APPLIED BOTANY



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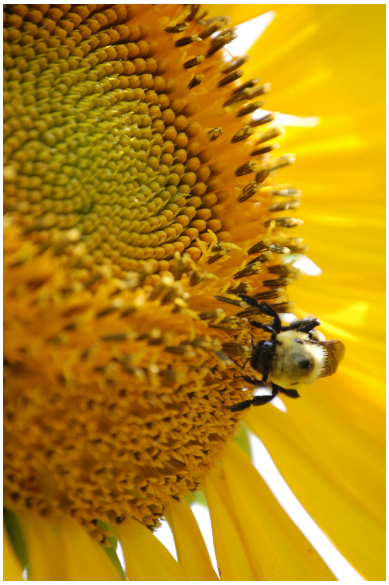
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Applied Botany: Introduction to Horticultural Science

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1: INTRODUCTION TO BOTANY AND THE SCIENCE OF HORTICULTURE



Mountain-laurel (*Kalmia latifolia*) is a broadleaf evergreen shrub native to the Eastern United States. It is known for its glossy foliage and intricate, cup-shaped spring blooms. (e.g., Harvey, 2026, CC-BY-NC).

Plants are all around us. They fill our forests and fields, our gardens and greenhouses, and our dinner plates, yet they are easy to overlook. Botany, the scientific study of plants, asks how plants are built, how they function, how they are classified, and how they interact with their environment and with us. Horticulture puts that knowledge to work, cultivating plants for food, medicine, beauty, and human well-being. In this chapter we survey the major fields of plant science, from anatomy and physiology to taxonomy, ecology, and horticulture. We then explore the critical roles plants play in the biosphere: as the primary producers at the base of nearly every food web, as the source of the oxygen we breathe, and as consumers of carbon dioxide. Finally, we look at how plants stabilize soils, moderate temperature and water, and supply humans with food, fiber, lumber, medicine, and fuel. By the end of the chapter, you should have a clearer picture of why understanding plants matters to all of us.

1.1: Plant Sciences

1.2: Role of Plants in the Ecosystem

1.3: Humans and Plants

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1.1: Plant Sciences

Plant Sciences

Botany is the study of plants. We define plants as organisms that include mosses, ferns, pines, broadleaf trees, grasses and other flowering plants (Figure 1). Plant Science is a vast and diverse field of study that covers many different areas. The following discusses Some of the major areas of study within botany.

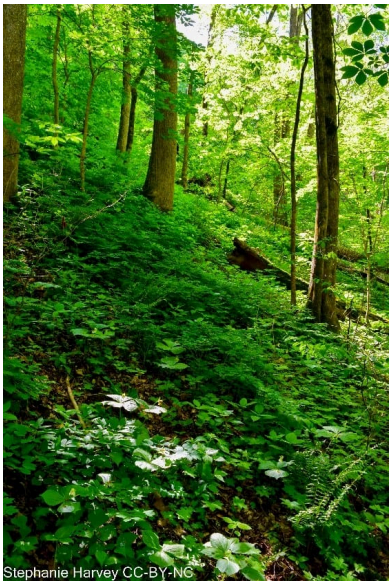


Figure 1. A forested slope in Northwest Georgia demonstrate the vast array of plant forms. (Harvey. 2023 CC-BY-NC)

Plant anatomy:

Plant anatomy is the study of the internal structure of plants. It involves the examination and understanding of the various tissues, organs, and cells that make up plants. The science of plant anatomy provides important insights into plant form and function, growth and development, and adaptations to different environments.

At the most basic level, plant anatomy is concerned with the cellular structure of plants. Plant cells are unique in that they have a rigid cell wall made of cellulose, which provides structural support and protection for the cell. Within the cell, there are various organelles, such as chloroplasts for photosynthesis and mitochondria for energy production.

Beyond the cellular level, plant anatomy also encompasses the study of plant tissues (Figure 2). Tissues are groups of cells that work together to perform specific functions within the plant. There are three main types of plant tissues: dermal, ground, and vascular. Dermal tissues are the outer protective layer of the plant, ground tissues are responsible for photosynthesis and storage, and vascular tissues are involved in water and nutrient transport.

In addition to tissues, plant anatomy also includes the study of plant organs. Organs are groups of tissues that work together to perform specific functions. The main organs of a plant are the roots, stems, leaves, and flowers. Each of these organs has a unique structure that reflects its specialized functions, such as anchoring the plant, conducting water and nutrients, or producing and storing food.

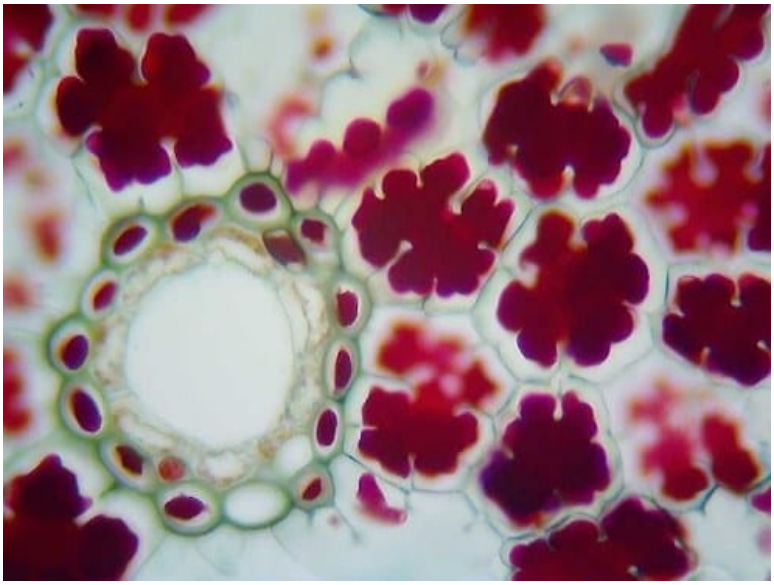


Figure 2. Cross section of a *Pinus* needle. A ring of cells indicates a resin canal while the red stain cells are of the mesophyll (Harvey. 2021 CC-BY-NC).

The science of plant anatomy also includes the study of plant development and growth. This involves understanding how cells divide and differentiate to form tissues and organs, and how these tissues and organs grow and change over time.

Finally, plant anatomy is important for understanding plant adaptations to different environments. For example, plants that grow in harsh, dry environments may have specialized structures such as thick leaves or a deep root system that allows them to survive in those conditions.

The science of plant anatomy is essential for understanding the structure, function, and diversity of plants. It is also critical for developing new insights and solutions for plant-related issues, such as improving crop yields or conserving plant biodiversity.

Plant physiology:

Plant physiology is the study of how plants function and interact with their environment. It involves the examination and understanding of the various biological and biochemical processes that occur within plants, including photosynthesis, respiration, transpiration, and growth.

Of fundamental concern in plant physiology is how plants use energy. Plants are autotrophic organisms that use sunlight to produce their own food through photosynthesis. This process involves the absorption of light energy by pigments, such as chlorophyll, and the conversion of that energy into chemical energy that is stored in carbohydrates.

Beyond photosynthesis, plant physiology also includes the study of plant respiration. Respiration is the process by which plants convert stored energy into a usable form. This involves the breakdown of carbohydrates to release energy, which is used to power various cellular processes and growth.

Plant physiology also encompasses the study of plant water relations. Water is essential for plant growth and is taken up by the roots and transported to other parts of the plant through specialized tissues. Transpiration, the loss of water through the leaves, is an important process for regulating the water balance of the plant and for controlling the movement of nutrients and other molecules within the plant.

Another important aspect of plant physiology is the study of plant growth and development. This involves understanding how plants coordinate cell division, cell elongation, and cell differentiation to form specialized tissues and organs. It also involves the study of how plant hormones, such as auxins, cytokinins, and gibberellins, control various aspects of growth and development.

Finally, plant physiology is important for understanding how plants respond to different environmental conditions, such as changes in temperature, light, and nutrient availability. For example, plants may undergo physiological changes, such as the opening and closing of stomata, in response to changes in temperature or humidity.

Overall, the science of plant physiology is essential for understanding the complex processes that occur within plants and for developing new insights and solutions for plant-related issues, such as improving crop yields, optimizing resource use efficiency, and developing sustainable agricultural practices.

Plant taxonomy:

Plant taxonomy is the branch of botany that is concerned with the identification, classification, and naming of plants. It is an essential aspect of plant biology and is used by scientists to organize and understand the vast diversity of plant species on Earth.

The science of plant taxonomy involves the use of various techniques to group plants into hierarchical categories based on their physical characteristics and evolutionary relationships. The most commonly used technique in plant taxonomy is morphological classification, which involves the examination of plant morphology, or physical characteristics such as leaf shape, flower structure, and growth habit.

The classification system used in plant taxonomy is based on a hierarchical structure that starts with the broadest category, the Domain, and becomes increasingly specific as you move down the classification hierarchy. The classification hierarchy is typically organized as follows: Domain, Kingdom, Division (or Phylum), Class, Order, Family, Genus, and Species.

Within each of these categories, plants are grouped based on shared characteristics. For example, the division Magnoliophyta, or flowering plants, is characterized by the presence of flowers and seeds, while the order Rosales is characterized by the presence of certain types of flowers and fruit.

Plant taxonomy also involves the use of nomenclature, or the system of assigning scientific names to plant species. The scientific name of a plant species is typically composed of two parts: the genus and the specific epithet. For example, the scientific name or species name of tomato is *Solanum lycopersicum*, where *Solanum* is the genus and *lycopersicum* is the specific epithet (Figure 3). Only together do they identify the species.



Figure 3. Tomato plant in greenhouse (*Solanum lycopersicum*) (Harvey. 2022 CC-BY-NC)

The use of scientific names is important for accurate communication among scientists and for avoiding confusion due to regional or common names for plants. The scientific names are standardized and universal, so scientists from all over the world can use them to refer to the same plant species.

Plant taxonomy plays a vital role in the study and understanding of plant diversity and evolution. By classifying plants into different groups, scientists are better able to understand their relationships, origins, and characteristics. This knowledge is important for conserving and managing plant diversity and for developing new plant-based products and technologies.

Plant ecology

Plant ecology is a branch of ecology that focuses on the study of plants and their interactions with the environment. It encompasses the scientific investigation of plant distribution, abundance, and diversity, as well as the processes that influence these patterns. Plant ecologists explore various aspects of plant life, including their physiological adaptations, growth patterns, reproduction, and responses to environmental factors.

One of the central areas of research in plant ecology is the study of plant communities and their dynamics. Plant communities are groups of plants that coexist and interact within a specific geographic area. Plant ecologists examine the composition, structure, and functioning of these communities, seeking to understand the processes that shape their assembly and change over time. They investigate how factors such as competition, predation, disturbance, and resource availability influence the diversity and distribution of plant species within communities.

Another important aspect of plant ecology is the study of plant interactions with other organisms. Plants interact with a range of organisms, including herbivores, pollinators, seed dispersers, and symbiotic partners such as mycorrhiza fungi. Plant ecologists investigate the nature and consequences of these interactions, examining how they influence plant fitness, population dynamics, and community structure. For example, they might study how plants defend themselves against herbivory or how mutualistic interactions with pollinators shape floral traits and reproductive success.

Plant ecologists also explore the role of environmental factors in shaping plant distribution and adaptations. They investigate how abiotic factors such as temperature, precipitation, soil properties, and light availability affect the establishment, growth, and survival of plants. These studies contribute to our understanding of plant biogeography and help predict how plant communities may respond to environmental changes, such as climate change or land-use modifications.

In recent years, plant ecology has increasingly embraced interdisciplinary approaches, incorporating techniques and theories from genetics, molecular biology, remote sensing, and computational modeling. This integration allows researchers to address complex ecological questions and unravel the underlying mechanisms that govern plant-environment interactions.

The findings of plant ecology research have practical applications in fields such as conservation biology, land management, and restoration ecology. By understanding the ecological requirements and dynamics of plant populations and communities, scientists can develop strategies for preserving biodiversity, managing invasive species, and restoring degraded ecosystems.

Horticulture

Horticulture combines scientific knowledge, practical skills, and artistic sensibility to cultivate plants for various purposes. It contributes to food production, environmental sustainability, aesthetic enhancement, and the promotion of human well-being. Horticulturists play a vital role in improving and managing our plant-based environments, making significant contributions to agriculture, landscaping, and urban development.

The field of horticulture covers a wide range of disciplines and areas of specialization, including plant propagation, crop production, plant breeding, plant physiology, plant nutrition, pest and disease management, landscape design, and post-harvest handling. Horticulturists apply their knowledge and skills to enhance plant growth, improve crop yields, and optimize the aesthetic, functional, and environmental qualities of plant-based spaces.

Plant propagation is a fundamental aspect of horticulture. Horticulturists employ various techniques such as seed germination, vegetative propagation (cuttings, grafting, layering), and tissue culture to reproduce plants and produce healthy, genetically identical individuals. This allows for the efficient production of desirable plant varieties and the preservation of rare or endangered species.

Crop production is another significant component of horticulture. Horticulturists cultivate crops for various purposes, including food production, ornamental plants, medicinal plants, and fiber crops. They select appropriate crop varieties, manage soil fertility, implement irrigation and pest management strategies, and optimize environmental conditions to ensure healthy plant growth and maximize yield and quality (Figure 4).



Figure 4. Basil plants growing in greenhouse (Harvey. 2023 CC-BY-NC).

Plant breeding plays a vital role in horticulture, involving the development of new plant varieties with improved traits such as disease resistance, increased yield, better flavor, or enhanced ornamental characteristics. Horticulturists use traditional breeding methods as well as advanced techniques such as genetic engineering to create novel plant cultivars that meet specific needs and preferences.

Horticulture also encompasses the study of **plant physiology and nutrition**. Understanding how plants function and respond to environmental stimuli allows horticulturists to optimize growing conditions, manage plant growth, and prevent or address issues related to nutrient deficiencies, water stress, and other factors that can affect plant health.

Pest and disease management is a critical aspect of horticulture. Horticulturists employ various strategies to monitor, prevent, and control pests and diseases that can damage or destroy crops and ornamental plants. They may utilize integrated pest management (IPM) approaches that combine cultural, biological, and chemical control methods to minimize environmental impact while effectively managing pests and diseases.

Landscape design and management are important aspects of horticulture that focus on creating aesthetically pleasing and functional outdoor spaces. Horticulturists design and plan gardens, parks, green roofs, and other landscapes, considering factors such as plant selection, spatial arrangement, soil composition, and maintenance requirements. They aim to create visually appealing and sustainable environments that promote human well-being and ecological balance (Figure 5).

Horticulture also extends to urban environments, where horticulturists work on greening initiatives, urban agriculture, and the integration of plants in cities to enhance air quality, reduce heat island effects, and provide recreational opportunities.

Other Fields of Plant Science

There are too many fields of science related to plants to discuss them all at length. Many of the fields overlap with each other or with non-plant related sciences. Below is a brief list of other plant related fields.

- Plant pathology: the study of plant diseases and their causes
- Plant genetics: the study of how genes control plant traits and how these traits are inherited
- Plant biotechnology: the use of plants to produce useful products or to solve environmental problems
- Plant evolution: the study of how plants have evolved over time and their relationships to each other
- Ethnobotany: the study of the traditional uses of plants by different cultures
- Paleobotany: the study of plant fossils and their evolution over geological time
- Plant molecular biology: the study of the molecular basis of plant functions
- Plant biogeography: the study of the distribution of plants around the world

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1.2: Role of Plants in the Ecosystem

The Role of Plants in Our lives



Figure 5. Pine forest after control burn (Harvey. 2013 CC-BY-NC).

It is important that, as productive citizens within our communities, country and world, we understand the role plants play in our lives and how our actions (or lack of actions) impacts them. Plants play three critical roles in the biosphere (the parts of the land, sea, and atmosphere in which organisms are able to live): as primary producers of most food webs, as oxygen producers and carbon dioxide consumers.

Trophic Levels and Food Webs

Energy flows through an ecosystem and the paths it can take are describe as a food chain. The trophic level of an organism is the position it occupies in a food chain. A food chain is a succession of organisms that eat other organisms and may, in turn, be eaten themselves. Most ecosystems don't have a single food chain but instead an intricate series of interconnecting chains often described as a food web.

Primary Producers

Plants are the primary producers in nearly all terrestrial ecosystems and contribute to many aquatic and marine ecosystems as well (Figure 6). Plants (with a few exceptions) are photosynthetic autotrophs. This means they can build complex organic molecules from simple carbon sources like carbon dioxide (autotroph- literally meaning "self-feeding") using energy captured from the visible light spectrum (thus photosynthetic). The complex organic molecules (like carbohydrates, proteins and lipids) can then be used by other organisms (chemoheterotrophs) in that ecosystem. Thus, plants and other photosynthetic organisms (algae, protists and cyanobacteria) are primary producers and are the base for nearly all food webs.



Figure 6. Wildflowers beside a lake, basking in the sunlight (Harvey. 2016 CC-BY-NC).

Consumers

Chemoheterotrophs are organisms (like us) that consume organic molecules as a source of energy and to provide the carbons necessary to build their own molecules. The “chemo” refers to the release of energy by breaking down molecules, while the “hetero” refers to the need to get carbon from “other” sources. All chemoheterotrophs are dependent on plants and other primary producers for their food. There are primary consumers (herbivores) like cattle, deer and zebra that eat the primary producers and secondary consumers such as snakes, lions and eagles that eat the primary consumers. Some carnivores and omnivores can be classified as tertiary and quaternary consumers. For example, a hawk might consume a rat snake that fed on a field mouse that eat a grasshopper that was feeding on a plant. For this food chain, the hawk is a quaternary consumer, the rat snake is a tertiary consumer, the mouse is a secondary consumer, the grasshopper the primary consumer and the plant the primary producer. We also fall in one or more of the consumer trophic levels and get our energy and carbon from plants either directly as consumers of vegetable and grains or indirectly through consumption of the meat of primary consumers like deer or cattle (Figure 7).

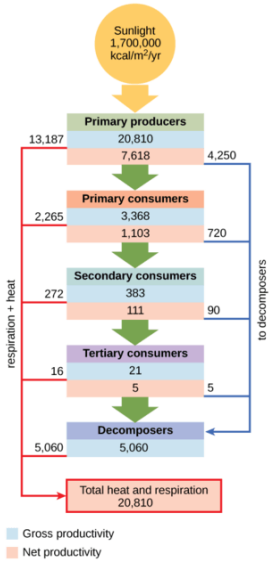


Figure 7. Trophic levels. Flow diagram of energy moving through trophic levels, in kilocalories per square meter per year. By CNX OpenStax - http://cnx.org/contents/GFy_h8cu@10....2/Introduction

Saprotrophs

It would be remiss of us not to discuss the saprotrophs; they are just as important to the ecosystem as the producers. Saprotrophic bacteria and fungi are decomposers (Figure 8). They break down organic materials to get energy and thus recycle materials back to their basic forms. These decomposers are critical in the cycling of nutrients needed by plants and other primary producers. Without them, dead animals, dead leaves and fecal material would remain intact, thus locking away all the nutrients and making them unavailable for future growth. Additionally, the breakdown of this material provides space for new growth. Imagine if the leaves from each fall remained, year after year. The earth's surface would be covered in detritus.



Figure 8. Bracket fungi breaking down cellulose of dead log (Harvey. 2013 CC-BY-NC).

Photosynthesis

The metabolic process of photosynthesis is critical to nearly all ecosystems. It is responsible for the energy transformation that makes plants primary producers, and it is responsible for both oxygen production and carbon consumption. We will not dwell on the biochemistry of photosynthesis in this introduction but will discuss it in general terms and how it impacts an ecosystem.



Figure 9. Light passing through Sycamore leaves (Harvey. 2016 CC-BY-NC).

Photosynthesis is the harvesting of light energy and its conversion to usable chemical energy in the form of the bond holding

together organic molecules like sugars (Figure 9). This complicated process occurs as two sets of reactions: light dependent reactions and light independent reactions (Calvin Cycle). The light dependent reactions are responsible for the harvesting of the light energy while the light independent reactions involve the making of sugars.

The Light Dependent Reactions

The light dependent reactions use chlorophyll pigments to capture light energy and a series of proteins to transfer some of the energy to carrier molecules called NADP+/NADPH and some to ADP/ATP. Some of the energy is lost to heat. To continuously capture and transfer this light energy requires a cheap source of electrons. The source can't be too toxic prior to the removal of the electrons and likewise can't be too toxic after the removal of electrons.

Water is the source. Water molecules consist of a single oxygen bound to two hydrogen atoms. While it is quite difficult to pull the electrons away from water, plants have an enzyme complex that can accomplish this. Once the electrons are removed, the hydrogen protons (so named because they are missing their electrons, have no neutrons and all that is left is the proton) separate from the oxygen atom. Two oxygen atoms combine to form a molecule of oxygen. This oxygen molecule is the oxygen released by plants (Figure 10).



Figure 10. Oxygen released from *Elodea* as a result of the light dependent reactions (Harvey 2013 CC-BY-NC).

The release of oxygen by photosynthetic organisms changed the course of earth history. Early cyanobacteria photosynthesized and produced enough oxygen to change the atmosphere of ancient earth from a reducing one to an oxidative one. A significant increase in atmosphere oxygen triggered a glaciation event that produced one of the largest extinctions discovered. The accumulation of oxygen in the atmosphere also made cellular respiration possible. Cellular respiration allowed for the more efficient harvest of energy from organic molecules and thus provided the opportunity for the development of large more complex organisms.

The Light Independent Reactions

There are three steps that happen during the light independent reactions (also called the Calvin Cycle). The first step is carbon fixations and is where plants "consume" carbon dioxide. During this step carbon dioxide is added to an existing 5-carbon molecule which results in the formation of two 3-carbon molecules. This fixation of carbon removes carbon from the atmosphere and sequesters it as organic molecules.

The second step of the cycle is the use of the energy captured in the NADPH and ATP from the Light Dependent Reactions to reduce the 3-carbon molecules from the fixation step to create higher energy molecules (sugars). The final step of the cycle is the regeneration of a starting component of the cycle. So, by the completion of this cycle, we have reduced atmospheric carbon dioxide and produced a high energy molecule that can be stored, used in the construction of other biomolecules or metabolized for energy by the plant cell. The storage molecules and some structural molecules are the source of energy for the primary consumers.

We have discussed the importance of oxygen production and primary production. The sequestering of carbon dioxide via carbon fixation is the third import role plants and other photosynthetic organisms play in the biosphere. Carbon dioxide in the atmosphere contributes to the greenhouse effect. It and other greenhouse gases traps energy between the atmosphere and the earth's surface. This energy heats the planet and helps moderate the temperature fluctuation between day and night. However, high levels of greenhouse gases can trap too much energy and cause increase global temperature. There is evidence that excessive sequestering of carbon dioxide by photosynthetic organisms contributed to the cooling of the planet as evidenced by the glacial oscillations occurring 2.4-2.1 billion years ago.

Habitats and Stability

If you discount the three critical roles that plants play in the biosphere, there are still others to consider. Within many ecosystems, plants provide structure in addition to serving as a source of food. As structural elements, plants provide habitats and allow partitioning of the ecosystems resources to support more organisms. For example, a tall tree can provide multiple shelters that allow different species to share a given area through vertical stacking. Plants serve as refuges for prey organisms and allow them to avoid predators. It can also work the other way with the plants providing cover for the predators as they hunt their prey. Plants help maintain a dynamic balance between the two groups.

Soil Stability

Plants stabilize soil and minimize erosion (Figure 11). Their roots hold soil in place while their leaf canopy and litter protect the soil from rain and wind. Not only does this help maintain the productivity of an area, but it also keeps the associated watersheds healthy. Plants help prevent the deposition of silts into the creeks, rivers and lakes. They also limit the movement of nutrients into these aquatic environments. Excess nutrients and silt can lead to significant changes in the aquatic ecosystems. Increases in turbidity (cloudiness of the water) can limit plant growth and impact the health and reproductive success of aquatic life. Too many nutrients can lead to alga blooms that can be toxic or can simply deplete oxygen levels as they die and are consumed by decomposers. Fish-kills can occur if oxygen levels become too low to support cellular respiration or when the toxin levels become too high.



Figure 11. The roots and leaf litter from plants help to stabilize areas easily eroded. (Harvey, CC-BY-NC CC-BY-NC)

Temperature

Microclimates are another way that plants can impact an ecosystem. Vegetation can moderate the climate of an area. Taller plants provide shade and can significantly impact temperatures in a small area. Surface temperatures of grass areas are cooler than hard surfaces (Armson, Stringer, & Ennosa, 2012). While this might not impact how organisms above the surface experience the temperature, those in direct contact would benefit from the vegetative effect. Shade provided by a tree canopy impacts surface temperature (15 °C cooler). The shade produced by trees can also change microclimates to favor herbaceous growth. In fact, a

synergistic effect is seen in arid environments. Shaded ground covers create a cooler microclimate than shade alone and reduce water needs of the ground covers by 50%.

Water

As noted in the statement above, plants also impact the water balance in ecosystems. Plants absorb water (typically from the soil) and then transpire 95% of it into the atmosphere. This increases the relative humidity within the vegetative area. Plants also increase the ecosystem water use efficiency of a given area. This is particularly true of herbaceous plants. In sandy soil, plant roots help trap water before gravitational forces move it out of the ecosystem. Detritus from plants such as leave and fruit litter, add to the humus layer of the soil and increase the organic component of the soil. This increases the water holding capacity of the soil.

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1.3: Humans and Plants

Humans and Plants

We briefly mentioned that humans use plants in a variety of ways. Let's look in a little more detail.

Food

As hunter gatherers we would have eaten native plants, but with the development of civilization and commerce, the plants grown and consumed for food declined in favor of crops easier to cultivate and store (Figure 12). Only a small fraction of the plants on earth are regularly consumed by humans for their nutritional value. Of the 328,000 vascular plants (Royal Botanic Gardens Kew, 2017), only about 6 thousand are cultivated for food (Leibniz Institute of Plant Genetics and Crop, 2017). Fewer than 200 species contribute significantly to global production with 66 percent of all crop production by weight is due to only nine crops (Fig 13; sugar cane, maize, rice, wheat, potatoes, soybeans, oil-palm fruit, sugar beet and cassava) (Food and Agriculture Organization of the United Nations, 2017). Except for the oil-palm fruit and soybeans, these pivotal crops are grown for their carbohydrates (starches and sugars).



Figure 12. Members of the Brassicaceae Family (Harvey. 2001 CC-BY-NC).

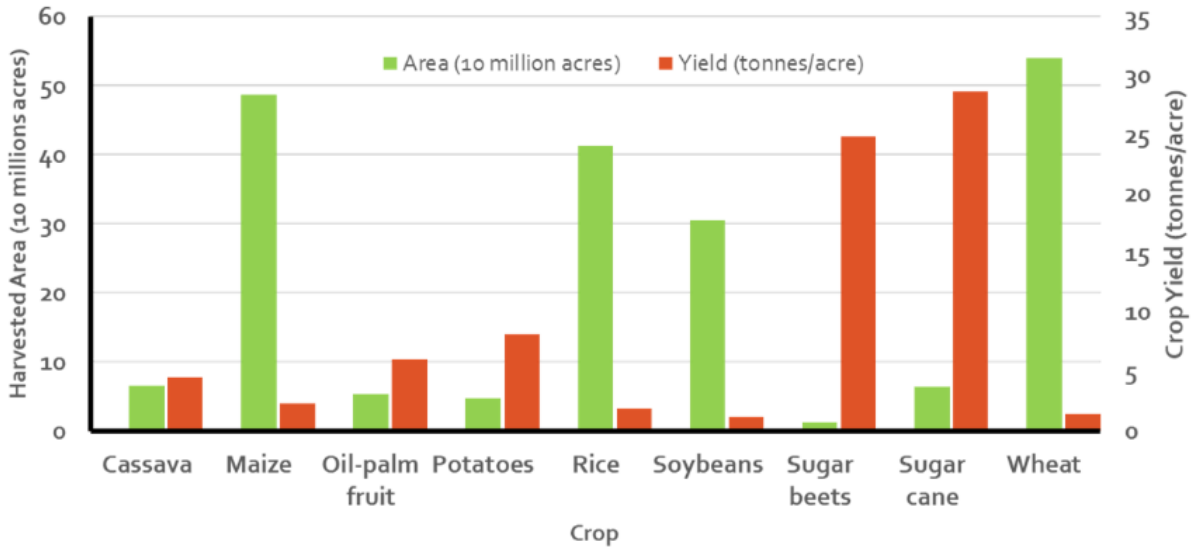


Figure 13. Nine major crops with the area harvested on left axis and yields on the right axis (Food and Agric. Org. 2017).

Recently there has been an interest in some of the "forgotten grains" and pseudocereal. Concerns about glutens and other anti-nutritional aspects of some of the common cereals have allowed the re-emergence of some these ancient foods. Amaranth grain for example, is the starch seed of a weed like plants that grows in North and South America and was cultivated by the Aztec. The seeds are small, but the productivity is comparable to that of rice or maize (Thomas Jefferson Agricultural Institute, 2006). Quinoa is another pseudocereal from South America. It was cultivated in the Andes of Bolivia and Peru first as animal fodder and later for human consumption. Like amaranth grain, it is a small seed that is produced in high quantities by a weedy annual plant (U.S. National Research Council, Advisory Committee on Technology Innovation, 1989).

Textiles

A textile is a flexible material consisting of a network of natural or artificial fibers (yarn or thread). Many plants can be used to make textiles of various textures and uses.

Clothing textiles are produced from the fibers of cotton, flax, jute, hemp, modal and even bamboo. These plants produce fibers that are soft enough to be comfortable and strong enough to resist damage. Piña (pineapple fibers) and ramie are also fibers used in clothing but are generally with a blend of other fibers such as cotton.

Linen (flax) is a bast fiber. In flax the bast fibers are found beneath the epidermal layer of the plant's stem. They vary in length from about 25 to 150 mm (1 to 6 in) and average 12–16 micrometers in diameter. There are two varieties: shorter tow fibers used for coarser fabrics and longer line fibers used for finer fabrics.

Cotton fibers are harvested from cotton seeds. The fibers extend from the cotton seed's seed coat. There are long fibers referred to as staples and short fibers called linters. The staples can be woven to produce thread while the short fibers are primarily used in paper production. The cotton plant is a perennial that is cultivated like an annual.

Rayon is a manufactured fiber made from regenerated cellulose fiber harvested primarily from wood pulp. Since the fibers are made from naturally occurring polymers, they are considered a natural fabric. The many types and grades of rayon can imitate the feel and texture of natural fibers such as silk, wool, cotton, and linen.

Lumber and Paper

Wood is a generic term that refers to a type of tissue produced by some plants. Plants classified as trees and shrubs produce secondary xylem (a transport tissue) that is made up of very strong cells (Fig 14). Lumber is a type of wood that has been processed into beams and planks, a stage in the process of wood production. It can also be processed into other construction materials such as plywood, chipboard, particle board and oriented strand board (OSB). Lumber is mainly used for structural purposes but has many other uses as well.

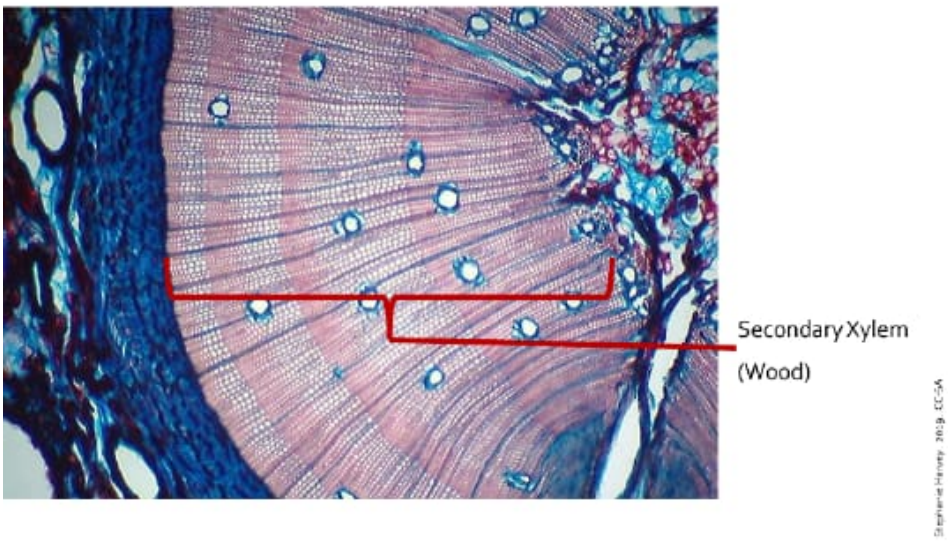


Figure 14. Secondary xylem is the "wood" of plants (Harvey. 2019 CC-BY-NC).

Paper is produced primarily from wood fibers extracted from softwoods like conifers. To make the wood pulp the wood chips must first be treated to remove the lignin. The resulting pulp can then be bleached to make white paper. To achieve a smooth finish, clays and other ingredients are added to the pulps before it pressed into thin sheet and dried. While wood is the primary source for fibers, cotton and other fibers can be used depending on the desired qualities of the finished product.

Medicine

Since the time of Hunter/Gatherers have been using plants in traditional medicine. Plants produce numerous secondary metabolites that provide service to the plant and have potential uses for humans. Many of the thousands of compounds synthesized by plants function in defense of the plants while other compounds may attract pollinators and dispersal agents. Many of these phytochemicals have potential or known biological activity. There are four primary groups of phytochemicals: alkaloids, glycosides, polyphenols, and terpenes.

Alkaloids are bitter-tasting chemicals found in many medical plants. They are very widespread in nature and often toxic. Medicines of different classes include atropine, scopolamine, and hyoscyamine (all from nightshade family -Solanaceae), the traditional medicine berberine (from plants such as *Berberis* and *Mahonia*), caffeine (*Coffea*), cocaine (*Coca*), ephedrine (*Ephedra*), morphine (opium poppy), nicotine (tobacco), reserpine (*Rauwolfia serpentina*), quinidine and quinine (*Cinchona*), vincamine (*Vinca minor*), and vincristine (*Catharanthus roseus*).

A glycoside is a molecule in which sugar is bound to another functional group via a glycosidic bond. Glycosides play numerous important roles in living organisms. Many plants store chemicals in the form of inactive glycosides. These can be activated by enzyme hydrolysis, which causes the sugar part to be broken off, making the chemical available for use. The cyanogenic glycosides - like amygdalin – hydrolyze to produce toxic hydrogen cyanide. Salicin is an alcoholic glycoside that is converted to salicylic acid by the body. There it has analgesic, antipyretic and anti-inflammatory effects.

Polyphenols play diverse roles in defenses against plant diseases and predators. Some are hormone-mimicking phytoestrogens and astringent tannins. Plants containing phytoestrogens have been administered for centuries for gynecological disorders, such as fertility, menstrual, and menopausal problems. Among these plants are kudzu, *Angelica*, fennel, and anise. Many polyphenolic extracts, such as from grape seeds, olives or maritime pine bark, are sold as dietary supplements and cosmetics without proof or legal health claims for beneficial health effects.

Terpenes are a large and diverse class of organic compounds, produced by a variety of plants, particularly conifers. They often have a strong odor and may protect the plants that produce them by deterring herbivores and by attracting predators and parasites of herbivores. Terpenes and terpenoids (which contain additional functional groups) are the primary constituents of the essential oils of many types of plants and flowers. Essential oils are used widely as fragrances in perfumery and traditional medicine, such as aromatherapy. Several terpenoids including thymol and Taxol. Thymol has antiseptic properties while Taxol is a cancer treatment drug. Vitamin A is a terpenoid.

Fuels

Just as plants can be used as fuel for our bodies, they can also be used for other fuel needs. Traditional use of plants materials for fuel involves direct combustion of plant biomass, primarily as woody tissue. This releases heat, light and energy to do work. The “harnessing” of fire is said to be one of man’s greatest achievements.

Much of the energy released when burning plant biomass cannot be directly captured and use for work. The conversion of plant material into other forms for combustion has led to more controllable energy release and thus more energy available to do the work needed. A fossil fuel is a fuel formed by natural processes, such as anaerobic decomposition of buried, dead organisms, containing energy originating in ancient photosynthesis. Fossil fuels such as crude oil and coal allow for a more controlled energy release but have consequences. The use of fossil fuels raises serious environmental concerns. The burning of fossil fuels produces around 21.3 billion tonnes (21.3 gigatonnes) of carbon dioxide (CO_2) per year. It is estimated that natural processes can only absorb about half of that amount, so there is a net increase of 10.65 billion tonnes of atmospheric carbon dioxide per year.

Alternative fuels using current biomass may offer better alternatives. While a number of postindustrial products (Black liquor and tall oil pitch) can be used as fuel, the most common types of biofuels are Bioethanol and Biodiesel (Figure 15) .

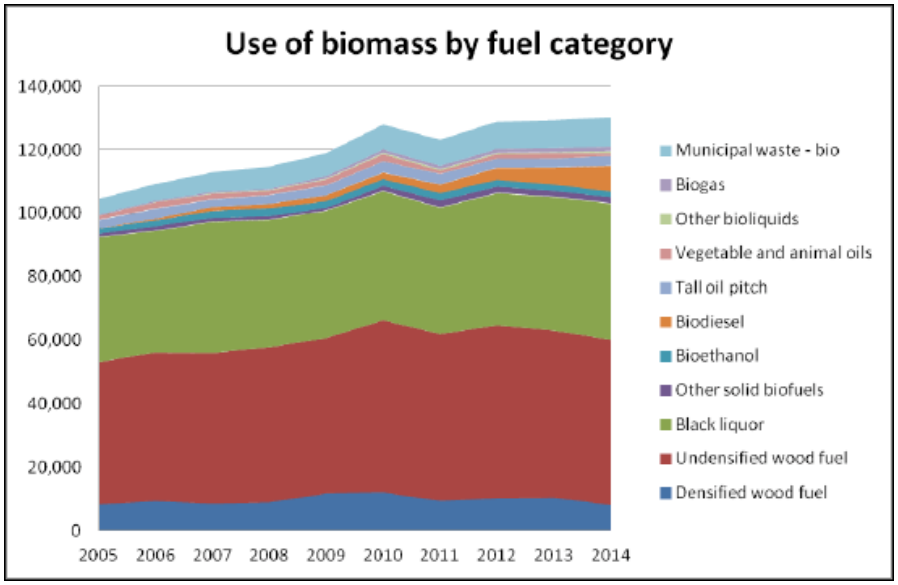


Figure 15. Use of Biomass by Fuel Category in Sweden, 2005-2014 (By Energimyndigheten - https://www.energimyndigheten.se/sta...=1#mainheading, CC BY-SA 4.0, Link).

Bioethanol is an alcohol made by fermentation, mostly from carbohydrates produced by crops such as corn, sugarcane, or sweet sorghum. Ethanol can be used as a fuel for vehicles in its pure form (E100), but it is usually used as a gasoline additive to increase octane and improve vehicle emissions. However, controversy exists with this biofuel. Six states (Iowa, Nebraska, Illinois, Minnesota, Indiana and South Dakota) accounted for 72% of U.S. fuel ethanol production in 2016, according to the most recent estimates from EIA’s State Energy Data System (Figure 16). As you might have noted, the primary crops grown for ethanol production are food crops. This means that as more of these crops are used for fuel, less are available for human/animal consumption.

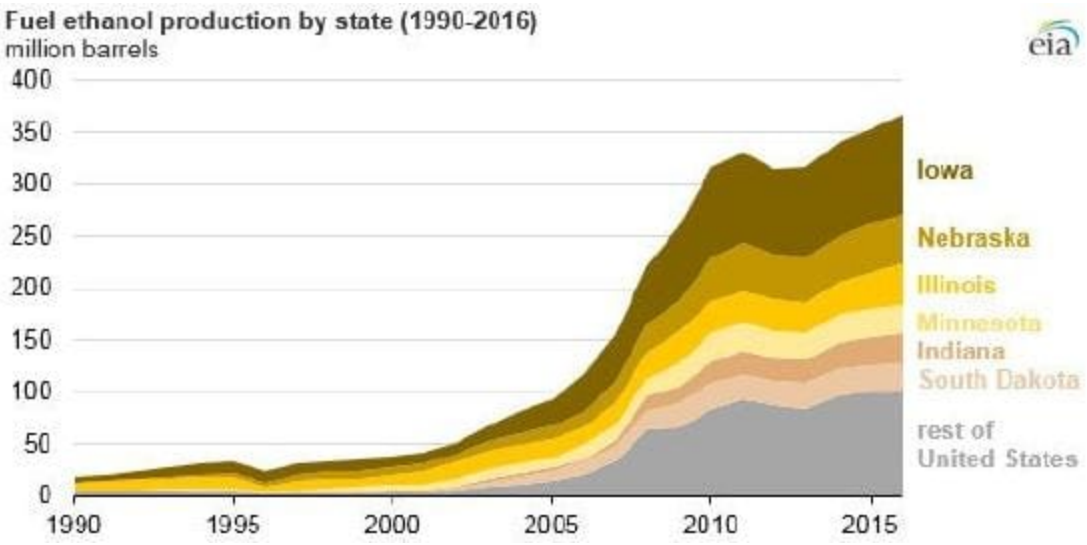


Figure 16. Fuel Ethanol production by state from 1990 to 2016 (U.S. Energy Information Administration (EIA).

Biodiesel is produced from oils or fats using transesterification and is a liquid similar in composition to fossil/mineral diesel. Plant oils and animal oils can be used to create biodiesel. Biodiesel is safer to handle and transport b/c it is non-toxic and biodegradable. It also has a high flash point of 148 °C compared to petroleum diesel fuel which has a flash point of 52 °C. This does create some difficulties if used in standard diesel engines in cold climates.

Oils

Much of the biodiesel is made from vegetable oils. Typically, these oils (and fats) are removed from seeds, but there are some other sources depending on the oils use. There are three types of plant oils that are categorized based on their extraction and nature of the resulting oil: Vegetable fats and oils, Macerated or infused oils and essential oils. Macerated or infused oils consist of a base oil to which plant parts are added. The hydrophobic components of the plant diffuse into the base oil, imparting fragrance and taste to the base oil. Essential oils are volatile aromatic compounds that are typically extracted from plants by distillations. Like the infused oils, their fragrance and taste make them valuable for food, perfumes but also medicines.

Vegetable fats and oils are historically extracted by putting parts of the plant under pressure and squeezing the oil out. Modern methods include continuous expeller presses and solvent based extraction systems. Most plant oils are extracted from seed where they act as fuel for the developing embryos. There are a few plants that have high oil content in their fruits – olives, avocados, coconuts and palm fruits. The evolutionary advantage of having expensive oils in what is essential a disposable organ is unknown and debated. Vegetable fats and oils are triglyceride-based, and include cooking oils like canola oil, solid oils like cocoa butter, oils used in paint like linseed oil and oils used for industrial purposes. Industry uses vegetable fats in a variety of ways including production of paints, medicines, foods, and plastics.

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1.4: End of Chapter Review

End of Chapter Summary

- Botany is the study of plants and encompasses many fields including anatomy, physiology, taxonomy, ecology, and horticulture.
- Plant anatomy examines the tissues, organs and cells that make up plants. Key structures include cell walls, chloroplasts, vascular tissues, roots, stems, leaves, and flowers.
- Plant physiology studies how plants function, looking at processes like photosynthesis, respiration, water transport, growth, and responses to stimuli.
- Plant taxonomy classifies and names plants based on physical characteristics and evolutionary relationships. Scientific naming uses a genus and specific epithet.
- Plant ecology examines plant distribution, diversity, and interactions with the environment including other organisms.
- Horticulture applies science and techniques to cultivate plants for human use and enjoyment, including food, ornamentals, landscaping, etc.
- Plants play critical roles as primary producers, oxygen producers, carbon dioxide consumers, habitat providers, soil stabilizers, and temperature moderators.
- Humans use plants for food, textiles, lumber, paper, medicine, and fuel. Key food crops provide most calories consumed.

Key Terms:

- Anatomy
- Horticulture
- Species
- Cell Wall
- Leaf
- Stem
- Chloroplast
- Photosynthesis
- Taxonomy
- Ecology
- Physiology
- Vascular Tissue
- Flower
- Respiration
- Transpiration
- Genus
- Root

Self-Review

1. What are the main organs of a plant?
2. What are the three main types of plant tissues?
3. What are the two main steps of photosynthesis?
4. What are the roles of roots, stems, and leaves in a plant?
5. What is the difference between plant anatomy and plant physiology?
6. What does the scientific name of a plant species consist of?
7. What field of botany studies plant evolution and relationships?
8. What techniques do horticulturists use to propagate plants?
9. What roles do plants play as primary producers?
10. How do plants help stabilize soils?
11. What are three ways humans use plants?
12. What are three plants critical for their fibers which are used to produce textiles?

13. What are the key differences between lumber and paper production from wood?
14. What are biodiesel and bioethanol?
15. What are the main categories of plant oils?

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2: PLANT DIVERSITY



The number of known plants alive today (extant) is estimated to be around 328,000. If you include yet to be discovered plants, the range varies from 500,000 to 1 million. In this chapter we will examine the principles of taxonomy, evolution of plants and diversity of plants. The image above shows water lilies - *Nymphaea alba* - in a pond in Sumter County Georgia. The plant is aquatic with large floating leaves that are produced from a rhizome (underground stem) that lies within the pond sediments (Photo: Stephanie Harvey. 2025 CC-By-NC).

2.1: Taxonomy

2.2: Plant Evolution

2.3: Non-Vascular and Seedless-Vascular Plants

2.4: Seeded Vascular Plants

2.4.1: Gymnosperms - "Naked" Seed Plants

2.4.2: Angiosperms - Flowering Plants

2.5: End of Chapter Review

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2.1: Taxonomy

The number of known plants alive (extant) today is estimated to be around 328,000. If you include yet to be discovered plants, the range varies from 500,000 to 1 million. In this chapter we will examine the principles of taxonomy and naming of plants, evolution of plants and diversity of plants.

Taxonomy is the science or technique of classifying, naming, and identifying of organisms. While precise communication is always a good ideal, in science it is critical. For scientists to share/compare their research it is critical that they know exactly the species to which the research refers. Differences in languages are always a barrier to communication, but this is particularly true with common names of organism that often do not directly translate. Even within a single language, common names can be difficult with different regions using differ names. Common names can also be misleading. For example, the calla lily, the canna lily, and the snake lily are not true lilies as their names would imply (Figure 2-1). True lilies are in the order Liliales, family Liliaceae and the genus *Lilium*. The canna lily is in the order Zingiberales, family Cannaceae, genus Canna. Both the calla and snake lilies are in the order Alismatales and family Araceae but different genera (*Zantedeschia* and *Dracunculus*, respectively.) To add to the confusion, there is a *Calla* genus, but the calla lily does not belong in it.

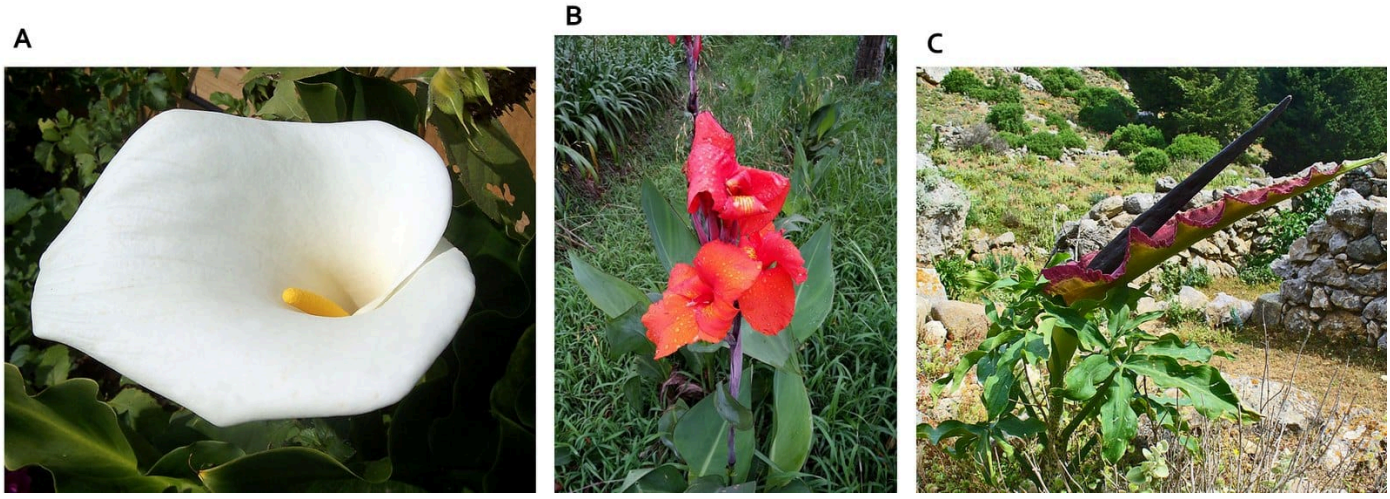


Figure 2-1. Common names are often misleading. The calla lily (A), canna lily (B), and the snake lily (C) all have names that implies they are related. They are not true lilies and are not closely related. Photo sources: (A) by User:Fir0002, own work, CC BY-SA 3.0; (B) by Saishreyaswiki, own work, CC BY-SA 4.0; (C) by H. Zell, own work, CC BY-SA 3.0.

The diversity of plants is staggering. To manage the complexity and volume of information we need a system of organization. To make it work it must have a basic principle or goal, and it must allow changes as we learn new information. The taxonomic hierarchy that used with all living organisms is based on a series of taxon ranks that range from the most inclusive rank to the most exclusive rank. The recognized scientific classification system's taxon includes (from most inclusive to most exclusive) Domain, Kingdom, Phylum (Division), Class, Order, Family, Genus, and Species. Variety or cultivar (cultivated varieties) are used sometimes to distinguish within a species. In our example here (Figure 2-2) for the "Nikko Blue" hydrangea, it would be in the Domain Eukarya, Kingdome Plantae, Phylum Magnoliophyta, Class Magnoliopsida, Order Cornales, Family Hydrangeaceae, Genus *Hydrangea*, Species *Hydrangea macrophylla* and the cultivar is 'Nikko Blue'.

Scientific classification

Binomial name

Hydrangea macrophylla
(Thunb.) Ser.



Domain:	Eukarya
Kingdom:	Plantae
Phylum:	Magnoliophyta
Class:	Magnoliopsida
Order:	Cornales
Family:	Hydrangeaceae
Genus:	*Hydrangea*
Species:	***Hydrangea macrophylla***
Cultivar:	'Nikko Blue'

Figure 2-2. The scientific nomenclature of a flowering plant - *Hydrangea macrophylla*.

Organisms are identified at the species level using a binomial nomenclature system. This two-name system means that at the species level a two-part name is used. The first is the **genus** name and tells you to which genus the organism belongs. The second is the **specific epithet** and tells you to which member of the genus you are specifically identifying. The specific epithet is typically an adjective that describes the specific member of the genus in some way.



Figure 2-3. *Hydrangea quercifolia* is the binomial name, the species, of the oak leaf hydrangea. (By Stephanie Harvey. 2018. CC-BY-NC.

For example, in *Hydrangea quercifolia*, *Hydrangea* is the genus and refers to a group of plants with common flowering characteristics (Figure 2-3). The specific epithet "*quercifolia*" describes which of the hydrangea's we are referring too. In this case, the one with oak (*querci-*) like foliage (*-folia*) instead of Hydrangea macrophylla (the big leaf hydrangea).

Linnaeus developed this naming system to replace long wordy Latin description of organism. Prior to this system to identify a specific organism you would have to provide 10-30 Latin adjectives. So, while the two Latin names may be difficult to spell and pronounce, it is a significant improvement over the old system.

When writing the species name for an organism a specific notation is used. The genus (either as part of the species name or alone as just the genus) is always capitalized and italicized. The specific epithet is lowercase (even if it is a proper name) and is also italicized. If the genus has been previously established, then the genus can be abbreviated to the first letter. For example, *Hydrangea macrophylla* can be abbreviated to *H. macrophylla* since it was already introduced to the reader. Please note that if

two different genera are being discussed that start with the same first letter, the full species name must be given.

Any of the taxon ranks can be used to describe groups of plant but the taxon level of Family is frequently used. Members of the same family share derived characteristics. This, however, does not mean they look (or act) alike. Selective pressures from predation, pollinators and the environment shape the individual populations. The plants shown here (Figure 2-4) are all from the Family Hydrangeaceae, but do not look like our common *Hydrangea* nor like each other.



Figure 2-4. Families share derived characteristics, but this does not mean they look alike.

Due to the vast number of plant species and their wide distribution, one additional component is used to help ensure that everyone is referring to the same species. A scientific name of a plant is not complete without the "authority." The authority is the name (or abbreviation thereof) of the person who first accurately described and named the plant. By citing the species name and authority, a reference is provided for the species identification (Figure 2-5).



Figure 2-5. Two examples of scientific names with authorities are given: *Hydrangea macrophylla* (Thunberg) Seringe and the common dogwood, *Cornus florida* L. The abbreviation "L" is used for "Linnaeus." In the case of the *H. macrophylla*, "Thunberg" first described it.

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2.2: Plant Evolution

The first oxygen producing photosynthetic organisms were prokaryote (Figure 2-6). Prokaryotes are single cell organisms that lack a nucleus. These photosynthetic organisms are referred to as cyanobacteria. They began what is often referred to as the "greening" of earth about 1.2 BYA. Terrestrial greening did not begin until 500 MYA.

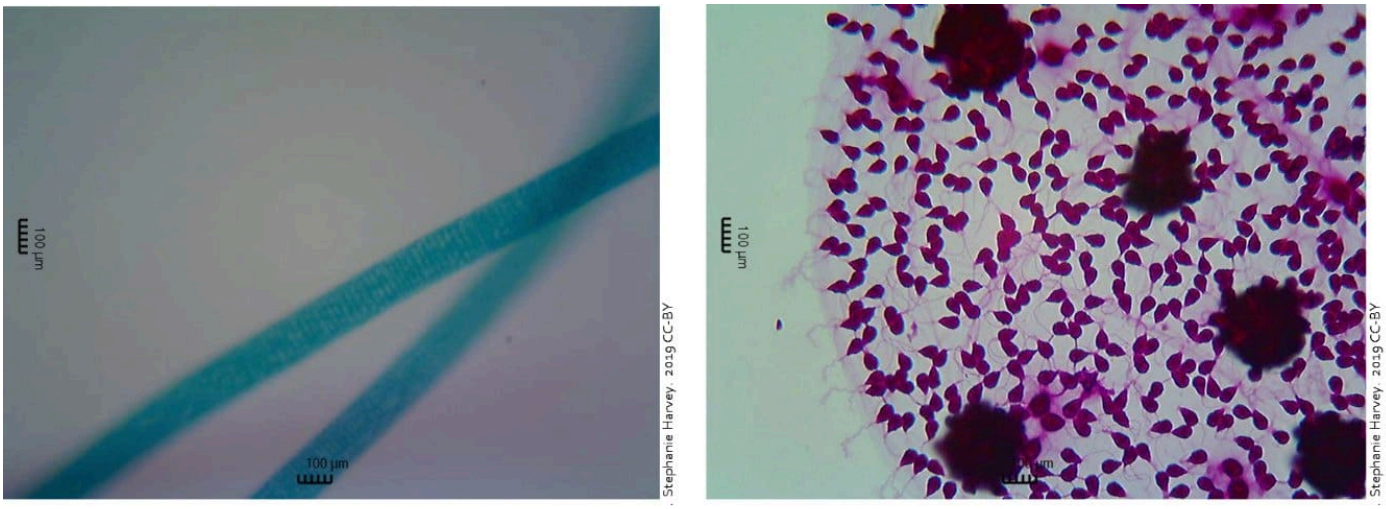


Figure 2-6. Photomicrographs of *Ocillatoria* (cyanobacteria) and *Volvox* (chlorophyte – stain here to see flagella)

Land plants evolved from green algae (Chlorophyta) and share some characteristics with them, such as the type of light harvesting pigment that are used. However, the nearest extant relative is a specific group of green algae called charophytes (Figure 2-7). This is evidenced by both physical and chemical characteristics shared between them but not found in other chlorophytes. This has been confirmed through genomic analysis of both nuclear and chloroplast DNA.



Figure 2-7. *Chara braunii*. A Charophyte that maybe the nearest living relative to the ancestral land plant.

The move into a terrestrial environment provided many benefits to plant organisms that could survive there. The sunlight, unfiltered by water, is more intense and provides significantly more energy for photosynthesis. Atmospheric carbon dioxide is at significantly higher concentrations and is easier to extract for building carbon molecules than the carbon dioxide dissolved in aqueous environments. Nutrient availability was also significantly higher in the soil than in water. Additionally, with minimal producers on land, there were few predators or pathogens.

However, there were a few significant challenges (Figure 2-8) that had to be overcome for survival on land. Water scarcity and water loss were significant problems. No longer submerged in water, the plants were exposed to a drying air environment leading to massive water loss. Since soil was the primary reservoir for water, getting that water to all the plant was an issue given a lack of transport tissue. Effectiveness of cell-to-cell transport declines at distance greater than five cells. This initial limited the size of terrestrial plants.



Figure 2-8. Kelp (a brown algae) and *Zea mays* demonstrate some of the disadvantages to terrestrial life - scarcity of water, lack of structural support and increase UV exposure.

Gravity was also an issue. Larger algae, like kelp, depended on the buoyancy of water to keep them upright. On land, the lack of structural support presents problem that limited the height that plant could obtain.

While the increase in sunlight allows for more photosynthetic productivity, too much solar input can present problems. Overloaded light harvesting system can create reactive oxygen species that damage cells. Increased solar exposure also presented heating issues for plant tissues. Evaporative cooling removed heat from exposed tissues but cost the plants water – a limited resource.

Algae present a classification conundrum. They were traditionally classified as plants since they are photosynthetic. However, our modern understanding of their phylogenetic heritage splits them into different groups (Figure 2-9). The green algae (Chlorophytes) share a more recent common ancestor with the land plants (known as embryophytes) than the red algae. Within the Chlorophytes, the charophytes share an even more recent common ancestor with the embryophytes than the rest of the group. If you include all the chlorophytes (including the charophytes) with the embryophytes, the plant kingdom is referred to as the Viridiplantae. If you include only the charophytes with the embryophytes, the kingdom is referred to as the Streptophyta. If you exclude all the chlorophytes and charophytes, the kingdom is referred to as Plantae. For our purposes we will define plants using the embryophytes only and the kingdom Plantae.

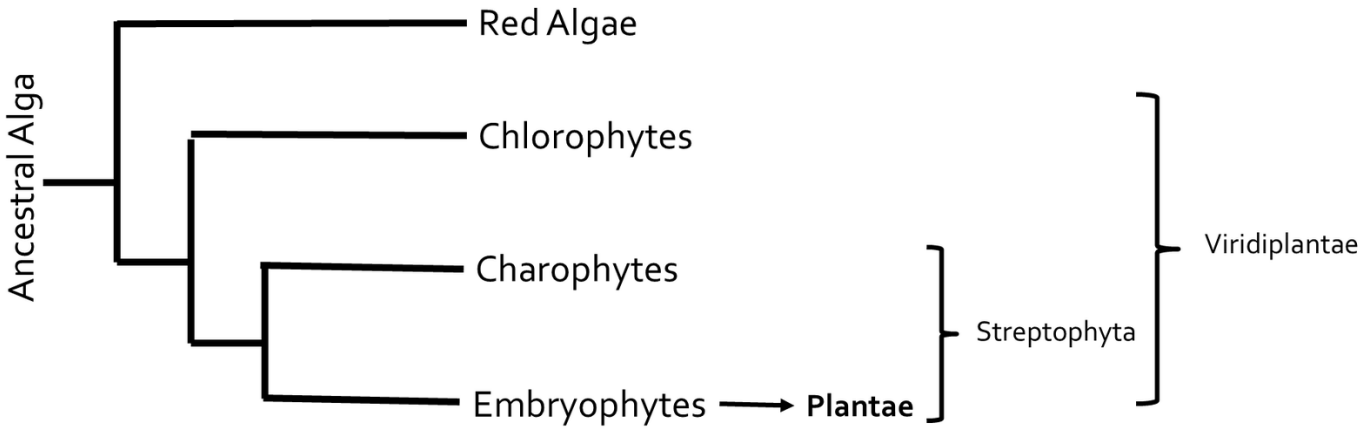


Figure 2-9. This tree shows the various definitions that have been suggested for the Kingdom Plantae. We will use embryophytes definition.

