interactions in a community can be represented by diagrams called food chains and food webs. Organisms in an ecosystem acquire energy in a variety of ways, which is transferred between trophic levels as the energy flows from the bottom to the top of the food web, with energy being lost at each transfer. Modeling of ecosystem energy is best done with ecological pyramids of energy, although other ecological pyramids provide other vital information about ecosystem structure.

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

- Describe the differences between intraspecific and interspecific interactions in reference to competition
- Describe what is herbivory
- Give examples of defenses against predation and herbivory
- Describe what is considered a symbiotic relationships between species
- Compare and contrast between commensalism, mutualism, and parasitism
- Describe symbiosis as it relates to nitrogen fixation
- Describe how saprophytes, epiphytes, and carnivorous plants depend on other orgnanisms
- Describe how species richness and relative abundance play a role on biodiversity
- Describe the role of keystone species in a community
- Describe the role of invasive species in a community
- Describe community structure and succession
- Describe the difference between a community and an ecosystem
- Describe how organisms acquire energy in a food web and in associated food chains
- Explain how the efficiency of energy transfers between trophic levels affects ecosystem structure and dynamics
- Compare and contrast betrween a food chain and a food webs
- Describe energy transfer efficiency as it relates to trophic levels

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5.3: CONSERVATION

Roughly 1.5 million species have been identified, and this is just a fraction of all the species on Earth. These species exist in a variety of ecosystems. Genetic differences among individuals within a species further contributes to the variety of life on Earth. While this **biodiversity** provides many benefits to humans, such providing food and building materials, recreational activities, and clean air and water, human population group and resource use threatens many species and ecosystems. **Conservation biology** is concerned with protecting biodiversity, which ultimately supports humans by promoting ecosystem function (Figure 5.3.1).



Figure 5.3.1: Fritillaria roderickii is an endangered plant that is **endemic** to California, meaning that it only occurs there. Protecting populations of rare plant species such as this is one component of conservation. Photo by Clare Golec/CDFW (public domain).

5.3.1: The Value of Biodiversity

5.3.2: Threats to Biodiversity

5.3.3: Preserving Biodiversity

5.3.4: Chapter Summary

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Image thumbnail: Maikal Hills in Kabirdham District, Chhattisgarh, India. The traditional healers take advantage of this rich biodiversity zone and use medicinal species in treatment of complicated diseases like different types of cancer, sickle cell anemia, etc. Image and caption (edited) by Pankaj Oudhia (CC-BY-SA).

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5.3.1: The Value of Biodiversity

Learning Objectives

- Define biodiversity.
- Distinguish among ecosystem, species, and genetic diversity, explaining the value of each.
- Define and provide examples of ecosystem services.
- Distinguish between species richness and species evenness.
- Explain the importance of biodiversity hotspots and identify the characteristics of endemic species.

Biodiversity is a broad term for the variety of life on Earth. Traditionally, ecologists have measured biodiversity by taking into account both the number of species and the number of individuals of each species. However, biologists now measure biodiversity at a number of organizational levels, including ecosystem, species, and genetic diversity. This focuses efforts to preserve the biologically and technologically important elements of biodiversity. Biodiversity is important to the survival and welfare of human populations because it has impacts on our health and our ability to feed ourselves through agriculture and harvesting populations of wild animals.

Ecosystem Diversity

Measuring biodiversity on a large scale involves measuring **ecosystem diversity**, the number of different ecosystems on Earth or in a geographical area as well as their relative abundances (Figure 5.3.1.1). The loss of an ecosystem means the loss of the interactions between species and the loss of biological productivity that an ecosystem is able to create. An example of a largely extinct ecosystem in North America is the prairie ecosystem (Figure 5.3.1.1). Prairies once spanned central North America from the boreal forest in northern Canada down into Mexico. They are now all but gone, replaced by crop fields, pasture lands, and suburban sprawl. Many of the species survive, but the hugely productive ecosystem that was responsible for creating our most productive agricultural soils is now gone. As a consequence, their soils are now being depleted unless they are maintained artificially at great expense.



Figure 5.3.1.1: The variety of ecosystems on Earth—from the tropical rainforest (top) to prairie (bottom)—enables a great diversity of species to exist. Top image by Frank Vassen. Bottom image modified from Jim Minnerath, USFWS.

The soil productivity described above is an example of an **ecosystem service**. These are the products and processes associated with biological systems are directly or indirectly of immense value to the well-being of people. Some ecosystem services are processes such as the regulation of climate, flooding, and disease. Nutrient cycling, pollination, and regulation of crop pests are

ecosystem services important to food production. A 2002 study by Claire Kremen and colleagues found that **native** pollinators in Central California (those that historically occurred there; Figure 5.3.1.2) provided full pollination to watermelon crops (Figure 5.3.1.3). This was only true on organic farms that were located near the natural habitat for these pollinators, highlighting the importance of sustainable farming practices and habitat conservation in preserving ecosystem services. The water cycle provides fresh water, and photosynthesis adds oxygen to our air. Other ecosystem services are human provisions including food, fuel, and fiber (such as cotton for clothing or timber). Medicines are another important provision (see Species Diversity). Furthermore, healthy ecosystems allow for recreational activities, such as hiking, kayaking, and camping, and educational opportunities, such as field trips. Nature is also the basis for a significant part of aesthetic and spiritual values held by many cultures.



Figure 5.3.1.2 and Figure 5.3.1.3: Figure 5.3.1.2 (left) The California bumble bee (*Bombus californicus*) is one of several native insects that provided watermelon pollination in Kremen and colleagues' study. Image by Rhododendrites (CC-BY-SA). Figure 5.3.1.3 (right) Watermelon flowers require multiple visits by bee pollinators to set fruits. Image by Sltan (CC-BY-SA).

In 1997, Robert Costanza and his colleagues estimated to annual value of ecosystem services to be $33 trillion dollars ($53 trillion in 2019 dollars), and many consider this to be an underestimation. For comparison the gross domestic product of the United States in 2020 was $21 trillion.

Species Diversity

Species diversity includes species richness and species evenness. **Species richness**, the number of species living in a habitat or other unit, is one component of biodiversity. Species richness varies across the globe. **Species evenness** is a component of species diversity based on **relative abundance** (the number individuals in a species relative to the total number of individuals in all species within a system). The area in question could be a habitat, a biome, or the entire biosphere. Areas with low species diversity, such as the glaciers of Antarctica, still contain a wide variety of living organisms, whereas the diversity of tropical rainforests is so great that it cannot be accurately assessed.

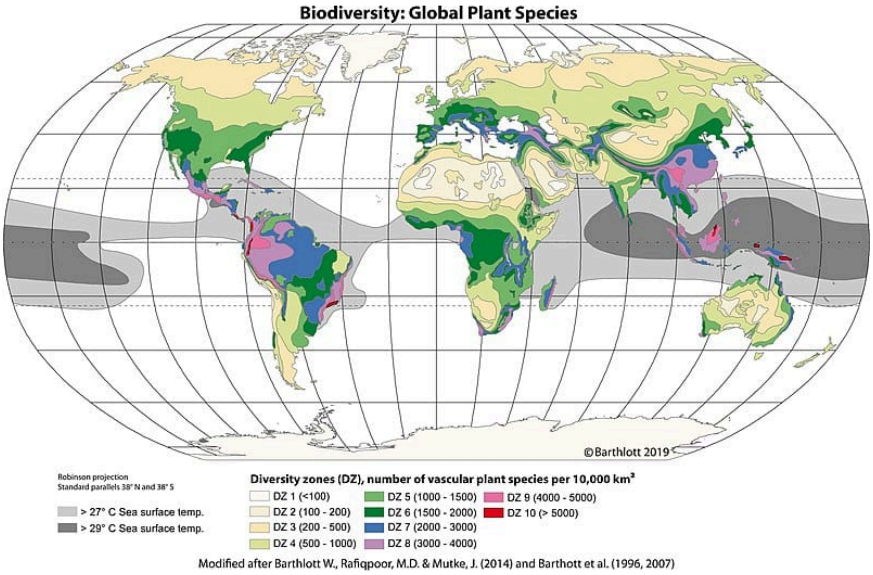


Figure 5.3.1.4: Global distribution of vascular plant species richness. Tropical regions have high species richness, with some tropical regions having more than 5000 species per 10,000 km^2. Temperate regions have intermediate species richness, ranging from 1000-4000 species per 10,000 km^2. Species richness further declines towards the poles. Image by Lotus Salvinia (CC-BY-SA).

Species richness is related to latitude: the greatest species richness occurs near the equator and the lowest richness occurs near the poles (Figure 5.3.1.4). Several hypothesis might explain this dyanamic, but the exact reasons for this pattern are still not clearly understood. One hypothesis is that tropical forests have consistently existed at the same location for a long period of time, allowing more time for speciation to occur. Another hypothesis is that speciation rate is simply higher in the tropics than other regions. The tropics also has a long growing season and a wide variety of ecological niches (different roles that species can occupy), partly due to the different vertical layers in a tropical forest (Video 5.3.1.1). Other factors besides latitude influence species richness as well. For example, ecologists studying islands found that biodiversity varies with island size and distance from the mainland.

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 5.3.1.1: This video discusses possible explanations for why species richness is high at the equator.

In 1988, British environmentalist Norman Myers developed a conservation concept to identify geographical areas rich in species and at significant risk for species loss: **biodiversity hotspots**. The original criteria for a hotspot included the presence of 1500 or more endemic plant species and 70 percent of the area disturbed by human activity. **Endemic species** are found in only one location. For example, giant lobelia (*Lobelia rhynchopetalum,* Figure 5.3.1.5) is only found in the alpine habitats in Ethiopia. Endemic species with highly restricted distributions are particularly vulnerable to extinction. If a population of a widespread species declines in one region, individuals from another region may be able to recolonize the first location, but this is not possible for endemic species. Endemic species are particularly common in isolated regions, such as mountaintops or islands. Identifying biodiversity hotspots aids with conservation efforts, a kind of conservation triage. By protecting hotspots, governments are able to protect a larger number of species. There are now 34 biodiversity hotspots (Figure 5.3.1.6) containing large numbers of endemic species, which include half of Earth's endemic plants.



Figure 5.3.1.5: Giant lobelia (*Lobelia rhynchopetalum*) in the Simien Mountains National Park, Ethiopia. Image by Bernard Gagnon (CC-BY-SA).

