

BOTANY IN HAWAI'I



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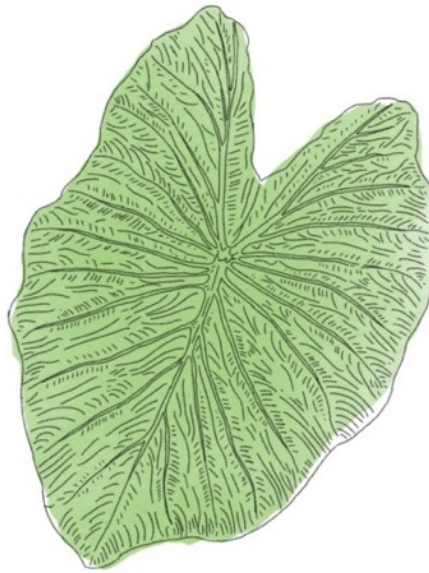
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1: INTRODUCTION TO PLANTS

Learning Objectives

After studying this chapter, you should be able to:

- Explain why plants are important for humans and the environment.
- Understand the process of scientific inquiry and follow the steps of the scientific method.
- Describe the difference between basic and applied science
- List some examples of what a botanist does and explain why it is important to learn about plants.



1.1: Why are plants important?

1.2: The science of Botany

1.3: Plant cells and tissues

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1.1: Why are plants important?

Plants are a common sight in our daily lives, the grass in the park, the flowers in our neighborhood, the shade trees in the streets, the palm trees on the beach, the green on the mountains, or even the leaves on our salad. However, we usually do not stop to think about the crucial role of plants in our ecosystems, their importance in our lives, or the basics of how they function.

For starters, plants provide us with food and oxygen. They belong to a group of organisms that can produce their own food (autotrophs) through a process called photosynthesis, and since they also produce the food for most animals, including humans, they are the basis (producers) for all terrestrial ecosystems (Figure 1.1.1). Besides food (in the form of sugars), photosynthesis also produces oxygen, which is required for all animals, fungi, and most bacteria to survive.



Figure 1.1.1: A wet forest ecosystem at Ka'ala, O'ahu. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

As the producers in terrestrial ecosystems, plants are found on all of the continents of Earth, in all types of ecosystems, like forests, deserts, and savannas. They provide not only food for animals but also shelter and nesting materials, among other things. Over millions of years of evolution, plants and other organisms, like insects, have created relationships that make them indispensable for each other's survival (Figure 1.1.2). Just think about bees and flowers, you cannot remove either from the equation without having dire consequences on the ecosystem. In the case of Hawai'i, these relationships are truly unique, given that the Hawaiian archipelago is one of the most isolated places on Earth. With over 47 million years of evolution in isolation from people and large terrestrial mammals, Hawaiian plants and animals have forged unique relationships, creating a delicate balance in the Hawaiian ecosystems. The majority of native Hawaiian plants are unique and cannot be found anywhere else on Earth. Hawai'i's climate and landscape play an important role in the diversity of native plants that can be found here. For example, 90% of native plants are endemic and therefore can only be found in Hawai'i.



Figure 1.1.2: Lava flow on Hawai'i Island with 'ōhi'a lehua, (*Metrosideros polymorpha*). Flowers of this species offer year-round nectar to native birds. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Not only do we need plants for food and oxygen, but our lives are intertwined with plants. We use plants for a variety of things: raw materials for paper, building materials, solvents and adhesives, fabrics, medicines, biofuels (i.e. biodiesels and ethanol), and many other products. Plants also play a crucial role in most cultures. If you think of a wedding or graduation, very likely plants are involved. Ceremonial uses of plants can be found in most cultures around the world.

Hawai'i is a special place due to people's cultural connection to plants. Once humans arrived in the islands, many new plant species were introduced eventually creating the collection of plants we find in Hawai'i today. The strong connection of Native Hawaiians to plants can be seen in hula, medicine, and agriculture (Abbott, 1992; Lincoln and Vitousek, 2017; Figure 1.1.3). It can also be seen in the inclusion of *kalo* as an intrinsic part of their genealogy. As Kalei Laimana articulated "the strongest evidence that Hawaiians sought to solidify their connection to plants occurred when they included the *kalo* plant into their genealogy as a Kaikua'ana (elder sibling) to the Hawaiian people. No other plant has ever been given such a place of honor and reverence. Such familial relationships set up the proper relationship of respect and endearment for future generations" (pers. communication).



Figure 1.1.3: Cultural use of plants is seen here in lei making using native Hawaiian plants: maile (*Alyxia stellata*), 'a'ali'i (*Dodonaea viscosa*), and palapalai (*Microlepia strigosa*). By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

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1.2: The science of Botany

The science that studies plants is called Botany. All natural sciences, including botany, aim to understand how the natural world functions. To be able to do this we need to make observations, run experiments, generate and test hypotheses, record data, and report results. In Western science, people use a series of steps, called the scientific method, that helps to answer a question in an unbiased way.

It is important to notice that indigenous peoples across the globe have their own knowledge systems that are different from the Western science approach, where “...knowledge for observing, collecting, categorizing, recording, using, disseminating and revising information and concepts that explain how the world works...” (Whyte *et al.*, 2016). Indigenous knowledge often takes place at a much longer time scale with knowledge and observations passed on from generation to generation. The two systems do not need to be isolated and sometimes are used together to answer questions. “Hawaiians like many indigenous people were careful observers of nature. They observed closely, developed possible explanations for what they observed, conducted experiments to either confirm or refine their understanding until they were confident in their understanding. Once their understanding was perfected, they then committed it to memory using such mnemonic devices as the mele (song), oli (chant) or mo’olelo (story) which was then passed on to the next generation. We only have to look at Hawaiian fishponds to realize how many observations, experiments, refinements that must have taken place before they made the immensely huge labor intensive commitment to build a fishpond. One thing we can be sure of, the perfection of the Hawaiian fishpond did not occur in one generation; it was a deliberate process. The western “Scientific Method” operates in much the same way, observations are made, hypotheses presented, experiments conducted to refine the observation, the main difference is that in the west every step is carefully written down and documented.” (Kalei Laimana, pers. communication).

The Scientific Method

Botanists and other scientists learn about the natural world by asking questions about it and using a systematic approach, known as the scientific method, to find answers. It might surprise you to learn that even you use this method in your life to solve everyday problems or answer questions that are apparently not related to science. The first step of the scientific method is an observation, which usually leads to a question. Imagine you have some beautiful *puakenikeni* plants in your garden and you notice their leaves start to turn yellow (Figure 1.2.1). This is an observation that can lead you to the question: “why are the leaves of my plants turning yellow?” Since you are not a plant expert, you turn to the internet or a member of the family that has a green thumb to try to answer the question and ultimately solve the problem. Scientists follow a similar process; they research information relevant to the question to try to find the answer to it, see if other scientists already tried to answer the question or came across a similar problem and how they solved it.



Figure 1.2.1: Puakenikeni plant (*Fagraea berteroana*) with yellowing leaves.

Going back to our example, after you search the internet for “plant leaves turning yellow” you find several potential reasons for the leaves of your plants turning yellow. Which one is the correct one? After reading more details about some of the causes you decide it must be lack of water, the soil around your plants seems dry so your plants are probably not getting enough water. Now you have a likely answer for your question, or a hypothesis. A hypothesis is a potential explanation for the question that can be tested. Hypotheses usually follow an “if ... then” format, that represents the question and the proposed solution. In this case your hypothesis could be: “If I water my *puakenikeni* plant more often, then the leaves won’t turn yellow.” In our example, there are different reasons that can cause the leaves on your plants to turn yellow, so there are several hypotheses that could be tested, and this is true for most questions in science.

Take a look at the scientific method flow chart presented in Figure 1.2.2. You can see that we have already followed several of the steps that compose the scientific method in our example: observation, question, and hypothesis/prediction. The following step is to run an experiment to test your hypothesis. Now, how would you test your hypothesis? Sometimes we imagine that scientific experiments are complex and advanced processes that need to be carried out in a super fancy and high-tech facility, but that is not always the case. To a certain extent, we all can run experiments in an easy and accurate way. After determining that your plants have been underwatered, the most logical experiment would be to add more water than normal to your plants to see if this solves the yellowing of the leaves. An experiment can be as simple as that; however, scientists need to be sure of exactly what is affecting the results. In order to do this scientific experiments have one or several experimental variables, which is (are) the part(s) of the experiment that can be changed. In our case the amount of water provided to the plants would be the experimental variable.

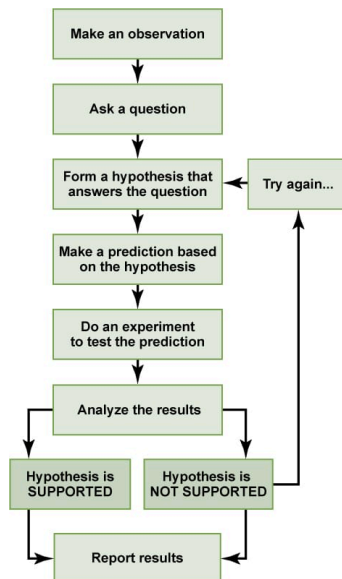


Figure 1.2.2: The scientific method consists of a series of well-defined steps. By OpenStax is licensed under CC-BY 4.0.

Experiments also need a control group, which is a group that has all the same characteristics as the experimental group (the one in which you are changing the variable), but in which we do not change the variable. By having a control group, we are making sure that the lack of water is the variable (characteristic) that is causing the yellowing of the leaves in your plants and that there is not another reason. In your garden a simple way to test this hypothesis accurately would be to set up an experiment that includes an experimental group and a control group. In the experimental group you are going to have at least one *puakenikeni* plant that you are going to water more frequently, so the variable you are changing is the water frequency. On the other hand, the control group will be at least one *puakenikeni* plant to which you will continue to water with the same frequency as you have done until now. You will continue to do this for several weeks, and then you can record your results. If a scientist wanted to run a similar experiment, she/he would probably run it in a greenhouse or nursery, to be able to regulate all other environmental conditions and any other variables, so that nothing else affects the results of the experiment. A scientist would also have several replicas or repetitions of the experiment, to ensure that the results are unbiased. For example, instead of increasing the watering on just one plant, a scientist might have a group of 30 plants that are watered more frequently as the experimental group and a group of 30 plants that are kept in the same watering regime as the control group.

The next step in the process is to analyze the results. For several weeks you have been watering at least one of your *puakenikeni* plants more frequently (experimental group) and kept watering at least one *puakenikeni* plant as before (control group), so it is time to analyze the results of your experiment. You take a good look at the leaves of both plants and to your dismay the leaves of both plants look similarly yellow. At this point you can conclude that it was not the water that was causing the yellowing of the

leaves in your plants, therefore your initial hypothesis was incorrect. What do you do next to save your plants? If you look at the flowchart of the scientific method (Figure 1.2.2), you see that if your hypothesis was not supported by your experiment then you need to try again.

Do you remember that there were other causes you found on the internet that could be causing the yellowing of the leaves in your plants? Well, you can now test another hypothesis: maybe your plant is suffering from a lack of nutrients in the soil. You need to run a new experiment to test this new hypothesis in a similar way you tested for the water hypothesis. So let's imagine you add fertilizer to at least one of your *puakenikeni* plants to increase the nutrients available in the soil (experimental group) and leave at least one *puakenikeni* plant without fertilizer (control group). After several weeks you analyze the results, and you see that the plant that had fertilizer added now has beautiful green leaves and looks healthy, while your control plant has yellow leaves. Congratulations, you have cracked the case and now you can help your plants live long and healthy lives by adding fertilizer to all of your *puakenikeni* plants! Normally, an experiment requires replication, so it would require that you had several plants in your control group and several in your experimental group. That's not always possible if you are doing that in your backyard, but it is important to know that researchers do that to make sure that the results are not the influence of a random variable (for example, the influence of the location of the plant).

The last step in the scientific method is to report or disseminate the results, which in the scientific community is usually done by publishing a scientific paper or report, doing a public presentation in a scientific meeting, or even publishing an article in a newspaper if the issue is of interest to the community. This last step is important, because it helps to build knowledge and advance science, so that we do not get stuck trying to solve the same issue over and over again. In our example, you could also share the results of your experiment with your family and friends to help somebody facing the same issue.

Experiments are not the only way to answer a question in science. Sometimes we use descriptive methods when an experimental approach is not feasible. For example, if you wanted to determine how many individuals of an endangered Hawaiian plant are left in the wild in Mount Ka'ala on O'ahu, the best approach would be to do a survey or record all the plants of that species in that mountain, instead of running an experiment.

Basic and applied science

There are two main types of science: basic and applied. Basic science aims to broaden knowledge; not seeking to find a practical utilization or creating a product, just the spread of knowledge in the subject. An example of basic science would be to record all the different species of plants that are present in Hawai'i. This does not seem to have any practical application, but we could actually use the knowledge gathered in basic science for applied science. Applied science aims to use science to create a product or solve a real-life problem. For example, if we recorded all the individuals of an endangered Hawaiian plant that are left in the wild in Mount Ka'ala on O'ahu, we could use this information to create a conservation plan to save this species from extinction by growing it in the lab and then planting it in the wild to restore native ecosystems. A great example of applied plant science is agriculture, because it uses the plant knowledge to create and improve plant varieties that are adapted to local environments, produce more fruit or yield, or increase resistance to drought. An example is tomato varieties that were developed by University of Hawai'i plant breeders that were resistant to several tropical diseases. This effort not only helped local food production from 1950-1980s, but helped breeding programs in many countries. The tomato varieties developed here were then used by other research programs to breed other varieties (Teves, 2017).



Figure 1.2.3: Kalo planting in Waihe'e, O'ahu. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Why is Botany important?

Botany is a broad science with many different sub-disciplines that encompass different aspects of plant sciences. Some botanists work on biotechnology, like people extracting compounds from plants to create medicines or studying the chemicals produced by different plants to find new uses for them. For example, we use some plant chemicals to treat certain types of cancer. One of these compounds is taxol, which is extracted from the Pacific yew (*Taxus brevifolia*) and is used to treat ovarian cancer. Botanists in the field of conservation, seek to preserve plant species and restore damaged ecosystems. They can also use biotechnology and grow a whole plant out of a single cell (tissue culture). Other botanists are interested in understanding how plants function (plant physiology), so they focus on studying things like photosynthesis, transportation of nutrients, and the movement of water in plants. Other botanists are more interested in exploring how plants have traditionally been used by people in cultural practices, medicine, or cooking (ethnobotany). Other botanists are interested in studying fossil plants and understanding how plants have evolved over time (paleobotany and plant evolution). These are just a few examples to illustrate the diversity of the botanical field.

Learning about plants is not only useful for botanists, but to all people. For example, learning about plants can help you grow and maintain healthy plants in your house and garden. In some booming businesses, like natural products and hemp/marijuana products, there is always the need for people with plant knowledge and, in some cases, lab experience, as the extraction of plant compounds can require the use of specific lab techniques. Learning about plants that have traditionally been used in your culture can also help you to connect with your family and community (Figure 1.2.4).

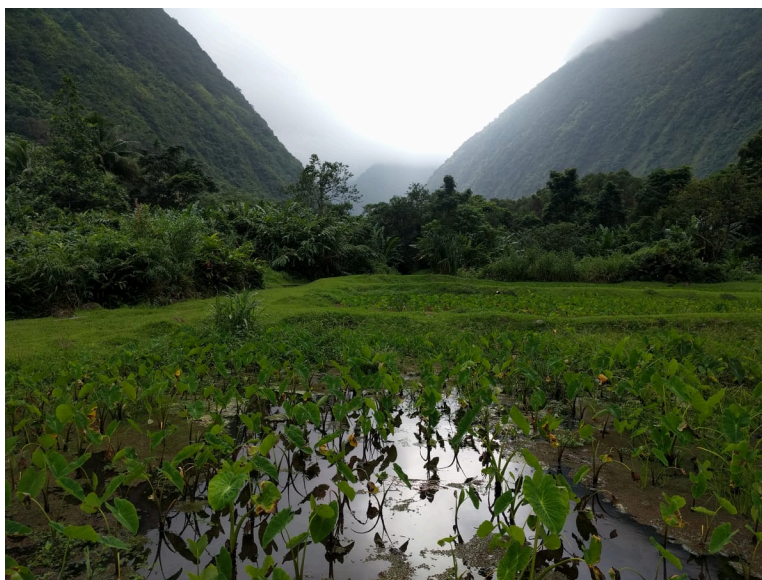


Figure 1.2.4: Kalo growing in Waipi'o Valley on Hawai'i Island. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

And of course, you cannot pass up the opportunity to answer some of the burning questions that you always had: Why are plants green? What is that smell when I cut grass? How do some plants move? What are those sticky things that attach to my socks? Do carnivorous plants eat human flesh?

1.3: Plant cells and tissues

Plant cells

Let's start with the most basic unit of life: cells. All living organisms are composed of cells, and are called unicellular when they are composed of a single cell or multicellular, when they have more than one cell. A plant is composed of millions of cells, organized into tissues (similar cells grouped together) and organs (different tissues grouped together). All living cells have common structures like the cell membrane, cytoplasm or ribosomes. Some groups of organisms have certain characteristics in their cells that are unique. Plant cells, for example, are different from animal, fungi, and bacteria cells. They have cell walls, a central vacuole, and chloroplasts. Cell walls in plants are made of cellulose, hemicellulose, and pectin, organic compounds called polysaccharides. The function of the cell wall is to protect the cell and provide mechanical support. A thicker cell wall provides more mechanical support and a thinner cell wall provides flexibility. The central vacuole is essential in the regulation of the turgor pressure, which is the pressure that liquid exerts against the cell wall (Figure 1.3.1). This internal pressure is important for the physiology of plants because that's how they are able to remain upright and not wilt. Plants also have unique organelles, called plastids, that have different functions: photosynthesis (chloroplasts), synthesis and storage of starches (amyloplasts), and synthesis of special pigments (chromoplasts).

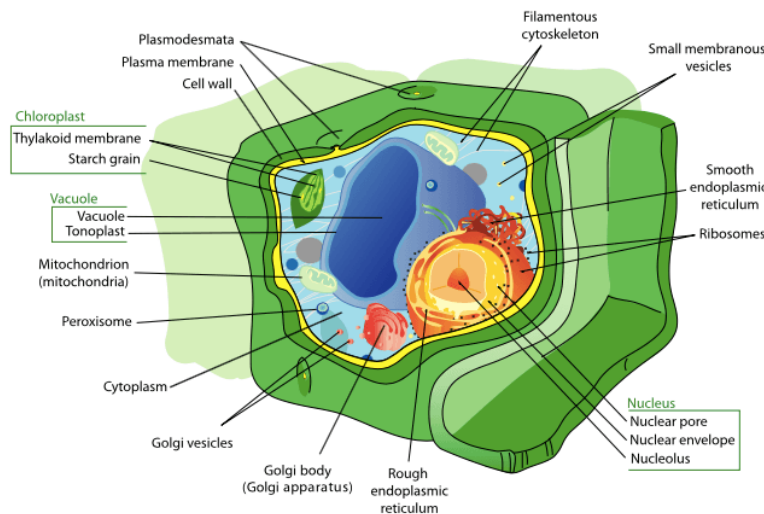


Figure 1.3.1: Typical plant cell. By LadyofHats is licensed under Public Domain via Wikimedia.

Plant tissues

Plants are composed of different types of cells, which have different functions. The cells group together into tissues, which in plants can be simple (one type of cell) or complex (more than one type of cell). Simple plant tissues are parenchyma, collenchyma and sclerenchyma.

- **Parenchyma** cells are the least specialized type of plant cell and the most abundant in plants. They are usually rounded and can be found in all plant organs. In leaves they make up the mesophyll, where photosynthesis takes place (Chapter 4). In stems and roots they make up the cortex, which is responsible for storing carbohydrates and other substances needed for plants to function (Chapters 2 and 3). Parenchyma cells also participate in plant support and the transfer of nutrients in the phloem. Parenchyma cells are the cells that divide and produce new cells when plants are growing. Parenchyma cells make up the parenchyma tissue.
- **Collenchyma** cells are elongated and provide support to growing plant organs, like leaves. Their primary cell wall is thick, but lacks lignin, making them flexible. Collenchyma cells group into a tissue of the same name.
- **Sclerenchyma** cells are thick as their cell walls contain lignin, a rigid polysaccharide. They are mostly dead when mature, and their main function is to provide mechanical support, for example in the stem.

Complex plant tissues are xylem, phloem, epidermis and periderm:

- **Xylem** is the tissue that transports water and nutrients from the roots to the leaves. It is composed of specialized parenchyma cells, tube shaped cells called vessels and tracheids, form long tubes for longitudinal transportation and are usually dead at maturity, and ray cells for lateral conduction.
- **Phloem** is the tissue that transports the sugars produced in photosynthesis. Unlike xylem, it is composed of live cells called sieve tube members (tube shaped cells) and companion cells, which help control the flow of liquid on the sieve tube members.
- **Epidermis** is usually a one cell layer on the outside of the plant tissues for protection, and secretes a protective layer called cuticle. Different cells can be found here: parenchyma cells, guard cells in the stomata (openings for gas exchange on leaves), trichomes (hairs), root hairs in the roots, and glands (production of substances).
- **Periderm** is the outermost layer of woody plants, or outer bark. It is composed of cork cells and lenticels, which are clusters of parenchyma cells that help bring more oxygen into the stem.

In the upcoming four chapters we will cover the different plant organs (Chapters 2 - 5). All plants have four main organs with different functions: roots, stems, leaves, and reproductive organs (flowers, fruits, and seeds). Stems and roots transport water and nutrients, and support the plant. Leaves are where photosynthesis happens. Flowers, fruits, and seeds play a role in plant sexual reproduction and dispersal.

1.4: References

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2: ROOTS

Learning Objectives

After studying this chapter, you should be able to:

- State the primary functions of roots.
- Distinguish the two types of root systems.
- Identify the different root regions and their corresponding function: root cap, region of cell division, region of elongation, and region of maturation.
- List the name and function of the main root tissues: epidermis, cortex, endodermis, pericycle, xylem, and phloem.
- Describe how water absorption happens in roots.
- List and describe the various types of specialized roots and provide examples of each.
- List economically important root crops.



2.1: Types of root systems

2.2: The regions of the root

2.3: Root Anatomy

2.4: Modified roots

2.5: References

2.1: Types of root systems

Roots are the plant tissue that we see less often because they are usually found underground, making them the plant tissue that we know the least about (Figure 2.1.1). Roots come in all sizes and lengths, being deeper for trees and more shallow for herbs. Some trees in arid places can grow very deep root systems in search of underground water. Kiawe (mesquite, *Prosopis pallida*), which is an introduced species in Hawai'i, can grow a root system as deep as 55 meters (180 feet). In contrast, some plants like giant redwoods have a widespread but relatively shallow root system. The giant redwood tree (*Sequoiadendron giganteum*) can be as tall as 75 meters (245 feet) with roots reaching only 12 -14 meters (39 - 46 feet) into the ground, but extending for over 4,000 square meters (1 acre).



Figure 2.1.1: Araucaria tree with root showing on the windward side of O'ahu. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Roots have three main functions in plants. First, they anchor the plant to the soil, providing mechanical stability and support. Second, they absorb water and dissolved minerals from the soil and transport them upward to be used by the plant. Third, roots store the carbohydrates produced in photosynthesis. Besides these basic functions, roots also produce and export the plant hormones cytokinins and gibberellins, which are involved in promoting cell division and plant growth respectively. Finally, in addition to their basic functions, some roots also have specialized functions which we will discuss later in this chapter.

There are two types of root systems: taproots and fibrous roots (also known as adventitious roots; Figure 2.1.2). Tap roots have a prominent primary root that develops when the seed germinates and the radicle emerges. From there, secondary or lateral roots grow. As the secondary roots grow they can also get thicker and develop further secondary roots, ending in a highly ramified root system. Taproots are characteristic of eudicots (Chapter 9), such as beans and carrots.

Fibrous roots, as the name suggests, look like fibers, with all the roots being of similar length and diameter. Fibrous roots usually form a dense superficial root system. Fibrous roots are also known as adventitious roots because the primary root that forms when a seedling germinates does not remain. Instead, roots grow out of the stem of the plant and are called adventitious. Fibrous roots are characteristic of monocots (Chapter 9), such as corn and grass (Figure 2.1.2).



Figure 2.1.2: A) Eudicot taproot and B) Monocot fibrous roots. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

2.2: The regions of the root

When a seed is germinating, one of the first things to emerge from the seed coat is the root. This initial “root” is called a radicle and as it grows it gives origin to the root system. To understand how roots grow, we need to take a peek inside of a growing root. If we look at a root tip, we can recognize four root regions: the root cap, the region of cell division, the region of elongation and the region of maturation (Figure 2.2.1). All of these regions are usually found within the first few centimeters of the root tip, so we are talking about a very small area.

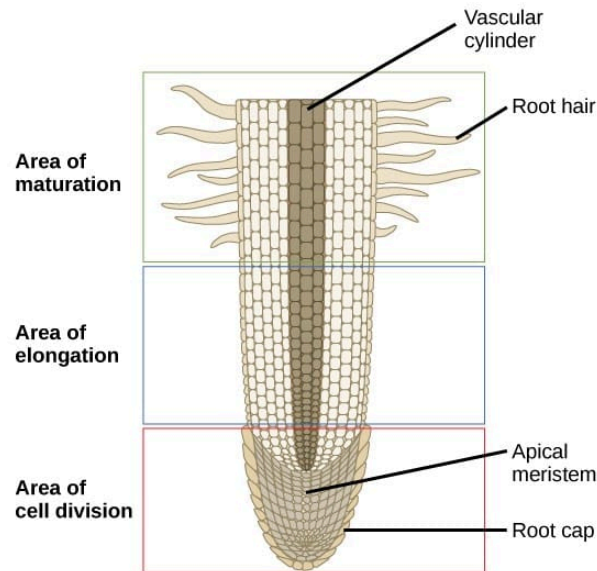


Figure 2.2.1: Regions of the Root by Openstax is licensed under CC BY 4.0.

Root Cap

A root growing into the soil faces physical challenges, like friction and potential damage from rock particles present in the soil. The root cap is a mass of cells (parenchyma cells) located at the tip of the root that protects it from mechanical damage. It also secretes a slimy substance called mucilage to help the root grow more smoothly into the soil. The root cap also plays a role in the plant perception of gravity (gravitropism), which makes plant roots always grow downward (Figure 2.2.2).

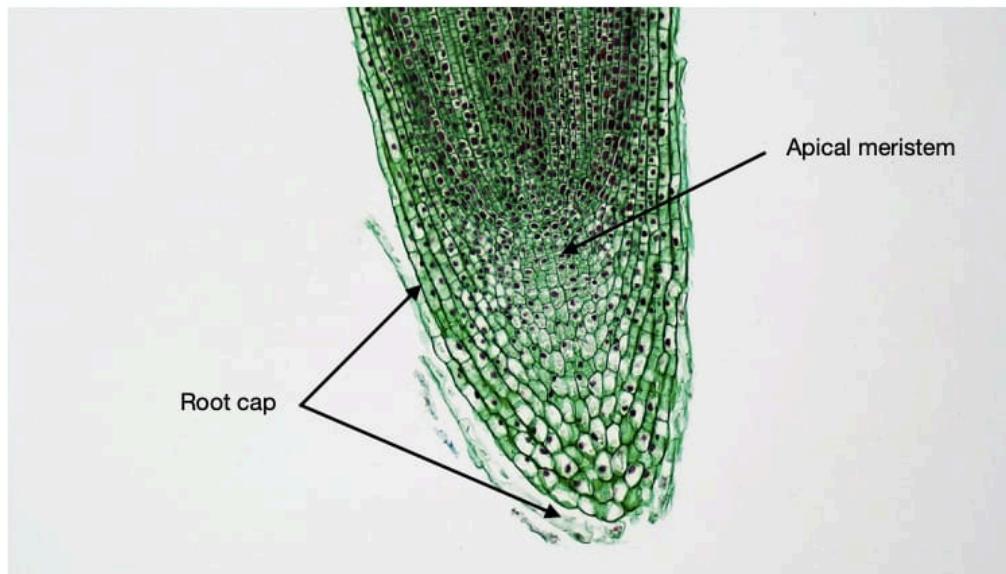


Figure 2.2.1: Root tip Longitudinal section. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr. Modified to include labels. A derivative of the original work of "Apical Meristem in Allium Root Tip" is licensed under Public Domain via Wikicommons.

The region of cell division

The region of cell division is found just under the root cap. In this region, cells are perpetually dividing (mitosis), meaning there is a constant generation of new cells, causing the root to grow in length (primary growth). These regions of active cell division in plants are found in the growing tips of roots and stems, and they are called apical meristems.

The region of elongation

Following the region of cell division is the region of elongation. When new cells are created in the apical meristem of the root they are small and rounded. In this region they grow in size, lengthening the root as they grow. The cells in this region are still undifferentiated; therefore they do not have a specific function yet.

The Region of Maturation

Following the region of elongation comes the final one, the region of maturation, where cells differentiate and become a specific type of cell. It is here that cells get their final function assigned depending on where they are located in the root. For example, cells in the center of the root will become specialized in transport (xylem and phloem), while the cells towards the periphery (outside) of the root will become specialized in protecting the root (epidermis).

In this region of maturation is also where root hairs are formed. Root hairs are extensions of some epidermal cells in the region of maturation (Figure 2.2.2). They extend the surface area of each cell, increasing their absorption capacity. In fact, most of the water and mineral absorption happens in the root hairs; therefore plants have massive amounts of them (in the range of several billion in a mature plant).

Root hairs are delicate and only survive for several days, but as the root grows, new root hairs are formed in the region of maturation. Root hairs can be easily damaged if you are transplanting seedlings to a new pot, which may limit the seedling's ability to absorb water and nutrients.

2.3: Root Anatomy

The main function of roots is the absorption of water and dissolved nutrients. To understand how water moves from the soil to the root and from there to the stems and leaves, we need to look at the different internal layers (tissues) that are inside of the root. If you take a carrot root and lay it flat on a cutting board, then cut it into thin slices, in each slice, you are able to see different concentric areas or tissues (Figure 2.3.1). A tissue is defined as a group of specialized cells that have a common function. This type of cut in botany is called a cross-section, and it allows us to have a top view of the tissues inside of a plant; in this case, a top view of the root tissues.



Figure 2.3.1: Cross-sections of carrot roots of different varieties. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Starting from the outermost layer in a root the first thing we find is the cuticle, which is not a tissue, but a waxy substance that covers all external parts of a plant. Its main function is to protect the plant from water loss and bacterial or fungal infection. In the roots, the cuticle is thin to allow water absorption. After the cuticle we find the true tissues of the root, starting on the outside of the cross-section to the inside we find: **epidermis**, **cortex**, **endodermis** with **Casparian strips**, and the **stele** or **vascular cylinder** which is composed of **pericycle**, **xylem** and **phloem** (Figure 2.3.2).

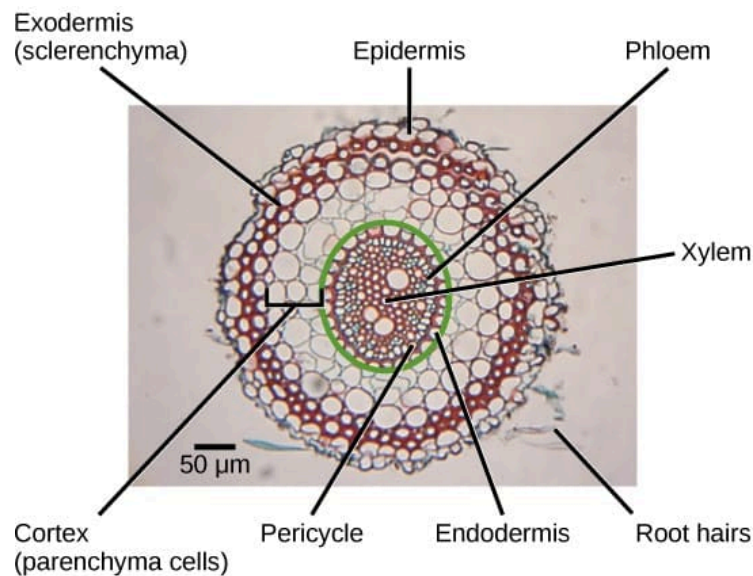


Figure 2.3.2: Light micrograph of a wheat (*Triticum*) root cross section. Sclerenchyma cells of the exodermis and xylem cells stain red, and phloem cells stain blue. Other cell types stain black. The stele, or vascular tissue, is the area inside the endodermis (indicated by a green ring). Root hairs are visible outside the epidermis. Biology 2e by Openstax is licensed under CC BY 4.0.

Root tissues

Epidermis (epi = outside; dermis = skin) literally translates as outer skin, and it delimits the root, protecting the inner tissues from the outer environment and physical damage. It usually is one cell layer thick.

Cortex is the tissue just underneath the epidermis and it is several cell layers thick. The function of the cortex is to store food and water.

Endodermis (endo = inner; dermis = skin) literally means the inner skin. It delimits the inner cylinder of the root and it is one single layer of cells. The cells of the endodermis are thicker than those in the cortex because the cell walls of the endodermal cells have lignin and suberin (structural plant compounds) that form bands called **Casparian strips**. These waterproof strips play an important role in the absorption of water in the roots, by not allowing the water and dissolved substances to pass in through the porous cell wall of the endodermal cells, but instead forcing the water to move to the inside of the endodermal cell to be transferred from there to the vascular cylinder. We will review this in more detail in the section below: Absorption of water and dissolved substances.