The embryophytes (land plants) have four traits that separate from charophytes. The first of these is "Alternation of Generations and multicellular, dependent embryos." Alternation of generation refers to the life cycle of the species in which a multicellular haploid and a multicellular diploid form alternate. The diploid form (2n) is called the sporophyte and produces haploid (n) spores via meiosis (Figure 2-10). The haploid spores germinate and give rise to the gametophyte -the haploid multicellular form. The gametophyte gives rise to haploid gametes (sperm and egg) via mitosis. The gametes fuse to produce a zygote which develops into an embryo and ultimately a new sporophyte. Some algae exhibit alternation of generations but none of the charophytes do. All embryophytes have this type of life cycle.

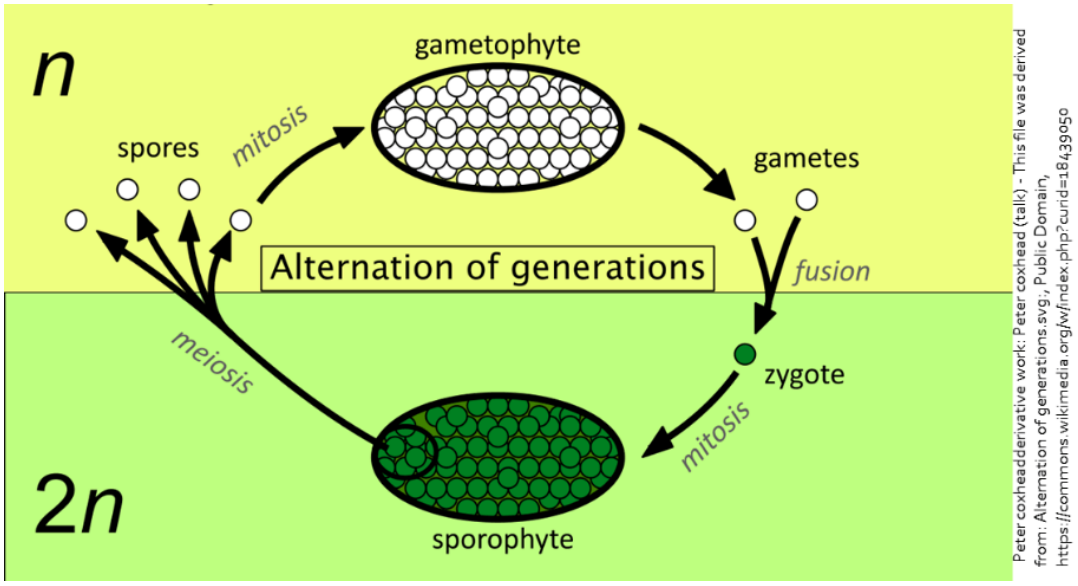


Figure 2-10. Alternation of generations with a multicellular, dependent embryos is characteristic of the embryophytes.

The second part of the statement is about the "multicellular, dependent embryo" means that the zygote develops into a multicellular embryo while still protected and supported by gametophytic tissues. This is in contrast to most algae where the sperm and egg fuse to form a free-living zygote.

The next of the four traits is "walled spores produced in sporangia." In embryophytes, spores are produced in organs called sporangia. Within these structures diploid spore-mother-cells undergo meiosis to produce haploid spores. The spores produced have walls that contain sporopollenin, a chemical that protects the spore from desiccation. Sporopollenin first evolved in charophytes but is found there in the cell walls not in the spore walls.

This image here is a photomicrograph (Fig. 2-11) of a cross section through a sorus on the back of a fern frond. Multiple sporangia are seen here clustered under a protective structure called an indusium. Within the sporangia, the walled spores are visible.



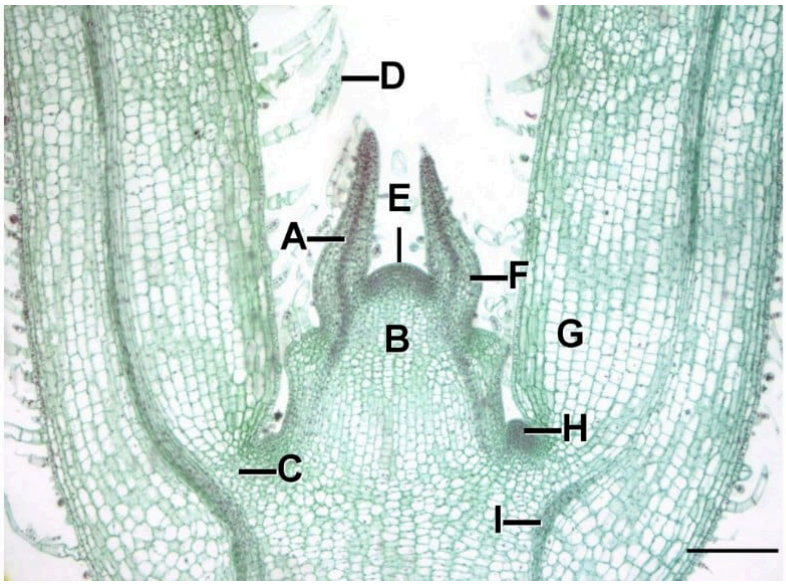
Figure 2-11. Fern Sorus with many sporangia (dashed arrow) each containing walled spores (solid line arrows). (S. Harvey 2016. CC-BY)

The third trait is the presences of "multicellular gametangia." A gametangium (singular) is an organ in which gametes are produced and in plants, the structure is part of the gametophyte. Thus, it is haploid and gives rise to gametes vial mitosis not meiosis as found in animals.

In this photomicrograph, the gametangia of a moss are visible. These gametangia are called antheridia and produce sperm.

The final trait that distinguishes embryophytes from charophytes is the presence of apical meristems (Fig. 2-12). Meristems are tissue in plants in which at least some cells remain undifferentiated. These meristematic cells give rise to various organs of a plant are responsible for growth. Apical meristems are the completely undifferentiated meristems of a plant and include both shoot apical meristems and root apical meristems. Both the SAM and the RAM are responsible for the elongation of the plant.

Photomicrograph of a *Coleus* stem tip.
A=Procambium
B=Ground meristem
C=Leaf gap
D=Trichome
E=Apical meristem
F=Developing leaf primordia
G=Leaf Primordium
H=Axillary bud
I=Developing vascular tissue.
Scale=0.2mm.



By Jon Houseman - Jon Houseman and Matthew Ford, CC BY-SA 4.0, https://commons.wikimedia.org/w/index.php?curid=35869276

Figure 2-12. Photomicrograph of a *Coleus* stem tip.

Embryophytes can be divided into groups based on characteristics that evolved over time. The diagram here shows the various phylogenetic splits that have occurred (Fig. 2-13). All embryophytes can be classified as either Non-vascular or Vascular plants. The Vascular plants diverged into the Seedless plants and the Seeded Plants. The Seeded plant clade diverged to form the Gymnosperms and the Angiosperms. The numbers given above each subgroup estimate the number of extant species.

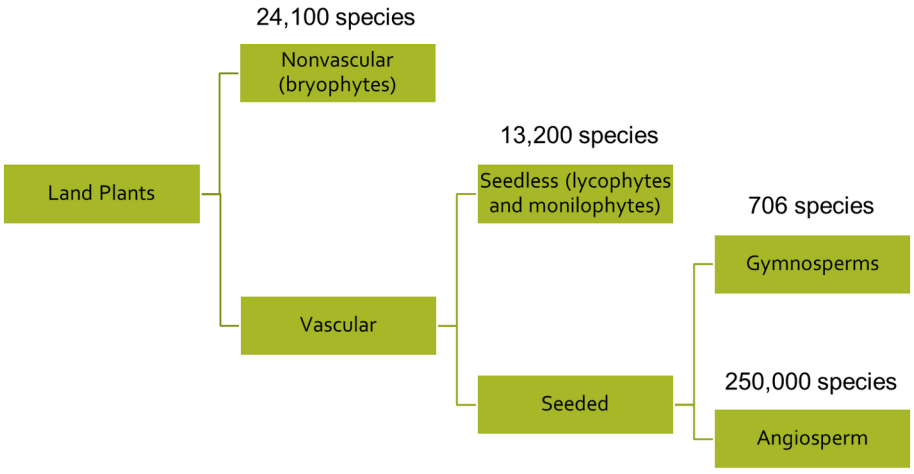


Figure 2-13. Evolution of land plants has produced many divergent branches. This diagram depicts the extant clades with an estimate of the number of species in each group.

We will look at the evolutionary path plants have taken to address the challenges of life on land and other challenges as they arose. We will start with the earliest plants - those with more relictual features (often referred to as “primitive”) - and move toward the new forms that have accumulated more derived traits and now dominate the planet.

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2.3: Non-Vascular and Seedless-Vascular Plants

Non-Vascular

Nonvascular plants, as their name would imply, lack the lignified vascular transport tissues found in higher plants. This lack of transport tissue places considerable constraints on these plants. Their size is limited by the need for all water and nutrients to diffuse from cell to cell. In general, the efficiency of cell-to-cell transport drop significantly a distance greater than five cells. Since a cell greater than five cells from a water source suffers from this limited transport potential, the plants stay small and close to the ground or water source.

The locations where they can survive are also limited. The plant body must be in contact with wet soil to prevent tissue desiccation. Their life cycle is also dependent on water being plentiful. The sperm of the gametophyte must swim to the egg for fertilization to occur. Without adequate water, the next generation would not be produced.

Another characteristic of the nonvascular plants is that they have a dominant gametophyte generation with a dependent sporophyte. This means that within the alternation of generation life cycle the haploid life form is typically larger and is present throughout the two-stage life cycle, while the sporophyte is only occasionally present and is completely dependent on the gametophyte for resources. For example, take the common moss – the green carpet like form that you often see is the haploid gametophyte generation (Fig. 2-14). The sporophyte only appears under certain conditions and is typical not green at maturity and does not contribute to the photosynthetic productivity of the moss. It depends on the gametophyte for water and carbohydrates. The sporophyte is in fact “rooted” into the gametophytic tissues.



Figure 2-14. Moss with tall sporophyte extending above grassy gametophyte. (S. Harvey 2022, CC-BY-NC)

There are three extant phyla of nonvascular plants: liverworts, hornworts, and mosses.

True mosses belong to the phyla **Bryophyta** (not to be confused with bryophytes – a generic term used to collectively refer to all nonvascular plants). There are approximately 12,000 species. We should point out that the use of the “moss” can be misleading. Many plants that are commonly called mosses are not really mosses. For example, clubmoss, spike moss, deer moss, and Spanish moss are not true mosses. (Spanish moss for example is a flowering plant, kin to the pineapple). Just another example of why common names can be problematic.

When you look at a true moss, the “grass” green carpet is the gametophyte stage. It is haploid and produces games via mitosis (as mentioned earlier). The gametophyte is responsible for the photosynthetic productivity for the plant and is the part in contact with the water supply.

In Fig. 2-14, you can see the reddish stalk-like structure with the green tip growing out of the top of the gametophytes. These represent the sporophyte stage. They are not photosynthetic and consist of a foot (unseen here) that anchors the sporophyte into the gametophyte's tissues, a seta that elevated the capsule for better spore release, and the capsule where the spores are produced via meiosis.

Most mosses are short, typically 0.2-10 cm, but there are a few larger ones such as *Dawsonia*, the tallest moss in the world that can grow up to 50 cm in height. The larger species can overcome the diffusion limitations because they have two types of transport tissue (Fig. 2-15). These tissues are fundamentally different than true vascular tissues in that they lack lignin, but their transport function is similar. Within the axis of the moss, hydroids help with water transport while leptoids move carbohydrates. Their lack of lignin however makes them less rigid than true vascular tissue and thus does not provide much in the way of structural support.

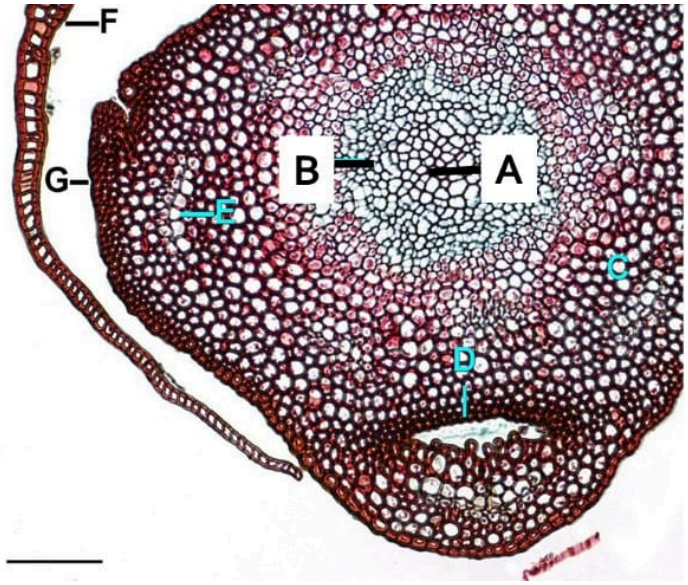


Figure 2-15. Photomicrograph of a cross section through a moss stem. A-Hydroid, B-Leptoid.

Marchantiophyta is the liverworts phylum. Like the mosses they have a gametophyte-dominant life cycle. There are about 9,000 species. The various species take one of two forms and are known as either thallus liverworts or leafy liverworts. The thallus form grows like a flattened, leafless ribbon while the leafy species look like flattened mosses. They are small, usually 2-20 mm wide and less than 10 cm long.

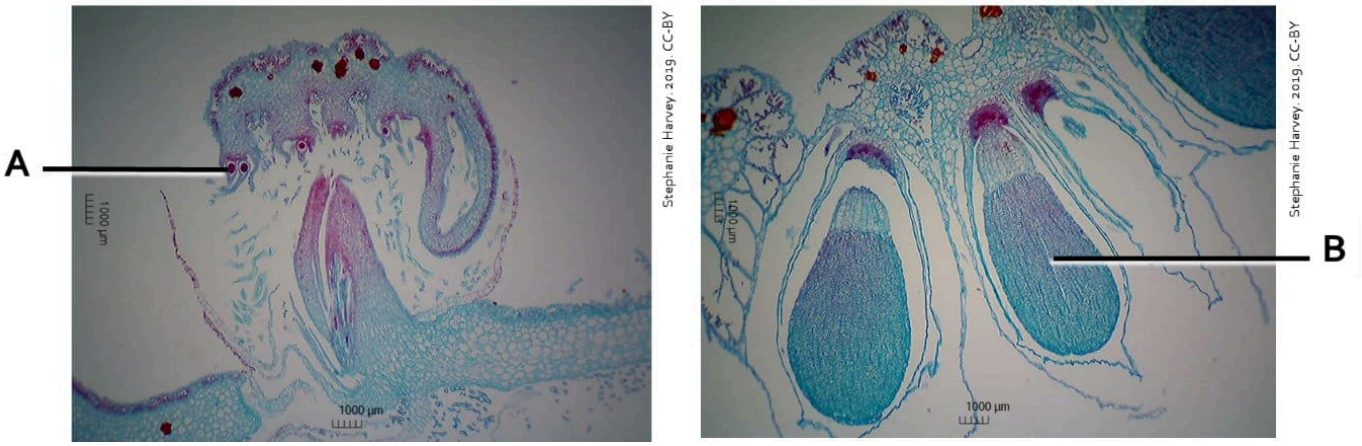


Figure 2-16. A) Micrograph from lateral section of a Gametophore with archegonia; B) the developing sporophyte within the sproganium. (Harvey 2019. CC-BY)

The sporophyte is hidden on the bottom side of a gametophore and has the same structure as the moss sporophyte but with a reduced seta (Fig. 2-16). The first photomicrograph shows a cross section through an archegonia containing gametophore, with the A line pointing to a single archegonium (gametangium producing an egg). If the egg gets fertilized by a sperm, it will develop into the sporophyte (seen in the second photomicrograph). The capsule is note by the line of letter B.

Anthocerophyta is the hornworts phylum and the sporophyte for this phylum is more advanced than that seen in the other nonvascular phyla (Fig. 2-17). At the base of the sporophyte is a meristem that allows the sporophyte to elongate indefinitely. It also produces pseudoelaters to help with spore dispersal. Although the sporophyte is photosynthetic, it is still dependent on the gametophyte. All research attempts at excising the sporophyte have failed.

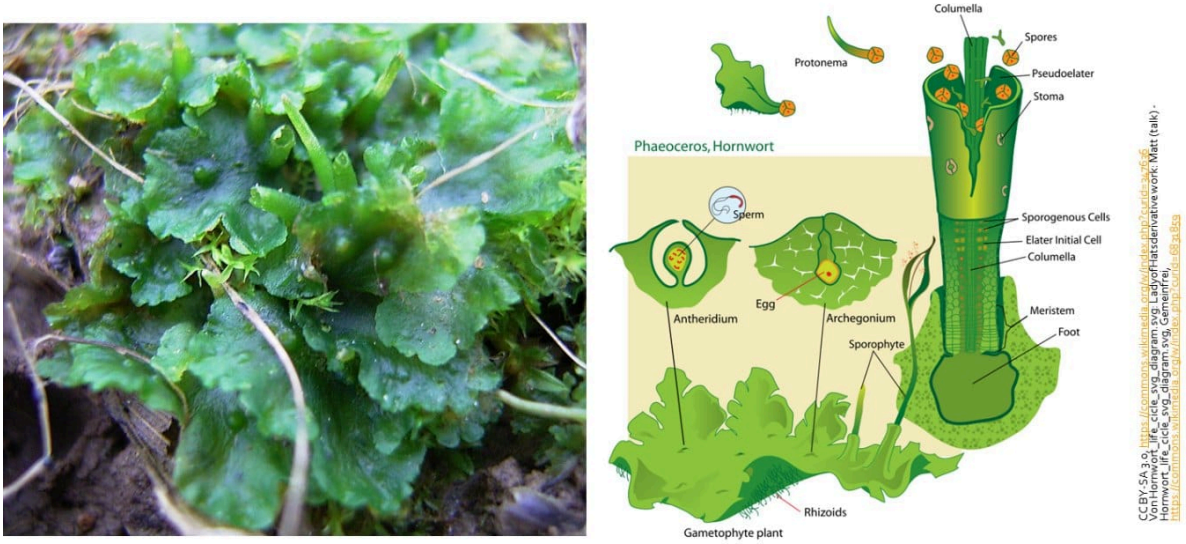


Figure 2-17. Hornworts showing green-leafy thallus (gametophyte) and green "horn" that is the sporophyte.

Seedless Vascular Plants

The development of vascular tissue allowed for taller plant growth due to increased transport efficiency and structural support. These benefits allowed vascular plants to out compete the nonvascular plants. The taller growth of these plants allowed them to intercept sunlight, shading out the nonvascular plant in some cases. Along with the development of vascular tissues can the formation of leaves and roots. Roots helped the vascular plants exploit areas where water was accessible by roots but not necessarily at the surface. Thus, drier environment could be colonized.



Figure 2-18. Mature sporophyte of Bird's Nest Fern and young sporophyte emerging from archegonia of gametophyte.

All vascular plants have dominant sporophyte lifecycles. In the seedless vascular plants, the gametophyte and the sporophyte are independent of each other although the gametophyte is reduced (Fig. 2-18). In the photograph, the sporophyte of a fern can be seen (Bird's Nest fern). In the photomicrograph on the right, the gametophyte of a fern is seen in the background while a new

forming sporophyte emerges from the gametophyte archegonia.

As the name implies, vascular plants have vascular tissues. The transport of water and dissolved minerals is carried out by the Xylem tissue which includes dead transport cells that are lignified. Carbohydrates and other products of photosynthesis are distributed by the living transport cells of the phloem. Xylem tissue and phloem tissues are often found together in columns called vascular bundles. The arrangement of tissues within the bundles and of the bundles themselves varies with the type of plant and the organ being examined.

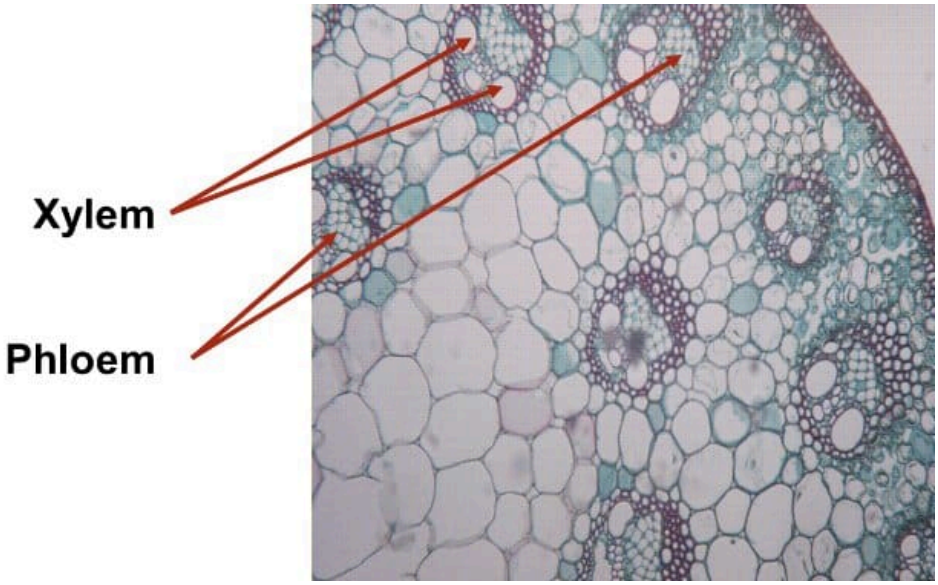
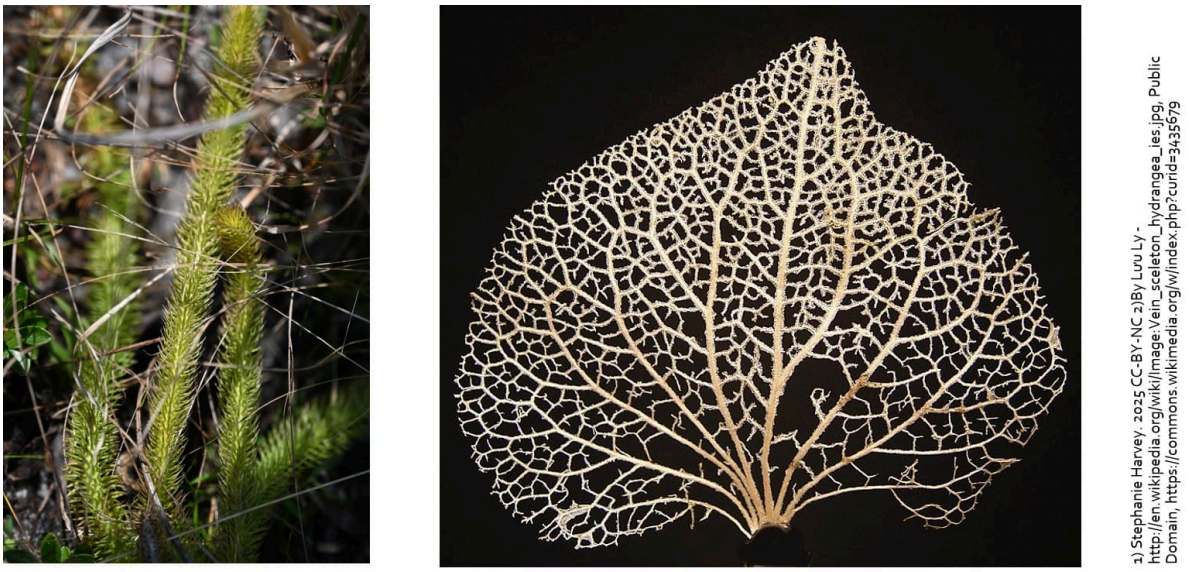


Figure 2-19. Micrograph of the cross-section of a monocot stem. Vascular bundles show xylem and phloem. (S. Harvey 2021. CC-BY-NC)

Only with the development of vascular tissues could true roots and leaves evolved. Branching of the plant axis occurred only after evolution of vascular tissues. With the branching of the vascular tissue came the ability to produce networks of roots and extensions of the stem that could form leaves. Two types of leaves developed – microphylls and megaphylls (Fig. 2-20). Microphylls (as seen in the first photograph) are small leaves with a single vascular bundle. Megaphylls (2nd photograph) are formed from webbing across numerous branches and thus multiple vascular bundles.



1) Stephanie Harvey. 2025 CC-BY-NC 2)By Luu Ly - http://en.wikipedia.org/wiki/Image:Vein_sceleton_hydrangea_ies.jpg, Public Domain, https://commons.wikimedia.org/w/index.php?curid=3435679

Figure 2-20. Branching allowed for the architecture that would support the development of both microphylls (fist image) and megaphylls (second image).

The vascular plants are divided into two groups: the seedless vascular plant and the seeded vascular plants. For the remainder of this segment, we will look at the seedless vascular plants. There are two groups of seedless vascular plants. The lycophytes (1300

species) and the monilophytes (9,000 species).

The **lycophytes** include the club and spike mosses as well as the quillworts. They differ from all other vascular plants by having microphylls instead of megaphylls. *Lycopodium clavatum* is an example of a club moss (Fig. 2-21). The sporangia of the club mosses are borne on the upper surface of specialized leaves arranged in a cone-like strobilus (plural: strobili) at the end of upright stems.



Figure 2-21. *Lycopodium clavatum* is in the class Lycopodiopsida and is commonly referred to as a "club moss."

Monilophytes include the ferns, horsetails and whisk ferns; they are often referred to as the “ferns and fern allies.” These vascular plants reproduce via spores and have neither seeds nor flowers. They have branched stems and megaphylls. The megaphylls or fronds arise from a rhizome.

Some ferns have fronds that can become sporophylls (spore bearing leaves) as the plant matures while other ferns have specialized fronds, known as fertile fronds, which are responsible for housing the sporangia (Fig. 2-22). In *Osmundastrum cinnamomeum* (the cinnamon fern) both sterile and fertile fronds are produced. It is the rusty-brown color of the fertile fronds that give the organism its names.

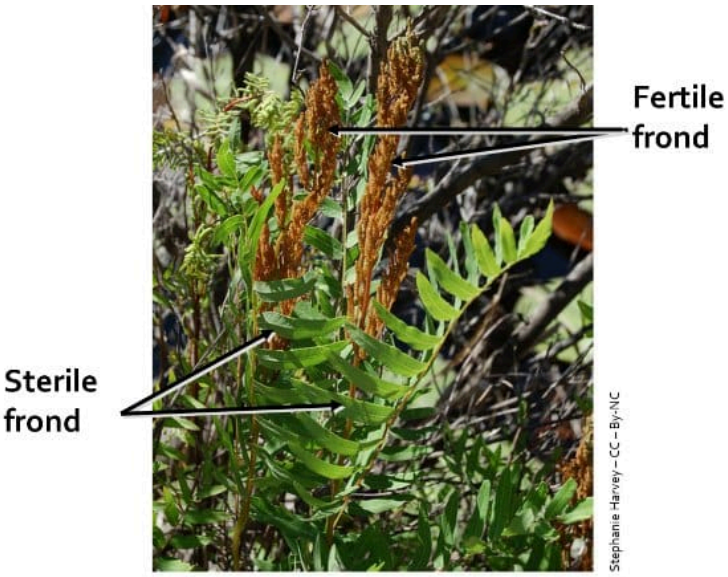


Figure 2-22. *Osmundastrum cinnamomeum* is in class Polypodiopsida and is an example of a fern with both fertile and sterile fronds. (S. Harvey 2021).

In the ferns with non-specialized sporophylls, sori are often produced on the back side of the frond. Sori are clusters of sporangia that produce spores for asexual reproduction. Some sori are protected by a covering called an indusium which gives them a shiny appearance. The arrangement of sori is often used to identify/classify various ferns (Fig. 2-23).

The first image is a photograph of the sori on *Athyrium filix-femina*. The photomicrograph in the middle is of a cross section through a sori while the last image, is a close-up photomicrograph of the sporangia of the sori. Note the spores within the walled structure.

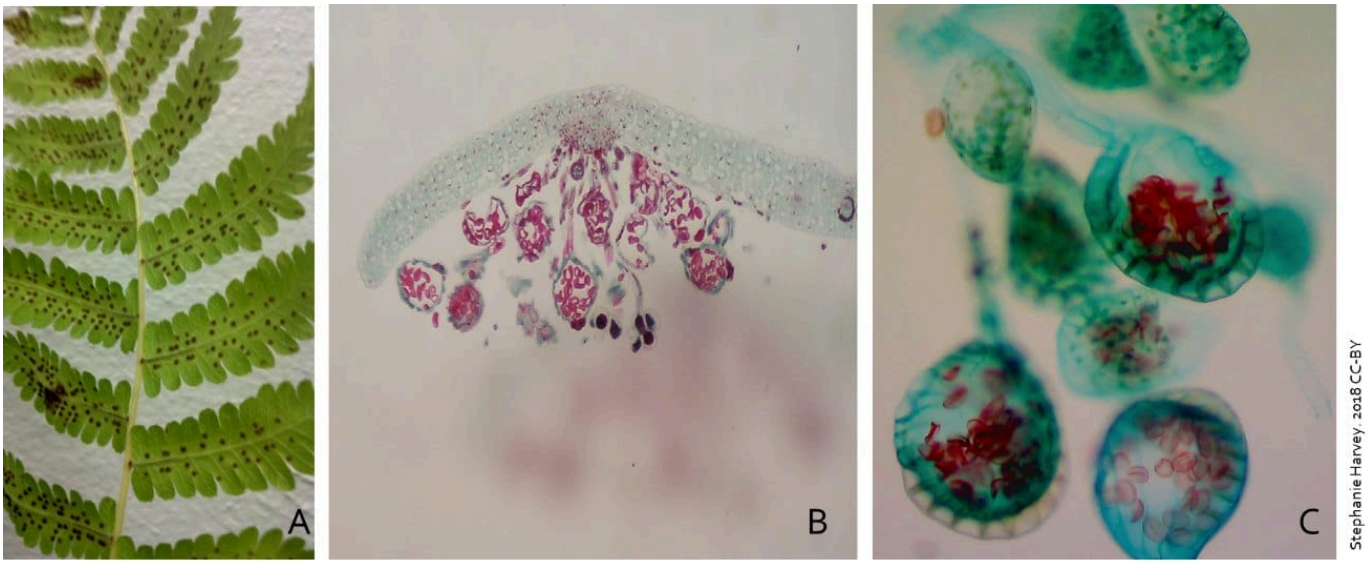


Figure 2-23. A - photograph of the sori on *Athyrium filix-femina*. B-Photomicrograph in the middle is of a cross section through a sori; C-close-up photomicrograph of the sporangia of the sori. (Harvey 2018).

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2.4: SEEDED VASCULAR PLANTS

The seeded vascular plants, also called the spermatophytes, are considered the most advanced of the land plants and represent the accumulation of many adaptations for terrestrial life. Four major adaptations are: a reduced, dependent gametophyte, secondary growth, pollen, and seeds.

As plants adapted to the terrestrial environment, a shift away from the dominant gametophyte of the bryophytes occurred. Ultimately in the seeded plants we find the gametophyte reduced in size and is retained by the maternal sporophyte. In this manner, the haploid tissues are not exposed to the potential damaging effects of the environment.

The female gametophyte is reduced to just seven cells (8 nuclei) with the ovule. One of these cells is the egg. The female gametophyte is always retained within maternal sporophyte. The male gametophyte is even more reduced with only two cells – a generative cell and a vegetative cell. The mature male gametophyte is ultimately released from the sporophytic tissue but only after maturation.

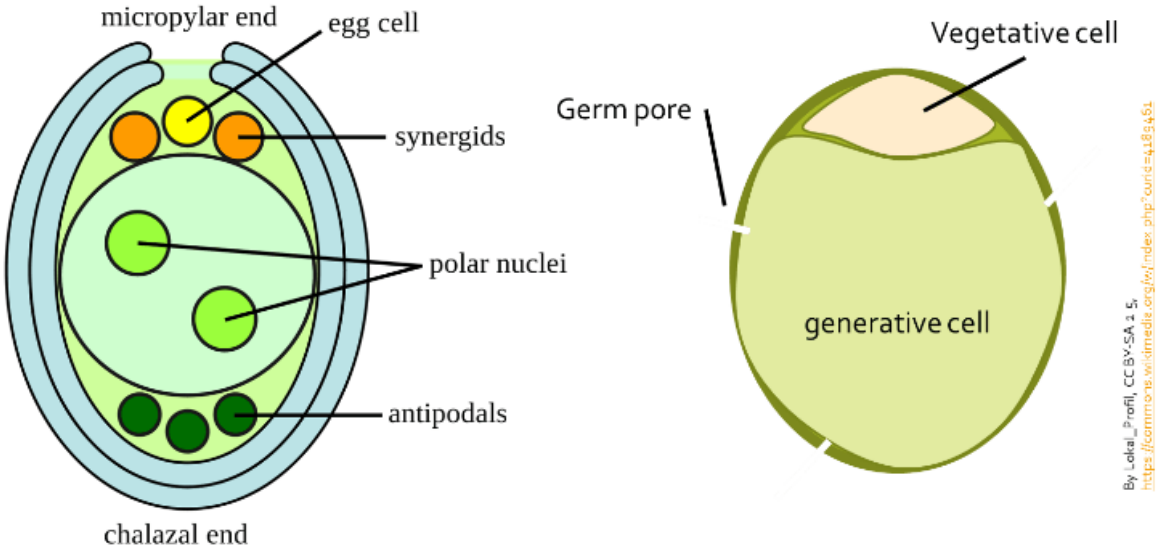


Figure 2-24. Diagram showing the reduced female and male gametophyte of the seeded plants.

One of the factors that allowed the seeded plants to outcompete the seedless plants was the development of second growth. A new meristematic tissue, the vascular cambium, allowed for lateral growth (lateral meristem). As the vascular cambium divides, one daughter cell matures into either second xylem or 2nd phloem (depending on its position) while the other remains as vascular cambium. This allows for the production of new transport tissue throughout the life of the organism. While the 2nd phloem does not accumulate overtime, the stronger cells of the 2nd xylem do accumulate and are what causes the increase in girth of tree trunks and branches. The photomicrograph shows a cross section through a 3-year-old pine stem. The pink (lighter) area is the 2nd xylem, and you can see the bands of growth associated with each year. Note the round holes throughout this region are resin canals.

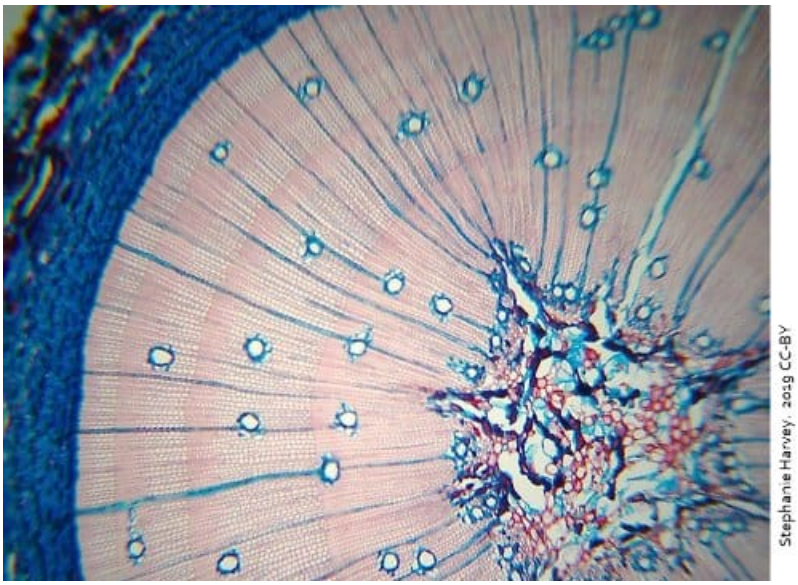


Figure 2-25. Cross section through a 3-year *Pinus* stem with 2nd growth visible (Harvey 2019 CC-BY-NC).

The evolution of pollen removed further environmental restrictions to plant expansion. Pollen grains are the mature male gametophytes of seeded plant. They are released from the maternal tissue only after they have developed resistant outer wall called an exine and an inner wall called the intine. The exine wall is largely composed of sporopollenin. The pollen wall protects the sperm from desiccation and UV exposure while the pollen grain is the sperm to the egg. Without the need for water as a medium for the sperm to swim to the egg, the vascular plants were able to move into drier areas without a decline in reproductive success.



Figure 2-26. Pollen released by male cones on a pine tree.

The evolution of seeds also allowed for colonization of new areas and had advantages over spores. A seed by definition is a multicellular embryo packed into a protective container with a food source. The nutritive tissue may be from the female gametophyte or a tissue that results from a fertilization event. The seed coat is a protective tissue derived from the maternal sporophyte.

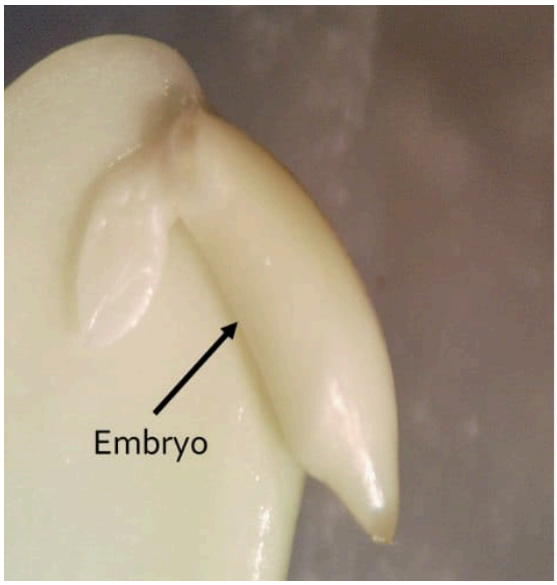


Figure 2-27. Well-developed embryo of a bean. (Harvey 2004 CC-BY-NC)

Seeds have a distinct advantage over reproduction by spores because the embryo gets a "jump start" will nurtured by the material tissues. It starts its independent life as a multicellular structure unlike spores that start as a single cell. So, the cost to the plant to produce seeds is higher than that of spores, but rate of successful germination and establishment of the next generation is significantly higher with seeds.

Gymnosperms, the "naked seed plants," were the dominant terrestrial plant from 251-65 MYA. They replaced rainforests of lycophytes in tropical regions. Today there are only about one thousand living species.

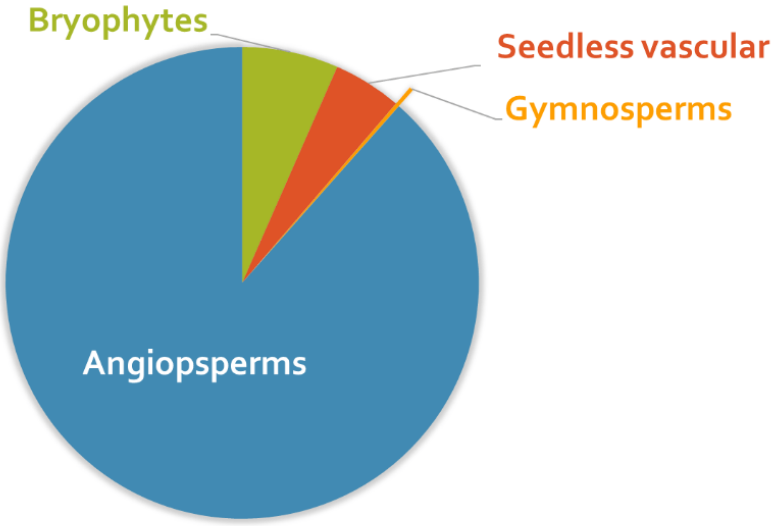


Figure 2-28. Distribution of extant plants among the various groups. (Harvey. CC-BY-NC)

Angiosperms, the "flowering plants," replaced gymnosperms as the dominant terrestrial plant. While they existed since about 160 MYA, they replaced conifers as the dominant trees between 100 to 60 MYA.

For extant plant species, about 88% are angiosperms, 7% are Bryophytes, seedless vascular make up 5% and the Gymnosperm less than 1%.

Like the gymnosperms, angiosperms have seeds and pollen. However, they also have specialized reproductive structures: flowers, ovaries, and fruits. These structures provide protection for the ovules and seeds. They also improved the potential for both pollination and dispersal of seeds. We will look at these differences more in the future.

2.4.1: Gymnosperms - "Naked" Seed Plants
2.4.2: Angiosperms - Flowering Plants

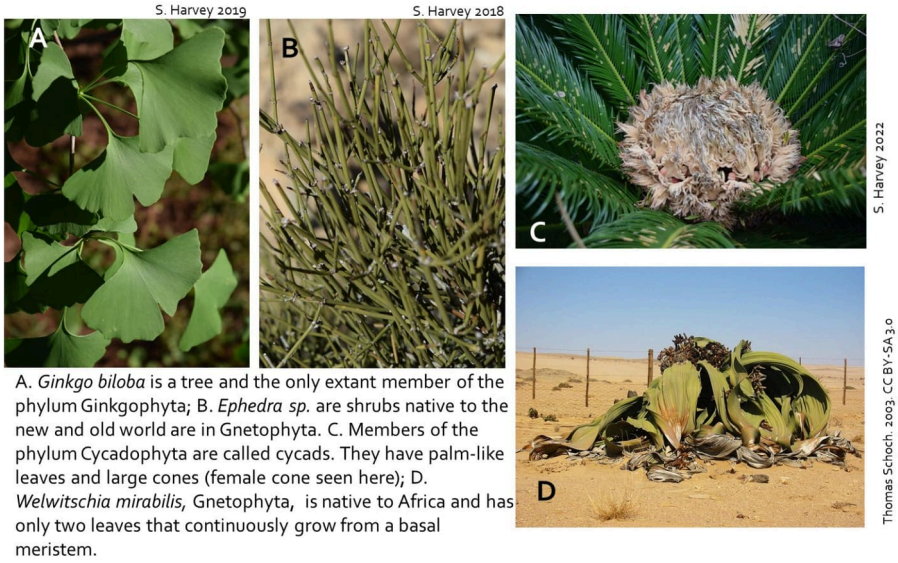
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2.4.1: Gymnosperms - "Naked" Seed Plants

Although gymnosperms make up less than 1 percent of the extant plant species, we will look at them more closely due to their overall importance. The success of a group of plants in a specific environment it typically linked to two factors: temperature and water availability. Gymnosperms are more drought tolerant and cold tolerant. They are often found in hot-dry environments and in cold-dry environments. Their economic importance as a source of fiber and lumber is also notable.

There are only four extant phyla: Cycadophyta, Gingkophyta, Gnetophyta and Coniferophyta. We will look briefly at each of these groups with a little extra attention to Coniferophyta.

Members of the phylum Cycadophyta are commonly called cycads (Fig. 2-29 C). They have palm-like leaves, large cones, and un-branching trunks. The palm-like leaves and un-branching trunk often have people confusing them with true palms. In fact, they are commonly known and sold as Sago palms. However, palms are angiosperms, so despite the similar appearance there is no close relationship. Cycads are dioecious, that is species takes two forms – one that bares female cones and one that bares male cones.



A. *Ginkgo biloba* is a tree and the only extant member of the phylum Ginkgophyta; B. *Ephedra sp.* are shrubs native to the new and old world are in Gnetophyta. C. Members of the phylum Cycadophyta are called cycads. They have palm-like leaves and large cones (female cone seen here); D. *Welwitschia mirabilis,* Gnetophyta, is native to Africa and has only two leaves that continuously grow from a basal meristem.

Figure 2-29. Collection of Gymnosperm plants

The phylum Ginkgophyta has only a single extant member (Fig. 2-29 A). This tree is not easily recognized as a gymnosperm due to its broad-leaf appearance. It has fan shaped leaves with dichotomous venation and is deciduous (drops it leave in the fall) like oaks and hickory trees.

The species is also dioecious. The female trees produce an apricot-like structure that looks like a fruit. However, it is really a seed with a soft-fleshy out section. While *Ginkgo*'s are often used in landscapes, only the male trees are desirable. That soft-fleshy section of the seed release butrizine – a compound that smells like vomit. The following seed production is so noxious most municipalities have ordinances outlawing female *Ginkgo* trees.

Gnetophyta contains only three extant families with a single genus each. These families are extremely different in physical appearance and in their range.

Welwitschia mirabilis (Fig. 2-29 D) is native to Africa in the xeric regions of Angola and Namibia. It has only two leaves that continuously grow from a basal meristem that circles the reduced stem. Wind rips the leaves into strips along specific sutures to minimize the damage done to the plant. These are also dioecious and will produce either male cones or female cones from the top of the reduced stem.

Gnetum species are typically tropical evergreen trees, shrubs, and lianas (woody vines). They are found in Africa, South America, and Southeast Asia.

Ephedra species (Fig. 2-29 B) are shrubs native to the new and old world. In the U.S. they are common in the southwest. Adapted to xeric environments, these plants lack leaves. Photosynthesis is carried out in the green stems of the plant. Like the *Ginkgo* trees, the *Ephedra* seeds have a fleshy coating that often gets them mistaken for fruits. *Ephedra* species are the original source for ephedrine and its isomers.



Figure 2-30. *Pinus* (pines) is the most common genus of the phylum Coniferophyta. (Harvey 2013 CC-BY-NC)

The phylum Coniferophyta, commonly called the conifers, contains perennial woody plants. Most are trees with strong monopodial growth (they grow upward from a single point) (Fig. 2-30). This phylum is by far the largest of the gymnosperm phyla. It includes several large families including pines, cypress, and yews.

The Cypress family (Fig. 2-31), Cupressaceae, includes junipers and redwoods with near-global distribution. *Taxodium ascendens*, seen in this image, is the pond cypress and occurs mainly in still blackwater rivers, ponds, and swamps.



Figure 2-31. *Taxodium ascendens*, the pond cypress, occurs mainly in still blackwater rivers, ponds, and swamps (Harvey 2017 CC-BY-NC)

The yew family, Taxaceae, are small evergreen trees and shrubs that branch frequently. The leaves are arranged spirally but are flattened to appear as two rows. Most produce seeds with red fleshy arils. While this fleshy structure does attract dispersal agents it is not a fruit. Of note in this family is the Pacific Yew, the source for the cancer drug – Taxol.

Pinaceae is the pine family, and it is the largest family in the gymnosperms with 629 extant species. Most members are trees or

shrubs with needle-like or scale like leaves. It includes pines, cedars, firs, hemlock, larches, and spruces.



Figure 2-32. *Pinus palustric* - longleaf pine- is native to the southeastern US and is highly pyrophytic. (Harvey, 2016 CC-BY-NC)

The image (Fig. 2-32) shows *Pinus palustris* – the longleaf pine. It is native to the southeastern US and is highly pyrophytic. This means it can survive (and in fact thrive) in areas frequently burned.

Pines are monoecious and thus will produce both male and female cones on a single plant. The male cones are the pollen cones (Fig. 2-33). These are typically smaller than the female cones and are papery in nature as they are only on the tree for a few months. The female (ovulate) cones are woody and significantly larger. The female cone stays on the tree until the seed mature or even after. Some female cones stay closed, storing the seeds, for up to 60-80 years. Thus, providing a new seed pool following a fire.



Figure 2-33. Male cones (pollen cones) are smaller than the female cones (ovulate cones) and are only present during pollen production. the foody female cones stay on the three for up to 3 years. (Harvey, 2016,2022 CC-BY-NC)

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2.4.2: Angiosperms - Flowering Plants

Traditionally the angiosperms, Phylum Magnoliophyta, were divided into two clades: monocots and dicots. However, our current understanding of angiosperm phylogeny divides Magnoliophyta into four (4) groups: monocots, eudicots, basal angiosperms and magnoliids.

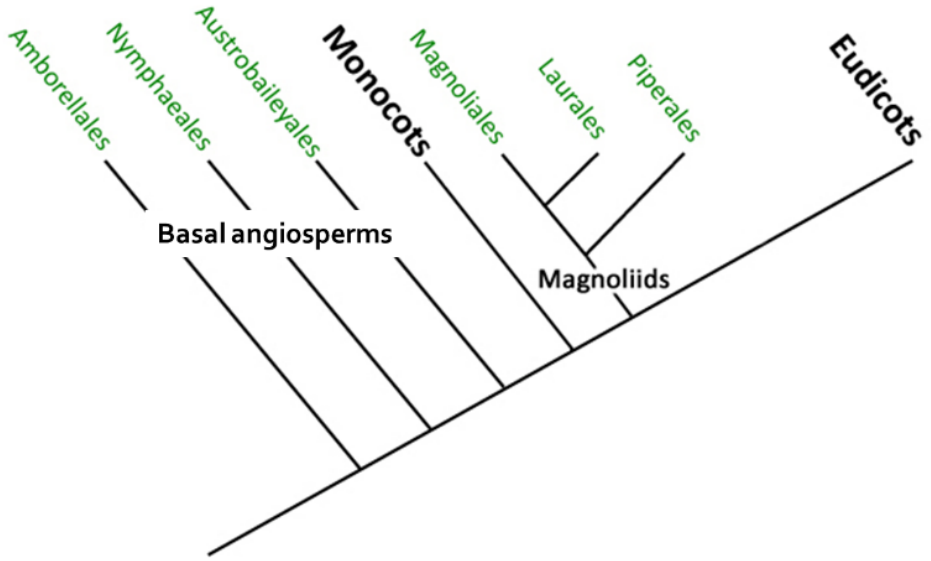


Figure 2-34. This cladogram demonstrates our understanding of the phylogenetic relationships amongst the flowering plants.

This cladogram, shows the three basal angiosperms diverging from the ancestral line first, followed by the monocots, then the magnoliids and finally the Eudicots.

Basal Angiosperms

Basal angiosperms are a group of plants that are considered to be among the most primitive or "basal" lineages of flowering plants (angiosperms). They represent a diverse array of plants that share certain characteristics and are believed to have diverged early in the evolution of flowering plants. Basal angiosperms are considered to be living fossils, providing valuable insights into the early stages of angiosperm evolution.

There are only a few hundred species in this grade. The group of basal angiosperms includes three main lineages: Amborellales (1 species), Nymphaeales 70-90 species, and Austrobaileyales (one hundred species). Amongst these lineages, the exact relationships are not clear. Let us explore each of these lineages and their defining features:

1. Amborellales: The Amborellales (Figure 2-35) are represented by a single living species, Amborella trichopoda. This plant is native to New Caledonia, a group of islands in the Pacific. Amborella is a small shrub with simple, opposite leaves. It produces small, inconspicuous flowers with spirally arranged floral parts. One notable characteristic of Amborella is its primitive reproductive features, such as a large number of spirally arranged stamens (male reproductive structures) and a lack of a well-defined carpel (female reproductive structure).



Figure 2-35. *Amborella trichopoda*. (Scott Zona of Miami, Florida, USA - *Amborella trichopoda*, CC BY 2.0)

2. Nymphaeales: The Nymphaeales include aquatic or semi-aquatic plants commonly known as water lilies (Figure 2-36). This group encompasses families such as Nymphaeaceae (water lilies) and Cabombaceae (water shield). Nymphaeales are characterized by floating or emergent leaves and showy, fragrant flowers. The flowers have numerous petals and numerous stamens, arranged in spirals or whorls. Water lilies often have large, round leaves that float on the water's surface.



Figure 2-36. *Nymphaea odorata* is also known as the American white waterlily or the fragrant water lily. (Harvey 2013 CC-BY-NC).

3. Austrobaileyales: The Austrobaileyales (Figure 2-37) lineage consists of a few families, including Austrobaileyaceae, Schisandraceae, and Trimeniaceae. Members of this group are predominantly found in tropical and subtropical regions, mainly in Southeast Asia. Austrobaileyales plants can be shrubs, small trees, or lianas. They often have simple, alternate leaves. Flowers of Austrobaileyales plants are usually small and not very showy, with an arrangement of floral parts that can vary among different families. Star Anise, *Illicium floridanum*, is a shrub native to Southern United States, from Florida to Louisiana.



Figure 2-37. Star Anise. Order Austrobaileyales (Harvey 2017 CC-BY-NC).

Basal angiosperms display several characteristics that differentiate them from more derived angiosperms. For example, they often possess numerous, spirally arranged floral parts, lack specialized floral organs, have simple leaves, and exhibit primitive features in their reproductive structures.

These traits provide insights into the early evolutionary stages of flowering plants and help scientists understand the diversity and adaptations of ancient angiosperm lineages. Their existence provides valuable clues about the characteristics and environmental conditions of the early angiosperm world. By examining the anatomy, genetics, and reproductive strategies of basal angiosperms, researchers can gain a deeper understanding of the origins and subsequent diversification of flowering plants.

Magnoliids

The magnoliids is an informal name that corresponds to a clade composed of Canellales, Laurales, Magnoliales and Piperales. This clade appears to have diverged from the lineage leading to eudicots after the divergence of the monocots. The magnoliids include a wide range of plant families, but some of the most well-known and recognizable members belong to the magnolia, laurel, and nutmeg families. Examples of magnoliids include magnolias (Magnoliaceae), tulip trees (*Liriodendron*), bay laurels (Lauraceae), sassafras (*Sassafras*), and nutmeg (*Myristica fragrans*).



Figure 2-38. *Magnolia grandiflora*, the southern magnolia is an evergreen with leathery leaves and large, fragrant, white flowers. (Harvey 2019 CC-BY-NC)

The Magnoliids share several characteristics. One of the defining features of magnoliids is their primitive floral structure (Figure 2-38). Their flowers typically have numerous petal-like tepals that are not clearly differentiated into distinct petals and sepals. The floral parts are often arranged in multiples of three (trimerous) or a multiple of three. Magnoliids possess primitive vascular tissues known as tracheids, which are elongated, water-conducting cells found also in the gymnosperms. Tracheids lack the specialized end walls found in more advanced angiosperms, called vessel elements. This distinction is one of the features that separates magnoliids from other flowering plants.

The leaves of magnoliids are generally simple, meaning they are not divided into leaflets. Their phyllotaxy is often alternate, meaning they are arranged singly along the stem, rather than opposite or whorled. Magnoliids have cultural significance, as some species, such as magnolias and bay laurels, are highly valued for their ornamental and aromatic qualities. They produce a variety of secondary metabolites, such as alkaloids, lignans, and essential oils. These compounds often contribute to the aromatic properties and medicinal uses of magnoliid plants. Additionally, certain magnoliids have historical uses as medicinal plants, flavorings, or sources of timber and essential oils. Some examples from this group include avocado, cinnamon species, black pepper, nutmeg, and bay laurel. The southern magnolia, *Magnolia grandiflora,* is often planted in landscapes.

Monocots

Monocots, short for monocotyledonous plants, make up more than 25% of the angiosperms. As their name implies, they develop a single cotyledon or seed leaf in their seeds. They also have other key characteristics that separate them from the other angiosperms.

The leaves of monocot are typically long, narrow, and have parallel venation, meaning the veins run parallel to each other from the base to the tip of the leaf (Figure 2-39). Most of the veins will be of equal size although some plants have a distinctly larger mid-rib. Examples of monocots with well-known leaves are grass, rice, wheat, and maize.



Figure 2-39. Cattails (*Typha*) exhibit the characteristct venation of a monocot.(Harvey, 2019 CC-BY-NC).

The floral structure of monocots often exhibits certain patterns. Monocot flowers typically have floral parts in threes or multiples of three. This is specifically true for petals, sepals, and stamens. If the ovary is compound it will form from three carpels (Figure 2-40). Not all monocots produce showy flowers. Grasses, for example, have lost their petal and sepal. Most people do not even recognize them as flowering plants. Another reproductive characteristic is that the pollen grain of the monocots typically has a single pore or furrow through which the pollen tube will immerge. Examples of showy monocots include orchids, lilies, and amaryllis.



Figure 2-40. Lilies are an example of a "showy" monocot. (Harvey 2019 CC-BY-NC).

In contrast to the taproot systems typical of the eudicots, monocots generally have a fibrous root system, with numerous thin roots that arise from the base of the stem. This occurs because the radical (the embryonic root) typically dies not long after seed germination. It is replaced by adventitious roots produced from the lower stem. These roots tend to stay the same size, and a taproot is not established.

If you are able to get a look at the stem or root of a monocot under the microscope you will see a pattern in the arrangement of the vascular bundles. In the monocot root, the vascular bundles are arranged in a ring. This creates two distinct areas – a cortex region and a pith region within the ring. In the stem, the arrangement of vascular bundles is usually scattered. However, this arrangement is not random. These are arcs of bundles produced by the sheathing bases of the leaves.

Monocots encompass a vast range of plants across different habitats and life forms. Some examples of monocots include grasses (Poaceae family), lilies (Liliaceae family), orchids (Orchidaceae family), palms (Arecaceae family), irises (Iridaceae family), and bananas (Musaceae family). They have ecological and economic significance. Grasses, such as wheat, rice, and corn, are major food crops that provide a significant portion of the world's caloric intake. Many ornamental plants, including lilies and orchids, belong to the monocot group. Additionally, several monocots are utilized for their fibers, such as sisal from Agave species.

Eudicots

The eudicots make up more than two-thirds of the angiosperms and as their name implies, they develop two cotyledons or seed leaves. There are many economically important members in this group including the rose family (Rosaceae), legume family (Fabaceae), squash family (Cucurbitaceae), oak family (Fagaceae) and many others (Figure 2-41). Their growth habits range from herbaceous plants to large trees.



Figure 2-41. Eudicots include many plants of ecological and economic importance. A - Corneace -the dogwood family; B - Fabaceae - the legume family (Harvey 2017, 2019 CC-BY-NC)

It is often useful to be able to distinguish between monocots and eudicots. It is often one of the first steps in identifying a plant species. It can also be helpful in more practical applications. For example, selective herbicides are available that will kill on group but not the other. So, if you have a weedy grass in your garden amongst your peas and beans, an herbicide that targets only monocots would work well without the potential to harm your crops.

One of the characteristics that is often used to determine if a plant is a monocot or eudicot is leaf venation (Figure 2-42). As mentioned in the previous section, monocots typically have leaf veins that run parallel to each other and the edge (margin) of the leaf. On the other hand, Eudicots have net-like venation. That is the veins branch and spread across the leaf surface.



Figure 2-42. Venation on a monocot verses a eudicot leaf (Harvey 2019 CC-BY-NC)

The number of floral parts (sepals, petals, stamen, carpels) with the flowers of the two groups also differs. Monocots have floral parts in sets of three. Eudicots have floral parts in sets of 4s or 5s. Within a flower, always count two different floral parts and determine if they agree with one another.

The type of root system may also be helpful in classification. While monocots typically have fibrous roots systems, while eudicots have a taproot (main root) present. This difference develops soon following germination of a seed. In eudicots, the embryonic root continues to grow, increasing in size and producing lateral roots. In contrast, the embryonic root of the monocot is replaced with multiple roots from stem tissue.

The onions (Figure 2-43) in the first image have many roots of about equal diameter and length. The white onion bulb visible is not a root – it is a collection of storage leaves attached to a compress stem disk. It is from this stem disk that the root emerges.



Figure 2-43. Roots typical of a monocot as compared to those of a eudicot.

There are other distinguishing characteristics as well, but not all are suited for use outside of a laboratory or classroom setting. This table lists the characteristic that differ between monocots and eudicots. The first three and the last we have already discussed.