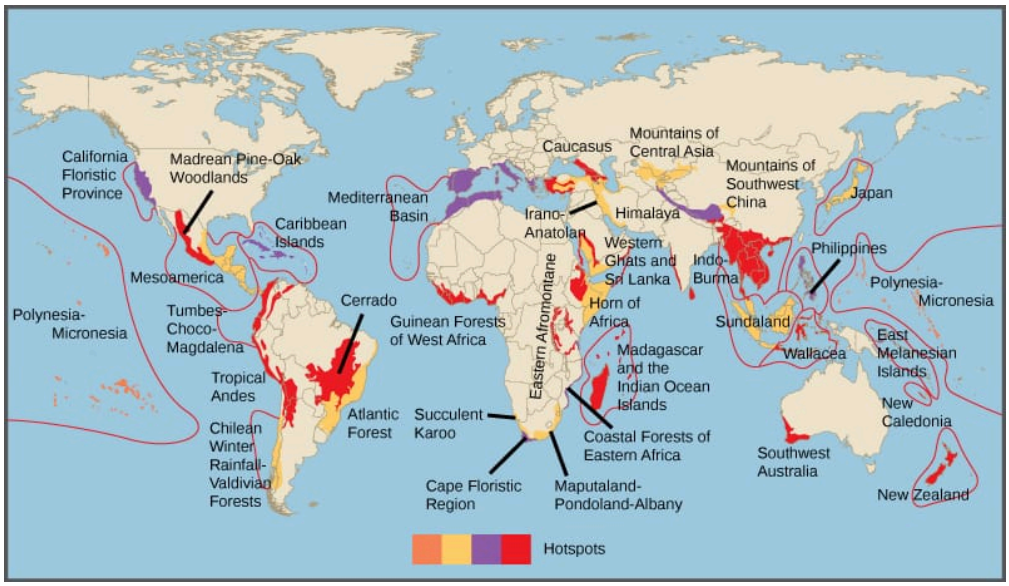


Figure 5.3.1.6: Conservation International has identified 34 biodiversity hotspots, which cover only 2.3 percent of the Earth's surface but have endemic to them 42 percent of the terrestrial vertebrate species and 50 percent of the world's plants. Hotspots are shaded in red, purple, yellow, or orange. Examples include the California Floristic Province, Tropical Andes, Mediterranean Basic, Cape Floristic Province, and Polynesia-Micronesia.

Regarding species evenness, foundation species often have the highest relative abundance of species. Two locations with the same richness do not necessarily have the same species evenness. For example, both communities in Figure 5.3.1.7 have three different trees species and thus a species richness of three. However, there is a dominant species (represented by six individuals) in community #1. In community #2, there are three of individuals of each species. Therefore, community #2 has a greater species evenness and greater species diversity overall.



Figure 5.3.1.7: Two hypothetical tree communities have the same species richness, but community #2 (bottom) has a greater species evenness. Both communities have nine trees and three tree species. In community #1, one species is dominant, represented by six individuals. There are two individuals of a conifer species, and only one individual of the final species. In community #2, there are three individuals from each species. Images compiled by Melissa Ha from Alone tree George Hodan, Old Tree Silhouette, and Tree (all public domain).

Healthy ecosystems contain a diversity of species, and each species plays a role in ecosystem function; therefore, species diversity as well as ecosystem diversity are essential to maintaining ecosystem services. For example, many medications are derived from natural chemicals made by a diverse group of organisms. For example, many plants produce compounds meant to protect the plant from insects and other animals that eat them. Some of these compounds also work as human medicines. Examples of significant medicines derived from plant compounds include aspirin, codeine, digoxin, atropine, and vincristine (Figure 5.3.1.8). It is estimated that, at one time, 25 percent of modern drugs contained at least one plant extract. That number has probably decreased to about 10 percent as natural plant ingredients are replaced by synthetic versions of the plant compounds. Antibiotics, which are responsible for extraordinary improvements in health and lifespans in developed countries, are compounds largely derived from fungi and bacteria. It is estimated that about 35 percent of new drugs brought to market between 1981 and 2002 were from natural compounds.



Figure 5.3.1.8: Catharanthus roseus, the Madagascar periwinkle, has various medicinal properties. Among other uses, it is a source of vincristine, a drug used in the treatment of lymphomas. (credit: Forest and Kim Starr)

Genetic Diversity

Genetic diversity is a measure of the variability among individuals within a single species. Genetic diversity is represented by the variety of **alleles** present within a population. Genetic diversity provides the raw material for **evolutionary adaptation.** Loss of genetic diversity makes a species less able to reproduce successfully and less adaptable to a changing environment or to a new disease. Small populations of species are especially susceptible to loss of genetic diversity. When a species loses too many individuals, it becomes genetically uniform. Some of the causes for the loss in genetic diversity include: **inbreeding** among closely related individuals and **genetic drift**, the process by which the genetic composition of a population fluctuates randomly over time. Genetic drift can lead to the loss of alleles from a population, even if those alleles are adaptive. For more on genetic drift, see Openstax 2e 19.1.

Genetic diversity is important to agriculture. Since the beginning of human agriculture more than 10,000 years ago, human groups have been breeding and selecting crop varieties. This crop diversity matched the cultural diversity of highly subdivided populations of humans. For example, potatoes were domesticated beginning around 7,000 years ago in the central Andes of Peru and Bolivia. The people in this region traditionally lived in relatively isolated settlements separated by mountains. The potatoes grown in that region belong to seven species and the number of varieties likely is in the thousands. Each variety has been bred to thrive at particular elevations and soil and climate conditions. The diversity is driven by the diverse demands of the dramatic elevation changes, the limited movement of people, and the demands created by crop rotation for different varieties that will do well in different fields.



Figure 5.3.1.9: The effects of potato blight, which is cause by the water mold *Phytophthora infestans*. Image by USDA (public domain).

The potato demonstrates a well-known example of the risks of low crop diversity: during the tragic Irish potato famine (1845–1852 AD), the single potato variety grown in Ireland became susceptible to a potato blight—wiping out the crop (Figure 5.3.1.9). The loss of the crop led to famine, death, and mass emigration. Resistance to disease is a chief benefit to maintaining crop biodiversity and lack of diversity in contemporary crop species carries similar risks. Seed companies, which are the source of most crop varieties in developed countries, must continually breed new varieties to keep up with evolving pest organisms. These same seed companies, however, have participated in the decline of the number of varieties available as they focus on selling fewer varieties in more areas of the world replacing traditional local varieties.

The ability to create new crop varieties relies on the diversity of varieties available and the availability of wild forms related to the crop plant. These wild forms are often the source of new gene variants that can be bred with existing varieties to create varieties with new attributes. Loss of wild species related to a crop will mean the loss of potential in crop improvement. Maintaining the genetic diversity of wild species related to domesticated species ensures our continued supply of food.

Since the 1920s, government agriculture departments have maintained seed banks of crop varieties as a way to maintain crop diversity. This system has flaws because over time seed varieties are lost through accidents and there is no way to replace them. In 2008, the Svalbard Global seed Vault, located on Spitsbergen island, Norway (Figure 5.3.1.10), began storing seeds from around the world as a backup system to the regional seed banks. If a regional seed bank stores varieties in Svalbard, losses can be

replaced from Svalbard should something happen to the regional seeds. The Svalbard seed vault is deep into the rock of the Arctic island. Conditions within the vault are maintained at ideal temperature and humidity for seed survival, but the deep underground location of the vault in the arctic means that failure of the vault's systems will not compromise the climatic conditions inside the vault.



Figure 5.3.1.10: The Svalbard Global Seed Vault is a storage facility for seeds of Earth's diverse crops. (credit: Mari Tefre, Svalbard Global Seed Vault)

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5.3.2: Threats to Biodiversity

Learning Objectives

- Name, define, and provide examples of the five major threats to biodiversity.
- Provide examples of the successes and failures of biological control in regulating invasive species.

Biodiversity loss refers to the reduction of biodiversity due to displacement or extinction of species. According to a 2019 United Nations report, 1 million species at risk of extinction. Considering there are estimated to be 8-11 million species total, that means up to 12.5% of species could go extinct, and many of them within our lifetimes. This will have dramatic effects on human welfare through the loss of ecosystem services.

The core threat to biodiversity on the planet is the combination of human population growth and the resources used by that population. The global population size is 7.8 billion as of August 2020. Population size is continuing to increase, although the rate of population growth is decreasing. Some argue that humans have already surpassed our **carrying capacity**, meaning that the environment cannot sustain our large population size indefinitely.

The human population requires resources to survive and grow, and many of those resources are being removed unsustainably from the environment. The five main threats to biodiversity are habitat loss, pollution, overexploitation, invasive species, and climate change. Increased mobility and trade has resulted invasive species while the other threats are direct results of human population growth and resource use.

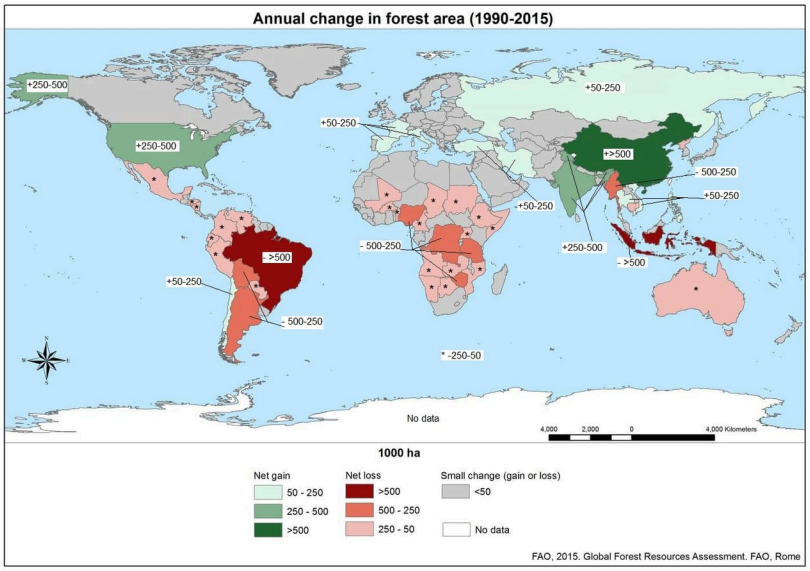


Figure 5.3.2.1: Average annual change in forest area globally from 2005 to 2015. China is dark green, indicating that have gained more than 500 "kilohectares" (kha) of forest. Medium green indicates countries that have gained 250-500 kha, including the the United States, India, Ghutan, and Bangladesh. Light green indicates countries that have gained 50-250 khA, including Chile, Spain, France, Italy, Turkey, Iran, Russia, Vietnam, and Thailand. Indonesia and Brazil lost more than 500 kha of forest (marked with dark red). Countries that lost 500-250 kha are marked with medium red, including Bolivia, Argentina, Nigeria, Democratic Republic of the Congo, Tanzania, Zimbabwe, and Myanmar. Countries that lost 250-50 kha are marked with light red and an asterisk (*). These include Mexico, Honduras, Nicaragua, Venezuela, Colombia, Ecuador, Peru, Paraguay, Mali, Burkina Faso, Benin, Cameroon, Chad, Sudan, Ethiopia, Somalia, Uganda, Angola, Namibia, Botswana, Zimbabwe, Mozambique, Cambodia, North Korea, and Australia. No data has been collected for Antarctica. All other regions have had lost or gained less than 50 kha in forest area. Image by FAO, 2015. Global Forest Resources Assessment. FAO. Rome (Open Access Policy).

Habitat Loss

Habitat loss includes habitat destruction and habitat fragmentation. **Habitat destruction** occurs when the physical environment

required by a species is altered so that the species can no longer live there. Human destruction of habitats accelerated in the latter half of the twentieth century. For example, half of Sumatra's forests, a biodiversity hotspot, is now gone. The neighboring island of Borneo has lost a similar area of forest, and forest loss continues in protected areas of Borneo. The forests are removed for timber and to plant palm oil plantations (Figure 5.3.2.1). Palm oil is used in many products including food products, cosmetics, and biodiesel in Europe. According to Global Forest Watch, 9.7% of tree cover was lost globally from 2002 to 2019, and 9% of that occurred in Indonesia and Malaysia (where Sumatra and Borneo are located). Figure 5.3.2.2 shows average annual change in forest area around the world from 1990 to 2015.

Habitat fragmentation occurs an the living space of a species is divided into discontinuous patches. For example, a mountain highway could divide a forest habitat into separate patches. **Wildlife corridors** mitigate the damage of habitat fragmentation by connecting patches with suitable habitat (Figure 5.3.2.2).