Pericycle is the tissue found just inside of the endodermis, commonly one cell thick and it is the first one found on the stele or vascular cylinder. Its main function is to produce lateral roots.

Xylem is the tissue in the middle of the root, usually looking as an X in young eudicots, and arranged in a ring around a central pith in monocots (Figure 2.3.3). The xylem is responsible for water and dissolved nutrient transportation. It transports water upward from the roots to the leaves.

Phloem is the tissue that transports the carbohydrates (sugars) produced in photosynthesis throughout the plant. In roots it is usually found in between the xylem in the vascular cylinder.

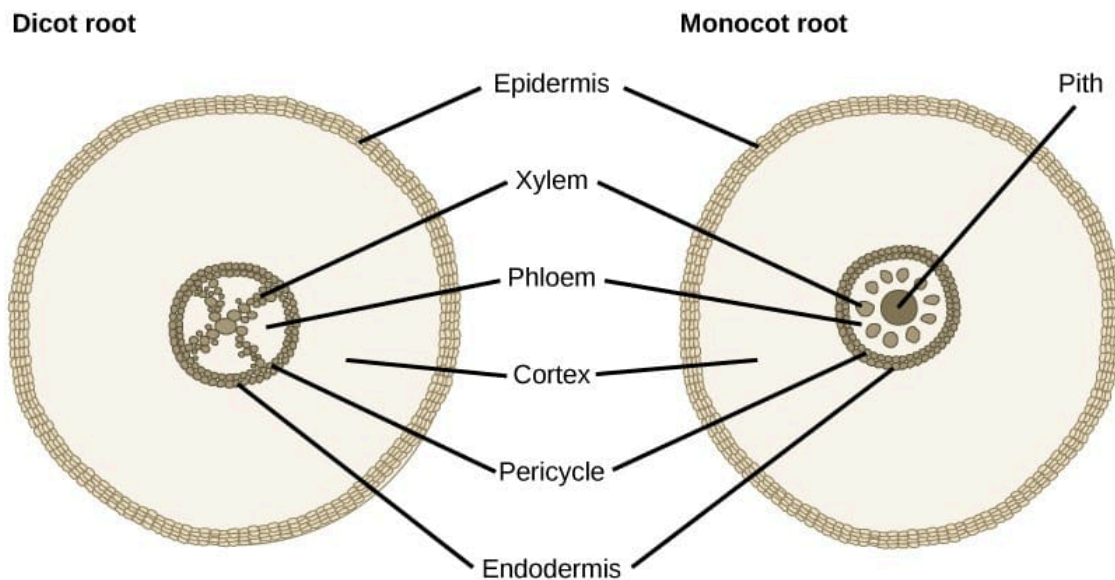


Figure 2.3.3: In typical eudicots, the vascular tissue forms an X shape in the center of the root (left). In typical monocots, the phloem cells and the larger xylem cells form a characteristic ring around the central pith (right). Open Stax Biology 2e is licensed under CC BY 4.0.

In Biology all transport tissues are referred to as vascular tissues. For example, when we talk about vascular diseases in humans, we are referring to a disease that affects our vascular tissues: arteries and veins. In plants we also use the term vascular when referring to the plant transportation system. Instead of arteries and veins, plants have xylem and phloem. As we just learned, roots have a vascular cylinder, which in simple terms is a cylinder in the middle of the roots that has xylem and phloem. These two tissues are found in all plant organs: roots, stems, leaves, and reproductive organs.

Absorption of water and dissolved nutrients

Plants need water for several physiological processes required for their survival, such as photosynthesis and transpiration. The water in soil is absorbed by the roots and transferred to the xylem to be transported to other parts of the plant. Water moves from the soil to the root hairs through a process called **osmosis**. In osmosis, water moves through a plasma membrane from a place with more water to a place with less water. Because of the presence of salts and other minerals inside of the root hairs, water is less abundant inside of the cells than on the outside in the soil, where there are less salts and minerals: therefore the water present in the soil moves to the inside of the root hairs. If you remember, water is transported by the xylem. Do you remember where the xylem is located in a root? It is the innermost tissue, found in the middle of the vascular cylinder. This means that the water that is absorbed by the root hairs has to be moved through every single tissue of the root until it finally reaches the xylem, where it will be transported upward to the plant. After water is absorbed by the root hairs it can move through the root tissues using two different routes: between the porous cell walls of the cells (apoplastic transport) or directly from cell to cell (symplastic transport), through tiny pores that join the cells called plasmodesmata. We can trace the water movement from the root hairs to the cortex and then to the endodermis. But here water finds an impenetrable barrier, the Casparian strips, that impede the water and dissolved substances from moving in between the cell walls, forcing them to go inside of the cell instead. Through this process the plants are able to control which dissolved substances will be transferred to the vascular cylinder for further transportation.

In the process of water absorption, the roots also absorb other substances, like minerals and nutrients, that are dissolved in the water. As with any other organism, plants require certain nutrients to be able to grow and survive. We can divide them into macro and micronutrients. Macronutrients (macro = big) are essential components of plants and they are available in large quantities. Examples of macronutrients are phosphorus (P), nitrogen (N) and Potassium (K). Micronutrients are also needed by plants, but they are available in small quantities. Examples of micronutrients are iron (Fe), copper (Cu) and manganese (Mn).

2.4: Modified roots

Some plant roots may be modified for special purposes in addition to accomplishing the root's basic functions.

Storage roots

Some plants store carbohydrates in the roots for use in case of emergency or in preparation for the winter months, as some plants lose their leaves and are unable to perform photosynthesis. Most of this storage in plants happens in the roots, where it can be safe from animals and be preserved better than aboveground. We are familiar with this strategy of food storage, as we animals also store extra food as fat in our bodies to use in case of food scarcity. For example, animals that hibernate accumulate fat to be able to survive the winter. Plants do not use fat to store food, instead they use mainly starch, which is more stable and lasts for longer periods of time. Roots have been sources of food for humans since the dawn of our species. Examples of economically important root crops are cassava, sweet potatoes (Figure 2.4.1), carrots, beets, sugar beets, turnips, radishes, parsnips, and horseradishes.

Currently, the most important root crop in the world is cassava (*Manihot esculenta*, Figure 2.4.2). There are dozens of common names for this crop. In Hawai'i, it can be known as tapioca. This plant is also originally from South America, but now it is widely cultivated in most tropical and subtropical regions including many Pacific islands. It is the third most important source of carbohydrates in the tropics, behind rice and corn. Cassava can grow in poor soils and in places with low rainfall. Proper cooking and preparation are important, as some varieties contain cyanide that needs to be removed before consumption. Cassava is a versatile crop and can be used in many ways: fried as in french fries, mashed as in mashed potatoes, fermented and made into an alcoholic beverage, and dried into different types of flour with long shelf life (e.g. tapioca flour). The tapioca balls in bubble tea are made of starches extracted from this root.

Another important root is 'uala or sweet potato (*Ipomea batatas*). They have been cultivated by Native Hawaiians since prior to European contact and were a very important source of carbohydrates for the population in the islands (Figure 2.4.1). Sweet potatoes are a very convenient crop as they grow in all kinds of environments: wet, dry, near sea level, and higher elevations. However, it was extensively cultivated in the Kohala agricultural system on Hawai'i Island (Lincoln and Vitousek, 2017). Many different varieties of sweet potatoes were grown in the past and this crop still is an important component of the diet today, although the majority of varieties grown locally are recent introductions to Hawai'i.

Sweet potatoes are native to South America, where they were first domesticated. They were cultivated in Hawai'i prior to European contact with Hawai'i and even the Americas. But how did they travel from South America to Hawai'i? There are a few hypotheses that try to explain this. One explanation is that the plant arrived by rafting, or getting a ride on oceanic currents (Montenegro *et al.*, 2008). However, there are linguistic similarities to the names used for sweet potato in Polynesia and the coast of Ecuador. The word for sweet potato in Polynesia is "kumala" which is similar to the original Ecuadorian Quechua word for sweet potato "kumara". In Hawai'i the sweet potato is known as 'uala (Adelaar, 2011). Therefore, it is plausible that Polynesians traveled by canoes as far as South America, traded with the native populations there and brought the sweet potato back home (Roullier *et al.*, 2013).



Figure 2.4.1: Sweet potato (*Ipomea batatas*). By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Adventitious roots

Roots usually grow underground, but some modified roots can grow above ground from the stem and they are called adventitious roots. We will subdivide adventitious roots into prop, buttress, and aerial roots.

Prop roots

Prop roots extend from the stem to the soil and provide extra mechanical support to the plant and an increased absorption capacity after they reach the soil. Hala (*Pandanus sp.*) is a great example of a plant with prop roots (Figure 2.4.2E). In this plant prop roots can grow 3- 4 meters (10-13 feet) long. Another good example is red mangrove (*Rhizophora mangle*) which is native to tropical and subtropical places; however, this species is not native to Hawai'i. The prop roots help to support branches, allowing the tree top to extend laterally, creating a beautiful maze of roots. This also helps the tree to withstand tidal changes and storm surges while creating habitat for fish and other aquatic organisms.

Buttress roots

These modified wall-like roots are characteristic of some large trees growing in the tropics, usually in shallow soils, providing the tree extra mechanical support. Ceibas are great examples of trees with buttress roots (Figure 2.4.2D).

Aerial roots

Most orchids are epiphytic, meaning they grow on top of other plants, like trees, and not in the soil. This means that their roots are not underground, but grow along the surface of the bark. However, this does not mean they are parasitic, as they are only using the tree as a place to grow and they still gather the water and nutrients from the environment to be able to carry on their photosynthesis. Orchid roots are covered in a thick layer of dead cells called velamen, which looks whitish, that helps to retain water (Figure 2.4.2B).

Parasitic roots

Some plants have specialized roots, called haustoria, that penetrate other plants to steal water and nutrients. These plants are called parasitic, but the level of parasitism differs among parasitic species. Some parasitic plants steal water and are still capable of undergoing photosynthesis to produce their own food, like the mistletoe plant. Other parasitic plants are absolute parasites that do not even have chlorophyll to be able to carry on the process of photosynthesis, meaning they must obtain water and food from

the host plant in order to survive. An example of a fully parasitic plant is dodder. The Kauna'oa kahakai (*Cuscuta sandwichiana*) is an example of a Hawaiian endemic plant that is fully parasitic (Figure 2.4.2C).

Reproductive Roots

Roots from certain species can produce new plants via asexual reproduction. This is very common in stems and relatively rare in roots. This type of modification allows the plant to grow a new individual from their root systems. This is the case of breadfruit. If the main breadfruit tree gets damaged by animals like pigs, the tree will send out new shoots from its root system. If the main tree dies, this new plant can grow and become a new tree. Even if the tree is only damaged, the new plant can grow and become its own individual. People all over the Pacific take advantage of this reproductive strategy to propagate breadfruit. Since many varieties do not produce seeds due to human domestication, the roots are used to propagate existing trees (Figure 2.4.2F).

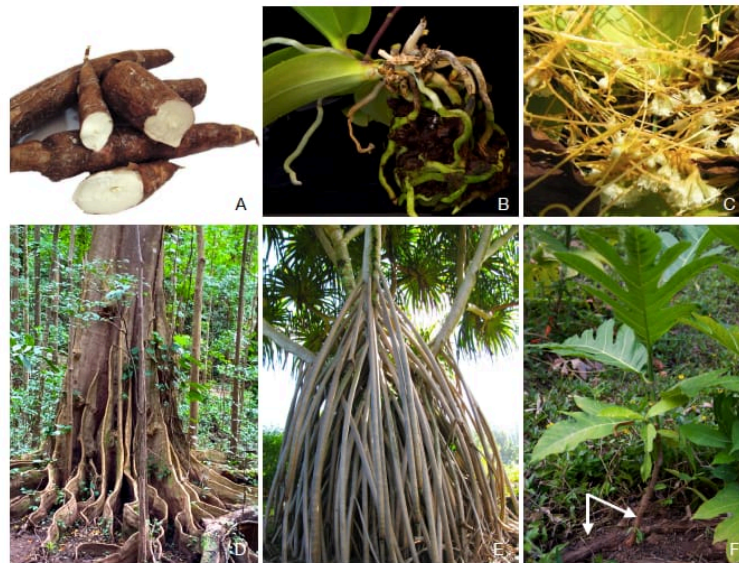


Figure 2.4.2: Modified root systems. A) Storage root (cassava), B) Aerial roots (orchid), C) Parasitic roots (parasitic vine, *Cuscuta sandwichiana*), D) Buttress roots (*Ficus* sp.), E) Prop roots (hala), and F) Reproductive roots (breadfruit). By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr. Modifications: Images A, C and E were combined with author's images (B, D and E) to form a plate/ A derivative from the original works (A: "Cassava Roots" is licensed by Renatosjoao, C: "Parasitic vine *Cuscuta sandwichiana*" and E: "*Pandanus tectorius* prop roots" by Forest & Kim Starr are licensed under CC BY 4.0).

Mycorrhizae

Mycorrhiza (myco = fungus; rhiza = root) is a symbiotic relationship that most plants have with fungi in their roots (Figure 2.4.3 ; mycorrhizae is the plural form of mycorrhiza). Symbiosis means "relationship" which can be mutualistic, commensalistic, or parasitic. Sometimes both partners get something from this relationship (mutualism), other times, the fungus or the plant may not get anything in return (commensalism; Pringle *et al.*, 2011). The fungal body is called mycelium (plural mycelia) and it is composed of root-like extensions called hyphae that absorb water and scavenge the soil for nutrients like phosphorus or nitrogen and give it to the host plant, increasing the total absorptive capacity of the plant. In exchange, the plant may give the fungus carbon (normally in the form of glucose) produced in photosynthesis.

There are two types of mycorrhizae: ectomycorrhizae (Figure 2.4.3A) where the fungi grows its hyphae (root-like fungi body) in the outermost layers of the cortex cells of the root. This type of mycorrhiza is commonly found in trees. Endomycorrhiza (Figure 2.4.3B) is when the hyphae penetrates the cortex cells, all the way to the endodermis. Sometimes the hyphae will swell up and form vesicles which store nutrients derived from the plant-fungus interaction (Figure 2.4.3B). The fungi does not damage the plant cells. Endomycorrhiza is found in woody as well as herbaceous plants.

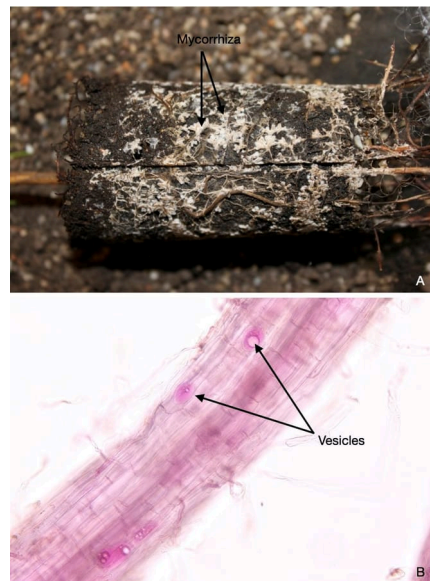


Figure 2.4.3: Examples of mycorrhizae. A) Ectomycorrhizal fungus on *Pinus muricata* seedlings, and B) Vesicles of an unidentified arbuscular mycorrhizal fungus on sunn hemp (*Crotalaria juncea*). By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr. A derivative from the original work by Nhu Nguyen is licensed under CC BY 4.0. Images were combined to form a plate and labels were added.

Root nodules

Nitrogen is one of the macronutrients plants need in order to grow. Although it comprises 79% of the air, plants cannot absorb it directly from the atmosphere. In fact, most organisms, including animals, cannot absorb nitrogen in its gaseous form. Fortunately, some nitrogen-fixing bacteria are capable of fixing or changing nitrogen into a usable form (i.e. nitrates). Some plants have the capability of forming a symbiotic relationship with some species of these bacteria in their roots, increasing nitrogen absorption. The plant forms a rounded structure in their roots called nodules that host and protects the nitrogen-fixing bacteria (Figure 2.4.4). Plants with this mutualistic association include plants in the legume family (Fabaceae) like beans, peas, and peanuts. Other families of plants are also able to have this kind of relationship with bacteria.

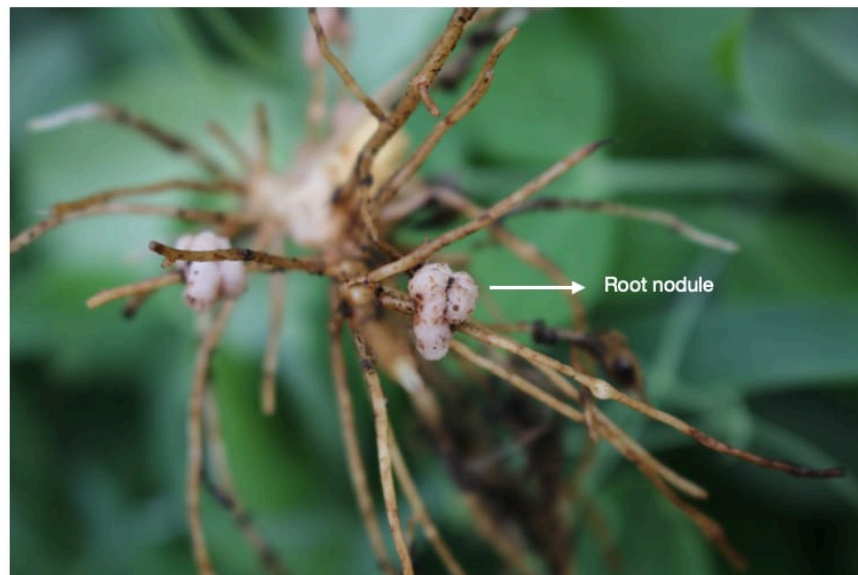


Figure 2.4.4: Root nodule of Fabaceae. Modified to include labels. By DutraElliott is licensed under CC BY BY-NC-SA 4.0 via Flickr. A derivative of the original work of "Cover crop Fabaceae nitrogen fixing root nodules with the bacteria Bradyrhizobium", by Foxy Tigre is licensed under CC BY 2.0 via flickr.

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2.5: References

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3: STEMS

Learning Objectives

After studying this chapter, you should be able to:

- Describe the parts of the stem and its main function.
- Describe the differences between the monocot and eudicot stems.
- List the name and function of the main woody stem tissues: bark, epidermis, phloem, vascular cambium, and xylem.
- Distinguish between primary growth and secondary growth in stems.
- Describe the composition of wood and its annual rings, sapwood, heartwood, and bark.
- List the main uses of stems.
- Describe the differences among modified stems: rhizomes, tubers, bulbs, stolons/runners, corms, and cladophylls.



3.1: Parts of the stem and primary growth

3.2: Secondary growth

3.3: Modified stems

3.4: References

3.1: Parts of the stem and primary growth

Stems play a huge role in our lives, as they have a vast range of uses, such as food, fuel, shelter, construction materials, furniture, light poles, musical instruments, and raw materials for a vast variety of paper products (paper towels, toilet paper, writing paper). One of the most important sources of carbohydrates worldwide is potatoes (*Solanum tuberosum*), which are a type of modified stem (tuber). Potatoes were first domesticated in South America about 8,000 -10,000 years ago and were taken to Europe in the 16th century. It is now cultivated worldwide and many cultures have incorporated it into their cuisines. In the Pacific many island nations cultivate taro/kalo (*Colocasia esculenta*), a modified stem called corm, which originated in China and migrated with people throughout the Pacific.

Stem anatomy

Stems are the vertical structures of plants where leaves attach. They are usually found above ground, providing mechanical support, conducting water and nutrients, and sometimes storing food. Stems can be woody (e.g. koa tree) or herbaceous (e.g. tomato), they can be tall as in sequoias (75 meters or 245 feet), or short as in 'ilima papa (12 cm or 5 inches); wide as in some cypress trees (11.5 meters or 36 feet) or thin as in sunflowers (2 meters or 6 feet).

In most woody flowering plants we can recognize **nodes** and **internodes** as the basic parts of the stem (Figure 3.1.1). The nodes are the places where leaves attach to the stem, while internodes are the spaces between the nodes.

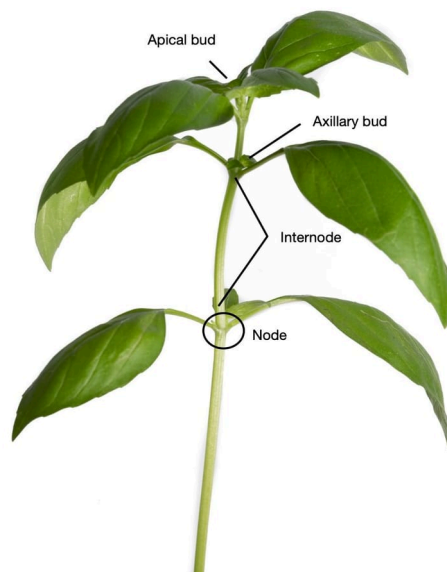


Figure 3.1.1: Herbaceous stem with opposite leaf arrangement in basil. By DutraElliott is licensed under CC BY-NC-SA 4.0.

Internal parts of the stem

Some stems are woody and some stems are herbaceous, which will define the type of tissues present inside of them. Monocots always have herbaceous stems, while eudicots can have herbaceous or woody stems. In both groups, the vascular tissue is arranged in bundles (vascular bundles), a region where you have both xylem and phloem grouped next to each other, and these bundles are surrounded by ground tissue, which is composed of cells called parenchyma. The organization of the vascular bundles is an identifying characteristic in monocots and eudicots. In monocots, like corn, these vascular bundles are scattered throughout the stem tissue. If you were to take a closer look at each vascular bundle in monocots, you will see alien faces, with big eyes (Figure 3.1.2). So if you are in the microscope and you find cute alien faces staring back, you know you are looking at a monocot stem. Eudicots, like beans and mango trees, are a little more complex. Eudicot stems can be herbaceous or woody. In herbaceous or young woody eudicots the vascular bundles are arranged in a ring fashion around the stem (Figure 3.1.2) and there are no cute alien faces on them. In older stems these bundles tend to fuse to form concentric rings.

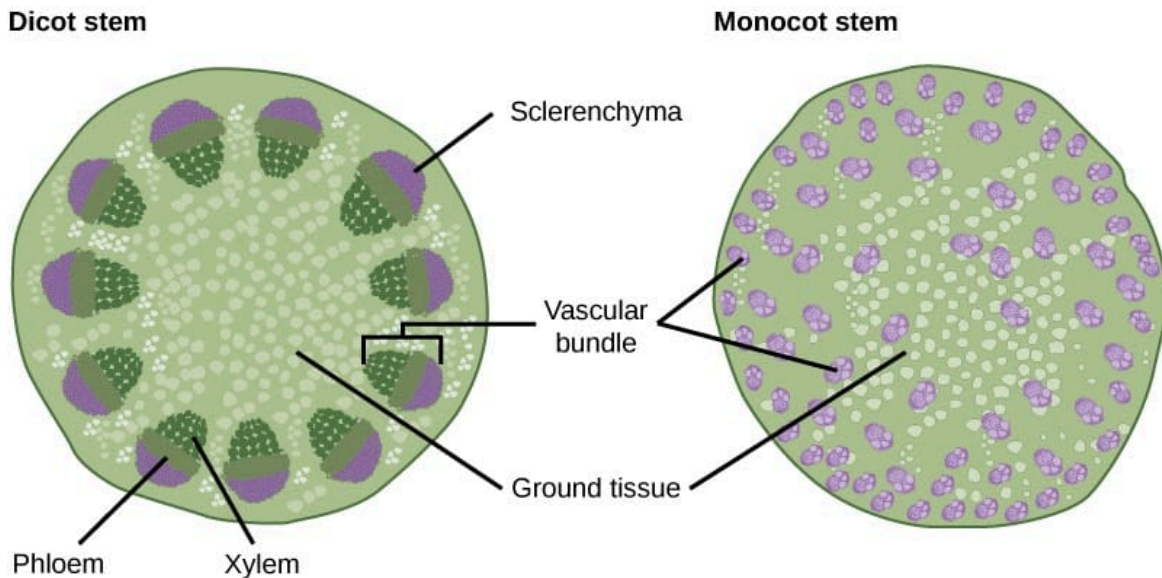


Figure 3.1.2: Distribution of vascular bundles in eudicots (ring) and monocots (scattered) by Openstax is licensed under CC BY 4.0.

Primary growth

Stems grow vertically and, similarly to roots, they have meristematic tissue on their tips, where cells are constantly dividing through mitosis, allowing the stem to elongate. This growth in length is called primary growth. Some plants can grow indefinitely for their entire lives, even for thousands of years. However, the rate of growth varies from plant to plant and it also depends on the environmental conditions where the plant is growing. Some plants can grow really fast, like albizia (*Falcataria moluccana*), an invasive species in Hawai'i, which can grow 4.5 meters (15 feet) per year (Little and Skolmen, 1989). Other plants grow very slowly, like the bristlecone pine trees in California, where a 5,000-year-old tree can measure just 18 meters (60 feet). Similarly, in Hawai'i, some o'hi'a lehua (*Metrosideros polymorpha*) trees are very short (30 centimeters or 12 inches) but can be as old as 300 years.

The meristem found on the tip of a stem is called the apical or terminal meristem, and it receives this name because it is located at the apex or end of the stem. In the stem, we also find meristematic tissue in the nodes, specifically in a little rounded bump found above the place of leaf attachment. They are called axillary buds and are found in the angle formed between the leaf stalk (petiole) and the stem (Figure 3.1.1). These buds are protected by bud scales, and they can become branches, flowers, or new leaves. Each new branch will develop its own apical meristem, ensuring that each branch can grow independently.

3.2: Secondary growth

Besides growing vertically, some plants also have secondary growth, meaning they also grow in diameter. This is especially true for plants that grow for several growing seasons (perennial), like woody plants (i.e. eudicots and gymnosperms). Herbaceous plants, like monocots and herbaceous eudicots, only grow for one growing season (annuals) and they do not present secondary growth. The tissues in woody stems, starting from the outer layer are bark, vascular cambium, sapwood, and heartwood (Figure 3.2.1). The bark consists of cork, cork cambium, and phloem. The vascular cambium is a layer of meristematic tissue that produces secondary xylem to the inside and phloem to the outside. This is the reason why woody plants can grow in diameter.

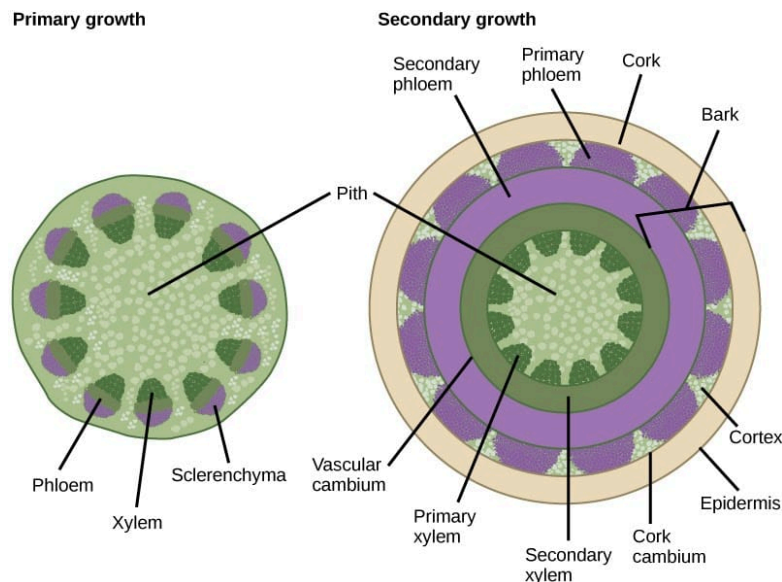


Figure 3.2.1: Primary versus secondary growth by Openstax is licensed under CC BY 4.0.

The tissue responsible for the secondary growth in woody stems is the vascular cambium. Vascular cambium is found in between the xylem and phloem in woody stems, it produces xylem to the inside of the stem and phloem to the outside of the stem. Because we are considering the secondary growth, we refer to the xylem produced by the vascular cambium as secondary xylem (wood). As the secondary xylem accumulates from one growing season to the next, the stem grows in diameter (this is called girth). In temperate climates plants grow according to the seasons, growing mainly during the spring and summer, resulting in clearly defined growth rings visible on woody stems (Figure 3.2.2). These growth rings provide information about the age of the tree, as usually, one growing season represents one year. Each ring consists of an area of light-colored wood (spring wood) that is formed during the spring when water is readily available for plant growth, and an area of dark wood (summer wood) that is formed late in the growing season when water availability is starting to decrease. Springwood consists of xylem cells that are larger in diameter (vessel elements), while the xylem cells in summer wood are smaller in diameter. The amount of water available during the growing season is correlated to the amount of spring wood produced in each ring; therefore, growth rings also provide insights into the climatic conditions prevalent during the growing season. For example, a thicker growth ring indicates a year with more precipitation/water availability than a thinner growth ring.

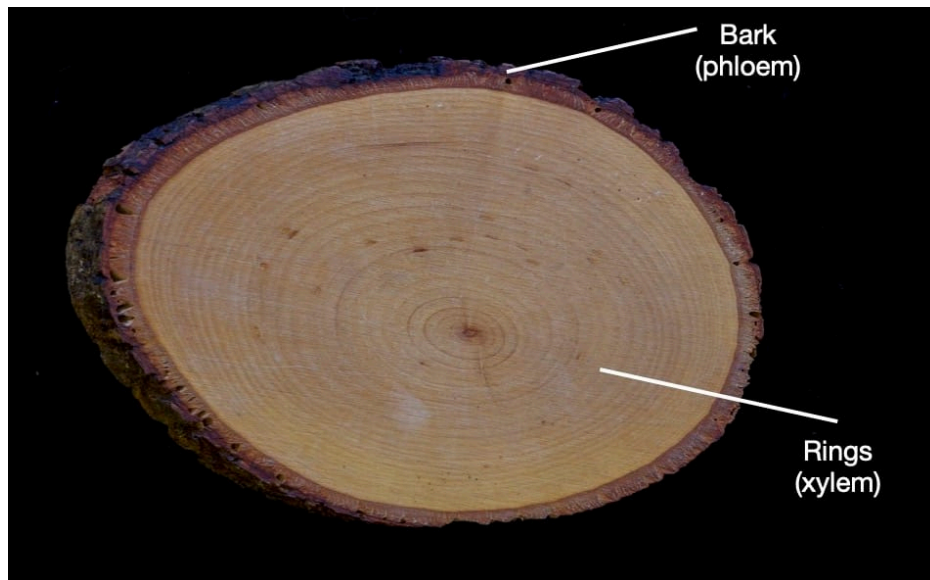


Figure 3.2.2: Growth rings in an eudicot tree. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Xylem in woody stems is what is called wood, and its main function is to transport water and nutrients. Functioning xylem (sapwood) is lighter in color and is found closest to the vascular cambium. Older xylem (heartwood) can be recognized because of its darker color, and it is found towards the center of the stem (Figure 5). This older xylem is no longer functional, however both sapwood and heartwood provide mechanical support for the plant. Many trees are able to survive and function normally after losing the heartwood, either to rotting or fire, as in the case of giant sequoias. Some trees in the tropics never stop growing because they may exist in a place without well-developed seasons. In this case, the tree may not produce rings (Figure 3.2.3).

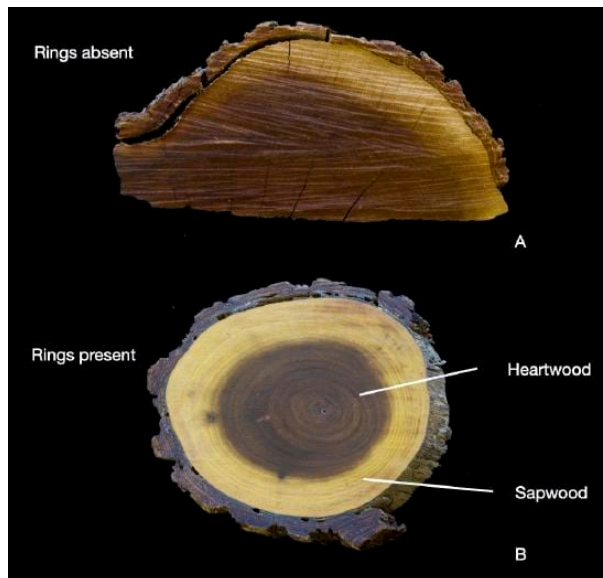


Figure 3.2.3: Woody stems. A) Eudicot woody stem showing no rings and B) Eudicot stem showing growth rings. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Wood or not wood?

It is important to note that not all woody stems are the same. The wood that is produced by eudicots is commonly called hardwood, while the wood produced by conifers, like pine trees is called softwood. The main difference between the wood from these two groups of plants is that wood from eudicots is composed of cells called vessel elements, fibers, and tracheids, while in conifers the wood is composed only of cells called tracheids. Other plants, like coconut or hala (*Pandanus sp.*, Figure 3.2.4), appear woody but they are not. Monocots are unable to produce wood, so they are mostly herbaceous, but that does not mean some species cannot grow tall. Some monocots can grow long stems by having thicker parenchyma cells in between the scattered

vascular bundles (e.g. coconut and hala), and other monocots have overlapping leaves with thick petioles wrapped around the stem that provide mechanical support (e.g. some palm trees), and other monocots have prop roots to increase the mechanical support of the stem (e.g. *hala*).