Table 2-1. *Characteristics that in the laboratory could help distinguish monocots from eudicots.*

Characteristic	Monocot	Eudicot
Leaf venation	Usually parallel	Usually netlike
Floral parts in multiples of	Three	Four or five
Roots	Fibrous	Taproot
Pollen grain openings	One pore	Three pores
Vascular bundles in stem	Scattered bundles	Bundles in a ring
Vascular bundles in root	Bundles in a ring	Bundles form a solid center
Embryo cotyledons	One cotyledon	Two cotyledons

The pollen grains of monocots have only a single pore in the pollen's exine while eudicots have three pores. The arrangement of the vascular bundles can be helpful if you can look at a cross section of the stem or root under a microscope. In the stem, vascular bundles of monocots appear scattered amongst the ground tissue. In eudicots, the vascular bundles are arranged in a ring dividing the ground tissue into two regions: cortex and pith. In contrast to the stem, it is the roots of monocots that have vascular bundles in a ring, while the eudicot root has the vascular bundles forming a solid central core.

Because members within either group have the potential to gain or lose specific traits through genetic changes, it is wise to ensure that 2-3 characteristics are met when trying to identify a specific plant into the monocot or eudicot group.

One of the most interesting aspects of angiosperm diversity is the changes brought about through co-evolution with animals, in particular insects. Initially, all pollination was carried out via the wind. This required an extensive investment by the plant toward the production of pollen. Copious amounts were needed to ensure that some would reach the correction species and the correct time so that fertilization could occur. Plants that could attract insects to move the pollen from site A to site B, had a distinct evolutionary advantage due to increased reproductive success. And if a very specific pollinator could be attracted, then even higher rates of reproductive success were possible while producing less pollen and thus saving resources.



Figure 2-44. *Rafflesia* flowers produce scents associated with rotting meat to attract flies for pollination; The bee orchid mimic the appearance and scent of a female bee to attract males for pollination.

The *Rafflesia* (Figure 2-44) has evolved a mechanism to attract a specific group of pollinators – flies. Its flower produces the scent of rotting meat. While not an attractive smell to us, to flies that are looking for rotting meat to lay their egg in, it must seem heavenly. They arrive at the flower and walk around its surface looking for meat all the while picking up pollen. When they do not find a suitable spot to lay their eggs, they fly off to find some rotting meat only to be misled again by another *Rafflesia*. Now while looking for that elusive rotting meat they transfer pollen to the new flower and pick up more pollen before moving on.

The bee orchid has a similar approach. It uses its appearance and the production of female bee hormones to lure male bees in. While they fruitlessly attempt to mate with the orchid flower, pollen is deposited on their head. They fly off, frustrated I am sure, only to lured back to mate with another false female and pollination is achieved.

While the previous examples make it seem like the insects are getting the short end of the stick, so to speak, co-evolution works both ways. Many plants produced secondary metabolic compounds that help prevent organisms from eating them. The milkweed family, for example, produces group of cardiac glycosides in their latex that should protect the plant from most grazers. However, the caterpillars of the monarch butterfly and milkweed bugs feed on milkweed plants without suffering any ill effects (Figure 2-45). To add insult to injury, they sequester the glycosides rendering the insects noxious to predators.



Figure 2-45. Milkweed bug (*Oncopeltus*) feeding on sandhill milkweed (*Asclepias hum strata*). (Harvey, 2023 CC-BY-NC)

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2.5: End of Chapter Review

In this lesson we have discussed how taxonomy and nomenclature allow us to categorize and identify different plants species.

- Covers plant taxonomy, naming, and the taxonomic hierarchy.
- Discusses the evolution of plants from aquatic to terrestrial environments.
- Explain adaptations like vascular tissue, seeds, and flowers that facilitated transition to land.
- Introduces alternation of generations in plant life cycles.
- Covers diversity of major plant groups:
  - Nonvascular plants (bryophytes)
  - Seedless vascular plants (pteridophytes)
  - Seeded vascular plants: gymnosperms and angiosperms.
- Outlines characteristics of basal angiosperms, magnoliids, monocots and eudicots
- Provides examples of plant adaptations like insect pollination (co-evolution)

Key Terms

- Alternation of Generations
- Angiosperms
- Binomial nomenclature
- Bryophytes
- Co-evolution
- Eudicots
- Flowers
- Gametophyte
- Gymnosperm
- Monocots
- Phloem
- Pteridophytes
- Seed
- Sporophyte
- Taxonomy
- Vascular tissue
- Xylem

Self-Review

1. What is the purpose of taxonomy and binomial nomenclature in biology?
2. What is alternation of generations and how does it differ between nonvascular and vascular plants?
3. How did the evolution of vascular tissue, seeds, and flowers facilitate the transition of plants to land?
4. What are three adaptations that allowed plants to survive on land?
5. What are the main groups of bryophytes?
6. How do roots and leaves of seedless vascular plants differ from those of nonvascular plants?
7. What are heterosporous plants and how did they facilitate plant evolution?
8. What are four key adaptations of seeded plants?
9. What are the four main groups of living gymnosperms?
10. How do pollen and seeds differ in gymnosperms versus angiosperms?
11. What are three features of basal angiosperms?
12. What are magnoliids and what traits define this group?
13. What are five characteristics that distinguish monocots from other angiosperms?
14. How can you distinguish between monocots and eudicots?
15. Provide one example of co-evolution between flowers and pollinators.

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3: PLANT STRUCTURE



Plants are living organisms composed of cells that create the structural components of the plant. The morphology (physical form) that the structure takes dictates its function. In this chapter we will look at the hierarchy of life and how plant structure follows this hierarchy from cells to organisms. Image above is of a thistle, *Centaurea nigra* (Black Knapweed) (Photo: Stephanie Harvey. 2024. CC-BY-NC). As a member of the Family Asteraceae, this plant demonstrates that a flower-like structure can instead be a collection of smaller flowers. Each of the small purple structures within the "bud" is a individual flower. As a collective, they are more attractive to pollinators than they would be as single small flowers.

3.1: Hierarchy of Life

3.2: Plant Cells

3.3: Plant Tissues

3.4: Vegetative Organs

3.4.1: Roots

3.4.2: Stems

3.4.3: Leaves

3.5: Reproductive Organs

3.5.1: Flowers

3.5.2: Fruits

3.5.3: Seeds

3.6: End of Chapter Review

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3.1: Hierarchy of Life

Plants are living organisms composed of cells that create the structural components of the plant. The morphology (physical form) that the structure takes dictates its function. In this chapter we will look at the hierarchy of life and how plant structure follows this hierarchy from cells to organisms.

With over 328,000 species in the Kingdom Plantae, great diversity of form exists. Even if we restrict our attention to the angiosperms, the variation is staggering. The smallest angiosperm belongs to the genus *Wolffia* (commonly called watermeal). They are under 2 millimeters in length (height of two stacked dimes). In comparison, *Eucalyptus regnans* (mountain ash) is the tallest angiosperm, towering up to 100 m (330 feet). Yet within these differences, there is a common hierarchy found in all living organisms.

In Chapter 2, we discuss the taxonomic hierarchy of plants. A compositional hierarchy can also be applied to plants and all other multicellular organisms (Figure 3-1). This hierarchy is commonly represented as a nested structure, with smaller units forming larger units, and ultimately leading to the entire organism. If we were to look for the smallest building blocks of an organism, chemists would surely argue that it would begin at the atomic level. In fact, atoms are the building blocks for all molecules including organic molecules. In turn organic molecules are the constructional units for the structure and functionality of organelles and then cells themselves.

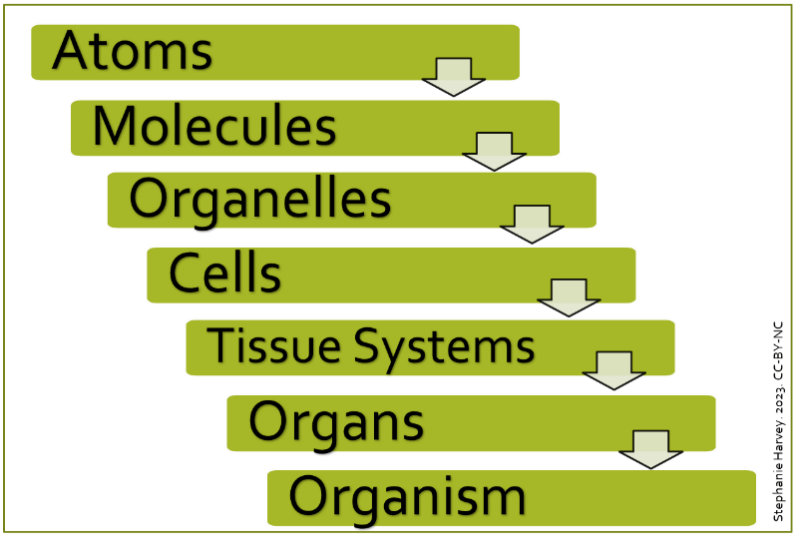


Figure 3-1. Across the highly varied multicellular organisms of the biosphere there is a common hierarchy (Harvey. 2023 CC-BY-NC).

Cells are the fundamental units of life. They are the smallest and most basic structural and functional entities of organisms. Single-celled organisms such as protists and bacteria exist but multicellular organisms have higher levels of organization. In multicellular organisms, groups of cells form tissues. These tissues may consist of only a single cell type (simple tissues) or multiple cell types (complex tissues). The cells of the tissue work together to perform specific functions and the tissues serve as building blocks for organs. Organs are structures composed of multiple tissues that work together to perform specific functions within an organism. Examples of organs in humans would include the heart, lungs, liver, and brain. Organ systems are groups of organs that work together to perform integrated functions and maintain homeostasis within an organism. Common organ systems in humans include the circulatory system, respiratory system, digestive system, nervous system, and reproductive system.

Finally, we have the organism. An organism is a complete, individual living entity composed of multiple organ systems working together. It is the highest level of the hierarchy within an individual. As mentioned, organisms can range from simple, single-celled organisms to complex multicellular organisms.

The hierarchy beyond the organism level with populations - a group of individuals of the same species that live in the same geographic area and have the potential to interbreed. Populations form the basis for studying ecology, evolution, and genetics. Next is the biological community which refers to the interaction and coexistence of populations of distinct species within

a particular habitat or ecosystem. It involves the study of species diversity, interactions, and ecological relationships. The community along with the physical environment within a specific area constitutes the ecosystem. For the purposes of this chapter, we will look at organelles within plant cells to organism itself.

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3.2: Plant Cells

A Generic Plant Cell

A plant cell is a eukaryotic cell (a cell with a nucleus) that is the basic structural and functional unit of a plant. Plants share many characteristics with other eukaryotic cells such as the cells of animals and fungi. There are differences as well. The simplified drawing of a plant cell (Figure 3-2) will guide us as we explore the fundamental organelles of a plant cell.

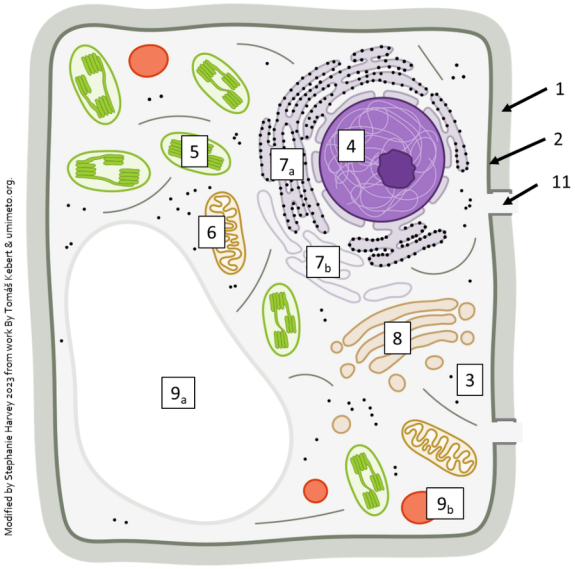


Figure 3-2. Simplified drawing of a plant cell (modified by Harvey 2023).

1. **Cell Wall**: Plant cells have a rigid cell wall surrounding the cell membrane. Fungi also have cell walls but while the fungi walls are primarily composed of chitin, the plant cell wall is composed mainly of cellulose. In both cases the walls provide strength, support, and protection for the cells.

2. **Cell Membrane**: All cells have a cell membrane, also known as the plasma membrane. It is a thin, flexible layer (a phospholipid bilayer) that encloses the contents of the cell. It controls the movement of substances into and out of the cell and plays a crucial role in maintaining cell homeostasis.

3. **Cytoplasm**: The cytoplasm is the gel-like fluid that fills the cell. It contains various organelles, including the nucleus, as well as cytosol, which consists of water, enzymes, and other molecules necessary for cell metabolism. All cells, both prokaryotic (without a nuclei) and eukaryotic cells have this.

4. **Nucleus**: The nucleus, found in all eukaryotic cells, is a membrane-bound organelle that houses the cell's genetic material, DNA. It acts as the control center of the cell, regulating gene expression and coordinating cellular activities. The nucleus is typically located near the center of the cell and is surrounded by a nuclear envelope, which separates it from the cytoplasm. The nucleolus is often visible with the aid of a light microscope. It is a dense structure within the nucleus that is responsible for ribosomal RNA synthesis.

5. **Chloroplasts**: Some plant cells contain chloroplasts, which are organelles responsible for photosynthesis. Chloroplasts contain chlorophyll, a pigment that captures sunlight and converts it into chemical energy. They have a double membrane and contain a 3rd membrane called the thylakoid membrane. The thylakoid is where chlorophylls are found and is where the light-dependent reactions of photosynthesis occur. Structures similar to chloroplast (called plastids) are found in non-photosynthetic plant cells.

6. **Mitochondria**: Mitochondria are organelles responsible for cellular respiration, where energy is generated in the form of ATP. Plant cells, like animal cells, have mitochondria to meet their energy needs. Mitochondria have a double membrane and contain their own DNA. Even plant cells with chloroplast have mitochondria.

7. **Endoplasmic Reticulum** (ER): The endoplasmic reticulum is a network of membranous tubules and sacs involved in protein synthesis, lipid metabolism, and the transport of molecules within the cell. The rough endoplasmic reticulum (RER) (7a) is studded with ribosomes and involved in protein synthesis, while the smooth endoplasmic reticulum (SER) (7b) lacks ribosomes and plays a role in lipid metabolism.

8. **Golgi Apparatus**: The Golgi apparatus is responsible for modifying, sorting, and packaging proteins and lipids for transport to their final destinations within or outside the cell. It consists of a stack of flattened, membrane-bound sacs called cisternae. While animal cells typically have one, plants often have many and they are sometimes referred to as dictosomes.

9. **Vacuole**: Plant cells typically have a large central vacuole (9a) that occupies a significant portion of the cell. The vacuole stores water, nutrients, ions, and waste products. It also helps maintain turgor pressure, which contributes to cell rigidity and support. Smaller vacuoles (vesicles; 9b) also have a single membrane and are important for moving material throughout the cell.

10. **Plasmodesmata**: Plasmodesmata are small channels that connect adjacent plant cells. The plasma membrane continues through the plasmodesmata and into the next cell, allowing for the exchange of materials, such as nutrients and signaling molecules. They enable communication and transport between cells within a plant tissue. There is some regulation as to what moves between cells – it is not just an open hallway.

Not labeled in the image are the ribosome, seen here as dots in the cytoplasm and on the RER. These structures made of protein and ribosomal RNA are part of the “factory” that assembles new proteins.

Of these structures, the chloroplast, central vacuole and plasmodesmata are unique to plants. Both plants and fungi have cell walls. The remaining structures are common to all eukaryotic cells.

These are some of the key structures found in a typical plant cell. While there may be variations in the structure and composition of plant cells depending on the specific cell type and function, these structures provide the foundation for plant growth, metabolism, and reproduction. Prokaryotic cells, simpler in structure have plasma membranes, cell walls (different type from that of eukaroytic cells), cytoplasms, DNA (not in a nucleus) and ribosomes. They completely lack internal membrane-structures.

Types of Plant Cells

All cells start as unspecialized units. They can specialize (differentiate) as they mature to perform specific tasks for the organism. This is often referred to as division of labor. There are three primary types of cells found in plants: **parenchyma**, **collenchyma,** and **sclerenchyma**.

All cells start their lives as parenchyma (Figure 3-3). They have thin, primary cell walls and are living at maturity. The primary cell wall is the flexible layer formed while the cell is growing, and many cells never have more than a primary wall. Due to its thinness, materials can more easily move in and out of parenchyma cells. This is needed in metabolically active cells.

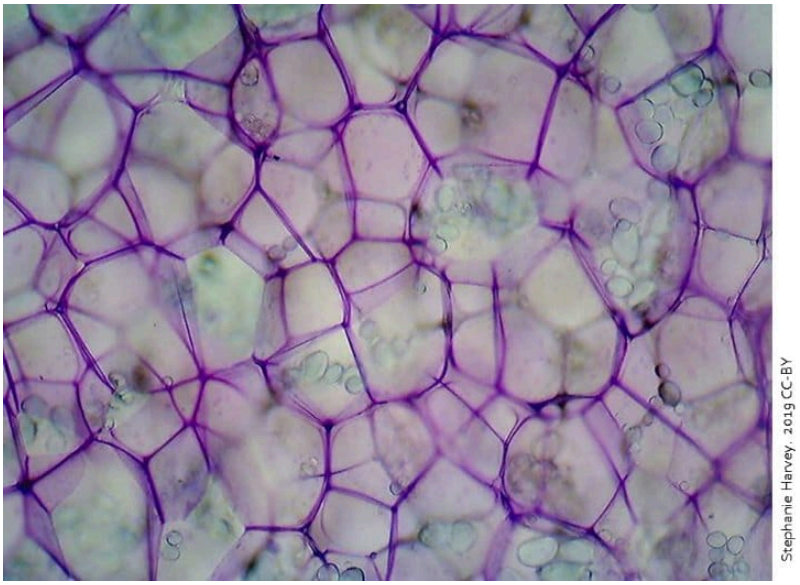


Figure 3-3. Cells from potato tuber stain to show cell walls. The round shapes in the image are starch grains (Harvey 2019 CC-BY-NC)

Most of the metabolic functions of a plant are carried out by parenchyma cells. These cells can specialize to provide specific functions: water storage, carbohydrate storage, photosynthesis, or chemical production. New, undifferentiated cells would also be considered parenchyma. The first photomicrograph (Figure 3-3) is from potato tuber – note the evenly thin walls.

Collenchyma cells live at maturity and only have a primary cell wall (Figure 3-4). But, unlike parenchyma cells, these have thick walls, often unevenly in deposition. The primary function for the plant is to provide support, particularly in growing regions of the plant. Collections of these cells make up the resilient strands in the stalks of celery. In Figure 3-4 the white (unstained) areas are the inside of the cell, and the darker material is cell wall. Note that the thickening primarily happens where three or more cells touch.

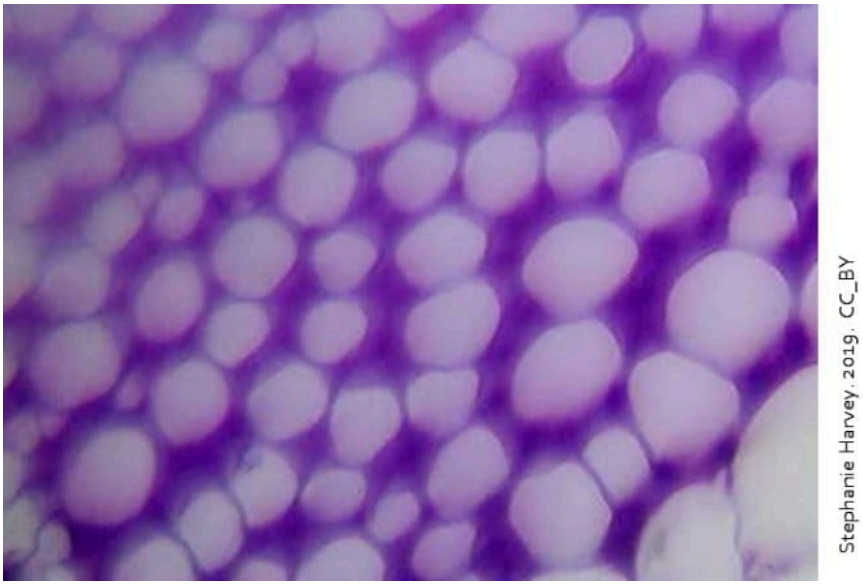


Figure 3-4. Collenchyma cells have unevenly thick, primary walls for added strength to plant structures (Harvey. 2019 CC-BY-NC).

As Sclerenchyma cells develop from undifferentiated cells, a thick, secondary wall is produced (Figure 3-5). Additionally, a chemical called lignin is added to the cell wall components. This produces an extraordinarily strong cell wall that can be used for structural support.

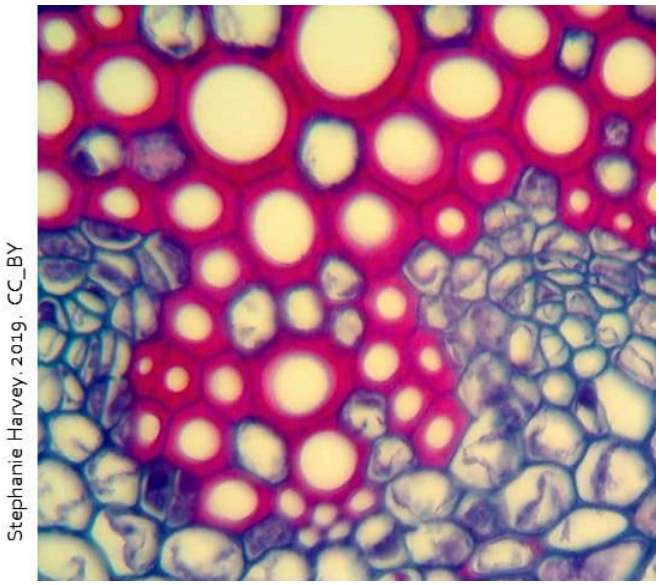


Figure 3-5. The sclerenchyma cells of the xylem are stain red. Note the even thickness of the walls. (Harvey, 2019 CC-BY-NC).

Unlike collenchyma, mature sclerenchyma cells are dead at maturity, and the thick secondary wall can make up to 90% of the cell volume. There are two types of sclerenchyma cells commonly found in plants. Fibers are long, slender cells that are typically found in bundles where they add strength. Sclereids (Figure 3-6) in contrast are more cuboidal and participate in protection and often form hard durable layers such as the woody “stones” around the seeds of peaches and cherries.

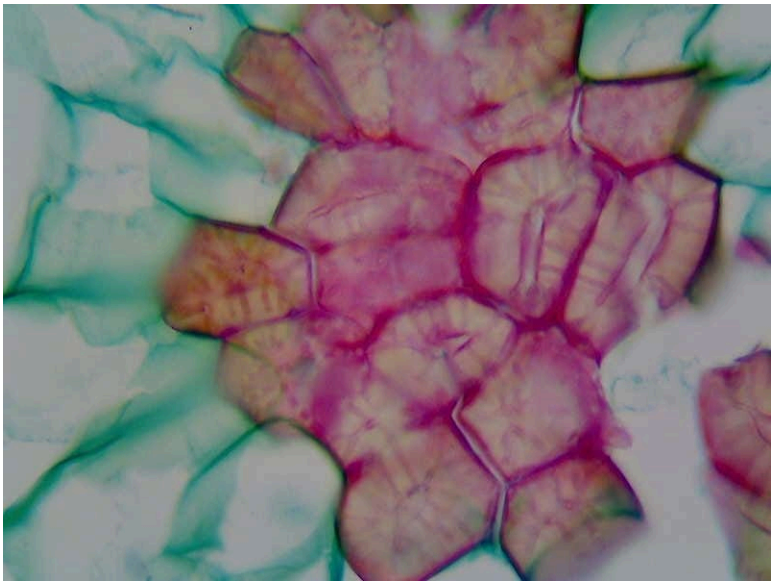


Figure 3-6. Sclereids from pear fruit tissues. The clusters of sclereids create the gritty texture (Harvey, 2021 CC-BY-NC).

Some specialized sclerenchyma cells play a vital role in water transport in vascular plants. The transport cells of the xylem are sclerenchyma cells. The photomicrograph Figure 3-5 shows the transport xylem cells. The cell walls show up red due to a stain that interacts with the lignin. The thickened secondary walls allow the structural support needed to prevent collapse and the lack of cytoplasm (since the cells are dead) allow for bulk flow of water.

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3.3: Plant Tissues

In the broadest sense there are two types of plant tissues: meristematic tissues and permanent tissues. Meristematic tissues are composed of cells whose main function is to divide and produce new cells (Figure 3-7). This is critical to growth since this is how cell numbers increase. Meristematic tissues are found as apical meristems at the tips of roots and stems, intercalary meristems at the bases of grass leaves and as vascular cambium of woody species.

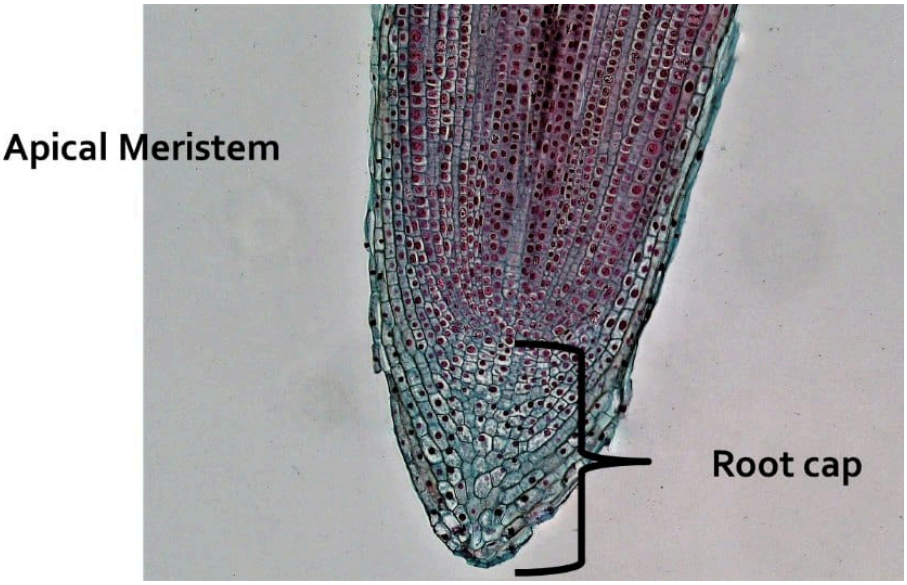


Figure 3-7. Onion root tip showing apical meristem and the root cap. (public domain, 2019)

When the cells of meristematic tissue divide, one daughter cell typically remains as an undifferentiated cell of the meristem, while the other completes its growth and differentiation and becomes part of the permanent tissue.

Permanent tissues make up the bulk of the plant. These tissues are composed of cells that have completed their growth and any differentiation that might need to take place. These tissues can be divided into three types of tissue systems: conductive, ground, and dermal tissues.

Conductive Tissue System

The conductive (or vascular) tissues consist of parenchyma and sclerenchyma cells. The tissue functions in both support and the transport of materials within the plants (Figure 3-8). Vascular tissue is typically found as vascular bundles in all organs of the plant. In this photomicrograph the vascular bundles of a monocot stem are clearly visible. The vascular bundles contain both xylem and phloem.

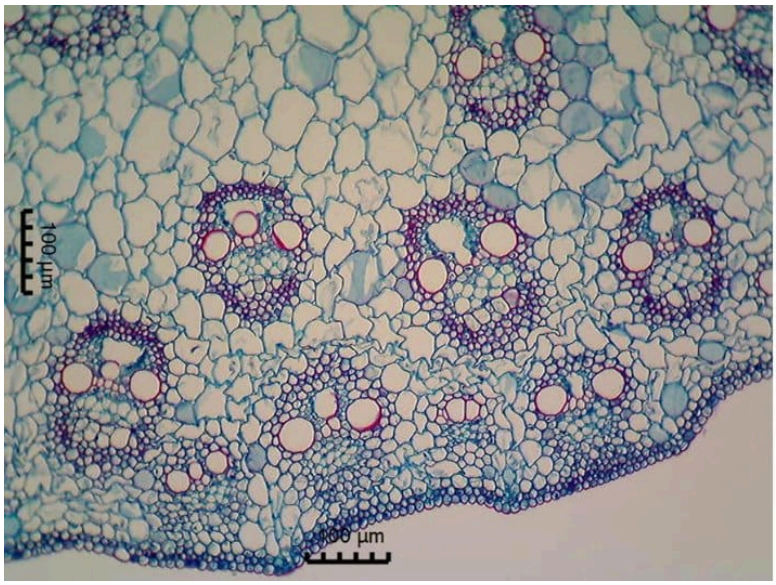


Figure 3-8. The vascular bundles of a monocot stem represent the conductive tissue system (Harvey, 2019 CC-BY-NC).

The xylem tissue transports water and dissolved nutrients from the roots to the shoots. The path is unidirectional and is powered by the evaporation of water from the surface of the plant (leaves and stems). The tracheary element are the transport cells of the xylem. They are sclerenchyma cells that dead at maturity. As such water moves through these cells unencumbered by cytoplasm or cell membranes. The secondary walls provide enough strength that the negative tension created via evaporation will not collapse the cells. Negative tension is a pulling force, like when you suck a milkshake through a straw. If the straw is too weak it collapses.

There are parenchyma cells and fibers also within the xylem tissue (Figure 3-9). The fibers provide additional support to the vascular bundles while the parenchyma act as a water reserve and helps with some lateral movement of water.

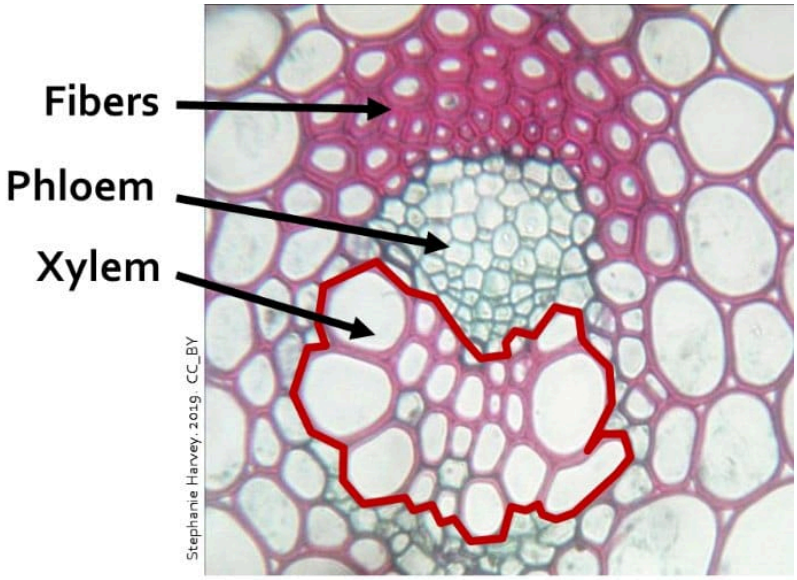


Figure 3-9. A cap of fibers for support is located at the top of the vascular bundle. Below the cap is the thin-walled cells of the phloem. At the bottom of the vascular bundle are the large transport cells of the xylem tissue (Harvey, 2019 CC-BY-NC).

Phloem tissues transport photosynthates and other dissolved substances throughout the plant. Unlike with the xylem, the flow of the phloem sap is not unidirectional. The transport of carbohydrates moves from source to sink but the direction can change depending on where the carbohydrates are coming from and to where they are going. For example, in the spring carbohydrates may be mobilized from root to shoots as new growth is initiated. Later when mature leaves photosynthesis, carbohydrates are moved from leaves to roots.

The transport cells of the phloem are living at maturity but are reduced. They have lost most of their organelle including the

ER, nucleus, and mitochondria. While it is a good adaptation for making the bulk flow of carbohydrates more efficient, it creates significant problems for the transport cells. They lack the infrastructure necessary for self-maintenance.

Companion cells are small parenchyma cells adjacent to the transport cells. They carry out many of the metabolic processes needed to support the transport cells. In this photomicrograph of a vascular bundle from the stem of a eudicot, the phloem tissue with both transport and companion cells is outlined. Also note that there is a cap of fibers for support to the outside of the phloem tissue.

Dermal Tissue System

Plants must maintain internal conditions in a rather hostile environment. Desiccation, infection, and predation can decrease productivity and lead to death. The dermal tissue is the first line of defense for the plant. The dermal tissue exhibits many of the adaptations needed to survive in the terrestrial ecosystem: wax and cuticles layers, epidermal cells, guard cells, and other specializations.

In this photomicrograph (Figure 3-10) from a cross section of a monocot leaf, the epidermal cells that cover the top and bottom of the leaf can be seen. The pinkish layer to the outside of the epidermal layers is the cuticle layer. The cuticle layer is a non-cellular layer excreted by the epidermal cells. It is extremely hydrophobic and prevents both water loss and infiltration of the leaf cells by pathogens. In the lower epidermis, guard cells can be seen flanking a stomatal pore. These pores are necessary for gas exchange since the cuticle not only stops water loss but also diffusion of gases into the cells of the leaf. The guard cell can close the pore when water loss is too costly.

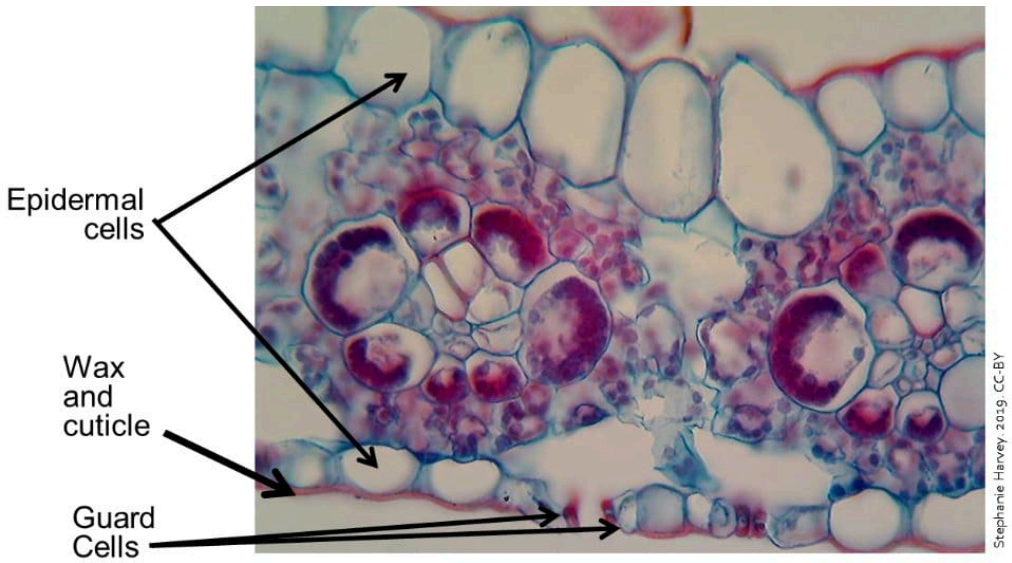


Figure 3-10. A cross section of a monocot leaf shows both the upper and lower epidermis (Harvey 2019 CC-BY-NC).

Some of the cells of the epidermis are specialized for defense of the plant (Figure 3-11). Diverse types of trichomes can extend from the dermal surface. Some are single cells while others are composed of multiple cells. Trichomes are often hair-like structures that come in a variety of shapes and sizes. They often deter grazing by insects and other animal – fuzzy food is not pleasant to consume. For a small insect, walking on a trichome covered stem it tantamount to marching through a dense forest; it expends energy and limits foraging times. Trichomes can also help reduce water loss and minimize solar damage.



Figure 3-11. Often hair-like structures, trichomes some in a variety of shapes and sizes (first two images) with some specialized as glandular trichomes that produce/secrete compounds (last image). (Harvey CC-BY-NC, Harvey CC-BY-NC, and Stojanovic CC-BY-SA).

Prickles are hard, sharp outgrowths of the epidermis people often mistake for thorns. This armor helps protect the plant from larger herbivores. Some specialized trichomes produce and secrete compound; they are called glandular trichomes. The chemicals they produce can have antibacterial, antifungal, and anti-herbivory properties. In Figure 3-11, the first photograph shows a closeup of short, ridged trichomes while the middle photograph shows dense coverage of the epidermis of a wooly mullein with long, soft trichomes. The third image is a photomicrograph showing glandular trichomes on the leaf of *Salvia*.

Ground Tissue System

Our last tissue system is the fundamental or ground tissue system. The best way to describe ground tissue is to say what it is not. It is not dermal tissue, vascular tissue, or meristematic tissue. However, this description understates the importance of the ground tissue system.

In herbaceous plants it makes up the bulk of the plant's mass. (In wood plants, the bulk belongs to the conductive tissue system.) The ground tissue system is comprised mostly of parenchyma cells and carry out numerous functions for the plant. The function is highly variable depending on the organ within which the system is found. In non-photosynthetic organs it is responsible for storage of both carbohydrates and water. In photosynthetic organs, it is the ground tissue system that is responsible for photosynthetic activity. In the photomicrograph of the monocot leaf (Figure 3-12), the tissue sandwiched between the epidermal layers and to the outside of the vascular bundles, is ground tissue system. This fundamental tissue is specifically called mesophyll (middle leaf).

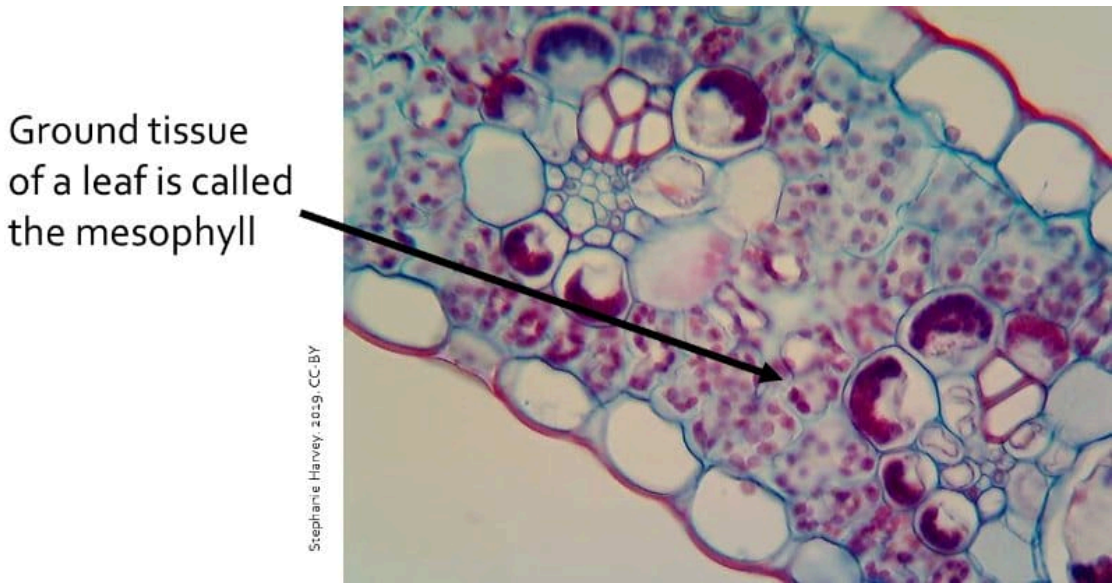


Figure 3-12. This cross section of a monocot leaf shows the mesophyll cells of the ground tissue. They are packed with chloroplasts (stained red) (Harvey, 2019 CC-BY-NC).

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3.4: VEGETATIVE ORGANS

The tissues systems work in concert to provide higher functions in the form of organs. All plant organs include dermal tissues, vascular tissues, and ground tissues. And even organs that lack meristematic tissues at maturity had them early in their development.

The organs of a plant can be divided into two categories: vegetative and reproductive. The vegetative organs are not part of the reproductive process of the plant and include the roots, stems and leaves. The reproductive organs are flowers, fruits, and seeds. They are all responsible for the reproductive success of the plant. While all plants have vegetative organs, although those may be reduced, the reproductive organs may only appear after a specific signal. This triggering may be due to age, season, nutrient availability, light duration, or light quality. Let start our exploration with the vegetative organs of a plant and specifically the roots.

3.4.1: Roots

3.4.2: Stems

3.4.3: Leaves

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3.4.1: Roots

Roots provide vital functions for the plants. They provide anchorage to keep the plant upright. They counterbalance the shoot weight and thus have a biomass typically equivalent to the aerial shoot.

They are the site of water and nutrient absorption. Water absorption is critical to plant survival. Plants lose water via transpiration and must have a nearly continuous flow into the plants. If intake of water does not meet water loss, the plant will wilt and eventually die. The importance of this function is underscored during seed germination (Figure 3-13). The embryonic root, the radicle, is the first thing to emerge from the seed.

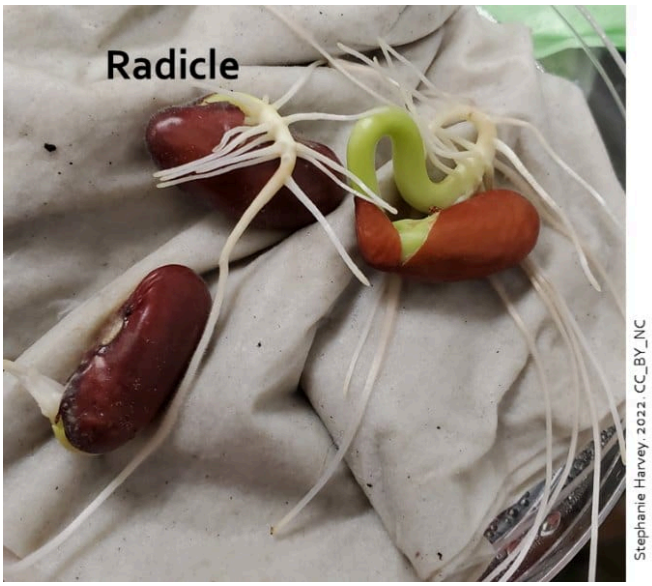


Figure 3-13. The radicle is the first part of the embryo to emerge from the seed (Harvey, 2022 CC-BY-NC).

With the exception of CO_2, the nutrients needed by the plant are absorbed from the soil matrix. This uptake and accumulation of nutrients in root tissue requires an elaborate system of passive and active transport.

Roots can also function in storage. Storage of high energy molecules underground is important b/c it provides a somewhat secure location for hording of energy because it is more difficult for herbivores to obtain. Root tissues typically store energy in the form of starch, but sugars and proteins are also used.

The features of a root, moving upward from the tip, include the root cap, root apical meristem, region of elongation and region of maturation (Figure 3-14). The root cap is a loose aggregation of cells that protect the meristematic tissues. As the root elongates, the tip pushes through the soil. This could damage the delicate meristem, so the root cap cells take the damage and are shed. The root cap also plays a role in sensing gravity. The root apical meristem is a region of cell division and above that is the region of elongation where cells begin to take on water and elongate. Some differentiation starts to take place. In the region of maturation, cells have differentiated into the three permanent tissues. This is visible by the presence of root hairs – hair-like extensions of some epidermal cells. They dramatically increase the surface area for water absorption. It is above this zone that lateral roots can emerge.

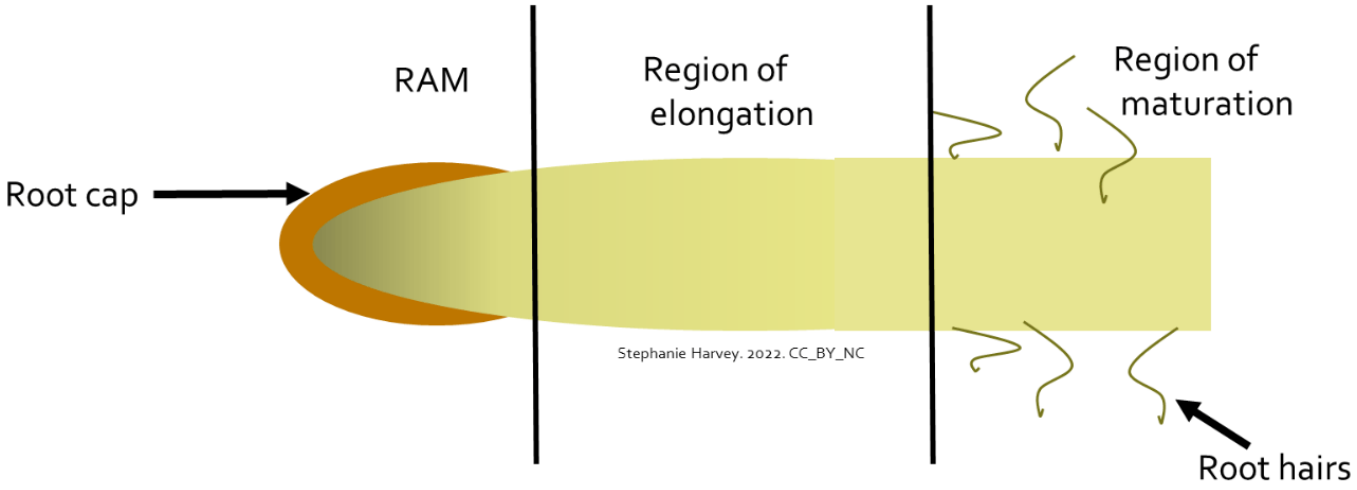


Figure 3-14. The features of root, moving upward from the tip, include root cap, root apical meristem, region of elongation and region of maturation (Harvey, 2022 CC-BY-NC)

A cross-section of a root reveals three distinct areas – epidermis (outmost layer of cells), the cortex (ground tissue – generally parenchyma) and then the stele (Figure 3-15). The stele is a central column of vascular tissue. In Monocots (plants like grasses and lilies) the stele consists of a ring of vascular tissue (phloem and xylem) surrounding a pith area (ground tissue). In Eudicots (plants with broad leaves like maples, cotton), the stele lacks a pith. Instead the xylem is arranged at the center of the stele in a star shaped pattern with the phloem in between the arms.

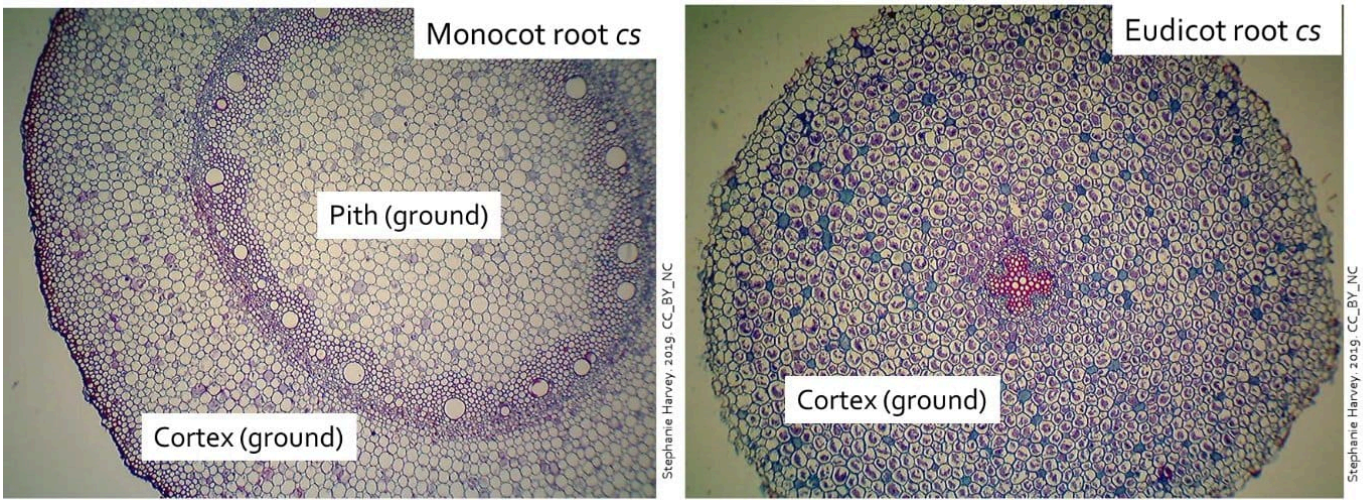


Figure 3-15. A cross-section of a root reveals our three distinct tissues: epidermis, ground tissue, and vascular tissue (Harvey, 2019 CC-BY-NC).

In both cases, just outside of the stele is the endodermis - a single layer of cortex cells running between the cells of this layer is a waterproofing material called the Casparian strip (stains red in these images) (Figure 3-16). The strip prevents water from entering the stele except through the cytoplasm of endodermal cells. This allows for finer control of water/nutrients entering the stele. As you move upward along a root the Casparian strip eventually covers most of the surface of the endodermis and stops water leaking out of the stele. As the root ages, the cortex will be lost, and the endodermis will give rise to a new periderm.

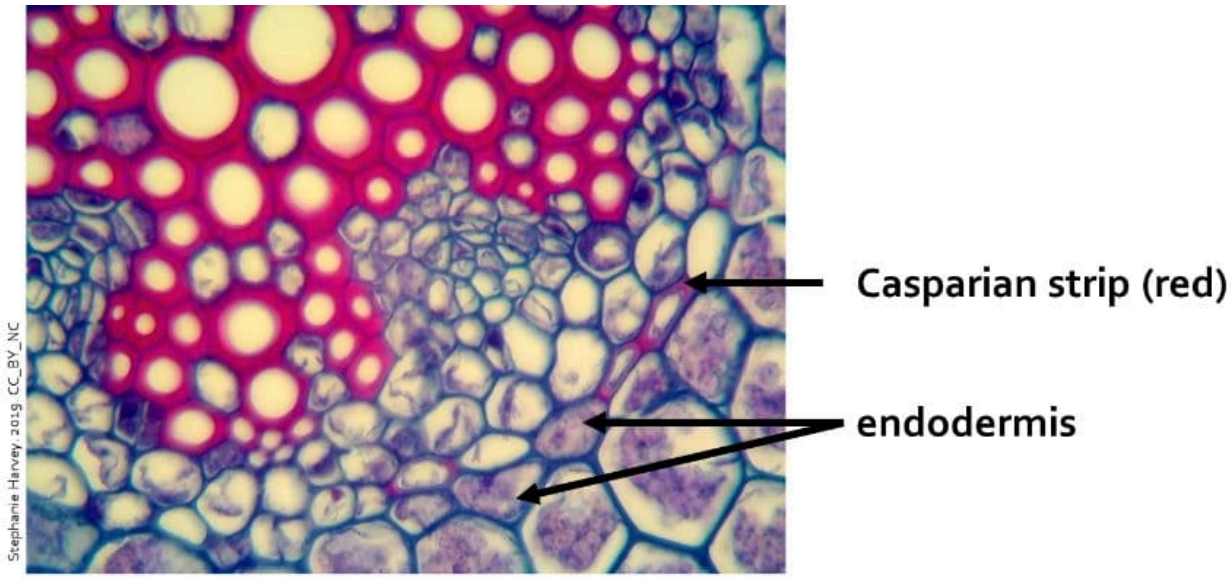


Figure 3-16. The inner most layer of cells of the cortex, the endodermis, has the Casparian strip (cross section of eudicot root) (Harvey, 2019 CC-BY-NC)

"True" roots are derived from those original embryonic roots, the radical (Figure 3-13). Adventitious roots arise from non-root tissue such as stems, leaves and branches. All monocot roots are adventitious since their embryonic root is not maintained post germination. New roots develop from stem tissue.



Figure 3-17. Adventitious roots such as the prop-roots seen here, develop from non-root tissue. (Harvey, 2022 CC-BY-NC).

Adventitious roots take many forms (Figure 3-17). The aerial roots like that of ivy and orchids that provide anchorage and water absorption above the ground. Arboreal roots like that of the Banyan Tree and other prop- or stilt roots help provide support for large branches or tall shoots.

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3.4.2: Stems

Stems are part of the aerial portion of the plant (the shoot) although there are some specialized stems that are underground and are referred to as Rhizomes. The function of the stem is structural in nature (Figure 3-18). It supports the leaves and puts them into positions that are advantageous for photosynthesis. The stems also are important for connecting the roots, where absorption is taking place, to the leaves which are very metabolically active.



Figure 3-18. Stems are the aerial part of the plant that supports the leaves and puts them into positions that area advantageous for photosynthesis (Harvey, 2014).

Stems can also act as storage tissues and may be photosynthetic depending on the species and age of the stem.

Stems are divided into regions called nodes and internodes (Figure 3-19). A node is where leaves (leaf scars – where leaves were attached), branches and axillary buds are attached. In between nodes are the internodes; only a few structures are associated with the internodes – prickles and lenticels. Stems increase in length primarily through internode elongation during early development and all lateral growth is associated with nodes. The pattern of nodes, leaves and branches is initiated in the terminal bud where the apical meristem is protected. The axillary buds also contain meristematic tissue and can give rise to lateral branches and other new growth.

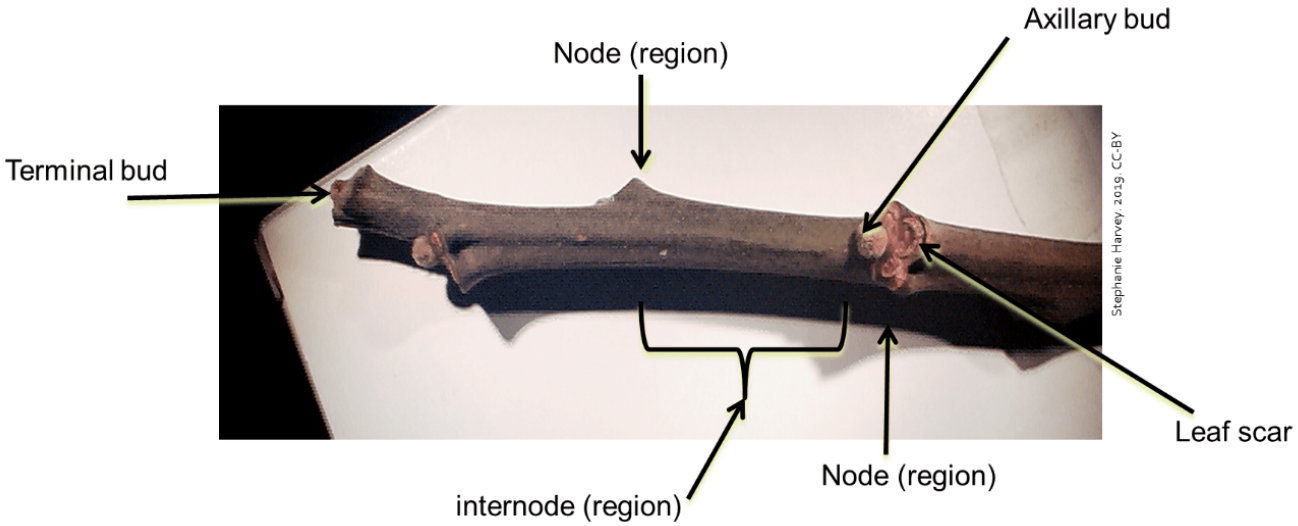


Figure 3-19. The regions along a stem are nodes (where leaves, branches and axillary buds are found) and internodes (regions in between two nodes) (Harvey, 2019).

When a twig (shoot without leaves) breaks dormancy in the spring, the terminal bud opens to allow the new nodes and internodes to expand. The scales of the terminal bud fall away leaving behind small scars. The tightness of the bud scales means the small scars are close together and ring the stem. This creates a mark called a growth ring. (Not to be confused with annual ring of a wood tree trunk). This new growth is often photosynthetic until the epidermis is replaced by bark.

With the loss of the epidermis with its stomata, a new structure is needed to allow gas exchange but limit water loss. Lenticels fulfill this need (Figure 3-20). A lenticel consists of porous tissue consisting of cells with large intercellular spaces in the bark of woody stems. The porous tissue provides a path for gas exchange while slowing the diffusion of water molecules into the atmosphere.

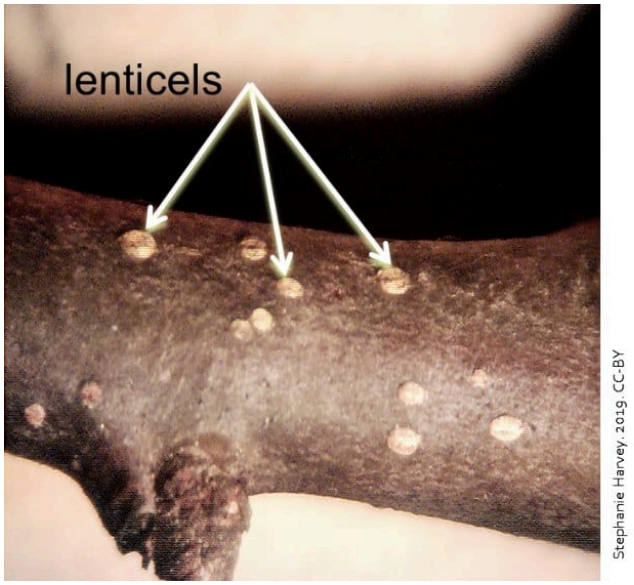


Figure 3-20. Lenticels replace stomata functionally as new bark forms (Harvey, 2019).

The arrangement of tissues in the herbaceous stems of monocots and eudicots differ (Figure 3-21). Monocot (as seen in the first photomicrograph) have vascular bundles that appear scattered through the ground tissue. The bundles themselves have a “face-like” appearance. The vascular bundles of eudicots have a more acorn shape and are capped with fibers. The vascular bundles are located in a ring that separates the ground tissue into two zones – cortex and pith tissue. The vascular bundles of the monocot may at first seem random, but a closer inspection will show they are arranged in a series of arches corresponding to the veins of the leaf bases.

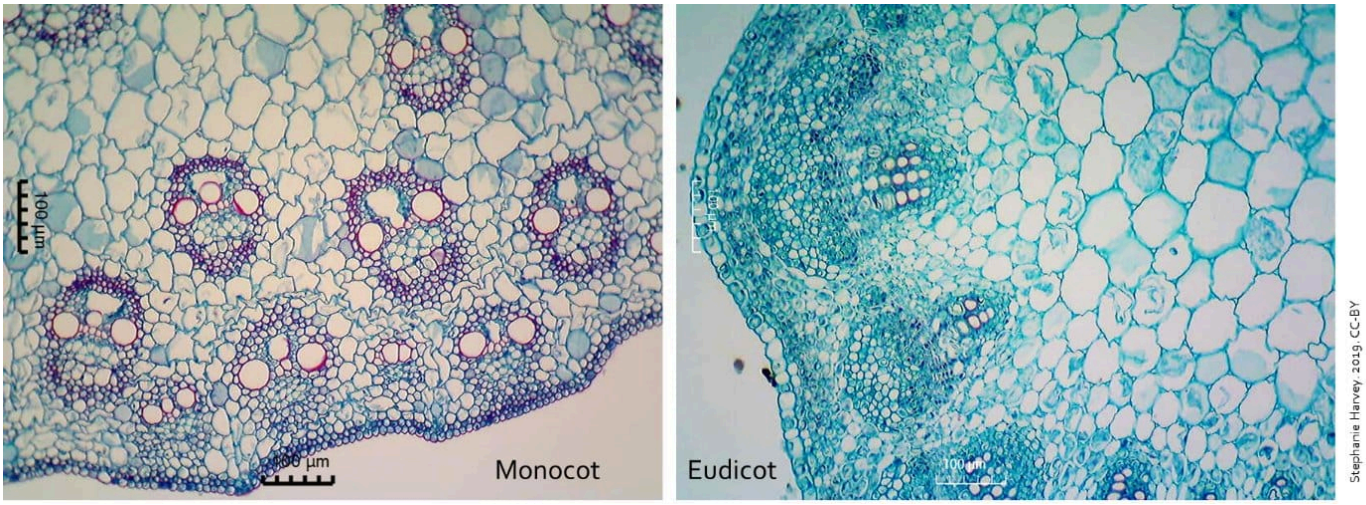


Figure 3-21. Monocots have arcs of vascular bundles spread throughout the ground tissue, while eudicots have vascular bundles in a ring separating the ground tissue into cortex and pith tissue.