Figure 5.3.2.2: This overpass on the Trans-Canada Highway between Banff and Lake Louise, Alberta, serves as a wildlife corridor. Image by WikiPedant at Wikimedia Commons (CC-BY-SA).

Overexploitation

Overexploitation (overharvesting) involves hunting, fishing, or otherwise collecting organisms at a faster rate than they can be replenished. While overfishing and poaching are common examples of overexploitation, some fungi and slow-growing plant species are also overexploited. For example, stocks of wild ginseng, which is valued for its health benefits, are dwindling. Peyote cactus, which causes hallucinations and is used in sacred ceremonies, is also declining. Yarsagumba, dead moth larvae that were infected by fungal parasites (caterpillar fungus, *Ophiocordyceps sinensis*), is overexploited because it is highly valued in traditional medicine and used as an aphrodisiac (Figure 5.3.2.3).



Figure 5.3.2.3: Yarsagumba is a combination of moth larvae and the fungus that infected and killed it. Image by Punya (CC-BY-SA).

Pollution

Pollution occurs when chemicals, particles, or other materials are released into the environment, harming the organisms there. Pollution has contributed to the decline of many threatened species. For example, a 2007 study by Kingsford and colleagues found that pollution was a major pressure on 30% of threatened species in Australia and surrounding regions.

Power plants, factories, and vehicles are common sources of air pollution. In some cases, the pollutants are directly toxic (for example, lead), but in other cases the pollutants indirectly cause ecological harm when they are present in unnaturally large quantities (for example, carbon dioxide emissions leading to climate change). Not only can air pollutants directly harm animals by causing respiratory issues and cancer as well as damage vegetation, but some interact with the atmosphere to form **acid deposition** (commonly called acid rain). Acid deposition which disrupts aquatic ecosystems as well as soil communities and plant growth.

Heavy metals, plastics, pesticides, herbicides, fertilizers, and sediments are examples of water pollution. Heavy metals (including copper, lead, mercury, and zinc) can leach into soil and water from mines. Nutrients, such as nitrate and phosphates, are healthy in bodies of water to an extent, but when fertilizer pollution adds too many of these nutrients at one time, algal blooms can result. This has cascading effects that can ultimately shade and kill aquatic plants and deplete oxygen needed by fish and other animals (**eutrophication**, Figure 5.3.2.4). A particularly concerning water pollution problem is **micropollutants**. For examples, some chemical residues affect growth, cause birth defects, and have other toxic effects on humans and other organisms even at very low concentrations.



Figure 5.3.2.4: Eutrophication in Dianchi Lake, China. Increase in nutrients from fertilizer pollution led to an algal bloom, and oxygen was depleted from the water as the algae decomposed, killing fish. Image by Greenpeace China (CC-BY).

Invasive Species

Invasive species are **non-native** organisms that, when introduced to an area out of its native range, disrupt the community they invade. **Non-native** (exotic) refers to species occurring outside of their historic distribution. Invasive species are have been intentionally or unintentionally introduced by humans into an ecosystem in which they did not evolve. Human transportation of people and goods, including the intentional transport of organisms for trade, has dramatically increased the introduction of species into new ecosystems. These new introductions are sometimes at distances that are well beyond the capacity of the species to ever travel itself and outside the range of the species' natural predators. Invasive species can cause ecological and economic damage.

Invasive plants like the purple loosestrife (*Lythrum salicaria*) and kudzu (*Pueraria montana*) threaten native plants through competition for resources, and they drastically altered the ecosystems they invaded (Figure 5.3.2.5). They indirectly harms the animals that depend on native plants to be primary producers and to provide habitat. Some invasive plants, like yellow flag iris (*Iris pseudacorus*) are toxic, directly poisoning the livestock and wildlife that eat them. The awns projecting from cheat grass (*Bromus tectorum*) during seed dispersal irritate and injure cattle (Figure 5.3.2.6). Invasive insects and plant pathogens harm crops and native species. The emerald ash borer (*Agrilus planipennis*) has killed millions of ash trees in the eastern and midwestern United States and Canada. In spreads through movement of firewood and other wood products. *Xylella fastidiosa fastidiosa* is an invasive bacterium that is native to Central America that causes several diseases including Pierce's disease of grapes in California and the southeastern United States (Figure 5.3.2.7). It is spread through an invasive insect, the glassy-winged sharpshooter (Figure 5.3.2.7).




Figure 5.3.2.5 (right)and 5.3.2.6: Figure 5.3.2.6 (left) Purple loosestrife growing in New England. Image by liz west (CC-BY). Figure 5.3.2.6 (right) Cheat grass has long awns that can injure cattle who eat the mature plants. Image by Matt Lavin (CC-BY).

One reason why invasive species proliferate dramatically outside of their native range is due to **release from predators**. This means that parasites, predators, or herbivores that usually regulate their populations are not present, allowing them to outcompete or otherwise decimate native species, which are still regulated. Based on this principle, organisms that regulate the invasive species populations have been introduced the newly colonized areas in some cases. The release of organisms (or viruses) to limit population size is called **biological control**. As described the examples below, biological control of invasive species has had varying success, exacerbating the problem in some cases and solving it in others.



Figure 5.3.2.7: The glass-winged sharpshooter (*Homalodisca vitripennis*), which spreads the bacterial pathogen *Xylella fastidiosa fastidiosa* on a grape leaf. Image by USDA ARS Photo Unit (public domain).

Introduced into Australia, this cactus soon spread over millions of hectares of range land driving out forage plants. In 1924, the cactus moth, *Cactoblastis cactorum*, was introduced (from Argentina) into Australia. The caterpillars of the moth are voracious feeders on prickly-pear cactus, and within a few years, the caterpillars had reclaimed the range land without harming a single native species. However, its introduction into the Caribbean in 1957 did not produce such happy results. By 1989, the cactus moth had reached Florida, and now threatens five species of native cacti there.

In 1946 two species of *Chrysolina* beetles were introduced into California to control the Klamath weed (St. Johnswort, *Hypericum*

perforatum) that was ruining millions of acres of range land in California and the Pacific Northwest. Before their release, the beetles were carefully tested to make certain that they would not turn to valuable plants once they had eaten all the Klamath weed they could find. The beetles succeeded beautifully, restoring about 99% of the endangered range land and earning them a commemorative plaque at the Agricultural Center Building in Eureka, California.

To summarize the lessons learned from biological control successes and failures, only candidates that have a very narrow target preference (eat only a sharply-limited range of hosts) should be chosen. Each candidate should be carefully tested to be sure that once it has cleaned up the intended target, it does not turn to desirable species. Biological controls must not be used against native species. Finally, introduction of non-native species into the environment should be avoided because they could themselves be invasive.

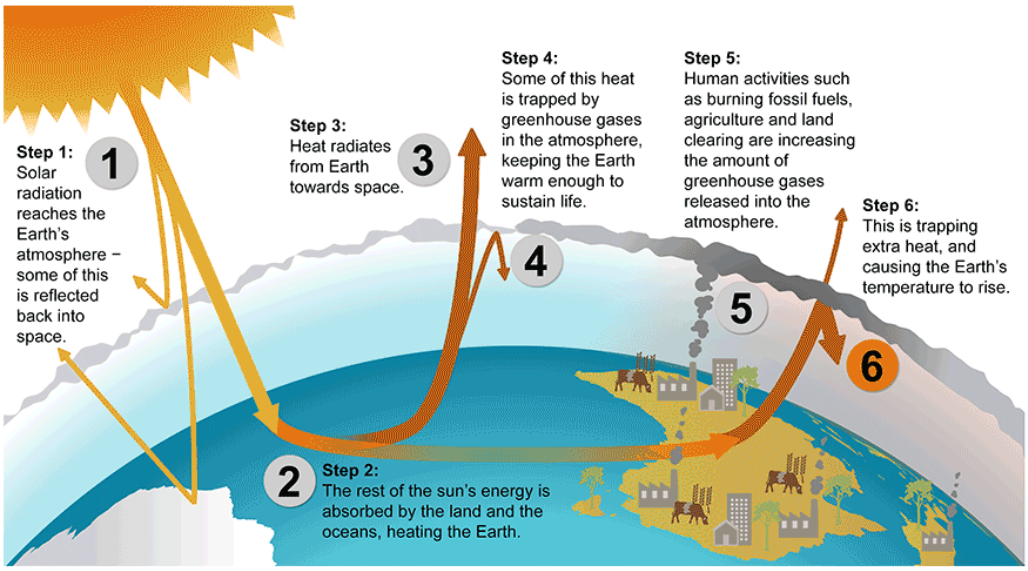


Figure 5.3.2.8: The enhanced greenhouse effect. Step 1: Some solar radiation reaches the Earth's surface, and some is reflected back into space. Step 2: The rest of the sun's energy is absorbed by the land and the oceans, heating the Earth. Step 3: Heat radiates from Earth towards space. Step 4: Some of the heat is trapped by greenhouse gases in the atmosphere, warming the Earth. Step 5: Human activities such as burning fossil fuels, agriculture, and land clearing have increased the concentrations of greenhouse gases in the atmosphere. Step 6: This is trapping extra heat, causing the Earth's temperature to rise.

Climate Change

Global **climate change** is also a consequence of human population needs for energy, and the use of fossil fuels to meet those needs. Essentially, burning **fossil fuels**, including as oil, natural gas, and coal, increases carbon dioxide concentrations in the atmosphere (see Nutrient Cycles for details about the carbon cycle). Carbon dioxide, methane, and other **greenhouse gases** trap heat energy from the sun, resulting not only in an average increase in global temperature but also in changing precipitation patterns and increased frequency and severity of extreme weather events, such as hurricanes (Figure 5.3.2.8). Scientists overwhelmingly agree the present warming trend is caused by humans.

Climate change is recognized as a major extinction threat, particularly when combined with other threats such as habitat loss. Scientists disagree about the likely magnitude of the effects, with extinction rate estimates ranging from 15 percent to 40 percent of species committed to extinction by 2050. By altering regional climates, it makes habitats less hospitable to the species living in them. While increased carbon dioxide levels can help plants conduct photosynthesis more efficiently, they are threatened by harsh temperatures and extreme weather events. Additionally, with warmer conditions, moisture from snow melt arrives earlier in the season, lengthening the fire season.

The warming trend will shift colder climates toward the north and south poles. Climate gradients will also move up mountains, eventually crowding species higher in altitude and eliminating the habitat for those species adapted to the highest elevations. Some climates will completely disappear. In response to changing conditions, range shifts have also been observed in plants, butterflies, other insects, freshwater fishes, reptiles, amphibians, and mammals. Because individual plants cannot physically move to cooler regions, plant range shifts result from seed dispersal. Seeds are often dispersed in all directions away from a parent plant, but more of the seedlings that establish in northern locations or higher elevations survive, resulting in a gradual shift

towards the poles or up mountains (Figure 5.3.2.9). However, species that cannot adapt to new conditions or shift their ranges quickly enough face extinction.



Figure 5.3.2.9: In a 2015 study by Monleon and Lintz, seedlings of the Pacific dogwood (*Cornus nuttallii*) were found at elevations 347 m (379 yards) higher than mature trees. Image by J Bres (CC-BY-SA).