Figure 3.2.4: Monocot stem crosssection showing fibers (hala). By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Putting this knowledge into practice: How to kill an invasive tree

Invasive plant species in Hawai'i can be very problematic. Not only do they displace native species, but they can also cause damage to property and roads. Plants like albizia (*Falcataria moluccana*) grow really fast and are susceptible to falling during strong winds. One strategy that arborists use to kill albizia is a technique called girdling (Figure 3.2.5), where the outer layer of the stem is removed all the way around and the tree is left standing. Eventually, the tree dies, because as the outer layer is removed, the phloem and the cambium are removed from the tree. The tree is still able to photosynthesize, but the sugars coming from above the girdled region cannot reach the roots to feed the cells there, therefore the plant eventually starves to death. Since the cambium is also removed, the tree cannot produce new phloem. The only thing the tree is left with is the xylem, so it is still able to transport water up the stem. The tree can survive like this for several months, but it will eventually die. A standing dead tree can be dangerous since it will drop branches and can damage structures and harm people. Tree killing and removal should be done by professional arborists so that accidents don't happen.

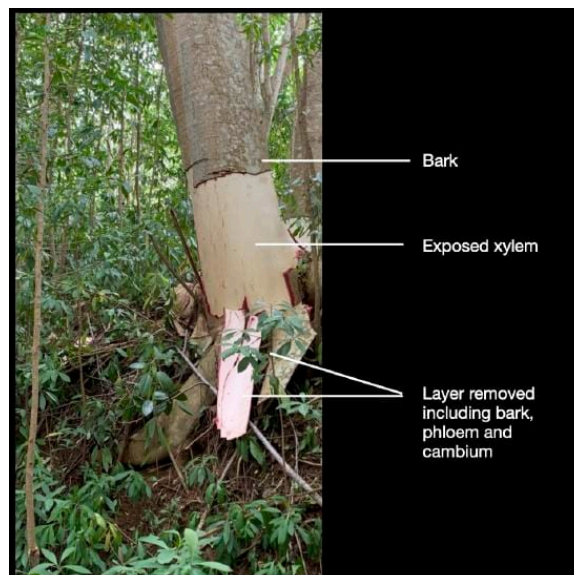


Figure 3.2.5: Girdling of an albizia tree. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

3.3: Modified stems

Stems come in different shapes and sizes and some plants have modified or specialized stems that serve other purposes. For example, some stems grow underground and are used by the plant to store food reserves. How can you tell if an underground plant structure is a stem or a root? Remember that stems have nodes and axillary buds, so if you look closely, you can see these structures in modified stems. Below are different types of modified stems.

Rhizomes

Rhizomes are underground stems that grow horizontally, with the function of storing nutrients and water. Examples of rhizomes include ginger (*Zingiber officinale*) and 'olena or turmeric (*Curcuma longa*). From these rhizomes, you can clearly see the nodes and internodes, with the roots emerging from the nodes (Figure 3.3.1).



Figure 3.3.1: Turmeric (*Curcuma longa*) A) Flower, B) Underground stem (rhizome), C) Leaves. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Stolons

Stolons are similar to rhizomes, but instead of growing horizontally underground, they grow mostly above ground (some will grow very shallow right below the surface). Stolons are used as asexual plant reproduction since a new plant (clone) can grow out of the nodes present in the stolons (Figure 3.3.2). Some grasses produce stolons and can spread from one area to another. At the base of each node, adventitious roots can grow and take hold.

Tubers

Some plants will form rounded or cylindrical structures called tubers on the tips of the stolons, which eventually detach from the main structure. The main function of tubers is the storage of carbohydrates. The plant may do this to store food underground to survive a drought or cold period. A good example of tubers is potato (*Solanum tuberosum*, Figure 3.3.2). If you look closely at a potato you will see little “eyes”. These “eyes” are the nodes and axillary buds, which can be used for plant propagation, as planting of these potato “eyes” will result in the growth of new plants. Another example is *pia* (*Tacca leontopetaloides*) which is a Polynesian introduced plant that is used for its starches (e.g. haupia).

Bulbs

Bulbs are modified short stems with many fleshy leaves. One example is onions and shallots. Bulbs have a very short and flattened stem that is called the “basal plate”. The structures above it are modified leaves (Figure 3.3.2).

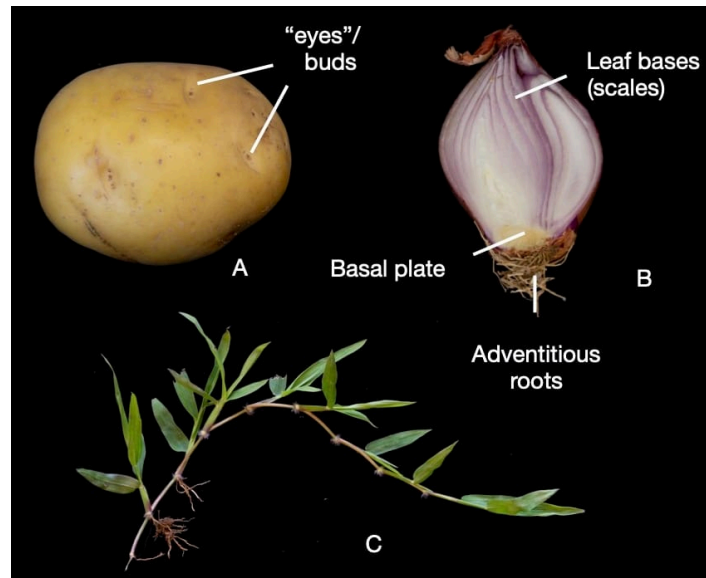


Figure 3.3.2: Examples of modified stems: A) Tuber (potato), B) Bulb (shallot), and C) Stolon (grass). By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Corms

Corms are underground stems that are vertical. It is normally an organ for the plant to store nutrients. In non-cultivated plants, this is important to survive winter or drought times. In cultivated plants, these structures are selected for and eaten for their carbohydrates. For example, the corm of taro/kalo (*Colocasia esculenta*) is steamed and made into poi or eaten in a diversity of dishes (Figure 3.3.3). Before European contact, kalo provided one of the main sources of carbohydrates for Hawai'i's population. About 80 kalo varieties remain in the Hawaiian Islands (Lincoln and Vitousek, 2017) which are cultivated in lo'i (wetland agricultural systems developed by Native Hawaiians) and dryland. Roots grow out of the nodes of the corm and they are normally removed before cooking. Axillary buds are also located on the nodes and will give rise to other shoots ('oha). All these plant parts have names in the Hawaiian language (see [Levin, 2008](#)) and are used as morphological keys to identify varieties. Before European contact, kalo provided one of the main sources of carbohydrates for Hawai'i's population.

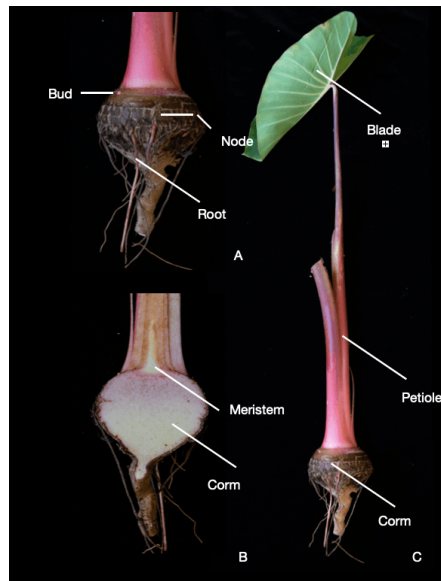


Figure 3.3.3: Taro/*kalo* (*Colocasia esculenta*). A) Corm close up with nodes, roots and buds, B) Corm dissection showing meristem or growing point where new leaves are produced and C) Whole taro plant showing petiole and blade. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Cladodes

Cladodes are flattened stems like the stems seen in cacti. Cladodes are green, sometimes may even look like leaves and they are capable of performing photosynthesis. In cacti, the spines found in the cladodes, are modified leaves that serve as a protection structure against herbivores (Figure 3.3.4).

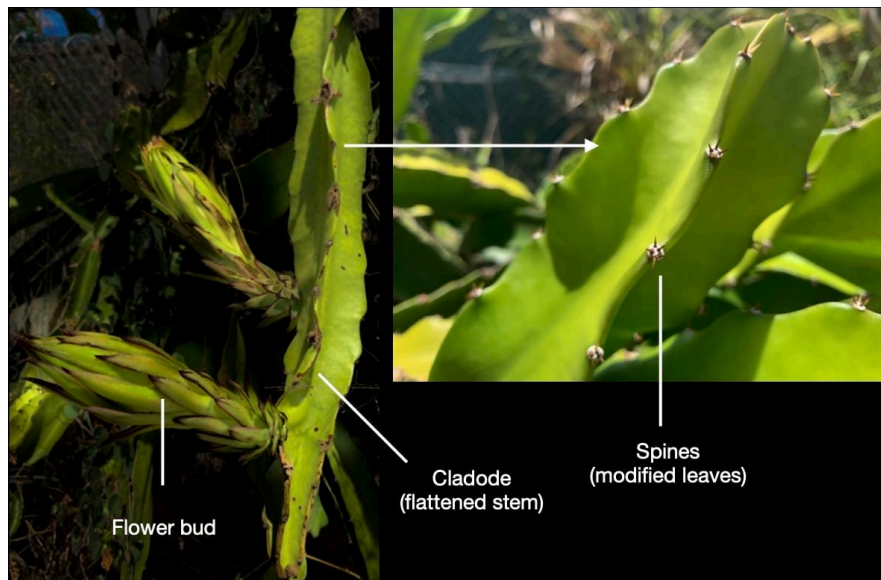


Figure 3.3.4: Dragon Fruit Cladode By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

3.4: References

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4: LEAVES

Learning Objectives

After studying this chapter, you should be able to:

- Identify where stomata are located.
- Identify the internal structures of a leaf.
- Identify the external forms and parts of leaves.
- List the leaf tissues and their functions.
- Describe the difference between pinnate, palmate, and parallel venation, and the differences between simple and compound leaves.
- List some of the most important economical uses of leaves.



4.1: Leaf structure

4.2: Internal leaf characteristics

4.3: Photosynthesis

4.4: Modified leaves

4.5: References

4.1: Leaf structure

Leaves are commonly used in our day to day lives, from the fresh salad we may eat for dinner to perfumes, leaves are used to make a diversity of products. Some leaves even have great economical importance. The most important product derived from leaves is tea (*Camellia sinensis*), which is the most widely consumed beverage. The growing, harvesting, and processing of tea is very intricate and the end product is highly valued around the globe, an industry worth billions of dollars per year. Other products derived from leaves include essential oils extracted used in cleaning products, medications and bug repellent. The oil from citronella/lemongrass leaves (*Cymbopogon citronella*) are extracted and used to enhance flavor in foods, in cosmetics, perfumery, and in vitamins, among other products. The leaves of lemongrass, mint (*Mentha spicata*), and *māmaki* (*Pipturus albidus*) are used to make herbal teas (Figure 4.1.1). Many people around the world use the leaves of hundreds of plant species for medicinal purposes. In Hawai'i, *māmaki* leaves are used for traditional medicinal uses.



Figure 4.1.1: Māmaki (*Pipturus albidus*) is a native plant that grows in the wild and can also be cultivated. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Leaves are variable in shape, size, and color. Some palm tree leaves can measure 4–6 m (13–20 ft) in length, while duckweed leaves are tiny as 1 millimeter (0.04 inch). In regards to shape, some leaves are like needles, as in pine trees, or they can be very broad like in *kalo* leaves. Plants are able to synthesize their own food using sunlight and carbon dioxide. In turn, humans and other animals rely on plants for food and oxygen that they also produce.

Parts of the leaf and leaf attachment

The flat part of the leaf is called the lamina or blade. Leaves normally attach to the stems by a short stalk called the petiole. The leaf lamina has a midrib where the vascular tissues are located. From the midrib, smaller veins, also containing vascular tissue, branch out. The edge of the blade is called the margin (Figure 4.1.2). Leaf margins differ in plants and are used as an identification tool for species. They can also vary in different environments, for example, most plants in tropical rainforests have entire (smooth) margins, while plants in temperate regions usually have margins with teeth.

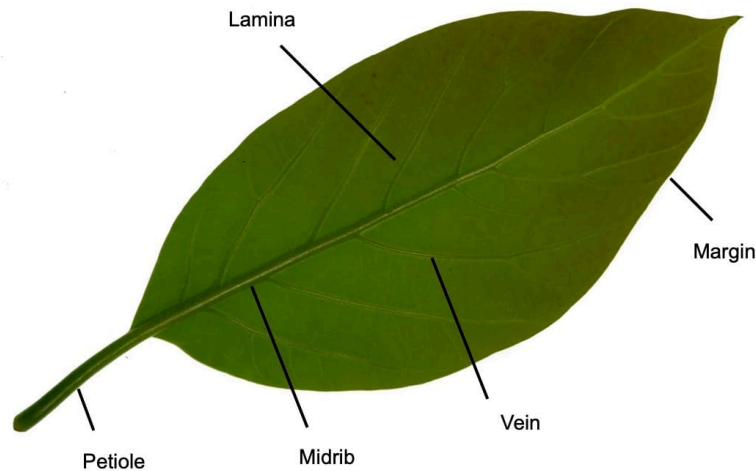


Figure 4.1.2: Parts of a simple leaf (avocado, *Persea americana*). By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Leaves attach to the stems at the nodes, and the space between nodes is called internodes. If we take a closer look at the nodes, we will find that in the angle between the leaf stalk (petiole) and the stem, there is a little rounded bump called a bud, which is composed of dormant meristematic tissue that can develop into flowers, branches, or leaves (Figure 4.1.3).

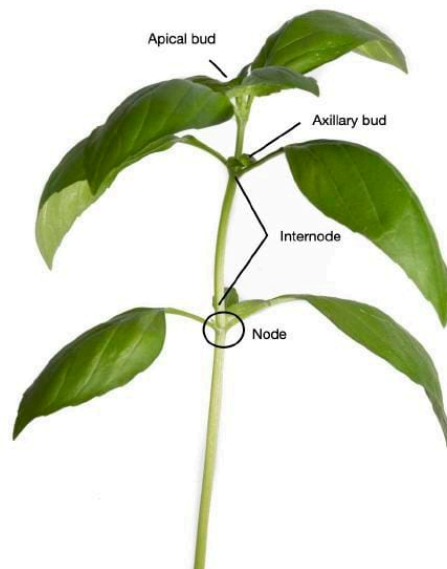


Figure 4.1.3: Basil stem showing nodes, internodes and buds. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

The pattern of leaf attachment to the stem (phyllotaxy) varies in plants and it is commonly used for identification purposes. For example, in some plants two leaves attach on opposite sides of a node (opposite), in others there is only one leaf per node (alternate), in others 3 or more leaves attach around the stem at the same node, forming a whorl of leaves (whorled), or even forming a spiral around the stem by slightly rotating the attachment position in each subsequent node (spiral; Figure 4.1.4).

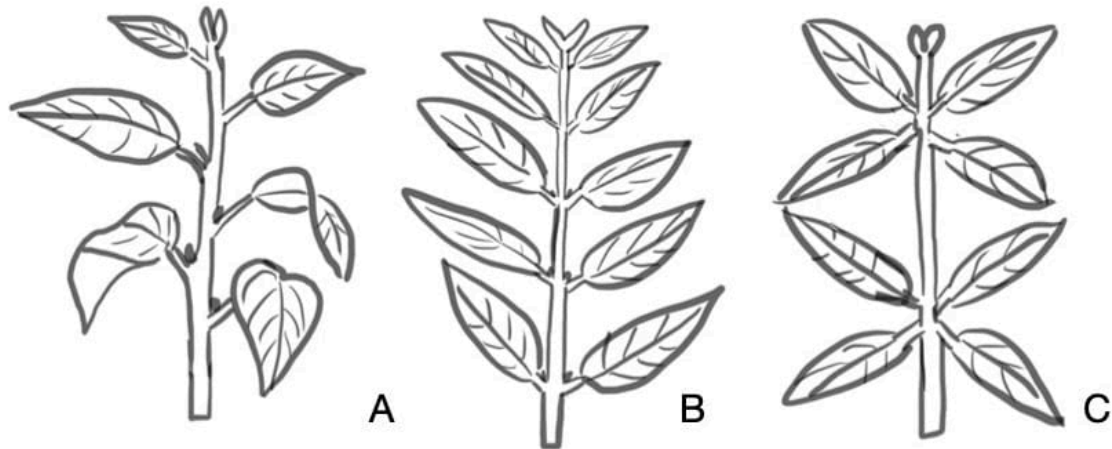


Figure 4.1.4: Examples of leaf attachment patterns. A) Alternate, B) Opposite, and C) Whorled. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Simple vs. Compound leaves

Leaves may be simple or compound, meaning they can have one or several lamina (blades). In a simple leaf, the lamina is undivided or it has lobes, but the lobes do not reach the midrib (Figure 4.1.5). In a compound leaf, the leaf lamina is completely divided, forming smaller independent “leaves” called leaflets (Figure 4.1.5).

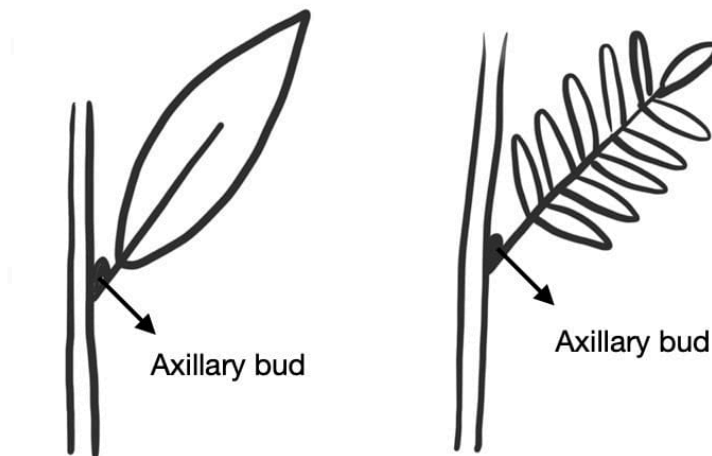


Figure 4.1.5: Simple vs. compound leaves. A) Simple leaf and B) Compound leaf showing leaflets. By DutraElliott is licensed under CC BY BY-NC-SA 4.0 via Flickr.

Each leaflet has its own petiole but is attached to the midrib, which in compound leaves is called rachis. There are different types of compound leaves, depending on how the leaflets are arranged. In pinnately compound leaves the leaflets are arranged on both sides along the rachis (e.g. starfruit, Figure 5B). Double pinnately compound leaves or bipinnately compound leaves are similar to pinnately compound leaves, but each leaflet is further divided into even smaller leaflets (e.g. albizia; Figure 4.1.6). In palmately compound leaves leaflets attach to a single point and radiate from there, resembling the palm of a hand (Figure 4.1.6). An example of a plant with palmate compound leaves is *Schefflera* sp. (umbrella plant).

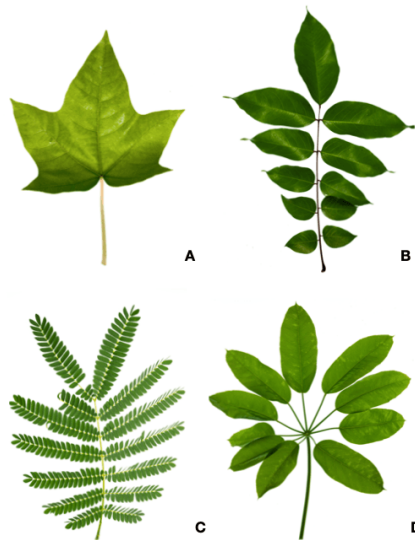


Figure 4.1.6: Examples of simple and compound leaves: A) Simple leaf (kukui, *Aleurites moluccanus*); B) Pinnately compound leaf (starfruit, *Averrhoa carambola*); C) Bipinnately compound leaf (albizia, *Falcataria moluccana*); and D) Palmately compound leaf (umbrella tree, *Schefflera actinophylla*). By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Leaf venation

Veins in leaves are arranged in different patterns and they are another characteristic that is very helpful in plant identification (Figure 4.1.7). Pinnate leaf venation is the first to come to mind when we think about a typical leaf. In pinnate venation, there is a midvein or midrib and secondary, smaller, veins branching to either side of the midvein. An example of a plant with pinnate venation on its leaves is avocado (Figure 4.1.7). In parallel venation, secondary veins are parallel to the midrib and each other. Parallel venation is characteristic of monocots, like grasses and kī/ tī (Figure 4.1.7), although there are some exceptions (e.g. kalo). In palmate leaf venation, there are several main veins of similar thickness that radiate from a single point at the base of the leaf (e.g. kukui leaf; Figure 4.1.7). In eudicots, the branching pattern seen as the veins further divide into smaller veins resembles a net, so it is called reticulate (netted) venation.

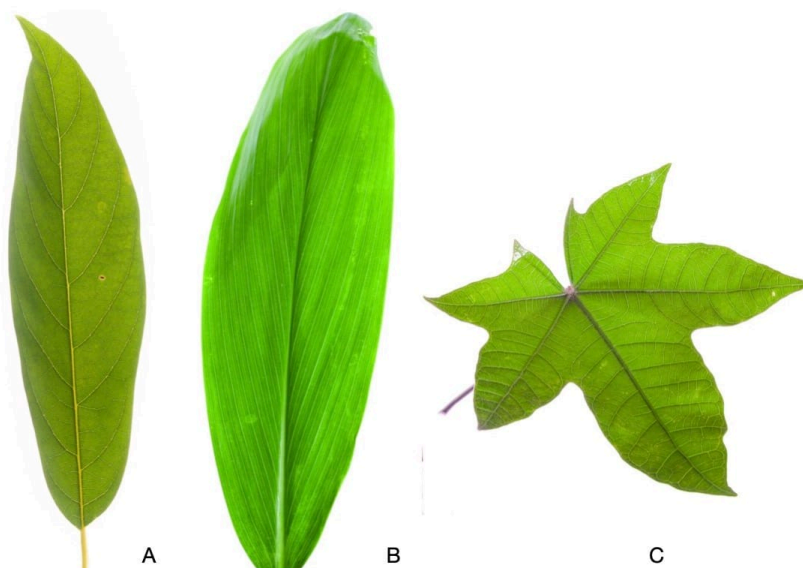


Figure 4.1.7: Types of leaf venation: A) Pinnate venation, B) Parallel venation, and C) Palmate venation. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Leaf Margins

Leaves have a diversity of margin types or edges, which is a very useful characteristic in plant identification. Examples of the most common margin types are entire, dentate, and serrate (Figure 4.1.8). If you are trying to identify a plant to the species level, you will likely encounter keys and descriptions that include leaf margins and there are many to choose from.

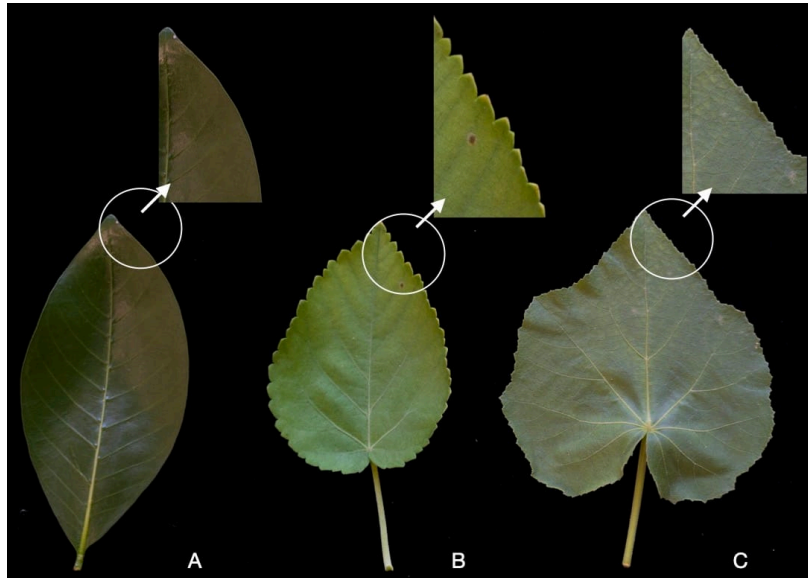


Figure 4.1.8: Simple leaves with different margins. A) Entire (*puakenikeni*, *Fagraea berteroana*), B) Dentate (*'ilima*, *Sida fallax*), and C) Serrate (*'akiohala*, *Hibiscus furcellatus*). By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

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4.2: Internal leaf characteristics

Leaves have three main internal regions; the epidermis, the mesophyll, and the veins. The epidermis is the outermost layer, being present on the top and bottom of the leaf, the upper and lower epidermis, respectively (Figure 4.2.1). The epidermis is usually one cell layer thick, but it can be several layers thick in plants growing in arid environments, to prevent excessive water loss. A waxy layer known as the cuticle is found outside of the epidermis. The cuticle is made of a waxy substance that helps to reduce water loss. Some leaves may have small hairs (trichomes) on the leaf surface, which help to decrease herbivory either mechanically (reducing insect movement) or chemically (producing chemicals). They can also reduce transpiration by reducing airflow on the leaf surface or by reflecting sunlight, protecting the plant against UV damage.

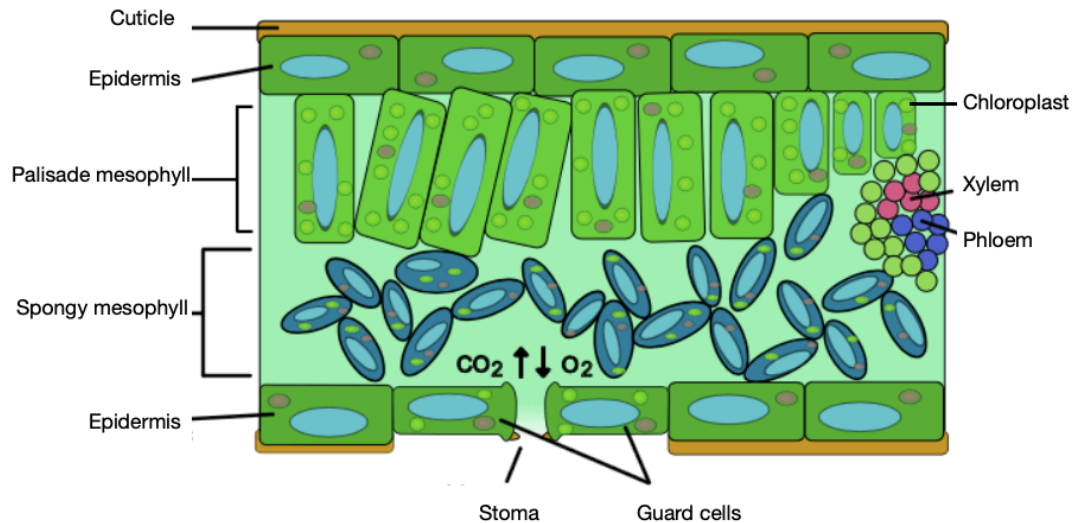


Figure 4.2.1: Internal leaf anatomy. Modified to replace Russian with English labels and added chloroplast. By Chan, CC BY 3.0, via Wikicommons.

The epidermis protects the inner leaf tissues and helps in the regulation of gas exchange. It possesses small openings called stomata, that facilitate gas exchange (Figure 4.2.2). Carbon dioxide (CO_2), needed for photosynthesis, enters the leaf through the stomata, while oxygen, a product of photosynthesis, and water vapor from transpiration exit. In most plants, stomata are usually located in the lower epidermis. The opening and closing of the stomata are controlled by guard cells, which surround each stoma. Climatic conditions, water availability in the soil, and the time of the day affect the opening and closing of stomata. For example, most plants close their stomata during the nighttime as the CO_2 required is only needed when sunlight is available for photosynthesis.

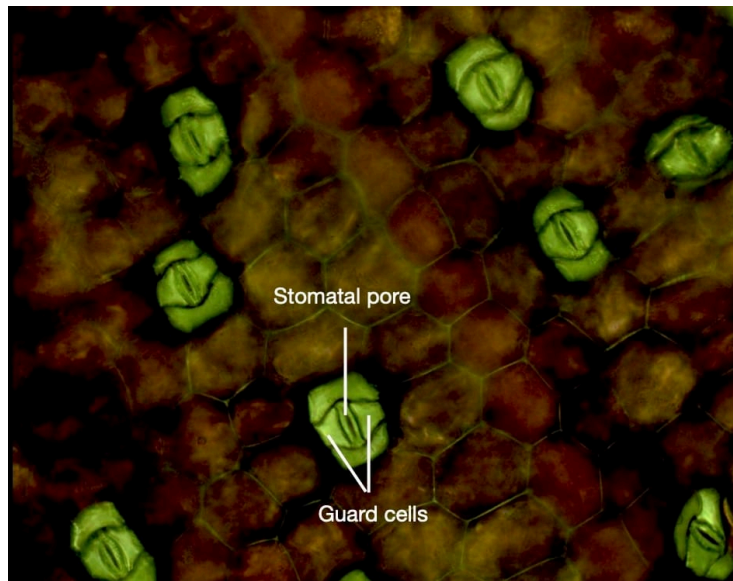


Figure 4.2.2: Stomata on the leave of purple heart (*Zebrina sp.*) By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr. A derivative from the original work "Stomata top view" by AioftheStorm, Public Domain, via Wikimedia Commons. Modified to include labels.

In between the upper and lower epidermis is the mesophyll, which has two differentiated regions. The palisade mesophyll is found just below the upper epidermis and it is composed of parenchyma cells closely arranged in a brick-like fashion. These cells are packed with chloroplasts and it is here where most of the photosynthesis takes place. The other region is called the spongy mesophyll and it is composed of loosely arranged parenchyma cells that have numerous air spaces in between (Figure 4.2.1). The veins are the third tissue present inside the leaves. Veins contain bundles of vascular tissue, xylem for transporting the water for photosynthesis and transpiration, and phloem for transporting the sugars produced in photosynthesis.

4.3: Photosynthesis

One of the most amazing things about plants is that they can make their own food through photosynthesis. Photosynthesis is the chemical process in which plants transform sunlight into chemical energy. The process has evolved for millions of years and thanks to it, humans can survive by eating the bounty produced by plants and breathing the oxygen released as a by-product. How does that happen? To photosynthesize plants need the energy of the sun, water from the soil, and carbon dioxide from the atmosphere. The chemical reaction then gives rise to glucose (sugars/carbohydrates), water, and oxygen (Figure 4.3.1). The sugars produced are either used by the plant for growth and development or are stored in the plant. Sweet potato plants are known to store carbohydrates in their roots while aloe plants store it in their leaves.

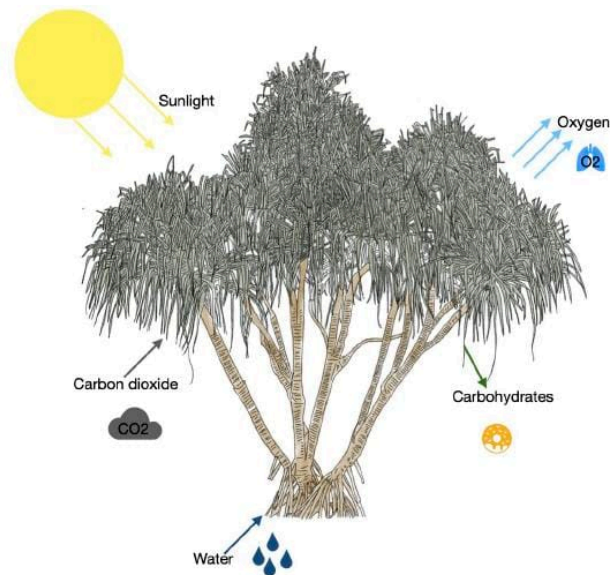


Figure 4.3.1: Simplified view of photosynthesis. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Photosynthesis happens in a cell organelle called chloroplast, which contains a pigment called chlorophyll. There are two main phases of photosynthesis. A light-dependent reaction and the Calvin Cycle (light-independent reaction). During the light-dependent reactions, sunlight and water are needed. Water molecules split, in a series of light reactions, releasing oxygen. The energy generated in this step is used to fix the carbon dioxide into glucose (sugar) during the second phase of photosynthesis or the Calvin Cycle (Figure 4.3.2).

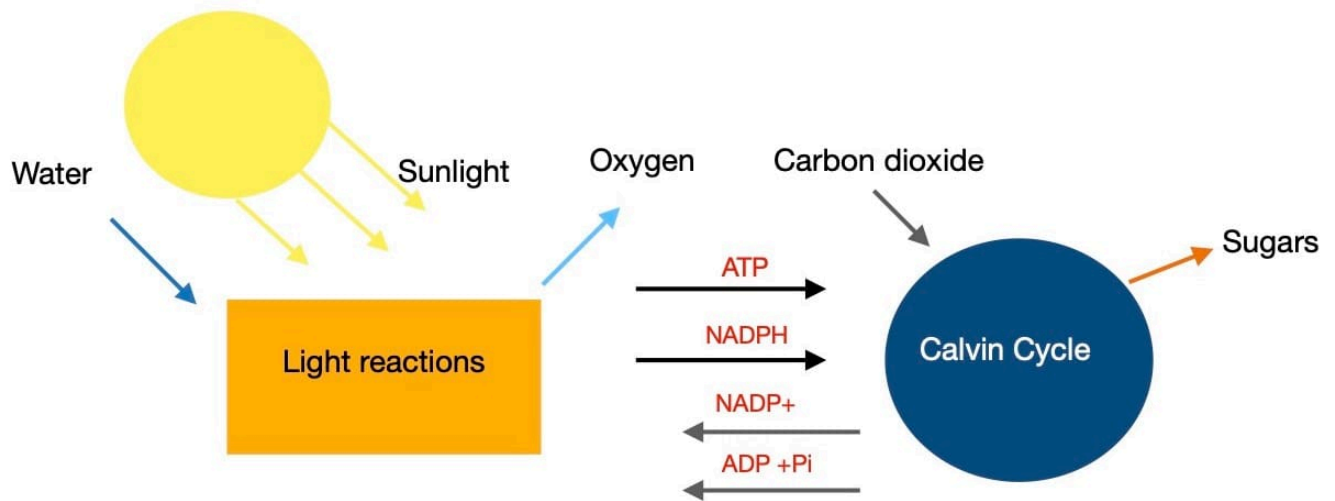


Figure 4.3.2: Photosynthesis light dependent and independent (Calvin Cycle) phases. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

4.4: Modified leaves

Some plants have leaves that have been modified to do jobs besides photosynthesis. Here are some examples:

Bracts

Leaves in some species are modified to have different colors and look like petals. Their main function is to attract pollinators. In the case of *Bougainvillea sp.*, flowers are small and creamy and are found in the middle of three pink petal-like modified leaves known as bracts (Figure 4.4.1A).