Secondary growth occurs in wood stems of some eudicots, magnoliids and basal angiosperms as well as gymnosperm (Figure 3-22). It is conspicuously absent from monocot. It appears secondary growth evolved fairly early in plant history but was lost from the monocot branch. Secondary growth is responsible for the increase in the girth of a plant stem or root. This new growth is created by the vascular cambium (a lateral meristem). A single layer thin, a cambial cell divides, and one cell remains as a meristematic cell with the other differentiates into either 2nd xylem or 2nd phloem. In this way the vascular cambium can be maintained throughout the growth of the plant.

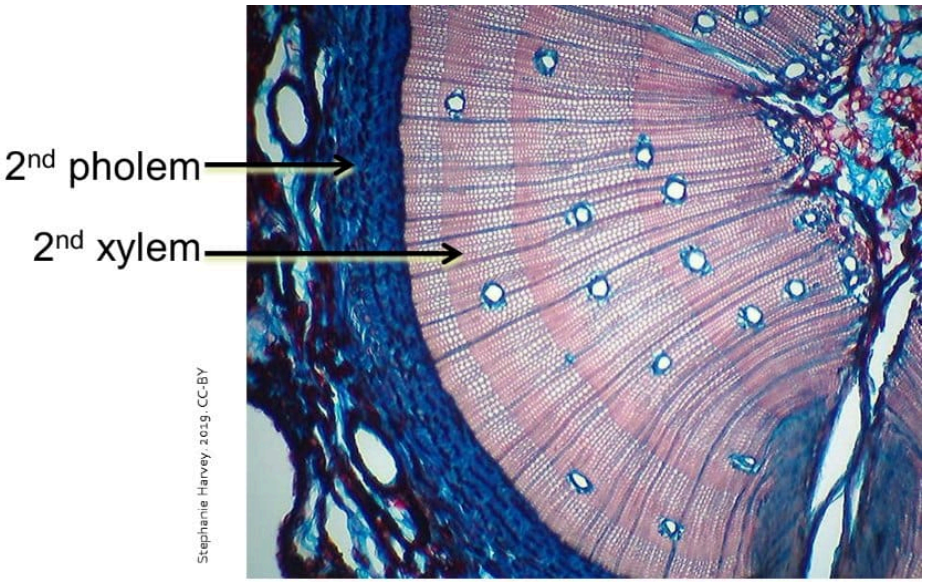


Figure 3-22. The vascular cambium (lateral meristem) adds both 2nd xylem and 2nd phloem. In temperate regions grown rings are easily seen (Harvey, 2019).

In temperate regions where growth slows considerably in the winter, the annual growth rings can easily be seen in the 2nd xylem which continues to accumulate year after year. 2nd phloem is eventually lost with the bark. Thus the “wood” of a tree trunk is 2nd xylem.

There are multiple directions for stem specialization (Figure 3-23). A common one seen in cacti, is that the stems become the primary photosynthetic organ. In cacti, leaves are highly reduced or loss to minimize surface area for water loss. The stem, with a lower surface area to volume ratio, is more able to retain water while providing some surface for light absorption.



Figure 3-23. The green pads of cacti are stems. Both tubers and rhizomes are underground stems for storage and asexual reproduction.

Stems may also play a role in storage. Tubers (such as potatoes) are underground stems (not roots). They have nodes ("eye") while roots lack nodes. Tubers are both storage organs and can be used for asexual reproduction. Tubers separated from the parent plant will sprout and produce new plants. The advantage in using tubers as storage organs is that their underground nature makes them less available to herbivores.

Rhizomes (like the bamboo rhizome seen in Figure 3-23)) are underground stems that give rise to above ground leaves and can be used to propagate a plant asexually. With the stem below ground it is, like the tuber, less available to predators. Additionally, it is less susceptible to the cold of winter. The above ground can die back, and the rhizome will produce new leaves above ground when conditions improve.

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3.4.3: Leaves

The other vegetative organ of the shoot is the leaf. The leaf, for most plants, is the sight of photosynthesis – the conversion of light energy to chemical energy. The leaf is a good example of how form and function interact.



Figure 3-24. Leaves consist of a lamina (blade) and petiole (stem-like supportive structure) (Harvey, 2019).

The structure of a eudicot leaf is simple: There is the leaf blade or lamina and the petiole (Figure 3-24).

The lamina is typically a flatten sheet of tissue that is the primary site of photosynthesis. It contains the veins that supply the leaf with water and nutrient and that carry away the products of photosynthesis – sugars.

The petiole is the stem-like portion of the leaf that attaches the leaf to the stem at a node. Not all leaves have petioles, in some the blades attach directly to the stem - these are referred to as sessile leaves.

Leaves exhibit determinate growth. That is, they grow to a specified size and stop. A maple leaf rapidly grows to its mature size and then stays that size until senescence (death) and abscission (dropping) from the tree.

The blade is typically thin to maintain a high surface to volume ratio. Because large surfaces for light absorption also present large surfaces for water loss, Plants have features that help them minimize water loss and these are associated with the upper and lower epidermis. Additionally, the ratio tends to shift in favor of volume in dry environments; plants that are adapted to drier climatic conditions tend to have thicker/fleshier leaves.

We discussed the features of the epidermis during the segment on the dermis tissue and will just mention them briefly here. The epidermis secretes the cuticle layer, an extremely hydrophobic, non-cellular covering, which prevents both water loss and infiltration of the leaf cells by pathogens. Guard cells in the epidermis regulate stomatal pore size to minimize water loss during gas exchange. Trichomes reflect the sun and help slow diffusion of water out of the leaf.



Figure 3-25. Leaves have features that help them minimize water loss: cuticle, trichomes and stomata with guard cells (Harvey, 2014;2019).

The internal organization of a leaf is fairly simple (Figure 3-26). Since monocot leaves have parallel veins a cross section through the leaf reveals many vascular bundles as rings spaced at regular intervals in the section as seen in this photomicrograph. The outermost layers are the upper and lower epidermis and sandwiched in between are the mesophyll and vascular bundles. The mesophyll is the photosynthetic tissue of the leaf.

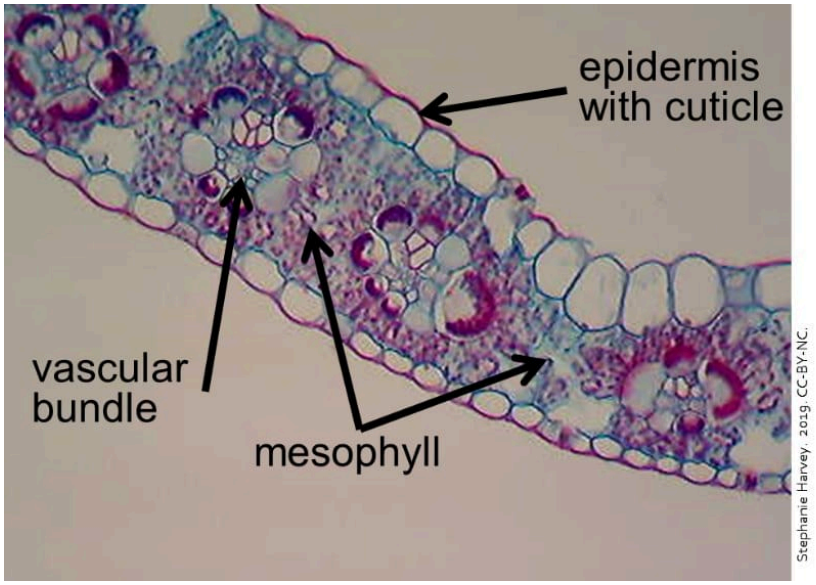


Figure 3-26. Monocot leaves have parallel veins and only general mesophyll (Harvey 2019).

In Eudicots with net-like venation, the vascular bundles are more difficult to since they don't run perpendicular to the cut of the cross section (Figure 3-27). In the photomicrograph seen here, a small section of a bundle is visible, but not as a ring. Like the monocot, there is an upper and lower epidermis but since eudicot leaves are more likely to have a shaded side and a sun side, most of the stomatal complexes are located in the lower epidermis (shade side). This helps reduce water loss from the leaf.

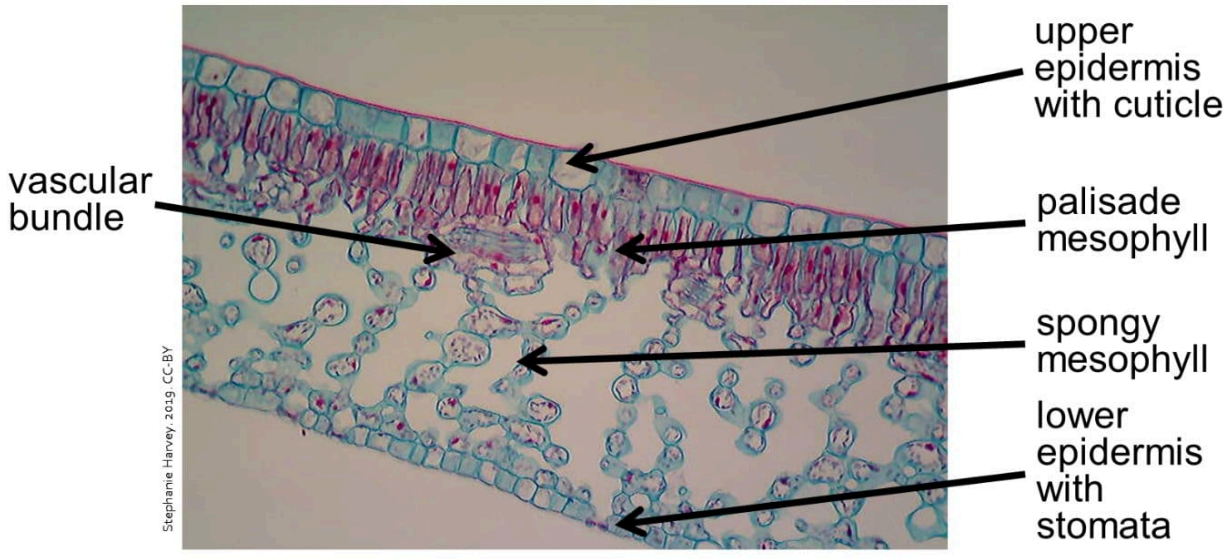


Figure 3-27. Eudicot leaves have net-like veins and often two types of mesophylls: palisade and spongy (Harvey, 2019).

Another difference is that there are two forms of mesophyll. The palisade mesophyll is located just below the upper epidermis and consists of column shaped cell pack together. Below the palisade layer is the spongy mesophyll made up of more spherical shaped cells with significant air spaces around them. Both layers are photosynthetic, with the palisade mesophyll capturing more light than the spongy due to its location and tightly pack nature. The air spaces associated with the spongy mesophyll help facilitate gas exchange.

Throughout the vascular plants and specifically the angiosperms, there is significant diversity in leaf morphology. From species to species the leaf shape, size, attachment, arrangement, pigments, and duration can vary significantly. For example, the leaves of bellwort are sessile having lost their petiole. Additional structure developed as well. Within some families it is common to have small leaflike structures at the base of the petioles. These leaf-like structures are called stipules.

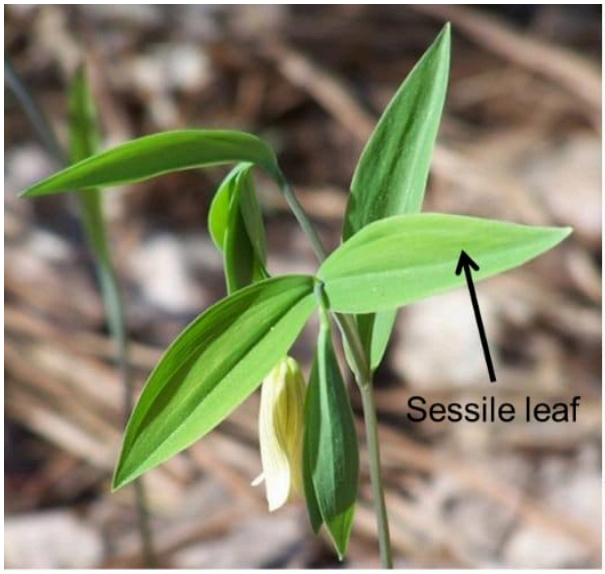


Figure 3-28. Some include loss of a structure, such as the petiole with sessile leaves (Harvey, 2019).

Leaves can be classified as simple or compound. Simple leaves consist of a single lamina while compound leaves are composed of multiple leaflets. Since the leaflets can vary in size it is sometimes difficult to determine if the organ in question is a leaf or a leaflet of a compound leaf. One way to distinguish the two is to look for the axillary bud. At the base of the petiole, where it attaches to the stem there should be an axillary bud. If there is no visible bud (always check several), follow the stem-like structure down until it connects to another stem and look for a bud there. Leaflets will not have associated bud. Additionally, if you are looking at a stem with leaves along it, there should be a terminal bud at the end of the stem.

Compound leaves are described by their arrangement of leaflets (Figure 3-29). Pinnately compound leaves have a central axis to which all the leaflets are attached. Palmately compound leaves extend of a central point on a single petiole. Compound leaves can also be doubly compound where the primary leaflets consist of secondary leaflets.

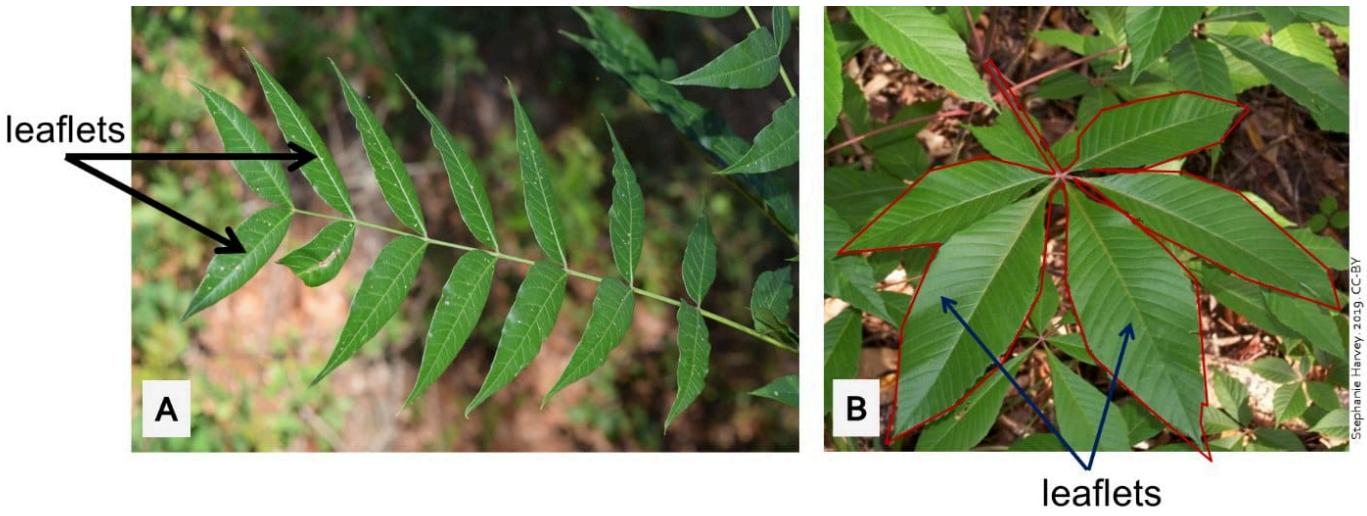


Figure 3-29. Pinnately compound have a central axis to which all the leaflets attach. Palmately compound leaves all come off the same point on the petiole (Harvey, 2019 CC-BY-NC).

Leaves can also be described based on their pattern of venation (Figure 3-30). As mentioned previously, monocot leaves typically have parallel venation but there are exceptions. The eudicot leave may have palmate venation or pinnate venation. As with the use of the terms in compound leaves, pinnate venation means there is a central axis of which secondary vein diverges. Palmate venation is when several veins of about equal size radiate from a single point, typically the base of the lamina.

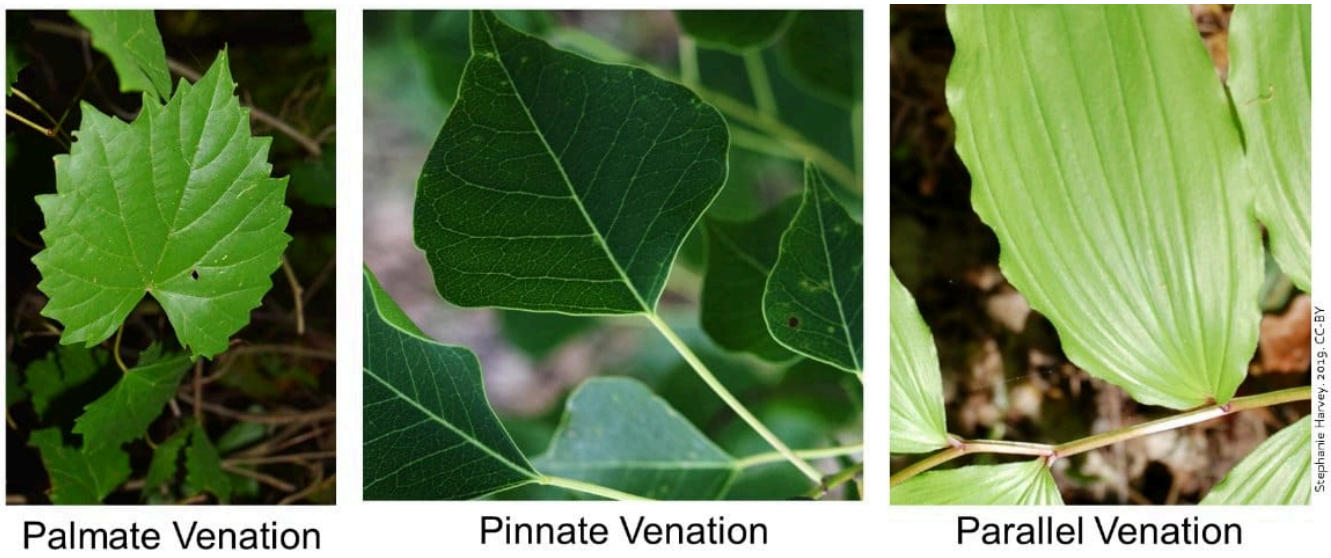


Figure 3-30. Net-like venation is associated with eudicots while parallel venation is associated with monocots but there are exceptions (Harvey, 2019).

Leaves are also arranged along stems in different patterns depending on species (Figure 3-31). The arrangement is referred to as phyllotaxy. The arrangements have evolved to minimize self-shading while maximizing solar exposure. The first thing to observe is how many leaves are present per node. With alternate phyllotaxy, there is a single leaf per node and the position of the leaf alternates from one side of the stem to the other. If there are two leaves per node the phyllotaxy is said to be opposite. The last, whorled, is when more than two leaves are attached to a single node. Whorled phyllotaxy is fairly rare and commonly mistakenly used when internodes don't expand and nodes are tightly packed as with basal rosettes of dandelions.

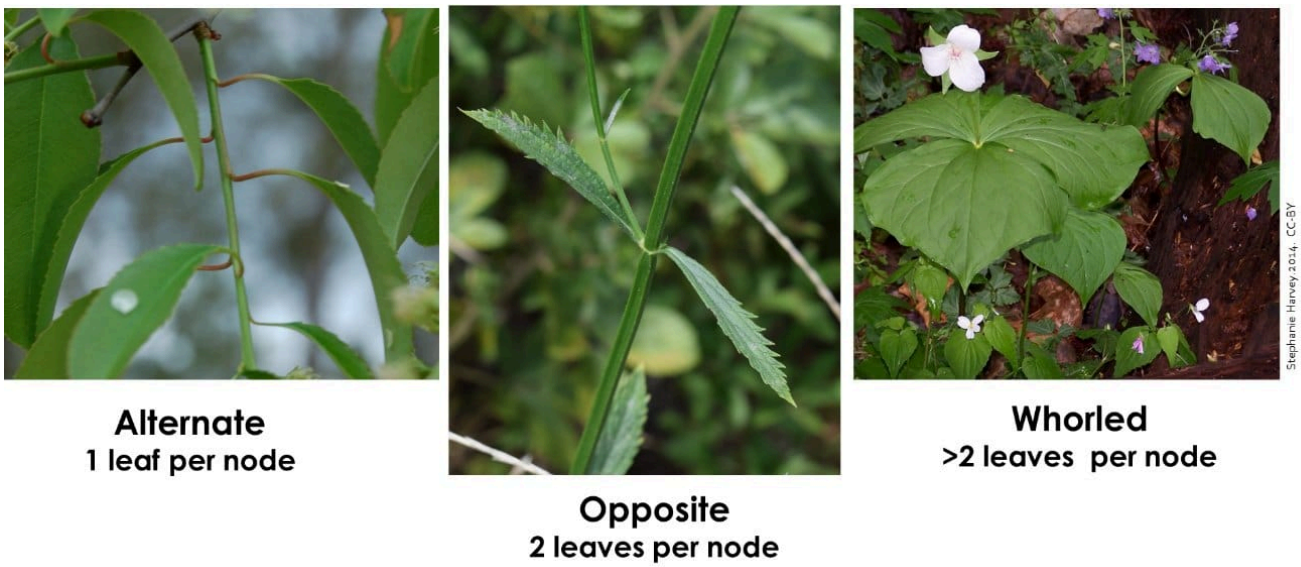


Figure 3-31. Leaves are also arranged along the stem in different patterns to minimize self-shading (Harvey, 2014).

Additionally, the leaf arrangement can be described by noting the "ranks" or rows of leaves along a stem. For example, if the leaves are opposite, but each node rotates 90 degrees from the one below, it would produce 4 rows when viewed down the stem axis and would be described as "opposite with rank of 4."

Some leaves have evolved to provide non-photosynthetic function for the plant (Figure 3-32). In Cacti, leaves are modified into spines. Spine are hard, sharp structures that are used as a defense mechanism by the plant.



Figure 3-32. Some leaves are specialized for defense, climbing, reproduction, or storage.

Please note that spines are often confused with thorns (modified branches) and prickles (outgrowths of the epidermis) due to their convergent form and function. Most rose "thorns" are in fact prickles. Some leaves, leaflets or even stipules have evolved to allow plants to climb and attach to structures. The most common of these structures are tendrils. These elongated structures coil around objects in the environment to allow the plant to attach itself for support. A bulb is an overwintering structure that consists of a compressed stem and modified leaves. The leaves are not photosynthetic but instead function as storage tissue. The stored reserves are used in the spring to power the production of new photosynthetic leaves and new flowers.

Some leaves are even modified to help the plant obtain essential minerals when the soils are chronically deficient (Figure 3-33). For example, nitrogen levels are often low in boggy soils, but plants such as the pitcher plants, sundews and Venus flytraps capture insects and other animals and digest them to provide the plant with much needed minerals. The traps are modified leaves. In the case of pitcher plants, leaves for hollow tubes that have digestive juices at the bottom. Sundews have pad-like leaves covered with sticky trichomes to trap the insects. Venus flytraps have hinged leaves that when triggered snap shut to trap the insects. All

of these are expense leaves to produce, so if adequate nitrogen is present then these specialized leaves will not be produced. Thus, fertilizing your Venus flytrap will not result in traps big enough to take out your roommate but instead will stop the plant from producing traps at all.



Figure 3-33. Some plants adapted to soils with low nitrogen levels digest capture and digest insects to supplement their nutrient intake (Harvey, 2017 CC-BY-NC).

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3.5: REPRODUCTIVE ORGANS

Reproduction in plants can vary greatly from spore producing, naked-seeded plants to flowering plants. Since angiosperms dominate the biosphere and are the most ecologically and economically important group of plants, we will focus on this clade. The reproductive organs of the angiosperms, the flowering plants, include the flowers, fruits, and seeds. These organs are critical to the production of the next generation of plants.



Sitka Rose. (Stephanie Harvey, 2023 CC-BY-NC)

3.5.1: Flowers

3.5.2: Fruits

3.5.3: Seeds

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3.5.1: Flowers

The flower is the primary reproductive structure of Angiosperms – flowering plants (Figure 3-34). On the most basic level a flower is a compressed stem of modified leaves. There are four whorls (or groupings) of modified leaves that produce 4 distinct floral parts. If viewing a flower from the proximal end of the floral axis to the distal end, the whorls are – sepals, petals, stamen, and carpels. The first two whorls are sterile (don't produce gametes) while the last two are reproductive in nature.



Figure 3-34. Flowers are essentially compressed stems of modified leaves (Harvey, 2016).

The lower or outermost whorl consists of sepals (Figure 3-35). Collectively they are referred to as the calyx. The calyx protects the unopened bud. They may be non-showy, or they may contribute to the colorful display used to attract pollinators. On occasions when the appearance of the sepals is such that they are difficult to distinguish from the petal, both are referred to as tepals.



Figure 3-35. The outer most whorl consist of sepals (collectively: calyx) and the colorful structures are the petals (collectively: corolla) (Harvey, 2016).

The next whorl is the petals, which are collectively called the corolla (Figure 3-35). In a typical flower, the petals are the showy, colorful bits that are to the interior of the sepals. The primary function of petals is to attract pollinators. Both the calyx and the

corolla are non-reproductive components of the flower and are collectively called the perianth (Greek - “around” “flower”).

The third whorl of modified leaves consists of stamen. Stamen are the equivalent of the “male” component of the flower. Stamen are composed of an anther (where pollen is produced) supported by a filament. Pollen grains carry the sperm nuclei required for fertilization.

The female pistil (carpel) is formed from the innermost whorl of modified leaves. The terms carpel is more precise as it refers to an individual modified leaf. A pistil can be made up of a single carpel or multiple carpels fused together. Some flowers have multiple pistils.



Figure 3-36. The third whorl is the stamen which produce the pollen while the inner-most is the pistil which produces the eggs (Harvey, 2016).

A pistil has three components: stigma that receives the transferred pollen, the style which connect the stigma to the ovary and the ovary – the site of the ovules that house the egg.

As with all the plant organs we have discussed, flowers come in a variety of forms with significant modifications. Some flowers are missing one or more of the whorls and are said to be incomplete (as compared to a complete flower with all four components) (Figure 3-37). In image here show the flower of a grass. It is missing the entire perianth – no sepals or petals. The protective role of the sepals is carried out by modified leaves from below the flower (called bracts) and since the grass is wind pollinated, the lack of petals doesn’t create a problem. The flowers of grasses, such as wheat and ryes, are incomplete.

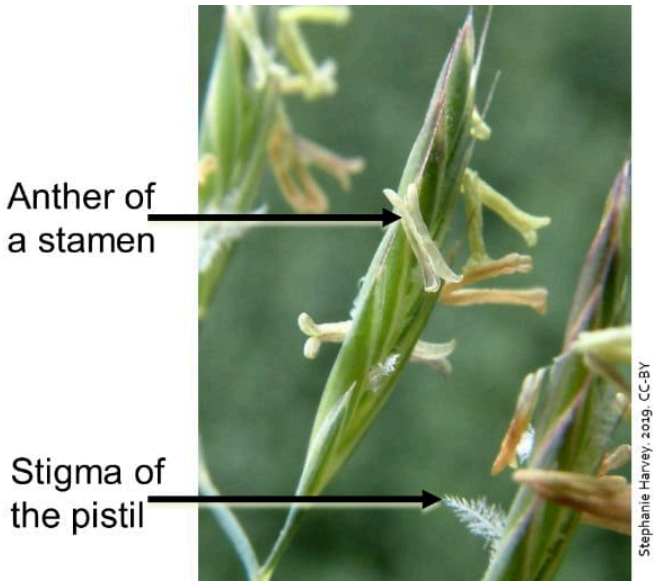


Figure 3-37. Some flowers, such as grasses, are missing one or more of the whorls and are said to be incomplete (vs. complete) (Harvey 2019).

A more specific set of terms can be used to describe the sexuality of a flower. If the flower has both stamen and pistil, it is said to be perfect or bisexual. If one of the reproductive structures is missing it is said to be imperfect or unisexual. A pistillate flower is a flower with no stamen while a staminate flower has no pistil. A complete flower must be perfect, an imperfect flower must be incomplete, but an incomplete flower could be perfect or imperfect.



Figure 3-38. A species with imperfect flowers may be monecious or dioecious. (one “house” or two “houses”).

A species of plants with imperfect flowers may be monecious or dioecious (Figure 3-38). Monecious species have a plant form that houses both pistillate flowers and staminate flowers. In contrast, dioecious species have two plant forms – one that has only pistillate flower and one that has only staminate flowers. (mono – one “house;” dioecious two “houses”).

An inflorescence is the organization of flowers. The simplest is the solitary flower – single flower supported by a peduncle (Figure 3-39). Others are compound and consist of multiple florets (flowers) supported by pedicels while the entire inflorescence is supported by a peduncle. The image here shows an example of a raceme. Collections of small flowers can have an advantage over a single large flower. Loss of a single small bud, has less of an impact on the reproductive success of the plant but provides the same visual appeal to pollinators that a single large flower could.



Figure 3-39. An inflorescence is an organization of flowers that can be simple as a solitary – one flower supported by a peduncle while the stalk supporting each individual flower is a pedicle (Harvey, 2016).

There are many types of inflorescences (Figure 3-40). Some look like a collection of flowers on a single stem. Others take on the attributes of a single flower. The common sunflower or Zinnia appears to be a flower but in reality, is an inflorescence referred to as a head or capitulum. The petal-like structures are individual flowers called rays and the central part that resembles a cluster of stamen and pistils are really hundreds of disk flowers.



Figure 3-40. Some inflorescences can look like a single flower or not a flower at all (Harvey, 2016).

Some inflorescences don't look like flowers at all. A spadix is an inflorescence consisting of a fleshy axis covered with minute flowers that lack perianths. A special bract called a spathe is associated with the spadix. In the case of Jack-in-the-pulpit, the spathe effectively wraps around and "hood" the spathe. The vast array of floral organs is mind blowing and we could spend an entire class just discussing them, but we will move on. However, next time you see a "flower" stop and take a good look at what is there and what is not.

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3.5.2: Fruits

Following pollination (the transfer of pollen from anther to pistil) and fertilization (union of egg and sperm), the ovary of the flower begins to mature into a fruit. In some species additional tissues may also contribute to the mature fruit. Culinary fruits are only a small segment of the types of fruits produced by plants. Many of the foods we describe as vegetables are in fact fruits. Eggplant, squash, cucumbers, and green beans are just some examples. These fruits are typically eaten while immature, so that seeds and seed coats are soft and chewable. If the structure has seeds it is botanically a fruit.

Fruits are groups into four categories based on the tissues that contribute to the structure: simple fruits, aggregate fruits, multiple fruits, and accessory fruits.

A simple fruit is one that develops from a single pistil of a single flower (Figure 3-41). The single pistil may consist of multiple carpels but that are fused to form as single ovary within the flower. Some examples of simple fruit include peaches, legumes, acorns, wheat, and sunflower “seeds.”



Figure 3-41. Developmental sequence of a typical simple fruit, nectarine (*Prunus persica*), flowering to fruit ripening in midsummer (By jjron, 2019)

An aggregate fruit (Figure 3-42) is derived from a single flower that houses many individual pistils each with an ovary clustered on a common receptacle. Each ovary develops into a small fruit (fruitlet). These stay together through the ripening process. Blackberry and raspberry fruits are the most common aggregate fruits but there are other non-culinary examples as well such as the fruit of the wildflower *Aquilegia* (columbine).



Figure 3-42. An aggregate fruit consists of a number of individual matured ovaries clustered as a unit on a common receptacle as a result of a single flower with multiple ovaries (Harvey).

A multiple fruit (Figure 3-43) develops from the mature ovaries of an entire inflorescence that fuse together to form a single fruit mass. You can often see remnants of individual flowers and the rachis in the mature fruit. Some examples of multiple fruits are pineapple, mulberry, and fig.



Figure 3-43. A multiple fruit develops from the mature ovaries an entire inflorescence (multiple flowers) that fuse together to form a single mass.

Please note that the terms “aggregate fruits” and “multiple fruits” are commonly confused. Remember aggregates are from groups of pistils with a single flower while multiple fruits come from multiple flowers of an inflorescence.

A fruit is classified as an Accessory “fruit” when non-ovary tissues contribute to the structure of the fruit. In many cases, an accessory fruit also belongs to the category of simple or aggregate fruit. Since multiple fruit by definition must contain parts of the inflorescence, it is not included in this group. Some accessory fruits that are simple fruits include fruits like apples and pears. The bulk of the fleshy tissue we consume when eating these pomes is derived from the wall of the receptacle. Other accessory fruits, like the strawberry, are aggregate fruits. The fleshy, red part we consume is receptacle tissue while the true fruit is the small “seeds” scattered across the surface. These “seeds” are a dry fruit called an achene. In the first image you can see the style and stigma attached to the achene while in the second you can see the vascular bundles feeding the individual ovaries/fruits.

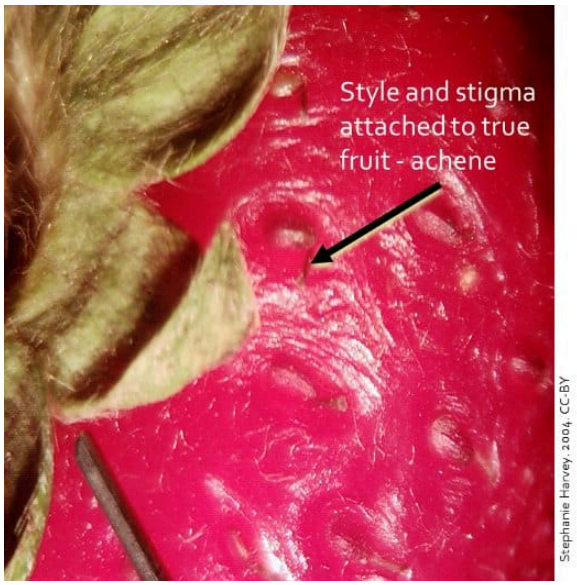


Figure 3-44. Some or all of the edible part of accessory fruit is not generated by the ovary. Accessory fruit can be simple, aggregate, or multiple (Harvey, 2014).

Fruits can also be categorized as either fleshy or dry fruits based on what happens the ovary walls – the pericarp - during maturation. In fleshy fruits the pericarp (or at least some of it) is soft and fleshy at maturity (Figure 3-45). There are several types of fleshy fruits depending on morphology and derivation.

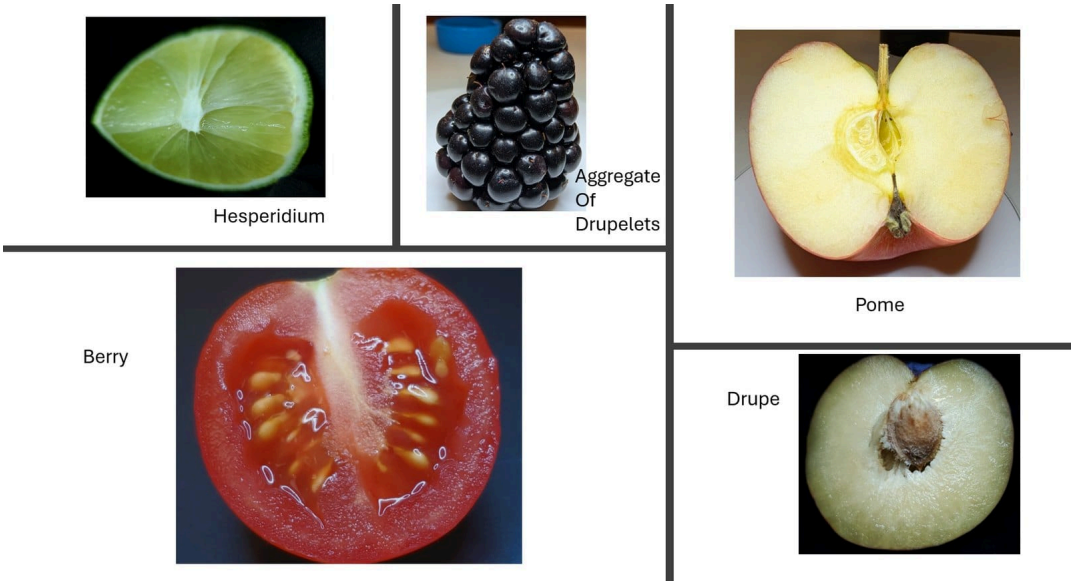


Figure 3-45. Examples of fleshy fruits (Harvey. 2026 CC-BY-NC).

A berry is a fleshy simple fruit and thus a single ovary. The ovary may be compound – made of several fused carpels. Tomatoes are examples of berries, while many things we call berries are not. Two specialized berries are the pepo – a berry of the cucurbits with hard skin (melons for example) and hesperidium – a berry of the citrus family with a rind and a juicy interior (oranges and lemons).

Drupes are simple fruits with “stones” and includes peaches, cherries, plums, and apricots. In these fruits the innermost layer of the pericarp (the endocarp) develops sclereids to form a hard, woody like shell around the seed. The exocarp remain soft and the mesocarp fleshy.

Pomes are accessory fruits composed of one or more carpels surrounded by an extension of the receptacle. This accessory tissue is the most edible part of the fruit. Apples and pears are some common examples of pomes. If you slice an apple in half (top to bottom) you can often see where the ovary wall starts due to a difference in texture from the accessory tissue.

Dry fruits have a pericarp that is hard and brittle at maturity. They can be segregated into two groups, dehiscent and indehiscent, depending on what happens at maturity. Dehiscent fruits have carpels that split along defined sutures at maturity in order to release the mature seeds (Figure 3-46).

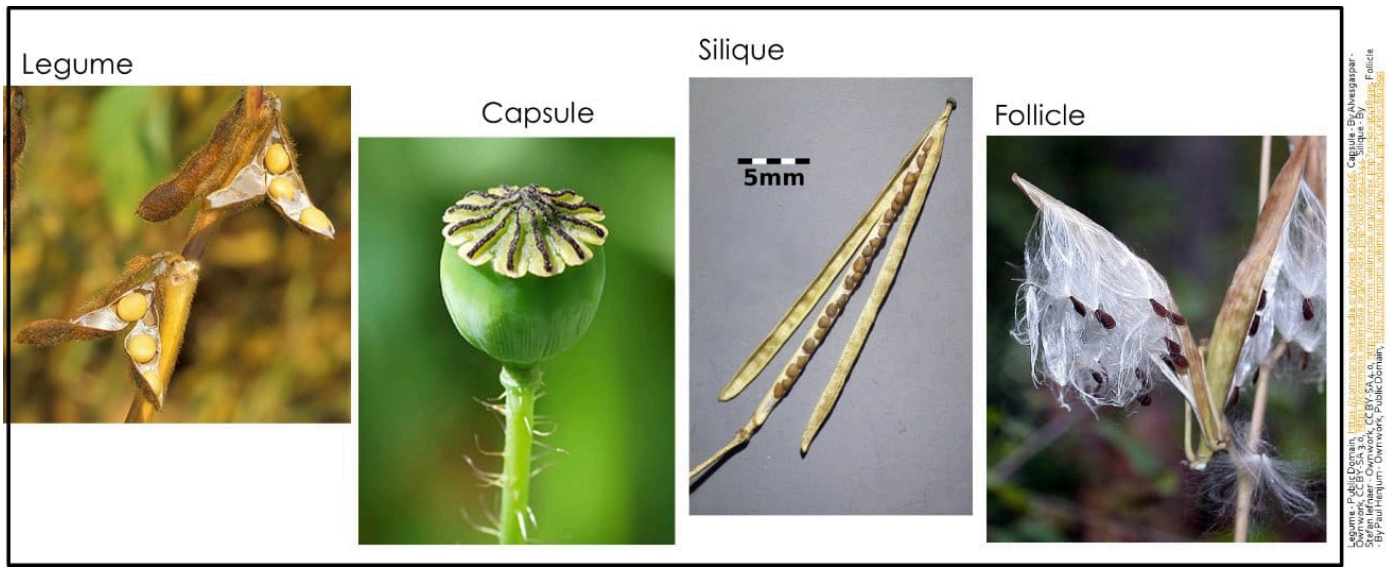


Figure 3-46. Examples of dry fruit that are dehiscent.

A Legume is a simple dry fruit that develops from a simple carpel and usually dehisces (opens along a seam) on two sides to disperse mature seeds. We often don't recognize this characteristic because we harvest fruits immaturely. In cultivation, this "shattering" is an undesirable trait, and we have bred many of our crops, such as soybeans, to retain the seeds. (Seeds that touch the ground are not harvestable.)

Capsule is a simple dry fruit composed of two or more carpels. The location and type of dehiscence varies from pores to longitudinal sutures between or within the carpels. The poppy capsule is an example of a poricidal capsule while lilies have loculicidal capsules.

Members of the mustard family (Brassicaceae) produce structures know as silique (if 3x longer than wide) and silicle (length less than 3x the width). Siliques are often confused with legumes, but when they open you can see two chambers separated by a septum.

A follicle is a dry unilocular fruit formed from one carpel, containing two or more seeds. It opens along a single suture in order to release seeds. Milkweed fruits are follicles.

Dry indehiscent fruits have a pericarp that is hard and brittle at maturity and the fruit wall does not split to release the mature seed(s). Instead, the embryo germinates from with the protection of the dry fruit.



Figure 3-47. Examples of dry fruit that are indehiscent.

Many of the objects we refer to as nuts are not true nuts. Some are legumes (peanuts) while other are the seeds of other fruits such as almonds, pecans, pistachios, walnuts, and Brazil nuts. True nuts are dry fruits where the seed remain unattached or free with the ovary wall. Hazelnuts, chestnuts, and acorns are examples of true nuts.

A caryopsis, often referred to as a grain, is the simple dry fruit from a single carpel where the pericarp fuses to a very thin seed coat. This is the typical fruit of the Poaceae family that includes corn, rice, and wheat.

Achene is similar to a caryopsis, but the seed does not adhere to the pericarp. In many species what is called the seed is, in fact, an achene. Examples include sunflower “seeds” as well as the fruits of quinoa, amaranth and dandelions.

A Samara is essentially a winged achene. The flattened wing of fibrous papery tissue develops from the ovary wall and enables the wind to carry the seed away from its source. A common example is the fruits of maple trees.

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3.5.3: Seeds

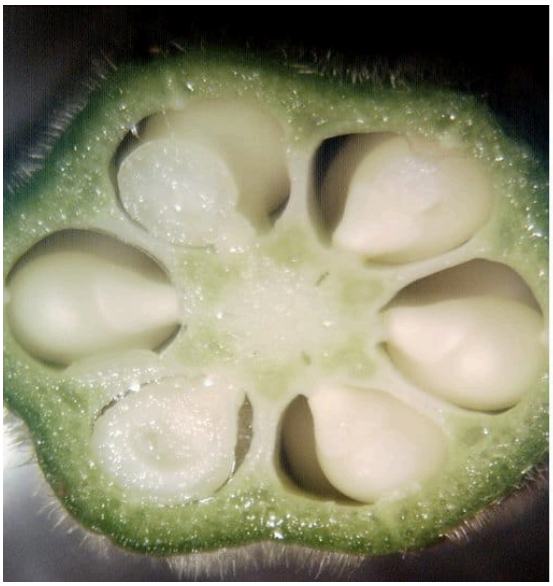


Figure 3-48. Seeds maturing with an okra fruit (capsule) (Harvey, 2016).

A seed is the product of the ripened ovule of gymnosperm and angiosperm plants. Seed development begins after fertilization and continues within the maternal plant tissues. In this image (Figure 3-48), the ovules within an okra capsule are visible. These ovules will develop into okra seed.

Seeds are remarkably diverse in size, from dust-like orchid seeds to the 30-60 lb. seed of the sea coconut. The larger a seed is the more resources the maternal plant must devote to its productions. Plants that produce large seeds are typically perennials. They are considered “K” – strategist – produce a few high-quality seed with better chances of development. Additionally, they can conserve resources for themselves since the survival of the species is not dependent on the seed producing the next generation. Small herbaceous annuals on the other hand are completely dependent on the seed to continue the species. Thus, they tend to be “R”-strategist – produce many, many seeds to insure some survive.

The anatomy of a seed is fairly basic and includes three parts: (1) an embryo, (2) a supply of nutrients for the embryo (maybe part of the embryo), and (3) a seed coat. In this diagram (Figure 3-49), (a)outer most layers are the seed coat, (b) represents the endosperm, (c) represents the cotyledon (part of the embryo), also called the seed leaves and (d) is the hypocotyl (part of the embryo’s axis).

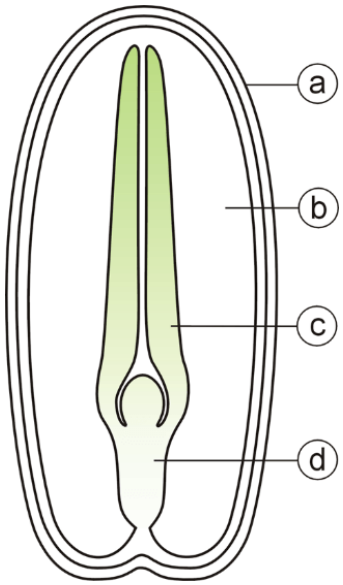


Figure 3-49. Diagram of a cross section of a seed.

Seeds can be categorized based on the presence or quantity of endosperm. For gymnosperm, the endosperm is produced from the haploid tissue of the maternal gametophyte and it remains such to nourish the embryo during germination (Figure 3-50). With angiosperms, the endosperm is the product of a second fertilization. While one sperm nucleus fertilized the egg, a second fuses with the two nuclei of the central cell and thus produces 3n (triploid) tissues. In some cases, like with monocots, the endosperm remains and provides the nutritive material for the germinating embryo. In eudicots some or all of the endosperm is absorbed, and its energy stored in the cotyledons or seed-leaves of the embryo.

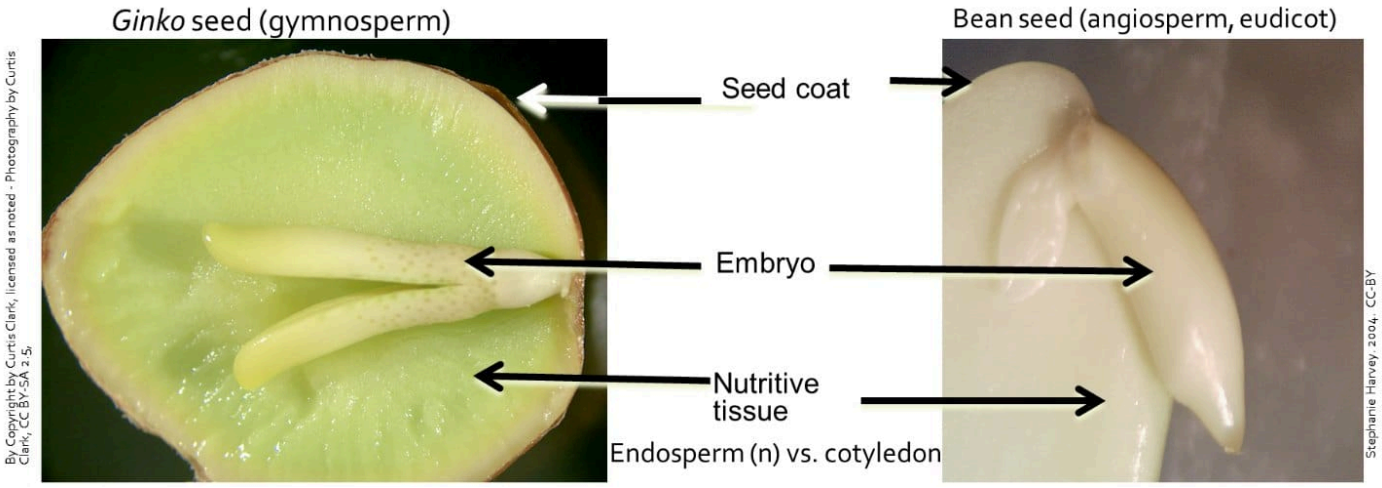


Figure 3-50. Comparison of a *Ginkgo* seed (gymnosperm) to that of a bean (angiosperm-eudicot).

In Figure 3-50, the image on the left is of a *Ginkgo* seed, a gymnosperm, with a well-developed embryo. The image on the right partially shows a bean with a well-developed embryo and cotyledons. The first true leaf is even visible at the top of the embryo's axis.

The seed coat develops from maternal tissues, called the integument. They surround and protect the ovules. In general, the seed coat protects the embryo from physical injury, predators and drying out. The nature of the seed coat can vary from a paper-thin layer (like a peanut husk) to very thick and hard like that of a coconut. In the case of a pomegranate, it is fleshy.

Plants have evolved mechanisms to disperse their seeds (Figure 3-51). Movement of seeds away from their maternal source is an important mechanism for colonization and to prevent competition between parent and offspring. Some mechanisms are relatively passive and use wind to move the seeds. The common dandelion is a notable example of wind dispersal.



Stephanie Harvey, 2023. CC_BY-NC.
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Figure 3-51. Plants evolved mechanisms to disperse their seeds from wind dispersal to animal dispersal.

Other mechanisms require interaction with animals. Fruits many be eaten by animals and seeds are dispersed with their droppings. In some cases, seeds have specialized structures to attract specific dispersal agents. Elaiosomes are soft, fleshy structures that contain nutrients for animals that eat them. The ants carry such seeds back to their nest, where the elaiosomes are eaten and then the seed remains untouched. Wither it is fruit or elaiosomes, plant resources are allocated to attract a dispersal agent, essentially “paying” for the dispersal. Animals can be used passively as well. Seeds with barbs or hooks can hitch a ride in animal fur (or clothing) until they are dispersed elsewhere.

The embryo is an immature plant from which a new plant will grow under proper conditions. The embryo has one cotyledon or seed leaf in monocotyledons, two cotyledons in almost all dicotyledons and two or more in gymnosperms. The radicle is the embryonic root. The plumule is the embryonic shoot. The embryonic stem above the point of attachment of the cotyledon(s) is the epicotyl. The embryonic stem below the point of attachment is the hypocotyl.

Typically, once as seed reaches maturity, it desiccates and enters dormancy. This prevents the seed from germinating too soon, before conditions are suitable, and to help stagger germination times to help avoid disasters. If all the seeds germinated at the same time, a single event (drought, flood, fire, pest, disease) could destroy the entire generation. Staggering germinations means a more resilient seed pool.

Dormancy is seed controlled and maintained through a balance of hormones. Changes in the balances due to external factors can break dormancy and trigger germination. Mechanisms for maintaining seed dormancy are varied. In some cases, the hard seed coat prevents imbibition (the uptake of water). Since this is the required first step in germination, preventing maintains dormancy. Chemical or physical scarification (abrading) of the seed coat can let water in. Chemical dormancy is when a chemical produced by the cell prevents germination. Depending on the plant species, the chemical may be washed out by rainfall or snowmelt or deactivated by other forces such as the heat of a fire. Other environmental factors that can play a role include exposure to cold temperature, exposure to sunlight, or just time.

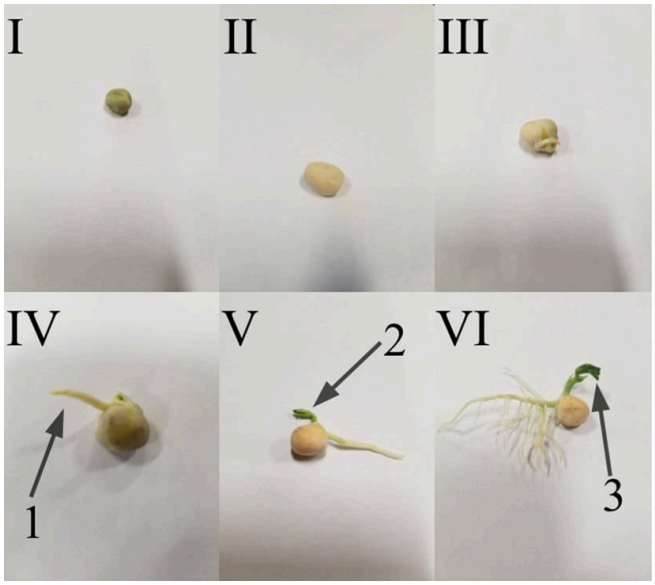
Typically, dormancy is maintained while the seeds are still attached to the parent. However, some seeds such as those of mangroves are viviparous; they begin to germinate while still attached to the parent (Figure 3-52). It the case of the mangrove seeds, it is critical that the germinating seed stick in the mud at low tide, so they are not washed out to sea. When the fruit falls, the dagger-like radical sticking out the bottom of the fruit, wedges itself into the mud, anchoring it in a suitable location.


By Forest & Kim Starr, CC BY 3.0 us, https://commons.wikimedia.org/w/index.php?curid=71935865

Figure 3-52. Seeds of some mangroves are viviparous; they begin to germinate while still attached to the parent.

Seed germination is the process by which a seed embryo develops into a seedling. Seed germination occurs in stages that can vary slightly with species, but typically five steps are seen in most seeds. Before germination can begin, three fundamental conditions must be met: 1) the embryo must be alive; 2) dormancy must be overcome; 2) proper environmental conditions must exist.

Assuming the above 3 conditions are met, the first step in the germination process is imbibition – the uptake of water (Figure 3-53). This uptake provides the water needed for many metabolic processes. In particular, it reactivates enzymes associated with release and mobilization of energy from the nutritive source to the embryo. The next observable change is the splitting of the seed coat. The water softens the seed coat and ass the tissues of the embryo and nutritive tissue swell, the seed coat splits open. The first part of the embryo to emerge from the seed is the radicle – the embryonic root. It establishes itself for anchorage and water absorption. With an adequate supply of water flowing in through the radicle, the cotyledons emerge. The role of the cotyledons varies depending on the species. They may be pulled above ground and become the first photosynthetic leaves of the seedling, or they may stay below ground as an energy reserve. The last step is the establishment of the first true leaf. The plumule unfurls, expands, and greens as it becomes a functioning leaf.



By Noahjgagne - Own work, CC BY-SA 4.0,

Figure 3-53. Germination in peas: I. Seed dormant/dry; II. Imbibition; III. Seed coat ruptures – radicle beginning to emerge; IV. Radicle emerged and elongating; V. Plumule emerges; VI. Lateral roots develop and plumule expands to true leaf.

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3.6: End of Chapter Review

- In this chapter we explored the hierarchy of life and how it applies to plant structure from the cellular level up to the whole organism.
- We looked at the three main types of plant cells - parenchyma, collenchyma, and sclerenchyma - and how they form simple and complex tissues like xylem, phloem, epidermis, and mesophyll.
- The major tissue systems (dermal, ground, vascular) make up the vegetative organs of roots, stems, and leaves as well as the reproductive organs of flowers, fruits, and seeds.
- There is incredible diversity in the form and function of these organs, from modified leaves to complex flower structures.
- Ultimately though, the role of these structures is to help the plant survive, grow, and reproduce.

Key Terms

- Carpels
- Collenchyma cells
- Cotyledons
- Cuticle
- Dermal tissue
- Dormancy
- Endosperm
- Epidermis
- Germination
- Ground tissue
- Internodes
- Meristematic tissue
- Mesophyll
- Nodes
- Ovules
- Parenchyma cells
- Perianth
- Petals
- Phloem
- Sclerenchyma cells
- Seed coat
- Sepals
- Stamen
- Stomata
- Vascular tissue
- Xylem

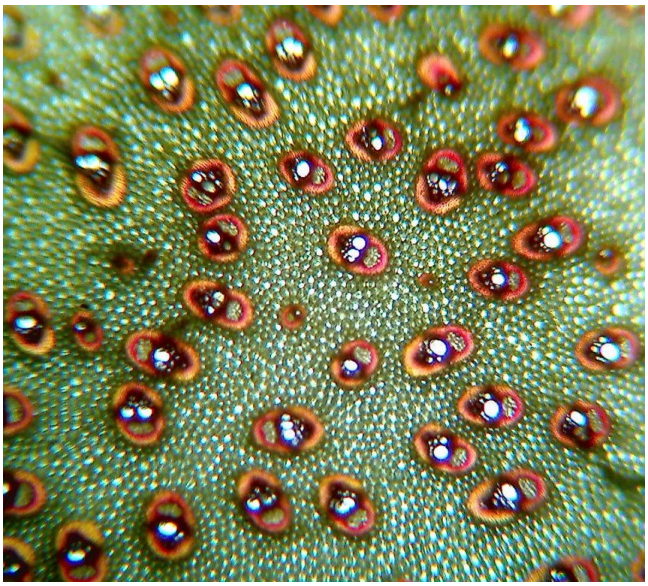
Self-Review

1. What are the three main types of plant cells and how do they differ in structure and function?
2. What are the main tissues that make up leaves and what are their roles?
3. Compare xylem and phloem tissues. What are their key structural differences and functions?
4. What is the difference between monocot and eudicot stems? How does this relate to their vascular tissues?
5. What are the main vegetative organs of plants? What key functions do they serve?
6. Define meristematic tissue and explain where it is located in plants.
7. What floral organs make up a complete flower? What is their arrangement?
8. How do fruits develop and what are the main types of fruits? Provide examples.
9. What are the three main parts of seeds and what does each part do?
10. What triggers the transition from a dormant seed to a germinating seed?
11. What is the sequence of events during seed germination?
12. What is a node? What plant structures are associated with nodes?

13. How does phyllotaxy arrangement minimize self-shading of leaves?
14. What adaptations help plants reduce water loss from their leaves?
15. How do plants disperse their seeds? Give examples of dispersal mechanisms.

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4: PLANT FUNCTION



In this Chapter, we will look at processes critical to plant survival. While discussing these processes, keep in mind plant structure - from the cellular level to whole plant level - supports and is often critical to these functions. In the light micrograph shows the vascular bundles of a palm leaf petiole. This bundles contain the transport tissue needed to move water into the leaf and move the products of photosynthesis out of the leaf (Stephanie Harvey. 2021 CC-BY-NC).

4.1: Photosynthesis

4.1.1: Chlorophyll

4.1.2: Required Reactants

4.1.3: Processes of Photosynthesis

4.1.3.1: Light-Dependent Reactions

4.1.3.2: Light-Independent Reactions (Calvin Cycle)

4.1.4: Photorespiration - When RuBisCO Errs

4.2: Cellular Respiration

4.2.1: Required Reactants

4.2.2: Glycolysis

4.2.3: Citric Acid Cycle (Krebs Cycle)

4.2.4: Electron Transport System and Oxidative Phophorylation

4.3: Water and Nutrient Movement

4.3.1: Cell-to-Cell Movement of Water & Solutes

4.3.2: Transport and Transpiration

4.3.2.1: Bulk Movement within Phloem Tissue

4.3.2.2: Bulk Movement within Xylem Tissue

4.3.2.3: Transpiration

4.4: Plant Hormones

4.5: End of Chapter Review

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4.1: PHOTOSYNTHESIS

Structure and functions are tightly linked. The structure of plant cells, tissues, organs, and organ systems has an impact on the functional role they play for the cell and organism. Often the “ideal” structure for one function must be sacrificed to meet other needs. For example, the broad surface of a typical leaf is ideal for light absorption (Figure 4-1) but it also provides a large surface for water loss. Thus, where water conservation is critical, leaves are often smaller. Compromise and adaptation are common themes in all living organisms.



Figure 4-1. Saw Palmettos (*Serenoa repens*) bathed in sunlight. Stephanie Harvey. 2013 CC-BY

All living organisms must process energy. Energy from outside the system (the plant) must be obtained to provide for growth, maintenance, and reproduction. Photosynthesis is a chemical process by which most plants, some protists and some bacteria transform light energy and carbon dioxide (CO_2) into carbohydrates.

Photosynthesis is a complex series of reactions that take place within some plant cells. Note that not all plant cells can photosynthesis – only those that exposed to light and contain chlorophyll can harvest this energy. The overall formula (Figure 4-2) for photosynthesis summarizes the required reactants and the resulting products. Photosynthesis requires carbon dioxide, water, and light (in the presence of chlorophyll) to produce sugars, oxygen, and water. Yes, water is on both sides of the equation since research shows water is both consumed and produced by this process.

$$6\ CO_2 + 12\ H_2O + \text{light} \xrightarrow{\text{(chlorophyll)}} C_6H_{12}O_6 + 6\ O_2 + 6\ H_2O$$

Figure 4-2. Summary equation for the process of photosynthesis.