Changing climates also throw off the delicate timing adaptations that species have to seasonal food resources and breeding times. Scientists have already documented many contemporary mismatches to shifts in resource availability and timing. For example, pollinating insects typically emerge in the spring based on temperature cues. In contrast, many plant species flower based on daylength cues. With warmer temperatures occurring earlier in the year, but daylength remaining the same, pollinators ahead of peak flowering. As a result, there is less food (nectar and pollen) available for the insects and less opportunity for plants to have their pollen dispersed.

Ocean levels rise in response to climate change due to meltwater from glaciers and the greater volume occupied by warmer water. Shorelines will be inundated, reducing island size, which will have an effect on some species, and a number of islands will disappear entirely. Additionally, the gradual melting and subsequent refreezing of the poles, glaciers, and higher elevation mountains—a cycle that has provided freshwater to environments for centuries—will be altered. This could result in an overabundance of salt water and a shortage of fresh water.

Finally, increased carbon dioxide levels in the atmosphere react with ocean water to form carbonic acid, a phenomenon called **ocean acidification**. In combination with warmer temperatures, **ocean acidification** is responsible for coral bleaching, the process by which coral expel the algae that typically conduct photosynthesis within the corals. Ocean acidification can also dissolve the calcium carbonate skeletons formed by the coral. Overall, climate change plays a major role in the loss of nearly one third of coral reefs.

The impacts of climate change extend to humans as well. Warmer temperatures will affect agricultural yield. In fact, a 2017 study by Zhao et al. found that for every degree Celsius increase in average global temperature, wheat yields are expected to decrease by 6%, rice yields by 3.2%, and maize by 7.4%. Additionally sea level rise and extreme weather events damage property and force people to move inland. Human health is directly impacted by heat-related illnesses and an expanding range of tropical diseases.

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5.3.3: Preserving Biodiversity

Learning Objectives

- Describe the legislative framework for conservation, providing and describing examples of national and state laws and international agreements.
- Summarize the role of non-profit organizations in conservation.
- Provide specific examples of species-level conservation and discuss the shortcomings of this approach.
- Explain the importance of protected areas.
- Describe principles preserve design.
- Define ecosystem restoration.
- Provide examples of how citizen science and botanical gardens contribute to conservation efforts.

The field of **conservation** focuses on preserving biodiversity. Effective conservation depends on ecological knowledge. Today, the main efforts to preserve biodiversity involve legislative approaches to regulate human and corporate behavior, setting aside protected areas, and ecosystem restoration. Additionally, citizen science, botanical gardens, and seed banks are critical to conservation efforts.

Policies

Within many countries there are laws that protect endangered species. For example, the **Endangered Species Act** (ESA) was enacted in 1973 in the United States. The U.S. Fish and Wildlife Service (FWS), which enforces the ESA, assesses candidates for protected status as threatened or endangered (Figure 5.3.3.1). Consideration of candidate species can be initiated by the FWS itself or at the request of the public. Through the Species Status Assessment Framework, the FWS compiles biological data, such habitat and population information and current threats to the species. This biological data is used to inform decisions.



Figure 5.3.3.1: Public Affairs Specialist for the U.S. Fish and Wildlife Service, Joanna Gilkeson, takes photos of federally endangered San Diego fairy shrimp in a vernal pool in Otay Mesa, California. Vernal pools are shallow seasonal ponds, and vernal pool species are uniquely adapted changes in water availability. Image by Maideline Sanchez/USFWS (public domain).

Once a species is listed, the FWS is required by law to develop a management plan to protect the species and bring it back to sustainable numbers. The ESA, and others like it in other countries, is a useful tool, but it suffers because it is often difficult to get a species listed or to get an effective management plan in place once a species is listed.

State laws can also aid in conservation. Through **California Endangered Species Act** (CESA), originally passed in 1970 and subsequently amended, the California Fish and Game Commission assesses species to be listed as threatened or endangered by the state. A listed species, or any part or product of the plant or animal, may not be imported into the state, exported out of the state, "taken" (killed), possessed, purchased, or sold without proper authorization.

The **Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES)** treaty came into force in 1975. The treaty, and the national legislation that supports it, provides a legal framework for preventing listed species from being transported across nations' borders, thus protecting them from being caught or killed when the purpose involves international trade.

Species can be listed in one of three CITES appendices. Trade is banned for Appendix I species, which are threatened with extinction. For example the trade of the cycad *Cycas beddomei,* which has medicinal value, is banned by CITES. Trade is regulated for Appendix II species, such the timber from the big-leaf mahogany (Figure 5.3.3.2). Appendix III species are protected in at least one country, and the local government needs a coordinated response through CITES. For example, several species of red and pink corals have been added to Appendix III at the request of China.



Figure 5.3.3.2: Big-leaf mahogany (*Swietenia macrophylla*) timber is used to make furniture, musical instruments, boats, and other products. It listed in CITES Appendix II, meaning that it is regulated. Specifically, a permit is required to ship big-leaf mahogany timber. Image by Forest and Kim Starr (CC-BY).

Approximately 35,800 species are protected by the CITES. The treaty is limited in its reach because it only deals with international movement of organisms or their parts. It is also limited by various countries' ability or willingness to enforce the treaty and supporting legislation.

Non-profit Organizations

The private non-profit sector plays a large role in the conservation effort both in North America and around the world. Some non-profit organizations are directed at specific groups of organisms, like the Orchid Conservation Coalition. Others are broadly focused, such as the International Union for Conservation of Nature (IUCN), which categorizes species based on extinction risk and maintains this information on the Red List. The Nature Conservancy (Figure 5.3.3.3) takes a novel approach. It purchases land and protects it in an attempt to set up preserves for ecosystems.



Figure 5.3.3.3: Jo-Ellen Darcy (left), Assistant Secretary of the Army for Civil Works, discusses the Hamilton City with Ryan Luster, project director for The Nature Conservancy, during a site tour in Hamilton City, Calif., June 3, 2014. The U.S. Army Corps of Engineers Sacramento District's Hamilton City project will let nature help do the work of reducing flood risk by restoring 1,500 acres of native habitat between the Sacramento River and a new setback levee to be built near the town. The Nature Conservancy assisted the project partners by helping acquire the land planned for restoration. Image by US Army Corps of Engineers (public domain).

Species-level Conservation

Some conservation efforts center around a single species. Often this is a charismatic animal that elicits public interest, such tigers, sea otter, or the California Condor. The specific approach depends on specific threats based by the species of focus. A common strategy is to propagate rare plants and reintroduce them to locations where they were **extirpated** (went locally extinct). Protecting or restoring habitat is another component of the conservation of rare plant species. For example, removal of the invasive iceplant *Carpobrotus edulis* from California coasts, restores conditions for endangered dune vegetation (Figure 5.3.3.4 -6).



Figure 5.3.3.4: Vegetation at Martin Dunes in California. Iceplant is visible in the forefront. Photo by USFWS (public domain).



Figure 5.3.3.5: Carpobrotus edulis is an invasive iceplant that forms thick mats and outcompetes coastal vegetation. Image by Dr. Dwayne Meadows, NOAA/NMFS/OPR (public domain).



Figure 5.3.3.6: Removal of the iceplant restores habitat for endangered species, such as Menzies' wallflower. Image by Gordon Leppig & Andrea J. Pickart, FWS (public domain).

Seemingly unimpressive species can still serve vital ecological roles, but they are often overlooked in conservation efforts. In fact, a 2007 study by Colléony and colleagues found that people more often donated to conservation efforts for species that were more similar to humans rather than choosing those that were at greatest risk of extinction. Broad approaches such as establishing protected areas and ecosystem restoration benefit charismatic and non-charismatic species alike. Additionally, broad approaches protect unidentified and species that have not been assessed.

Protected Areas

It is important to protect natural areas (Figure 5.3.3.7) for several reasons. Some people feel a cultural or spiritual connection to the wilderness. Every year, millions of people visit recreational lands such as parks and wilderness areas to experience attractions of the great outdoors: hiking among the giant sequoias in California, traveling on a photo safari in Kenya or just picnicking at a local county park. Besides providing people with obvious health benefits and aesthetic pleasures, recreational lands also generate considerable tourist money for government and local economies. Outdoor recreation activities such as hiking and camping benefit tourist industries and manufacturers of outdoor clothes and equipment.



Figure 5.3.3.7: Contractors survey Keesler Air Force Base's sensitive wetlands. One contractor inventories the vegetation that must be removed to preserve the wetlands. The other contractor monitors the process to ensure no damage is being done to the wetlands. Image by Kemberly Groue/U.S. Air Force (public domain).

Establishment of preserves is one of the key tools in conservation efforts. A **preserve** is an area of land set aside with varying degrees of protection for the organisms that exist within the boundaries of the preserve. Governments or private organizations establish nature preserves. In 2016, the IUCN estimated that 14.7 percent of Earth's land surface was covered by preserves of various kinds. This area is large, but only 20% of the key biodiversity areas identified by the IUCN were sufficiently protected.

There has been extensive research into optimal preserve designs for maintaining biodiversity. Preserves can be seen as "islands" of habitat within "an ocean" of non-habitat. In general, large preserves are better because they support more species, they have more core area of optimal habitat for individual species, and they have more niches to support more species. One large preserve is better than the same area of several smaller preserves because there is more core habitat unaffected by less hospitable ecosystems outside the preserve boundary. For this same reason, preserves in the shape of a square or circle will be better than a preserve with many thin "arms." If preserves must be smaller, then providing wildlife corridors between two preserves is important so that species and their genes can move between them. All of these factors are taken into consideration when planning the nature of a preserve before the land is set aside. In addition to the physical specifications of a preserve, there are a variety of regulations related to the use of a preserve. These can include anything from timber extraction, mineral extraction, regulated hunting, human habitation, and nondestructive human recreation.

Public lands differ in their level of protection. For example, national parks and forests allow camping whereas wildlife refuges place more limitations on human activities. **Wilderness areas**, comprise ecosystems in which human activity has not significantly affected the plant and animal populations or their environment. National parks and forests and wildlife refuges can contain wilderness areas. The **National Park System** consists of more than 80 million acres nationwide. Their mission is to "preserve unimpaired the natural & cultural resources & values of the national park system for the enjoyment, education, and inspiration of this & future generations". Science, conservation, and outreach are a big part of the National Park (Figure 5.3.3.8).



Figure 5.3.3.8: Shelton Johnson, a National Park Service Park Ranger, has dedicated his work at the park on connecting minorities, especially African Americans, to the natural world. He is famous for his work in sharing the history of the Buffalo Soldiers who protection public lands. (Wikipedia; Public domain)

The **California State Park System** manages more than one million acres of parklands including: coastal wetlands, estuaries, scenic coastlines, lakes, mountains and desert areas. The **National Forest System** manages more than 170 forestlands and grasslands, which are available for activities such as camping, fishing, hiking and hunting. The Coronado National Forest in Arizona is famous for "sky islands", or steep mountain ranges surrounded by low-lying areas. The dramatic increase in elevation is associated with changes in the flora and fauna (figure 5.3.3.9). Explore national forests using this interactive map. The U.S. Fish and Wildlife Service manage more than 500 national **wildlife refuges**, which not only protect animal habitats and breeding areas but also provide recreational facilities.



Figure 5.3.3.9: The Santa Teresa Mountains of the Coronado National Forest form "sky islands". Image by Jstuby (public domain).