Spines

Spines are modified leaves used for protection against herbivores. They have also evolved as a water-saving strategy in some plants. For example, most cacti, like dragon fruit, have spines instead of regular leaves (Figure 4.4.1B).

Reproductive leaves

Some plants, like *Bryophyllum daigremontianum*, produce plantlets along the margins of their leaves. Eventually, the new plants fall off and become separate from the main plant. This is an example of asexual reproduction. The new plants are identical to the mother plant (Figure 4.4.1C).

Tendrils

Tendrils are modified leaves used for climbing or support. For example, cucumbers use tendrils to climb and serve as a support structure for the plant (Figure 4.4.1D).

Storage leaves

These leaves are modified to store water and/or nutrients for the plant. One example is aloe. There are about 500 species in this genus, and most of them are drought-resistant. *Aloe vera* is cultivated as a medicinal plant and the leaves are used to treat sunburn, among other things (Figure 4.4.1E).

Trap leaves

Some leaves are modified to trap insects. These trapping leaves have evolved due to low nutrient availability in the soil where they grow, so plants with these leaves can gather nitrogen and other nutrients from the bodies of the insects they trap. For example, the Venus flytrap (*Dionaea muscipula*) and sundew (*Drosera spp.*) grow in bogs where nitrogen is not easily available. *Drosera anglica* or mikinalo is indigenous to the island of Kaua'i. Its leaves are covered with glands that secrete mucilage used for trapping insects (Figure 4.4.1F).



Figure 4.4.1: Types of modified leaves. A) Bracts, B) Spines, C) Reproductive leaves (e.g. *Bryophyllum daigremontianum*), D) Tendrils (e.g. cucumber), E) Storage (e.g. aloe), F) Trap leaves (e.g. *Drosera anglica*). "Types of modified leaves" by DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr. A derivative from the original works ([C](#), [D](#), [E](#), [F](#)) put together on a plate with labels and the addition of two photos by the author (A and B).

4.5: References

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5: FLOWERS, FRUITS AND SEEDS

Learning Objectives

After studying this chapter, you should be able to:

- Identify the parts of a flower.
- Identify a monocot or an eudicot based on the flower characteristics.
- Identify different types of fruits .
- Identify the parts of a seed.
- List some uses of flowers, fruits, and seeds.



5.1: Flowers

5.2: Plant reproduction- pollination and fertilization

5.3: Fruits

5.4: Seeds

5.5: References

5.1: Flowers

Angiosperms (flowering plants) are the only group of plants to produce flowers. Flowers are rather diverse, coming in different colors, sizes, and shapes (Figure 5.1.1). Some have fragrances to attract pollinators and many offer pollen and nectar to reward the pollinator's visit. Flowers are in great part responsible for the incredible success of this group, as they can enlist help from animals like bees, butterflies, and birds to transfer pollen from one flower to another, while other groups of plants, like conifers, have to rely only on the wind for this same purpose. Flowers co-evolved with pollinators assuring that flowering plants could reproduce successfully and ensuring genetic diversity in the population. Nectar and pollen are not the only rewards offered by plants, flowering plants also offer fruits as a reward to dispersers who, in turn, take the seeds away from the mother plant and are; therefore, able to colonize new areas.

For thousands of years, humans have been fascinated by flowering plants' reproductive structures; flowers and fruits. Many fruits are sweet and can be eaten, while flowers have been used in cultural, medicinal, and religious practices. For example, in pre-European contact Mesoamerica, in what is now called Mexico, flowers were used in many aspects of day-to-day life. Today these traditions remain strong, with flowers being used to decorate altars and graves, as well as for medicinal purposes. In Hawai'i cultural practices can be observed with the use of flowers, fruits, and seeds for hula, lei making, and celebrations such as weddings and graduations.



Figure 5.1.1: Examples of tropical flower diversity. A) Koki'o 'ula (*Hibiscus clayi*), B) Pua kala (*Argemone glauca*), C) 'Ōhai (*Sesbania tomentosa*), D) Orchid (*Dendrobium sp.*), E) Liliko'i (*Passiflora edulis*), F) Anthurium (*Anthurium sp.*). By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Flower Parts

To understand how flowers are involved in the sexual reproduction of plants, we first need to identify the flower parts. Flowers contain the female and male reproductive structures of flowering plants. The female reproductive structures are organized into the **pistil**, which consists of the **stigma**, **style**, and **ovary**. The stigma is the very top part of the pistil. It is usually flattened and sticky, as pollen grains that come from other flowers need to be collected here for sexual reproduction to happen. The style is a tube that connects the stigma to the ovary. And finally, the ovary is the rounded portion at the base of the flowers, and it contains the eggs (ovules). The male parts of the flower, on the other hand, are called **stamen** and they are composed of the **anther** and the **filament**. The anther is a double canoe-like structure where pollen grains are produced, and the filament is the stalk that supports the anther (Figure 5.1.2).

Besides containing the plant's sexual organs, flowers also have other parts, which are collectively called the perianth. The perianth is composed of **petals** and **sepals**. The petals are the colorful flower parts that attract pollinators. At the base of the flower are

the sepals, which are green leaf-like structures that protect the flower in bud.

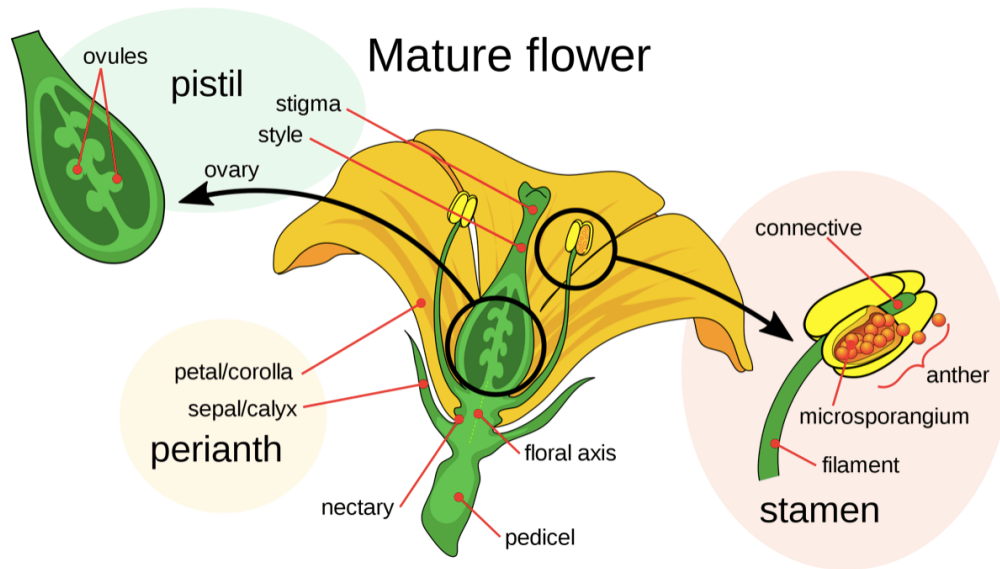


Figure 5.1.2: Diagram of a perfect flower. Image by LadyofHats is licensed under Public Domain via Wikimedia Commons.

Flowers from different species are unique, with variations in the way these basic parts described above are distributed. When you think about a typical flower, as the one shown above (Figure 5.1.2), the stamen and pistil are normally found independently. However, this is not always the case. Flowers in the *Hibiscus* genus, for example, have the style from the pistil and the filaments from the anthers fused forming a single long tube, in which the anthers branch out close to the stigma (Figure 5.1.3).



Figure 5.1.3: Flower parts and dissection of Koki'o ke'oke'o (*Hibiscus arnottianus*) flowers. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Flowers can be **perfect**, having both male and female parts, or **imperfect**, having just one sex (male or female). Koki'o ke'oke'o is an example of a perfect flower, with both stamen and pistil (Figure 3). Imperfect flowers also come in different arrangements. Male and female flowers (imperfect) may be found growing in the same plant, as it happens in the breadfruit tree (*Artocarpus altilis*, Hawaiian 'ulu or Samoan and Tongan ma'afala), pictured below (Figure 5.1.4).

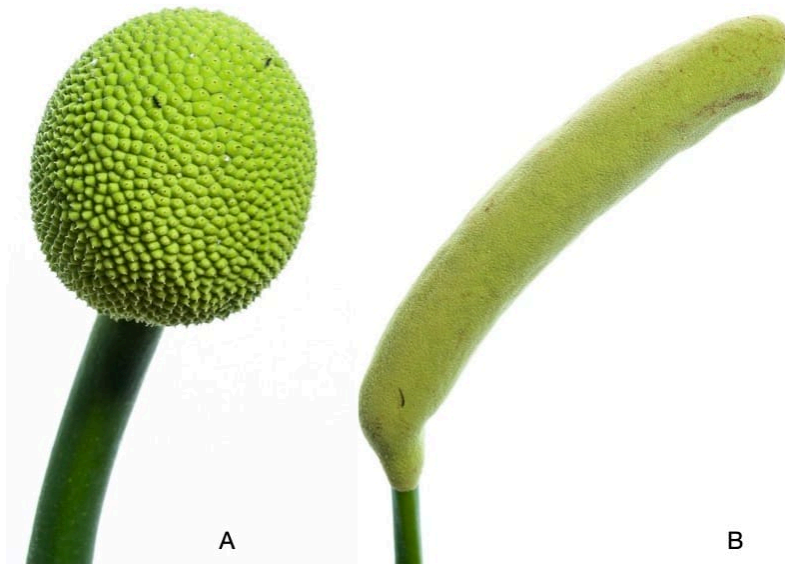


Figure 5.1.4: Flowers of breadfruit (*Artocarpus altilis*): A) Female flower, variety of ma'afala. B) Male flower. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Imperfect flowers can also be found in separate trees. For example, hala (*Pandanus*) has female flowers growing on one plant while male flowers grow on another, so the plant is either male (Figure 5.1.5) or female (Figure 5.1.6). A plant is called **dioecious** when it has male and female flowers on separate plants. This only happens in a minority of plants, as most plants are **monoecious**, having both male and female flowers on the same plant. How can you remember this? Breaking down the words into their roots is a good way. For example “di” means two, so you have two houses while “mono” means one (one house). Or just think about animals, we are dioecious because you can have either a male or a female.

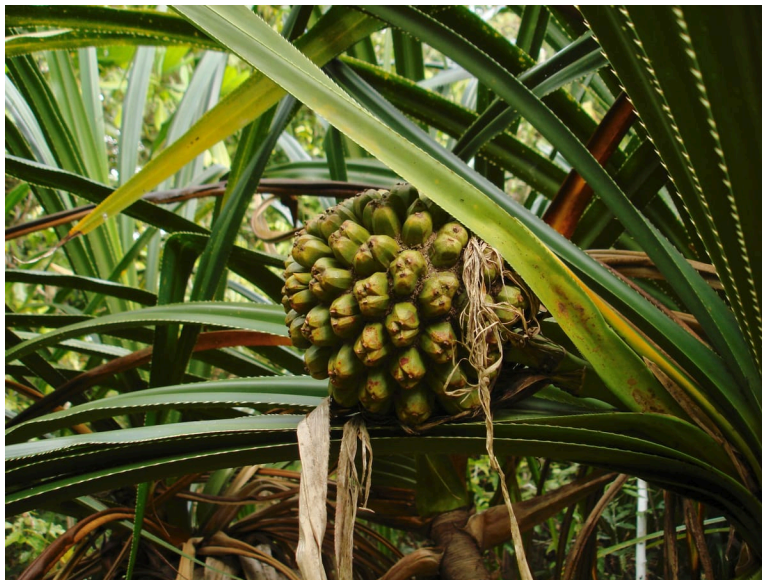


Figure 5.1.5: Female hala tree (hala hua, *Pandanus tectorius*) with fruit ('āhui hala). “Hala (*Pandanus tectorius*)” by Lauren Gutierrez is licensed under CC BY-ND 2.0.



Figure 5.1.6: Male hala tree with (male) flowers (hīnano). “Hala (*Pandanus tectorius*)” by David Eickhoff is licensed under CC BY-ND 2.0.

Flowers of Monocots and Eudicots

Monocots and eudicots are the two largest groups of flowering plants, and they can be easily recognized based on their flower parts. Flower parts (e.g. petals, sepals, stamens) in monocots are arranged in 3 or multiples of 3, while eudicot flowers are arranged in 4 or 5 or multiples of 4 or 5. Therefore a monocot flower may have 6 stamens and 6 petals (Figure 5.1.7). Eudicot flowers, on the other hand, may have 5 petals (Figure 5.1.8). This comes in handy when you are trying to identify plants in the field. Finding out if a plant is a monocot or an eudicot is the first step in plant identification because you can rule out several plant families. If the plant is a monocot, then you will only look at monocot families from that point onward.

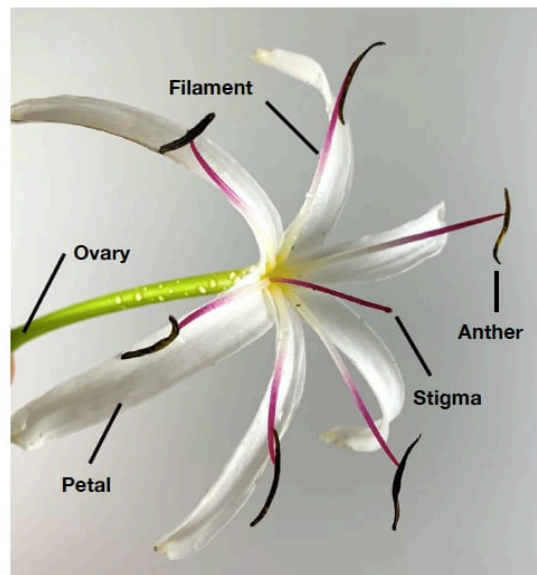


Figure 5.1.7: Spider lily (*Crinum asiaticum*) is a monocot and a recent introduction to Hawai‘i. The large flowers can be easily used to identify flower parts. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.



Figure 5.1.8: Example of an eudicot flower. Ha'u (*Hibiscus tiliaceus*) flower dissection. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

5.2: Plant reproduction- pollination and fertilization

The process of sexual reproduction in plants consists of several chronological steps:

1. Production of flowers
2. Pollination
3. Fertilization (produces seeds)
4. Formation of fruits

As with animals, for sexual reproduction to happen in plants the sperm needs to join the egg. The sperm of plants is contained in the pollen grains, therefore the **pollen** must be transferred to another plant for sexual reproduction to take place. Since plants cannot walk to find a mate, they have to use other means of bringing the pollen to the egg. **Pollination** is defined as the transfer of pollen from the male part of a flower to the female part of the flower, usually the flower on another plant. Some species of plants will self-pollinate (pollen is transferred to the stigma of the same flower); however, the majority of flowering plants out-cross (are pollinated by another plant). This interchange of genetic material, a characteristic of sexual reproduction, increases diversity in the population. Genetic diversity is important because that's how plants can adapt to new challenges. If all plants in a population have the same genetic makeup (clones), as is the case with plants that reproduce mainly asexually (e.g. bananas), they may all get killed by a disease. However, if some plants in the population have a different gene that provides resistance to that disease, they will survive and be able to pass on their genetic material to their offspring. Flowers provide a clear advantage to flowering plants, allowing them to reproduce sexually. This is one of the reasons why flowering plants are so successful and are the dominant group of plants in most of the terrestrial ecosystems on our planet.

In some plants, like pine trees, the pollen is transported by water or by wind. This strategy is very energy-consuming for the plant, as it requires the plant to produce millions of pollen grains to ensure that at least some of them will reach a nearby female flower of another plant. Flowering plants have evolved an innovative strategy where they enlist the help of animals to transfer the pollen to the female parts. Through this strategy plants do not need to produce as much pollen, since pollinators will visit the same type of plant, ensuring the successful transfer of pollen to the right target. However, the plant will likely have to produce other substances, like nectar, to attract pollinators. Insects are the most famous pollinators, with bees and butterflies attracting the attention of many of us. However, some plant species are pollinated by birds, bats, or even lizards. In Hawai'i, native plants have coevolved with certain animals for millions of years, forming some unique pollination strategies. For example, lobeliads can only be pollinated by native nectariferous birds like the 'i'iwi (*Drepanis coccinea*). If you look at the shape of the lobeliads flowers you will see how they fit to the shape of the bird's beak (Figure 5.2.1). Because of the specificity of this pollination strategy, these plants are in danger of extinction, as many of the native Hawaiian forest birds have gone extinct or are so rare that the plants are not getting pollinated.



Figure 5.2.1: 'I'iwi (*Vestiaria coccinea*) visiting a Hawaiian lobeliad flower. By USFWS Pacific Region is licensed under CC BY-NC via Flickr.

Once the pollen that is brought in by a pollinator comes in contact with the stigma of the flower, a pollen tube grows down into the style of the flower. The tube elongates to reach the ovary, where it releases two sperm cells. One of these sperm cells will find the ovule (egg) and it will fertilize it to form the zygote. **Fertilization** is the fusion of the male and female gametes (reproductive cells), forming a zygote and eventually an embryo (baby plant). Flowering plants have a unique process of fertilization, called double fertilization, where through the process of fertilization they produce an embryo as well as an energy pack to feed the embryo (endosperm). We will describe this process here in the simplest terms. As mentioned above, one of the two sperm cells that were released from the pollen grains and delivered to the ovary via the pollen tube will join the egg to give rise to an embryo, while the other sperm cell will fuse with a structure, found inside of the plant egg, called the polar nucleus giving rise to a nutritive tissue called the endosperm. Both embryo and endosperm are located inside the **seed** (Figure 5.2.2). The endosperm is important because it is the energy reserve that the embryo will use to grow during the germination process.

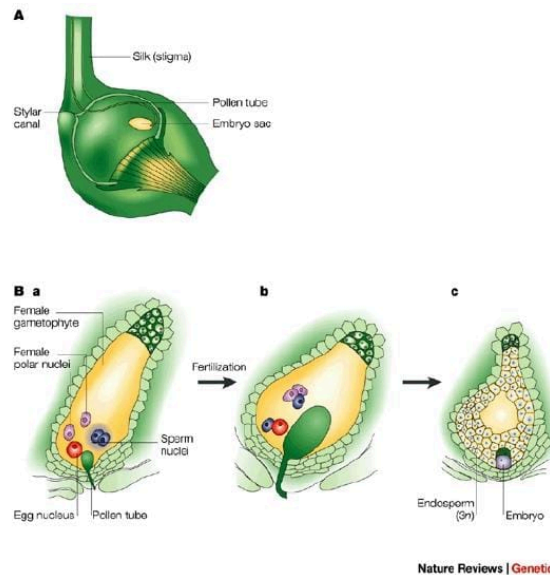


Figure 5.2.2: Double fertilization. By Triploid at English Wikipedia., CC BY 3.0, via Wikicommons.

5.3: Fruits

A fruit is the swollen ovary of the flower, the last step in the process of sexual reproduction of flowering plants. After seeds are formed through fertilization, the tissue around those seeds starts to grow, forming the fruit. Fruits help the plant to disperse the seeds, through different mechanisms that depend on the type of fruit. Fruits can be either dry or fleshy fruits. Animals who eat fruits will often disperse the seeds to other areas. Some dry fruits can attach themselves to the feathers and fur of animals and “catch a ride” to another area where they can grow without competition. Other fruits resemble wings and will fly with the wind. Here we will review only some of the types of fruits.

Fleshy Fruits

Berries

In Botany, berries are defined as a fleshy fruit where the two innermost tissues are fleshy (endocarp and mesocarp) and they usually contain lots of seeds inside (Figure 5.3.1). The endocarp is the tissue that is directly in contact with the seeds (endo = inside), while the mesocarp (meso = middle) is the tissue found in between the endocarp, and the external fruit tissue, the exocarp (exo = outside). This definition might be very confusing because, in the English language, we use the term “berry” to describe fruits that don’t necessarily comply with this botanical definition. For example, strawberry fruits are not considered berries in a botanical sense because their fruits and seeds are located on the outside of the edible red fleshy part (Figure 5.3.1).

If we follow the botanical definition, then liliko’i (passion fruit), tomato and bananas are berries (Figure 5.3.1). The banana varieties you see in the supermarket have been heavily domesticated by humans and no longer produce seeds. The brown specks you see inside a banana are unfertilized ovules. Wild bananas still produce seeds because their flowers get pollinated. Orange liliko’i (*Passiflora laurifolia*), native to Brazil, is an invasive species in Hawai’i. Its berries contain lots of pulp and seeds inside. This species is not as tart as yellow liliko’i or passionfruit (*Passiflora edulis* var. *flavicarpa*), and it is not cultivated commercially.

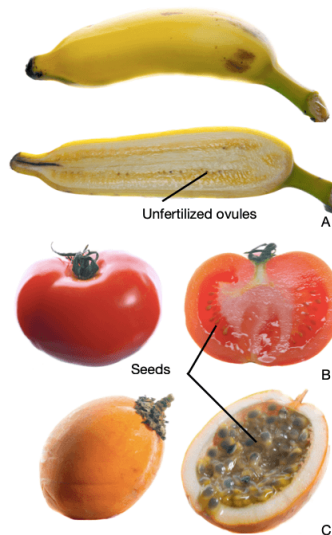


Figure 5.3.1: Examples of berries. A) Banana (*Musa* sp.), B) Tomato (*Solanum lycopersicum*), and C) Orange liliko'i (*Passiflora laurifolia*). By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Drupes

Drupes are fleshy fruits where the endocarp forms a hard enclosure (pit) that surrounds the seed (Figure 5.3.2). Drupes usually have a single seed. Examples of drupes include mangoes, peaches, nectarines, and apricots.

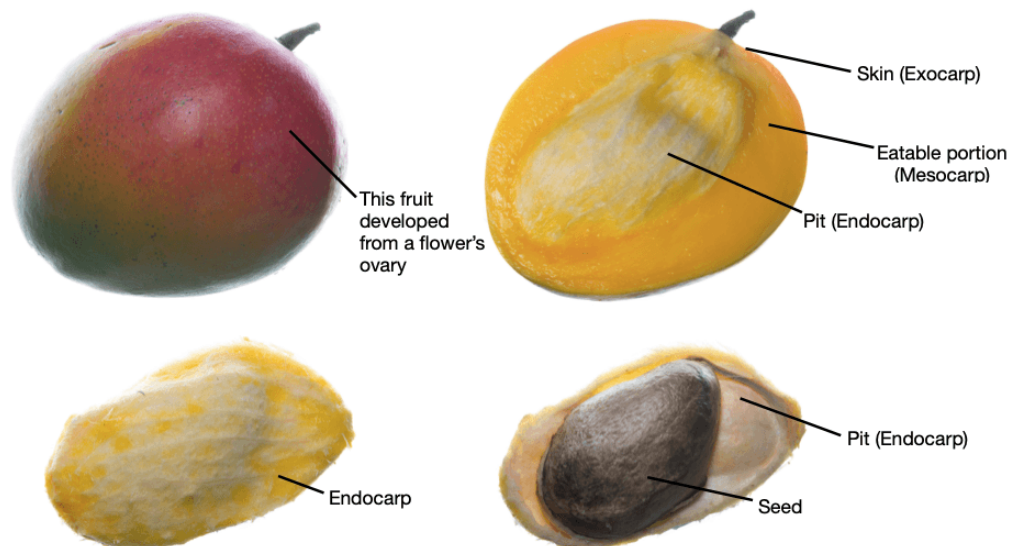


Figure 5.3.2: Example of a drupe: parts of a mango fruit (*Mangifera indica*). By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Hesperidium

The hesperidium is a modified berry where the endocarp is separated into segments, and the mesocarp is a thick and leathery whitish tissue, that we usually call a rind. This includes many citrus varieties, like the cara cara orange below (Figure 5.3.3).



Figure 5.3.3: Example of a hesperidium: cara cara orange (*Citrus x sinensis*), which grows well in Hawai'i. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Pepo

Squashes, watermelons, and cucumbers are all examples of pepos. Pepos are modified berries with a hard rim (exocarp). Just like berries, they have fleshy endo and mesocarp and contain lots of seeds inside (Figure 5.3.4).



Figure 5.3.4: Cross-section of a pepo: Japanese squash or kabocha (*Curcubita maxima*). By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Multiple fruits

Multiple fruits are formed as the result of fused ovaries of nearby flowers. Each “eye” in a noni fruit (*Morinda citrifolia*; Figure 5.3.5) is the scar where each flower used to be located. After pollination, they fall off the fruit. Examples of multiple fruits include noni, pineapple, mulberry, and breadfruit.



Figure 5.3.5: Example of a multiple fruit: progression of a noni (*Morinda citrifolia*) inflorescence from a cluster of flowers to a mature multiple fruit. Noni is a Polynesian introduced crop to Hawai'i and it has been used medicinally. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Dry Fruits

Achenes

Achene is a type of dry fruit that does not split open (indehiscent) and contains a single seed (Figure 5.3.6). The small brown dots on top of strawberries are examples of achene fruits. Strawberries are a special type of fruit called an accessory fruit, which does not develop from the ovary of the flower but instead develops from the receptacle (the part that connects the flower to the stem).

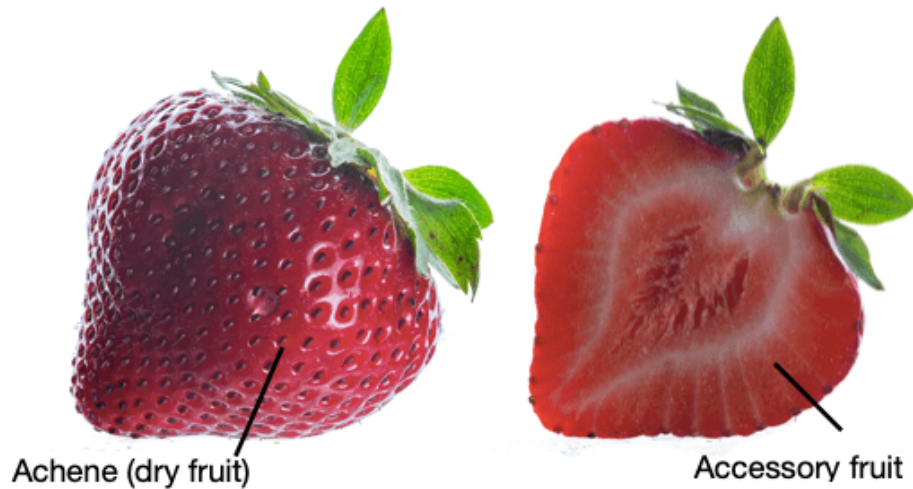


Figure 5.3.6: Achene fruits on the surface of a strawberry (*Fragaria × ananassa*). By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Capsules

A capsule is a dry fruit that splits open (dehiscent) in 3 or more ways. Pua kala (Hawaiian poppy; *Argemone glauca*) is a native Hawaiian species that produces capsule fruits. The capsules pop open when dry, releasing dozens of black seeds (Figure 5.3.7).



Figure 5.3.7: Dry fruit example, capsules of Puakala (*Argemone glauca*). By DutraElliott is licensed under CC BY-NC 4.0 via Flickr.

Legumes

Legumes are fruits commonly found in the members of the Fabaceae family (legume or bean family). These dry fruits normally split open along two seams when mature (Figure 5.3.8).



Figure 5.3.8: Dry fruits. Legume, violet's butter beans (*Phaseolus lunatus*) seeds and fruit. By DutraElliott is licensed under CC BY-NC 4.0 via Flickr.

Caryopsis

The caryopsis is a dry fruit that has the seed coat fused with the ovary wall or pericarp (Figure 5.3.9). You can't distinguish between the seed and the fruit because the two are fused. Cereal grains in the family Poaceae such as rice, barley, and corn have this type of fruit.



Figure 5.3.9: An example of a caryopsis: Corn kernels (*Zea mays*). By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

5.4: Seeds

Seeds are contained inside fruits. This is a good characteristic that you can use to differentiate between a fruit and another plant part. If it has seeds then it is a fruit (e.g. tomato, watermelon, pepper). If it does not have seeds then it is another plant part (e.g. sweet potato, cassava, onion). These other plant parts are normally referred to as “vegetables”. Keep in mind that there are some varieties of fruits, like bananas, that for our convenience have been bred to be seedless. Seeds come in all shapes and sizes (Figure 5.4.1).



Figure 5.4.1: Seed diversity. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

A seed is a flowering plant's unit of reproduction and has all the materials needed to develop into another plant. Seeds have three main parts: an embryo, a seed coat (testa), and the endosperm (cotyledon; Figure 5.4.2). The function of each of these parts is very specific:

Seed coat (testa): The outer layer that surrounds the seed. It protects the embryo against microbes and the environment.

Embryo: Embryo is the end product of fertilization (the baby plant). The embryo will germinate and become a new plant.

Endosperm (cotyledon): A second product of the double fertilization process previously discussed. The endosperm is the nutrient tissue that will feed the embryo during germination. Seeds of monocot plants have 1 cotyledon (e.g. corn) while seeds of dicot (eudicot) plants have 2 cotyledons (e.g. beans).

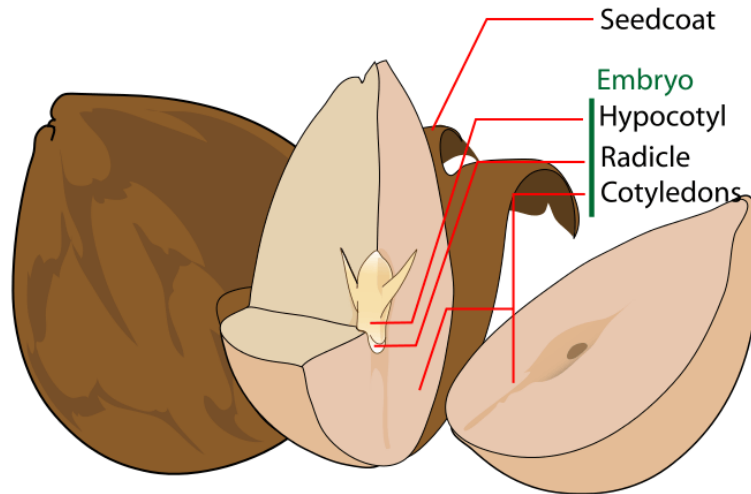


Figure 5.4.2: Avocado seed (*Persea americana*; eudicot) split open showing two cotyledons. By LadyofHats is licensed under Public Domain via Wikicommons.

Seed germination

Seed germination is a process by which the embryo contained in a seed develops into a seedling. Usually, seeds are dormant, meaning they are in a state of inactivity. When seeds find the right conditions, there is a metabolic activation (chemical reactions) in the seed, which leads to seed germination or growth of the embryo to become a new plant. There are three distinct phases of seed germination:

1. Water uptake by the seed (imbibition): The embryo soaks up water from the environment causing the seed to swell. The seed coat then splits.
2. Lag phase: In this phase, the metabolism of the seed kicks in, the endosperm starts to break down, and those sugars are used by the embryo to grow.
3. Radicle emergence (part of the embryo that will become the root): In this phase, the radicle grows out of the seed coat and starts to develop into a root (Figure 5.4.3).

Once these three phases are completed, the embryo will continue to grow and develop into a photosynthetic seedling that will be able to make its own food.