The summary equation is misleading because it represents the process as if it were only a single reaction. It is not. There are many reactions that take place to move from reactants to products. These reactions are divided into two sets: light-dependent reactions, in which plants capture the energy of light to make ATP and NADPH, and the light-independent reactions, in which ATP, NADPH and CO_2 are used to create high energy biological molecules like carbohydrates. Before we go on to look at these reactions, let us look at the required reactants for the overall process.

4.1.1: Chlorophyll

4.1.2: Required Reactants

4.1.3: Processes of Photosynthesis

4.1.3.1: Light-Dependent Reactions

4.1.3.2: Light-Independent Reactions (Calvin Cycle)

4.1.4: Photorespiration - When RuBisCO Errs

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4.1.1: Chlorophyll

For photosynthetic eukaryotes photosynthesis takes place in specialize organelles called chloroplasts (Figure 4-3). These bacteria-like organelles have three membranes. There are an outer membrane and inner membrane and thylakoid membrane. This creates three spaces or lumens. The one between the outer and inner membranes is not used. The stroma is the area between inner membrane and the thylakoid membrane. The stroma region of the chloroplast contains an aqueous solution of proteins, starch granules, lipid, ribosome, and a ring of DNA. This area is very metabolically active. The third lumen is within the sack-like structures of the thylakoid. The thylakoid lumen is also a space utilized during photosynthesis.

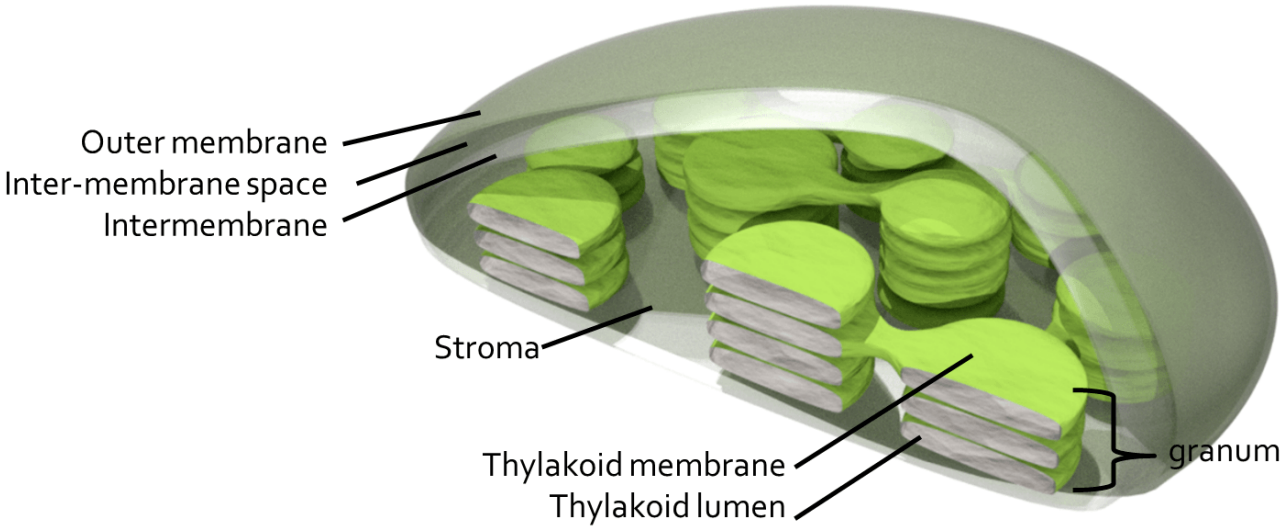


Figure 4-3. Artist rendering of a chloroplast. It consists of an outer membrane and an inner membrane. The two membranes enclose a liquid filled space called the stroma. Within the stroma is a third membrane the thylakoid. The thylakoid membrane has the chlorophyll molecules embedded. This membrane encloses another space - the thylakoid lumen. (Modified from By DataBase Center for Life Science (DBCLS) - https://doi.org/10.7875/togopic.2017.50, CC BY 4.0.)

It is the thylakoid membrane of the chloroplast that contains the light absorbing pigment chlorophyll. A chlorophyll molecule (Figure 4-4) has two regions: a hydrophilic region that contains a series of carbon rings and four nitrogen atoms that trap a Mg^{2+} and a hydrophobic tail that can embed in the thylakoid membrane. Chlorophylls absorb light most strongly in the blue portion of the electromagnetic spectrum as well as the red portion. Chlorophyll-containing tissues will appear green to our vision since the green light is poorly absorbed and thus reflected and transmitted.

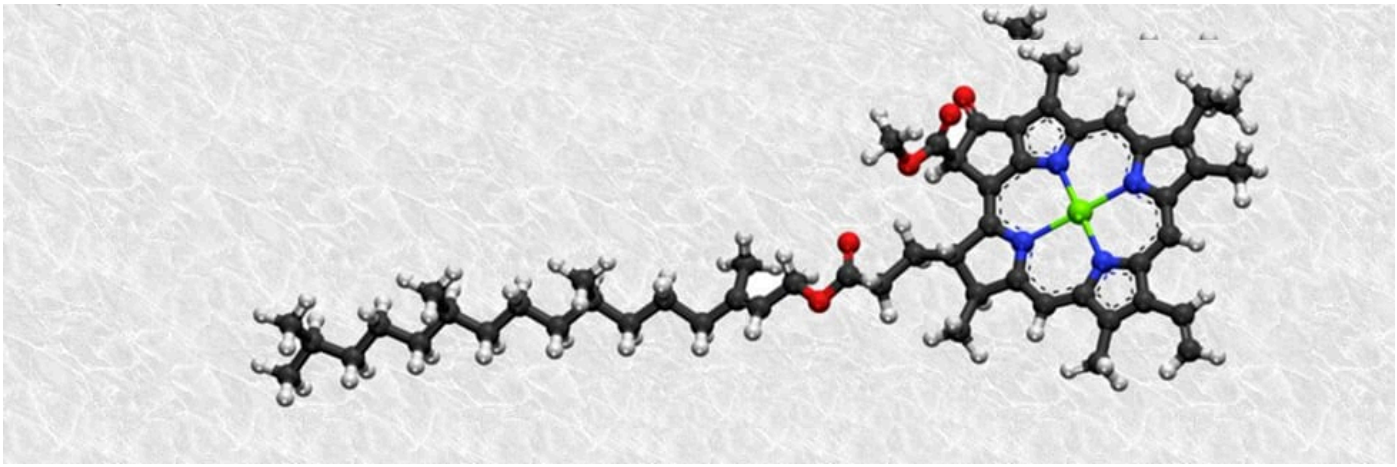


Figure 4-4. Molecular structure of Chlorophyll-a. Ball-and-stick model of Chlorophyll-a. Parts of interest are the large head area made up of multiple rings (light absorbing part) and the long fatty acid tail that anchors the pigment into the thylakoid membrane. (By Alejandro Porto - Derivada de File:Chlorophyll-a-3D-balls.png de Jynto y File:Chlorophyll a b d.svg de Yikrazuul, CC BY-SA 3.0, https://commons.wikimedia.org/w/inde...curid=31750856)

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4.1.2: Required Reactants

Carbon Dioxide

As photoautotrophs, plant can produce their own organic molecules from inorganic sources such as carbon dioxide (CO_2). Carbon dioxide (a gas) is plentiful in the atmosphere. It can reach the chloroplast in the mesophyll cells of a leaf by diffusing through the stomatal pores and into the interior of the leaf. The cuticle prevents desiccation of the leaf tissue but also prevents carbon dioxide from diffusing directly through the epidermis. The Figure 4-5 shows a cross-section through a monocot leaf. The chloroplasts are stained red, and we can be seen in the mesophyll and in the bundle sheath cells that surround the veins (aka. vascular tissue). Not the deep pink layer to the outside of the leaf this is the cuticle.

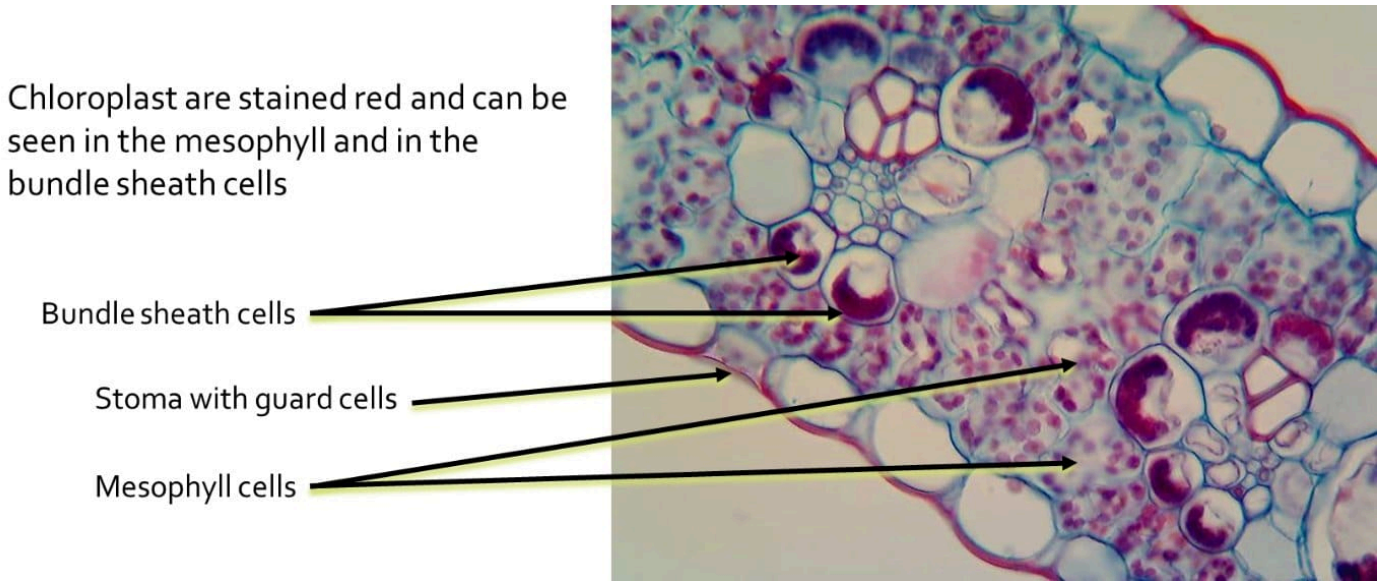


Figure 4-5. A monocot leaf in cross-section shows an upper and lower epidermis with a waxy cuticle and stomata often distributed on both surfaces. Small guard cells flank the stomatal pore. The mesophyll is typically undifferentiated, lacking distinct palisade and spongy layers. Vascular bundles are scattered throughout the mesophyll, each surrounded by a bundle sheath, with xylem positioned toward the upper surface and phloem toward the lower surface. (Stephanie Harvey. 2019. CC-BY-NC)

Water

Water is required for photosynthesis as well as most metabolic processes (Figure 4-6). Water is obtained through the roots of a plant and is transported in the xylem. The tissues of a plant are flushed with water, and it is not a reactant that limits the photosynthetic process - at least not directly.

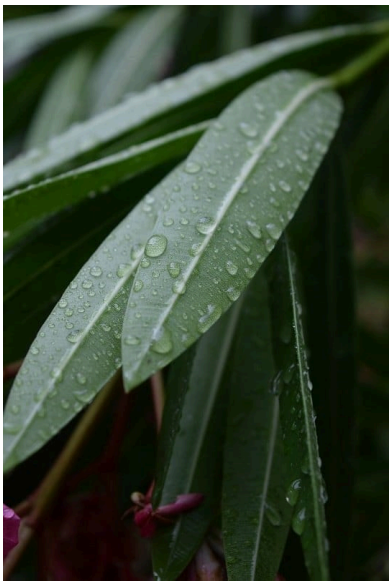


Figure 4-6. Water beading on the back of oleander leaves after a spring rainfall. Stephanie Harvey. 2018. CC-BY

As a plant's stomatal pores open to allow for diffusion of carbon dioxide, critical water is lost through the same pores. As much as 99% of the water taken in by plants is lost due to the need for gas exchange. Plants are in a constant struggle between water conservation and gas exchange. Ultimately, the need to conserve water wins out over the need for gas exchange and the guard cells close the stoma. But there is a cost. Without carbon dioxide, the plant cannot continue to transform light energy into carbohydrates.

Light

Light energy is only a small part of the electromagnetic spectrum with wavelengths from approximately 400 nm to 700 nm. Leaves are the primary site of light absorption. They are typically thin, flat structures that allow for maximum surface area with minimal resource expenditure. Leaves commonly absorb about 80% of the visible light that reaches them. Photosynthetic efficiency is affected by light intensity, quality, and duration. These characteristics vary with the time of day, season, altitude, latitude, and atmospheric composition. This will be discussed more in a later chapter.

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4.1.3: PROCESSES OF PHOTOSYNTHESIS

As mentioned previously, these reactions are divided into two sets. The light-dependent reactions, often called the light reaction, involve the capture and conversion of light energy into chemical energy. As seen in Table 4-1, the light reactions require light for energy and water as an electron source. The light reactions produce ATP, NADPH, and oxygen. The oxygen produced by the light reactions of photosynthesis dramatically altered the earth's atmosphere and made aerobic cellular respiration possible.

The light-independent reactions have been referred to by several other names. One commonly used in the past it the "dark reactions" since light is not needed for this process. However, this was deemed misleading since "dark" is not a requirement for this process. It is often just referred to as the Calvin Cycle. Within this cycle, carbon dioxide is fixed to an existing organic molecule and then the captured energy from the light reactions (ATP and NADPH) is used to reduce that newly formed molecule to a high energy organic molecules (sugars) (Table 4-1).

Table 4-1. *The two processes of photosynthesis along with their requirements and products.*

Light-Dependent Reactions	Light-Independent Reactions (Calvin Cycle)
Requires light for energy	Requires ATP & NADPH from the light-dependent reactions
Requires water as an electron source	Requires carbon dioxide
Produces ATP	Produces a three-carbon sugar (G3P)
Produces NADPH	
Produces oxygen	

4.1.3.1: Light-Dependent Reactions

4.1.3.2: Light-Independent Reactions (Calvin Cycle)

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4.1.3.1: Light-Dependent Reactions

Light-Dependent Reactions

There are four primary components that make up the light reactions (Figure 4-7). There are two photosystems (PS I and PSII) that include the pigments that harness the light energy. These work in concert with the ETS – electron transport system – which shuttles excited electrons from PSII to PSI and builds the hydrogen-proton gradient that powers ATP synthesis via the fourth component – ATP synthase.

Now for a closer look at these components. The process starts with PSI. Photons of light excite electrons in the light harvesting pigments. This excitation energy is passed to a pair of special chlorophyll molecules (reaction center) on the lumen side of the PSI complex. These excited electrons are then pulled away from the reaction center and ultimately passed to NADP+ to yield NADPH. This takes place on the stroma side of the thylakoid membrane.

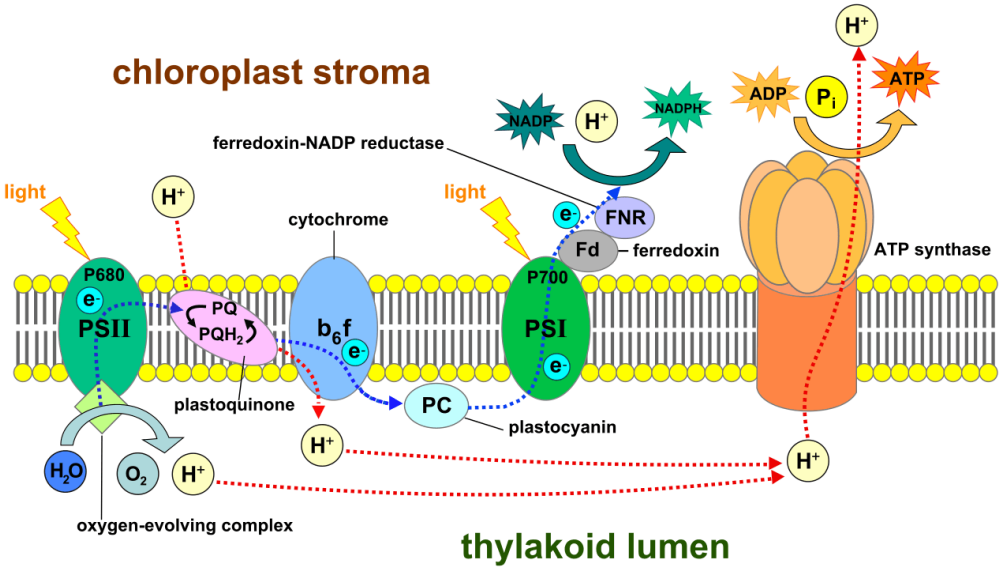


Figure 4-7. Thylakoid membrane with photosystems and ATP synthase. The electron transport system (ETS) in the thylakoid membrane consists of several protein complexes. embedded in the membrane that work together during the light reactions of photosynthesis. Photosystem II (PSII) and Photosystem I (PSI) are large protein complexes containing chlorophyll and other pigments. Between them lies the cytochrome b6f complex, and ATP synthase spans the membrane as well. When light strikes PSII, it energizes electrons from water molecules, releasing oxygen as a byproduct. These high-energy electrons move through the cytochrome b6f complex to PSI. As electrons pass through the ETS, protons (H⁺) are pumped from the stroma into the thylakoid lumen, creating a concentration gradient. At PSI, light energy boosts the electrons again, and they ultimately reduce NADP⁺ to NADPH. Chemiosmosis: The proton gradient created by the ETS drives ATP synthesis. Protons flow back through ATP synthase from the lumen to the stroma, powering the phosphorylation of ADP to ATP. (By Somepics - Own work, CC BY-SA 4.0, https://commons.wikimedia.org/w/inde...urid=38088695_

The problem now is that the PSI reaction center chlorophylls are missing electrons and cannot do their trick (reduction of NADP+) again. It is also too expensive to make another reaction center. So, the answer to this problem is to simply replace the lost electrons.

That is what PSII helps with. Like with PSI, the light harvesting pigments of PSII absorb light energy and electrons get excited. The excitation energy is passed to the reaction center of PSII where its electrons become excited and are pulled away by a series of electron acceptors, until ultimately the electrons are passed to the reaction center of PSI. As the electrons pass from acceptor to acceptor, energy is lost so they electrons arrive at PSI in the un-excited (or ground) state.

While this solves the problem of the lost electrons at PSI, PSII is now short a pair of electrons. It would be inefficient to continue this type of “robbing Peter to pay Paul” scenario. What is needed is a cheap, readily available sources of electrons. And this is where water (H_2O) comes into the reaction.

Associated with the PSII complex is the “oxygen-evolving complex.” This complex is a series of enzymes that strip electrons from a water molecule and passes them to the depleted reaction center of PSII. As a result, oxygen is released, and hydrogen-protons (H+) are released into the thylakoid lumen.

The path the electrons take from PSII to PSI is the electron transport system (ETS). It is a series of complex electron acceptors, some of which are mobile in the thylakoid membrane. The electrons are pulled away from the acceptors of PSII and are passed down the ETS. While the electrons are being passed through the ETS, hydrogen-protons (H+) are pumped into the thylakoid lumen. They effectively follow the electrons from the stroma when the electrons near the stroma side of the thylakoid membrane and proceed to enter the thylakoid lumens as the electrons move in that direction toward the PSI reaction center.

Between the hydrogen-protons released by the oxygen-evolving complex and those pumped into the thylakoid lumen by the ETS, a steep H+ gradient develops across the thylakoid membrane (the concentration on the stroma side – low – and the concentration on the lumen side – high). This gradient represents potential (stored) energy. Think of it like water trapped behind a dam; it can be harnessed to do work. The impermeability of the thylakoid membrane prevents the H+ from just diffusing through the membrane. Instead, their only path of escape is the channel created by ATP synthase. As the H+ move forcefully through the ATP synthase, their energy causes the enzyme to rotate. This forces an ADP molecule together with a phosphate group to produce ATP.

Thus, by the end of the light reactions ATP and NADPH are created (the chemical energy needed to make carbohydrates) and oxygen has been released as a waste product.

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4.1.3.2: Light-Independent Reactions (Calvin Cycle)

Light-Independent Reactions (Calvin Cycle)

The light independent reactions occur in the Calvin cycle. The purpose of this process is to take in carbon (in the form of carbon dioxide) and add it to an organic molecule. Then the molecule is reduced and phosphorylated to produce a high energy molecule (a sugar) for use by the cell. The reactions of the Calvin cycle (Figure 4-8) can be divided into three phases: 1) carbon fixations; 2) Reduction; 3) Regeneration of ribulose 1,5-bisphophate.

In Phase I, carbon dioxide is added to an existing 5-carbon (5-C) organic molecule - ribulose 1-5-bisphosphate (RuBP). The enzyme RuBisCO (which stands for Ribulose Bisphosphate Carboxylase/Oxygenase) catalyzes the reaction. The resulting six carbon molecule is extremely unstable and immediately splits into two 3-C molecules.

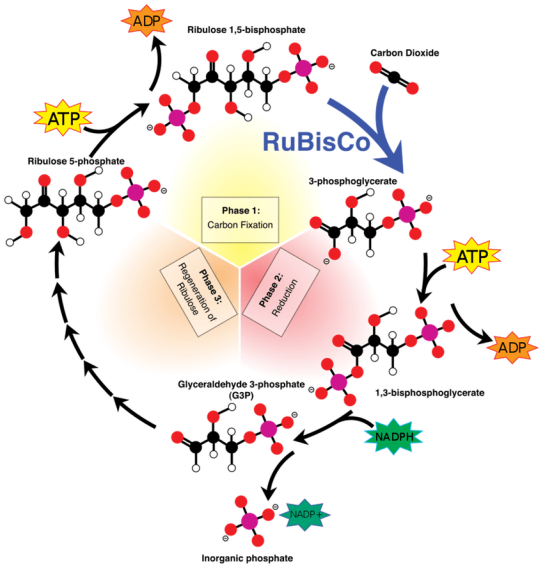


Figure 4-8. The Calvin Cycle showing the three phases: Carbon fixation, Reduction and Regeneration. By Mike Jones - Own work, CC BY-SA 3.0, https://commons.wikimedia.org/w/inde...?curid=9504547

In Phase 2, the two 3-C molecules are phosphorylated 2 ATP molecules (one for each). The second step is the reduction of each molecule using the electrons carried by NADPH. The product of this step is glyceraldehyde 3-phosphate (G3P), a high energy molecule that can be used to make glucose and other biomolecules. At the end of phase two, the energy captured in the light reactions (ATP and NADPH) has been converted to a stable carbohydrate. Since only a single carbon is fixed per turn of the cycle, to remove a 3-C molecule, like G3P, free and clear the cycle must turn three times. So, one G3P leaves but five stay behind to move on to Phase-3.

Phase 3 involves the regeneration of starting 5-C molecule of the cycle. The five 3-carbon molecules (G3Ps) have the carbon necessary to rebuild the 3 RuBP (the 5-carbon molecule) that starts the cycle. We will not discuss the complex chemical rearrangements that have to occur to go from five 3-C to three 5-C molecules. It is a delicate ballet of transfers and shifts. Three more molecules of ATP are needed for this phase – one for each of the newly formed RuBP.

The RuBPs must be regenerated. Without this part of the Calvin cycle, the RuBP pool would be depleted, and carbon fixation and the subsequent production of sugars would stop.

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4.1.4: Photorespiration - When RuBisCO Errs

The enzyme RuBisCO fixes carbon in the first phase of the Calvin cycle. However, the enzyme also has the ability to fix oxygen (the "O" stands for oxygenase). If oxygen level increase and CO_2 levels decrease, the oxygenase function of RuBisCO can kick in. The detrimental process, called **photorespiration**, causes the plant to lose carbon instead of fixing it and requires the expenditure of energy. This situation usually occurs when stomatal pores are closed to conserve water. Oxygen builds up as it is released by the light reactions while carbon dioxide level drops as molecules are fixed by the Calvin cycle. On a hot, dry day a standard plant can lose more carbon than it fixes.

Some plants, such as the cacti (Figure 4-9) have evolved mechanisms to minimize if not eliminate this problem of photorespiration.



Figure 4-9. Cacti have evolved mechanisms to minimize the chance of photorespiration. Stephanie Harvey. 2018. CC-BY

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4.2: CELLULAR RESPIRATION

While parts of a plant undergo photosynthesis to capture light energy, the ATPs and NADPHs generated in the light reactions are not readily available to non-photosynthetic parts of the plants nor are they available during night hours. The sugars created in the Calvin Cycle can be stored and transported for later use by non-photosynthetic organs and at night. The energy stored in this sugar molecules (like glucose) must be released slowly so it can be captured without excessive losses as heat. A series of controlled reactions are used to extract energy from these high-energy molecules and to make smaller amounts available to perform cellular work. This process is referred to as cellular respiration since the release of energy is accompanied by release of carbon dioxide molecules (Figure 4-10).

Cellular respiration can be broken down into four stages: (1) glycolysis – not unique to cellular respiration; (2) Krebs cycle (Citric Acid Cycle); (3) Electron Transport Chain and (4) Chemiosmosis/oxidative phosphorylation. The energy released is captured ultimately as ATP and aerobic respiration (with oxygen) yields 28-32 ATPs (Figure 4-11).

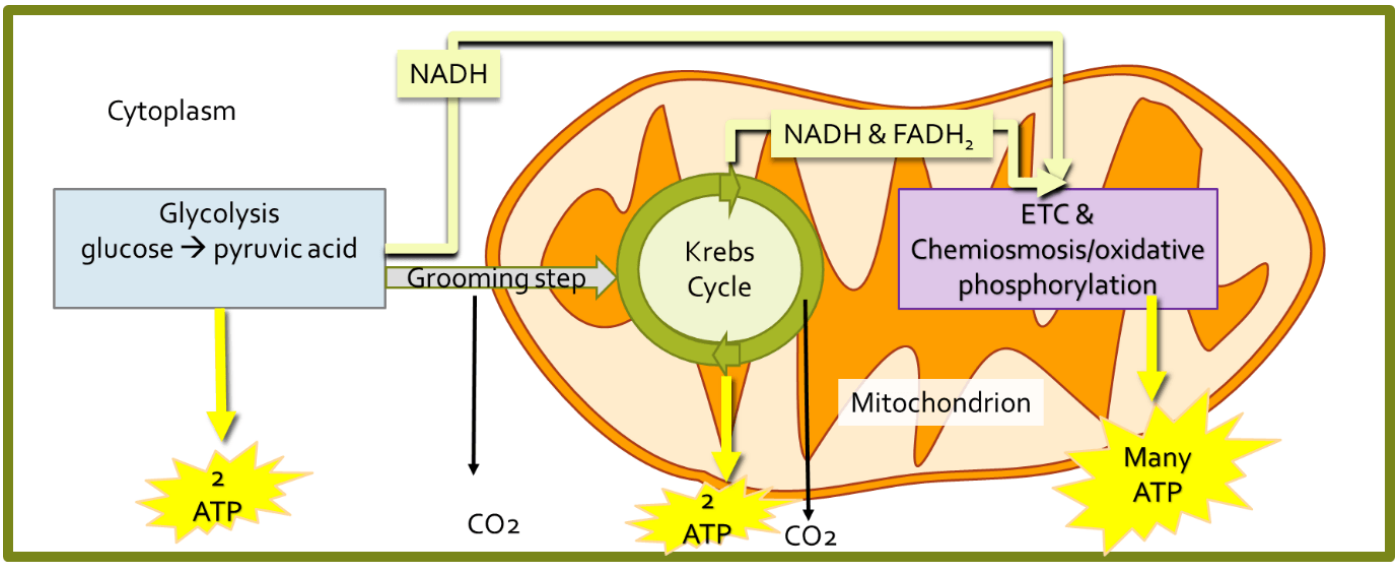


Figure 4-11. Cellular respiration within a cell. Stephanie Harvey. 2019-CC-BY

4.2.1: Required Reactants

4.2.2: Glycolysis

4.2.3: Citric Acid Cycle (Krebs Cycle)

4.2.4: Electron Transport System and Oxidative Phophorylation

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4.2.1: Required Reactants

$C_6H_{12}O_6 + 6\ O_2 \text{ --> } 6\ CO_2 + 6\ H_2O + ATP$

Figure 4-10. Summation Equation for Cellular Respiration.

The summation equation is similar to what we saw with photosynthesis but is reversed. In photosynthesis the goal was to build a sugar. For cellular respiration, the goal is to breakdown a glucose to produce the more cellularly friendly ATP. It requires glucose and oxygen while it releases carbon dioxide, water, and energy. The need for oxygen makes this an aerobic process. ATP production is possible via an anaerobic process, but it is far less efficient and not carried out long term in any plant tissues.

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4.2.2: Glycolysis

The first stage in the extraction of usable energy from glucose is glycolysis. This mechanism can be part of aerobic cellular respiration or can be used anaerobically (without oxygen) with fermentation to extract a small amount of energy from glucose (Figure 4-12). Glycolysis yields only 2 ATP and 2 NADH. If oxygen is not present to allow cellular respiration to occur, fermentation must occur to oxidize NADH back to NAD+. Without NAD+ to accept electrons in glycolysis, glycolysis would stop.

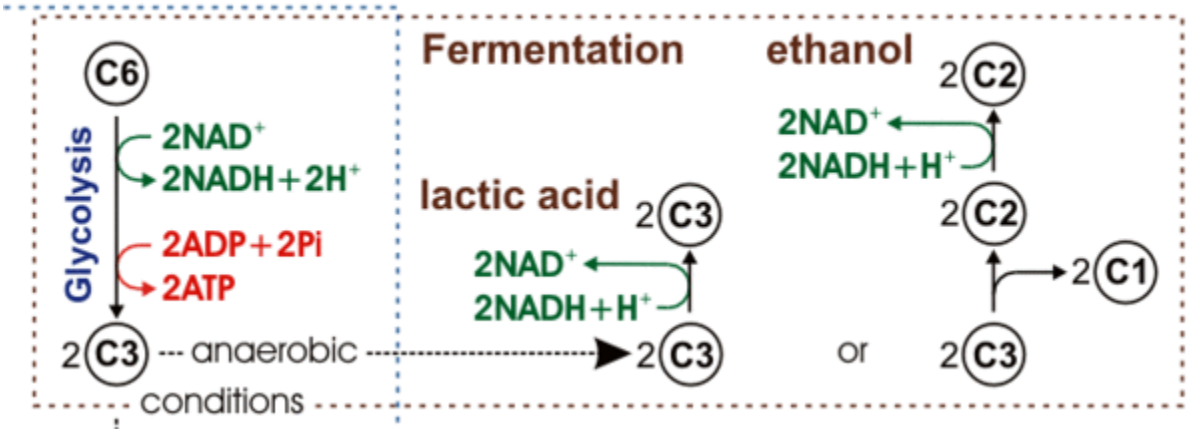


Figure 4-12. Glycolysis with fermentation variants. Diagram of glycolysis with fermentation: glucose (6 carbons) is split into two 3-carbon molecules, reducing 2 NAD+ to 2 NADH and producing 2 ATP. Under anaerobic conditions, fermentation regenerates NAD+ by producing either lactic acid (3 carbons) or ethanol (2 carbons) plus carbon dioxide. (By Darekk2 - Own work, CC BY-SA 3.0, https://commons.wikimedia.org/w/inde...curid=21712725)

There are two types of fermentation. Lactic acid fermentation is where the electrons from the NADH are passed to the three carbon products of glycolysis thus creating lactic acid. In ethanol fermentation, the 3-C product is de-carboxylated (it loses carbon dioxide) and then the resulting 2-C molecules are reduced by the electrons of the NADH, thus regenerating the NAD+ pool. The anaerobic breakdown of glucose thus yields only two ATPs. This small yield may be sufficient for a bacterial cell or single cell organism. It might also be a short term (very short) method of getting energy if oxygen is temporarily unavailable. For example, the oxygen debit seen during exercise or low/no oxygen situations for roots in flooded soils.

If aerobic cellular respiration is an option (Figure 4-13), the 2 3-C products (pyruvic acid/pyruvate) move into the mitochondria. Each is "groomed" by removing a CO_2 and the addition of Coenzyme-A. This yields two Acetyl CoA. Additionally, 2 NAD+ are reduced to 2 NADH during the grooming step. By the end of this step 2 CO2 have been released and 2 ATPs and 4 NADH formed. The two acetyl-CoA molecules can enter the Citric Acid Cycle.

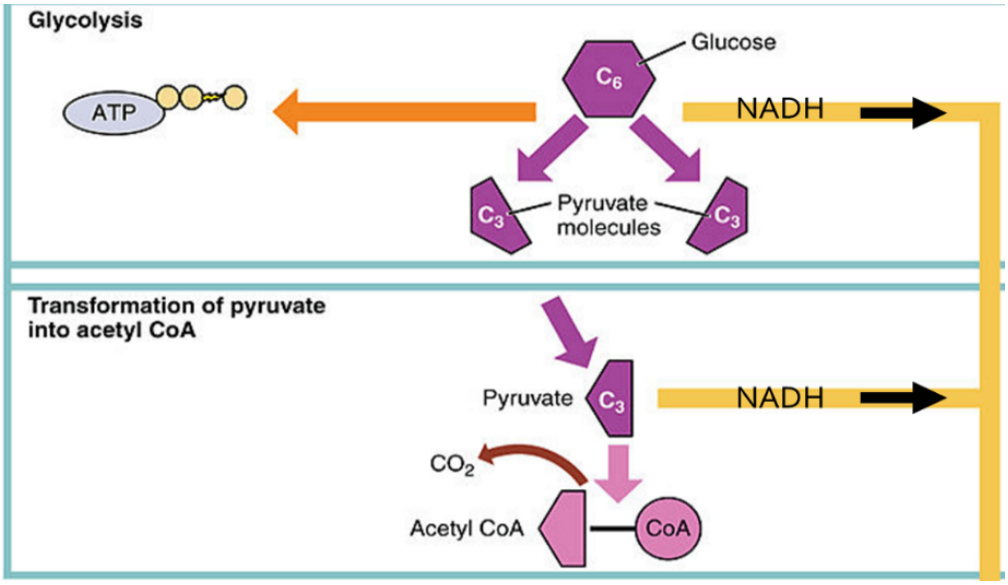


Figure 4-13. Glycolysis is the breakdown of a 6-carbon molecule into two 3-carbon pyruvates. This process produces ATP and NADH. The pyruvates are then groomed with the release of one carbon each as CO2 and NADH, and acetyl CoA. (By OpenStax College - Anatomy & Physiology, Connexions Web site. http://cnx.org/content/col11496/1.6/, Jun 19, 2013., CC BY 3.0)

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4.2.3: Citric Acid Cycle (Krebs Cycle)

Within the mitochondrial matrix (interior to the inner membrane) one of the acetyl-CoA (2-C) is added to a 4-C molecule to produce a 6-C molecule in the first step of the Citric Acid (aka Krebs) cycle (Figure 4-14) . To return to the 4-C molecule at the start of the cycle, 2 CO_2 molecules must be removed. Additionally, energy is transferred with the production so ATP, 3 NADH and 1 $FADH_2$. Remember that for each glucose that goes through cellular respiration we get two pyruvates and thus 2 Acetyl-CoA molecules.

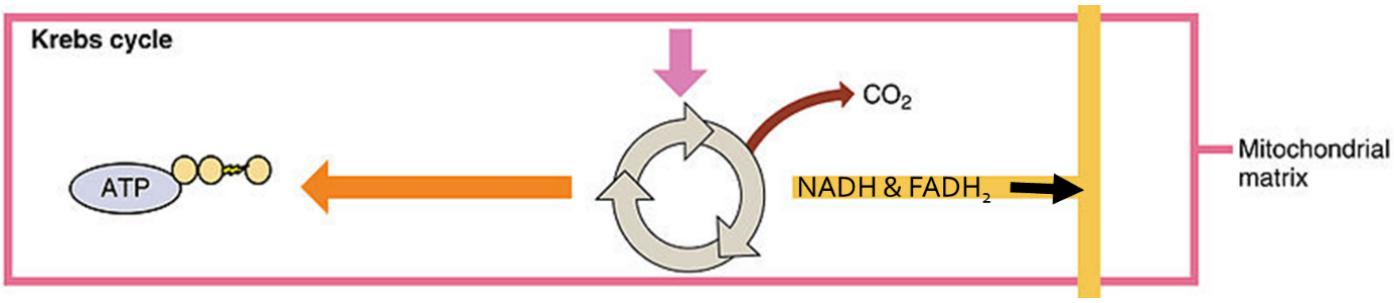


Figure 4-14. The Citric Acid Cycle produces in a single turn, 1 ATP, 3 NADH, 1 $FADH_2$ and 2 CO_2 molecules. By OpenStax College - Anatomy & Physiology, Connexions Web site. http://cnx.org/content/col11496/1.6/, Jun 19, 2013., CC BY 3.0.

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4.2.4: Electron Transport System and Oxidative Phophorylation

The electron carriers, NADH and $FADH_2$, pass their electron to the Electron Transport Chain (ETC) where they are passed through a series of electron acceptors (Figure 4-15). To keep the electrons moving cheaply, available electron acceptor is needed as the final electron acceptor; oxygen meets these requirements. The electrons passed to oxygen which combine with 2 H+ to produce water (H_2O). The redox reactions of the ETC power the movement of hydrogen protons (H+) across the inner membrane of the mitochondrion into the inner membrane space. This establishes a strong gradient that can subsequently power the oxidative phosphorylation of ADP to ATP via ATP synthase. This is the same process we saw in photosynthesis to produce ATP.

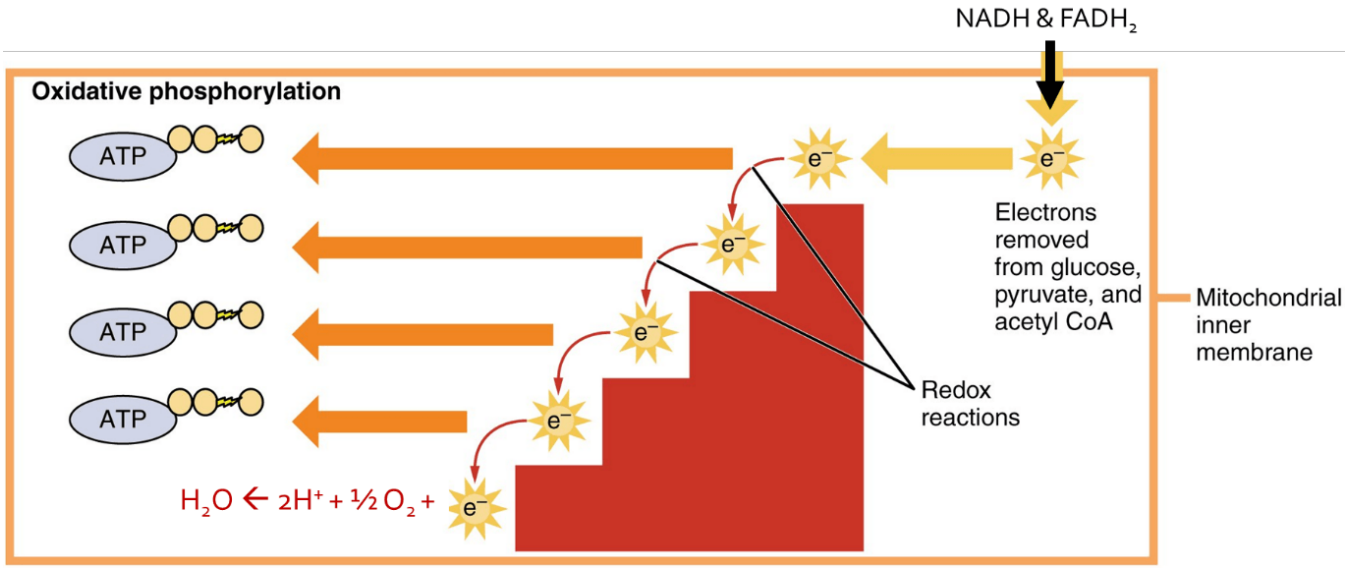


Figure 4-15. ETC powers the oxidative phosphorylation that creates ATP. The final electron acceptor is oxygen and produces a waste product of water. (By OpenStax College - Anatomy & Physiology, Connexions Web site. http://cnx.org/content/col11496/1.6/, Jun 19, 2013., CC BY 3.0.)

Note the oxidation of NADH and $FADH_2$ by the ETC sustains the pool of oxidized electron carriers (NAD+ and FAD) needed for glycolysis, the grooming step, and the Krebs cycle. Without this oxygen consuming process, the oxidized electron acceptor pool would be depleted and stop the production of most of the ATPs.

In summary a single glucose molecule can yield approximately 28-32 ATPs if it is completely oxidized. This yield can be lower for a specific molecule since throughout the process of cellular respiration intermediate molecules (pyruvic acid, for example) can be pulled away and used in the synthesis of other biomolecules.

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4.3: WATER AND NUTRIENT MOVEMENT

Plants are quite self-sufficient organisms since they can use light as an energy source. On of the elements they need in high quantities, such as carbon and oxygen, can be obtained from the atmosphere. However, the most limiting resource to plant growth is water followed by the nutrient nitrogen. In this lesson we will discuss water and nutrient uptake.



Figure 4-16. Roots play an active role in nutrient uptake. (Stephanie Harvey 2025 CC-BY-NC)

While oxygen, hydrogen and carbon can be easily obtained from the atmosphere, water and most other nutrients are extracted from the soil. The roots play a vital and active role in the uptake of nutrients along with water. And once absorbed, the water and its dissolved cargo must be transported throughout the plant (Figure 4-16).

4.3.1: Cell-to-Cell Movement of Water & Solutes

4.3.2: Transport and Transpiration

4.3.2.1: Bulk Movement within Phloem Tissue

4.3.2.2: Bulk Movement within Xylem Tissue

4.3.2.3: Transpiration

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4.3.1: Cell-to-Cell Movement of Water & Solutes

Along the length of a root, only the last few inches contribute significantly to absorption. The region of newly mature epidermis cell, specialized epidermis cells develop root hairs. Root hairs are not cells but extensions of the cell wall and cytoplasm of the epidermal cells. The roots dramatically increase the surface area in the region of the root and maximize absorption through osmosis and active transport.

Over 60% of the water-absorbent surface of the root comes from the root hairs. But root hairs are extremely fragile and short-lived (Figure 4-17). As the root grows and extends, new epidermis cells will mature and develop new root hairs. During transplanting seedlings, the damage to root hairs is extensive so it necessary to frequently water transplants for the first two weeks as root hairs are placed.

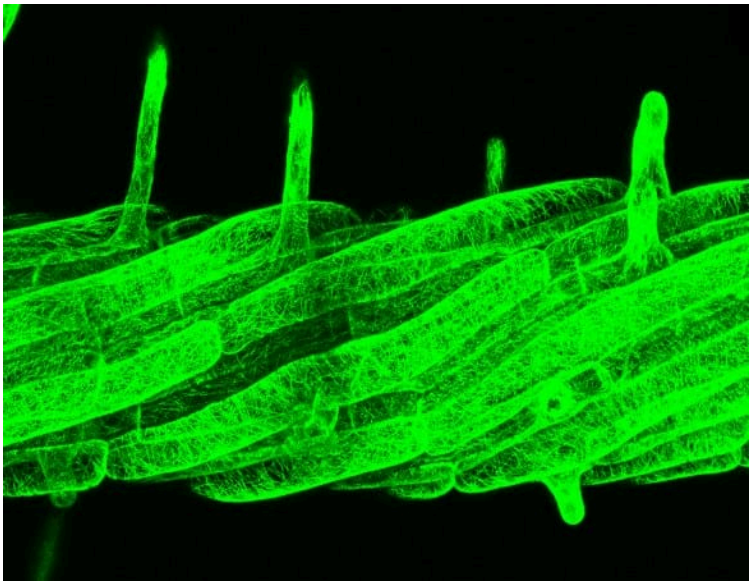


Figure 4-17. Root hair extending from individual epidermal cells. Photo by Dr. Masa Hiko Sato. Permission to use granted 8/1/2019 via personal communication.

Along with water, root must take up various nutrients. There are three processes by which these nutrients can be taken up depending on their concentration gradient and the charge of the nutrient (Figure 4-18). In simple diffusion, a solute dissolved in the water diffuses (moves) from an area of high concentration (the soil water surrounding the root hair) to an area of lower concentration (within the cytoplasm of the root hair or along its cell wall. This movement does not require any energy expenditure by the plant cells.

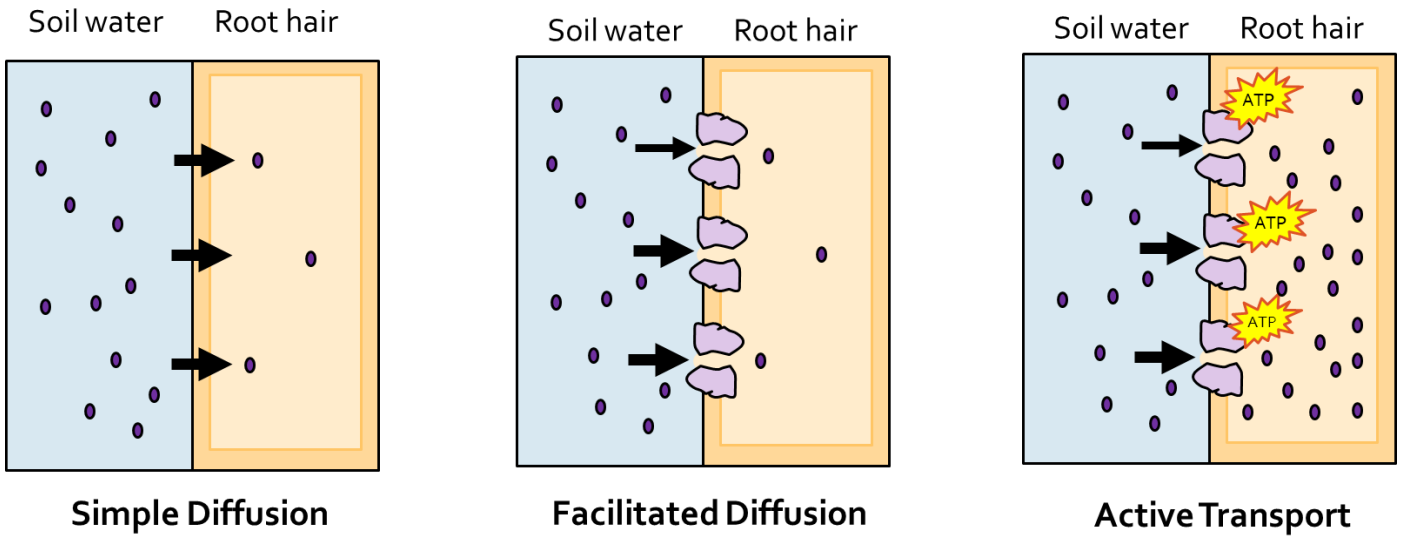


Figure 4-18. Three processes by which solutes move. A) Simple diffusion - with a high concentration of solute in soil water, solute will move from area of high concentration to lower (root hair). B) Like simple diffusion but solute must move into root hair via a protein channel. C) In Active transport, solute is moved against its gradient from low to high concentration area with the use of a protein pump and ATP. Stephanie Harvey. 2019 CC-BY-NC.

Facilitated diffusion works like diffusion but is aided by the presence of channel protein. These membrane proteins allow charged nutrients to move across the membrane and enter the plant cell. The proteins are needed due to the hydrophobic nature of the membrane which excludes most molecules with charges. No energy is expended directly to transport the nutrients, so this is considered a passive process. However, energy and other resources were used to produce channel proteins.

Active transport requires the use of specialized membrane proteins to pump nutrients across the membrane and is powered by ATP. Such pumps are required when a nutrient needs to move against its gradient. For nutrients that need to be accumulated at high concentrations within or outside a cell. Or when larger molecules that do not move easily across the membrane.

The epidermal cells of the root actively pump hydrogen protons into the soil solution to facilitate the uptake of some minerals in a process called Cation Exchange. We will discuss this in more detail when we cover soils.

Water and dissolved minerals can move into the root body and ultimately into the stele (the vascular cylinder) via two primary routes (Figure 4-19). As demonstrated by the purple line in the diagram, materials moving via the apoplast pathway remain outside the cell membrane (grey line) and instead move through the root via the cell walls. The cell walls are not solid structures but matrices of cellulose, hemi-cellulose and pectins. It is porous to water and other small molecules. This pathway avoids some of the regulatory properties of the cell membrane.

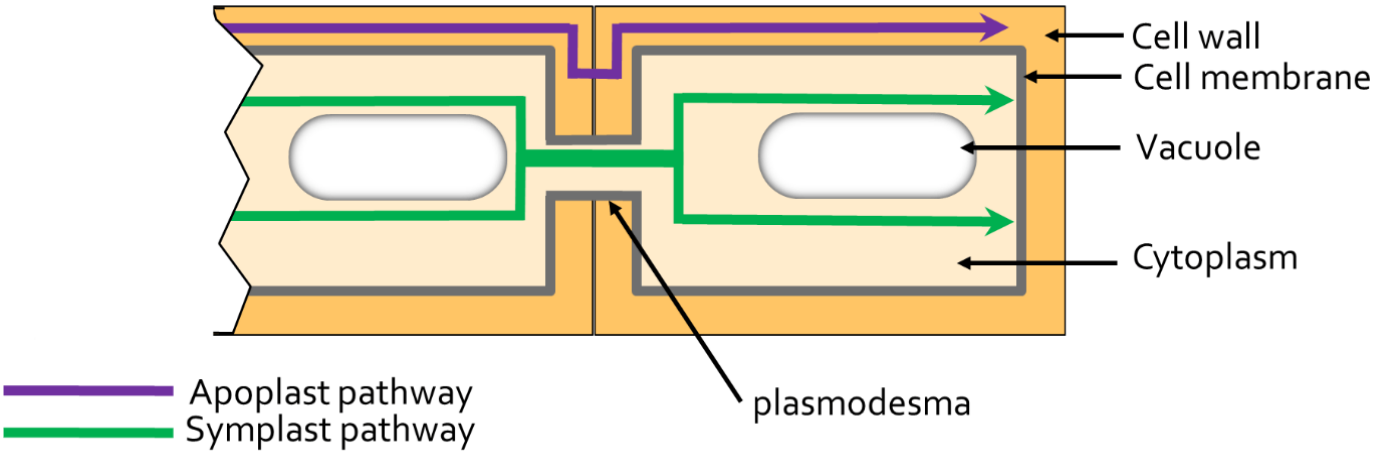


Figure 4-19. Minerals moving via the symplast must cross the membrane into a cell and then travel from cell to cell without crossing it again. Minerals in the apoplast do not cross a membrane. Stephanie Harvey. 2019. CC-BY

Materials moving along the symplast pathway (green line) enter a cell by passing through the cell membrane and becoming part of the cytoplasm. One inside one cell movement can continue to the next cell via plasmodesmata without re-crossing membranes.

At any point along their travel, water and dissolved minerals can switch paths. In fact, a third, infrequently seen, route has the materials crossing into a cell through the membrane (symplast) only to leave by exiting the membrane to move through the apoplast just to re-enter the next cell by crossing the membrane. This pathway is referred to as the transmembrane pathway, and it demonstrates how easy it is to move between the two spaces.

As the water approaches the stele, the vascular cylinder within the root, all water (with the dissolved minerals) is forced to take the symplast route through the endodermis (Figure 4-20– red cells). The endodermis is the inner-most layer of cortex cells and lies just outside the stele. These cells have a waterproof strip (the Casparian strip) that prevent water from entering the stele via the apoplast pathway. Essentially, the Casparian strip acts similar to weather stripping around a door or window, preventing leakage between or around the endodermis cells.

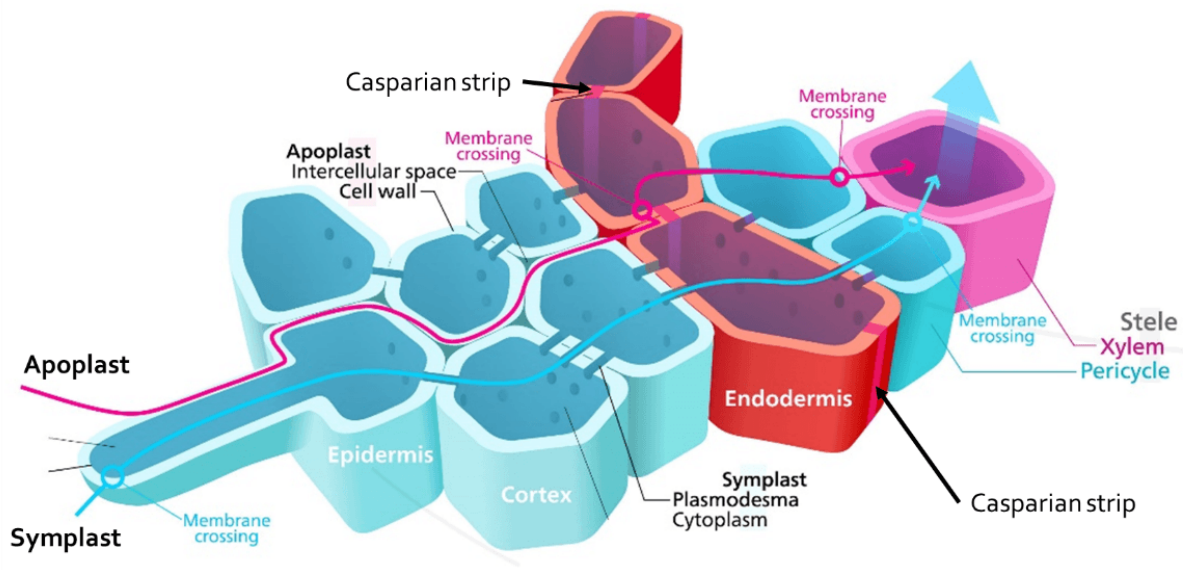


Figure 4-20. The endodermis, with its Casparian strip, forces the water and nutrients to use the symplast pathway to enter the stele. Diagram showing water movement from root hair to xylem in a plant root. Water enters through root hairs and travels across the cortex via two pathways: the apoplast pathway (through cell walls and intercellular spaces) and the symplast pathway (through cytoplasm via plasmodesmata). Water must pass through the endodermis, where the Casparian strip forces all water into the symplast pathway. Water then enters the xylem in the vascular cylinder for transport upward through the plant. (By Kelvinsong - Own work, CC BY-SA 3.0, https://commons.wikimedia.org/w/inde...curid=25917225)

Once through the endodermis, the water with it dissolved minerals can return to either pathway. However, it ultimately will enter the transport cells of the xylem. Since these cells are dead and thus have no cytoplasm, this pathway becomes apoplastic. In the next segment on transport and transpiration, we will look at how materials move throughout the plant.

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4.3.2: TRANSPORT AND TRANSPIRATION



Figure 4-21. Trees must transport fluid throughout their structures without the aid of a pump. Stephanie Harvey. 2023. CC-BY

Plants need to move materials (water, sugars, dissolved nutrients, and chemical messengers) through their tissues. Unlike the transport systems seen in many animals, plants lack a pumping organ (heart) to facilitate the needed movement (Figure 4-21).

In the section on absorption of water via root hairs, we discussed some mechanisms of cell-to-cell movement: this can be achieved via passive diffusion, facilitated diffusion and active transport. However, cell-to-cell movement is not very effective and only works for short distance transport. Efficiency drops dramatically with distances of over five cell lengths. For liverworts, hornworts, and the mosses – our non-vascular plants - this level of transport works but dramatically restricts their size.

For most plants, cell-to-cell movement is not satisfactory, and a long-distance transport is needed. This type of transport takes place in the vascular tissues – a collection of specialized transport cells and supportive non-transport cells.

Plant vascular tissues can be classified as two types: Xylem **tissue** is responsible for the unidirectional movement of water from roots to shoots. **Phloem tissue** is responsible for the source-to-sink movement of sugars. The direction of the flow in phloem is variable depending on the season, type of day or stage of growth. It can even move in different directions in different regions of the same plant.

4.3.2.1: Bulk Movement within Phloem Tissue

4.3.2.2: Bulk Movement within Xylem Tissue

4.3.2.3: Transpiration

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4.3.2.1: Bulk Movement within Phloem Tissue

Phloem Tissues

Sugars are transported from a source location via a process called translocation. The movement takes place in the sieve tubes of the phloem. The source of sugars could be the photosynthetic activity of a leaf cell or a storage cell located in a storage tissue like the cortex tissues of a root. Figure 4-22 provides a diagram of this process with corresponding numbers.

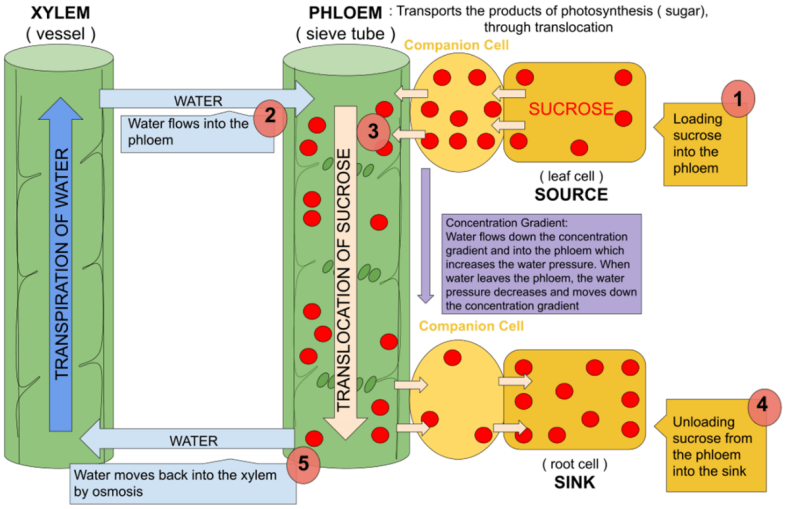


Figure 4-22. Translocation of sugars is performed by the sieve tubes of the phloem. Diagram illustrating sugar translocation from source to sink in plants. On the left, a green cylindrical xylem vessel shows upward water transport. Adjacent to it, a green cylindrical phloem sieve tube shows bidirectional movement of sucrose (represented as red dots). At the top, a yellow source cell (leaf cell) loaded with sucrose connects to the phloem. At the bottom, a yellow sink cell (root cell) receives sucrose from the phloem. Blue arrows indicate water movement: water flows from xylem into phloem at the source, increasing pressure, then returns to xylem at the sink as sucrose is unloaded. The diagram shows five numbered steps of the pressure-flow mechanism driving translocation. (By Alyssa Pham - Own work, CC BY-SA 4.0, https://commons.wikimedia.org/w/inde...curid=79163371)

Step 1 is the loading of sucrose into the phloem. Sugars move from the source cell into the companion cells which then load them into the sieve tube. The accumulation of sugar molecules creates a water gradient between the sieve tube (low water) and the vessels of the xylem containing water (high water). In **Step 2,** water flows from the xylem into the phloem. This creates hydrostatic pressure gradient and induces bulk flow within the sieve tube that pushes the sugars toward the sink (**Step 3**). The sink location is where the sugars will be stored or used, in our example it is a storage root cell. The sugars are unloaded by the companion cells and then moved into the storage root cell (**Step 4**). The loss of sugar from the sieve tube again creates a water gradient but now in reverse so the water moves from the sieve tube back into the vessel of the xylem (**Step 5**).

This process allows for the translocation of sugars in both directions. Sugars can be moved from the shoot to the root while photosynthesis is being carried out. Sugar can also be moved from root storage cells to shoot cells to power the flush of leaves in early spring. This same technique is how sugars are moved into fruits from leaves (typically the leaf cluster above the fruit). In this case the fruit is the sink.