Ecosystem Restoration

Ecosystem restoration is the process of bringing an area back to its natural state, before it was impacted through destructive human activities. Reintroducing wolves, a top predator, to Yellowstone National Park in 1995 led to dramatic changes in the ecosystem that increased biodiversity. The wolves (figure 5.3.3.10) function to suppress elk and coyote populations and provide more abundant resources to the detritivores. Reducing elk populations has allowed revegetation of **riparian areas** (those along the banks of a stream or river), which has increased the diversity of species in that ecosystem. In this ecosystem, the wolf is a

keystone species, meaning a species that is instrumental in maintaining diversity within an ecosystem.

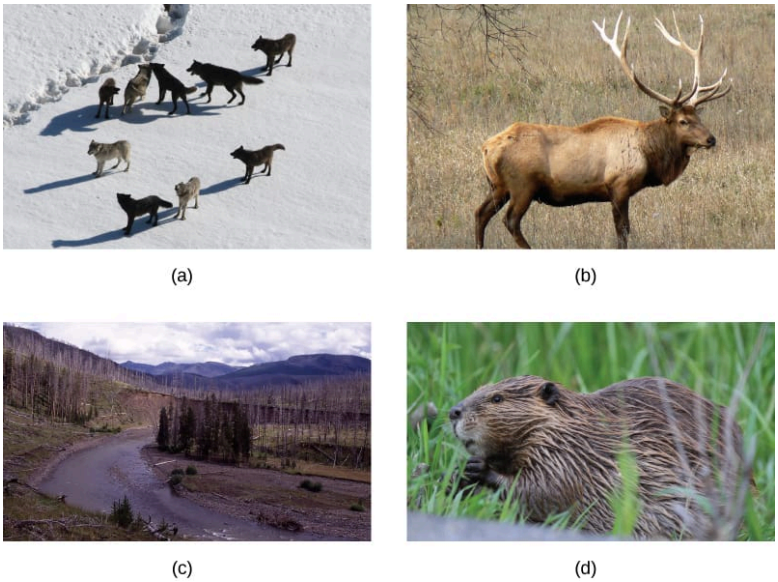


Figure 5.3.3.10: (a) The Gibbon wolf pack in Yellowstone National Park, March 1, 2007, represents a keystone species. The reintroduction of wolves into Yellowstone National Park in 1995 led to a change in the grazing behavior of (b) elk. To avoid predation, the elk no longer grazed exposed stream and riverbeds, such as (c) the Lamar Riverbed in Yellowstone. This allowed willow and cottonwood seedlings to grow. The seedlings decreased erosion and provided shading to the creek, which improved fish habitat. A new colony of (d) beaver may also have benefited from the habitat change. (credit a: modification of work by Doug Smith, NPS; credit c: modification of work by Jim Peaco, NPS; credit d: modification of work by "Shiny Things"/Flickr)

Citizen Science

Citizen science, research conducted by laypeople (non-scientists), provides the opportunity to be directly involved in biological conservation efforts. In other words, it is scientific research that engages the public. For some opportunities, like the Flora of the California Floristic Province, data can be collected independently and submitted online. Others, like mapping the urban heat island effect (the phenomenon of higher temperatures in cities than surrounding areas), are scheduled events in which experts train a group of volunteers to collect data. The federal government's citizen science database lists many such opportunities.

Botanical Gardens

Botanical gardens maintain live specimens of a variety of plant species, including those facing extinction (Figure 5.3.3.11). Some botanical gardens have programs to research the cultivation, ecology, and disease prevention of rare species. Additionally, they emphasize the value of preserving biodiversity to the public and provide education on conservation efforts.



Figure 5.3.3.11: The Berlin Botanical Garden. Image by Paul VanDerWerf (CC-BY).

Supplemental Reading

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5.3.4: Chapter Summary

Biodiversity exists at multiple levels of organization, including ecosystem diversity, species diversity, and genetic diversity. Biodiversity is negatively correlated with latitude for most taxa, meaning that biodiversity is higher in the tropics.

The core threats to biodiversity are human population growth and unsustainable resource use. These are habitat loss, overexploitation, pollution, invasive species, and climate change. Deforestation is an example of **habitat loss**. Water and air **pollution** introduce toxic substances into the environment that harm plants and animals. The collection of plants and fungi at faster rate than they can be replenished is an example of **overexploitation**. **Invasive** plant species can outcompete native plants, poison livestock and wildlife, and cause plant diseases. **Climate change** is causes range shifts and extinctions and disrupts species interactions. Climate change will also raise sea levels, eliminating some islands and reducing the area of all others.

Conservation involves a variety of approaches, and many factors influence the success of conservation efforts. In the United States, the **Endangered Species Act** protects listed species but is hampered by procedural difficulties and a focus on individual species. International treaties such as **CITES** regulate the transportation of endangered species across international borders. The non-profit sector is also very active in funding and organizing conservation efforts. **Species-level conservation** of rare plants can involve propagating and reintroducing rare plant species and restoring their habitat by removing invasive species. Presently, 14.7 percent of Earth's land surface is protected in some way. **Preserves** are a major tool in conservation efforts, and large, interconnected preserves favor biodiversity. **Ecosystem restoration** promotes biodiversity, improves conditions for native species, and reinstate ecosystem services. Through **citizen science** and **botanical gardens**, the public can engage directly in conservation efforts.

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

- Define biodiversity.
- Distinguish among ecosystem, species, and genetic diversity, explaining the value of each.
- Define and provide examples of ecosystem services.
- Distinguish between species richness and species evenness.
- Explain the importance of biodiversity hotspots and identify the characteristics of endemic species.
- Name, define, and provide examples of the five major threats to biodiversity.
- Provide examples of the successes and failures of biological control in regulating invasive species.
- Describe the legislative framework for conservation, providing and describing examples of national and state laws and international agreements.
- Summarize the role of non-profit organizations in conservation.
- Provide specific examples of species-level conservation and discuss the shortcomings of this approach.
- Explain the importance of protected areas.
- Describe principles preserve design.
- Define ecosystem restoration.
- Provide examples of how citizen science and botanical gardens contribute to conservation efforts.

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5.4: TERRESTRIAL BIOMES



Figure 5.4.1: Left, Desert Sunflower in Mojave National Park. Right, tropical rainforest in Costa Rica. Images by Kammy Algiers (CC-BY).

A **biome** is a large geographical area characterized by climate and vegetation. Biomes may be terrestrial or aquatic, but this chapter will focus only on terrestrial biomes. Terrestrial biomes are characterized by their plant life. The types of plants depend on the amount of precipitation in an area as well as the temperature. Different adaptations evolve based on the abiotic factors. For example, desert environments with less rainfall will have a different type of vegetation and plant life will be more scarce than tropical rainforests which have plenty of rainfall throughout the year (Figure 5.4.1).

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5.4.1: Introduction

Learning Objective

Identify the two major abiotic factors that determine terrestrial biomes.

Plants are main components of terrestrial ecosystems as they are primary producers. Almost all terrestrial life if based on the types of plants found in the area. These types of plants are able to survive in the given environment based on the temperature and precipitation range of the biome. Annual totals and fluctuations of precipitation affect the kinds of vegetation and animal life that can exist in broad geographical regions. Temperature variation on a daily and seasonal basis is also important for predicting the geographic distribution of a biome. Since a biome is defined by climate, the same biome can occur in geographically distinct areas with similar climates (Figure 5.4.1.1)

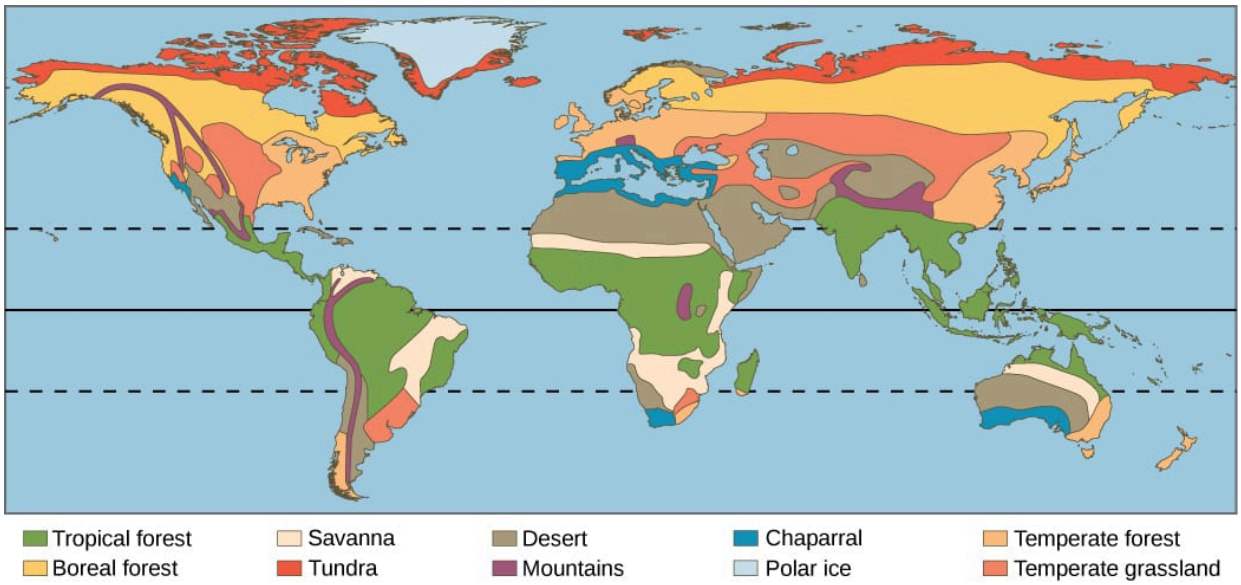


Figure 5.4.1.1: Some of the major biomes, distinguished by characteristic temperatures and amount of precipitation. Tropical forests, deserts and savannas are found primarily in South America, Africa and Australia. Tropical forests also dominate southeast Asia. Deserts dominate the Middle East and are found in the southwestern United States. Temperate forests dominate the eastern United States, Europe and Eastern Asia. Temperate grasslands dominate the midwestern United States and parts of Asia, and are also found in South America. Boreal forest is found in northern Canada, Europe and Asia, and tundra exists to the north of the boreal forests. Mountainous regions run the length of North and South America, and are found in northern India, Africa and parts of Europe. Polar ice covers Greenland and Antarctica. The latter is not shown on the map.

Given the amount of rainfall, for example, tall evergreen trees can dominate one area, whereas small shrubs may dominate another. The plants, thus, determine the *types of vegetation* (i.e., visually different plant communities). We will explore some of the most important types (also called *biomes*).

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5.4.2: Climate and Biomes

Learning Objective

The Identify the role of temperature and percipitation play on distribution of biomes.

Biomes are large-scale environments that are distinguished by characteristic vegetation and climate (Figure 5.4.2.1). Biomes are also characterized by the animals and other organisms there, which are influenced by vegetation and climate patterns. The Earth's biomes are categorized into two major groups: terrestrial and aquatic. **Terrestrial biomes** are based on land, while **aquatic biomes** include both ocean and freshwater biomes. Altitude and latitude, which affect temperature and precipitation determine the distribution of biomes.