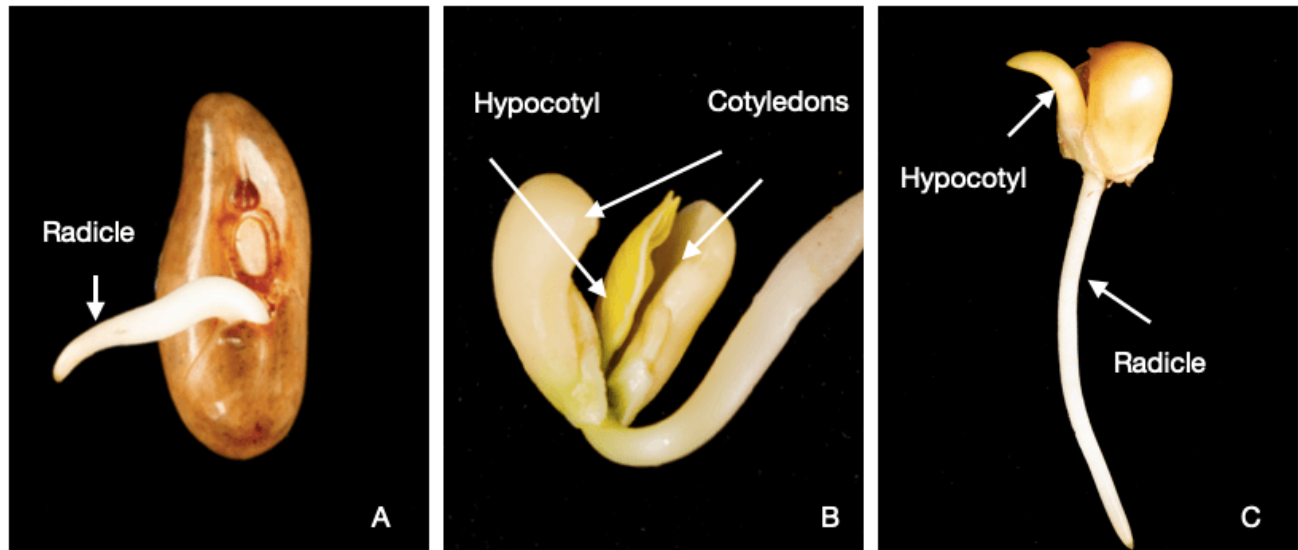


Figure 5.4.3: Germinating seeds. A) Bean seed with first root (radicle), B) Bean seed without seed coat, C) Corn seed with shoot and root. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Seed viability and dormancy

Three requirements must be met before germination can happen:

1. The embryo must be alive. Seed **viability** is the ability of the embryo to germinate. If the embryo is dead, non-functional, or non-existent (some seeds do not have embryos. a.k.a. empty seeds), the seed will not germinate.
2. **Dormancy** must be overcome. Seeds can lay dormant for many years. For wild species this is very important and a matter of survival. A seed will remain dormant until the right conditions are in place. For example, a seed lays dormant when there is a drought and will only germinate when there is enough water in the environment.
3. The right environmental conditions must be in place: water, oxygen, temperature, and light. Some seeds will not germinate in high temperatures or the presence of light. All seeds will not germinate in the absence of water.

In agriculture and conservation, there is a need for high-quality seeds. When you purchase a seed packet in the store, you should feel confident that most of the seeds in the package will germinate. There are federal and state standards for this, but the quality of seeds vary widely depending on where you are getting your seeds from. This is why some gardeners and farmers decide to save their own seeds. When looking into seed quality, people consider a few things. In the conservation field, for example, people are always trying to understand how long seeds will last in the ground before they germinate or when is the best time to harvest seeds for restoration projects.

High viability of seeds is what people look for if they are trying to grow a crop. This can be measured by looking at the **germination percentage** and the **rate of germination**. The **germination percentage** is the proportion of seeds that germinate from all seeds subject to the right conditions for growth. If you try to germinate 100 seeds and 20 of those do not germinate, you have an 80% germination percentage. This number should be included in the seed package when you purchase one in the store. It gives you a clue that the seeds you are purchasing are good. The **germination rate** is the length of time it takes for the seeds to germinate. Again, if we tried to germinate 100 seeds in 7 days and only 50% of the seeds germinated, this is your rate of germination. Why is the rate of germination important? Imagine you planted a field of beans. In the first 7 days, 50% of your seeds germinated, and the other 50% germinated a month later. This can be very frustrating for a farmer who wants to harvest all the crops at the same time. In nature, this is not a bad strategy, since it may give the plants some advantages. For example, if the environmental conditions are not right when the first batch of seeds germinates, a second germination event a month later may have better success. Finally, **seed vigor** is a measure of the quality of seed, and involves the viability of the seed, the germination percentage, germination rate, and the strength of the seedlings produced.

Seed Saving and Conservation

Wild plants have evolved in their natural habitat for millions of years. In certain instances, plants become endangered due to

negative human impacts on the environment, such as the introduction of invasive species and habitat destruction. One strategy used in plant conservation is to collect seeds of threatened and endangered plants, store them in the right conditions, and eventually germinate them to reintroduce them to restored areas so that the future of the species can be ensured. Seeds of native species are collected all over the world by different organizations involved in conservation and are stored in seed banks. In Hawai'i several organizations, like the Plant Extinction Prevention Program (PEPP), collect seeds of endangered Hawaiian plants, grow them in greenhouses, and then outplant them in the wild to restore native ecosystems.

Seeds are crucial in agriculture. Humans have been domesticating crop species for the past 15,000 years. Once wild species, **crop species** have been selected by humans for some characteristics that benefit us such as seed and fruit, taste, and uniformity in maturation. For example, corn (*Zea mays*) was domesticated in Mexico around 9,000 years ago (Figure 5.4.4).



Figure 5.4.4: Varieties of Mexican corn (*Zea mays*). By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

The **wild relative** of corn, Teosinte (Figure 5.4.5), looks like a large grass. Several changes needed to happen for teosinte to develop into modern corn. Humans played a direct role by selecting plants with larger and larger seeds and growing only those. This process is called artificial selection. If you were relying on corn for subsistence, you would want plants that produce larger seeds for higher caloric intake.

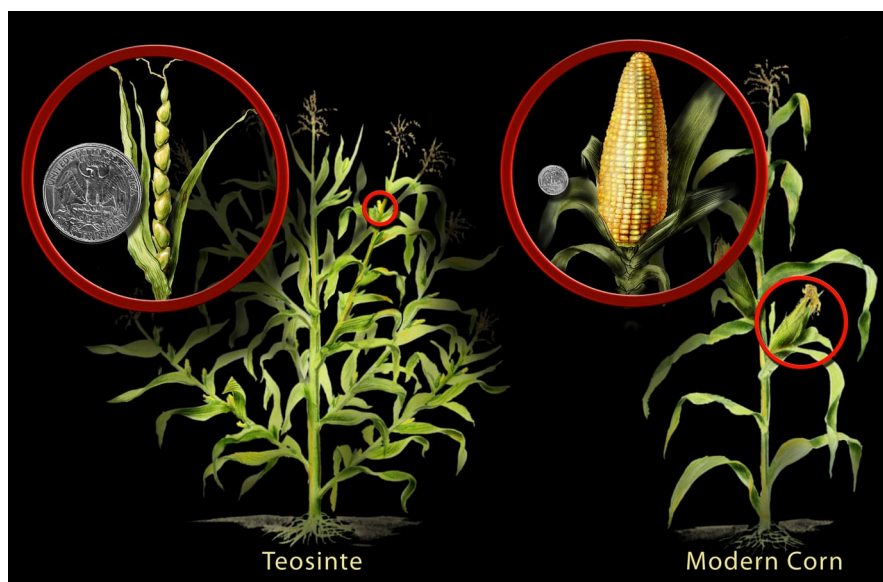


Figure 5.4.5: Teosinte the wild relative of corn and modern corn. By National Science Foundation is licensed under Public domain via Wikicommons.

Saving seeds from the wild relatives of crop species (like Teosinte) is important because those genes can be used for future plant breeding. The Crop Trust Project has been doing just that. Sometimes plant breeders will look for wild relatives to cross with domesticated crops so that they can acquire genes that provide some resistance to diseases or drought. An example of this application is the use of the Hawaiian species of cotton, ma'o (*Gossypium tomentosum*, 5.4.6) in breeding projects to increase disease resistance in domesticated cotton (Akhtar *et al.*, 1996). Although the fibers of ma'o (Figure 5.4.6) are short and are not used commercially to make cotton, the plants have been crossed with varieties of commercial cotton to make stronger varieties.



Figure 5.4.6: Ma'o (Hawaiian cotton), *Gossypium tomentosum*. A) Open fruit (capsule) with seeds and B) Flower. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

5.5: References

References

Akhtar L. H., J. Gorham, M. A. Mirza, and A. L. Sheikh. 1996. Heat stress tolerance in the wild species of the genus *Gossypium* measured by chlorophyll fluorescence. *Pakistan Cottons* 40:49-58

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6: PLANT EVOLUTION AND NON-VASCULAR PLANTS

Learning Objectives

- List the features that distinguish the Plant Kingdom from other Eukarya Kingdoms.
- Describe the general concept of alternation of generations in plants.
- Recognize the gametophyte and sporophyte life stages of a moss.
- List the main characteristics of non-vascular plants.
- Within non-vascular plants identify mosses, liverworts and hornworts and list their main characteristics.
- List five uses of non-vascular plants by humans.



6.1: What defines a plant?

6.2: Alternation of generations

6.3: Non-vascular plants

6.4: References

6.1: What defines a plant?

All living organisms on Earth are divided into three domains (groups): Bacteria, Archaea, and Eukarya. Bacteria and Archaea are grouped in an informal category called prokaryotes, small unicellular organisms (smaller than the tip of a needle) that lack a nucleus and membrane-bound organelles. Eukaryotes, on the other hand, are composed of bigger cells that have a nucleus and membrane-bound organelles and they can be unicellular or multicellular. Domain Eukarya is further divided into four Kingdoms (groups; Figure 6.1.1): plants (Plantae), animals (Animalia), fungi (Fungi), and protists (Protista). Both prokaryotes and eukaryotes have cell membranes, ribosomes, and genetic material (DNA and RNA).

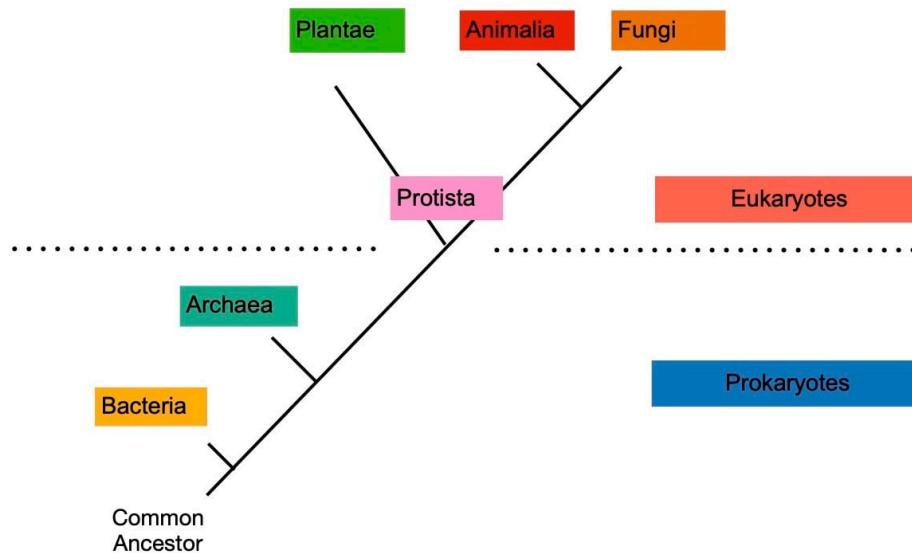


Figure 6.1.1: Simplified phylogenetic tree of life. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Plants are multicellular photosynthetic organisms that have unique organelles and compounds, setting them apart from other eukaryotes. Specialized plant organelles, that are not found in animal cells, are chloroplasts for photosynthesis, a central vacuole to store water, and a cell wall to provide protection and structure to the plant cell. Other groups of organisms also have cell walls, like some bacteria, fungi, and some protists, but in plants, the cell wall is mainly composed of a substance called cellulose, while in other organisms it is composed of other substances, like chitin in fungi. There are also other organisms capable of performing photosynthesis, like some bacteria, and some protists (algae). Plants have green pigments called chlorophyll a and chlorophyll b, which are involved in photosynthesis.

Origin of plants

Plants are well known for their crucial role in producing oxygen. About 16% of the modern Earth's atmosphere is constituted by oxygen, but a couple of billion years ago it did not have any oxygen, so it could not support life as we know it today. Around 2.8 billion years ago a group of bacteria started to perform an innovative process called photosynthesis in the Earth's oceans, and over time oxygen accumulated in the atmosphere until it was high enough to support oxygen-breathing creatures, like animals.

For millions of years, algae and blue-green algae (bacteria) were the main photosynthetic organisms on Earth. The first true plants evolved from green algae, probably from a Class (group) of green algae called Zygnematophyceae (Cheng *et al.*, 2019; Figure 6.1.2). Because the ancestors of terrestrial plants were aquatic, land plants had to adapt to new challenges brought by the dry conditions inherent to terrestrial environments. Some of the most notorious plant adaptations to life on land were the development of a physical barrier to prevent desiccation (drying out), specialized cells for water and nutrient transport, mechanical support to stay upright, anchoring mechanisms, specialized mechanisms to transfer the reproductive cells (gametes) from one plant to another, and the development of protective cell layers around the spore- and gamete-producing structures.

The physical barrier plants developed to prevent desiccation is called a cuticle, a waxy layer that covers all the aerial surfaces of a plant to help prevent desiccation. All living land plants have a cuticle. The Zygnematophyceae algae are hypothesized to have

acquired genes from soil bacteria that help prevent desiccation (Cheng *et al.*, 2019). These genes are currently found in land plants and bacteria, but not any other algae, adding support to the hypothesis that these green algae are the ancestor of all land plants. When plants colonized land they also had to redesign the way sexual reproduction took place. In aquatic environments, gametes just swim or float to another plant, which is not possible in most terrestrial environments. Land plants developed drought-resistant spores that could survive on dry land, as well as enclosed gamete or spore producing structures with several layers of cells to protect them from drying out. Some land plants, like bryophytes, still have swimming sperm, which confine them to wet environments.



Figure 6.1.2: Filamentous algae, *Spirogyra* spp. (Class Zygnematophyceae). Scale=0.1mm. By Andrei Savitsky CC BY 4.0 via Wikicommons.

In aquatic environments water and dissolved minerals are readily available and easily absorbed by plants via osmosis. Land plants, in contrast, had to develop specialized cells to be able to transport water and dissolved nutrients from the soil. Most of these specialized cells look like narrow tubes, where water is transported from the roots to the leaves via the stem. These transporting cells are also related to the newly required mechanical support, as they have fortified cell walls to be able to withstand the physical forces involved in transporting fluids (Niklas, 1997). Mechanical support is required for vertical growth outside of a water environment and as plants seek to reach the most sunlight to be able to perform photosynthesis, growing vertically is beneficial for many of them. Most land plants developed a cylindrical stem that provided efficient means of mechanical support (Niklas, 1986), which could explain the general shape of most plant stems. Bryophytes do not have these conducting tissues, and therefore are short, while plants that have them, like flowering plants, can grow taller. The development of an upright position in plants was also accompanied by the development of an anchoring mechanism, or roots. The earliest evidence of roots dates back to the early Devonian 408 million years ago (Erick *et al.*, 1998).

The major extant (living) groups of plants are non-vascular plants, seedless vascular plants, Gymnosperms, and Angiosperms. The first evidence of terrestrial plants is fossil spores from the late Ordovician (~450 Ma; Gray, 1985; [Appendix 1](#)). From bryophytes (the oldest plant group) to flowering plants (the most recent plant group), plants have acquired unique characteristics that allow them to survive and thrive in different terrestrial environments (Figure 6.1.3). Plants have been able to colonize all terrestrial ecosystems on Earth, including mountains, islands, sand dunes, rainforests, and deserts.

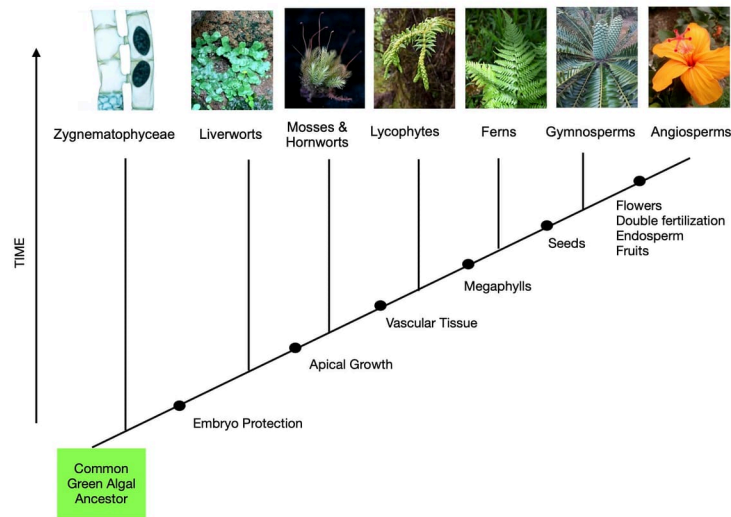


Figure 6.1.3: Evolutionary tree of land plants and algae ancestor. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

In the following chapters, we will explore the main characteristics of each plant group and learn about important economic or cultural uses for each. Learning about the basic characteristics of each group is the first step in identifying plants. For example, if you go hiking and find an interesting plant you want to identify, you can start by identifying the plant's group. By eliminating the other groups, you can get closer to an identification.

6.2: Alternation of generations

Before embarking on the exploration of the different groups of plants, let's introduce the concept of alternation of generations in plant life cycles, which is inherited from the green algal ancestors of land plants. Alternation of generations means that plants alternate between two different life stages, or generations, in their life cycle; a haploid stage called **gametophyte** and a diploid stage called **sporophyte**. The terms haploid and diploid refer to the number of chromosomes contained in the cells. For example, most of the cells in the human body contain two sets of chromosomes (n) meaning they are diploid ($2n$): one set that we inherit from our mother (n) and one set we inherit from our father (n). However, humans also have special reproductive cells (eggs and sperm) that only have one set of chromosomes, and we call this haploid (n). These reproductive cells are called gametes and they are produced via cell meiosis (reductive cell division). When a male gamete (n) joins a female gamete (n) through fertilization, they form a diploid organism ($2n$).

Most of the plants we are familiar with, like trees, grasses, and tomatoes, have a dominant sporophyte stage, so the visible plant is diploid. Just like humans, plants also have specialized gametes that are haploid (n), which are found in their reproductive organs like flowers. However, instead of producing their gametes on a specialized structure on their diploid body (e.g. a flower on a tree), some plants have a prominent life stage where the whole plant is composed of haploid cells (n), and that haploid plant produces gametes. We call this haploid plant a gametophyte. The visible green body of some plants, like mosses, is actually the gametophyte. The alternation of generations in plants is an alternation between the gametophyte stage and the sporophyte stage.

In general, this is how the alternation of generations works: a male gametophyte (n) and a female gametophyte (n) produce gametes (sperm and eggs, respectively), which combine in fertilization to form a diploid plant called a sporophyte ($2n$). This sporophyte will grow and then produce spores, through meiosis, that will germinate into a new gametophyte (n), thus the alternating cycle is complete (Figure 6.2.1). The specifics of this alternation are unique for each plant group, so we will revisit the alternation of generations for each one of the plant groups in subsequent chapters.

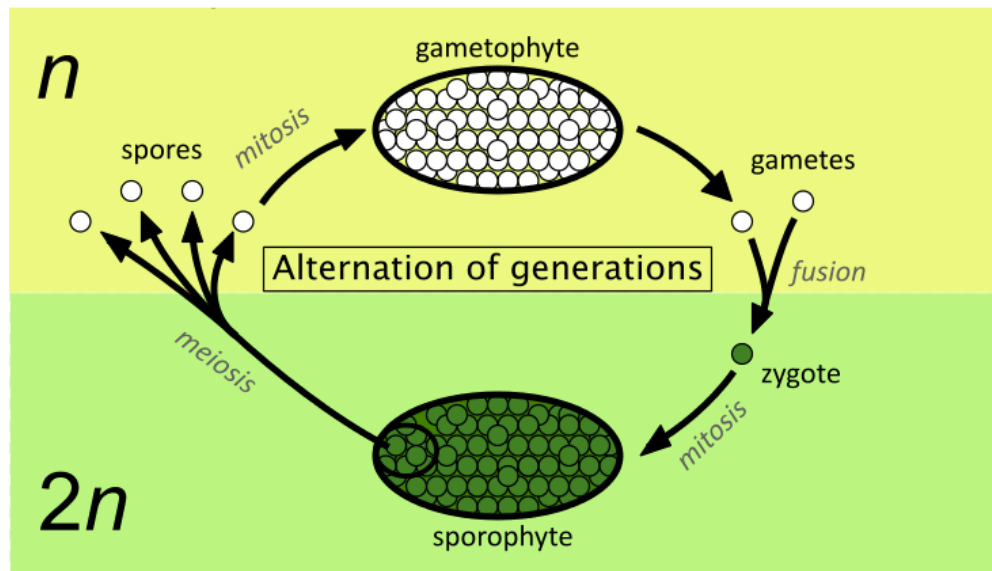


Figure 6.2.1: Alternation of generations. By Peter Coxhead is licensed under Public domain via Wikicommons.

6.3: Non-vascular plants

Non-vascular plants are a diverse group of plants with approximately 20,000 living species presenting a wide geographical distribution, ranging from tropical forests to high-latitude tundra, to high mountain ranges. They are the most ancient group of land plants, being the closest relatives to green algae and the earliest diverging lineages of land plants. Informally, they are called “bryophytes” which include mosses, liverworts, and hornworts. In this chapter, you will see the term used to refer to non-vascular plants.

Bryophytes can grow in a variety of substrates, like rocks, tree stems, or fallen logs. They are an important part of the environment because of their ability to grow on bare surfaces, interact with non-living elements like rocks and boulders as part of the biogeochemical cycles (Lindo and Gonzalez, 2010), and even filter water. Bryophyte communities (also known as Bryospheres), are complex micro-ecosystems that house a variety of species of bacteria, fungi, and other organisms. They are small so most people won't notice them; however, they are very important for ecosystem functioning. For example, a bryophyte mat can retain water and serve as a nursery for native plants (Figure 6.3.1).



Figure 6.3.1: Native wet forest in Hawai'i where an 'ōhi'a lehua (*Metrosideros polymorpha*) seedling is growing in a bryophyte community dominated by *Leucobryum gracile* (endemic to the Hawaiian Islands). By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Bryophytes lack vascular tissue which translates into them being short, as they cannot perform any significant vertical transportation of water. Instead, they absorb water directly from their surroundings through osmosis, especially via the lower surface of the leaf. Consequently, they are mostly confined to places where water is readily available. They also require water for sexual reproduction, as bryophyte sperm is flagellated and needs to swim to the egg. With this in mind, in which type of ecosystems would you likely find bryophytes? Here in Hawai'i, they can be found in areas with high precipitation and high humidity, like on the Windward side of the islands, or along stream banks. On higher elevations where precipitation is high, they can be found growing on rocks and logs on the forest floor. Bryophytes are an ancestral group of plants because besides lacking vascular tissue they also lack true roots and true leaves, which are characteristic of more recent plants. There are three main bryophyte groups (liverworts, hornworts, and mosses), each one possessing easy-to-recognize characteristics (Figure 6.3.2).

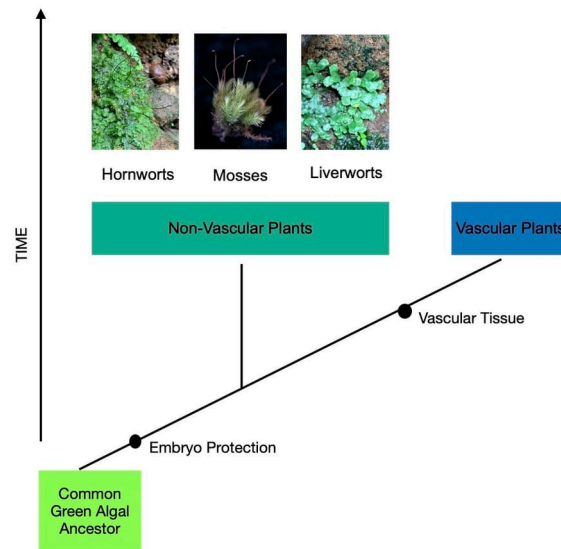


Figure 6.3.2: Bryophyte groups: Mosses, Liverworts and Hornworts. Please note that new studies have suggested that bryophytes are not a monophyletic group. We keep this simplified view in this chapter until more studies better elucidate their relationships. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Liverworts (Phylum Hepaticophyta)

There are about 9,000 species of liverworts on Earth (Christenhusz and Byng, 2016). The name of this group originated at a time when botanists thought the shape of a plant could be used to treat diseases of the part of the human body it resembled. In this case, liverworts look like human livers because they are lobed. This method of treating diseases took place in the 15th century and it is no longer an accepted practice, but the name stayed. Liverworts play a crucial role in their habitats. For example, in tropical forests, they play a role in water absorption and retention. In arid regions, they help form a soil crust that allows other species to survive while stabilizing the area.

Some species of liverworts have the characteristic flattened leaf-like body (thallus) from which the group name is derived and are small (less than 10 centimeters or 4 inches) with lobed “leaves” (Figures 6.3.3). Interestingly, most species of liverworts are similar to mosses and can be differentiated from them by the presence of single-cell rhizoids in liverworts (primitive root structure), rather than the multicellular rhizoids present in mosses. This might not be very useful when trying to identify a mossy-looking liverwort in the field because you would need a microscope to see these structures. Some characteristics that can help tell the difference in the field are that most mosses have spirally arranged leaves, a distinct midrib, and, same size leaves.



Figure 6.3.3: Liverwort population. A) Liverwort (*Dumortiera hirsuta*) growing on shady and wet rocks of the Mānoa cliff trail on O'ahu. B) Endemic liverwort (*Marchantia marginata*) growing on a stream bank on the windward side of O'ahu. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

The dominant life stage of a liverwort is the gametophyte, which is the green leafy part of the body. From the gametophytes, they produce the male and female reproductive structures, archegonium and antheridium, respectively. These photosynthetic structures usually tower over the thallus and it is here where eggs and sperm are produced. Liverworts, just like mosses and hornworts, require water for reproduction because the sperm needs to swim to the female structure for sexual reproduction to take place. The sperm swims through a hollow tube in the archegonium (female) to reach the egg. Once fertilization is accomplished, the embryo becomes the diploid sporophyte (2n) and it remains attached to the gametophyte (Figure 6.3.4).

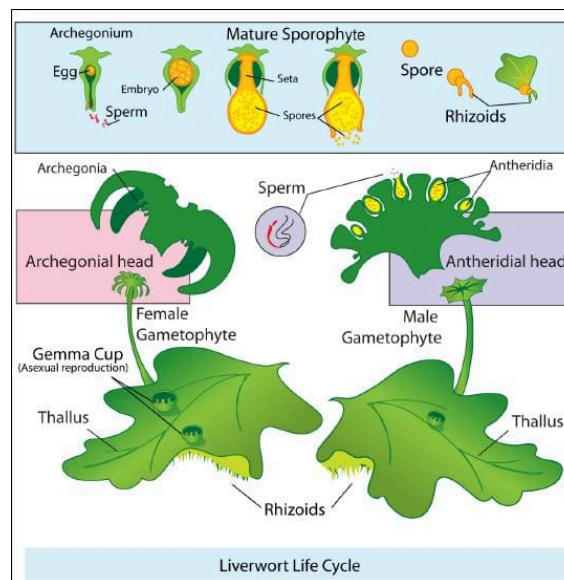


Figure 6.3.4: Liverwort life cycle. By LadyofHats, Public Domain.

Liverworts also reproduce asexually, by producing gemmae in cup-like structures on their gametophytes (Figure 6.3.4). Gemmae are small pieces of haploid tissue that can grow into new gametophytes. Rain usually splashes the gemmae out of the cups, dispersing them to other environments. A few liverworts are very popular in the aquarium hobby as submerged plants or as plants growing in terrariums. Floating crystalwort (*Riccia fluitans*), Asian liverwort (*Monosolenium tenerum*), and mini peltia (*Riccardia chamedryfolia*) are all species used by hobbyists.

Mosses (Phylum Bryophyta)

There are about 12,700 species of mosses in the world (Christenhusz and Byng, 2016). In Hawai'i, there are approximately 255 species of mosses, consisting of 75 endemic, 166 indigenous, and 14 introduced species (Staples *et al.*, 2004). If you are walking around a wet rural or urban area you will likely find mosses. By looking closely, you may see mosses growing in cracks of a sidewalk or on the bark of trees on the windward side of O'ahu (Figure 6.3.5). If the environment is moist enough, mosses will be there. Some moss species can live in drier environments, going dormant during times when water is not available only to spring back to life when it rains.



Figure 6.3.5: A) Mosses (*Hyophila involuta*) growing in the cracks on the asphalt of a paved road, B) Mosses growing on a tree in an urban park. By DutraElliott is licensed under CC BY-NC 4.0 via Flickr.

The visible green fluffy plant that we call moss is the gametophyte, which is their dominant stage. Since mosses are part of the bryophyte group, they don't have true roots to absorb water; instead, they can do it directly from the surface of the gametophyte via osmosis. Once mosses are ready to reproduce, the egg and sperm combine to form a sporophyte that grows from the top of the gametophyte (Figure 6.3.6) or on lateral areas of the stem in prostrate species, and produces spores, which germinate into male and female gametophytes (Figure 6.3.7). These, in turn, will produce eggs and sperm that when combined, will give rise to a new sporophyte (the cycle continues!). Sporophytes are not photosynthetic, and they depend on the gametophyte. Some mosses may live a long time without undergoing sexual reproduction. Instead, they form colonies composed of gametophytes. Sometimes small clumps will break off due to a flood or animal disturbance and one of those clumps may start a new colony elsewhere in the process of asexual reproduction via fragmentation.

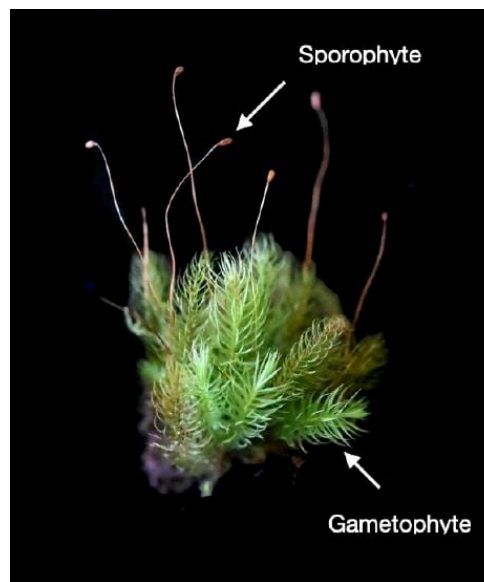


Figure 6.3.6: Moss (*Pyrrhobryum spiniforme*) sporophyte and gametophyte. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

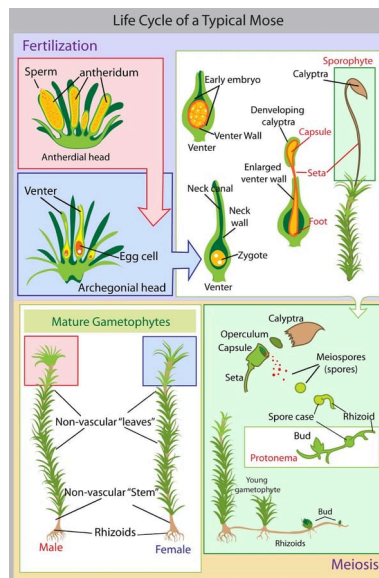


Figure 6.3.7: Lifecycle of a moss. By LadyofHats, Public Domain.

Mosses are important ecologically for several reasons. They act like sponges that can absorb and retain rainwater. For this reason, they are important in the establishment of epiphytic fern gametophytes because they can retain moisture for prolonged periods so that spores can germinate and develop (McCarthy 2007, Miles Thomas Pers. Com.). They can also serve as a nursery for native seedlings (Rehm *et al.*, 2019; Kimmerer, 2003); when a seed is dispersed, if it finds a moss colony it can be protected from predators and will have a moist environment to develop and grow (Figure 6.3.8).



Figure 6.3.8: Moss community on Waiāhole stream. *Pyrrhobryum spiniforme* (indigenous). By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Mosses have been used for quite a long time by humans. Because of their immense absorptive capacity, native people in different regions have used mosses as diapers and for menstrual supplies. Given their antimicrobial properties, they were used as bandages by several native communities and even during WWI (Kimmerer, 2003). They have also been extensively used as packaging material, and even today they are used for live shellfish shipping. Today, mosses are used in the horticultural industry as potting media for plants (peat moss) and decorations. The harvest of moss from natural communities can have a significant impact on these populations because they may take a very long time to recover.

Hornworts (Phylum Anthocerophyta)

There are about 225 species of hornworts worldwide, the smallest group of bryophytes (Christenhusz and Byng, 2016). In Hawai'i there are a total of 8 species (one endemic, three indigenous, 2 introduced, and two of dubious origin). The sporophyte of this group looks like a little horn, which gave the group its name (Figure 6.3.9). On the evolutionary scale, hornworts seem to have diverged from the green algae common ancestor much earlier than mosses and liverworts. They have a unique gene not found in mosses or liverworts called LCIB. This gene is also found in algae and is responsible for concentrating carbon dioxide in the chloroplasts of the cells, making the production of sugars more efficient. The gametophyte, which is the dominant stage in hornworts, grows in a loose circular arrangement from where the green photosynthetic horn-like sporophytes grow. Hornworts have stomata in their sporophytes, a feature that is absent in liverworts and most mosses (Figure 6.3.10).

On O'ahu, hornworts can be found on stream banks (Figure 6.3.9), which may be one of the only places they can grow without competition from weeds or leaf cover (Vitt *et al.*, 2018). There, colonization is facilitated by the presence of exposed mineral substrates and microhabitats full of moisture (Figure 6.3.9).



Figure 6.3.9: Hornworts at Waiānu stream on the windward side of O'ahu. A) *Phaeoceros carolinianus* is indigenous to Hawai'i, and B) Habitat of *Phaeoceros carolinianus* on a rock wall on stream bank. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

The dominant life stage of a hornwort is the gametophyte (Figure 6.3.10). From the gametophytes, they produce the male and female reproductive structures, archegonium and antheridium, respectively. These structures are located on the surface of the gametophyte and are where eggs and sperm are produced. Hornworts, just like mosses and liverworts, require water for reproduction because the sperm needs to swim to the female structure for sexual reproduction to take place. Once the sperm reaches the egg and fertilization takes place, a zygote (diploid, $2n$) forms which then develops into the sporophyte which remains attached to the gametophyte (Figure 6.3.10).