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4.3.2.2: Bulk Movement within Xylem Tissue

Xylem Tissues

The movement of xylem “sap” (mostly water with dissolved mineral nutrients) occurs in the tracheary elements (transport cells) of the xylem. The system allows water to be moved from root cells to the shoot. This path is unidirectional; that is water cannot move from shoot to root.

Water enters the tracheary elements (tracheids and vessels element) in the root stele. Tracheary elements are dead at maturity and thus lack cytoplasm; they are essential hollow tubes. Two properties of water are critical in the movement of water through the xylem system. Water molecules experience significant cohesion due to the partial charges on the molecule. Cohesion means that the molecules stick together and in doing so create a strong column of water (Figure 4-23). Adhesion also contributes to the movement process by holding the water molecules in place and preventing them from “back-sliding” toward the roots. Adhesion of water molecules means the water is attracted to other materials like the cell walls of tracheary elements. The combination of cohesion and adhesion makes the water column very strong. You might have experienced this strength if you have ever tried to separate two pieces of glass that have a thin layer of water between them. It takes considerable effort to break the cohesion and adhesion forces.

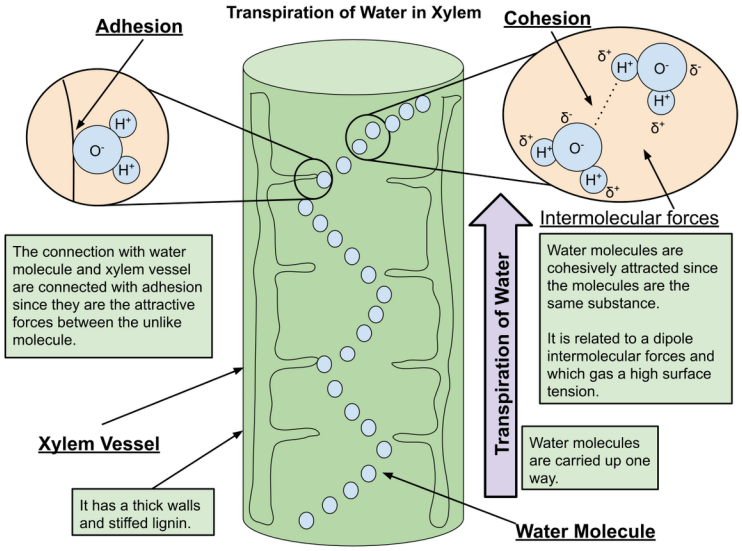


Figure 4-23. Movement of xylem sap is powered by transpiration via evaporation. Diagram of water moving up a xylem vessel, titled Transpiration of Water in Xylem. Water molecules form a continuous column inside the thick, lignified vessel. Callouts explain adhesion (water molecules attracted to the vessel wall) and cohesion (water molecules attracted to one another by intermolecular forces), and an arrow shows water being pulled upward by transpiration. (By FeltyRacketeer6 - Own work, CC BY-SA 4.0, https://commons.wikimedia.org/w/index...curid=79163087)

Cohesion and adhesion alone do not move the water, however. The water column moves upward due to tension placed on the water column. This tension (negative pressure) is created as water molecules evaporate from cells and diffuse out of the leaves and stems of the shoot. So, the loss of water molecules at the leaves (a process known as **transpiration**), causes the entire column of water to be pulled upward. This explanation of water movement is referred to as the Cohesion-Tension theory.

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4.3.2.3: Transpiration

Transpiration

Transpiration is the process of water evaporating from aerial organs (leaves, shoots, flowers, and fruit). Due to the cuticle and waxy layers that cover the epidermis of the shoot, very little water evaporates through the epidermal layers. Of the water loss by a plant 95% leaves through stomata. A stoma (singular form) is a pore in the epidermis that allows for gas exchange and water loss. Transpiration losses (and guttation which will be discussed later) account for 97-99.5 % of the water taken up by plant roots (Figure 4-24).

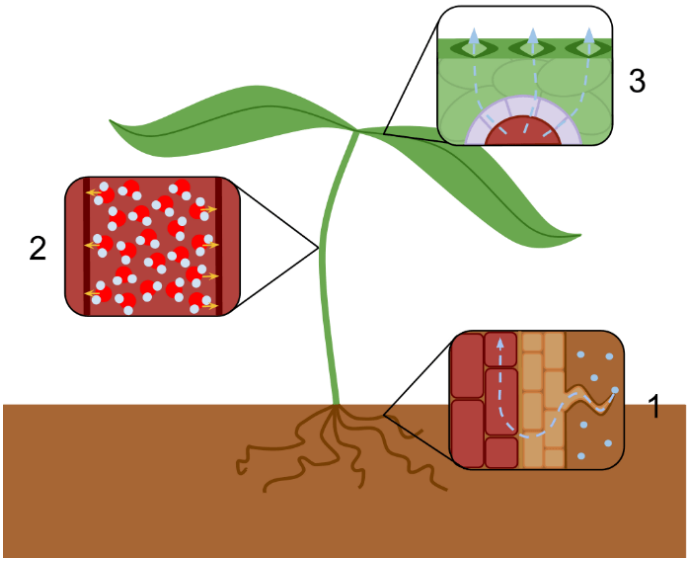


Figure 4-24. This illustration depicts the pathway of water from soil to air and provides a nice summary for the movement of water in plants. Diagram of a plant showing the path water takes from the soil to the air, with three numbered insets: 1) water entering a root and moving across the cortex to the xylem; 2) a column of water in the xylem; 3) water evaporating from the spongy mesophyll of a leaf out through an open stomatal pore. The numbered steps are described in the text. (By Laurel Jules - Own work, CC BY-SA 3.0, https://commons.wikimedia.org/w/inde...curid=26331125)

1-Water molecules from the soil enter the roots passively, passing through the cortex, and are guided to xylem tissue by the Casparian strip. A concentration gradient of solutes within the xylem leads to further passive transport of water into the vessel elements or tracheids.

2-Once the water has entered the xylem, the forces of adhesion and cohesion take effect. Adhesion causes the molecules to adhere to sides of the vessels, and cohesion causes the molecules to adhere to each other, forming a column of water that extends from the roots to the top of the plant.

3-Water from the xylem is let into the spongy mesophyll, where it can come into contact with stomata. When the stomata are open, the cells in this layer are exposed to the outside air, and evaporation occurs. When water molecules evaporate out of the stomata, they create tension in the water column, as the forces of cohesion pull nearby molecules up with them, creating pulling force down the length of the xylem.

While we often consider transpiration in a negative light, it does have positive aspects like powering the movement of water in the xylem. In addition to providing the mechanism for water movement, transpiration also helps cool plant surfaces through evaporative cooling. As water transitions from a liquid to a gas, heat is removed from the surface on which the evaporation occurs. This can prevent overheating of leaves exposed to excess solar radiation.

Excessive water loss, however, is detrimental to plants. Since stomata are the primary site of water loss, plants have evolved specialized cells to help regulate transpiration. Two specialized cells, guard cells, surround the stomatal pore (Figure 4-25) and control the aperture of the opening. During photosynthetic periods, the guard cells are turgid, and the pore is open to allow for

the gas exchange necessary for the process. However, if water loss becomes critical, this can be overridden, and the guard cells become flaccid, and the stomata is closed.

While closure of the stomata allows for water conservation, photosynthetic productivity declines and plants can undergo photorespiration (further cost to the plant). The struggle between water conservation and photosynthetic productivity is significant and a species ability to minimize the impacts of the necessary compromises may mean the difference between thriving and surviving.

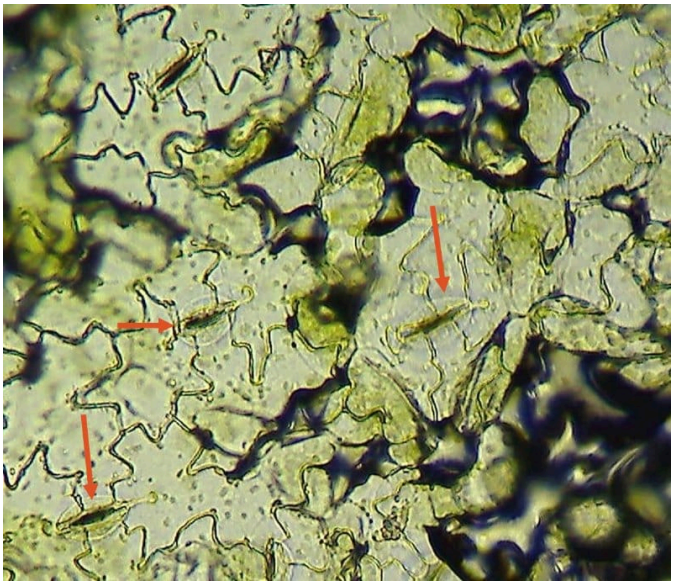


Figure 4-25. Lower epidermis removed from a spinach leaf. Layer is slightly green due to "spilled" chloroplast during the removal process. Orange arrows indicate stomata with guard cells. By Stephanie Harvey. 2023. CC-BY-NC

Before we leave the concept of water movement in plants, we should discuss root pressure and the observable phenomenon of **guttation** (Figure 4-26). When soil moisture is high, water pressure in the soil can push water into the plants; a process defined as root pressure. Root pressure was once thought to be responsible for water movement from root-to-shoot, but the pressures achieved were too low to account for its movement in plants over one foot tall. It can however contribute, and in small plants can supply enough pressure to move water through the entire plant.

When root pressure is high and transpiration is not occurring (typically at night), the internal pressure can force water through release valves called **hydathodes**. These small valves are located at the ends of leaf veins. The small droplets of water clinging to the leaves in early morning are often mistaken for dew. However, as you can see in this image of strawberry leaves, the position of the drops aligns with the termination of a leaf vein at the leaf margin.



Figure 4-26. Guttation is the exudation of drops of xylem sap due to root pressure. It is often mistaken for dew. (Stephanie Harvey, 2026 CC-BY-NC)

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4.4: Plant Hormones



Figure 4-27. Inflorescence of Devil's club (*Oplopanax horridus*). By Stephanie Harvey. 2023. CC-BY-NC

In plants, growth, development, and regulation is governed by hormones (Figure 4-27). Hormones are signal molecules that at extremely low concentrations illicit a response in a target tissue. Plant hormones – called **phytohormones** are slightly different than animal hormones in that the target tissue for plants can be the same tissue (tissue of origin) in which the hormone was produced. For Animal hormones the target tissue must be different from the tissue of origin.

This may seem like a dramatic change in focus, but it is these signaling molecules that regulate, and control, may of the processes we discuss earlier in this chapter.

Historically, there were five phytohormones: abscisic acid, auxin, cytokinins, ethylene and gibberellins. However, in recent years four more have been added to the list: brassinosteroids, jasmonates, salicylic acid and strigolactones.

Table 4-2 lists these nine phytohormones and their general activity. Please note that for most plant growth, development and regulations, there are multiple phytohormones involved and it is their relative concentration that effects change in the plant or plant tissue.

Table 4-2. *Phytohormones can be grouped into classes.*

Hormone class	Abbreviation	General activity
Abscisic acid	ABA	Growth inhibitor, drought responses
Auxins	IAA, IBA, IPA	Cell enlargement, bud formation and root initiation
Brassinosteroids	BR	Cell division and growth regulation (potential cancer treatment?)
Cytokinins	CK	Cell division and shoot formation
Ethylene	C_2H_4	Fruit ripening; cell growth and cell shape
Gibberellins	GA	Promotes seed germination, internode elongation
Jasmonates	JA	Plant defense; seed germination
Salicylic acid	SA	Plant defense; response to abiotic stress
Strigolactones	SL	Promotes growth of mycorrhizal fungi; shoot branching

Auxins

Auxins were the first of the major phytohormones discovered. This class of phytohormones was first described by Frits Went in the 1920's although their effects were noted far earlier. In general, auxins are often described as juvenility hormones due to their roles in growth and development. There are a number of different forms of auxin (IAA, IBA, IPA). Auxin is present in all plant tissues. The concentration of auxin (relative to other phytohormones) at specific locations is critical to guiding plant development and response to the environment.

In terms of plant growth, auxins trigger cell elongation (particularly in combination with gibberellins) and cell division (if cytokinins are present). From a developmental standpoint, auxins are critical to the formation and organization of the vascular tissue (xylem and phloem) and are important in root initiation. They also induce shoot apical dominance which impact the architecture of the plant. They also play a role in fruit growth, development, and delays fruit senescence (dropping from the tree).

Auxins also turn up in other places. In Figure 4-28, the tumor-like growth as crown galls that have formed due to a bacterial pathogen (*Agrobacterium tumefaciens*). The bacteria excrete auxin and cytokinin in ratios that trigger cell division leading to the formation of these tumors. Another interesting place to find auxins is in herbicides. At high concentrations, auxins will kill plants. The herbicides 2,4-D and 2,4,5-T are synthetic auxins.



Figure 4-28. Crown galls are caused by *Agrobacterium tumefaciens* bacteria; they produce and excrete auxin and cytokinin, which interfere with normal cell division and cause tumors. (This image is Image Number 1436062 at Forestry Images, CC-BY-SA)

Gibberellins

Gibberellins (Gibberellic Acid or GAs) were first discovered in rice plants infected with fungi. The fungus produced exogenous GAs that induced the rice plants to grow extremely tall. The condition was called "foolish-seedling disease" because the plants grew so tall that when they produced seeds, they could not support the added weight and fell over. Similar compounds were discovered to naturally occur in plants and to induce stem elongation via internode elongation. GAs are involved in the natural process of breaking dormancy and other aspects of germination.

GA and GA inhibitors are used in multiple horticultural industries to control plant and fruit development. For example, GAs are applied to table grapes to trigger internode elongation within fruit cluster so that there is more room to produce larger grapes. Alternatively, many ornamental plants (like mums) are treated with GA inhibitors to prevent internode elongation. This creates tight, compact plants that are visually appealing (Figure 4-29). It is thought that the "green revolution" of the 1960 was due in part to selectively breed plants deficient in GAs and thus creating higher yielding cultivars.



Figure 4-29. The tight compact form seen in these chrysanthemums is due to the use of GA inhibitors. By Jebulon - https://commons.wikimedia.org/w/inde...curid=17194779

Brassinosteroids

Brassinosteroids are a class of plant hormones that were first discovered in the 1970's by researchers studying plant growth. The first brassinosteroid identified was brassinolide, which was isolated from rapeseed pollen. Since their discovery, over 50 different brassinosteroids have been identified in plants. Since Brassinosteroids are found throughout the plant kingdom and are essential for normal plant growth and development, they were added eventually added to the list of phytohormones.

The key role of brassinosteroids is to regulate cell elongation and cell division. Brassinosteroids cause cells to elongate and divide, stimulating growth (Figure 4-30). They interact with other plant hormones like auxins and gibberellins to control developmental processes like germination, photomorphogenesis, and flowering. Brassinosteroids are especially important for stem elongation, vascular differentiation, and fruit development. Mutant plants unable to synthesize brassinosteroids show stunted growth and abnormal development. The application of brassinosteroids can rescue these defects, underscoring their significance as growth-promoting hormones in plants.



Figure 4-30. Plant on left is Brassinosteroid deficient. Plant on right is normal. (https://www.psb.ugent.be/groups/brassinosteroids)

Cytokinins

Cytokinins are a class of plant hormones that promote cell division and were first discovered in the 1950's. The first cytokinin compound identified was kinetin, which was isolated from autoclaved herring sperm DNA. Since then, over 25 naturally occurring cytokinins have been found in plants. Cytokinins are synthesized in actively growing tissues like roots and shoots and can move to other parts of the plant.

The key functions of cytokinins include regulation of cell division and shoot initiation and growth. Cytokinins stimulate the formation and activity of shoot meristems, areas of cell division that enable plant growth. They also promote chloroplast development and delay leaf senescence. Cytokinins interact with other plant hormones like auxins to coordinate plant development. Some key developmental processes regulated by cytokinins include embryogenesis, apical dominance, root growth, and nutrient mobilization. Mutant plants with reduced cytokinin synthesis or signaling capacity exhibit stunted shoot growth and defects in vascular development. Exogenous application of cytokinins can restore normal growth, highlighting their essential role in plant growth and morphology. Recent research indicates they may also play a role in pathogen resistance.

Ethylene

Ethylene is an interesting phytohormone because it is a gas. At trace levels it stimulates/regulates ripening of fruits, opening of flowers and abscission of leaves. Ethylene is autocatalytic – that is, exposure to ethylene triggers (up-regulates) production of ethylene. This can be problematic in postharvest situations since ethylene is also produced in response to wounding. So, if a single apple is bruised or punctured during transport, it begins to produce high levels of ethylene which will trigger all the surrounding apples to produce ethylene thus speeding up their own ripening and eventual spoilage. This scenario is where the saying “one rotten apple can spoil the whole barrel” comes from.

Being able to control ethylene and thus the ripening process has made some fruits more marketable. For example, bananas can now be harvested when mature but not ripe, shipped in containers that scrub (absorb) ethylene released and then ripened by exposure to ethylene at their destination. In other fruits, it does not induce ripening but does cause de-greening. Most of our fresh market citrus is treated with ethylene to produce a nice, uniform orange color (Figure 4-31).



Figure 4-31. Tinges of green on imperial mandarins can be removed with applications of ethylene. (https://www.abc.net.au/news/rural/20...life/102320506

Abscisic Acid

Abscisic Acid (ABA) is important in several processes. It often works antagonistically to growth stimulating hormones like cytokinins, auxins and gibberellins. ABA (as its name suggests) was once thought to be involved in the abscission of plants organs (leaves, buds, fruits) but is now known that this is true in only a few plants. ABA induces dormancy in buds by slowing the growth of

within the bud and forces the formation of bud scales that protect the delicate bud tissues throughout winter. Another winterizing effect is that ABA inhibits the cells of the vascular cambium from dividing. This helps the plant adjust to cold conditions by suspending primary and secondary growth.

ABA also inhibits seed germination and can prevent the loss of seed dormancy. The relative concentrations of the ABA to GA determines if the seed will break dormancy or not. In most cases, seed remain dormant while attached to the parent plant. In mangrove plants (Figure 4-32), a drop in ABA trigger seed germination early. This produces an elongated spike-like root. When the seed falls the spike sticks into the mud and prevents the seed/seedling from washing away with the tides.



Figure 4-32. Vivipary is common in mangrove plants where seed germinate while still attached to the trees. (Prony, New Caledonia; Photo N.C. Duke 2006)

In addition, ABA plays an important role in a plant's response to environmental stresses such as drought, salinity, wounding, and extreme temperatures. Under water stress situations for example, ABA induces stomatal closure (overriding the blue-light signal to open them) and stimulated root production. This minimizes water loss and improves the plant's ability to uptake water.

Jasmonates

Jasmonates (JA) are critical for plants defenses against herbivory. They, like ABA, also play a role in the plants' ability to respond to biotic and abiotic stress. Some JA are volatiles organic compounds (VOCs). Released into the air in response to damage by a pathogen or herbivore, JA communicates the danger to adjacent plants. The adjacent at-risk plants are able to up-regulate their defense mechanisms.

Salicylic Acid

Salicylic Acid is involved in the system acquired resistance (SAR) seen in plants. SAR is often likened to the immune system seen in animals, although it lacks the specificity seen in our immune system. When a pathogen attacks part of a plant, salicylic acid is released and induces the production of special proteins and induces resistance to the pathogen in other parts of the plant. The signal can also move to nearby plants as salicylic acid is modified to a volatile form.

Strigolactones

Strigolactones are a new class of plant hormones that were first discovered in the 1960's during studies on seed germination. Strigolactones were originally isolated as germination stimulants for parasitic plant seeds. It was not until the 2000's that strigolactones were identified as a new class of plant hormones in plants. Since then, over 20 naturally occurring strigolactones have been found across the plant kingdom.

The primary role of strigolactones is to inhibit shoot branching. They suppress the growth of axillary buds, limiting the outgrowth of new shoots. This helps regulate above-ground architecture and branching patterns. Strigolactones also promote root growth and root hair elongation, enabling better nutrient scavenging. They interact with other plant hormones like auxins and cytokinins to control plant development. Mutant plants unable to synthesize strigolactones show excessive shoot branching and reduced root growth. Exogenous strigolactone application restores normal branching patterns, demonstrating the key growth regulatory effects of this hormone class in plants. Strigolactones also facilitate beneficial symbiotic associations between plant roots and mycorrhizal fungi.

Interactions

Early on in the study of phytohormones, scientists were looking for signal molecules that would control specific aspects of plant growth. Today, we know that plant responses, growth and development are typically under the control of several hormones. The developmental direction a tissue takes is determined by the ratio of multiple hormones. For example, in tissue culture the ratio auxin to cytokinin will determine if cells develop into shoots or roots.

In Figure 4-33, a purple coneflower (*Echinacea purpurea*) exhibits the condition of phyllody. This is a plant abnormality that occurs when leaf-like structures replace the floral organs. Phyllody is caused by a hormonal imbalance.



Figure 4-33. Phyllody on a purple coneflower (Echinacea purpurea), a plant development abnormality where leaf-like structures replace flower organs. (By Estreya - Own work, CC BY-SA 3.0, https://commons.wikimedia.org/w/index.

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4.5: End of Chapter Review

- Photosynthesis is the process plants use to convert light energy into chemical energy in the form of carbohydrates. It takes place in chloroplasts and involves light-dependent reactions that produce ATP and NADPH, and light-independent reactions (Calvin cycle) that fix CO_2 into sugars.
- Cellular respiration breaks down sugars to release energy in the form of ATP. It takes place in mitochondria and involves glycolysis, Krebs cycle, electron transport chain, and chemiosmosis.
- Water and minerals are absorbed by root hairs through passive and active transport. Root pressure and transpiration help move water and minerals through the xylem.
- Sugars are transported through the phloem tissue via translocation. This process relies on pressure gradients created by loading and unloading sugars.
- Transpiration helps cool plants and facilitates water movement through xylem but must be balanced against water loss through open stomata. Guard cells regulate transpiration rate by opening and closing stomata.
- Plant hormones like auxins, cytokinins, gibberellins, etc. regulate growth, development, and responses to stimuli at very low concentrations. They often work together in complex ways.

Key Terms

- Abscisic Acid
- Adhesion
- Auxins
- Calvin Cycle
- Cellular Respiration
- Chemiosmosis
- Chlorophyll
- Chloroplast
- Cohesion
- Cytokinins
- Electron Transport Chain
- Ethylene
- Gibberellins
- Glycolysis
- Guard cells
- Krebs Cycle
- Light-dependent reactions
- Light-independent reactions
- Photosynthesis
- Phytohormones
- Stomata
- Thylakoid
- Transpiration

Self-Review

1. In which organelle does photosynthesis take place?
2. What are the products of the light-dependent reactions?
3. What is the main enzyme involved in carbon fixation during the Calvin cycle?
4. What are the three phases of the Calvin cycle?
5. Where in the cell does cellular respiration occur?
6. What are the products of glycolysis?
7. How many ATP molecules are produced from the complete breakdown of one glucose molecule during cellular respiration?
8. What provides the driving force for water movement through xylem?
9. Through what leaf structures do most water loss occur?
10. What cells regulate the opening and closing of stomata?

11. In what vascular tissue does translocation of sugars occur?
12. What physiological process involves the loading and unloading of sugars into phloem?
13. At what concentrations do plant hormones elicit responses?
14. Which hormone stimulates shoot growth and lateral bud development?
15. Which hormone induces seed and bud dormancy?

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5: LIGHT- AN ABIOTIC INFLUENCE ON PLANTS

With the fundamentals of plants – diversity, structure and function complete. We can now take a look at how abiotic (non-living) components impact plants. In this chapter we will look at light.

As discussed previously, photosynthesis requires light as its energy source. Plants, as photoautotrophs, need light. It should be noted however that not all plants are photosynthetic. Some plants, like the American cancer-root (*Conopholis americana)* are achlorophyllous (Figure 5-1). That means they lack chlorophyll. Since these plants do not photosynthesis, they need another source of energy. They are chemoheterotrophs like fungi and animals. They get their energy and organic carbon by parasitizing other plants. They feed off the sugars stored in the roots of woody plants. So technically light does provide their energy but only indirectly through the food web.



Figure 5-1. Not all plants are photosynthetic. *Conopholis americana*, American cancer-root or bear corn, is a non-photosynthesizing. parasitic plant. (Stephanie Harvey. 2019. CC-BY-NC)

Since light is a critical abiotic factor for life on our plant, whether directly or indirectly, we will look at multiple aspects of light: physics of light, quality of light and the quantity of light. We will discuss some ways that plants respond to light and finish with how we as humans can manipulate light to impact plant growth and function.

5.1: Physics of Light

5.2: Light Quality

5.2.1: Visualizing Light Quality

5.2.2: Refraction and Reflection

5.2.3: Non-photosynthetic Uses of Light

5.3: Light Quantity

5.3.1: Daily Light integral

5.3.2: Plant Light Requirements

5.4: Plant Responses to Light

5.4.1: Photosynthetic Responses to Light

5.4.2: Non-Photosynthetic Reponses to Light

5.4.3: Photoperiodism
5.4.4: Phototropism

5.5: Light Manipulation

5.5.1: Shading
5.5.2: Artificial Lighting
5.5.3: Lighting Sources

5.6: End of Chapter Review

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5.1: Physics of Light

The electromagnetic spectrum consists of all known forms of electromagnetic radiation (Figure 5-2). This includes radio waves, microwaves, ultraviolet, X-rays, gamma rays, infrared and visible light. Types of electromagnetic radiation can be described based on their respective wavelengths, frequencies and photon energies.

Figure 5-2 provides both the frequencies and wavelengths (in meters) for the various types of radiation. Additionally, they have provided an approximate scale to help you visualize the differences. The energy of this spectrum travel as waves and differ parts of the electromagnetic spectrum have different wavelengths. A wavelength is the distance from one crest to the next crest of the wave. The largest wavelengths are radio waves with a range of wavelengths from 1 millimeter to 1000 meters. At the other end of the spectrum, we have gamma rays with wavelengths at 10^{-12} meters (around 0.000000000001 M or one picometer or 1 trillionth of a meter). For scale, a radio waves wavelength could be as long as the height of skyscrapers while gamma rays are the width of an atomic nucleus.

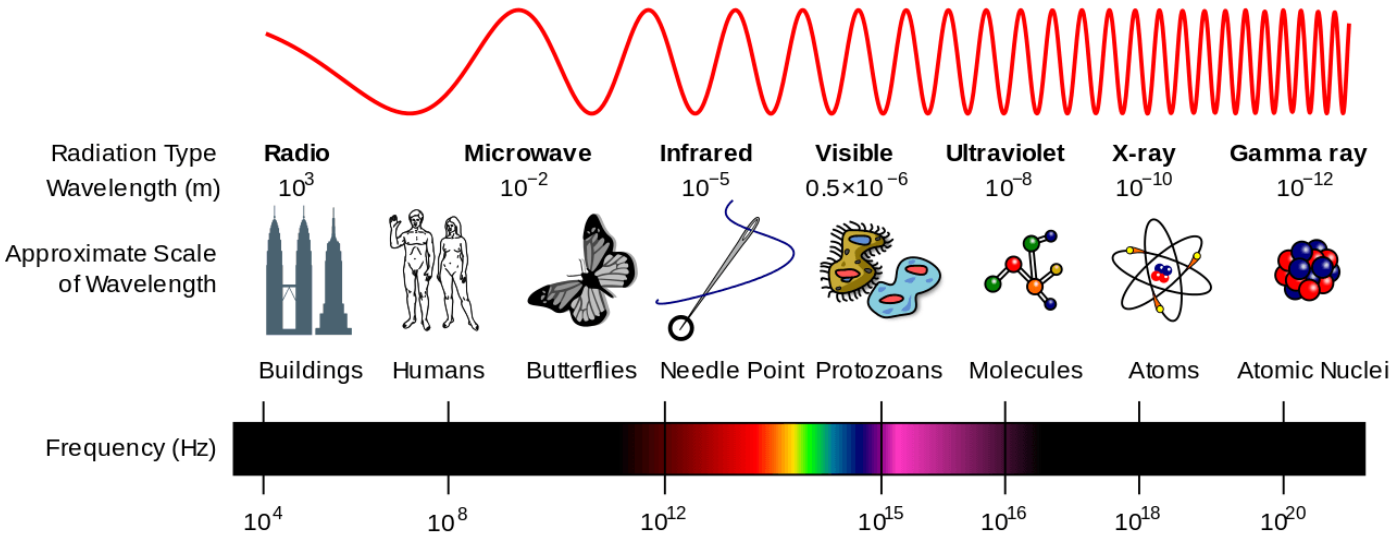


Figure 5-2. Electromagnetic spectrum shows the relationship between wavelength and frequency. The images provide a visual scale to help with understanding sizes. (By Inductiveload, NASA - self-made; https://commons.wikimedia.org/w/inde...?curid=2974242)

There is a relationship amongst the wavelength, frequency and photon energies of electromagnetic radiation. The wavelength (identified using λ - Greek letter lambda) is inversely proportional to the wave's frequency (*f*) and the frequency is directly proportional to the photon energy(*E*). This means that as the wavelengths get longer their frequencies decrease and energy decreases as well. For example, a microwave with lambda of 10^{-2} m has a frequency of 10^{10} Hz, while X-rays with lambda 10^{-10} m (smaller) has a frequency of 10^{18} Hz (larger). The higher the frequency the more energy. This is why we are concerned about exposing our bodies to too many X-rays (high energy) but not concerned about radio waves (low energy).

Visible light (VL) is only a small range of the electromagnetic spectrum with wave lengths of 400 nm (4 x 10^{-7} m) to 700 nm (7 x 10^{-7} m) (Figure 5-3). The range for VL is literally "in the eye of the beholder." The range will shift with species and even within species. Some large cats can see further into the long wavelengths while many insects can see deeper into the UV range. Even amongst humans, the range for "visible light" can vary.

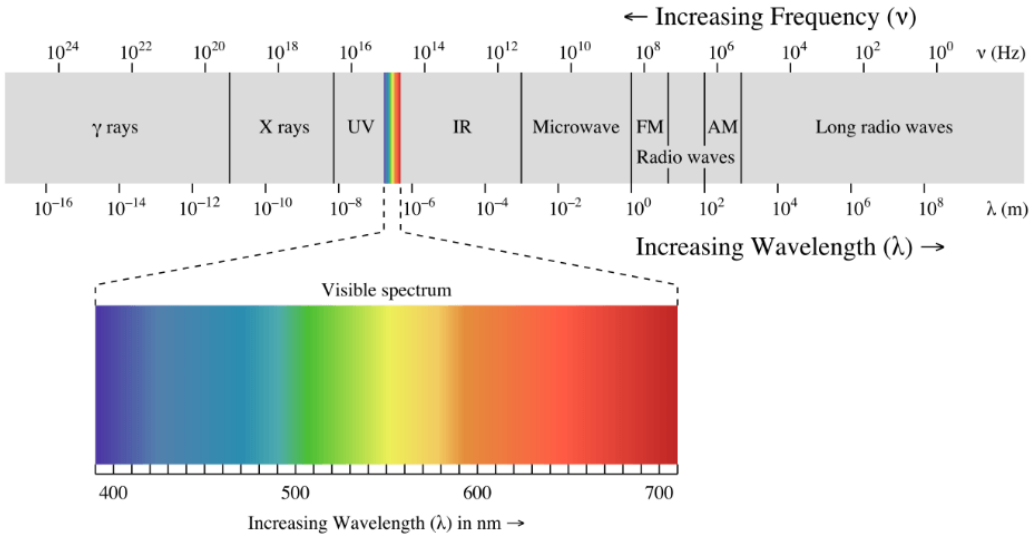


Figure 5-3. The visible light spectrum is but a small region of the electromagnetic spectrum. The top section of the image shows the relative size of the VL spectrum compared to the other spectrums. The lower image zooms in to show the region that comprise the VL spectrum (CC BY-SA 3.0, https://commons.wikimedia.org/w/inde...?curid=2521356)

Light is often described by its wavelength, however for physiological activities such as photosynthesis, it is often easier to describe it in terms of photons – discrete packages of light energy. As was mentioned earlier, as wavelengths increase, frequencies decrease. This also hold true for the energy of photon.

Table 5-1. *Chart of colors with their associated bands of wavelength, frequency, and photon energy. THz = terahertz. eV=electronvolts.*

Color	Wavelength	Frequency	Photon energy
Violet	380–450 nm	680–790 THz	2.95–3.10 eV
Blue	450–485 nm	620–680 THz	2.64–2.75 eV
Cyan	485–500 nm	600–620 THz	2.48–2.52 eV
Green	500–565 nm	530–600 THz	2.25–2.34 eV
Yellow	565–590 nm	510–530 THz	2.10–2.17 eV
Orange	590–625 nm	480–510 THz	2.00–2.10 eV
Red	625–740 nm	405–480 THz	1.65–2.00 eV

In Table 5-1 each row represents a color in the VL spectrum from violet to red. For each color the corresponding range for the wavelength (in nm), frequency (in Terahertz) and photon energy (in electron-volts) is given. (Electron-volts are a measure of energy; it takes 6.24×10^{18}eV to equal 1 joule.) Notice that as you read down the list (from violet to red) the wavelengths get larger, while both the frequencies and the photon energies decrease. Because of this, while both blue and red light are used in photosynthesis, blue is more photosynthetically productive than red.

When we perceive light energy, our eyes interpret the different wavelengths as colors from violet (380-450nm) to red (625-740nm) (Table 5-1). Our perception of color is due to specific wavelengths of light reflecting off surfaces. If a car appears blue to you, it is because the wavelengths being reflected to your eyes fall within the blue range. That is within the range of 380-450 nm. We perceive the color black when no wavelengths of VL are being reflected. In contrast, we perceive white when all wavelengths are reflected equally. The term “white light” refers to light containing all the colors of the spectrum. (See Colors and Light Extended).

Colors and Light Extended

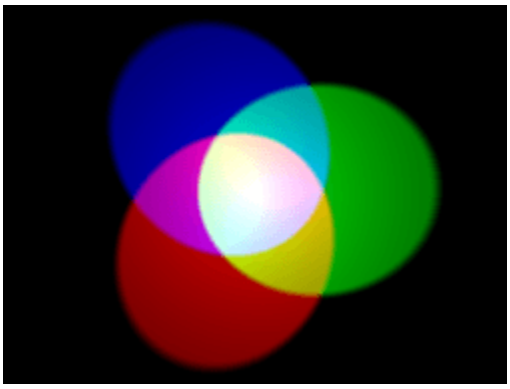


Figure 5-4. A simulated example of additive color mixing. Additive color mixing: overlapping circles of red, green, and blue light on a black background. Where two colors overlap they make cyan, magenta, or yellow, and where all three overlap the center is white.

What would a white surface look like if illuminated by red-light only?

Since the only wavelengths of light that can be reflected back to our eyes are red, we would see a red tile. To see white, red, green and blue wavelengths must reflected. When working with beams of light, additive color mixing comes into play (Figure 5-4). This method is used to product color on TVs, computer monitors and cell phones. Additive primaries act as sources of light. The primaries red, green, and blue combine pairwise to produce the additive secondaries cyan, magenta, and yellow. Combining all three primaries (center) produces white. Subtractive mixing relies on the colored material, like pigments, being lit by an external white light source.

The sun is our primary source of light, and it showers the earth with both VL and other types of wavelengths. Of the solar energy striking a leaf surface, 50 percent exist as wavelengths that can't be absorbed and 15% is reflected or transmitted (passes through the leaf) (Figure 5-5). About 10% is dissipated as heat. That leaves on 25% for used by the plant. Metabolism by the cells of the leaves accounts for 20% of that 25%. This energy is used to maintain the cells; it includes ATP from in the light reactions used for cellular work and in the consumption of intermediates used in anabolic (molecular building) activities. Only 5% gets converted into carbohydrates.

Since much of the solar energy is not absorbed, physiologist studying photosynthesis are typically only concerned with **PAR** – photosynthetic active radiation (400-700 nm). It is this range of light that powers photosynthetic activity.

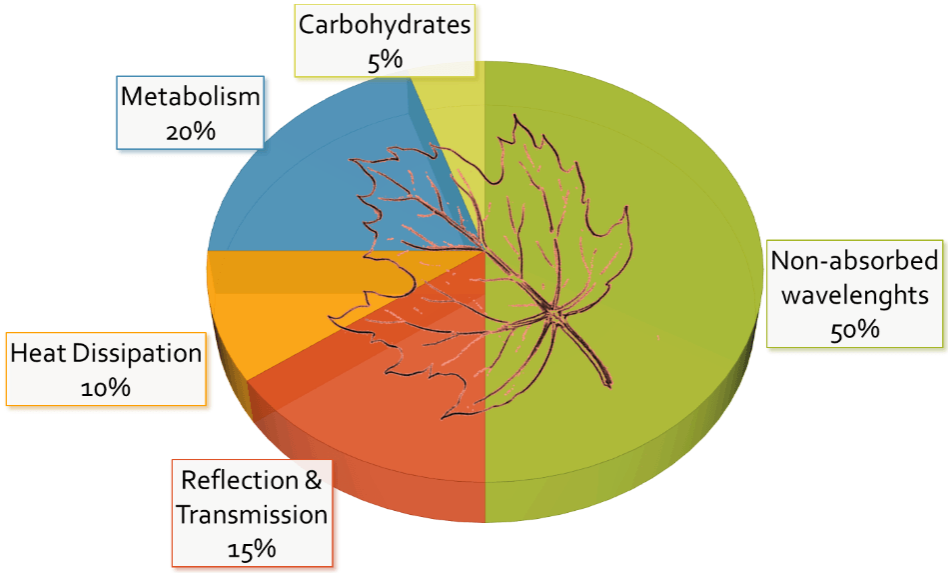


Figure 5-5. What happens to all the solar energy striking a leaf surface? Pie Chart of solar energy striking a leaf surface. 50% non-absorbed wavelengths; 20 % metabolism; 15% reflection and transmission; 10% heat dissipation and 5% carbohydrates. (Stephanie Harvey, 2022)

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5.2: LIGHT QUALITY

Not all wavelengths of light are created equal, as we saw in the last section (Table 5-1). Visible light (VL) is made up of many wavelengths with different colors and energy. PAR (photosynthetically active radiation) is the band of wavelengths that participated in photosynthesis. By definition, PAR is the band from 400 nm to 700nm. But even within the PAR band, not all wavelengths are equally absorbed and utilized.



Sunlight in a late summer sky falling on grasses. (Stephanie Harvey. 2024 CC-BY-NC)

5.2.1: Visualizing Light Quality

5.2.2: Refraction and Reflection

5.2.3: Non-photosynthetic Uses of Light

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5.2.1: Visualizing Light Quality

There are two ways to observe how the wavelengths of light affect photosynthesis. An **action spectrum** depicts the physiological activity (photosynthesis) in response to various wavelengths. Either oxygen production or carbon dioxide consumption can be used to determine the photosynthetic rate. The first action spectrum was created by a researcher using photosynthetic bacteria. He used their growth rate as a measure of photosynthetic activity so the bacterial growth would be the highest in cultures irradiated with the most photosynthetically active wavelengths.

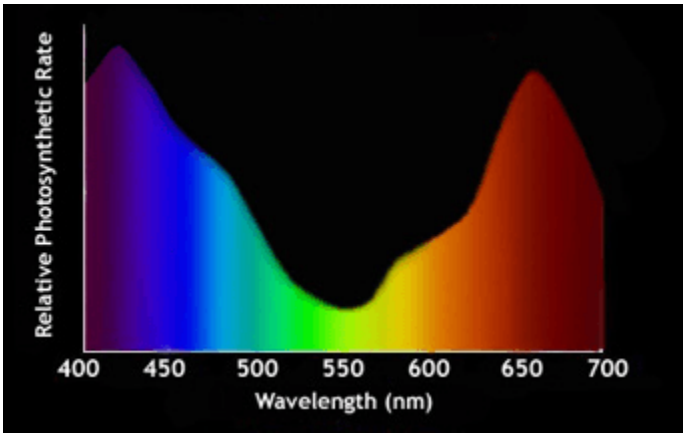


Figure 5-6. Photosynthetic action spectrum. Action spectrum graph with relative photosynthetic rate on the y-axis and wavelength from x-axis, shaded in the matching colors. Activity is highest in the blue-violet and orange-red wavelengths and lowest in the green to green-yellow wavelengths. (http://projects.ncsu.edu/project/bio...thesis2.html#1)

In Figure 5-6, the graph has the y-axis label is “Relative Photosynthetic Rate” while the X-axis show the continuum of wavelengths from 400 nm to 700nm. The colored regions depict the level of activity and the color that corresponds to the particular wavelength. Notice that the two areas with the highest activity correspond to the blue-violet and orange-red wavelengths. The lowest activity is associated with the green-yellow wavelengths.

Since the principle pigments involved in photosynthesis are (in higher plants) Chlorophyll *a* and *b*, we can also use their **absorbance spectra** to see what wavelengths they absorb and thus use for photosynthesis. In Figure 5-7 the graph, has the y-axis label is “Absorbance” and the x-axis is wavelengths (like in Figure 5-6). This graph shows two spectra – the blue line represents the absorbance spectrum for Chlorophyll *a* and red the spectrum for Chlorophyll *b*. Chlorophyll *a* absorbs light within the violet, blue and red wavelengths while chlorophyll *b* absorbs blue and orange wavelengths. The uniqueness of their individual spectra helps maximize solar absorbance (although there is some overlap). Neither pigment absorbs wavelengths associated with green, with Chlorophyll *a* reflecting green-yellow and *b* reflecting green.

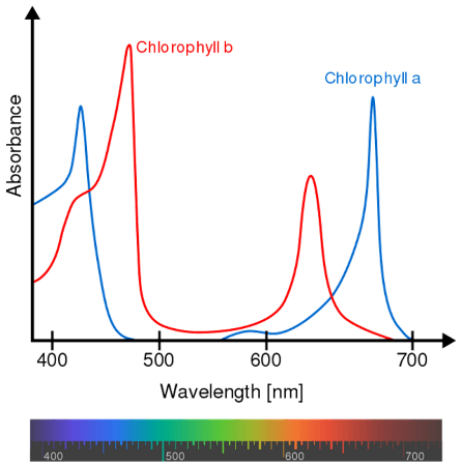


Figure 5-7. Absorbance spectra for chlorophyll a and b. Graph with absorbance on y-axis and wavelength (nm) from 400 to 700 on x-axis. Two absorbances are plotted. Chlorophyll b has a peak at 480 and 620. Chlorophyll a has a peak at 420 and 680. Very little absorbance is seen between 500 and 600. (By Chlorophyll_ab_spectra2.PNG: Daniele Pugliesi derivative work: M0tty - This file was derived from: Chlorophyll ab spectra2.PNG: CC BY-SA 3.0, https://commons.wikimedia.org)

While the action spectrum and the absorbance spectra do not match up exactly, both demonstrate that the quality of the light maters.

Chlorophyll molecules

PAR is absorbed primarily by chlorophyll molecules. Remember for plants these pigments are only found within the chloroplast, and these are mostly located in the mesophyll cells of leaves. These pigments are partially embedded in the thylakoid membranes of the chloroplast. The molecular structure can be described in two parts: a fatty acid tail and a multi-ring head with Mg^{2+} bond in the center (Figure 5-8). There are several types of chlorophylls but in higher plants we find chlorophyll-*a* and chlorophyll-b. They differ in that Chlorophyll-b has an oxygen bound to one of the rings that is not found on Chlorophyll-a. This slight structural change accounts for the difference in absorbance spectra.

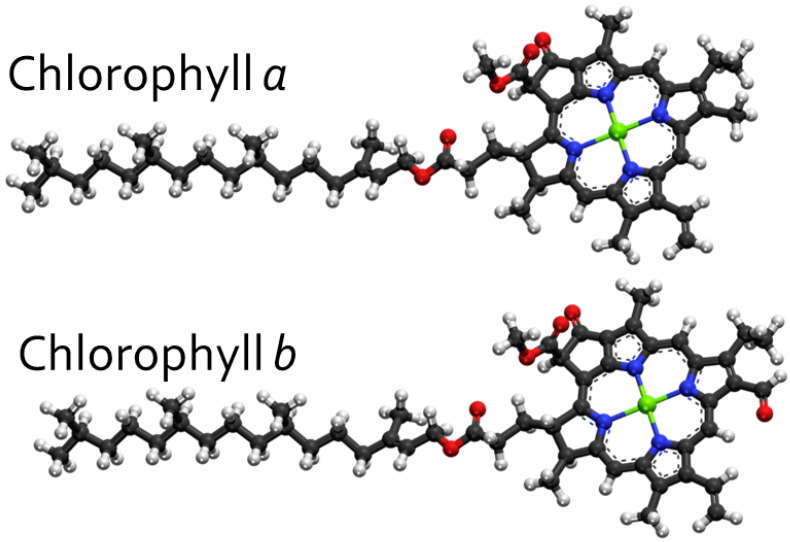


Figure 5-8. The structure of chlorophyll a and b. Molecules differ only slightly. Both have large head group of many cyclic compounds and long fatty acid tail.(Red=oxygen; black=carbon; white=hydrogen; blue=nitrogen; green= magnesium ion). (By Jynto (talk) - Own work This image was created with Discovery Studio Visualizer., CC0, https://commons.wikimedia.org)

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5.2.2: Refraction and Reflection

All solar energy striking a leaf has passed through multiple and/or complex media before reaching its destination. These media, like the atmosphere, impact light quality. Some wavelengths of light may be absorbed, while others get reflected (scattered). For example, a significant amount of UV radiation is filtered by the atmosphere (specifically the ozone layer). As VL passes from one medium to another with a different refractive index, these changes can often be seen (Figure 5-9). You have encountered this phenomenon. A straw in a glass of water appears bent or water in a pool looks shallower than it is.

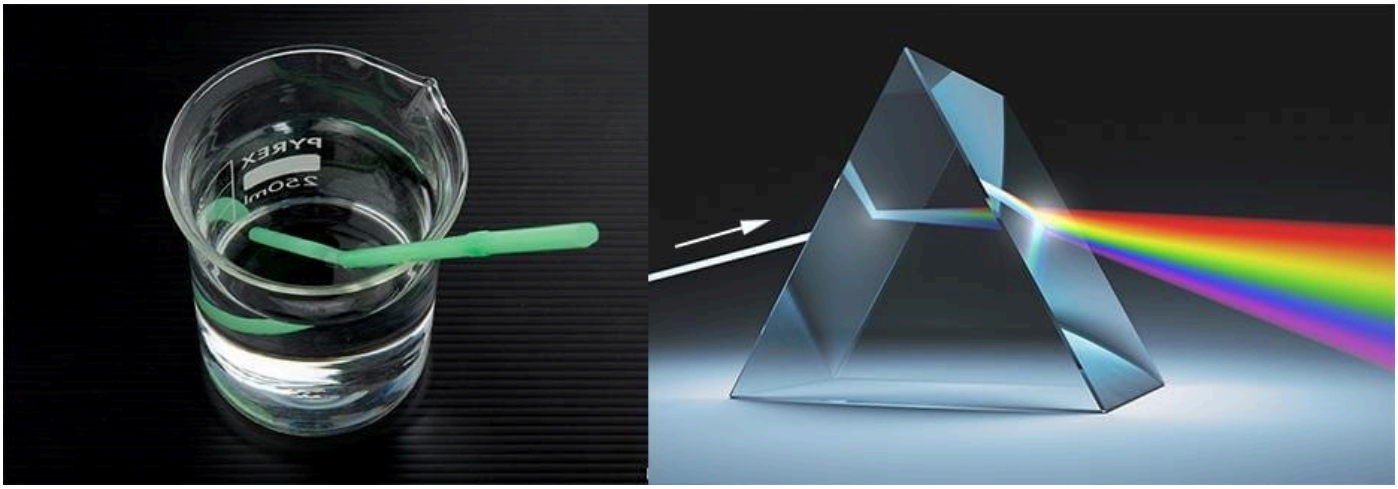


Figure 5-9. The first image demonstrates refraction using a straw in a beaker of water. The straw appears to bend due to refraction. In the second image, light passing through a glass prism is refracted and dispersed into colored bands of light. (Science Photo Library, NTB Scanpix. CC BY-NC)

A prism is often used when demonstrating refraction because you can see a distinct change in the path of the light. You can also see a dispersal effect as the light exists the prism. In the second image in Figure 5-9, we can see the refraction and dispersal effects. As beam of light passes through air and then through a prism, the various wavelength interacts differently with the prism causing them to separate into the distinct color bands we associate with a rainbow.

As light passes through the leaf canopy, the quality of light changes. There is a shift toward red with little light in the violet regions (Figure 5-10). This shift has a significant impact on the efficiency of chlorophyll *a* which absorbs heavily in that region. To compensate plants that live below the canopy have higher concentrations of chlorophyll *b* to take advantage of the available light since it absorbs more in the blue region than violet. Shaded plants also restrict their production of chloroplast and chlorophyll. With the limited light available, energy and resource expenditures to produce them would not be returned with increased photosynthetic productivity.

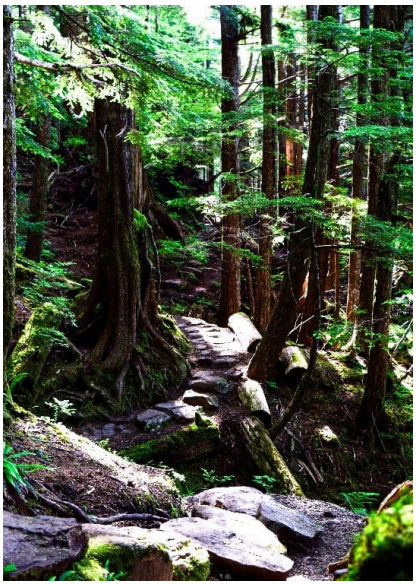


Figure 5-10. Sunlight filtered through tree canopies along Rainbird Trail in Ketchikan, Alaska. (Stephanie Harvey. 2023. CC-BY-NC.)

As the earth rotates, solar radiation passes through different thicknesses of the atmosphere. At sunrise and sunset, the distance that light travels is greater than when the sun is directly overhead. This creates more scattering of violet and blue wavelengths. Thus, the orange and reds tend to dominate creating colorful displays.

Shifts in the atmosphere's composition can affect the light waves that pass through it. Volcanic eruptions, fires, and other events can increase scattering of light and impact the wavelengths that are available for plant growth (Figure 5-11).



Figure 5-11. Wanaka, New Zealand at sunset after Tonga volcanic eruption. (By Marian Predescu, https://commons.wikimedia.org)

Archeological digs in England found mass graves initially thought to be due to the Black plague. However, dating processes determined that the deaths did not occur during the plague outbreak. What else could cause high mortality rates? Ice cores drilled in the arctic held a clue - ash. Researchers scoured ancient written records looking for a volcanic eruption that coincided with mass graves. They found one that occurred in South America and it was massive. The ash clouds blocked a significant amount of sunlight creating an induced winter. While the ash settled from the atmosphere, the chemical reactions that also took place in the atmosphere following this large-scale eruption extended the impact for nearly 2 years. The result was diminished sunlight and exceptionally cold weather leading to famine and high fatality rates.

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5.2.3: Non-photosynthetic Uses of Light

Plants use light for activities beyond photosynthesis. The wavelengths at the red end of the spectrum, red & far-red, provided less energy for photosynthetic activity than the violet and blue regions. However, the red & far-red wavelength are important for plant regulation and development.

Phytochromes are red-light photoreceptors that regulate light responses in plants, fungi, and bacteria. This regulation is accomplished through the reversible photoconversion of the phytochrome to between it two states: the P_r form that absorbs red light and the P_{fr} form that absorbs far-red light (Figure 5-12). When the P_r form absorbs red light, it is converted to the P_{fr} form. When the P_{fr} form reverts to the P_r form when it absorbs far-red light.

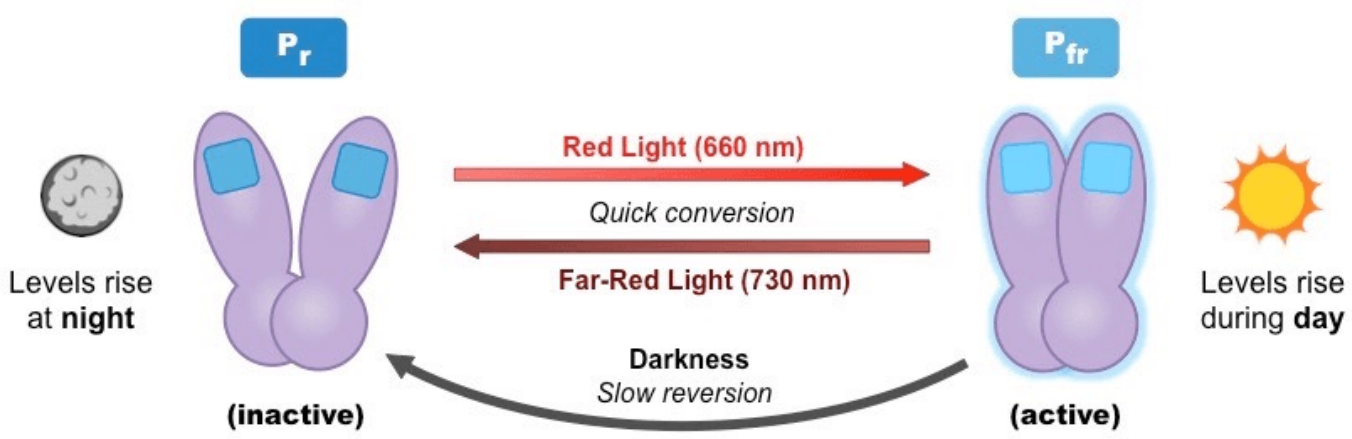


Figure 5-12. Inter-conversion of the phytochrome between the active P_{fr} form and the inactive form P_r controls physiological and morphological responses in plants.

One example of the role of red/far-red light, as demonstrated in this illustration, is on initiation of floral initiation. Short-day plants bloom when nights are long, while long-day plants bloom when the nights are short. We will discuss this more in a later section.

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5.3: LIGHT QUANTITY

The quality of the light can have impacts on plants and so can the **quantity**. To discuss light quantity, we first have to determine how light can be measured. There have been many different units used due to the different roles light can play. From a human perspective, we are typically quantifying for purposes of visual clarity. How well can an object be seen at given quantities of light? For this purpose, light is typically measured in **lumens** with the quantity of light falling onto a surface measured as illuminance with units of **lux** (lumens per square meter) or in **foot-candles** (lumens per square foot).



Figure 5-13. A foot-candle is a measurement of illuminance defined as lumens per square foot.

When discussing light quantities for plants, only PAR is used. Remember PAR is photosynthetic active radiation. The quantity of PAR that falls onto a surface is measured as **PPFD** – photosynthetic photon flux density- with units of micromoles per meter squared per second ($\mu mol/m^2/s$).

5.3.1: Daily Light integral

5.3.2: Plant Light Requirements

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5.3.1: Daily Light integral

PPFD is the number of photosynthetically active photons that fall on a square meter of surface each second. This works well for instant readings – for recording what is happening "right now." Two readings taken only minutes apart can vary greatly is a thick cloud obscured the sun for one of the measures but not the other (Figure 5-14). However, plant growth and development depend on what happening over longer periods of time – day, week, and month – so PPFD is not a great for determining how plants will respond.



Figure 5-14. Clouds over Camel Lake, Florida. (Stephanie Harvey. 2022. CC-BY-NC)

Instead of PPFD, a measure referred to as the **daily light integral** (DLI) is used. It measures the number of PAR photons that accumulate in a square meter over the course of the day. The units of this measurement are moles per meter square per day (mol/m^2/day).

The DLI range will vary from location to location and month to month. The map in Figure 5-15 shows the ranges of DLI for each month for the US. For most of Georgia, the DLI ranges from a low of 15-20 mol/m^2/day (Dec & Jan) to a high of 40-45 mol/m^2/day (April-July). As you move northward the DLI is lower particularly in the winter months. Although the northern latitudes (northern Canada and Alaska) experience only a few months of high DLI, their DLI during those months is high (50-55 mol/m^2/day) due to their long day length.

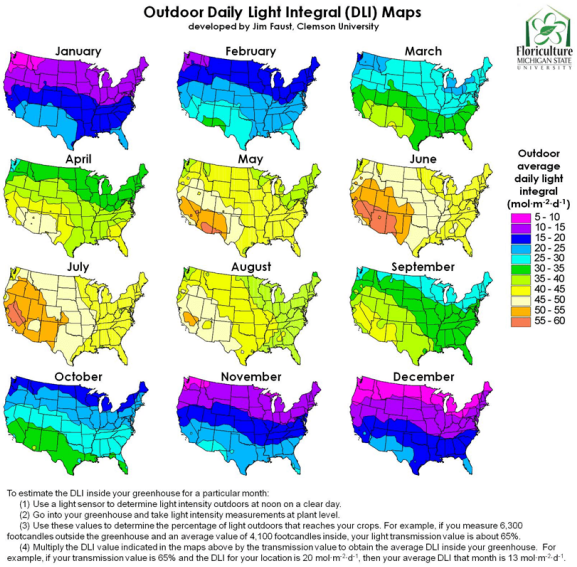


Figure 5-15. Monthly maps of USA showing the daily light integral by color gradient. In Jan most of US is receiving less than 20 moles per meter squared per day. By June most of US is receiving over 40 moles per meter squared per day. The farther north we move the more months at lower levels. (Source: Mapping monthly distribution of daily light integrals across the contiguous United States (Pamela C. Korczynski Joanne Logan, and James E. Faust; Clemson University, 2002)

The longer days of summer and shorter days of winter can account for the seasonal changes in DLI. The changes are most significant at the poles. This is demonstrated in Figure 5-16. The lines represent the apparent "path" of the sun across the horizon through the course of the day for an observer at 56°N latitude (just north of Port Moller Alaska and Moscow, Russia). The y-axis describes how far above the horizon the sun appears. Imagine you are standing outside at 56°N and are watching the sun rise and the set at different times of the year. On the Winter solstice (blue line, lowest line), the shortest day of the year in the Northern hemisphere, the sun rises only 40 degrees east of north and sets only 40 degrees west of north. Additionally, it only rises to a maximum of 10 degrees about the horizon. This means not only is there a very short window of light it is of extremely low quality as it passes through a significant thickness of the atmosphere. In contrast, at Summer solstice, the longest day of the year the sun rises sun rises only 120 degrees east of north and sets 120 degrees west of north (red line, upper most). The sun crests the sky about 60 degrees above the horizon. This makes it the longest day and the day with the greatest solar intensity at this latitude (although still lower than what would happen at the equator).