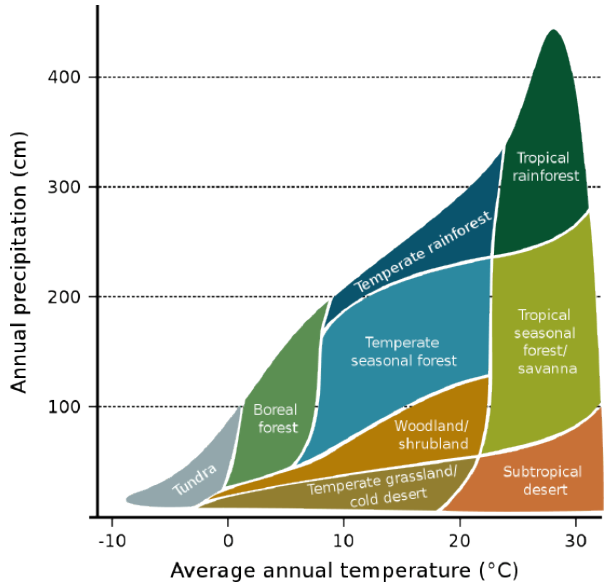


Figure 5.4.2.1: Average annual temperature and annual precipitation are two climatic factors that determine the distribution of biomes. This graph shows annual precipitation in centimeters on the y-axis and average annual temperature in degrees Celsius on the x-axis. Tropical rainforests have the highest temperatures and most precipitation. Tropical seasonal forests and savannas have high temperatures (20-30°C) with precipitation from approximately 50 to 270 centimeters. Subtropical deserts have similarly high temperatures but dry conditions. Temperate grasslands and cold deserts range in average annual temperature from below 0 to 22°C and have less than 50 centimeters of precipitation per year. Woodlands/shrublands (such as the chaparral) have the same temperature range as cold deserts but can receive a little over 100 cm of precipitation per year. Temperate forests have intermediate temperatures (approximately 16-22°C), but temperate rainforests receive more precipitation than temperate seasonal forests. Boreal forests receive a little less precipitation than temperate forests, but are colder (approximately 1-10°C). The tundra has the coldest temperatures and little precipitation. Deserts have a range of temperatures but low precipitation. Image by Navarras (public domain).

Low latitudes (near the equator) have high temperatures and low latitudes (near the poles) have low temperatures. This is because the sun hits the equator more directly. Sunlight hits the poles at an angle, reducing the intensity of light (and heat energy) per unit of area. Temperature also decreases with altitude. At high altitudes, the atmosphere is thinner and traps less heat energy from the sun. Because temperatures decline with altitude as well as latitude, similar biomes exist on mountains even when they are at low latitudes. As a rule of thumb, a climb of 1000 feet (about 300 m) is equivalent in changed flora and fauna to a trip northward of some 600 miles (966 km).

Where precipitation is moderately abundant — 40 inches (about 1 m) or more per year — and distributed fairly evenly throughout the year, the major determinant is temperature. It is not simply a matter of average temperature, but includes such limiting factors as whether it ever freezes or length of the growing season. Biomes are thus characterized not only by average temperature and precipitation but also their seasonality.

Not only does latitude influence temperature, but it also affects precipitation. For example, deserts tend to occur at latitudes

of around 30° and at the poles, both north and south, driven by circulation and prevailing wind patterns in the atmosphere. The engine that drives circulation in the atmosphere and oceans is solar energy, which is determined by the average position of the sun over the Earth's surface. Direct light provides uneven heating depending on latitude and angle of incidence, with high solar energy in the tropics, and little or no energy at the poles. Atmospheric circulation and geographic location are the primary causal agents of deserts. At approximately 30° north and south of the equator, sinking air produces **trade wind deserts** like the Sahara and the Outback of Australia (Figure 5.4.2.2 and Video 5.4.2.1).

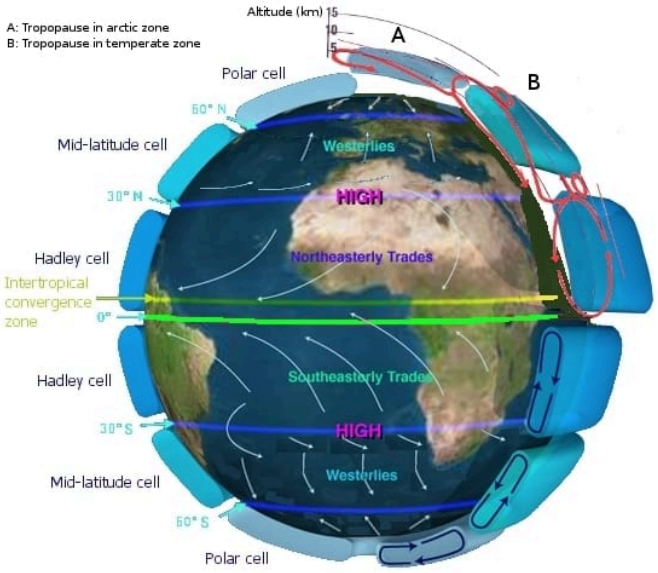


Figure 5.4.2.2: The generalized circulation of the atmosphere. Solar energy falling on the equatorial belt heats the air and causes it to rise. The rising air cools and its contained moisture falls back on the tropics as rain. The drier air then continues to spread toward the north and south where it sinks back at about 30 degrees north and south latitudes. This sinking drier air creates belts of predominant high pressure along which desert conditions prevail. These belts of predominantly high pressure have air that descends along these belts and flows either north to become the westerlies or south to become the trade winds. Note the arrows indicating general directions of winds in the latitude zones. The trade winds are predominant in the tropics and the westerlies in the mid-latitudes.

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 5.4.2.1: This MinuteEarth video discusses the global climate patterns which lead to deserts.

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5.4.3: Tropical Rainforest

Learning Objective

- Recognize distinguishing characteristics of tropical rainforests & plant adaptations of the biome.

Also referred to as tropical wet forest, this biome is found in equatorial regions. Tropical rainforests are the most diverse terrestrial biome. This biodiversity is still largely unknown to science and is under extraordinary threat primarily through logging and deforestation for agriculture. Tropical rainforests have also been described as nature's pharmacy because of the potential for new drugs that is largely hidden in the chemicals produced by the huge diversity of plants, animals, and other organisms. The vegetation is characterized by plants with spreading roots and broad leaves that fall off throughout the year, unlike the trees of deciduous forests that lose their leaves in one season. These forests are "evergreen," year-round, meaning they retain they leaves throughout the year.

The temperature and sunlight profiles of tropical rainforests are stable in comparison to that of other terrestrial biomes, with average temperatures ranging from 20°C to 34°C (68°F to 93°F). Month-to-month temperatures are relatively constant in tropical rainforests, in contrast to forests further from the equator. This lack of temperature seasonality leads to year-round plant growth, rather than the seasonal growth seen in other biomes. In contrast to other ecosystems, a more constant daily amount of sunlight (11–12 hours per day) provides more solar radiation, thereby a longer period of time for plant growth.

The annual rainfall in tropical rainforests ranges from 250 cm to more than 450 cm (8.2–14.8 ft) with considerable seasonal variation. Tropical rainforests have wet months in which there can be more than 30 cm (11–12 in) of precipitation, as well as dry months in which there are fewer than 10 cm (3.5 in) of rainfall. However, the driest month of a tropical rainforest can still exceed the *annual* rainfall of some other biomes, such as deserts.

Tropical rainforests have high net primary productivity because the annual temperatures and precipitation values support rapid plant growth (Figure 5.4.3.1) . However, the high rainfall quickly leaches nutrients from the soils of these forests, which are typically low in nutrients. Any nutrients that reach the soil (fallen leaves, tree branches, or dead animals) quickly decompose and are used by plants as raw material. Thus, the nutrients are always above ground, and not stored in the soil.

Tropical rainforests are characterized by vertical layering of vegetation and the formation of distinct habitats for animals within each layer. On the forest floor is a sparse layer of plants and decaying plant matter. Above that is an understory of short, shrubby foliage. A layer of trees rises above this understory and is topped by a closed upper **canopy**—the uppermost overhead layer of branches and leaves. Some additional trees emerge through this closed upper canopy. These layers provide diverse and complex habitats for the variety of plants, animals, and other organisms within the tropical wet forests. Many species of animals use the variety of plants and the complex structure of the tropical wet forests for food and shelter. Some organisms live several meters above ground rarely ever descending to the forest floor.

Rainforests are not the only forest biome in the tropics; there are also tropical dry forests, which are characterized by a dry season of varying lengths. These forests commonly experience leaf loss during the dry season to one degree or another. The loss of leaves from taller trees during the dry season opens up the canopy and allows sunlight to the forest floor that allows the growth of thick ground-level brush, which is absent in tropical rainforests. Extensive tropical dry forests occur in Africa (including Madagascar), India, southern Mexico, and South America.



Figure 5.4.3.1: Species diversity is very high in tropical wet forests, such as these forests of Madre de Dios, Peru, near the Amazon River. (credit: Roosevelt Garcia)

Adaptations

Plants living in tropical rainforests have many unique adaptations. For example, due to the poor nutrient soil, they cannot have deep roots. They withstand many rain events and compete with other plants for sunlight, causing them to sometimes grow at an angle. Due to all these restrictions, trees often have **buttresses**, which are large aerial extensions of the lateral surface roots, to help stabilize the tree. Another common adaptation are **epiphytes**. These are plants that live on the surface of other plants, using moisture and nutrients from the air or rain. They grow on plants instead of the shady forest floor, where they cannot obtain enough sunlight. Epiphytes do not have any attachment to the ground and are not parasitic on the plant. Orchids, bromeliads, and mosses are common epiphytes. Some plants have leaves with **drip tips,** pointy tips that help remove water off the leaves quickly to reduce the cumulating of fungi and bacteria. It also helps protect the leaves from breakage during heavy rains.

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5.4.4: Tropical Deciduous Forest

Learning Objective

Recognize distinguishing characteristics of tropical deciduous rainforests & plant adaptations of the biome.

This biome is distinguished by seasonal rainfall and a constant warm temperature throughout the year. There are two seasons in this biome, are often referred to as the dry season (with no to little rain) and the wet season (with heavy rain). This biome receives up to 80 inches of rain per year and temperatures range between 68°F to 77°F.

One would find this biome on the north and south ends of tropical rainforests, generally between 10° and 20°. Parts of South America, including parts of amazon and southern Mexico, as well as parts of south east Asia and India contain tropical deciduous forests. This biome is also sometimes called Monsoon forest or mixed deciduous forest, depending on its location and slight variations.



Figure 5.4.4.1: Cat Tien National Park in Vietnam showing tropical deciduous forest in the early dry season. (credit: Roy Bateman)

Adaptations

Though there is less biodiversity in this biome than tropical rainforests, there are still a large number of species, including many endemic species that reside here. Deciduous trees lose their leaves during the dry season and re-grow them during the rainy season. This allows the plants to save energy when liquid water is not as available. During the rainy season, the forest is lush and full of foliage, whereas the dry season creates an open canopy, allowing plants under the canopy to access sunlight. You can still see the various layers of vegetation in this biome, including lianas (woody vines) and epiphytes such as bromeliads and orchids. The canopy contains tall trees above and smaller trees and shrubs underneath. Though most of the tall trees are often deciduous, there are still plenty of evergreen plants that retain their leaves throughout the year. Many birds and mammals live in this biome and use the vegetation as habitat and food.

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5.4.5: Savannas

Learning Objective

Recognize distinguishing characteristics of savannas & plant adaptations of the biome.