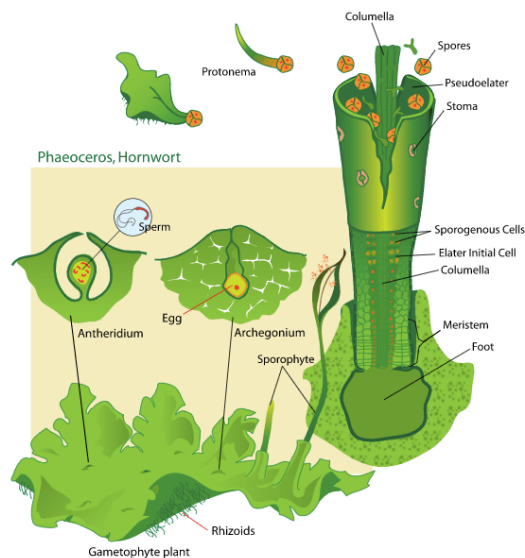


Figure 6.3.10: Life cycle of a typical hornwort *Phaeoceros*. derivative work: Smith609 (talk)Hornwort_life_cicle_svg_diagram.svg: Mariana Ruiz user: By LadyofHats is licensed under CC BY 3.0, via Wikicommons.

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7: FERNS AND LYCOPHYTES

Learning Objectives

- List and describe the distinguishing characteristics of lycophytes and ferns.
- Identify the gametophyte and sporophyte generations in the life cycle of a fern.
- List five important uses of seedless vascular plants.



7.1: Seedless vascular plants

7.2: Lycophytes

7.3: Ferns

7.4: References

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7.1: Seedless vascular plants

Seedless vascular plants reproduce via spores but, unlike non-vascular plants (hornworts, mosses, and liverworts) have a vascular system with xylem and phloem, which transport water and nutrients (Figure 7.1.1). They do not produce flowers, fruits, or seeds. There are two major distinct evolutionary lineages: lycophytes (Lycopodiopsida) and ferns (Polypodiopsida) with approximately 12,000 species worldwide (PPG I, 2016). On an evolutionary scale, ferns are more closely related to seed plants than to lycophytes, but these two classes of plants are usually grouped as seedless vascular plants because they share several characteristics. These relationships are still being studied by evolutionary biologists and they will likely be clarified in the near future.

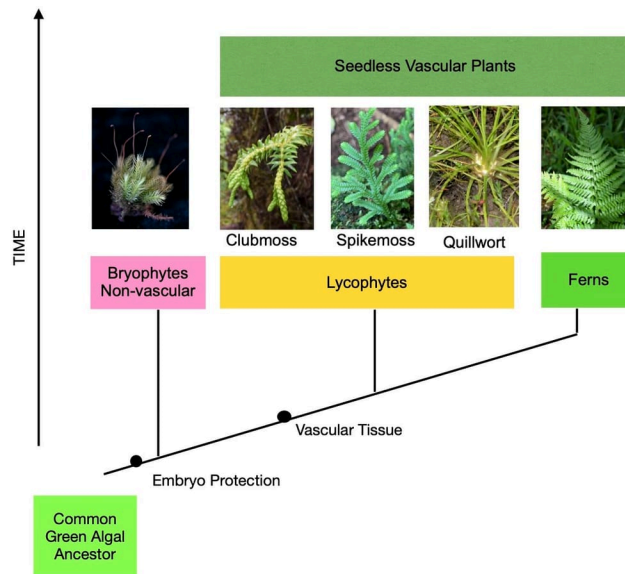


Figure 7.1.1: Phylogenetic tree depicting the evolutionary relationships among plants, based on PPG I (2016). By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Lycophytes and ferns share a similar life cycle with independent photosynthetic gametophytes and sporophytes, with the sporophyte being the dominant phase. This is different from bryophytes, where the sporophyte grows from and remains attached to the gametophyte, and the gametophyte is dominant. The sporophytes of vascular plants are usually large and visible, having differentiated plant organs, as leaves, roots, and stems, while the gametophytes are small. Lycophytes have **microphylls** (leaves with single unbranched veins), while other vascular plants (ferns, gymnosperms, and angiosperms) have **megaphylls** (leaves with multiple branched veins).

7.2: Lycophytes

There are approximately 1,300 species of lycophytes worldwide (Christenhusz and Byng, 2016) and they can be found in arctic, temperate, and tropical regions. In Hawai'i, there are 17 native species and varieties and at least 4 introduced species that have become naturalized (Ranker *et al.*, 2019).

Lycophytes first appeared in the Silurian period approximately 425 million years ago ([Appendix 1](#)). By the Carboniferous period (350 million years ago), they had become the dominant plant group and formed extensive dense forests. The species living at that time and that are now extinct, ranged from short plants to massive trees up to 30 meters (98 feet) in height (Figure 7.2.1). These plants were very common in swamp forests and their biomass was responsible for the formation of coal deposits, from which we extract coal today. In the late Carboniferous, the climate on Earth changed, drying the swamps and pushing most lycophytes to extinction. Today the living species of lycophytes are all relatively few and small compared to their once lush diversity.

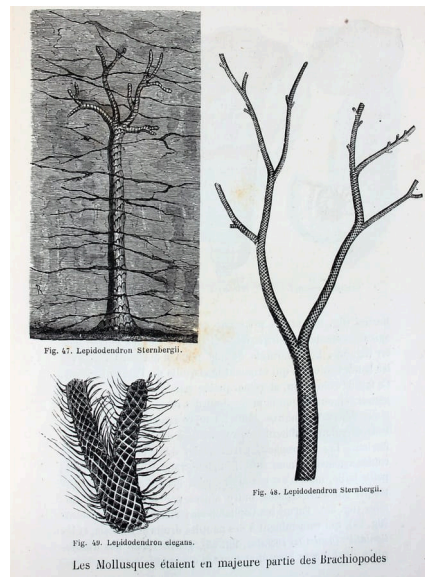


Figure 7.2.1: Artistic reconstruction of Lycophytes from the Carboniferous period. *Lepidodendron sternbergii* and *Lepidodendron elegans* by Biblioteca Rector Machado y Nuñez, Public Domain.

Lycophytes are divided into three groups (orders): Lycopodiales, Selaginellales and Isoetales:

Lycopodiales (club mosses, fir mosses)

There are four groups of Lycopodiales in Hawai'i (*Huperzia*, *Lycopodium*, *Palhinhaea*, *Phlegmariurus*, per PPG I, 2016). Some species may resemble small pine trees with “cones” growing on the tip of their branches. These cones are spore-bearing structures called strobili (singular, strobilus). They are made up of tiny, closely spaced leaves with sporangia (spore cases) hiding at their bases. Species in this group are usually smaller than 30 centimeters (1 foot) but can reach more than a meter (5 feet) tall in some tropical ecosystems. Hawai'i has fifteen species and a few hybrids (Ranker *et al.*, 2019), which are commonly found in wet forests (Figure 7.2.2).



Figure 7.2.2: Wāwae'iole (*Phlegmariurus phyllanthus*), is a species in the Lycopodiales native to the Hawaiian Islands. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr. A derivative of the original work by Forest and Kim Star licensed under CC BY 3.0 via Wikicommons. Modified to include labels.

Selaginellales (spike mosses)

Spike mosses have stems with many branches and scale-like leaves that grow in a spiral-like pattern, each having a little tongue-like extension called a ligule (Figure 7.2.3). Spike mosses can be found in wet environments, growing alongside mosses and liverworts. In Hawai'i, there are 2 native species (one endemic and one indigenous) and four introduced species that became naturalized (Ranker *et al.*, 2016).



Figure 7.2.3: *Selaginella arbuscula* (Lepelepe a moa) is a spikemoss native to Hawai'i. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Isoetales (quillworts)

Quillworts are aquatic plants with long narrow leaves that are wider at the base and are arranged in a spiral (Figure 7.2.4B). Hawai'i only has one species of quillwort, *Isoetes hawaiiensis*, which is endemic (Taylor *et al.*, 1993). This species is quite rare and has only been found on Maui and Hawai'i Island. On Maui, it occurs in the West Maui Mountains (Mauna Kahālāwai) on top of Pu'u

‘Eke elevation 1372 meters (4,500 ft; Figure 7.2.4A).



Figure 7.2.4: A) Pu'u Eke on the Island of Maui, where populations of *Isoetes hawaiiensis* are found (Photo Credit: Royce Bair). B) *Isoetes hawaiiensis*, a quillwort species endemic to the Hawaiian Islands (Photo Credit: [Earth.com](https://www.earth.com/)). By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

7.3: Ferns

There are about 10,560 species of living ferns worldwide (PPG I, 2016). Hawai'i has approximately 188 species with 111 of them being endemic and 35 indigenous to the Hawaiian Islands. Additionally, 40 species of introduced ferns have become naturalized (Ranker *et al.*, 2019). As with lycophytes, the sporophyte is the dominant stage in the fern's life cycle, and the gametophyte is a separate, free-living plant (Figure 7.3.1).



Figure 7.3.1: Sporophyte of *palapalai* (*Microlepia strigosa*), an indigenous fern species. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Ferns are a common sight in most rural and urban areas and are widely used as indoor plants and in landscaping. In Hawaiian forests, remaining fern understories play critical roles. Fern leaves (megaphylls) are commonly referred to as fronds, which grow from an erect creeping rhizome (stem). They start as fiddleheads that uncurl. Fern sporophytes range in size from small, herbaceous plants of a few centimeters to tree-like plants more than 7 meters (25 feet) tall.

The spore-bearing structures in ferns are called sporangia (singular sporangium), which are clustered together in structures called sori (singular, sorus; Figure 7.3.1). Sori are usually found on the underside of fertile fronds, and they can be rounded or linear, depending on the species. Sori shape and arrangement are used as key characteristics for the identification of different fern species.



Figure 7.3.2: Fern gametophyte. "Tender Brake (*Pteris tremula*)" by Poytr is licensed under CC BY-NC 2.0.

Spores germinate into gametophytes (Figure 7.3.2), which then produce gametes (sperm and egg) that, when combined, grow into sporophytes (what we typically see and think of as 'ferns'), completing the fern life cycle (Figure 7.3.3). The gametophyte is smaller than a fingernail, and independent from the sporophyte (Figure 7.3.2).

Ferns can grow in a variety of environments, but they are more common in wet ecosystems since they need water for sexual reproduction so that the sperm can swim to the egg on the gametophyte (Figure 7.3.3).

Ferns can also reproduce asexually (vegetative reproduction) from the rhizome with new plants emerging from it. In the horticulture field, ferns are propagated by division (a plant can be split up into many).

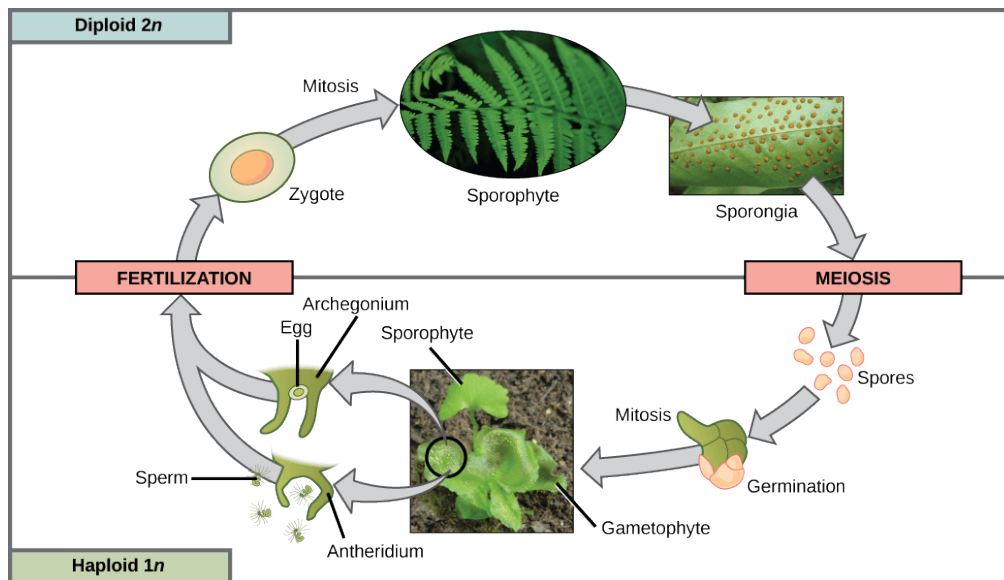


Figure 7.3.3: This life cycle of a fern shows alternation of generations with a dominant sporophyte phase. (credit "fern": modification of work by Cory Zanker; credit "gametophyte": modification of work by "Vlmastra"/Wikimedia Commons) by Biology OpenStax Attribution-NonCommercial 4.0 International (CC BY-NC 4.0).

Ferns are divided into four main groups (subclasses; PPG I, 2016): Equisetidae, Marattidae, Ophioglossidae, and Polypodiidae.

Equisetidae (horsetails)

Equisetales were once a diverse group of seedless vascular plants that were very common in the Carboniferous (300 million years ago) and have a rich fossil record. Today there is only one living genus, *Equisetum*, which is herbaceous, commonly reaching up to 1 meter in height (3 feet), but with some species able to reach 10 meters (32 feet). The name of this group is derived from the horsetail appearance that some branched species have. They are easy to recognize because of their green photosynthetic stems with vertical ridges (Figure 7.3.4). Leaves are usually brown or black, triangular, small, and arranged as a whorl around the stem at the nodes (dark rings on Figure 7.3.4).

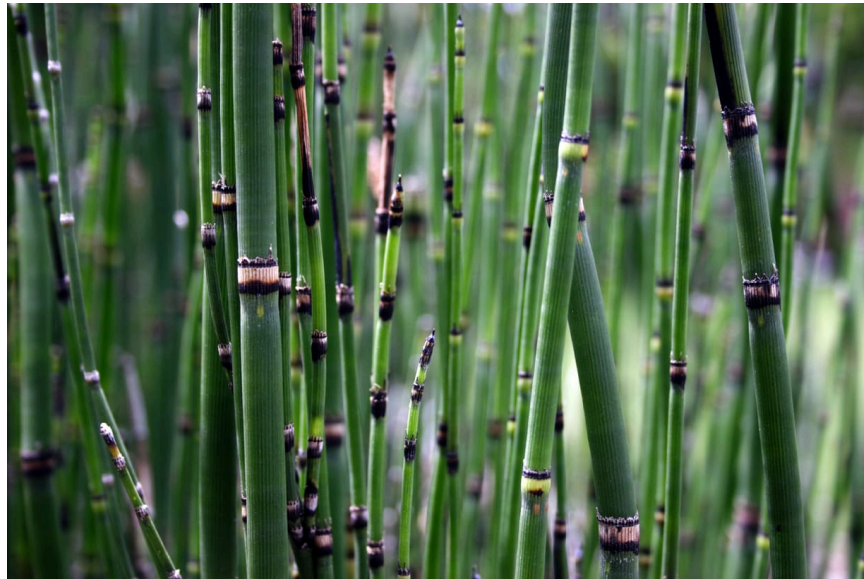


Figure 7.3.4: Cluster of horsetail (*Equisetum* sp.) stems by Christian Ostrosky CC BY-NC-ND 2.0 via Flickr.

Stems have silica on their cells, making these plants useful as polishing material. Some species have been used medicinally in Europe, the Americas, and Asia (especially in India) including as a diuretic and an anti-inflammatory medication (Carneiro *et al.*, 2013). They are also used as food, eaten boiled or raw in different cultures, especially the tender young stems. There are no native species of this group in Hawai'i. Several horsetail species were recently introduced to the islands to be used in gardening and landscaping, especially around ponds.

Marattiidae (mule's foot)

This group has only one living family and 110 species worldwide (PPG I, 2016). It is the most ancient group of ferns. These species are known to have very large, vertical rhizomes. The leaf bases are swollen, with large fleshy stipules on either side (stipules of some species can be eaten). Mule's foot leaves can be very large, reaching up to 9 meters (30 feet) in length.

Hawai'i has one native species, pala (*Marattia douglasii*). Another species, *Angiopteris evecta*, known as Madagascar's tree fern or mule's foot, has been introduced and is listed as an invasive species in Hawai'i (Figure 7.3.5).



Figure 7.3.5: Ferns in the Marattiaceae in Hawaii. A) Pala (*Marattia douglasii*) and B) Madagascar's tree fern (*Angiopteris evecta*). By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr. A derivative of the original work by Forest & Kim Starr, CC BY 3.0, via Wikicommons.

Ophioglossidae (whisk ferns, adder's-tongues)

Subclass Ophioglossidae has two orders: Psilotales (whisk ferns) and Ophioglossales (adder's tongues). Whisk ferns are very easy to recognize since they look like a green whisk broom with triangular stems that branch dichotomously (in twos). They do not have roots. Their leaves are tiny, therefore the green stems perform most of the photosynthesis. Their sporangia (spore-bearing structures) are rounded, yellow, and can be seen suspended on the upper portions of the branches. Whisk ferns are found in all tropical environments around the world. In Hawai'i, there are two indigenous species of whisk fern (Figure 7.3.6). *Moa nahele* (*Psilotum complanatum*) has flat stems and moa (moa or *Psilotum nudum*) grows upright. These species are found in a wide variety of environments on all the main Hawaiian islands. Traditionally moa has been used for lei making as well as medicine; for example, as a laxative tea, and the spores were used as powder to prevent chafing (Krauss 1974).



Figure 7.3.6: Whisk fern species in Hawai'i. Left: moa nahele (*Psilotum complanatum*) and right: moa (*Psilotum nudum*). By David Eickhoff is licensed under CC BY 2.0 via Wikimedia Commons.

Species of the Ophioglossales (adder's-tongue ferns) are often characterized by producing only one fleshy leaf at a time. Also, their gametophytes occur underground and they rely on mycorrhizal fungi for nutrition. Hawai'i has four indigenous and one endemic species in the Ophioglossales. An example is puapua moa or old-world adder's-tongue (*Ophioderma pendulum*). Its

sporangia are held within a spike that dangles from the middle of a leaf (Figure 7.3.7).



Figure 7.3.7: Puapua moa or old-world adder's-tongue (*Ophioderma pendulum*) with fertile spike. By Forest & Kim Starr, CC BY 3.0, via Wikicommons.

Polypodiidae

This is the largest group of ferns with most species of ferns in Hawai'i belonging to it. Species in this group are very important for the ecology of native ecosystems in Hawai'i. They flourish in wet and mesic forests, in which they may become the dominant group covering the soil, as well as being present in the mid-canopy as epiphytic species (growing on trees without harming them). Some ferns are pioneers on recent lava flows, where they start to break down the rock into soil and prepare the way for subsequent plant colonization, an important step in the formation of plant communities. Ferns also colonize areas where landslides have occurred. For example, uluhe (*Dicranopteris spp.*) can be seen growing in steep areas where the soil has been exposed by landslides (Figure 7.3.8). Uluhe species grow in thick mats, preventing invasive seeds from germinating and establishing, which helps the native species in the area by reducing competition.



Figure 7.3.8: Uluhe (*Dicranopteris linearis*) covers areas of recent landslides and steep slopes. © 2021 by DutraElliott is licensed under CC BY-NC 4.0 via Flickr.

In native forests, Polypodiidae species cover the soil surface (Figure 7.3.9). Ferns break the force of the rain passing through the

forest canopy so more water can get absorbed by the soil, and go into the aquifer, and erosion is reduced. Water runoff can be seen in areas where ferns and native forests are either disturbed or not present. After heavy rains, the ocean will turn brown due to all the sediment carried by the rain runoff from these mid-elevation disturbed areas.

The presence of introduced ungulates (pigs, deer, and mouflon sheep) has negatively impacted fern communities in Hawai'i. Pigs dig around the soil to uncover worms and insects, disturbing the root system of ferns. Once the fern ground cover is removed, invasive species have a better chance to colonize the area. Fencing to keep pigs out has been a successful strategy in Hawai'i that tremendously helps the conservation of native ecosystems. It gives fern communities a chance to recover, improving the chances that other native species can thrive.



Figure 7.3.9: An example of a wet forest ecosystem with native ferns (Ka'ala, O'ahu). © 2021 by DutraElliott is licensed under CC BY-NC 4.0 via Flickr.

In Hawai'i there are several traditional uses for ferns in this group: lei making, fiber, and food. Some species of ferns were used medicinally (see Gutmanis, 1976). There are at least two species of ferns used for food. One species, hō'i'o or pohole (*Diplazium sandwichianum*), is endemic to the Hawaiian Islands and grows in mid-elevation mesic to wet forests. The most common fern used for food is *Diplazium esculentum*, an introduced fern often called hō'i'o or warabi in Hawai'i. Throughout the Pacific and Southeast Asia it is known as paca (Palmer, 2003). It grows very well in lowland wet areas. The newly emerged fiddleheads of both species are harvested before they uncurl (Figure 7.3.10) and are eaten raw or steamed.



Figure 7.3.10: Calvin Hoe collecting hō'i'o or paca (*Diplazium esculentum*) in Waiāhole, O'ahu. © 2021 by DutraElliott is licensed under CC BY-NC 4.0.

Another native Hawaiian fern, the hāpu'u pulu (*Cibotium glaucum*) is a species of tree fern that produces hairs on its unfolding fronds, at the base of the stem (Figure 7.3.11). These soft hairs were used as filling material, including for the stuffing of pillows. These ferns are also ornamentals, being transplanted into gardens for their beauty, and their stems are often used as a substrate for other plants such as orchids (Buck, 1982). Wild harvest of tree ferns has been of conservation concern in some parts of the globe including Hawai'i.



Figure 7.3.11: Hāpu'u pulu (*Cibotium glaucum*) at Hawai'i Volcanoes National Park, Hawai'i Island. © 2021 by DutraElliott is licensed under CC BY-NC 4.0 via Flickr.

In Hawai'i, ferns are also commonly used in lei making (Figure 7.3.12), with two native species often used: pala'ā (*Sphenomeris chinensis*) and palapalai (*Microlepia strigosa*). Both of these ferns have special connections to Hawaiian culture and are seen as the physical representations (kinolau) of Laka, goddess of hula (palapalai), and Hi'iaka (pala'ā). The fronds of palapalai are also used to decorate hula altars (Ticktin *et al.*, 2006). Both species are harvested from the wild and in some areas, there are protocols in place to maintain populations that have been negatively impacted by invasive species (Ticktin *et al.*, 2006). The cultivation of pala'ā in gardens can be challenging, however, palapalai is easy to grow and is used in landscapes in urban areas. If grown in the right conditions, this fern can produce many fronds that can then be harvested.



Figure 7.3.12: Pala'ā (*Sphenomeris chinensis*) being used for lei making. © 2021 by DutraElliott is licensed under CC BY-NC 4.0 via Flickr.

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8: GYMNOSPERMS

Learning Objectives

- List the four major groups of gymnosperms and provide distinguishing features and examples of each.
- Explain the characteristics that made gymnosperms and other seeds plants dominate in terrestrial ecosystems compared to bryophytes and earlier vascular plants.
- List at least five uses of gymnosperms.



8.1: Gymnosperms

8.2: Conifers

8.3: Cycads

8.4: Ginkgo

8.5: Gnetophytes

8.6: References

8.1: Gymnosperms

Gymnosperms produce seeds (Figure 8.1.1) and, together with flowering plants, constitute the seed plants. Although gymnosperms do not produce flowers and fruits, they still have embryos enclosed in a protective barrier or seed coat. This neat little package called a **seed** is an innovative step in plant evolution that helped some plants thrive in terrestrial ecosystems. Seeds allowed plant embryos to withstand freezing, desiccation, and ultraviolet light damage in terrestrial environments while providing energy storage (endosperm). The name gymnosperm is derived from gymno meaning naked, and sperm meaning seeds (i.e., their seeds are uncovered). On the other hand, angiosperm (flowering plants) seeds are usually covered by a fruit. Most gymnosperms produce seeds in structures called **cones** or strobili (singular strobilus; Figure 8.1.2). Cones evolved from modified leaves, and they can either be male cones that produce pollen, or female cones that produce ovules.

There are approximately 1,100 gymnosperm species in the world today (Christenhusz and Byng, 2016) representing only 1% of plant diversity on the planet. However, they are an important part of the ecology of boreal regions (located in the Northern Hemisphere between 50° to 70°N latitude) and high-elevation environments including in the tropics (Crepet and Niklas, 2009). For example, in North America, entire forests are composed of large gymnosperm trees: redwoods, cedar, and pines.

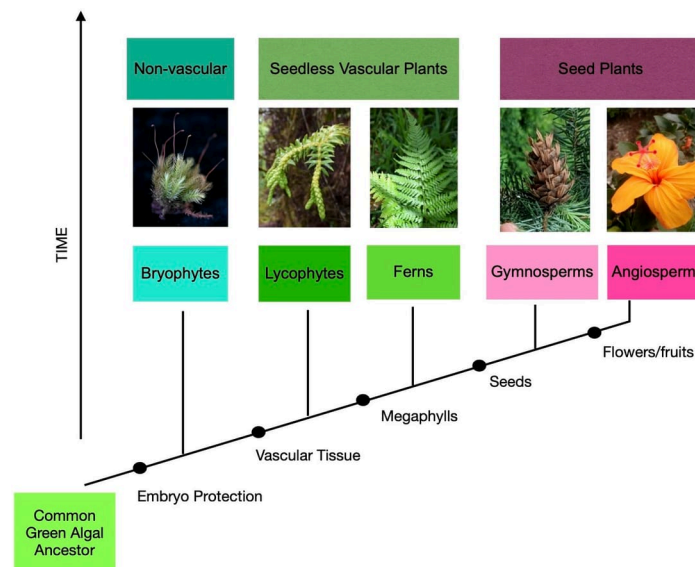


Figure 8.1.1: Phylogenetic tree depicting the evolutionary relationship of plants. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Besides having a protected embryo, seed plants also protect and nourish the gametophytic stage of their lifecycle, an advantageous characteristic for terrestrial life. In non-vascular plants (bryophytes), the gametophyte is the dominant stage, while in seedless vascular plants (ferns and lycophytes) the gametophyte is independent and reduced in size, leaving the sporophyte as the dominant stage. This pattern of gametophyte reduction continues in seed plants, in which the gametophyte becomes so reduced that it is only a microscopic entity found inside the ovules and pollen grains that grow on the sporophyte. Because the gametophyte develops inside the sporophyte, they are protected from environmental pressures and get nourishment from the sporophyte.

Another advantageous characteristic is the type of spores seed plants produce. While ferns produce one type of spore, making them **homosporous**, gymnosperms and other seed plants produce two types of spores (**heterosporous**), **megaspores**, which give rise to female gametophytes inside the ovule, and **microspores**, male gametophytes inside the pollen grain. The development of pollen and ovules has contributed to the success of seed plants on land. The pollen containing the male gametophyte gets transported via wind and sometimes by pollinators so that seed plants no longer rely on water for fertilization to take place. Most gymnosperms are wind pollinated, therefore they produce millions of pollen grains to increase the chances of them reaching the eggs on the female cones.

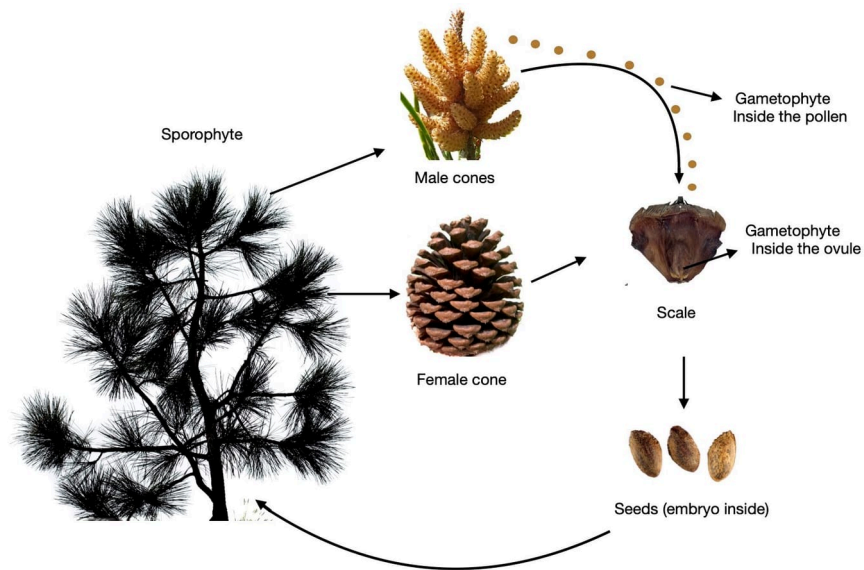


Figure 8.1.2: Gymnosperm life cycle. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Today, Gymnosperms are the group of plants most threatened by extinction with 40% of species being categorized as high risk (Forest *et al.*, 2018). For example, ginkgo is cultivated outside its natural range, but in China only a few natural populations remain, making it vulnerable to extinction. Another example is *Araucaria* (*Araucaria angustifolia*) which is native to Brazil and Argentina. This species has received critically endangered status because its natural habitat has decreased by 97% in the past century (Forest *et al.*, 2018).

Gymnosperms are divided into four groups: Conifers, Cycads, Ginkgo, and Gnetophytes.

8.2: Conifers

8.2 Conifers (Phylum Pinophyta)

Conifers are the most diverse group of gymnosperms, with 629 species worldwide (Christenhusz and Byng, 2016). A large number of conifer species are native to the Northern Hemisphere where they are an important part of native ecosystems, providing forest structure with many organisms depending on them for survival. The majority of conifer species are trees with secondary growth (wood formation) and are evergreen, not shedding their leaves seasonally. Leaves on most species are adapted to cold climates and snowy conditions by growing in a needle-like shape, which prevents snow from accumulating on the tree and eventually breaking it. Instead, the snow falls through the needles and releases the pressure caused by its weight. Another advantage of the needle-like leaf shape is resistance to desiccation in the cold dry winter. All species of conifers are wind pollinated, with some species having male and female plants (dioecious), while others have male and female cones on the same tree (monoecious).

There are several economically important species of conifers such as pines, cedars, and junipers, which are used for lumber and paper making. Conifers are the main source of raw material for paper products in North America, with numerous species grown in timber lots and constituting a big part of the world's economy.

Culturally, many species of conifers are important and are used during the holidays for decorations or as part of celebrations. For example, several species of Christmas trees are grown on tree farms, and pine cones and juniper foliage are used for wreaths and other seasonal decorations (Figure 8.2.1). Another example of how conifer species are used by people is the harvesting of juniper berries to make gin. The berries are female cones, not real fruits, that are used to flavor the alcoholic beverage. The seeds of two *Araucaria* species are also eaten in Chile and Australia by indigenous peoples.



Figure 8.2.1: Washington Christmas tree farm. A) Holiday ornaments, and B) Field of Christmas trees. By Washington State Department of Agriculture is licensed under CC BY-NC 2.0 via Flickr.

Pine trees are the most iconic group of conifers (Figure 8.2.2). They are considered by many as the most important genus of trees, as they have been used extensively by humans and their range of distribution occupies a vast area that extends from subtropical areas to subarctic zones. Pine trees grow in the coastal plains of Florida, mid-elevation forests in Mexico, and the boreal forests of Canada (Richardson *et al.*, 2007). Pine “nuts,” which are pine seeds, are very nutritious and are harvested from 29 species of pine trees in different parts of the world, including most of the Mediterranean, Asia, and the Middle East (Awan and Pettenella, 2017), as well as in the Southwestern United States.



Figure 8.2.2: White pine (*Pinus strobus*) native to the Eastern United States. A) Needle like leaves, B) Female cone, and C) Four year old seedling. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Redwood trees, *Sequoia sempervirens*, and *Sequoiadendron giganteum*, are important species in the conifer group in California (Figure 8.2.3). These trees are the tallest trees on Earth and can reach up to 110 meters (330 feet) in height and 11 meters (33 feet) in diameter. They can also live up to 2,200 years (Watson, 1993). These trees depend on humidity carried by fog for survival and can absorb water directly through their leaves (Burgess and Dawson, 2004). When fog or light rain occurs, the xylem reverses its direction, absorbing water directly from the leaves and transporting it to other places in the plant such as stems and sometimes to the roots (Burgess and Dawson, 2004). This impressive mechanism is important for the survival of the California redwoods because during the summer months when droughts are common, fog coming from the ocean is still commonly present (Limm et al., 2009).



Figure 8.2.3: *Sequoia sempervirens* in the Big Basin Redwoods State Park, California. By Allie_Caulfield, CC BY 2.0, via Wikicommons.

Douglas fir (*Pseudotsuga menziesii*) is a conifer native to the Pacific Northwest (Oregon, Washington, and British Columbia). It has been used extensively by native peoples, who eat the seeds, harvest and consume crystallized sugar from the branches at certain times of the year, and use the sap for medicine. This species has been logged for over 160 years (late 1800s to today) in the Pacific Northwest, and is one of the most important US timber exports (Cubbage et al., 2020; Walter and Maguire, 2004). Its wood is used to make poles, plywood, and railroad ties, among many other things. This tree can live up to 1,300 years and it is an integral part of the ecosystem where it is native (Figure 8.2.4). Several mammal and bird species depend on its seeds as a source of food and the structure of the forest created by these tall trees allows a high diversity of plant and animal species in

these areas.