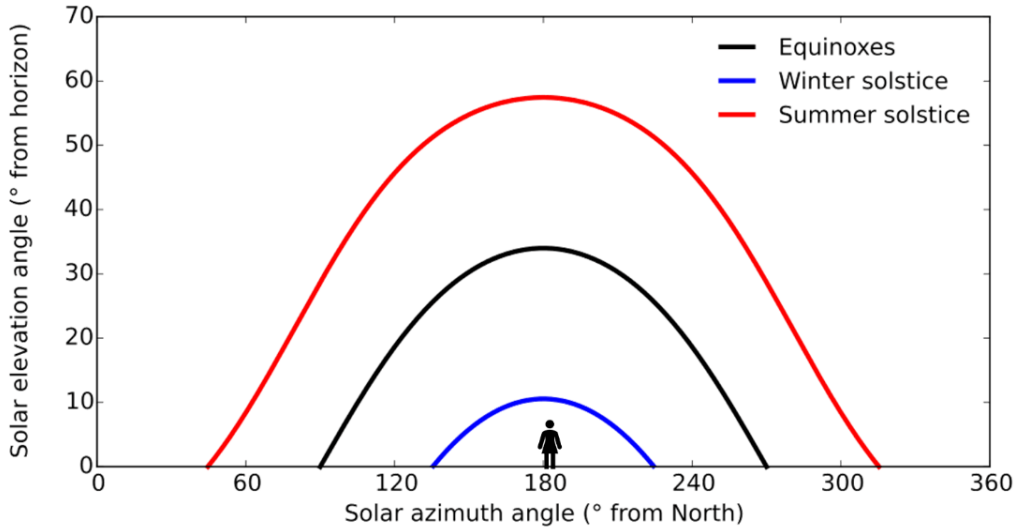


Figure 5-16. Path of sun in the sky to an observer at 56°N latitude. The upper line represents the Summer solstice path while the lowest line is the Winter solstice path. The middle line represents the path on either Fall or Spring equinoxes. (By Deditos - Own work, CC BY-SA 4.0, https://commons.wikimedia.org/w/inde...curid=37904452)

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5.3.2: Plant Light Requirements

While sunlight is required for all photosynthetic plants, the quantities needed can vary. From a horticultural standpoint, plants can be divided into three categories based on their light needs: Low-light plants, medium-light plants, and high-light plants (Table 5-2). Low-light plants need 3 to 6 mol/m^2/day. Plants that fall into this category represent adaptations for the lower light under a dense canopy. While they may thrive in a vegetative state, they seldom bloom at these lower light levels. Examples include many house plants used as "greenery." Medium-light plants need the DLI to be 6 to 12 mol/m^2/day. Most annuals fall into this category. They often germinate and mature in early spring before light levels get intense. Plants like many perennials and vegetable crops need a minimum of 12 mol/m^2/day and thus are called high-light plants. While they might survive at medium light levels, they will not bloom or produce fruit and since production of blooms and fruits is often desired this is a limitation. For plants being grown in the greenhouse, this can be an issue. Greenhouses DLI's rarely exceed 25 mol/m^2/day on the best of days and can be as low as 1-5 mol/m^2/day.

Table 5-2. *Typical plant categories described in horticulture and their required DLI.*

Categories	DLI needed (mol/m^2/day)	Plant examples
Low-light plants	3 to 6	House plants (typically don't flower)
Medium-light plants	6 to 12	Most annuals
High-light plants	Minimum of 12	Perennials and vegetable crops
Greenhouse values rarely exceed 25 on the best day and can be as low as 1–5 mol/m^2/day.		

In addition to reproductive success, DLI impacts many aspects of plant growth. In an experiment, DLI was manipulated from 1.3 to 10.8 mol/m^2/day for groups of "New Guinea" impatiens cuttings to determine the effect DLI has on propagation (Figure 5-17; Lopez and Runkle, 2008). Cuttings exposed to higher DLI demonstrated increased rooting, greater biomass accumulation, reduced stem elongation (higher quality) and less time to flowers. In Figure 5-17, the center two plants are classified as "marketable liners" (which means they are ready to pot and sale) at day 16 but the two groups set at the higher DLI levels are marketable in 13 day and produced more biomass. Thus, not only are they available to sell earlier, but they are more vigorous than the older cuttings at lower DLI.

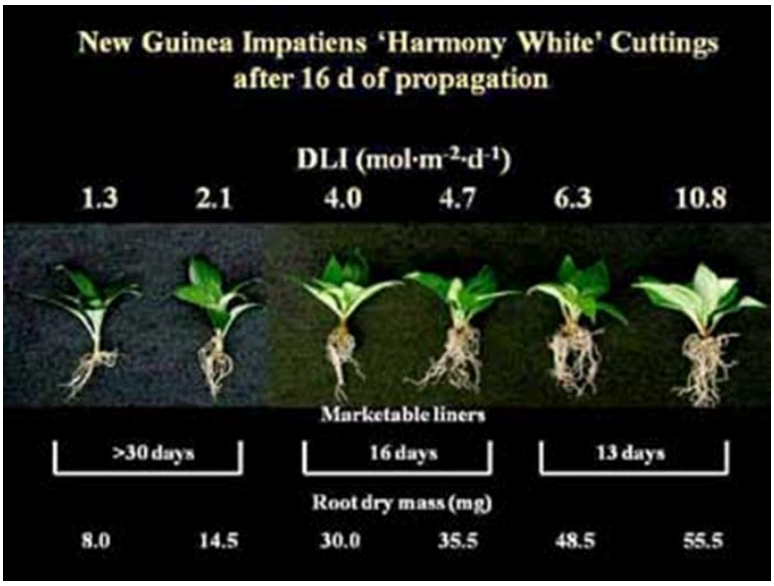


Figure 5-17. Exposure to increasing DLI impacts many aspects of cutting development including increase rooting, biomass accumulation, reduced stem elongation and decreased time to flowering. ((Lopez and Runkle, 2008).

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5.4: PLANT RESPONSES TO LIGHT

Plants use light for photosynthesis. However, it is also critical to development, morphology changes, and reproductive success of plants. Plants respond to illumination in four ways: photosynthesis, phototropism, photoperiodic and photomorphogenesis.



Seedlings exhibiting phototropism. They are bending toward the light source. (Stephanie Harvey. 2026 CC-BY-NC)

5.4.1: Photosynthetic Responses to Light

5.4.2: Non-Photosynthetic Reponses to Light

5.4.3: Photoperiodism

5.4.4: Phototropism

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5.4.1: Photosynthetic Responses to Light

Photosynthesis, as was discusses in a previously Chapter 4, is the conversion of the electromagnetic energy of light to chemical energy (via chemical bonds of biomolecules such as sugars). This is the most obvious plant response to light. For most plants it is critical to their survival. However, when one examines a plant response to increasing light levels, the response is not a completely linear one.

Figure 5-18 demonstrates how the rate of net photosynthesis changes as light intensity increases. The x-axis has the PAR (micromoles per meter squared per second) while the y-axis measures photosynthetic rate via carbon dioxide uptake (micromoles per meter squared per second). At zero PAR (and up to about 150 µmol/m2/s), the net carbon dioxide uptake is negative as more CO_2 is released (via cellular respiration) than is taken up via photosynthesis. At the light level of 150 µmol/m2/s the **light compensation point** is reached. This is the light level at which photosynthetic CO_2 uptake cancels out the CO_2 release by cellular respiration and thus the net uptake is zero. As light intensity increases the photosynthetic rate increases (as seen via the CO_2 uptake). However, the photosynthetic apparatus of the chloroplast can only handle so much light and can become saturated. This light level is referred to at the **light saturation point** (for this graph at 1000 µmol/m2/s). At this light level, the maximum net photosynthetic rate has been reached and increased light intensity does not increase the rate further. If fact at some point (beyond what this graph shows) increased light intensity can have negative impacts on photosynthetic rates as the photosystem become damaged due to overexcitation.

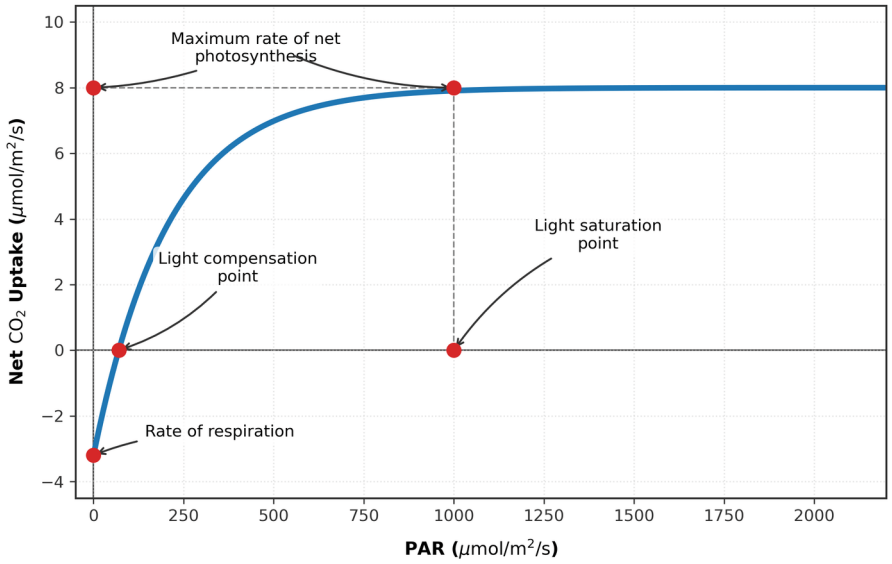


Figure 5-18. Net CO2 uptake on y-axis versus quantity of light (PAR in micromoles per meter squared per sec) on x-axis. Line graph shows steep incline then flatten out as maximum rate of photosynthesis occurs at the light saturation point.

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5.4.2: Non-Photosynthetic Reponses to Light

The three other responses plant have to light, (phototropism, photoperiodism and photomorphogenesis) involve changes in development or growth patterns. In the most general sense, both phototropism and photoperiodism could be classified as photomorphogenesis but are typically addressed separately due to their specifications. Both involve phytochromes and other photochromic sensory receptors, but phototropism is directional growth in response to light while photoperiodism involves morphological changes in response to day length. Meanwhile the term photomorphogenesis constitutes a diverse group of morphological responses with various light triggers – including UV-A, UV-B, blue and red portions of the spectrum.

One example of photomorphogenesis is the hypocotyl hook seen in some dicot seedlings (Figure 5-19). In the dark, an apical hook is present following germination from the seed. With exposure to light, the hypocotyl will straighten, pulling the cotyledons above the ground and in position to photosynthesize.



Figure 5-19. Dicot seedling emerging from the ground. The apical hook (in the hypocotyl) is a response to dark condition. With exposure to light, the hypocotyl will straighten, pulling the cotyledons above the ground and in position to photosynthesize. (By Zanchetta Fabio (faxstaff) - http://ladriditalee.faxstaff.net/, CC BY-SA 2.5.)

Phytochromes are light sensitive molecules that change their structure when irradiated by select wavelengths (Figure 5-12). The P_r form, which is considered the inactive form of the photochrome, absorbs red light and is converted to P_{fr} (Figure 5-20). P_{fr} is considered the active form and absorbs far-red light which converts it back to P_r form. P_{fr} will also slowly revert to P_r during the dark periods without the absorbance of far-red light.

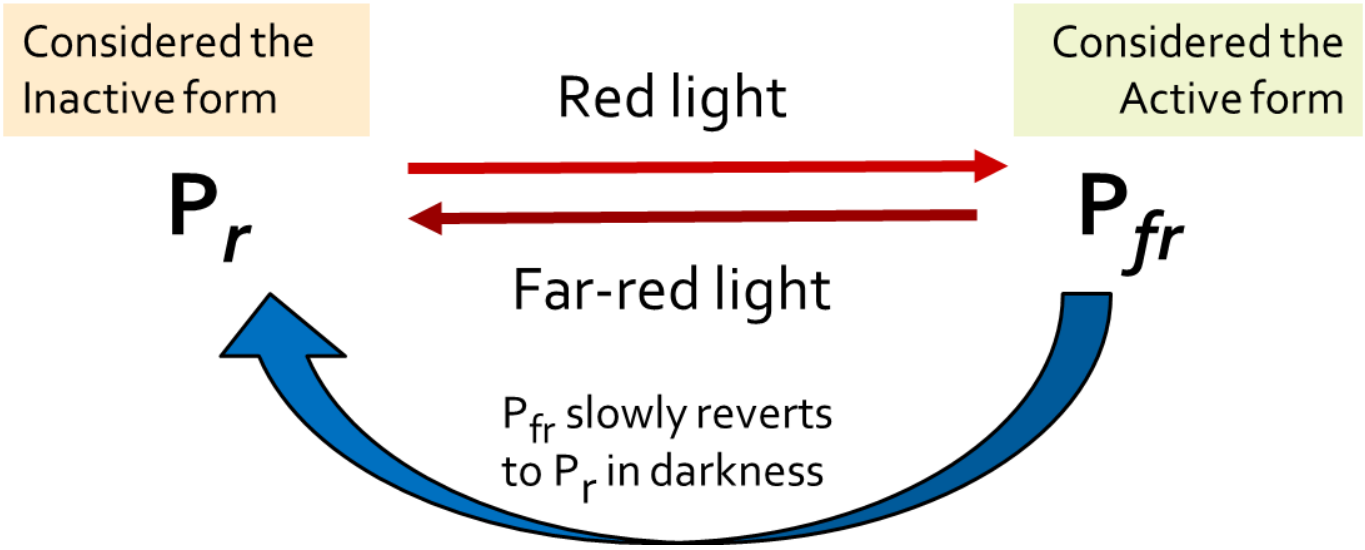


Figure 5-20. Photochromes interconvert between the P_r from and P_{fr} form. The Pr form, which is considered the inactive form of the phytochrome, absorbs red light and is converted to Pfr. Pfr is considered the active form and absorbs far-red light which converts it back to Pr form. Pfr will also slowly revert to Pr during the dark periods without the absorbance of far-red light.(Stephanie Harvey, 2023. CC-BY-NC)

There are a variety of plant responses that depend on form that the phytochrome stays in. The responses also vary with organism, developmental stage, and tissue (Table 5-3).

Table 5-3. *Common plant responses to red light and effected developmental stage.*

Group	Genus	Stage of development	Effect of red light
Angiosperms	*Lactuca* (lettuce)	Seed	Promotes germination
Angiosperms	*Avena* (oat)	Seedling	Promotes de-etiolation
Angiosperms	*Sinapis* (mustard)	Seedling	Promotes formation of leaf primordia, development of 1° leaves; anthocyanin production
Angiosperms	*Pisum* (pea)	Adult	Inhibits internode elongation
Angiosperms	*Xanthium* (cocklebur)	Adult	Inhibits flowering
Gymnosperms	*Pinus* (pines)	Seedling	Enhances rate of chlorophyll accumulation
Pteridophytes	*Onoclea* (sensitive fern)	Young gametophyte	Promotes growth
Bryophytes	*Polytrichum* (moss)	Germling	Promotes replication of plastids
Chlorophytes	*Mougeotia* (alga)	Mature gametophyte	Promotes orientation of chloroplasts to directional dim light

Lettuce (*Lactuca* sp) seeds germinate in response to exposure to red light (phytochrome in P_{fr} form). These seeds have minimal resources to help the seedling, so the seedling must reach light quickly and begin photosynthesizing. The red-light trigger helps prevent the tiny seeds from germinating when they are too deep.

In contrast, in adult pea plants (*Pisum* sp) red light inhibits internode elongation. Therefore, plants receiving adequate light stay compact and do not expend unnecessary energy on vertical growth. If, however, significant foliage is experiencing self-shading the phytochrome reverts to the Pr form and it triggers internode elongation that separated the leaves and allows more light penetration.

From Table 5-3, you can see that exposure to red light inhibits cocklebur plants (*Xanthium* sp) from flowering. This response to

the phytochrome form is an example of photoperiodism.

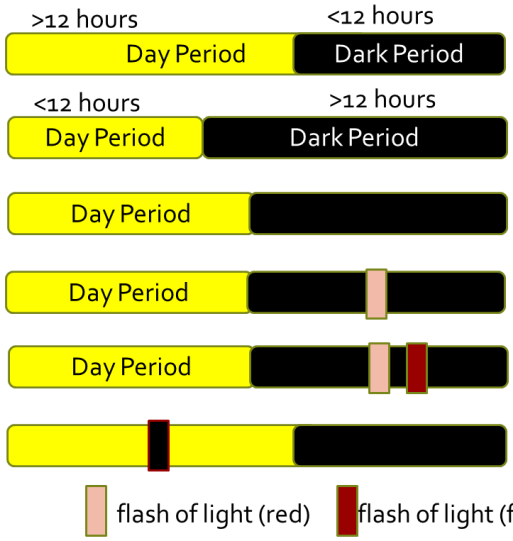
Flowering is a reproductive activity in Angiosperms. Ideally, for maximum genetic diversity, it requires cross pollination between different plants of a given species. To make that more likely, it is necessary for the plants of a given species to bloom at the same time of year. It is the phytochrome Pr/Pfr enables plants to determine the time of year and synchronize their reproductive development.

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5.4.3: Photoperiodism

Photoperiodism is a photomorphogenic response triggered by the number of nighttime hours. The plant's response is either the induction of flower bud formation or not. Plants can be grouped into one of three categories based on how they respond: Short-day plants, Long-day plants and Day-neutral plants. The names are somewhat a misnomer since they imply that it is the length of the day that determines if the plants will flower. It is instead the night hours that are critical. So, short-day plants bloom when the nights are long, long-day plants bloom when the nights are short and day-neutral are unaffected by the number of night (or daylight) hours (Figure 5-21). It is the form of phytochrome that triggers this shift from vegetative to reproductive growth.

Long-day plants flower when the night length falls below their critical photoperiod. Under these short-night conditions not all the P_{fr} is converted to P_r. The high levels of the active P_{fr} induces flowering. These plants will not flower if the night length is longer than the critical time – when days are "short." However, we know that is the night length that is controlling this induction because when the long night is interrupted by a short flash of light, effectively creating two short nights, the long day plants will flower even though the day length has not changed. Likewise, if a long day is interrupted by a short period of dark, it has no impact on the floral induction.



Short-Day Plants	Long-Day Plants
Vegetative	Flowering
Flowering	Vegetative
Vegetative	Vegetative
Vegetative	Flowering
Flowering	Vegetative
Vegetative	Flowering

Figure 5-21. Response of long-day and short-day plants to different intervals of light and dark periods. When flash of light interrupting the dark period, the plants respond as if the nights were short. If a flash of far-red is given after the light, the plants respond as if the night is long regardless of the night length. A brief dark period interrupting a long day has no impact.

In short-day plants flowering is triggered by long (>12 hours) dark period. During this long dark period all the P_{fr} reverts back to P_r. In short-day plants flower induction is suppressed by the P_{fr} from. Thus, the long nights allow only low level to accumulate and flower set occurs. If a long dark period is interrupted by a flash of light no flowering occurs for the short-day plants. However, if a flash of light is followed by a flash of far-red light, flowering occurs. Why? The P_{fr} is quickly converted into the P_r form and thus does not need the night to slowly have this happen. No P_{fr} means that the short-day plants flower despite the short night.

So, regardless of the day length, in most cases a last flash of light, red or far-red, determines the form of the phytochrome and thus the plants' response. This reversibility is for a limited period of time after which the response is said to have "escaped" from the reversal control of light.

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5.4.4: Phototropism

Tropisms in plants are when growth occurs directionally toward a stimulus or away from a stimulus. In phototropism, the stimulus is light. Most shoots exhibit positive phototropism; they grow toward light. This is advantageous since leaves need to be exposed to light for photosynthesis. Some specialized shoot organs exhibit negative phototropism. For example, the tips of some vine respond negatively as they search for an object to which to anchor.

Phototropic responses are induced through the light mediated, asymmetric distribution of auxin (Figure 5-22). Remember, auxin is a plant hormone that triggers cell elongation. In a shoot tip, auxins accumulate at higher concentrations on the shaded side. The higher concentration trigger cell on the shade side of the stem while the cells of the sunlit portion of the stem do not. This differential growth results in the curing of the shoot time toward the light source.

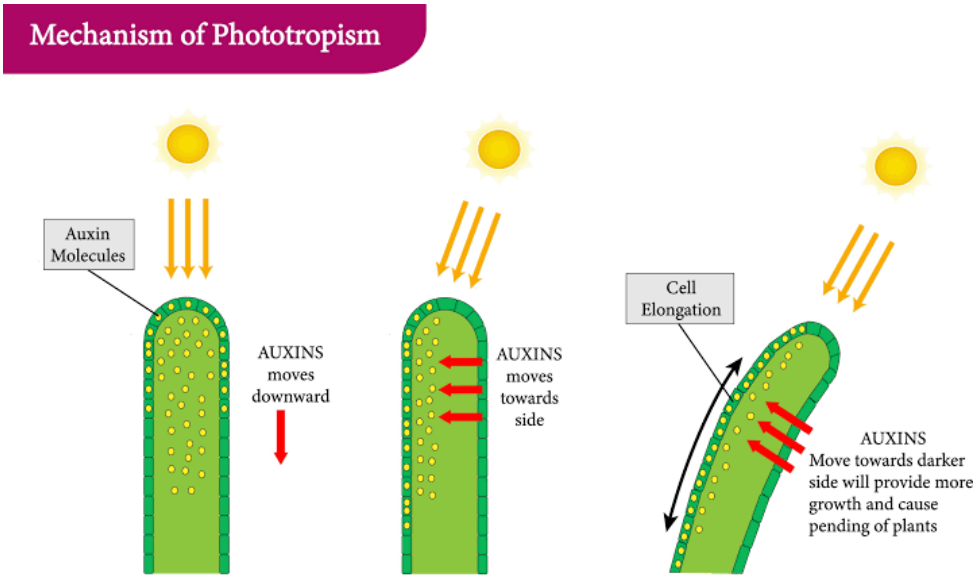


Figure 5-22. Phototropic response. 1) shows even distribution of light across the shoot tip and the resulting eve distribution of auxin. 2) With the sun to the right side of shoot tip, auxin accumulated on the left side. 3) Cells on left exhibit elongation while the sunlit cells do not – producing a curved shoot. (Google (2026). Created with prompts by Stephanie Harvey)

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5.5: LIGHT MANIPULATION



Figure 5-23. A yellow daffodil backlit by sunlight. (Stephanie Harvey. 2021 CC-BY-NC).

Plants are critical resources in nearly all ecosystems. Since light is critical to their success, being able to control light provides significant control over plant growth. To maximize yields and produce crops when and where we humans desire, we often manipulate the light quantity and quality.

Plants have varied light requirements. In landscaping, plants are often classified based on light needs. Commonly used categories include Full Shade, Partial Shade/Sun, and Full Sun (Table 5-4). Full shade plants require environments where they rarely get direct sunlight – less than 3 hours per day. Some examples of full shade plants include Hosta, begonia, and ferns. These plants will also do well in dappled or filtered light. Plants categorized as “Filtered Light” plants prefer environments where there is no direct light. All light is filtered through a leafy canopy. On the other end of the spectrum are the “Full Sun” plants which need to receive direct light all day (more than 6 hours). These sun-loving plants include sunflower, coneflower, butterfly weed and lavender. The term “Partial Shade” or “Partial Sun” tend to be used interchangeable. The plants such as New Guinea impatiens, bleeding hearts and primroses only receive direct sunlight for about one-third of the day.

Table 5-4. *Horticultural plant categories based on light requirements.*

Category	Light requirement	Examples
Full shade	Rarely gets direct sun; <3 hr	Hosta, begonia, ferns, ivy, lily of the valley
Filtered light (dappled), a subset of full shade	Only light admitted through leaf canopy	Same as full shade
Partial shade	Receives direct sunlight for 1/3 of day	New Guinea impatiens, bleeding heart, primroses
Full sun	Receives direct light all day; >6 hr	Sunflowers, purple coneflowers, butterfly weed, lavender

5.5.1: Shading

5.5.2: Artificial Lighting

5.5.3: Lighting Sources

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5.5.1: Shading

In landscaping, plants should be purchased to fit the light levels of the environment. To meet the light demands of horticultural crops, light is often controlled through application of shading materials or through artificial light sources. Light intensity can be too much for some plants. To minimize their exposure to light in outdoor spaces, natural and artificial shading can be employed. Shade-loving plants can be placed in the landscape to take advantage of natural shade from buildings, fences, and other plants. If natural shade is inadequate, artificial shade can be created.

Lath shade houses (Figure 5-24) are structures that provide dappled light. The strips of wood block light coming in. The resulting shadow (shade) moves as the solar angle changes throughout the day. Shade houses are often seen in big gardens and in commercial nurseries. Shade sails or canopies can provide shade for both people and plants. These shades can be easily erected at little cost.



Figure 5-24. Lath shade house. https://www.bourtonhouse.com

Greenhouse can also benefit from filtering out some of the light, particularly during summers. Most plants cannot use all the solar radiance of a bright summer's day. While the greenhouse structure itself will block some of the light, excess light entering the house can cause plant damage directly (over excitation of the photosystems) or indirectly (heat damage and water loss).

Shade cloths are synthetic tarps that can be installed either inside or outside of the greenhouse depending on specific needs of the plants (Figure 5-25). Shade cloths placed outside the greenhouse block the light before it enters and are most effective at keeping the house cooler in the summer. Shade cloths inside the house a slightly less effective for heat control since the light enters the house before encountering the barrier. There are, however, some advantages to having the cloth inside the greenhouse. One benefit is that the cloth is not subjected to the elements and thus tends to have longer life expectancies. With interior shade cloths, coverage and non-coverage can be mechanized. With the shade cloth on tracks, it can be manipulated based on PPFD (photosynthetic photon flux density). Automated systems can open and close the shade curtains throughout the day as light levels change.

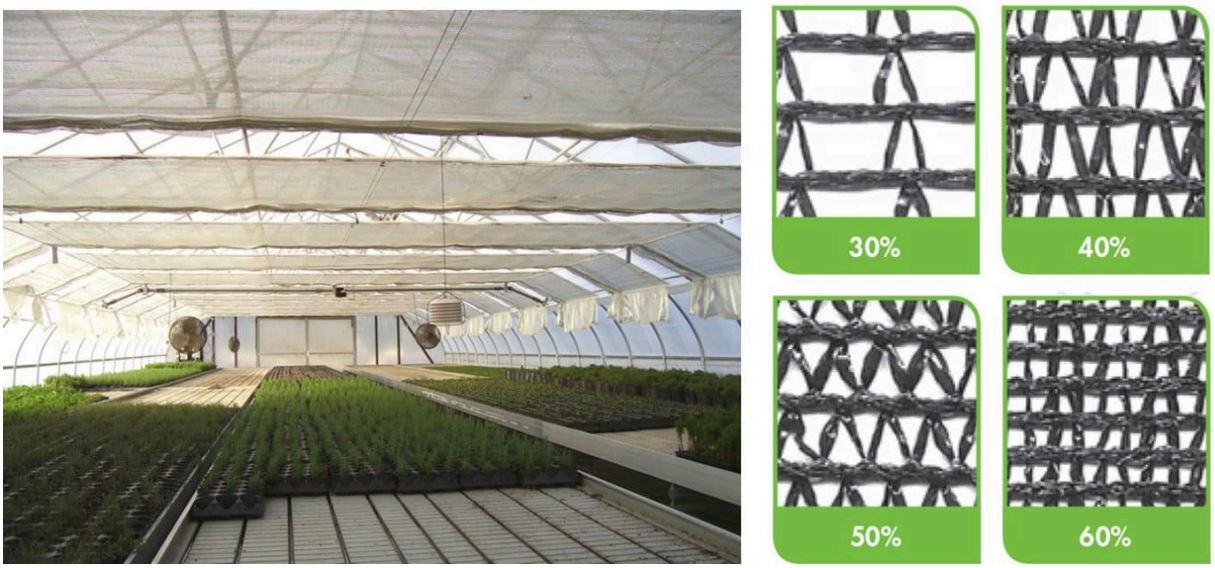


Figure 5-25. A -Shade cloth deployed inside a greenhouse. B-Shade cloth at various shading levels. (A-John Bartok, Jr. 2016; B- https://green-tek.com/shadenets/)

Shade cloth comes in a variety of meshes to filter out more or less light. They are rated based on how much of the light intensity is lost with the cloth. A 30%-shade cloth blocks out 30% of the solar input while a 60%-cloth blocks out 60% of the light.

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5.5.2: Artificial Lighting

The average greenhouse crop needs about 10 to 12 mol/m^2/d. The structure of the greenhouse itself blocks about 35% of the incoming solar radiation. During the winter months, when DLI is low, the light levels can fall below the required levels (Figure 5-26). For example, on a cloudy day in winter levels can drop to as low three mol/m^2/d outside which means within the greenhouse levels would be approximately 1.95 mol/m^2/d.

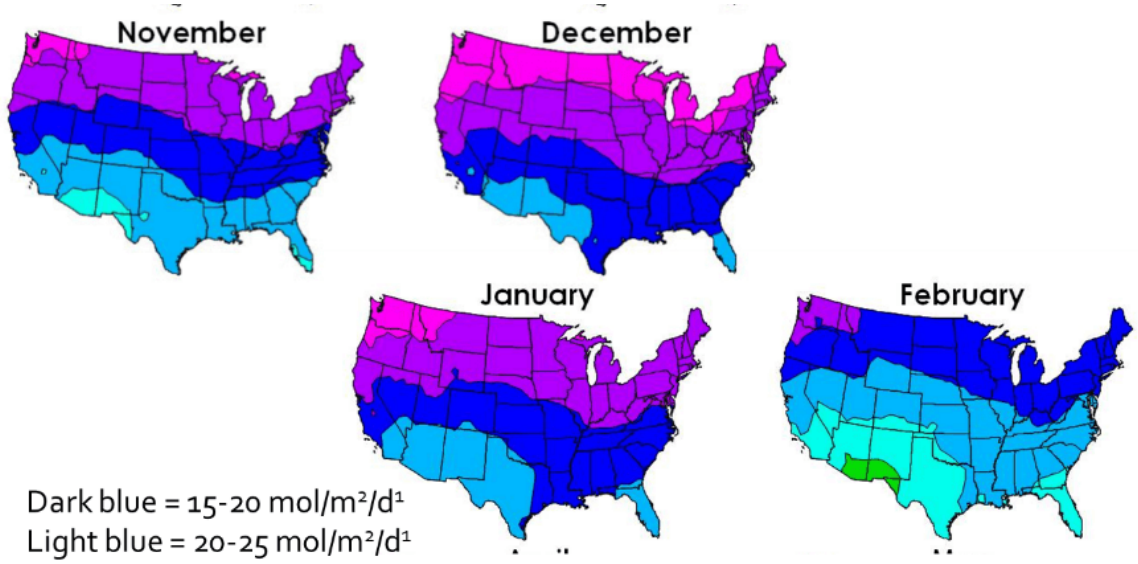


Figure 5-26. USA DLI maps for November, December, January and February. Demonstrates the low levels of DLI in Georgia during winter months. In November to January, Georgia receives 15 to 20 mol/m2/d. By February it increases to 20-25 mol/m2/d.

Artificial light can also be added to make-up the difference and enhance growth. Plant quality generally increases as the average DLI (daily light interval) increases even beyond “required” amount (with exception of true shade plants). The use of artificial lighting with plants is typically categorized into three types: Supplemental lighting, Photoperiodic lighting, and Sole-source lighting.

Supplemental Lighting

Supplemental light is used to boost existing light levels. These lamps emit moderate light intensity. Adding 60-120 µmol/m^2/s to the ambient light level. Supplemental lighting is used when the natural DLI is low. This may be due to the low intensity of the solar radiation or too short day length. Plants can be illuminated from directly above or, for tall dense canopies, from within the canopy to provide light to lower levels of the plant. This ability to hang lights within the crop canopy is only possible due to the invention of low-heat emitting lights – for example LEDs sources.



Figure 5-27. LED light sources can be hung within a tight canopy to increase productivity. (Runkle, Erik. 2017.)

Photoperiodic Lighting

For plants that are sensitive to photoperiods, photoperiodic lighting can be used to influence plant growth and development. Photoperiodic lighting is accomplished with low intensity lamps (1-2 µmol/m^2/s^1). Depending on the nature of the plant, the addition of this low intensity light can induce or inhibit flowering. The most common method for this technique is to deliver 1 to 2 µmol/m^2/s^1 of light for four hours during the night (or at the end of the day) from lamps that at least partly emit red +/- far red light. Incandescent lamps – rich in the red – were the traditional instrument used to deliver this light. However, modern LEDs have replaced the incandescent lamps as they are more efficient.



Figure 5-28. Red light is used for photoperiodic lighting. (© 2019 Great American Media Services & Greenhouse Product News.)

Sole-source Lighting

Sole-source lighting is used when plants are completely dependent on artificial light for their energy and developmental cues. This occurs when plants are grown indoors without natural light exposure (Figure 5-29). To reach the light requirements of the plants, high-intensity lighting (150 to 200 µmol/m^2/s^1) is needed, and it typically runs 18-24 hours per day. Night cycles and

photoperiodic lighting can be added if necessary for plant health and development.



Figure 5-29. Sole-source lighting must provide all the necessary energy for the plants. (https://konodesigns.com/pasona-o2/)

There are multiple lighting solutions available for growers. The addition of artificial light can be costly so there are multiple things to consider.

1. **The cost to purchase and install** – Are the fixtures themselves expensive? Do they include the lamps (bulbs)? Does it take specialized training to install the fixtures?
2. **Cost to operate** – How much energy is consumed to produce the needed light intensity? How long will the lamps last before they need to be replaced? What is their cost and what is the labor involved in replacing old lamps?
3. **Spectrum of light needed** – different sources emit different light spectrum. If you need red light to induce flowering, does your light source have enough red, or do you need to include additional sources to provide photoperiodic lighting?
4. **Intensity of light produced** – Can the source produce the light intensity needed for your crop under you growing conditions? Will this intensity modify the temperature or water requirements of the plants?
5. **Structural Requirements** – Can your existing structure (greenhouse) support the weight of the lighting units? Will the units create problems for existing mechanization in the greenhouse?

With the cost, both in time and funds, getting the lighting correct for your specific situation is critical. For large spaces, working with an engineer to calculate loads, cost, square-footage, energy consumption is advisable. Many lighting companies will provide this service.

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5.5.3: Lighting Sources

Today there are multiple light sources available to meet the needs of different applications. They vary in initial cost, light intensity, spectrum produced and cost of operation.

Incandescent lamps produce light as electricity moves through a wire filament. Much of the energy consumed is lost as heat rather than usable light. These lamps produce approximately 17 lumens per watt. The light spectrum produced (Figure 5-30) is predominately red with very little emitted in the violet and blue regions. The primary benefit is that both the fixtures and the lamps themselves are cheap. However, the cost of operating is significant and only produces low intensity light. With most of the emitted light in the orange-red region of the spectrum they are suited for use in photoperiodic lighting.

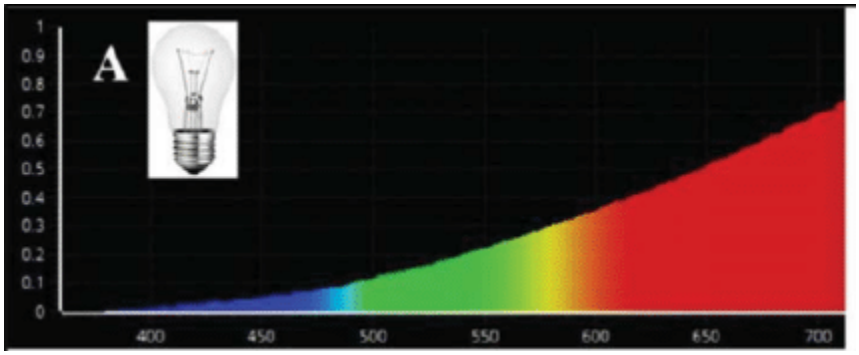


Figure 5-30. Output spectrum of an incandescent lamp, with intensity on the y-axis and wavelength on the x-axis. There is very low or no intensity in the blue, and intensity rises steadily to its highest in the red. (https://www.researchgate.net/figure/...fig1_312320039)

Fluorescent tubes produce light as electricity excites mercury vapor. The short-wave ultraviolet light it produces causes a phosphor coating on the inside of the lamp to glow. Most of the energy consumed is converted to usable light and thus these lamps are significantly more efficient than incandescent lamps. They produce approximately 50 lumen per watt. The light intensity produced is low to moderate but with more blue light and very little red (Figure 5-31). The low/moderate light intensity typically means the light sources need to be relatively close to the plants. Since they produce so little heat, placing the lights close to vegetation is not detrimental. Fluorescent fixtures and bulbs are relatively cheap and do not require any specialized knowledge for installation. However, their low/moderate intensity means that they work for supplemental lighting, but only in crops that have moderate light demands. They are useless for photoperiodic lighting due to the lack of red in their spectra.

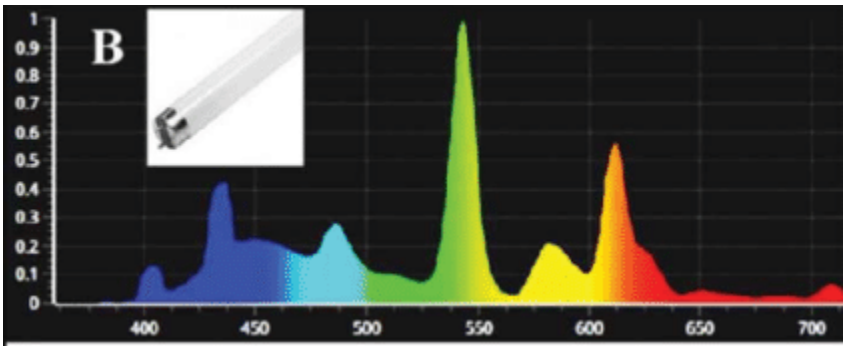


Figure 5-31. Output spectrum of a fluorescent tube. Graph with intensity along y-axis and wavelengths along x-axis. Low intensity with spikes in blue and green but none in red. (https://www.researchgate.net/figure/...fig1_312320039)

Compact fluorescent lamps produce the same spectrum of light as the tube fluorescent types. One benefit is that they can be used in fixtures designed for incandescent lamps since the lamps have integrated electric ballasts. Tubes require special fixtures that include ballast. For plant growth, tubes are typically preferred as they provide more coverage area than the compact style.

It is important to note that the presence of the mercury vapor in fluorescent tubes and lamps means they are classified as hazardous waste. They should be disposed of or recycled appropriately.

Commonly used in street lighting, **high-pressure sodium (HPS) lamps** produce light by passing energy through vaporized

sodium under high pressure. HPS lamps are more efficient than fluorescent or incandescent lamps. They produce approximately 80-120 lumens/watt. The spectrum they produce is dominated by orange and red (Figure 5-32). While significantly more efficient than incandescent lamps they still emit a lot of heat which may impact plants or require other environmental controls. The fixtures and lamps are pricey and may take some specialized knowledge for installation. The fixtures for these lamps must include a rather bulky ballast. This may require strengthening of structural supports due to the ballast unit's weight. Additionally, the bulk of the instrument blocks natural lighting. To avoid these issues, some manufacturers have ballasts independent of the light fixture. These ballasts can be placed some distance away and can power multiple fixtures. In the greenhouse, HPS lamps are used for supplemental lighting and can be used for sole-source lighting as well.

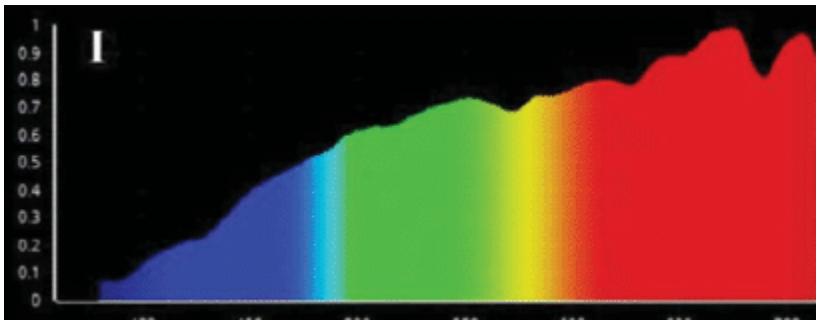


Figure 5-32. Output spectrum of a high-pressure sodium lamp, with intensity on the y-axis and wavelength on the x-axis. Intensity is low in the blue and rises through the green and yellow to its highest in the orange and red. (Scientific Figure on ResearchGate. Available from: https://www.researchgate.net/figure/...fig1_312320039 [accessed 13 Sep 2019])

Metal halide (MH) lamps are often preferred for some applications because they provide a more "natural sunlight" illumination as compared to the orange cast of the HPS lamps. The MH lamps produce light by passing energy through a mixture of vaporized mercury and compounds of metals with bromine or iodine (some versions use other halides) (Figure 5-33). They produce a high intensity light that emits well across the spectrum, as can be seen in the graph on this slide. Their energy efficiency is slightly higher than that of the HPS at 90-130 lumens/watt. The cost of the fixtures and lamps is about the same as the HPS. The MH lamps have some of the same drawbacks as the HPS. They require ballast and thus specialized fixtures. Modern ballasts are smaller, which does help with the weight and shading issues. The bulbs, however, have shorter life expectancy and thus any financial savings from energy efficiency is usually negated. These lamps are typical of sole-source lighting and can be used for supplemental as well.

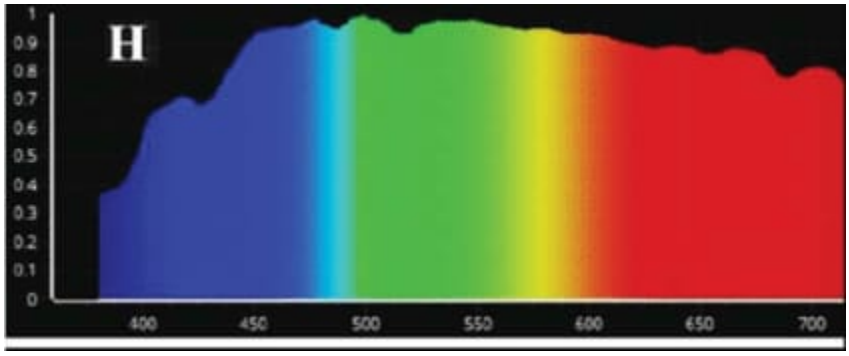


Figure 5-33. Light spectrum emitted by Metal halide lamps. (Scientific Figure on ResearchGate. Available from: https://www.researchgate.net/figure/...fig1_312320039 [accessed 13 Sep 2019])

The newest trend in plant lighting is the use of **LED** (Light emitting diodes). Each LED light produces a very narrow band of light (Figure 5-34). LED "grow lights" are made by creating large banks of LEDs emitting different wavelength. This can allow for the "tuning" of the light spectrum produced to complement the crops. For example, LED grow lights concentrate on producing red and blue light. Use of only red and blue lights provides the most cost-efficient method of growth; however, some studies have detected benefits associated with the addition of green light.

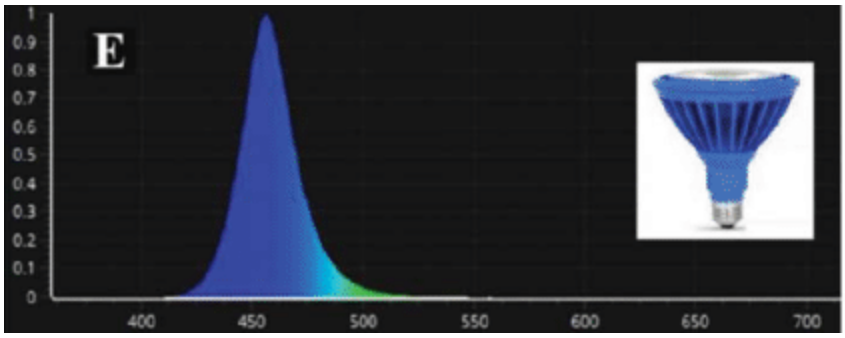


Figure 5-34. Output spectrum of a blue LED lamp. Graph with intensity along y-axis and wavelengths along x-axis. Produces a single peak at 460 nm. No other color is produced. (Scientific Figure on ResearchGate. Available from: https://www.researchgate.net/figure/...fig1_312320039 [accessed 13 Sep 2019])

LED equipment is more expense to purchase; however, the energy efficiency typically pays for the price difference within two years. Their energy efficiency varies with the array of colors emitted but it is typically 60-80% more efficient than HPS or MH lamps (100-300 lumens/watt are reported). They can be used for supplemental, photoperiodic, or sole-source lighting. Their low heat production makes the ideal from many applications.

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5.6: End of Chapter Review

Chapter Summary

1. Light is electromagnetic radiation.
   a. Characterized by wavelength (λ)frequency (f), and photon energy (E).
   b. These are inversely related, so longer wavelengths have lower frequencies and energies.
   c. The electromagnetic spectrum ranges from long radio waves to short gamma rays.
   d. Visible light makes up a small portion from 400-700 nm.
2. Photosynthetically active radiation (PAR) refers to visible light from 400-700 nm.
   a. Can drive photosynthesis.
   b. Blue (400-500 nm) and red (600-700 nm) wavelengths tend to be most effective due to absorption by chlorophyll pigments.
   c. Absorbance spectra of chlorophylls show peaks in the blue and red regions.
   d. Action spectra depicting photosynthetic activity also show peaks in blue/violet and orange/red.
   e. As light passes through leaf canopies, the blue/red portion is preferentially absorbed leading to a shift toward green and far-red light at lower depths.
3. Light quantity can be measured.
   a. Instantaneously as photosynthetic photon flux density (PPFD) in $\mu mol/m^2/s$
   b. Cumulatively as daily light integral (DLI) in $mol/m^2/day$.
   c. Most plants need at least a DLI of 10-12 $mol/m^2/day$ for growth and development.
   d. DLI varies by latitude, season, and weather conditions.
4. In addition to driving photosynthesis, light impacts phototropism, photoperiodism, and photomorphogenesis through photoreceptor molecules like phytochromes.
   a. Phytochromes exist in two photo-interconvertible forms: inactive P_r absorbs red, active P_{fr} absorbs far-red. The relative levels control development.
   b. Photoperiodism allows plants to flower based on night length. Short day plants flower with long nights while long day plants need short nights.
   c. Phototropism causes directional growth toward or away from light, often mediated by asymmetric auxin distribution.
5. Light levels can be manipulated.
   a. Shade reduces excess light through natural (trees, buildings) or artificial means (shade cloths, whitewash). It prevents overexcitation of photosystems.
   b. Supplemental lighting is added to boost PPFD when levels are suboptimal. Photoperiodic lighting manipulates day length for flowering. Sole-source lighting provides all light needs.
   c. Various electric lights can be used like LEDs, fluorescents, high-pressure sodium, and incandescent. They differ in spectrum, intensity, efficiency, and costs.

Key Terms

- Absorbance spectrum
- Action spectrum
- Daily light integral (DLI)
- Electromagnetic spectrum
- Incandescent lamps
- LED lamps
- Light compensation point
- Light saturation point
- Metal halide lamps
- PAR
- P_{fr}/P_r
- Photomorphogenesis
- Photoperiodism
- Phototropism

- Phytochrome

Self-Review

1. What is the range of wavelengths for photosynthetically active radiation (PAR)?
2. Which wavelengths within the PAR range tend to be most effective for photosynthesis?
3. How do the wavelength, frequency, and photon energy of light relate to each other?
4. What are two ways to quantify light levels for plant growth? Describe the units used for each.
5. How does light quality change as solar radiation passes through a plant canopy?
6. Compare the light absorption properties of chlorophyll a and chlorophyll b.
7. What is a phytochrome and how does it exist in two photo-interconvertible forms?
8. Explain the difference between long-day and short-day plants in terms of photoperiodism.
9. Describe how phototropism allows shoots to grow toward light.
10. What are three ways that humans can manipulate light levels for horticulture?
11. How do shade cloths reduce light intensity in greenhouses? What are their advantages?
12. Compare supplemental, photoperiodic, and sole-source lighting in terms of intensity and purpose.
13. What are the key properties and uses of LED grow lights versus high pressure sodium lamps?
14. Which type of lamp would you choose for photoperiodic lighting - incandescent, fluorescent, or metal halide? Why?
15. If electricity costs $0.12/kilowatt-hour, how much more expensive is it to operate a 250-watt incandescent bulb for 12 hours per day than a 25-watt LED bulb?

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6: WATER - CRITICAL FOR LIFE



Figure 6-1. Water can exist as a liquid, solid (ice) and gas (water vapor in air) in the same environment. Dawes Glacier in Alaska. (Stephanie Harvey. 2023. CC-BY-NC)

Water is critical to life, at least as we know define life. For example, in humans a large portion of our mass is water – up to 60%. Water is a vital nutrient to the life of every cell and acts first as a building material. Water regulates our internal body temperature as we sweat and breathe. The carbohydrates and proteins that our bodies use as food are metabolized and transported in the bloodstream by blood – which is on average 51% water. Water assists in flushing waste mainly through urination. It acts as a shock absorber for brain, spinal cord, and fetus. Saliva, 99% water, initiates the digestive process and lubricates the food to facilitate swallowing. In addition, it is the major component (70-80%) of synovial fluid which lubricates joints.

Water is equally important to plants and is the resource that most restricts plant growth. In this chapter we will take a brief look into several aspects of water including its chemistry (Figure 6-1), impact on the environment, impact on plants and how we can meet the water needs of plants.

6.1: Chemistry of Water

6.1.1: Water and Heat

6.2: Water and the Environment

6.2.1: The Water Cycle and Climate

6.2.2: Chemical and Physical Changes

6.2.3: Human Impacts

6.3: Water and Plants

6.3.1: The Need for Water

6.3.2: Shifting Needs

6.4: Water Delievery

6.4.1: Water for Crops

6.5: End of Chapter Review

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6.1: CHEMISTRY OF WATER

Water is a small compound made of one oxygen atom with two hydrogen atoms each attached to it via polar covalent bonds (Figure 6-2). Covalent bonds are formed when a pair of electrons are shared between two atoms. The bond becomes a polar covalent bond when one member of the bond retains the electrons more than the other. In the case of water, the oxygen atom is highly electronegative and this higher affinity for the electrons means they spend more of their time with the oxygen than with their respective hydrogens. This creates a partial positive charge (δ+) on each of the hydrogens and two partial negative charges (δ-) on the oxygen. It is this unequal sharing of electrons and the resulting partial charges on atoms of the compound that lead to the unique physical and chemical properties of water.

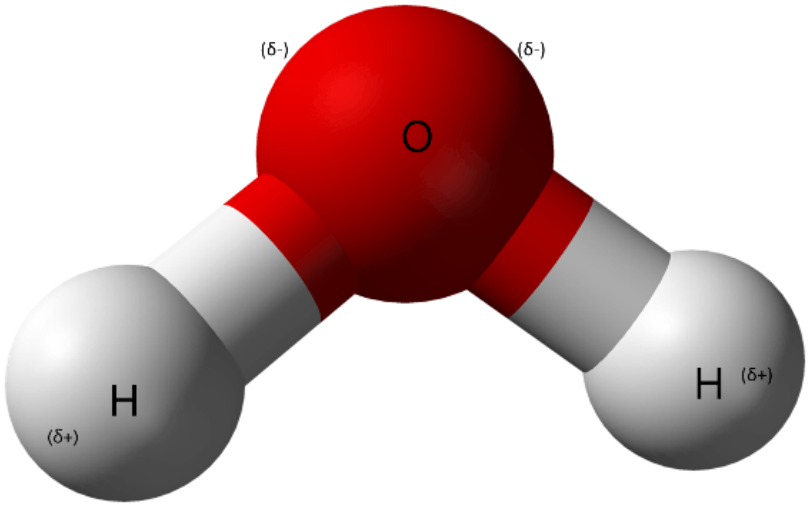


Figure 6-2. Ball-and-stick model of a water molecule: an oxygen atom attached to two hydrogen atoms at a bond angle of about 104.5 degrees. The partial negative charges (δ–) on the oxygen and partial positive charges (δ+) on the hydrogens are labeled. (Stephanie Harvey. 2023. CC-BY-NC.)

Water is the only naturally occurring substance that can exist in all three physical states in the environment. The physical states of matter are liquid, solid and gas. Solid matter is composed of tightly packed particles. It will retain its shape since the particles are not free to move around. Liquid matter is made of more loosely packed particles and will take the shape of its container. In a liquid the particles are free to move around but are packed tight enough to maintain their volume. Gaseous matter is composed of particles packed so loosely that it has neither a defined shape nor a defined volume. The state of the matter depends on the energy of the system. As demonstrated in Figure 6-1, water can be solid (ice), liquid and gas (clouds of water vapor) in the same system – although it may be changing states based on conditions such as temperature and pressure. For example, ice in your water melts if it is exposed to temperatures above zero degrees Celsius.

Water molecules can interact with each other via the partial charges on their surfaces. The partial negative on the oxygen is attracted to the partial positive on the hydrogen of an adjacent water molecule (Figure 6-3). This attraction produces a hydrogen bond. Hydrogen bonds are relatively weak. However, since each water molecule has 4 partial charges there is the potential for up to 4 hydrogen bonds. Collectively this creates a strong force – called **cohesion** -- that can hold water molecules to one another. Likewise, the partial charges can also interact with charges on the surface of other compounds leading to **adhesion**. Water's properties of cohesion and adhesion are important to how water behaves in various systems.

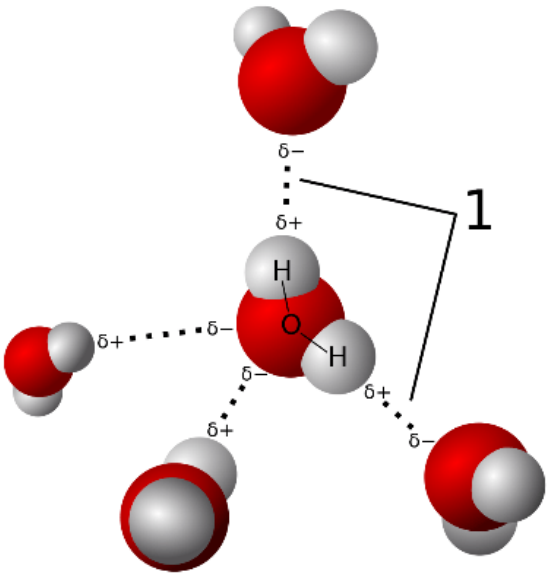


Figure 6-3. Model of five water molecules. The central molecule forms hydrogen bonds (dotted lines) from its partially positive hydrogens and partially negative oxygen to four neighboring molecules. Lines designated as #1 indicate two of the possible four bonds that can form.

In Figure 6-4, the spheres (drops) of water cling to a spider's web. The water molecules closest to the web's silk adheres via their adhesion properties. Additional layers of water molecules attach to the first layer of water via cohesion. At some point, the weight of the water droplet will overcome the adhesion, and the drop will fall from the web.



Figure 6-4. Cohesion and adhesion hold the water droplets in this spider's web. (Luc Viatour / www.Lucnix.be).

If you remember back to the chapter on plant processes, transport of water from roots to shoots relies on cohesion and adhesion. The cohesion keeps the column of water together as it is pulled from the top of the shoot due to evaporation. Adhesion keeps the column from slipping back down when tension is lost.

The potential formation of hydrogen bonds between water molecules allows water molecules to interact with each other to a high degree. At an interface between water and another media, like air, the water molecules are more likely to interact with other water molecules than air. As a result, more hydrogen bond form at this interface which creates a thin layer of water with greater cohesive power and thus greater surface tension. Surface tension allows the water's surface to support more weight than the water below the surface. Some insects, like this water strider (Figure 6-5), can spread their weight across the surface so that they can walk on the water. Other organisms, like some mosquito larva, hang downward from the surface of the water.



Figure 6-5. Water striders stay at on top of the water because of surface tension. Water is slightly depressed where the weight of the insect presses down. (By PD - Wikipedia English, CC BY-SA 3.0, curid=1095618

6.1.1: Water and Heat

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6.1.1: Water and Heat

For water to change physical states the number of hydrogen bonds occurring in the water much change. As liquid water freezes to ice, the molecules must slow and more bonds form. As water transitions from liquid to vapor (gas) bonds must be broken as the molecules move faster. For either of these transformations to occur energy has to be transferred. Evaporative cooling occurs as energy is absorbed by the water molecules causing them to move faster and causing bonds to break. The absorption of the energy by the water leaves the surface from which the water evaporated cooler.

Our bodies use this mechanism to help cool us off. When you exercise, excess heat is produced but to maintain normal body temperature, we sweat (Figure 6-6). As the sweat evaporates, it leaves us cooler. Evaporative cooling works best when humidity is low (sorry Southwest Georgia).



Figure 6-6. Evaporative cooling can be an area or our bodies cool. A sweating athlete being interviewed directly following a game. The water vapor (sweat) can be seen rising off the player. (By Haneburger - Own work, Public Domain).

If heat is absorbed as water evaporates, what would happen as water freezes? Although it seems counter intuitive, heat is released. Frost protection is a phenomenon in which growers spray their citrus trees (and strawberry plants) with water when the temperature drops to freezing (Figure 6-7). The small amount of heat release from the water as the molecules slow down and hydrogen bonds form is enough to keep delicate tissue from being damaged by the cold. Water freezes at 32^{o}F but most tissue is hardy to about 28^{o}F. This is a delicate balance however, because if windspeed pick up and increase the evaporation of the water this will chill the plant rather than warm it.



Figure 6-7. Grape vines protected from the cold via frost protection. Water is constantly sprayed on the plant where it freezes and releases a small amount of heat. (https://commons.wikimedia.org/w/inde...curid=10051921)

As water cools, the molecules slow down and move closer together and the water becomes denser like any other liquid material. At least until its temperature drops below 4^{o}C. Below this temperature, the slow-moving molecules start to form more hydrogen bonds and fewer are being broken. The bonds restrict the movement of the water molecules and force them further apart. Thus ice (solid water) is less dense than the liquid form. As a result, ices floats (Figure 6-8). Additionally, ice acts as a good insulator. Ice covering the surface of a lake prevents the extreme cold of the atmosphere from having as much impact on the water below the ice.



Figure 6-8. Iceberg floating in the Endicott Arm Fjord, Alaska. (Stephanie Harvey. 2023. CC-BY-NC).

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6.2: WATER AND THE ENVIRONMENT

Water is essential for all life on Earth. It makes up the majority of living organisms and is required for many environmental processes. Water plays a key role in shaping Earth's environments through its various states, abundance, movement, and chemical properties.

The most obvious impact of water is its sheer amount; it covers around 75% of Earth's surface. The water can be fresh, saline or a mixture of both. The oceans contain about 96.5% of Earth's water. They support a huge diversity of life from microbes to whales. Freshwater accounts for only about 3% of Earth's water supply but is vital for terrestrial ecosystems. Approximately 1.7% is stored in the polar icecaps, glaciers, and permanent snow. The remaining exists as surface water in lakes, rivers, and streams, as well as underground as groundwater. Only a tiny fraction, around 0.001%, exists as water vapor in the atmosphere.



Wetland at Seney National Wildlife Refuge, Germfask, MI. (Stephanie Harvey 2022 CC-BY-NC)

6.2.1: The Water Cycle and Climate

6.2.2: Chemical and Physical Changes

6.2.3: Human Impacts

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6.2.1: The Water Cycle and Climate

The hydrologic or water cycle describes how water circulates between these various reservoirs (pools) (Figure 6-10). Fluxes are how the water moves between the pools. Evaporation and transpiration transfer water to the air as vapor. This vapor condenses into clouds and precipitates back to the surface as rain, snow, sleet, or hail. Precipitation may directly return to the oceans or gather into surface waters that eventually drain back to the sea. Some water infiltrates the ground as groundwater. Global wind patterns and local topography determine where precipitation falls. For example, prevailing westerly winds bring moisture from the Pacific Ocean onshore in Seattle, resulting in abundant rainfall. The Cascade Mountains force clouds upward on their westward side, dropping rain, while leaving lands to the east in a drier "rain shadow."

As water moves through the hydrologic cycle, it shapes Earth's environments and moderates Earth's climate. The high specific heat capacity of water enables it to absorb energy without large changes in temperature. Bodies of water thus stabilize temperatures (Figure 6-9). During the day, light energy striking water. The energy is absorbed by the water with little change to the temperature. This heat-sink ability keeps the areas around these bodies of water slightly cooler than areas with the same solar input but without water. At night, the bodies of water radiate the heat in to surrounding air. This increases the atmospheric temperature adjacent to the waters. Thus, oceans and lakes act as heat reservoirs, warming air in winter and cooling it in summer.