Savannas are rolling grasslands scattered with shrubs and isolated trees. Not enough rain falls on a savanna to support forests. Savannas are also known as tropical grasslands. They are found in a wide band on either side of the equator on the edges of tropical rainforests. One can find savannas in Africa, South America, and northern Australia. Savannas are hot, tropical areas with temperatures averaging from 24°C –29°C (75°F –84°F) and an annual rainfall of 51–127 cm (20–50 in). Savannas have both a wet season and an extensive dry season with frequent fires. As a result, scattered in the grasses and **forbs** (herbaceous flowering plants) that dominate the savanna, there are relatively few trees (Figure 5.4.5.1) . Since fire is an important source of disturbance in this biome, plants have evolved well-developed root systems that allow them to quickly re-sprout after a fire.



Figure 5.4.5.1: Although savannas are dominated by grasses, small woodlands, such as this one in Mount Archer National Park in Queensland, Australia, may dot the landscape. (credit: "Ethel Aardvark"/Wikimedia Commons)

Adaptations

In the dry season, plants have adapted to the lack of water in Savannas. For example, trees and larger shrubs have deep roots so they can access underground water during the direst time of the year. Some trees, like the Baobob tree in Madagascar, store water in their trunk (up to 120,000 liters or 32,000 US gallons) to endure harsh drought conditions. Some trees may lose their leaves (deciduous) and grow them back during the rainy season, when water is available. In general, many savanna plants have small leaves to reduce water loss. Grasses are dormant during the drought, with their growth season mainly during the wet season.

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5.4.6: Desert

Learning Objective

Recognize distinguishing characteristics of Deserts & plant adaptations of the biome.

Subtropical deserts exist between 15° and 30° north and south latitude and are centered on the Tropic of Cancer and the Tropic of Capricorn. Deserts are frequently located on the downwind or lee side of mountain ranges, which create a **rain shadow** after prevailing winds drop their water content on the mountains Figure dd This is typical of the North American deserts, such as the Mohave and Sonoran deserts. Deserts in other regions, such as the Sahara Desert in northern Africa or the Namib Desert in southwestern Africa are dry because of the high-pressure, dry air descending at those latitudes. Subtropical deserts are very dry; evaporation typically exceeds precipitation. Subtropical hot deserts can have daytime soil surface temperatures above 60°C (140°F) and nighttime temperatures approaching 0°C (32°F). The temperature drops so far because there is little water vapor in the air to prevent radiative cooling of the land surface. Subtropical deserts are characterized by low annual precipitation of fewer than 30 cm (12 in) with little monthly variation and lack of predictability in rainfall. Some years may receive tiny amounts of rainfall, while others receive more. In some cases, the annual rainfall can be as low as 2 cm (0.8 in) in subtropical deserts located in central Australia (“the Outback”) and northern Africa.

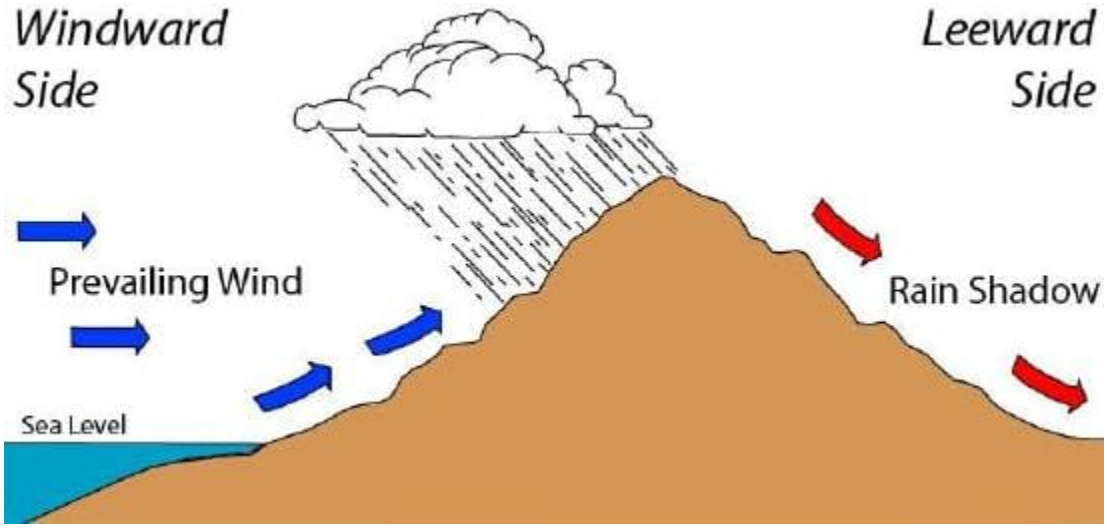


Figure 5.4.6.1: Effect of a rain shadow. Credit Meg Stewart. (CC BY-SA)

Adaptations

The low species diversity of this biome is closely related to its low and unpredictable precipitation. Despite the relatively low diversity, desert species exhibit fascinating adaptations to the harshness of their environment. Very dry deserts lack perennial vegetation that lives from one year to the next; instead, many plants are annuals that grow quickly and reproduce when rainfall does occur, then they die within the year. Perennial plants in deserts are characterized by adaptations that conserve water: deep roots to tap groundwater., reduced foliage to reduce water loss, and large, fleshy, water-storing stems (Figure 5.4.6.2). Seed plants in the desert produce seeds that can lie dormant for extended periods between rains. The Namib Desert is the oldest on the planet, and has probably been dry for more than 55 million years. It supports a number of endemic species (species found only there) because of this great age. For example, the unusual gymnosperm *Welwitschia mirabilis* is the only extant species of an entire order of plants.

In addition to subtropical deserts there are cold deserts that experience freezing temperatures during the winter and any precipitation is in the form of snowfall. The largest of these deserts are the Gobi Desert in northern China and southern Mongolia, the Taklimakan Desert in western China, the Turkestan Desert, and the Great Basin Desert of the United States.




Figure 5.4.6.2: Many desert plants have tiny leaves or no leaves at all to reduce water loss. The leaves of ocotillo, shown here in the Chihuahuan Desert in Big Bend National Park, Texas, appear only after rainfall and then are shed. (credit “bare ocotillo”: "Leaflet"/Wikimedia Commons)

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5.4.7: Mediterranean (Chaparral)

Learning Objective

Recognize distinguishing characteristics of Mediterranean (Chaparral) & plant adaptations of the biome.

The Mediterranean ecosystem occurs only in five relatively small areas around the planet: the area bordering the Mediterranean Sea, central Chile, the Cape region of South Africa, southwestern and southern Australia, and the California Floristic Province (CFP) located on the Pacific Coast of North America. These areas occur along the western edges of continents and are distributed between roughly 30 and 40 degrees latitude in the northern and southern hemispheres. Mediterranean ecosystems are characterized by mild, rainy winters and warm, dry summers and are moderated by cold ocean currents offshore. The annual rainfall in this biome ranges from 65 cm to 75 cm (25.6–29.5 in) and the majority of the rain falls in the cool, wet winter. Summers are very dry and many chaparral plants are dormant during the summertime.

Mediterranean regions make up only 2.5% of the earth's land but contain more than 16% of the world's plant species, an impressive level of diversity concentrated in a relatively small area. In the CFP, the majority of the primary vegetation has been damaged or completely removed. The threat of habitat destruction continues today along the coast of California due to the high number of attractive living locations (e.g. close proximity to the ocean) and desirable climate. In addition to the high level of biodiversity, more than a third of the plant species found in the CFP are endemic (not found anywhere else in the world). Because of all these qualities, the CFP is considered to be one of the earth's **biodiversity hotspots,** an area of high biodiversity and endemism at risk of destruction. There are a number of widely recognized plant communities in this biome, including Coastal Sage Scrub, Chaparral, Grassland, Wetland, Riparian, Coastal Salt Marsh, and Oak Woodland (Figure 5.4.7.1).

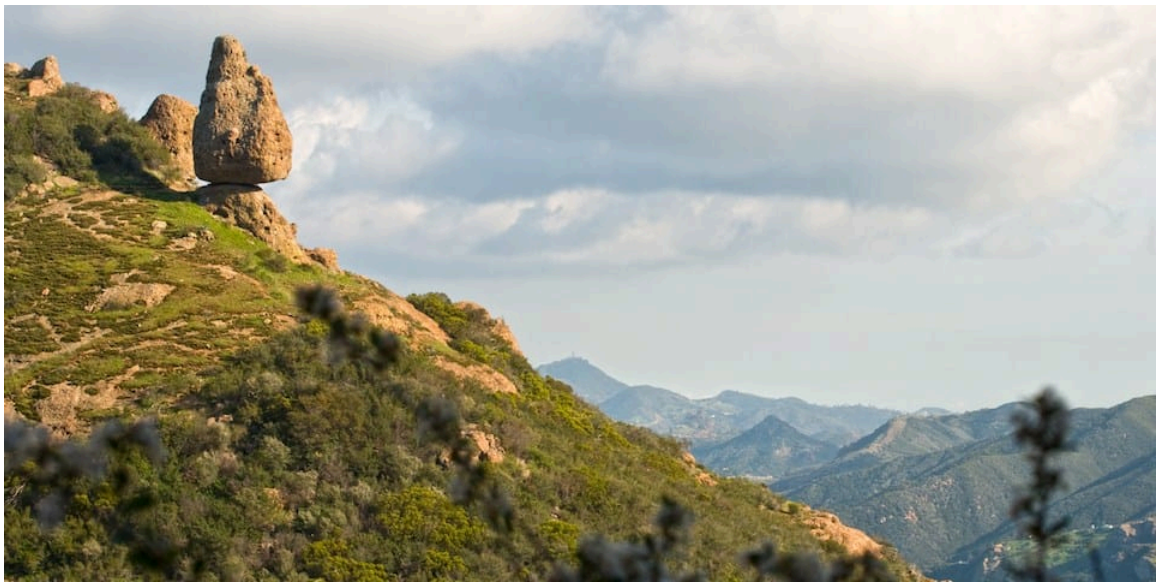


Figure 5.4.7.1: Chaparral dominated hillside, a common vegetation type found in the CFP. (credit: NPS, Public Domain).

Adaptations

The chaparral vegetation is dominated by shrubs and is adapted to periodic fires, with some plants producing seeds that germinate only after a hot fire. The ashes left behind after a fire are rich in nutrients like nitrogen that fertilize the soil and promote seeds to germinate. Other plants store nutrients in their roots and will recover after a fire by re-sprouting from the root crown. Many have fire resistant bark that protects the plant from harm. Periodic fire is a natural part of the maintenance of this biome. Though these communities are well adapted to infrequent, early season fires that are naturally ignited by lightening (and follow rain), they are not adapted to the frequent, late season fires caused by humans. These late season fires often occur during the dryer part of the year, when high Santa Ana winds can produce devastating results. Fires that occur during Santa Ana wind

conditions burn longer and hotter, and since they are more frequent, native plant recovery is more difficult (Figure 5.4.7.2).

Plants in the Mediterranean biome are also well adapted for conserving water. Small leaves, waxy cuticles, trichomes, and succulence are some adaptations you find on such plants. Others may be deciduous, or have large, deep taproots.



Figure 5.4.7.2:The Woolsy fire of 2018 burned over 96,000 acres of Los Angeles and Ventura County. (credit: NPS, Public Domain).

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5.4.8: Temperate Grasslands (Prairie)

Learning Objective

Recognize distinguishing characteristics of Temperate Grassland (Prairie) & plant adaptations of the biome.

Temperate grasslands are found throughout central North America, where they are also known as prairies, and in Eurasia, where they are known as steppes. Temperate grasslands have pronounced annual fluctuations in temperature with hot summers and cold winters. The annual temperature variation produces specific growing seasons for plants. Plant growth is possible when temperatures are warm enough to sustain plant growth, which occurs in the spring, summer, and fall. Annual precipitation ranges from 25.4 cm to 88.9 cm (10–35 in).