Figure 8.2.4: Pacific Northwest Douglas fir (*Pseudotsuga menziesii*). By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

There are no native gymnosperms in Hawai'i, but conifers can be found in different parts of the islands as introduced species. Several conifer species were introduced in experiment plots. In the 1920s and 1930s, approximately 15 million trees were planted by different organizations as an experiment to reforest degraded areas (Woodcock, 2003). If you go hiking in a forest reserve, you will likely see stands of these species in their original plots as well as naturalized species that escaped cultivation. The following are some of the species that were planted in O'ahu: Sugi (*Cryptomeria japonica*; 499,000 trees), Monterey cypress (*Cupressus macrocarpa*; 216,000 trees), maritime pine (*Pinus pinaster*; 173,000 trees), redwood (*Sequoia sempervirens*; 130,000 trees), Monterey pine (*Pinus radiata*; 121,000 trees) and several *Araucaria* species, including Cook's pine (Woodcock, 2003). Araucarias are native to the Southern hemisphere and they eventually became naturalized in Hawai'i after being introduced as part of these experimental plots. Now these areas have trees growing and producing seedlings that compete with native species (Figure 8.2.5).



Figure 8.2.5: Araucaria experimental plot on the windward side of O'ahu. A) Female cone, B) Cone dispersing seeds and C) Araucaria mature trees. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

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8.3: Cycads

Cycads (Phylum Cycadophyta)

Cycads are easy to recognize because they look like a palm tree. However, they bear large cones rather than fruits. Their leaves are quite large compared to the stem and grow out in a rosette around the stem (Figure 8). They can be either male or female, and their cones vary in shape and size, depending on the species. There are approximately 340 species worldwide (Christenhusz and Byng, 2016), and are native to tropical and subtropical areas. They can grow in deserts as well as wet forests. Even though we don't have any native cycad species in Hawai'i, you have probably seen them around homes, botanical gardens, and parks.

There are two main families of cycads: Cycadaceae and Zamiaceae (another family, Stangeriaceae, has only two living species). Many cycad species are endangered in their natural habitat, although some species are very common in cultivation.



Figure 8.3.1: Examples of cycad species growing in Hawai'i. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

The seeds in some cycad species are considered toxic and can negatively affect humans by entering the food cycle through bats, which eat the seeds. Humans then eat the bats, acquiring the poison through second-hand exposure. Another interesting characteristic of cycads is that their roots form a special relationship with bacteria that can fix nitrogen.

8.4: Ginkgo

Ginkgo (Phylum Ginkgophyta)

There is only one living species of ginkgo, *Ginkgo biloba*, which is native to China but is cultivated across the world in temperate regions. The fossil record shows that this group was once diverse and had a widespread distribution in the Northern Hemisphere during the middle Jurassic (170 million years ago). Fossils of these Jurassic plants look very similar to modern ginkgo, indicating their characteristics have changed little over time, granting the status of “living fossil” to the only surviving species.

Ginkgo is easy to recognize because of its fan-shaped leaves (Figure 8.4.1). It is also known as the maidenhair tree, as the leaves resemble maidenhair fern fronds. Ginkgo can be either male or female. They are widely cultivated in urban areas because of their beautiful leaves, which change color in the fall. However, female plants produce a “fruit-like” structure that is actually a seed surrounded by a fleshy seed coat (they do not produce cones; Figure 8.4.2). Seeds emit a foul odor, therefore male trees are preferred for cultivation in most urban areas. In Asia, however, ginkgo seeds are consumed boiled or roasted, therefore female trees are predominantly grown. Ginkgo is also used for medicine, such as a dietary supplement that is used to improve blood circulation.



Figure 8.4.1: Ginkgo biloba being grown in cultivation. A) Tree and B) Leaves. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.



Figure 8.4.2: *Ginkgo biloba* seed. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

8.5: Gnetophytes

Gnetophytes (Phylum Gnetophyta)

Gnetales are the least familiar group of gymnosperms. There are 112 species in the world (Christenhusz and Byng, 2016), being divided into three main subgroups: *Welwitschia* (1 species), Gnetales (43 species), and Ephedrales (68 species). *Welwitschia* is an odd-looking plant adapted to extremely arid environments, being native to the Namibian Desert in Africa (Angola and Namibia). It has a short stem and only develops two leaves over its long lifetime. Some of the oldest plants can be 3,000 years old. The leaves can reach up to 2 meters (6 feet) in length and will continue to grow the entire life of the plant. The leaves usually coil and get split by the wind (Figure 8.5.1).



Figure 8.5.1: *Welwitschia* is an example of a gnetophyte. A) Close up of a female *Welwitschia mirabilis*, and B) *Welwitschia mirabilis* plant in its natural environment. By DutraElliott is licensed under CC BY-NC 4.0 via Flickr. A derivative of the original works of A) by Tris T7, CC BY 3.0, via Wikicommons. And B) wolfgang.mller54, CC BY 2.0, via Wikimedia Commons. Modifications: Photos were put together in a plate and labels added.

An example of a plant in the Ephedrales group is Mormon tea (*Ephedra spp.*), which is common in arid regions of the Southwestern United States (Figure 8.5.2). Mormon tea, and a similar species in China from which ephedrine is extracted, have been used for millennia for treating asthma. Currently, ephedrine is used to prevent low pressure during anesthesia and most of it is synthetically manufactured, although some *Ephedra* species are still cultivated for extraction of natural ephedrine.



Figure 8.5.2: Mormon tea at Natural Bridges National Monument, Utah. By PaulaMejia is licensed under CC BY-NC-SA 2.0 via Flickr.

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9: ANGIOSPERMS

Learning Objectives

- State the basic differences between angiosperms and gymnosperms.
- Within angiosperms, identify and describe monocots and eudicots.
- Identify some economically important families.



9.1: Angiosperms

9.2: Monocots and eudicots

9.3: Angiosperms families

9.4: References

9.1: Angiosperms

Angiosperms are the group of plants that we are most familiar with, as most of the fruits and vegetables we eat belong to this group. They are currently the dominant group of plants in most terrestrial ecosystems and are easy to recognize since they produce flowers (Figure 9.1.1). Angiosperms are the most diverse group of plants, with 416 families and approximately 352,000 species (APG, 2016). The first fossils of angiosperms date back to the Lower Cretaceous (~130 million years ago; Magallón *et al.*, 2013; [Appendix 1](#)). Over time, they diversified and became more prominent in terrestrial ecosystems, slowly displacing and replacing gymnosperms and other plants. Today, angiosperms represent 90% of terrestrial plants on the planet. The remaining terrestrial plant species comprise gymnosperms (approximately 1% of species; Crepet and Niklas, 2009) and bryophytes, lycophytes, and ferns (9% of species).

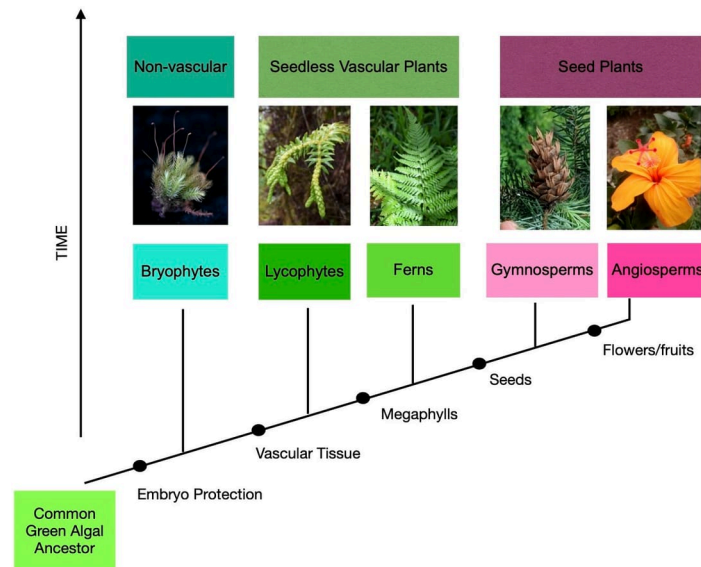


Figure 9.1.1: Phylogenetic tree depicting the evolutionary relationship of plants. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

The diversity and success of angiosperms can be attributed to the evolution of flowers and fruits within this group. The development of flowers was an innovative characteristic, as it allowed the ovules to be enclosed and protected inside an ovary, which after fertilization turns into a fruit that aids seed dispersal. Flowers also allowed for male and female parts of the plant to be clustered into a single structure (Figure 9.1.2).

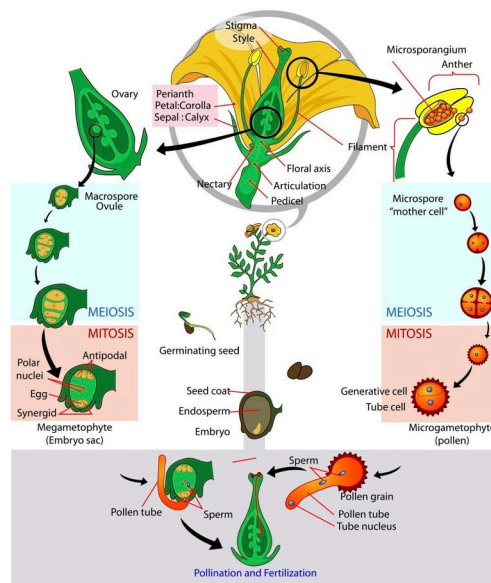


Figure 9.1.2: By LadyofHats is licensed under Public domain via Wikimedia Commons.

Flowering plants developed relationships with pollinators (Hu *et al.*, 2008). Instead of dispersing their pollen via wind, like gymnosperms, early angiosperms started to offer rewards in their flowers to attract animals, who in turn started to visit the flowers of a given species for the food rewards they offered. Through this relationship, flowering plants got the guarantee that their pollen would likely reach another individual of the same species: therefore, increasing the probability of successful fertilization (Figure 9.1.3). This transfer of pollen from one plant to another, otherwise known as cross-pollination, ensured higher genetic diversity in the population.



Figure 9.1.3: Flower diversity in angiosperms, and examples of pollinators. A) European honey bee pollinating guava flowers, B) Fly pollinating an avocado flower, C) European honey bee pollinating macadamia flowers and D) Carpenter bee (*Xylocopa* sp.) pollinating passion flower/*liliko'i*. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Since the origin of flowers, pollinators have driven floral diversity in angiosperms by increasing the richness of species (Van der Niet and Johnson, 2012). Pollinators have preferences for flower shape, size, color, and even type of reward. They also come in all shapes and sizes and they include birds, reptiles, beetles, and bats. Over time, some plants and pollinators have developed a specific relationship, where a plant species is pollinated by a specific animal. However, many plants (and animals) are generalists and are pollinated by different species of pollinators.

The Hawaiian honeycreepers are a great example of the relationship between pollinators and flowering plants. At least five genera of a group of plants called Hawaiian lobeliads (*Delissea*, *Clermontia*, *Cyanea*, *Lobelia* and *Trematolobelia*) are pollinated by native

forest birds (Pender *et al.*, 2014). The shape of the flowers, the nectar content, and other characteristics match this kind of pollination syndrome. The native Hawaiian honeycreeper 'i'iwi (*Vestiaria coccinea*) feeds on the nectar produced by these flowers thanks to its long, curved beak which has a similar shape to the curved flowers of many of the Hawaiian lobeliads (Figure 9.1.4). When feeding on nectar, pollen from the flower is deposited on the head of the 'i'iwi, and the bird inadvertently moves pollen between flowers. Unfortunately, it is believed that many Hawaiian lobeliad species produce reduced amounts of seed because some native bird species are so rare or have become extinct; therefore, the flowers are not adequately pollinated by these native birds.



Figure 9.1.4: 'i'iwi (*Vestiaria coccinea*) visiting a lobeliad flower. By USFWS Pacific Region CC BY-NC via Flickr.

A long, tubular Hawaiian lobeliad flower could not be pollinated by insects like bees because of its curved shape. On the other hand, some plant species like 'ōhi'a (*Metrosideros polymorpha*) are known as generalists, as they can be pollinated by either birds or insects (Figure 9.1.5). The flower shape and other characteristics, like color, allow for this type of pollination strategy.

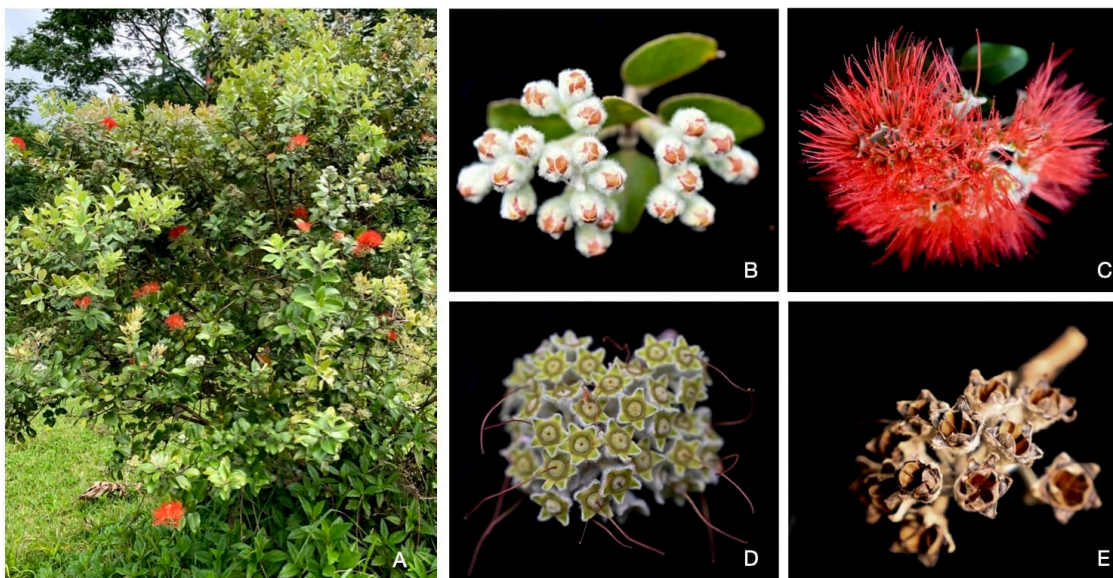


Figure 9.1.5: Fruits and flowers of 'ōhi'a lehua (*Metrosideros polymorpha*), an angiosperm species. A) Whole plant, B) Unopened flowers, C) Fruit capsules, D) Flower, and E) Dried capsules. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Fruits are another evolutionary adaptation present in angiosperms. Once the plants are pollinated and the ovules fertilized, the ovary grows into a fruit. One of the main functions of the fruit is to assist in the dispersal of the seeds, which is achieved through different mechanisms. For example, fruits can be attractive to animals because they offer a food reward. After being eaten, the seeds contained in the fruit are usually dispersed a distance from the parent plant, allowing the species to spread. Other fruits

have spurs to attach themselves to animal fur and bird feathers to aid the dispersal of seeds. An example of the importance of animals in the dispersal of angiosperm seeds is exemplified by the long-distance dispersal of seeds to Hawai'i from distant land masses; bird dispersal is the principal mode in which native plant genera arrived in the islands.

9.2: Monocots and eudicots

Angiosperms can be divided into several groups: Basal clades, Magnoliids, Monocots, and Eudicots. Most angiosperm families fall into the monocots and eudicots groups. These two groups have very specific morphological (external) characteristics. We will look at them closely here, but they were also explored briefly in previous chapters of this book.

Seeds

Monocots have one cotyledon (mono = one; cotyledon = seed leaf), while eudicots have two (eu = true; di = two; cotyledon = seed leaf). For example, beans are eudicots and when their seeds germinate it is easy to see the two cotyledons (Chapter 5, Figure 9.2.1). The same thing happens when you cook beans, some of the seeds may split into two parts. Monocot seeds don't do that, they stay intact. Corn is an example of a monocot.

Flowers

Dicot flower parts are organized in multiples of four or five, while in monocots flowers are organized in multiples of three. Some plants have petals and sepals while others have tepals. Tepals are the ancestral condition in flowering plants and are undifferentiated (they look the same). You may see a flower that has flower parts that look identical and you can't tell if they are sepals or petals like in daylilies (*Hemerocallis* spp.; Figure 9.2.1) and in spider lily (*Crinum asiaticum*; Chapter 5). An example of a monocot is a spider lily, which has six petals, while an example of a dicot is a *Hibiscus*, which has five petals (Figure 9.2.1; Chapter 5).

Roots

Overall, eudicots generally have tap roots while monocots have fibrous roots (Figure 9.2.1; Chapter 2). There are exceptions to this rule, for example, eudicot species may have adventitious roots. Tap roots have a prominent primary root that develops when the seed germinates and the radicle emerges. From there, secondary or lateral roots grow. Fibrous roots, as the name suggests, look like fibers, with all the roots being of similar length and diameter. Fibrous roots usually form a dense shallow root system. Fibrous roots are also known as adventitious roots because the primary root that forms when a seedling germinates is eventually replaced by lateral roots from the stem of the plant.

Leaves

Eudicots have reticulate (net-like) venation on their leaves, while monocots usually have parallel venation (Chapter 4). However, there are exceptions to this rule. For example, kalo/taro is a monocot that does not have parallel veins on the leaves (Figure 9.2.2). In reticulate venation, the branching pattern further divides into smaller veins resembling a net. In parallel venation, several secondary veins are parallel to the midrib and to each other.

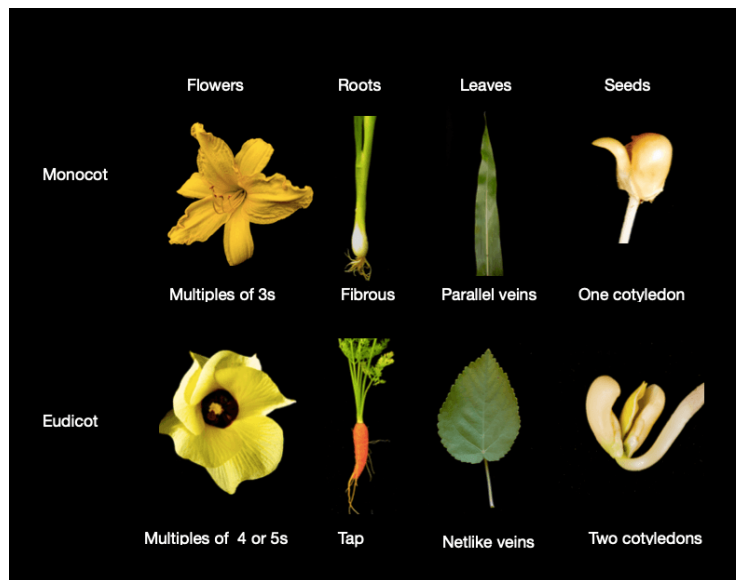


Figure 9.2.1: Characteristics of monocots versus eudicots. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.



Figure 9.2.2: Common monocots of Hawai'i. A) Niu/coconut (*Cocos nucifera*) ; B) Kī or ti (*Cordyline fruticosa*); C) Mai'a/banana (*Musa sp.*); D) Loulu (*Pritchardia sp.*); E) Kalo/taro (*Colocasia esculenta*); F) Sugarcane/Kō (*Saccharum* spp). By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Other characteristics

Several anatomical characteristics can also be used to distinguish monocots and eudicots. focus on the internal structure of plants (anatomy). You won't be able to see them with the naked eye, but you could use them to differentiate between plant groups if you had a microscope. For example, monocots have their vascular bundles scattered in the stem, while eudicots have them organized in a ring around the stem (Chapter 3). In monocots, like corn, these vascular bundles are scattered throughout the stem tissue. Eudicots, like beans, are a little more complex. Eudicot stems can be herbaceous or woody. In herbaceous or young woody eudicots the vascular bundles are arranged in a ring around the stem. In older stems, these bundles tend to fuse to form concentric rings. Also, pollen grains in eudicots have three apertures, while monocots have only one.

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9.3: Angiosperms families

Families are large groups within the Kingdom Plantae (plants) that share certain characteristics and have a common ancestor. Originally, these families were defined based on their morphological characteristics (shape). Today, we can use additional sources of data, like DNA to group plants into families and to more accurately reconstruct the evolutionary relationships of plants. The visible characteristics of plants (morphology) are still very useful for plant identification and can have practical uses. For example, some diseases may affect members of a specific family, some families are known to produce poisonous compounds, or some families may have specific germination requirements, like the case of Orchidaceae. The more you learn about plant families and their characteristics, the easier it is to identify plants. You start to notice that a plant you know may have similar characteristics to other plants.

Here we will cover just a few examples of plant families in the monocot and eudicot groups (Figure 9.3.1). These families have been selected due to their diversity of species, cultural, ecological, and economic importance. Of course, we encourage you to learn about other plant families; the ones listed here are just to get you started.

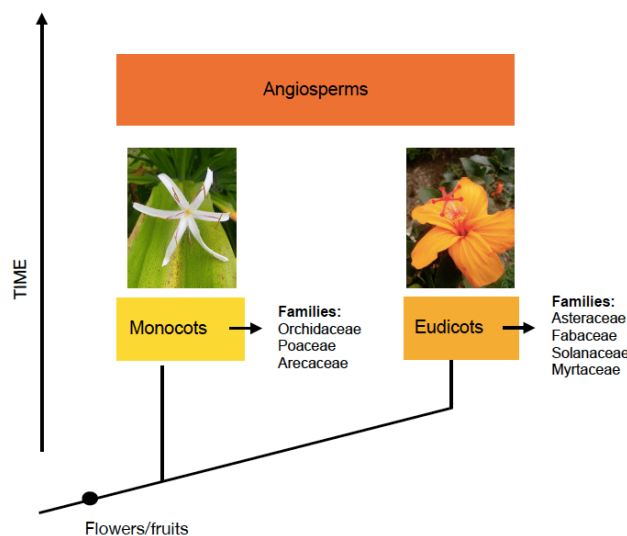


Figure 9.3.1: Angiosperm evolutionary tree. Please note this tree is simplified and excludes some information, like the basal groups and Magnoliids. It includes examples of families we will be referring to in this chapter. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Examples of Monocot families

Orchidaceae

The Orchidaceae is the largest plant family with approximately 28,000 species (Christenhusz and Byng, 2016). All species are herbs, but they can either be terrestrial or epiphytic. Terrestrial orchid species in temperate zones spend part of their lifecycle under the ground and at a certain time of the year the leaves may grow above ground and they may bloom and form fruits. The cycle may continue with the plant dropping its leaves and going dormant for a period of the year. In the tropics, terrestrial species may grow year-round. Epiphytic orchid species are found in tropical and subtropical environments. They use trees for support without damaging them. This is an important strategy when growing in a forest since little sunlight gets to the forest floor. These plants can grow high up in the canopy of trees where they benefit from more sunlight and access to pollinators.

Orchid species are highly diverse, presenting different flower shapes and colors. Researchers attribute the diversity of species in the Orchidaceae to co-evolution with pollinators and fungi. Some orchid species offer nectar as a reward, while others mimic insect shapes or pheromones that trick insects into believing the flowers are their mating partner. Many species in this family rely on specific animals for pollination. For example, vanilla (*Vanilla planifolia*), which is native to Mexico, is pollinated by a native species of bee. When the plant is grown outside of its natural range, like in Hawai'i, hand pollination is required for plants to

produce fruit capsules (Figure 9.3.2). The fruit of vanilla is the part of the plant used to make vanilla extract.

Hawai'i has three native orchid species, all found in high elevations. All of them are terrestrial and likely arrived here by air currents. Non-native orchids are very popular in Hawai'i and many growers focus on propagating hybrids for the horticultural market.

Common Characteristics

Habit: Either epiphytic or terrestrial herbs.

Flower: Instead of having petals and sepals, orchids have six tepals including a modified lip. The anthers are grouped into a structure called the pollinia.

Fruits and Seeds: The fruit in this family is a capsule. Seeds are very small and do not have food reserves. Instead, they rely on fungi to germinate (mycorrhizal association). When the seed gets dispersed from the capsule, it needs to land in a location with a specific fungus present. This fungus then inserts its mycelium into the seed and provides it with nutrients. The seed is completely dependent on the fungus until it can photosynthesize. Figure 9 shows orchid seeds that are germinating in association with mycorrhizae.

Leaves: Leaves are often simple with parallel veins (i.e. typical monocot leaf characteristics).

Stems: All species have herbaceous stems. Stems can either be monopodial (grow from a single shoot like in vanilla; Figure 9.3.2) or sympodial (grow from new shoots emerging from a rhizome base). Many species have a specialized stem called a pseudobulb which can store water and nutrients.

Other: Epiphytic orchids have velamen (specialized epidermis) on their roots which protects the exposed roots from ultraviolet light damage while allowing the root to absorb nutrients and water directly from the surrounding environment.



Figure 9.3.2: *Vanilla planifolia* A) Vanilla flower, B) Vanilla grower pollinating flowers by hand, C) Vanilla capsules, and D) Orchid seeds and E) Orchid embryos germinating with the help of mycorrhizae. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Poaceae

The Poaceae is the fifth largest plant family with 12,000 species (Christenhusz and Byng, 2016), and includes some very important species for human consumption: corn, rice, wheat, barley, and millet, as well as for animal feed (corn), construction materials (bamboo and grasses for thatching), and biofuels (ethanol made from corn and sugarcane). Several species of grasses were domesticated thousands of years ago and today they are known as cereal crops. For example, corn was domesticated in central Mexico around 10,000 years ago (Tian *et al.*, 2020). The ancestor of corn (wild relative) is teosinte, a large grass. Since its domestication, corn has been taken all over the globe and it is now one of the most important crops worldwide.

Grasses are very important for the ecology of natural habitats. Grasslands can be found all over the globe, sustaining diverse food webs, as in the African savannas. Grasses are also important components of forests, tundras, wetlands, and even in marine habitats. For example, marine grasses provide food and habitat to organisms like the Florida manatee, while also providing nursery grounds for the young of many fish species.

Polynesians introduced bamboo (*ohe*; *Schizostachyum glaucifolium*) to Hawai'i. It has been used to make musical instruments (e.g. nose flutes). They also introduced sugarcane (*kō*, *Saccharum* spp.). *Pili* grass (*Heteropogon contortus*), which is a native grass species and an important component of drylands, was used to thatch roofs. Hawaii's environment did not evolve with large herbivores such as cattle, goats, or deer, so native grasses have been severely impacted by the introduction of these large herbivores, as well as by the introduction of non-native grasses that have become invasive. Native grasses are still important in the native environments, being part of the understory and crucial for coastal erosion control. For example, 'aki'aki grass (*Sporobolus virginicus*) is a native grass species that plays an important role in reducing the erosion of coastal environments in Hawai'i.



Figure 9.3.3: Sugarcane/*kō* (*Saccharum* spp.). One of the main characteristics of the Poaceae family is the leaf-sheath, the base of the leaf that surrounds the stem. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.



Figure 9.3.4: Caryopsis: fruit type in Poaceae. Kernels of different varieties of corn (*Zea mays*). By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Common Characteristics

Habit: Herbs.

Flowers: Small and normally wind-pollinated. Flowers are formed into a spikelet which is composed of many different parts (glume and lemma).

Fruits and Seeds: The fruit is a caryopsis (Figure 9.3.4) and the seed has one cotyledon as in other monocots.

Leaves: The leaves are normally alternate and have parallel veins. The base of the leaf encloses the stem of the plant creating a “leaf-sheath” while the top of the leaf (the blade) is detached from the stem (Figure 9.3.3).

Stems: The stems are hollow except at the nodes.

Areaceae

The Areaceae or palm family has 2,600 species (Christenhusz and Byng, 2016). This family is known for its tree-like species (palm trees) which inhabit tropical and subtropical areas. Even though palms are monocots, which do not develop wood, the stems of these species are extremely strong. They are used to make furniture and musical instruments. The species are also used for food (e.g. coconut, palm sugar, and heart of palm), thatching, as well as hand crafts such as baskets and hats. Many palm species have edible fruits that are consumed in different locations. For example, dates (*Phoenix dactylifera*) are grown in dry areas and are part of the cuisine in the Middle East, North Africa, and certain parts of Asia. Açai palm (*Euterpe oleracea*) is cultivated in the Amazon and its fruit is used to make very nutritious and savory meals. It has been a staple part of the diet of local habitants for centuries. Recently, açai became a health food trend around the world and it is now eaten as a sweet treat.

Hawai'i has an incredible diversity of native palms, with 22 endemic species of *loulou* (*Pritchardia* spp.; Figure 9.3.5). Most species are native to specific islands or even specific mountain ranges on an island. The large leaves of these species were used to thatch roofs and make baskets and other items. The trunks were used for construction. The immature fruit (a drupe) was used as food (Hodel, 2012). Many *loulou* species are currently threatened or listed as endangered due to damage from invasive animals, such as pigs and rats. Rats eat the fruits, impacting the ability of the population to regenerate. In some areas you can find old trees, but no young plants or seedlings. This happens when rats remove all the viable seeds making it impossible for new seedlings to establish. Eventually, the old trees die and the population disappears from the wild. Pigs damage the bark and root systems as well, negatively impacting older plants in the populations.



Figure 9.3.5: Loulu palm trees (*Pritchardia* spp.). By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

The coconut palm (*Cocos nucifera*) is very important in many cultures. The fruit can be used as food and for coconut milk, the fiber can be used for cordage, and the leaves for handcrafts. The oil is important for many African (including the diaspora in the Americas) and Pacific Island cultures. Coconut oil has recently begun being used worldwide due to its nutritional benefits. Polynesians introduced coconut (*niu*) to Hawai'i and this plant has been used for the purposes described above. This plant is considered one of the most versatile plants since every part of the plant has a use (Figure 9.3.6).



Figure 9.3.6: *Cocos nucifera*. A) Young coconut still attached to the fruit. B) Coconut stem showing stem fibers. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Common Characteristics

Habit: Lianas (climbers) and tree-like (palms).

Flowers: Small and symmetrical with three petals and three sepals. The flowers are arranged in an inflorescence (a cluster of flowers originating from a main branch).

Fruits and Seeds: Drupe with a single seed inside (sometimes two).

Leaves: Leaves are large and either palmately compound or pinnately compound.

Stems: Most common species have a single dominant stem that does not branch. Although some species grow in clusters. Like in other monocots, the stems do not produce wood (secondary growth).

Examples of Eudicot families

Fabaceae

The Fabaceae, also known as the bean or legume family, is a very important plant family with approximately 19,500 species. Many members of this family can grow in soils with low nutrient levels because they can form root nodules and house nitrogen-fixing bacteria, making them an important crop in areas with poor soil. Fabaceae are also known for being very rich in protein, which makes it a staple food in many diets. Plants in this family are important for human food (beans, lentils, peas, beans, soybeans), cattle forage (e.g. *Leucaena*), and as cover crops (species that are planted to enhance soil health on a farm). Several species in this family are known for their hardwoods, making them important as a source of lumber.

There are several native species in this family in Hawai'i (Figure 9.3.7). These include *koa* (*Acacia koa*; Figure 9.3.8), *wiliwili* (*Erythrina sandwicensis*) and *māmane* (*Sophora chrysophylla*; Figure 9.3.7). The wood of *koa* is highly valued and it is used to make furniture, jewelry, and art. The wood of *māmane* was used for house posts, fences, and digging sticks (o'o), and the seed is used for lei making (Figure 9.3.9). On Mauna Kea, the palila bird (*Loxioides balleui*) depends on the seeds of this plant as a food source, and the plants as nesting and roosting habitat. In ancient times, Native Hawaiians used *wiliwili* to make surfboards because its wood is buoyant. The beautifully colored seeds are used in lei making (Figure 9.3.10).



Figure 9.3.7: Diversity of flowers in the Fabaceae family. These are examples of three faboid subfamilies. A) Green bean flower (*Phaseolus vulgaris*, subfamily Faboideae), B) Orchid tree (*Bauhinia variegata*; Cercicoideae subfamily), C) Monkey pod flower (*Samanea saman*; Caesalpinoideae subfamily), D) *Māmane* (*Sophora chrysophylla*, subfamily Faboideae) and E) *Wiliwili* (*Erythrina sandwicensis*, subfamily Faboideae). By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.



Figure 9.3.8: Koa (*Acacia koa*). By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr. This work is a derivative of the original work of Forest and Kim Star CC-BY 2.0 via Wikicommons. Modified to combine photos and include labels.



Figure 9.3.9: Māmane (*Sophora chrysophylla*) seed lei. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.



Figure 9.3.10: Wiliwili (*Erythrina sandwicensis*) seeds. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Common Characteristics

Habit: Herbs, shrubs, trees, vines and lianas.

Flower: Flowers are very diverse, varying among the six subfamilies in this family. Three of the most common flower types can be seen in Figure 14. Pea-shaped flowers are in the subfamily Faboideae. Flowers with multiple stamens and very small petals (as in monkey pod; Figure 14) can be found in the Caesalpinioideae subfamily. From afar they may look like puff balls. Flowers of the orchid tree (*Bauhinia variegata*) are large and colorful with five petals and are in the Cercicoideae subfamily.

Fruits and Seeds: Most fruits are legumes or loment. The seed is bean-like.

Leaves: Alternate and entire. Compound.

Stems: Stems can be herbaceous or woody.

Other: Nodules on roots contain nitrogen-fixing bacteria.

Solanaceae

The Solanaceae is also known as the nightshade family and it has about 2,600 species (Christenhusz and Byng, 2016). Many species are poisonous, while others have medicinal and ornamental uses. For example, belladonna/deadly nightshade (*Atropa belladonna*) is very toxic and causes hallucinations if ingested, as it contains several alkaloids. An ornamental plant that is commonly seen in Hawai'i and that is extremely poisonous is the angel's trumpets (*Brugmansia* sp.). This plant is used as a psychoactive drink in rituals in some cultures in South America and causes hallucinations. It was introduced to Hawai'i in the 1800s from South America and can be seen growing in gardens. Tobacco (*Nicotiana* sp.) is also in this family. It can be highly addictive because it contains the alkaloid nicotine, which is a stimulant.

Many plants in this family are not toxic and are widely used for cooking. For example, many crop species such as potato tubers, tomatoes, peppers, and eggplants are used in cuisines all over the globe. Potatoes, tomatoes, and peppers are originally from the Americas, where they were first domesticated, and were introduced to the rest of the globe after European contact (Figure 9.3.11). Tomatoes, for example, were first domesticated in Mexico and were introduced to Europe after the Spanish colonized the Americas in the 16th century. They are now an iconic component of several European cuisines. It is hard to imagine Italian food without the tomato, or even peppers, but it was only after Europeans brought those crops back from the Americas that they were introduced to Italy. The same thing is true about peppers anywhere in Asia. Thai food did not have hot chilies until they were introduced from the Americas.

Common Characteristics

Habit: Herbs, shrubs, trees, and vines.

Flowers: Flowers have five petals and five sepals. The stamens also occur in multiples of five and can fuse together around the pistil, forming a column (Figure 9.3.11A).

Fruits and Seeds: Fruits are either berries or capsules.

Leaves: Frequently have prickles.

Stems: Stems are very diverse in this family due to different growth habits.

Other: Many species are poisonous and many are edible domesticated crops (e.g. tomato, pepper, eggplant, and potato).



Figure 9.3.11: Examples of plants in the Solanaceae: A) Tomato (*Solanum lycopersicum*) flower showing fused stamens, B) Tomato fruits (berries), and C) Pepper (*Capsicum annuum*) fruits. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Asteraceae

The Asteraceae, also known as the sunflower family, has 24,700 species (Christenhusz and Byng, 2016). Species in this family can grow in a wide range of environments, but they most commonly occur in dry areas and deserts, including high-elevation zones. In Hawai'i, for example, āhinahina or silversword (*Argyroxiphium sandwicense* subsp. *macrocephalum*) grows near the summit of Haleakalā at approximately 3,000 meters (10,000 feet) in elevation. The plant has leaves with furry hairs (trichomes) to protect the plant against sun and wind (Figure 9.3.12).



Figure 9.3.12: Haleakalā silversword (*Argyroxiphium sandwicense* subsp. *macrocephalum*). A) flowers and B) Plant body. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

This family has many economically important species that are used to make oil (e.g. sunflower), teas, and medicine (e.g. chamomile, echinacea). Several species are used for food: lettuce (*Lactuca sativa*), artichoke (*Cynara cardunculus* var. *scolymus*), and sunflower (*Helianthus annuus*). There are many ornamental species and cultivars in this family including marigolds (*Tagetes* spp.), chrysanthemum (*Chrysanthemum* spp.), zinnia (*Zinnia* spp.), and dahlia (*Dahlia* spp.), which are very important to the horticultural industry.

Asteraceae have very characteristic flowers. They are grouped into clusters called heads or capitulum, which are made up of dozens and sometimes hundreds of individual small flowers (Figure 9.3.13). There are two main types of flowers composing the head. Ray flowers are on the outside of the heads with the petals on the very outside. Disk flowers, on the other hand, are in the inner part of the head. This arrangement likely evolved to attract pollinators.

Common Characteristics

Habit: Mostly herbs, but also shrubs and trees.

Flower: The inflorescences (cluster of flowers) are showy and the numerous flowers are packed in heads. A single flower can fall into one of three different types: disk florets, ray florets, and ligulate florets (Figure 9.3.13).

Fruit and Seeds: Achene.

Leaves: Leaves can be arranged differently on the stems depending on the species (opposite, alternate or whorled).

Stems: The stems are most often herbaceous.



Figure 9.3.13: CA) Sunflower head with many individual flowers, B) Close up of a sunflower head with ray flowers on the outside of the head, and C) Zinnia with disc flowers at the center of the head. By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Myrtaceae

This family has many important edible species in Hawai'i such as guava, strawberry guava, and mountain apple/'*ohi'a* 'ai (Figure 9.3.14). Today, 5,950 species exist worldwide in this family. The petals on the flowers can be reduced and the stamens numerous, giving the flower a fluffy appearance (Figure 9.3.14). Some species in this family are important sources of timber (e.g. *Eucalyptus* spp.). Some species in this family produce essential oils (e.g. allspice; *Pimenta dioica*). One of the most important native forest species in Hawai'i is *ōhi'a*, *Metrosideros polymorpha*, which belongs to this family (Figure 9.3.14D). Native birds depend on their flowers for nectar, they play an important role as watershed forests and are also highly important culturally.



Figure 9.3.14: Mountain apple/'*ohi'a* 'ai (*Syzygium malaccense*) fruits, B) Flowers, C) Guava (*Psidium guajava*), D) 'Ōhi'a (*Metrosideros polymorpha*). By DutraElliott is licensed under CC BY-NC-SA 4.0 via Flickr.

Common Characteristics

Habit: Woody trees and shrubs.

Flowers: Flowers have five petals but they are often reduced, with numerous colorful stamens present (Figure 9.3.14D).

Fruits and Seeds: Fruits are capsules or berries.

Leaves: Essential oils are present in the leaves of some species.

Stems: Stems are woody.

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10: PLANTS IN HAWAI'I

Learning Objectives

- Learn the terminology associated with plants in Hawai'i.
- Describe how native Hawaiian plants originated.
- Summarize how the original colonizers of native Hawaiian plants arrived in Hawai'i.
- Describe Polynesian introduced and recently introduced plants.



10.1: Native plants

10.2: Polynesian introduced plants

10.3: Recent introduced plants

10.4: References

10.1: Native plants

Hawai'i is a special place with diverse ecosystems such as alpine deserts, ocean coastlines, dry shrublands, and rainforests. Learning more about the plants and the different environments present in the Islands can enhance our relationship with nature and our role in island sustainability. Humans have strong connections to plants and animals. We depend on them for food and medicine, and they are utilized in cultural practices, stories, and belief systems. A great way to get to know the place we live is by knowing local plant names and their stories. How did they get here? Who or what brought them in? What is their significance?

While strolling anywhere in the Hawaiian Islands, we may find ourselves surrounded by an astonishing diversity of plants. However, not all the plants that currently inhabit Hawai'i are native to Hawai'i. Every single plant you find has a different history: some evolved here; some are found elsewhere on the planet but arrived in Hawai'i without any human assistance, and others were brought by humans.

A species is considered **native** when it naturally inhabits a region and arrived there without any human assistance. Native plants are divided into two categories: endemic and indigenous. **Endemic** plants are plants that are only found naturally in a specific area and nowhere else in the world. These terms are used anywhere on the globe. For example, a plant that is endemic to China grows naturally only in China. An example of a Hawaiian endemic plant is *koki'o 'ula* (*Hibiscus clayi*) which does not naturally occur anywhere other than Hawai'i. **Indigenous** plants are native plants that can be found in a specific area as well as in other locations. For example, *naupaka kahakai* (*Scaevola taccada*) is a plant that naturally grows in Hawai'i, but also grows on other Pacific islands (Figure 10.1.1).



Figure 10.1.1: Examples of endemic and indigenous plants in Hawai'i. *Koki'o 'ula* (*Hibiscus clayi*) is endemic to Hawai'i, (left) and *naupaka kahakai* (*Scaevola taccada*) is indigenous (right). Both endemic and indigenous plants are considered native. © 2021 by DutraElliott is licensed under CC BY-NC 4.0 via Flickr.

Hawai'i has 1,606 species of native plants, divided as follows:

- 421 non-vascular plants (Staples and Imada, 2006; Staples *et al.*, 2004)
- 146 ferns and 15 lycophytes (Ranker *et al.*, 2019)
- 1,039 angiosperms (Price *et al.*, 2018).

The flora of Hawai'i is very unique compared to other parts of the world, with 88% of those species being endemic to the Hawaiian Islands.

How did plants originally get to Hawai'i?

The Hawaiian archipelago is one of the most isolated places on Earth. It is located 3,700 km (2,300 miles) from the coast of the United States and 5,863 km (3,643 miles) from Asia. Plants in Hawai'i evolved in isolation from people and other influences for 47 million years (Gustafson *et al.*, 2014). This long history of isolation coupled with the many diverse environments on the islands gave rise to a great diversity of endemic species evolving from the original plants that arrived in the archipelago.

The Hawaiian archipelago was created by volcanic activity. A stable hot spot beneath the ocean floor releases magma while the Pacific plate moves northwest over it. This creates seamounts underwater that eventually break the surface and become islands. As the plate moves away from the hot spot, the hot spot starts creating another island under the ocean. This is why islands away from the hot spot such as Kaua'i, O'ahu and Maui no longer have active volcanoes while Hawai'i's volcanoes are still active, and those farther away from the hot spot are smaller, due to erosion of the once massive shield volcano islands. The hot spot has already started creating a new island called Lō'ihi, east of the island of Hawai'i that is still submerged (Figure 10.1.2). Some cultural practitioners call this island Kama'ehu ("reddish child").

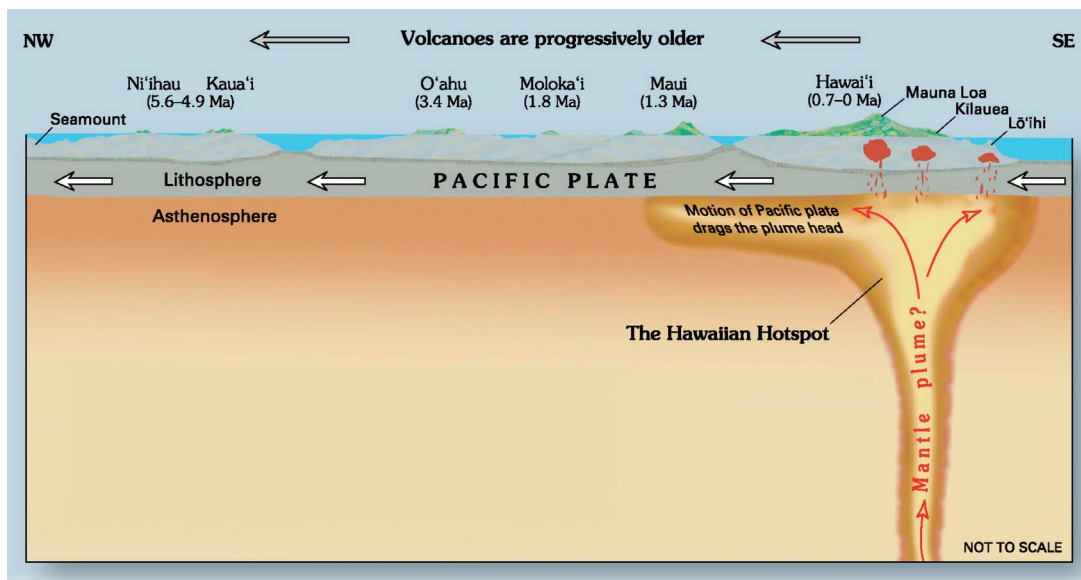


Figure 10.1.2: Hawaiian Hotspot Cross-sectional Diagram by Joel E. Robinson is in the Public Domain via Wikimedia Commons.

When the first plants arrived in the Hawaiian Islands millions of years ago, they encountered a land devoid of vegetation. These plant arrivals were rare; for flowering plants (angiosperms), it is estimated that there were only 259 colonizing events. These original 259 events gave rise to the 1,039 species we have today (Price *et al.*, 2018). These species originally arrived in Hawai'i carried by wind, water, and wings (birds).

Wind (1.4%)

Transportation by trade winds and storms is responsible for the arrival of the smallest percentage of ancestral species. This is probably because seeds or spores have to be light enough to be carried by the air, and need to be able to survive the very cold temperatures in the upper atmosphere. *Ōhi'a lehua*, *Metrosideros polymorpha*, seeds likely arrived in Hawai'i carried by the wind, as they are small and light.

Water (17%)

Plants also arrived in Hawai'i attached to clumps of soil and wood (rafting) or by floating in the ocean (oceanic drift). To do this, their seeds had to float and be able to survive long-term saltwater exposure. One example is *naupaka kahakai* (*Scaevola taccada*), which is naturally found in coastal environments and has fruits that float in saltwater.

Wings (83%)

The most successful way for plants to reach the Hawaiian archipelago was by catching a ride with a bird. Sticky fruits and seeds could attach themselves to a bird's feathers or even to the bird's feet with the help of some mud. Seeds and fruits could also be eaten by birds elsewhere and end up in Hawai'i after passing through the bird's digestive system.

Where did early plants come from?

Some people are very interested in figuring out where the plants that gave rise to the Hawaiian flora came from. Plant 'colonizers' arrived from different parts of the globe (Figure 10.1.3).

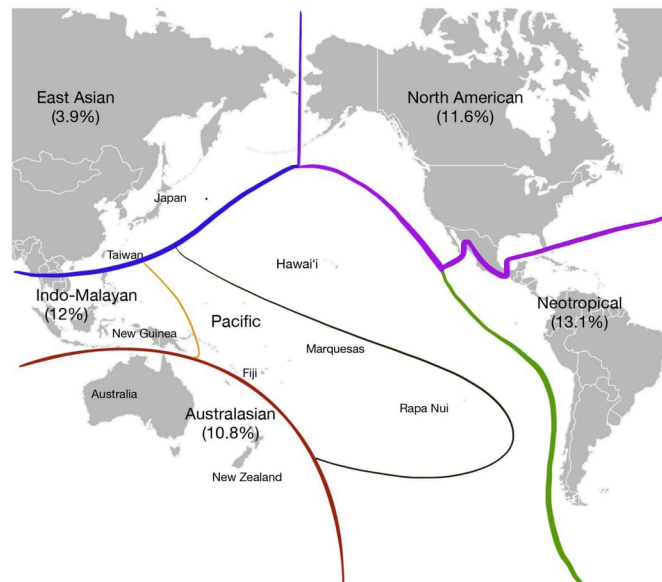


Figure 10.1.3: Map of the Pacific source regions with percentages of plant colonists. Each colored line indicates approximate boundaries of major source regions. Black line indicates the area including Pacific islands likely to serve as stepping stones. Map statistics are from Price *et al.* (2018). © 2021 by DutraElliott is licensed under CC BY-NC 4.0.

Some plants arrived directly from their home regions while others “island hopped” arriving on other Pacific islands and then eventually getting another ride to Hawai'i. Some of these plants (30%) are native to more than one region and are therefore classified as “widespread”. Below are the descriptions for each region along with the percentages for the plant colonists that arrived in Hawai'i from each source:

Australasian (10.8%)

This region includes Australia and New Zealand which is 6,832 km (4,245 miles) from Hawai'i.

Indo-Malayan (12%)

This region includes tropical areas of South and Southeast Asia. It encompasses the Malay Archipelago, New Guinea, and nearby islands. This region is 5,841 km (3,629 miles) from Hawai'i.

East Asia (3.9%)

This region includes non-tropical areas of Asia. This region is 5,863 km (3,643 miles) from Hawai'i.

Neotropical (13.1%)

This region includes tropical regions of Mexico, and Central and South America. This region is 4,648 km (2,888 miles) from

Hawai'i.

North American (11.6%)

This region includes the non-tropical areas of North America. This region is 3,631 km (2,256 miles) from Hawai'i.

Widespread (30.1%)

If the colonist species comes from more than one of the regions above, then it falls into this category.

Unknown (18.5%)

A large percentage of plants have unknown origins and fall into this category.

Pacific

This area includes the islands of Fiji 4,715 km (2,930 miles), the Society Islands 3,937 km (2,446 miles), and the Marquesas 3,398 km (2,111 miles). This area serves as a series of stepping stones for island-hopping species. Plants may arrive in one of these islands from one of the regions included above, and eventually arrive in Hawai'i by one of the dispersal methods (likely by birds or oceanic currents).

How did early plants colonize Hawai'i?

Besides having some of the characteristics discussed above that helped plants get to Hawai'i, they also needed traits that once here allowed them to settle, compete, reproduce, and flourish in their new environment. These plants are often referred to as "early colonists" because they were the first ones to arrive. Some of the characteristics early colonists had were self-pollination, fast growth, and adaptations to coastal environments. Plants that were able to self-pollinate had a clear advantage because the chance of finding another plant of the same species in the same place at the same time for cross-pollination to occur was quite small. Plants that were able to produce seeds without the need to pollinate with another plant of the same species were one step ahead in the game.

Fast-growing plants are often considered "weedy" because they can grow fast and in environments that are not very specific or ideal. For example, they will grow on sandy soils without a lot of nutrients. For the plants arriving in Hawai'i, being annual (only living for one year), or being able to complete their life cycles relatively quickly, was a good way to establish new populations faster.

Finally, plants that were adapted to coastal environments (Figure 10.1.4) often had an advantage. Since the largest percentage of plants arrived in Hawai'i with birds, many of them seabirds, they had to be able to grow near the coast where seabirds spend much of their time and, therefore, are most likely to deposit the seeds they inadvertently carried. Initially, each of the Hawaiian Islands was barren with very little or no vegetation. Eventually, some of the arriving plants were able to move inland, but originally they had to survive in the coastal environments. An example of a plant that originally arrived in a coastal environment and made it to higher elevations is *naupaka kahakai* /beach naupaka (*Scaevola taccada*) which is an indigenous species. This species is also native to several Pacific islands. There is another naupaka species, *naupaka kuahiwi*/mountain naupaka (*Scaevola gaudichaudiana*) which grows in wet forests of higher elevations. This species is endemic to Hawaii. It likely originated from naupaka kahakai through speciation (a process in which populations of a species split and become new species).



Figure 10.1.4: A coastal environment on O'ahu. Some of the environmental conditions of coastal environment are strong winds, salty sea spray, and intense light. © 2021 by DutraElliott is licensed under CC BY-NC 4.0.

Some plants did not arrive in coastal areas but likely got deposited by birds directly in high-elevation areas. For example, the Hawaiian raspberry, 'ākala (*Rubus hawaiensis*; Figure 10.1.5), likely arrived in Hawai'i from North America in the digestive tract of birds (Carlquist 1974; Morden *et al.*, 2003).



Figure 10.1.5: Hawaiian raspberry, 'ākala (*Rubus hawaiensis*), at Ha'ikū Uka, Maui, Hawai'i. By Forest & Kim Starr, CC BY 2.0, via Flickr.

Once in Hawai'i, these early plant colonizers diversified because they encountered new and different environments. They eventually dispersed from coastal areas and moved inland towards the mountains, became isolated from their original populations, and often evolved into new species. Approximately 88% of the native Hawaiian plants are endemic, all derived from those early colonizers who were able to arrive, survive, and establish populations here. For example, one colonizer species in the Lobeliad group (Campanulaceae family, Figure 10.1.6) gave rise to 126 new species, and the Silversword alliance (Asteraceae family, Figure 10.1.7) likely originated from one colonist species that came from California and diversified into 30 new species (Price, 2004).



Figure 10.1.6: *Lobelia gaudichaudii* by Nate Yuen.

When you compare the native flora of the Hawaiian Islands to the flora of the mainland source regions, you will notice that several families of plants are missing (a concept called disharmony; Christian *et al.*, 2019). This is because not all seeds and spores were able to make the long trip to get here. Also, as discussed above, seeds had to be salt tolerant to survive floating in oceanic currents, small enough to travel in air currents or have the right shape and size to be carried by birds. A mango seed, for example, could never reach Hawai'i, because they are not salt tolerant and are too heavy to be carried by a bird or by air currents. Therefore many plant families are not naturally present in the Hawaiian Islands.



Figure 10.1.7: Silversword Alliance diversity. A) *Iliou* (*Wilkesia gymnoxiphium*) is endemic to the island of Kaua'i, B) 'Āhinahina/ Haleakalā silversword (*Argyroxiphium sandwicense* subsp. *macrocephalum*) is endemic to the island of Maui; and C) Na'ena'e (*Dubautia menziesii*) is endemic to Maui. © 2021 by DutraElliott is licensed under CC BY-NC 4.0 via Flickr. Picture A, *Wilkesia gymnoxiphium*, is derivative of the original work by c87144, licensed under CC BY NC 2.0, via Flickr. The image was modified by cropping and was added to this figure with two original photos from the author. Labels were added.

10.2: Polynesian introduced plants

Polynesian Introductions are plants introduced by early Polynesians who migrated to the Hawaiian islands from other islands in the Pacific. The history of Polynesian migration is well documented through archeological, linguistic, and DNA studies as well as through oral histories passed on through generations. Humans started to migrate eastward from Southeast Asia and Melanesia around 3,500 years ago (Kirch, 2010). They initially migrated to islands that were relatively easier to get to, as ocean levels were lower at this time. As they moved east, the distance between islands became greater and the biodiversity decreased. This meant the technology for successful voyaging had to become more advanced, such as the development of double-hulled canoes that could withstand longer journeys in open water. The dependency on domesticated plants and animals also increased because more distant islands did not have wild plants and animals that could be used for food and other survival means, compared to islands closer to Asia.

Polynesians arrived in Hawai'i around 800 years ago (Kirch, 2010) and brought with them approximately 23 species of plants (Table 1). These plants were incredibly important, as they ensured the survival of the newly established human populations. While the first arrivals could survive for a time on native bird populations and seafood, successful human settlements depended on the successful introduction and production of domesticated agricultural crops (Kirch, 2010; Figure 10.2.1).



Figure 10.2.1: Example of a Polynesian introduced plant brought to Hawai'i on long-distance voyaging canoes. *Kalo* (*Colocasia esculenta*) growing in lo'i (wetland) system on the left and māla (dryland) on the right. © 2021 by DutraElliott is licensed under CC BY-NC 4.0 via Flickr.

The plants introduced by Polynesians did not all arrive at the same time, as there were multiple trans-oceanic voyages to and from the Hawaiian Islands. For example, 'ulu (*Artocarpus altilis*, Figure 10.2.2) arrived much later, and voyages to acquire it are well documented through oral histories.



Figure 10.2.2: “Ulu or breadfruit (*Artocarpus altilis*). The variety shown here is ma’afala, a Sāmoan and Tongan variety introduced more recently. © 2021 by DutraElliott is licensed under CC BY-NC 4.0 via Flickr.

‘Uala or sweet potato (*Ipomea batatas*, Figure 10.2.3) was very likely acquired by Polynesians who traveled by canoe from islands in the Pacific Ocean to South America where this plant was first domesticated by indigenous people there.



Figure 10.2.1: Sweet potato or ‘uala (*Ipomea batatas*) is a Polynesian introduction that came from South America. © 2021 by DutraElliott is licensed under CC BY-NC 4.0 via Flickr.

These plants were part of highly sophisticated agricultural systems developed over time and passed on from generation to generation. For more information regarding traditional agricultural systems in Hawai‘i, see [Lincoln and Vitousek \(2017\)](#).

Table

: Plants introduced by the Polynesians to Hawai'i.

Common Name(s)	Species
Kukui/Candlenut	<i>Aleurites moluccana</i>
‘Ape	<i>Alocasia macrorrhizos</i>
‘Ulu/Breadfruit	<i>Artocarpus altilis</i>
Wauke	<i>Broussonetia papyrifera</i>
Kamani	<i>Calophyllum inophyllum</i>
Niu/Coconut	<i>Cocos nucifera</i>
Kalo/Taro	<i>Colocasia esculenta</i>
Kī/Ti	<i>Cordyline fruticosa</i>
‘Ōlena/Turmeric	<i>Curcuma longa</i>
Uhi	<i>Dioscorea alata</i>
Hoi	<i>Dioscorea bulbifera</i>
Pi’a	<i>Dioscorea pentaphylla</i>
‘Uala/Sweet potato	<i>Ipomea batatas</i>
Ipu	<i>Lagenaria siceraria</i>
Noni	<i>Morinda citrifolia</i>
Mai’a/Banana	<i>Musa spp.</i>
‘Awa	<i>Piper methysticum</i>
Kō/Sugarcane	<i>Saccharum officinarum</i>
‘Ohe/Bamboo	<i>Schizostachyum glaucifolium</i>
‘Ōhi’a ‘ai/Mountain apple	<i>Syzygium malaccense</i>
Pia	<i>Tacca leontopetaloides</i>
‘Auhulu/Fish poison	<i>Tephrosia purpurea</i>
‘Awapuhi/Shampoo ginger	<i>Zingiber zerumbet</i>
Unknown origin (native and/or Polynesian Introduced):	
Hau	<i>Hibiscus tiliaceus</i>
Hala	<i>Pandanus tectorius</i>
Milo	<i>Thespesia populnea</i>

*Based on Whistler (2009).

10.3: Recent introduced plants

Plants introduced to Hawai'i after 1778 (post European contact) are known as recent introductions. Starting in the 1800s, different crops were brought in and tested to determine the viability of growing them in the Islands (Table 10.4.1). For example, pineapple and coffee were introduced to the Islands in 1813. Coffee became one of the most important crops, along with pineapple and sugarcane. Although sugarcane was introduced to Hawai'i by Polynesians before European contact, the first variety for commercial production ('Lāhainā') was introduced in 1854 to Maui (Lincoln, 2017). Pineapples were tested in 1885 in Mānoa, O'ahu; the starting point for commercial production. Rice was first introduced in 1858. Later trials were conducted to see if it could be grown commercially, and it soon became one of the most commonly grown crops in the 19th century (HDOA, 1998). Today, rice is no longer grown commercially in Hawai'i, but it is still part of the diet.

Table 10.3.1: Some commercially important crops introduced to the Hawaiian Islands. Sources: HDOA, 1998 and *Lincoln, 2017.

Crop name	Species	Year Introduced
Orange	<i>Citrus × sinensis</i>	1792
Coffee	<i>Coffea spp.</i>	1813
Pineapple	<i>Ananas comosus</i>	1813
Mango	<i>Mangifera indica</i>	1824
'Lāhainā' sugarcane	<i>Saccharum spp.</i>	1854*
Eucalyptus	<i>Eucalyptus spp.</i>	1870
Macadamia	<i>Macadamia spp.</i>	1881
Rice	<i>Oryza sativa</i>	1858
'Solo' Papaya	<i>Carica papaya</i>	1911
Seed corn (commercial)	<i>Zea mays</i>	1966

Pineapple and sugarcane production drove the plantation era (1850-1980s) in Hawai'i with many immigrant groups coming to the Islands for work. People from different cultures who arrived brought with them their own staples, and these crops were frequently incorporated into the plants that are grown and consumed in Hawai'i today (Figure 10.3.1).



Figure 10.3.1: Examples of plants recently introduced to Hawai'i: A) Kabocha (*Cucurbita maxima*), B) Corn (*Zea mays*), C) Cacao (*Theobroma cacao*), and avocado (*Persea americana*). © 2021 by DutraElliott is licensed under CC BY-NC 4.0 via Flickr.

Plantation agriculture changed the way land and water were managed, used, and controlled, and had negative impacts on traditional agriculture (Figure 10.3.2). Starting with plantations, water was taken from the windward side of islands to the leeward sides to irrigate sugar and pineapple fields, negatively impacting *kalo* production. Today, plantations have mostly disappeared from Hawai'i, and seed crops such as corn, as well as diversified agriculture have taken hold (Perroy *et al.*, 2016).



Figure 10.3.2: Wailuku Sugar Plantation (between 1883 and 1905). Gabriel Bertram Bellinghausen, Public domain, via Wikimedia Commons.

The horticultural trade also brought many ornamental plants to Hawai'i over the past century. For example, plumeria (*Plumeria* spp.) and monkeypod (*Samanea saman*) are introductions from Latin America (Figure 10.3.3). These plants have become part of life in Hawai'i since they are abundant in gardens and lowland areas where people live. Many of these introduced species remain in cultivation and do not naturalize (grow and reproduce in wild spaces without human assistance). For example, plumerias do not produce seedlings that can grow without human help. They need to be propagated by cuttings. However, many other horticultural species have become naturalized and have become invasive.



Figure 10.3.3: Plumeria tree (*Plumeria* spp.). By Daniel Ramirez, CC BY 2.0, via Wikimedia Commons.

Although some Polynesian introduced plants escaped cultivation and have become naturalized (e.g. kukui), most naturalized species are plants introduced after 1778. The **invasive species** we have in the Islands are mostly recent introductions. These have escaped cultivation and naturalized in wild habitats. Some of the names used for this group of recent introductions are exotics, aliens, and weeds. There are hundreds of naturalized species in Hawai'i, and many have negative impacts on native ecosystems. For example, strawberry guava (*Psidium cattleianum*), from South America, grows in such thick stands that they

overcrowd native species, eventually killing them (Figure 10.3.4).



Figure 10.3.4: *Acacia koa* (center left) surrounded by strawberry guava (*Psidium cattleianum*) at Kīpahulu Forest Reserve, Maui, Hawai'i. Forest & Kim Starr, CC BY 3.0, via Wikimedia Commons.

Another example of an invasive species in Hawai'i is fountain grass (*Pennisetum setaceum*) which is native to Africa and southeast Asia. Fountain grass dominates the understory of native dryland forests and competes with native trees. It also creates a fire risk in an environment that did not evolve with the frequent wildfires we see today (Cordell and Sandquist, 2008). On O'ahu, for example, the introduction of fire-prone grasses has created problems not only to native ecosystems, but also to communities on the west (leeward) side of the Islands. Fires have become far more common in the past decades, and increasingly cause damage to houses and businesses. The fires open dry lowlands to the invasive *koa haole* (*Leucaena leucocephala*), from Central America, which, along with fire prone grasses, dominates these areas (Figure 10.3.5).



Figure 10.3.5: *Koa haole* (*Leucaena leucocephala*) has spread to a lowland area on Moloka'i. Forest & Kim Starr, CC BY 3.0, via Wikimedia Commons.

The introduction of numerous invasive plant and animal species, along with other factors, has resulted in the decrease of native species, to the point where a significant number of them have become endangered. Hawai'i has more **endangered species** (species that have a higher risk of extinction) per square meter than any other place on Earth, and this is linked to habitat loss and invasive species (Czech *et al.*, 2000). Invasive species displace natives species, and a plant community dominated by non-native species does not function the same way as a native-dominated community (Kagawa *et al.*, 2009). For example, water gets

absorbed into the soil way less in non-native forests compared to native forests, and during big rain events the water runs towards the ocean instead of recharging the aquifer. This has a direct impact not only on the environment, but on the quality of life for humans as well since we all need freshwater.

Learning about the plants in Hawai'i can not only be interesting, but it connects us to our environment, to cultural practices, and to food security. We depend on plants for survival in many ways, and plants bring beauty to our lives. Plants bring us together around the table for a good meal, while helping us celebrate cultural traditions through food recipes and as part of life rituals.

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wind pollination

- [8.2: Conifers](#)

woody

- [3: Stems](#)

woody plants

- [3.2: Secondary growth](#)

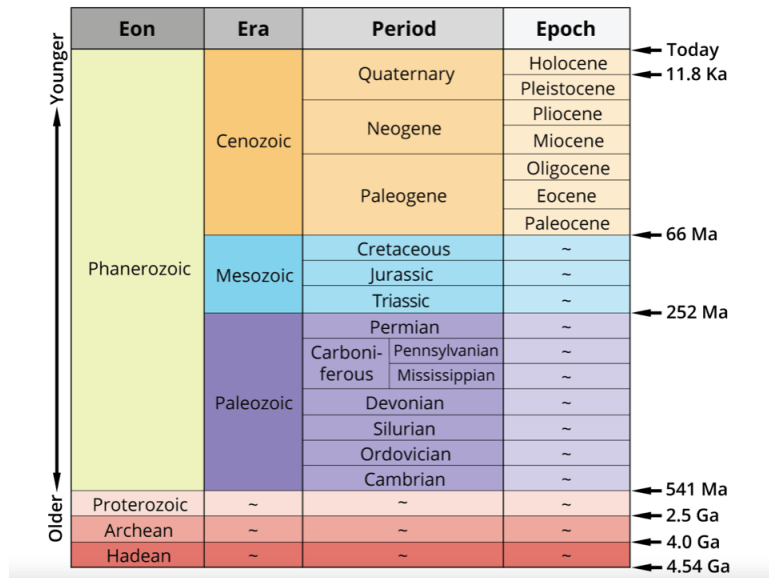
X

xylem

- [2: Roots](#)
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Appendix

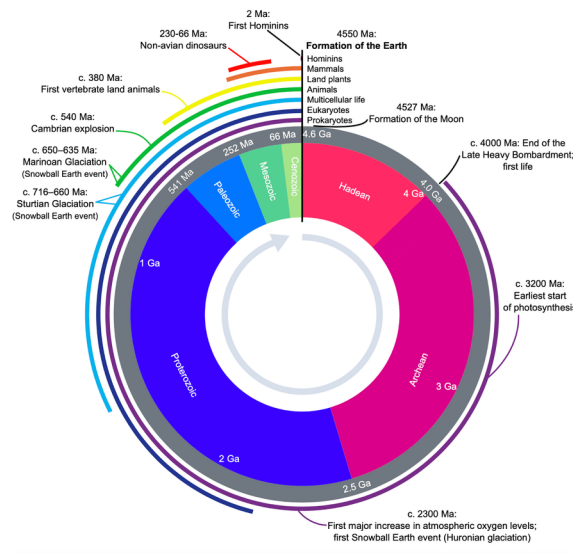
1. Geological time scale



The geological time scale. Image by Jonathan R. Hendricks. This work is licensed under the license CC-BY 4.0.

Note: To learn more about geological time scales and how to interpret them, visit the [Digital Atlas of Ancient Life](#).

2. Geological time scale



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