Adaptations

Temperate grasslands are areas of open grass with few trees, most of which are found growing along rivers or streams. The treeless condition is maintained by low precipitation, frequent fires, and grazing (Figure 5.4.8.1). The vegetation is very dense and the soils are fertile because the subsurface of the soil is packed with the roots and rhizomes (underground stems) of these grasses. The roots and rhizomes act to anchor plants into the ground and replenish the organic material (humus) in the soil when they die and decay. Thus, temperate grasslands contain some of the most fertile soils in the world. Agriculture and development is often associated with this biome due to its rich soil.



Figure 5.4.8.1:The American bison (*Bison bison*), more commonly called the buffalo, is a grazing mammal that once populated American prairies in huge numbers. (credit: Jack Dykinga, USDA ARS)

Fires, which are a natural disturbance in temperate grasslands, can be ignited by lightning strikes. It also appears that the lightning-caused fire regime in North American grasslands was enhanced by intentional burning by humans. When fire is suppressed in temperate grasslands, the vegetation eventually converts to scrub and dense forests. Often, the restoration or management of temperate grasslands requires the use of controlled burns to suppress the growth of trees and maintain the grasses.

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5.4.9: Temperate Deciduous Forests

Learning Objective

Recognize distinguishing characteristics of temperate forests & plant adaptations of the biome.

Temperate deciduous forests are the most common biome in eastern North America, Western Europe, Eastern Asia, Chile, and New Zealand. This biome is found throughout mid-latitude regions and is the second most common biome in the world at 25% forest cover. Temperatures range between –30°C and 30°C (–22°F to 86°F) and drop to below freezing on an annual basis. These temperatures mean that temperate forests have defined growing seasons during the spring, summer, and early fall. Precipitation is relatively constant throughout the year and ranges between 75 cm and 150 cm (29.5–59 in). However, in the winter, the precipitation falls in the form of snow.

Deciduous trees are the dominant plant in this biome with fewer evergreen conifers. Deciduous trees lose their leaves each fall and remain leafless in the winter. Thus, little photosynthesis occurs during the dormant winter period. Each spring, new leaves appear as temperature increases. Due to the dormant period, the net primary productivity and diversity of tree species is less than that of tropical rainforests. Yet, since deciduous trees lose their leaves during the drier part of the year, the sunlight that reaches the ground provides energy for the growth of wildflowers, ferns, mosses, and lichens. The thick layer of leaf litter on forest floors allows provides cover for invertebrates. Decay of leaf litter and the reduced leaching of nutrients by rainfall allows detritivores and decomposers to thrive, returning nutrients to the soil. The leaf litter also protects soil from erosion & insulates the ground (Figure 5.4.9.1).

Adaptations

Deciduous trees in this biome begin to lose their leaves in autumn. As light levels are reduced, leaves stop receiving nutrients from the tree due to changes in hormone level and nutrients are instead stored in the root for future use. Chlorophyll molecules begin to break down within the leaves. This allows the carotenoid pigments, which are orange, red, and yellow, to become visible. By winter, the trees have shed their leaves completely. The thick bark of the tree will be protected from the cold as the tree stays dormant for the winter. However, as spring arrives, an increase in sunlight and liquid water from melted snow triggers new growth of leaves and the stored nutrients within the soil are used to begin leaf growth.



Figure 5.4.9.1: Deciduous trees are the dominant plant in the temperate forest. (credit: Oliver Herold)

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5.4.10: 22.10 Temperate Rainforest

Learning Objective

Recognize distinguishing characteristics of temperate rainforests & plant adaptations of the biome.

Temperate rainforests, sometimes called mixed evergreen forests, are common on the western coast of the United States, from Alaska to California. However, smaller patches of this biome can be found on other contents as well. The conditions of this biome are similar to temperate deciduous forests but winters are colder and last longer. The soil in this biome is generally poor in nutrient levels. Being close to the coast, the temperature rarely goes below freezing, averaging between 39°F and 54°F. Precipitation averages about 55 inches but can reach up to 100 inches a year.

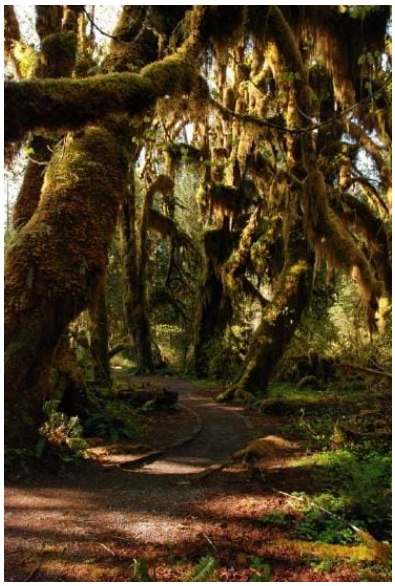


Figure 5.4.10.1: Hall of Mosses at Olympic National Park. (Copyright *Carmen Bubar,* NPS, Public Domain)

The term mixed evergreen forest comes from the fact that both deciduous and evergreen (coniferous) trees are common in this biome. These evergreen trees are often tall and conspicuous. The tallest trees in the world, the coast redwoods, can be found in this biome. Often, moss and epiphytes can be found growing on the tall trees as they reach out for the sun (Figure 5.4.10.1) . In the understory, ferns are common, as well as other shade tolerant plants. Showy wildflowers and fungi can also be seen in the understory.

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5.4.11: Boreal (Coniferous) Forests

Learning Objective

Recognize distinguishing characteristics of boreal (coniferous) forests & plant adaptations of the biome.

The **boreal forest**, also known as coniferous forest, is found roughly between 50° and 60° north latitude across most of Canada, Alaska, Russia, and northern Europe. Boreal forests in North America are sometimes referred to as Taiga. Boreal forests are also found above a certain elevation (and below high elevations where trees cannot grow) in mountain ranges throughout the Northern Hemisphere. This biome has cold, dry winters and short, cool, wet summers. The annual precipitation is from 40 cm to 100 cm (15.7–39 in) and usually takes the form of snow; little evaporation occurs because of the cold temperatures.

Though evergreen, the net primary productivity of boreal forests is relatively low, as is species richness. The aboveground biomass of boreal forests is high because these slow-growing tree species are long-lived and accumulate standing biomass over time. Boreal forests lack the layered forest structure seen in tropical rainforests or, to a lesser degree, temperate forests. The structure of a boreal forest is often only a tree layer and a ground layer. When conifer needles are dropped, they decompose more slowly than broad leaves; therefore, fewer nutrients are returned to the soil to fuel plant growth (Figure 5.4.11.1).



Figure 5.4.11.1: The boreal forest has low lying plants and conifer trees. The snowcapped mountains of the Alaska Range are in the background. (credit: L.B. Brubaker, NOAA, Public Domain)

Adaptations

The long and cold winters in the boreal forest have led to the predominance of cold-tolerant cone-bearing plants. These are evergreen coniferous trees like pines, spruce, and fir, which retain their needle-shaped leaves year-round. These small, waxy leaves are adapted to little water loss during the winter where liquid water is not available.

Evergreen trees can photosynthesize earlier in the spring than deciduous trees because less energy from the Sun is required to warm a needle-like leaf than a broad leaf. Evergreen trees grow faster than deciduous trees in the boreal forest. In addition, soils in boreal forest regions tend to be acidic with little available nitrogen. Leaves are a nitrogen-rich structure and deciduous trees must produce a new set of these nitrogen-rich structures each year. Therefore, coniferous trees that retain nitrogen-rich needles in a nitrogen limiting environment may have had a competitive advantage over the broad-leafed deciduous trees.

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5.4.12: Arctic Tundra

Learning Objective

Recognize distinguishing characteristics of arctic tundra & plant adaptations of the biome.

The **Arctic tundra** lies north of the subarctic boreal forests and is located throughout the Arctic regions of the Northern Hemisphere. Tundra also exists at elevations above the tree line on mountains. The average winter temperature is –34°C (–29.2°F) and the average summer temperature is 3°C–12°C (37°F –52°F). Plants in the Arctic tundra have a short growing season of approximately 50–60 days. Though the sun is low to the ground and the days are limited, there are almost 24 hours of daylight and plant growth is considerably rapid. The annual precipitation of the Arctic tundra is low (15–25 cm or 6–10 in) with little annual variation in precipitation. And, as in the boreal forests, there is little evaporation because of the cold temperatures.

Adaptations

Plants in the Arctic tundra are generally low to the ground and include low shrubs, grasses, lichens, and small flowering plants with small leaves (Figure 5.4.12.1). There is little species diversity, low net primary productivity, and low aboveground biomass. The soils of the Arctic tundra may remain in a perennially frozen state referred to as **permafrost**. The permafrost makes it impossible for roots to penetrate far into the soil and slows the decay of organic matter, which inhibits the release of nutrients from organic matter. The melting of the permafrost in the brief summer provides water for a burst of productivity while temperatures and long days permit it. During the growing season, the ground of the Arctic tundra can be completely covered with plants or lichens.



Figure 5.4.12.1: Low-growing plants such as shrub willow dominate the tundra landscape during the summer, shown here in the Arctic National Wildlife Refuge. (credit: Arctic National Wildlife Refuge, USFWS)

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5.4.13: Chapter Summary

Plants are main components of terrestrial ecosystems as they are primary producers. Almost all terrestrial life if based on the types of plants found in the area. Biomes are large-scale environments that are distinguished by characteristic vegetation and climate. Since a biome is defined by climate, the same biome can occur in geographically distinct areas with similar climates. In terrestrial biomes, temperature and precipitation determine the type of biome. There are ten major terrestrial biomes: tropical rainforests, deciduous rainforests, savannas, deserts, Mediterranean (or chaparral), temperate grasslands (or prairie), temperate deciduous forests, temperate rainforests, boreal (or coniferous) forests, and Arctic tundra. Some biomes, such as temperate grasslands and temperate forests, have distinct seasons, with cold weather and hot weather alternating throughout the year. In warm, moist biomes, such as the tropical rainforest, net primary productivity is high, as warm temperatures, abundant water, and a year-round growing season fuel plant growth and supply energy for high diversity throughout the food web. Other biomes, such as deserts and tundras, have low primary productivity due to extreme temperatures and a shortage of available water.

After completing this chapter, you should be able to

- Identify the two major abiotic factors that determine terrestrial biomes.
- The Identify the role of temperature and precipitation play on distribution of biomes.
- Recognize distinguishing characteristics of tropical rainforests & plant adaptations of the biome.
- Recognize distinguishing characteristics of tropical deciduous rainforests & plant adaptations of the biome.
- Recognize distinguishing characteristics of savannas & plant adaptations of the biome.
- Recognize distinguishing characteristics of deserts & plant adaptations of the biome.
- Recognize distinguishing characteristics of Mediterranean (chaparral) & plant adaptations of the biome.
- Recognize distinguishing characteristics of temperate grasslands (prairie) & plant adaptations of the biome.
- Recognize distinguishing characteristics of temperate deciduous forests & plant adaptations of the biome.
- Recognize distinguishing characteristics of temperate rainforests & plant adaptations of the biome.
- Recognize distinguishing characteristics of boreal (coniferous) forests & plant adaptations of the biome.
- Recognize distinguishing characteristics of Arctic tundra & plant adaptations of the biome.

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