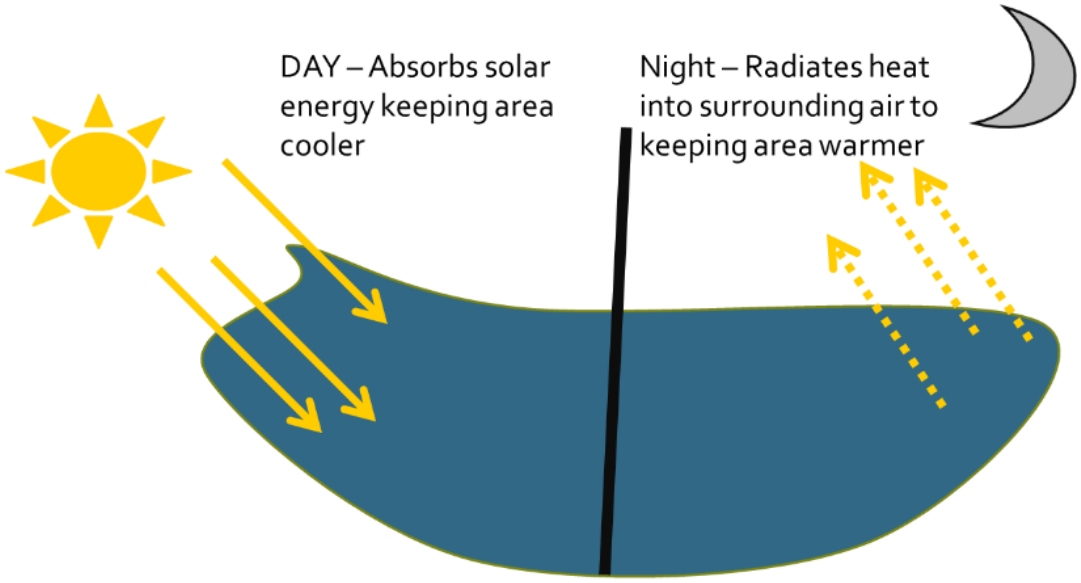


Figure 6-9. Light energy absorbed by bodies of water during the day and radiated during the night. (Stephanie Harvey, 2021. CC-BY-NC).

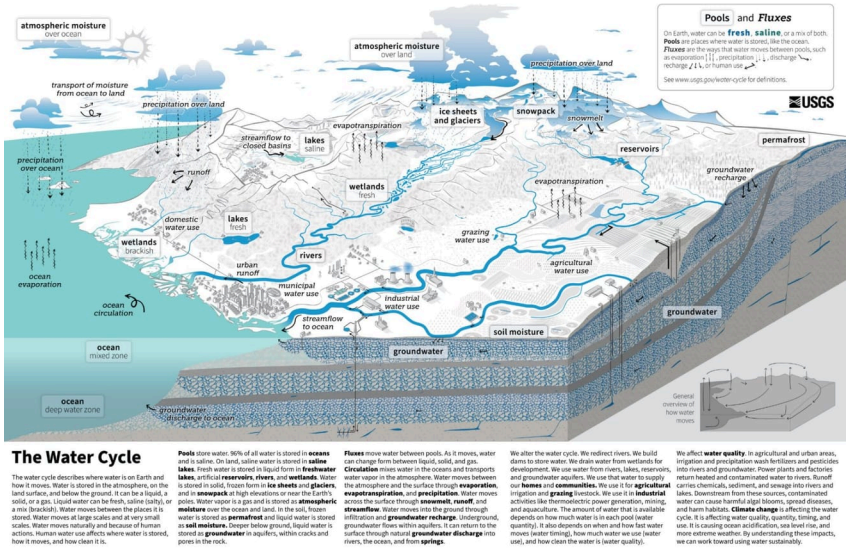


Figure 6-10. detailed diagram depicting the global water cycle. The direction of movement of water between reservoirs tends towards upwards movement through evapotranspiration and downward movement through gravity. The diagram also shows how human water use impacts where water is stored and how it moves.(By Hayley Corson-Dosch, Cee Nell, Rachel Volentine, Althea Archer, Ellen Bechtel, Jennifer Bruce, Nicole Felts, Tara Gross, Dianne Lopez-Trujillo, Charlotte Riggs, Emily Read - https://www.usgs.gov/media/images/water-cycle-png, Public Domain.

This moderating effect decreases farther inland and way from the large bodies of water. This can be seen in more extreme temperature ranges in continental interiors like Wichita, Kansas compared to coastal cities like San Francisco (Figure 6-11). The prevailing winds at 37°N latitude blow from west to east. San Francisco's temperature is moderated by the Pacific Ocean. Both Wichita and Norfolk are more heavily influenced by the continent.

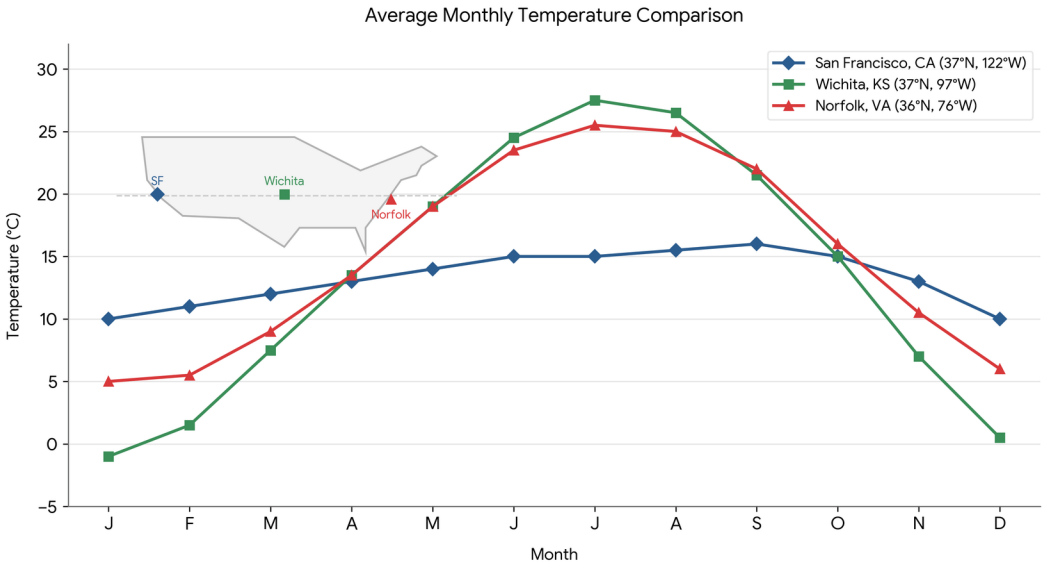


Figure 6-11. Yearly temperature variations at three midlatitude weather stations. Line graph of monthly average temperatures (°C) for San Francisco, CA; Wichita, KS; and Norfolk, VA. San Francisco's line rises only moderately in summer and stays moderate in winter. Wichita's and Norfolk's lines change dramatically over the year, peaking around 25–27 °C in summer and dropping to about 0–5 °C in winter. (Stephanie Harvey. CC-BY-NC)

Water's heat capacity also drives global circulation patterns by heating air masses over warm tropical oceans and cooling them over cold polar oceans. This creates major wind and precipitation belts around the planet. As the global winds drag across the ocean's surface, currents develop. Five major ocean-wide currents (gyres) occur, North Atlantic, South Atlantic, North pacific, South pacific and Indian Ocean gyres (Figure 6-12). The North Atlantic gyre has a very strong western boundary current referred to as the Gulf Stream. The Gulf Stream originates in the Gulf of Mexico, exits through the Strait of Florida, and then follows the eastern coastline of the United States and Newfoundland. It travels at speeds of 25 to 75 miles per day at about 1.15-3.45 miles

per hour. It influences the climate of the east coast of Florida, keeping temperatures warmer in the winter and cooler than the other southeastern states in the summer. It also influences severe weather patterns such as hurricanes.

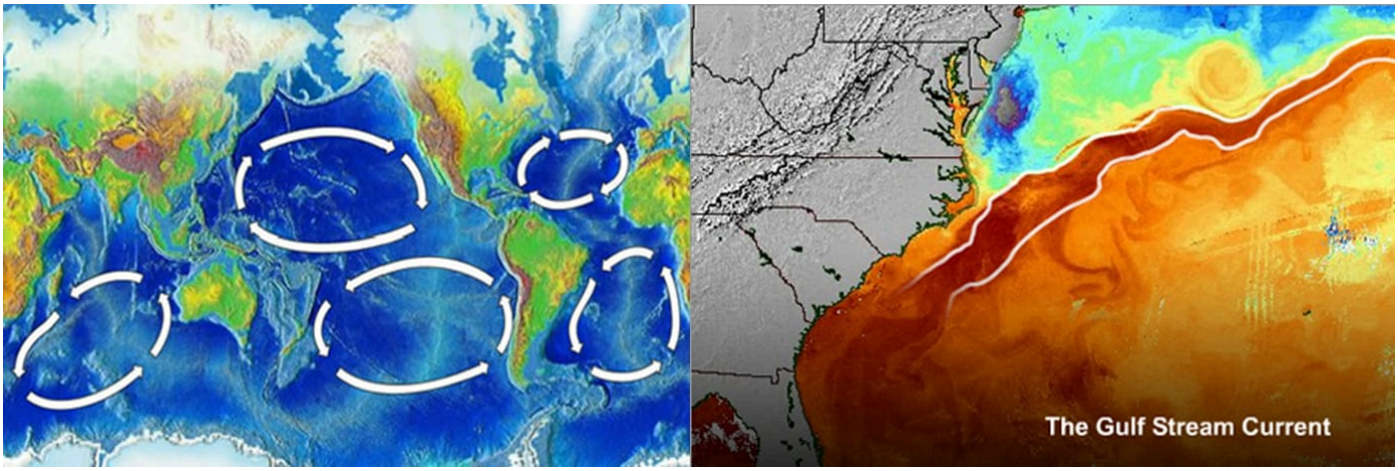


Figure 6-12. Left Image -Five major ocean-wide gyres: North Atlantic, S. Atlantic, N.Pacific, S. Pacific and Indian Ocean gyres. Right image - The North Atlantic gyre has a very strong western boundary current referred to as the Gulf Stream. The Gulf Stream originates in the Gulf of Mexico, exits through the Strait of Florida, and then follows the eastern coastline of the United States and Newfoundland. (Ross, 1995[1]).

[1]Ross, D. 1995 Introduction to Oceanography. New York: HarperCollins College Publishers. pp. 199-226, 339-343.

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6.2.2: Chemical and Physical Changes

The partial charges on the water molecules influences water role as the “Universal Solvent.” The chemical properties of water enable it to dissolve, pick up, transport, and deposit chemicals and nutrients around the planet. Water's polarity allows it to separate and transport ions, enabling processes like wet deposition where precipitation transfers compounds like sulfur and nitrogen oxides through the atmosphere. Rivers and groundwater transport dissolved nutrients like phosphorus and nitrogen that are essential for ecosystems.

By dissolving and mobilizing the building blocks of life, water facilitates chemical reactions necessary for life, both in organisms and entire ecosystems. Photosynthesis relies on water to transport reactants and split water molecules, releasing oxygen into the atmosphere. Water's solvent properties help distribute nutrients within organisms and maintain cellular homeostasis. On the ecosystem scale, the cycling of chemical elements like carbon and nitrogen by water is essential for life.

The movement of water also shapes the planet's surface through processes like erosion and deposition. Running water carves valleys, moves sediment, and deposits material downstream. Moving glaciers carve out basins, scrape away soil, and deposit rocky till. Wave action erodes shorelines and redistributes coastal sediments. As these processes reshape the land, they also provide diverse habitats for plants and animals.

The Grand Canyon is a great example a landscape shaped by water movement – both deposition and erosion (Figure 6-13). The layers (strata) seen in the exposed walls of the canyon reveal multiple deposition events. The canyons carved through these layers are the result of erosion by the Colorado River and its tributaries.



Figure 6-13. South rim of the Grand Canyon. Landscape produced through years of deposition and erosion. (Stephanie Harvey. 2018. CC-BY-NC).

Water also shapes ecosystems through its physical presence and movements. Lakes, rivers, wetlands, and coastlines create habitat and influence what life can exist within a given area. Many organisms have adapted to living near or in water, with entire ecosystems centered around rivers, lakes, or estuaries. The flow of water connects otherwise disconnected habitats, transporting nutrients, chemicals, organisms, and other materials. Many organisms rely on currents for transportation, food dispersal, and access to varied habitats throughout their life cycles.

The abundance and flow regimes of water dictate the types of organisms supported and govern population dynamics. Floods and droughts impose disturbances that structure ecological communities. Many species have life history strategies aligned with wet and dry periods. Environmental flows describe the quantities and patterns of water flows required to sustain freshwater ecosystems. Managing water resources to maintain key aspects of an ecosystem's natural hydrologic regime is crucial for conserving biodiversity.

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6.2.3: Human Impacts

Human activities profoundly impact water's distribution and movement through the hydrosphere. Actions like damming rivers, overdrawing groundwater, and paving land alter natural hydrologic patterns, degrading ecosystems (Figure 6-14). Pollution disrupts water's chemical properties. Nutrient loading from fertilizers produces algal blooms and dead zones in lakes and coastal areas. Acid rain alters water chemistry as sulfur and nitrogen oxides dissolve in precipitation.

Climate change is rapidly transforming the global water cycle by warming oceans, melting glaciers, intensifying storms, increasing evaporation, and shifting precipitation patterns. Rising seas endanger coastal habitats and communities. Changes to water availability threaten everything from food production to electricity generation.

Water mediates countless processes essential for life at scales from cells to the biosphere. Its unique thermal, chemical, mechanical, and biological roles arise from water's structure and abundance. Any environmental shifts that reduce water quality or availability reverberate throughout interconnected ecosystems. A holistic understanding of water's diverse functions is necessary to protect the health of both human communities and the natural world. Sustainable management of water resources will be critical as climate change stresses Earth's interlinked human and natural systems.



Figure 6-14. Hoover Dam - a hydroelectric power plant that impounds Lake Mead. Image taken when water was very low so four intake towers stand high above the waterline. (Stephanie Harvey. 2018. CC-BY-NC).

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6.3: WATER AND PLANTS

The transition of an ancestral algae to terrestrial life required adaptations associated with water acquisition, sequestration, and avoidance of evaporation. All plants need water and the limited availability of water in the terrestrial environment significantly restricted early plants. Early colonizers were restricted to areas where surface water was readily available. The limitation on transport of water within the multicellular form of non-vascular plants (such as the mosses) limited their size. With the evolution of vascular plants, some of these limitations were overcome. Soil water could be extracted and efficiently transported throughout the plant. But even these non-seeded vascular plants (lycophytes and ferns) depended on water for reproductive success since flagellated sperm had to swim to the egg for fertilization. The evolution of pollen (non-flagellated sperm) and seeds allowed plants to stretch their colonization to new areas. But still water is the most limiting factor to plant productivity, germination, growth, and reproduction. Water availability and temperature are the key characteristics that separate the world's biomes.



Native azalea by stream in North Georgia, The Pocket Recreation Area. (Stephanie Harvey. 2022, CC-BY-NC)

6.3.1: The Need for Water

6.3.2: Shifting Needs

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6.3.1: The Need for Water

At a cellular level, some water is needed for metabolic work. For example, hydrolysis of starch requires water. However, most of the water taken up by plants is lost to transpiration and evaporation (refer back to Chapter 4 – Section: Transport and Transpiration). Plants have evolved a sophisticated array of adaptations to control water loss.

Water efficiency can be expressed as mm of water lost per day. Adaptive strategies often involve sacrifices in other areas of efficiency, so plants that evolved in environments where water was plentiful are often less water efficient. Some plants, like C_4 plants and CAM plants, are more water efficient while photosynthesizing than the typical C_3 plants. If less water is lost during this process, the plants' need for water is also less. The C_4 plants and CAM plants specialized for tolerate drought and fair better under limited rainfall than C_3 plants. The C_3 plants on the other hand are more photosynthetically efficient. Thus, when water is plentiful, they are more productive (and can out compete) the C_4 and CAM plants. The changes made to make the $C_4$and CAM plants more water efficient are both biochemical and physiological.

Morphological differences are also a common adaptation. Large leaves are ideal for maximizing photosynthetic surfaces, but this increase in surface is also marked but increases in water loss. Plant adapted to regions with lower water availability often exhibit reduced leaf area. The reduction in leaf surface area can be extreme in some cases (Figure 6-15). *Ephedra* species have evolved photosynthetic stems, and the leaves are reduced to small scalelike structures at the stem nodes. The stems have a lower surface to volume ratio which helps reduce water loss.



Figure 6-15. *Ephedra* growing in the Valley of Fire, Nevada. Ephedra, a leafless plant that grows in arid regions of the American Southwest. The green stems are the photosynthetic part of the plant. (Stephanie Harvey. 2018. CC-BY-NC).



Figure 6-16. Pubescence along the sepals in inflorescence of Canadian Lousewort. (Stephanie Harvey. 2025. CC-BY-NC).

Plants have also evolved methods to prevent water loss from exposed tissues. Terrestrial plants produce a hydrophobic mixture that is deposited by the plant epidermis on the plant's outer surfaces. This cuticle layer is extremely efficient at stopping evaporation of water – less than 5 percent of the water loss by plant is trans-cuticular. Plants can also increase the density and type of hairs found on their epidermis to minimize water loss and thus water demand (Figure 6-16).

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6.3.2: Shifting Needs

The water demand by a plant can vary depending on the growth stage of the plant. A newly germinated plant is small and has a relatively low water demand as compared to the same plant weeks later as it undergoes vigorous growth. New flushes of leaves or flowers, or engorgement of fruit can dramatically increase the water demand. For deciduous perennial plants, the springtime flush of new leaves creates a heavy demand for water. To help meet this demand tree will produce larger diameter vessel elements - transport cells in the xylem. As the need drops off in late spring/summer the diameter of the vessel element decreases (Figure 6-17).

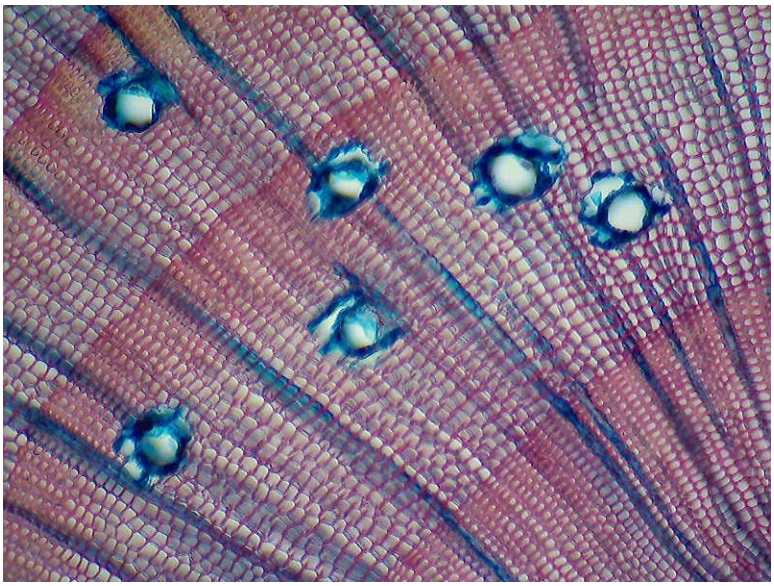


Figure 6-17: Annual growth rings as seen in cross section of a *Pinus* stem. The large cells of spring produced xylem are very distinguishable form the smaller cells of the summer produced xylem. (Stephanie Harvey. 2019 CC-BY-NC)

Daily changes in the weather can change the water needs of a plant. You might think that a hot, still day would create the highest water demand. Not necessarily true. The slight breeze that may feel good to us on a warm day can strongly impact water demand. Under still conditions, the water vapor leaving the plant stays close to the leaf. This effectively humidifies the air boundary adjacent to the plant. With the adjacent air humidified, water evaporates from the leaf more slowly. Even a moderate breeze will strip this humid boundary away from the leaf, leaving the dryer air that leads to higher evaporation rates. And remember, the reason for most water loss is the need for gases exchange to keep photosynthesis going. So, on heavy overcast days, plants are more likely to hold onto water than lose it to when low photosynthetic efficiency is likely.

If water demand is not met, plants will close their stomata pores and sacrifice photosynthetic efficiency in favor of water efficiency. If water loss continues to outstrip uptake, plants will wilt as water loss impacts rigidity of herbaceous plants. Plants can recover if water is supplied prior to the plant reaching a stage referred to as permanent wilt. Once permanent wilt is reached, no amount of water will stimulate recovery. Wilt is less visible in woody plants where the ridged xylem maintains the support not hydrostatic pressure. However, loss of water will take its toll on large trees even when leaves look normal. Large branches can break without warning due to large cavitation (breaking of the water columns within the xylem transport cells).

Water pressure (turgor pressure) powers cell expansion (Figure 6-18). Following cell division, animal cells must manufacture cytoplasm to increase in size. Plant cells increase to their “adult” size with the addition of water into the central vacuole. The cellulose microfibrils of the plant cell wall restricts the enlargement of the cell along a single axis. From the experiment shown in Figure 6-18, you can see that the bead placed on the surface of the cells are further apart following a period of growth. The growth is accompanied by a nastic movement – a non-directional response to stimuli – that results in a slight twisting of the stem during cell expansion.

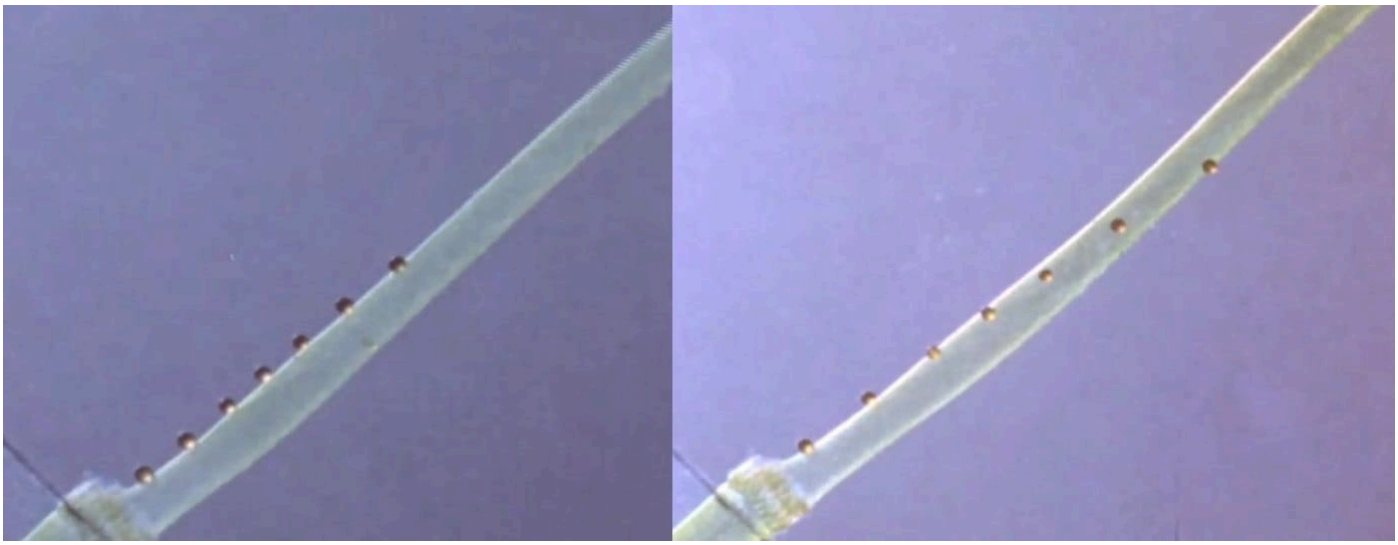


Figure 6-18. Growth of a *Nitella axillaris* stem is demonstrated by adhering small beads to the surface of the stem. The first image is after their application while the second image is just hours later. Also note how the line twists slightly as the cells expand. (Images captured from Growth & Morphogenesis in Plant Cells. (1971); capture 10/2023 by Stephanie Harvey).

For crops, the water need can vary with developmental stage, crop type and even by cultivar. Some crops inherently need more water than others. In Figure 6-19, crabgrass is surviving drought condition while other grasses fail. Crops such as rice and sugarcane need more water than crops like beans and wheat. However, modern techniques such as creation of genetically modified cultivars may lessen the differences.



Figure 6-19. Crabgrass emerging in drought-stressed turf. (Photo by Kevin Frank, MSU.)

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6.4: WATER DELIEVERY

Most plants get their water via precipitation in the form of rain or snow. Other forms of precipitation can also contribute to the water available for plants. For example, San Francisco's dense fog (Figure 6-20A) deposits water directly on the leaves or on surfaces from which water can drip (fog drip). Many of the plants within the Golden Gate Park depend on almost daily deposition. The heavy fog is caused by moist air over the Pacific Ocean passing over cold upwellings along the coast (Figure 6-20B).

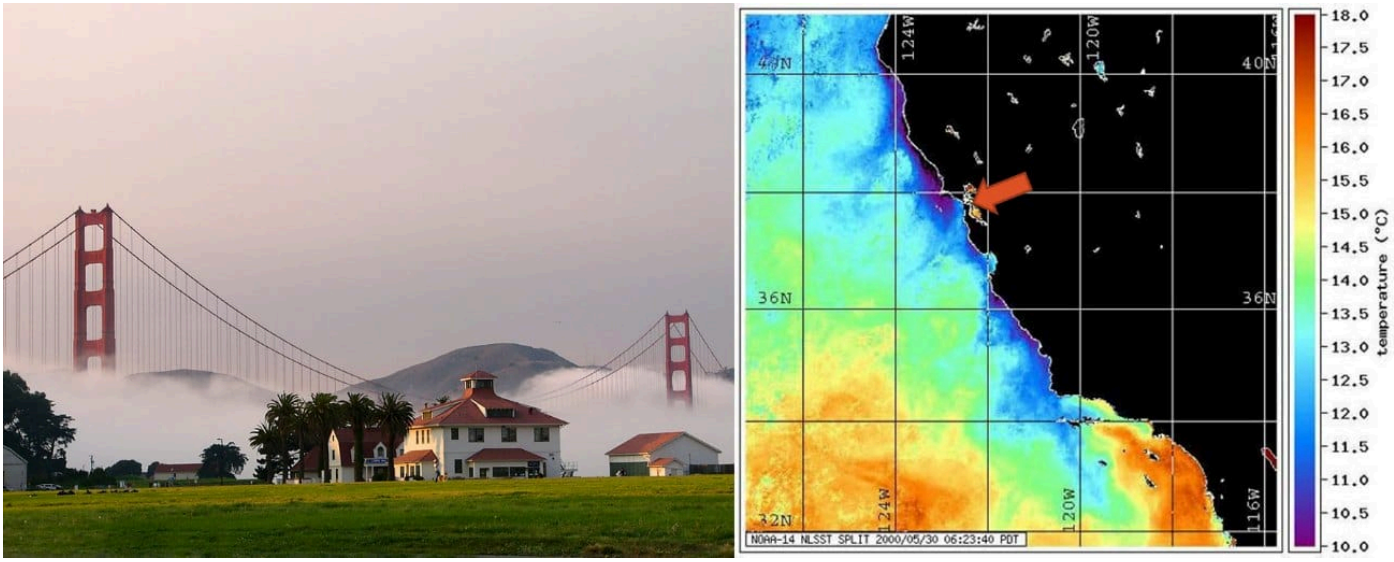


Figure 6-20. A. Fog bank rolling inland from San Francisco Bay. B. Map of water temperatures along the California coast with arrow marking San Francisco. The dark blue color signifies the cold upwellings. (http://www.nps.gov; curid=864900; NOAA - https://oceanexplorer.noaa.gov/)

Precipitation is subject to seasonality and can be difficult to predict. Plants native to a region are well adapted for surviving on the rain/snow fall typical of their native range. For regions where rain fall is infrequent, adapted plants have mechanism to "wait it out." They may restrict growth or reproductive efforts during acute drought. Global climate change may place these native species under pressure as precipitation patterns change (Figure 6-21). Much of the US experiences drought periodically. However, longer, and more critical drought levels are being seen. In Figure 6-21, the colored areas are all experiencing lower than expected precipitation. The darker the color the more severe the drought. Additionally, areas marked with "L" are experiencing long term (>6 months) impacts (hydrology and ecology), "S" areas are experiencing short-term (<6 months) impacts (agriculture and grasslands) and "SL" are areas experiencing both short- and long-term impacts.

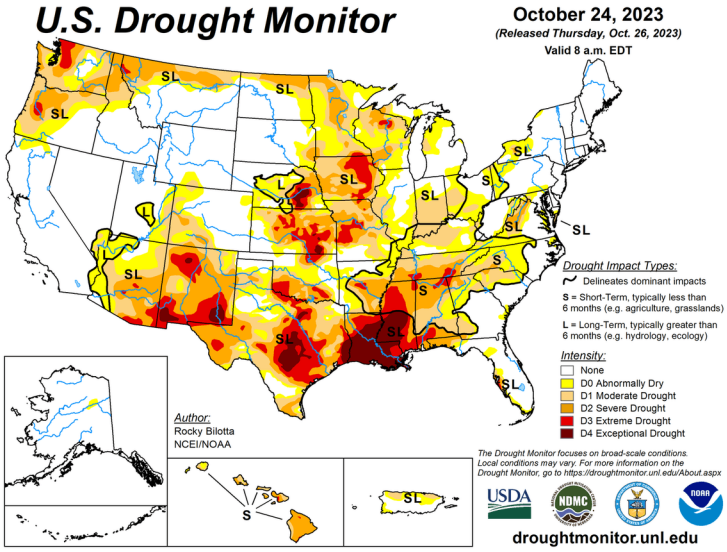


Figure 6-21. U.S. Drought Monitor map indicates the areas under drought as of October 24th 2023. Shows exceptional drought in parts of Louisiana, Mississippi and Texas. Moderate drought covers about 1/2 the US. The East Coast is mostly unaffected as is California, Nevada, Colorado, Utah, Wyoming and most of Idaho.(https://droughtmonitor.unl.edu/Maps/MapArchive.aspx)

Drought and the Mississippi River

The Mississippi River and its tributaries experiencing extremely low water flow due to limited precipitation (second year) and extreme summer heatwave. Lack of water is something new to Southern Mississippi and Louisiana; typically, their issue is too much water from tropical storms and hurricanes. At the Mississippi Delta – the area where the river empties into the Gulf of Mexico, the lower flow of water is causing multiple problems. The river is a major transportation route, and lower water levels are making parts of the river unnavigable. Irrigation pumps and drinking water systems along the river have inlets above the current water levels. This results in areas where drinking water is at risk.

An invisible hazard has also developed. At the delta, saltwater, and freshwater mix. Salt water, which is heavier, sinks below the freshwater. Normally, the flow of freshwater prevents saltwater intrusion so far up the river. In the summer of 2023 however, a massive saltwater wedge was moving up the river. It threatened to expose about a million residences to dangerous levels of salt water. By mid-October it retreated six miles due to river flow increased and installation of an underwater sill created. (The sill was created as a wall on the bottom of the river that holds back the saltwater.) This retreat saves the freshwater supply for most of Orleans and Jefferson Parishes but smaller communities in Plaquemines and St. Bernard Parishes were already inundated. More than 8 million gallons of fresh water are barged each day to help flush the water systems.

6.4.1: Water for Crops

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6.4.1: Water for Crops

For crops it is not just about surviving a season. It is about productivity – plants need to flourish to meet our demands. They need an optimum supply of water, and they need it on a specific schedule. Too much at the wrong time can be just as damaging as too little.

If the environment cannot provide the water needed by plants, supplemental watering can be employed. Water rights, control of water sources, is a growing issue Worldwide. In the US, the tension is growing with the droughts cities and states fight over water. Sources of water tend to vary with location and geology. Water for large scale irrigation systems can be pulled from rivers or streams if there is a source close by. Holding ponds – farm/irrigation ponds – can be created it surface water by damming or diverting existing creeks and streams. A holding pond might also be created and fed by springs. If the region has aquifers below it, wells can be drilled to bring the water to the surface for use. Or for small scale irrigation such as your garden or lawn, municipal water sources can be an option.

There are many techniques that can be employed to deliver water to plants. For small scale application water can be added to individual plants or to groups of plants using a watering wand and/or a “fog-it”nozzle (Figure 6-22). These devices allow the user to modify the amount of water an individual plant gets and can be particularly useful in mixed plant settings where one plant might have a plant with a high demand adjacent to a xeric plant (dry habitat). The size of the water droplets can impact plant health. The larger droplet of a wand may be for larger, established plants but smaller droplets work better for young seedlings. “Fog-it nozzles” spray a very fine mist of water that is beneficial for seeded flats and young tender seedlings. The fine mist helps prevent displacement of seeds in a tray or the flatting of young seedlings as can happen with larger water drops. The downside is that the fine mist is not delivering much water at a time. While the surface may look saturated, the soil beneath is bone dry. The surface water quickly evaporates, leaving the seedling without water. Care must be taken that enough water is applied to penetrate the soil completely.



Figure 6-22. Watering wand and fog-it nozzles allow for hand application of water. (Lynn Ketchum. 2014. CC-BY-SA.; https://www.greenhousemegastore.com)

For large scale agricultural fields, center pivot irrigations systems are more practical (Figure 6-23). These systems consist of a pipe (typically aluminum) that supplies water to sprinkler heads along its length. The pipe (with the sprinkler heads) is moved on wheels around a center pivot, creating an irrigated circle. Originally the movement was powered by water pressure, but most systems today move via electric motors. Older systems had sprinkler heads along the top of the pipe, but modern systems now use dropped sprinkler heads to position the water just above the crop. The “drop” can be changed based on the crop’s height. This helps limit evaporative losses.



Figure 6-23. Center pivot irrigation system. (By Gene Alexander, USDA Natural Resources Conservation Service - photogallery.nrcs.usda.gov No. NRCSCO87001, Public Domain.)

Smaller fields of horticultural crops and home gardens can be irrigated using drip and micro-irrigation systems. These systems deliver water at or near the root zone of the plant in significantly smaller amounts than large broadcast systems. This minimizes evaporation and runoff, making this the most efficient method of irrigation.

Drip systems can consist of either a hose with small holes that leak water at set intervals or a hose with drip emitters inserted. Figure 6-24 (left image) show a blue drip emitter. Emitters are selected based on the water volume needed by the plant. This works well in a mixed setting where different plants might have different water needs. Simple emitters allow water to flow outward at a set rate. Some applications require more sophisticated emitters that only allow water to leave the emitter under pressure. This prevents overwater that can happen as water drains out the lowest emitters post irrigation event.

In micro-irrigation systems, water is sprayed on the plants using small sprinkler heads (Figure 6-24-Right image). Again, the type of head selected will allow for control of volume, droplet size as well as spray patterns for highly customizable water delivery.

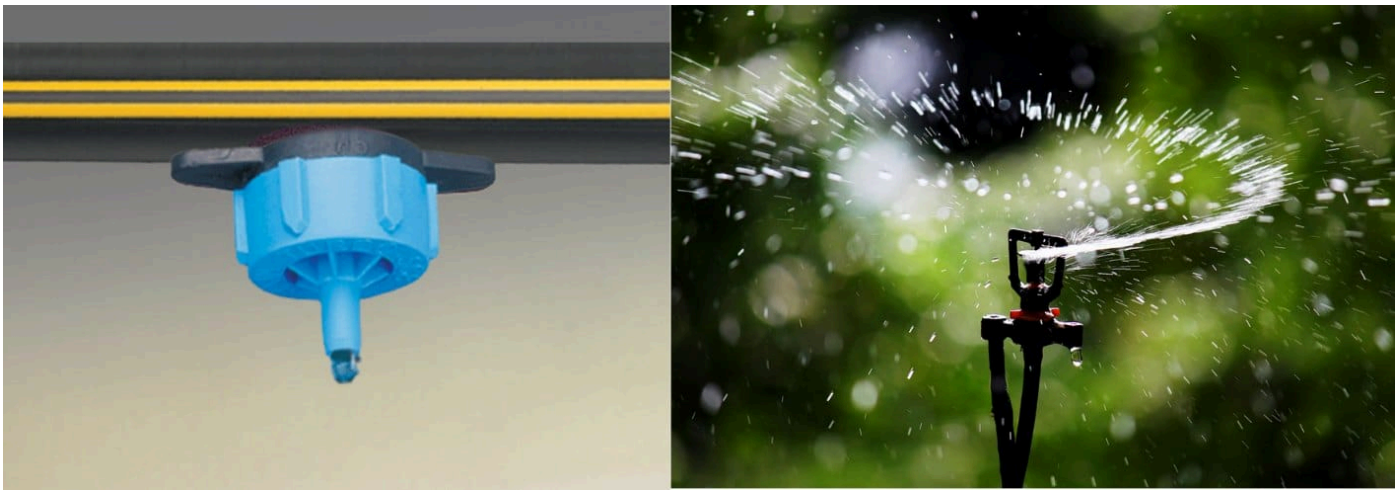


Figure 6-24. Left image - drip emitter installed in a supply line. Right image - Water being sprayed in a circle by a micro-irrigation sprinkler head. (By Jisl, CC BY-SA 3.0, curid=37688342; By Anton - Own work, CC BY-SA 4.0, curid=18120755.

Water delivery can be automated by using timers to turn valves on and off (Figure 6-25). Depending on application and controllers, triggers for water can be based on time/day. For example, watering can be scheduled for 6 am every morning. Some controllers use light to control irrigation. A light sensor detects sunrise and triggers a watering cycle. It then counts the cumulative solar radiation (such as the DLI) until a threshold is reached, triggering another water cycle. This type of control can help conserve

water since solar radiation often drives the plant's water demand. On a cloudy day when little water is lost by the plants, less irrigation occurs.

Other adaptors can be used with the controllers to help determine when irrigation is needed. Soil moisture probes detect the level of water in the soil and can trigger a water cycle when needed. Rain sensors can detect rain fall and prevent irrigation cycles during rain events. Together these systems can help make sure adequate water is supplied but water is not wasted.



Figure 6-25. Automation of watering can be done using a controller. Triggering can be based on sunrise, time, soil moisture, or DLI. (www.rainbird.com; link4controls.com.)

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6.5: End of Chapter Review

Chapter Summary

- Water is essential for life. It makes up a large portion of living organisms and enables important chemical reactions and transport processes.
- Water has unique chemical properties due to its polar structure. These allow it to dissolve materials, adhere to surfaces, and form hydrogen bonds.
- Water's high heat capacity stabilizes temperatures. Its ability to change states regulates climate.
- The water cycle circulates water between the atmosphere, land, and oceans through processes like evaporation, condensation, and precipitation.
- Water shapes the environment through physical processes like erosion and chemical processes like dissolving and transporting materials.
- Plants need water for metabolism, rigidity, growth, and cooling. Adaptations like sunken stomata and C4 photosynthesis increase water efficiency.
- Water availability, especially precipitation, limits plant distribution and growth. Supplemental irrigation helps agriculture flourish.
- Humans impact the water cycle through actions like pollution, groundwater pumping, and altering flow regimes. Sustainable water management is crucial.

Key Terms

- Adhesion
- Aquifer
- Cohesion
- Condensation
- Cuticle
- Deposition
- Drought
- Erosion
- Evaporation
- Hydrogen bond
- Irrigation
- Precipitation
- Stomata
- Transpiration
- Water Cycle

Self-Review

1. What are the three physical states that water can exist as in the natural environment?
2. What causes water molecules to stick together?
3. How does water's high heat capacity impact climate?
4. What processes are involved in moving water through the water cycle?
5. How does moving water shape the land surface on Earth?
6. Why is water essential for the cells and bodies of living organisms?
7. What adaptations help plants reduce water loss from their leaves?
8. What photosynthetic pathways make some plants more water efficient?
9. How does a plant's water demand change throughout its life cycle?
10. What are two ways that fog can impact the water availability for plants?
11. How have human activities disrupted natural water availability and quality?
12. What factors influence how much water a crop plant needs?
13. How can the method of water delivery impact plant health?

14. What are some techniques used to automate irrigation systems?
15. How could shifts in global precipitation patterns threaten native plant communities?

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7: SOIL



Figure 7-1. Soil with fungal hyphae visible. Also notice the porous nature of the soil. (Stephanie Harvey. 2000. CC-BY-NC.)

Soil, as defined by geologist is “the loose surface of the earth as distinguished from solid bedrock.” While this covers a significant part of the soil (mostly abiotic), it does not include the elements critical for biologists. Biologists would include biotic and organic materials in their definition of soil. Or they might refer to a more traditional definition that required the additional phrase that soil “nourishes and supports plant growth.”

Soil is a complex medium with both abiotic (non-living) and biotic (living) components (Figure 7-1). In this chapter we will mostly focus on how soils impact plant growth. To do so we will have to examine both the abiotic and biotic components of soils.

7.1: The Abiotic Nature of Soils

7.1.1: Soil Formation

7.1.2: Soil Texture

7.1.3: Soil Structure

7.1.4: Soil Horizons and Profiles

7.1.5: Soil pH

7.1.6: Soil Cation Exchange Capacity

7.2: The Biotic Nature of Soils

7.2.1: Microscopic Inhabitants

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7.1: THE ABIOTIC NATURE OF SOILS

As plants evolved from aquatic algae to terrestrial life one of the major changes was the uptake of needed resources. No longer surrounded by water, plants needed support --physically and chemically. With limited uptake from the atmosphere, the only other environmental interface was the earth. Soil is a matrix in which plant roots can anchor and from which plants obtain their nutrients and water. Additionally, the plant roots must have oxygen for cellular respiration, and this too must be obtained from the soil matrix. As such soil is a vital resource and both its chemical and physical properties impact plants and their ecosystems.

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7.1.1: Soil Formation

Soil is an important resource in natural and agricultural settings. It is renewable but the formation is very slow. It is estimated that to produce a single inch (2.5 cm) of topsoil, it takes about 100 years. That same inch can be lost in a single severe weather event. Soil formation through weathering is a complex process that breaks down rocks and minerals over time. Weathering can be physical, chemical, or biological.

Physical weathering processes do not involve chemical changes. They simply mechanically break down parent rock material into smaller fragments to create sediments and soils. The mechanical forces needed to fracture and disintegrate rocks come from a variety of sources:

- Freeze-thaw weathering: Water seeps into cracks and pores in rock. When temperatures drop below freezing, the water expands as it turns to ice. This expansion exerts outward pressure on the rock, enlarging the crack or pore. Over many freeze-thaw cycles, this wedging action splits rocks apart along fractures (Figure 7-2).
- Thermal expansion: Rocks expand and contract with heating and cooling. These stresses can eventually cause cracks and fractures. Exfoliation of surface sheets or onion-skin weathering often results from thermal expansion.
- Abrasion: Rock-on-rock collisions, such as in a stream or along a cliff face, effectively grind rocks into smaller pieces. Glacial movement is an extreme example of this as the pressure and motion of the glacier causes abrasion as rocks embedded in ice scour the underlying rock surface.
- Crystal growth: Minerals like salt crystallize and grow in the pores and cracks of rock, exerting pressure that can break rocks apart. In coastal areas, saltwater-spray can penetrate pores and cracks in the rock. As the water evaporates the salts crystalize within the rock. As the salt crystals heat up, they expand.
- Plant growth: Small plant root can grow into fissures within rocks. As the roots expand in girth, the growth this can literally splits rocks apart.



Figure 7-2. Freeze-thaw cycles eventually fracture larger rocks into smaller pieces. (By Till Niermann - Own work, CC BY-SA 3.0, curid=745814)

Chemical weathering alters rocks and minerals through chemical reactions. One cause of chemical weathering is oxidation. From a chemical standpoint, oxidation is the loss of electrons from an element. Iron atoms within rock can be oxidized to rust which weakens the rock material. Oxidation of sulfide minerals results in the creation of sulfuric acid. Acids often play a role in chemical weathering and can come from a variety of sources. Carbon dioxide mixes with water to produce carbonic acid. Pollutants like sulfur and nitrogen oxides dissolve in rainwater to produce acid rain which chemically weathers rocks upon contact. Acids secreted by lichens, mosses and plant roots can impact rocks as well. These acids dissolve rock, creating channels and pits. These channels and pits can then create more entry points to facilitate both physical and chemical weathering. The type and rate of weathering depend on factors like climate, topography, and rock characteristics.

The smaller particles created through weathering accumulate as sediments like sand, silt, and clay. With continued weathering,

these sediments break down into finer particles with more surface area. The texture of the soil becomes finer. In warm, wet climates, high rates of chemical weathering decompose feldspar minerals into clays. In drier grasslands, physical weathering may dominate, with a higher percentage of sand and silts from broken rock pieces.

Colonization of newly formed inorganic soil components starts with plants such as lichens and mosses. They attract other organisms and initiate the addition of organic matter through secretions and decay. New organisms move into the area and effect soil formation including microbial organisms - such as protozoa, bacteria, and fungi- plants and animals â€“ such as earthworms, nematodes and insects. As weathering continues, soils develop characteristic horizons, with organic accumulation on top. Soil formation is a gradual process dependent on climate, biology, parent material, and topography over long timescales. Weathering continually generates soil from solid rock and mineral material. Not all soil comes from newly weathered local rocks. Soils can be translocated by flooding and landslide. Glaciation moves soil across the landscape while volcanic eruptions add new land to the landscape.

We tend to think of soil as a solid material, but it is not. It is composed of mineral matter, organic matter, air and water. For a given volume of typical soil, solids only make up about 50% with 45% inorganic and 5% organic matter. The other 50% of the soil is made up of voids that are filled with gases (25%) and water (25%). All four of these components are critical to plant success. The pie graph (Figure 7-4) shows the components of a loam soil by percent volume. Here the mineral matter (collectively 45%) has been separated into sand, silt and clay. Soils are broadly classified as their inorganic (mineral) or organic based on the organic material in the top 80 cm of soil. There is no universally accepted threshold for exact percentage required to make this classification but in general it is 20-30%. Peat and â€œmuckâ€ soils have some of the highest organic matter contents, often 50% or greater (Figure 7-3).



Figure 7-3. Organic soils can be very productive as they hold nutrients well but can become waterlogged. (https://www.flickr.com/photos/soilsc...in/dateposted/. Photo by John A. Kelley, USDA Natural Resources Conservation Service.)

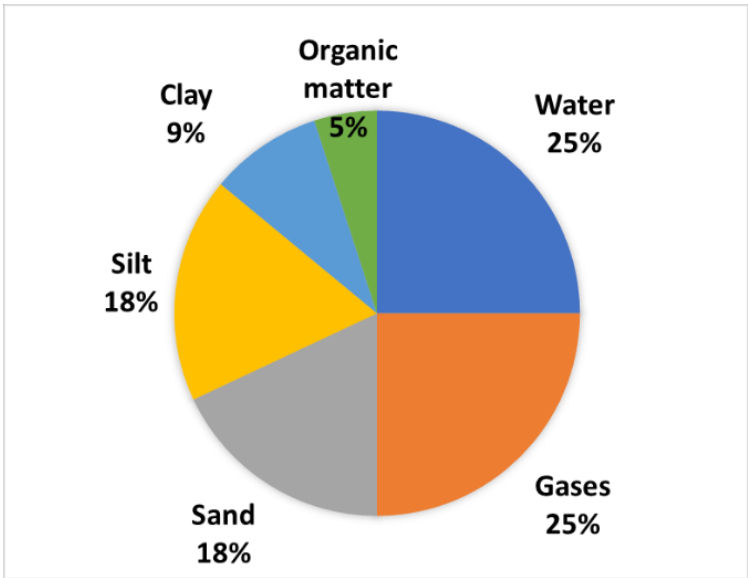


Figure 7-4. Components of a loam soil by percent volume.Relative composition of a loam soil by percent volume. Water 25%, gases 25%, sand 18%, silt 18%, clay 9% and organic matter 5%. (Stephanie Harvey. CC-BY-NC)

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7.1.2: Soil Texture

The two most important physical properties of soil are texture and structure. These terms are easy to confuse since they both deal with particles. Texture is related to the soil particles size while soil structure involves the arrangement of the particles.

Soil texture refers to the relative proportion of the primary particle sizes in the soil. As soil forms, the parent material is broken down to increasingly small sizes, from gravel to clays. For formed soils, we only care about particles that fall into one of three categories: Sand particles which range in size from 2 mm to 0.05 mm; silt particles which range in size from 0.05mm to 0.002 mm (2µm); clay particles which are smaller than 0.002mm. In Figure 7-5, the relative size (not actual) is depicted for the three particles with sand (purple), silt (blue) and clay (grey). For reference, a dime is about 1 mm thick.

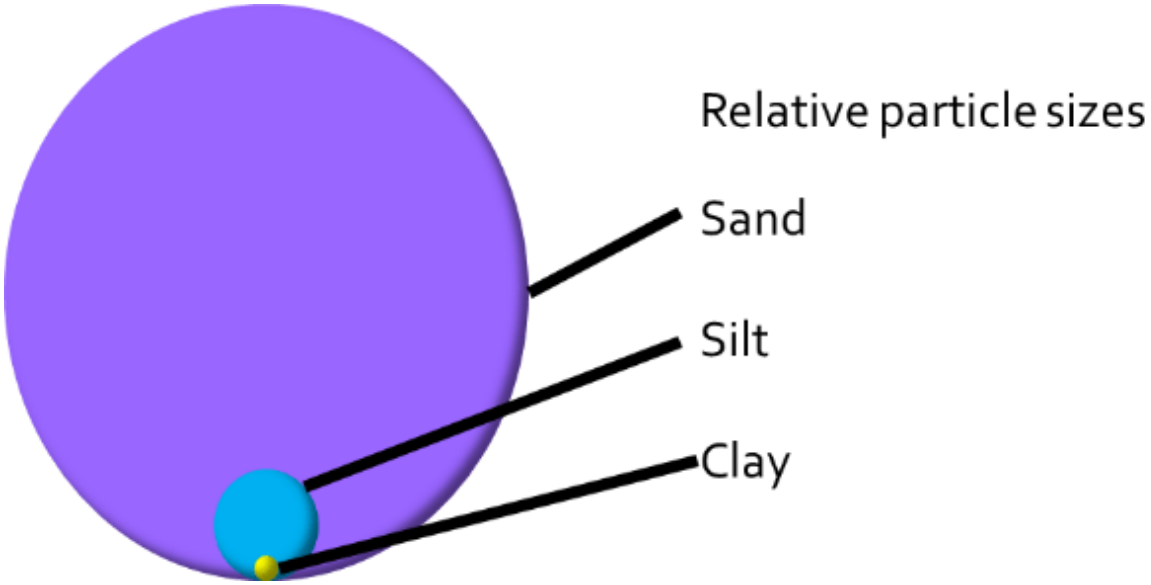


Figure 7-5. Soil texture is the relative proportion of the primary particles in the soil with sand at 2mm-0.05mm, silt at 0.05-0.002mm and clay with particles sizes less than 0.002mm. As a comparison, if a sand particle were the size of a basketball, silt would be about the size of a tennis ball and the largest clay particles about the size of a marble. (Stephanie Harvey. 2023. CC-BY-NC).

Sand has a significant impact on soil characteristics. The large particles of sand do not pack tightly together (Figure 7-6). This increases the volume in large-pore-spaces within the soil matric. Due to the large size of the pores, water is not held well due to the low level of adhesion to volume of water. The water (termed gravitational water) stays in the soil only for a short time before it percolates downward due to gravitational pull. Soils dominated by sand are course and drain well. Because water moves easily through these soils so do water soluble nutrients.



Figure 7-6. Sand and emeralds from Austria. (Renee1137~commonswiki assumed based on copyright claims). - Public Domain, curid=860).

Clay particles, on the other hand, are the smallest of the soil particles at less than 2µm (2/1000 mm). They pack tightly together and thus have very small pore spaces (Figure 7-7). These small pore spaces provide water with a high level of adhesion per volume of water. Water stays in the pores instead of being pulled away by gravity. Since there is less flow through the soil there is less nutrient leaching occurs. Thus, plants grown in clay soil tend to demonstrate few nutrient deficiencies than sandy soil (given no fertilizers are applied).

However, because of their high water-holding capacity, these soils can become waterlogged. These leads to poor aeration and possible anoxia (lack of oxygen leading to cellular death) in the roots. Compaction is another issue often seen in clay soils. When compressed (for example under the weight of passing cars, the clay particles align leaving even smaller pores for aeration. Additionally, compaction can make it difficult for the roots of plant seedlings to penetrate soil.

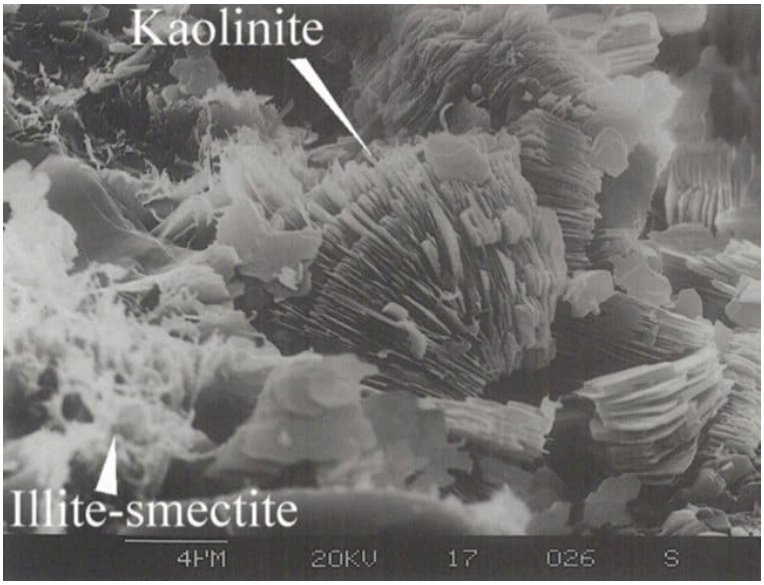


Figure 7-7. Two types of clays: Kaolinite and Illite-smectite. The small scale-like pieces are individual particles. Scale bar is 4 µm (0.004mm or 4/1000000m). (http://pubs.usgs.gov/dds/dds-033/USG...txt/figure.htm. Accessed 2019.)

Silt, the third particle size, lies between the size of sand and clay. The silt particles originate from quartz and feldspar. In the scanning electron micrograph (Figure 7-8) you can see both the smaller clay particles and the larger silt particles. Note the scale bar here is 100 µm. Due to their small size, silts along with clays, are easily carried in water or in the air. Silts contribute to the shallowing of bodies of water and the initial turbidity seen in waterways after a rain event.

Soils are typically mixtures of all three particle sizes. The overall texture of the soil is based on the relative amount of the three particles. Soils are often described as coarse textured soils or fine textured soils. Coarse textured soils have higher proportions of the large particles - sand. These would include soil types such as Sand, Loamy sand and Sandy loam. Fine texture soils have a higher proportion of the smaller particles (i.e., clay). These soils would include soil types such as: Clay, Silty clay and Sandy clay.

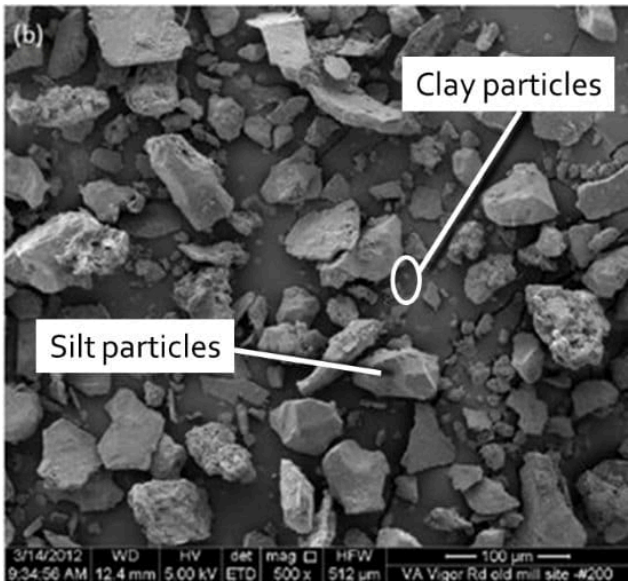


Figure 7-8. Silt particles along with clay particles as seen in a scanning electron micrograph. Silt appears as large rubble compared to the barely visible clay particles. Scale bar is 100um. (Russell A Green. Dynamic Properties of Coal Combustion Products (CCP) October 2012.

To determine the soil texture, we need to know the relative proportions of the three soil particles. This can be achieved in a lab using a known volume of soil and a graduated cylinder (Figure 7-9). The soil is mixed with water for a specified period of time using a shaker device to create a homogenized slurry. The shaker is then turned off, and the sample is allowed to sit undisturbed. The sand particles will quickly sink to the bottom of the cylinder (within a minute or two). The volume of sand can be recorded. After two hours, the silt will have settled to the bottom, and its volume can be recorded. After 48 hours, the final component, the clays will have settled to form the uppermost layer within the cylinder and its volume can be recorded. With the volume of each component now know, we can calculate the percentage each particle size contributes to the soil. With those percentages, can then be looked up on a soil textural triangle (Figure 7-10) the soil textural classification can be determined.



Figure 7-9. An at home, jar-test works similar to the lab method. The depth of each layer can be measures to find the relative amounts of each soil particle. Layers are visible with sand in bottom (~1.5 inches), then silt (~0.5 inch) and on top a fine layer of clay (0.06 inch). A small amount of clay is still suspended in the water. (Andrew "Drew" Jeffers, ©2018, Clemson Extension).

To use the soil triangle, start with the percent sand along the bottom of the triangle. Next, find the percent silt along the right side of the triangle. Follow the line for each component to where they cross. For example, if you have a soil with 20% sand, 60% silt and 20% clay your soil is a “silt loam.”



Figure 7-10. Soil textural triangle can be used to determine a soil's classification based on the relative percentages of the different particles. Soil texture triangle diagram classifying soil types based on percentages of sand, silt, and clay. The triangle has three axes: sand (0-100% along bottom, left to right), silt (0-100% along right side), and clay (0-100% along left side). The triangle is divided into twelve soil texture classes based on particle size proportions: sand (highest sand content, bottom left corner), loamy sand, sandy loam, loam (center, roughly equal proportions), silt loam, silt (highest silt content, bottom right corner), sandy clay loam, clay loam, silty clay loam, sandy clay, silty clay, and clay (highest clay content, top apex). To determine soil type, locate the intersection point of the three particle percentages within the triangle. (By Mikenorton - Own work, CC BY-SA 3.0, https://commons.wikimedia.org - curid=17074432.

Try this one: A sample with 65% sand, 10% Silt and 25% clay would be classified as __?__.

Show answer

Sandy clay loam

Soils classified as loams and loam-adjacent (clay loam, sandy loam and silt loam) are ideal soils for growing most plants. A loam soil has roughly equal amounts of clay/silt/sand (clay on short side) with solids making up about 50% of the soil volume. The aeration and drainage are good due to the larger pores created by the sand component, but some water is retained because of the silts and clays. Thus 25% of the soil volume is air and 25% is water. With the increase in surface area due to clay components as well as the slowed drainage of the water, loam soils are good at holding nutrients.

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7.1.3: Soil Structure

In addition to soil texture, soil structure can impact water and nutrient holding capacities as well as aeration and compaction. Soil structure is due to the binding of soil particles into aggregates (Figure 7-11). Not only do aggregates affect the structural function of the soil but they also store and release nutrients into the aggregates.

Aggregates of soil particles bind together through the actions of organic substances. These organic substances include plant roots, mycorrhizae and decomposing organic matter. Other particles can produce aggregates – iron oxides, carbonates, clays and silica play a role. Organisms, the biota, also contribute. Earthworms, for example, play an important part in the formation of aggregates. Climactic factors can also contribute to the formation of aggregates - freeze/thaw cycles and wetting and drying cycles.



Figure 7-11. Aggregates of soil sorted by size (left). Drawing showing aggregates linking to form larger aggregates(right). (By Lewis Fausak - Own work, CC BY-SA 4.0, https://commons.wikimedia.org - curid=68611993.)

The soil pore space is impacted by soil texture and by soil structure. Larger particles (from soil texture or structure) create large pore spaces while smaller units pack more tightly together and have smaller spaces (Figure 7-12). The larger pore spaces drain easily and provide air spaces from which oxygen can be extracted. In contrast, the smaller pores hold water better and are less prone to leaching of nutrients. Aggregates provide both types of pore spaces – large between aggregates and smaller pores within the aggregate. Overworking the soil can cause loss of soil structure as aggregates are broken up. This can change the characteristics of the soil and dramatically impact crop yields.

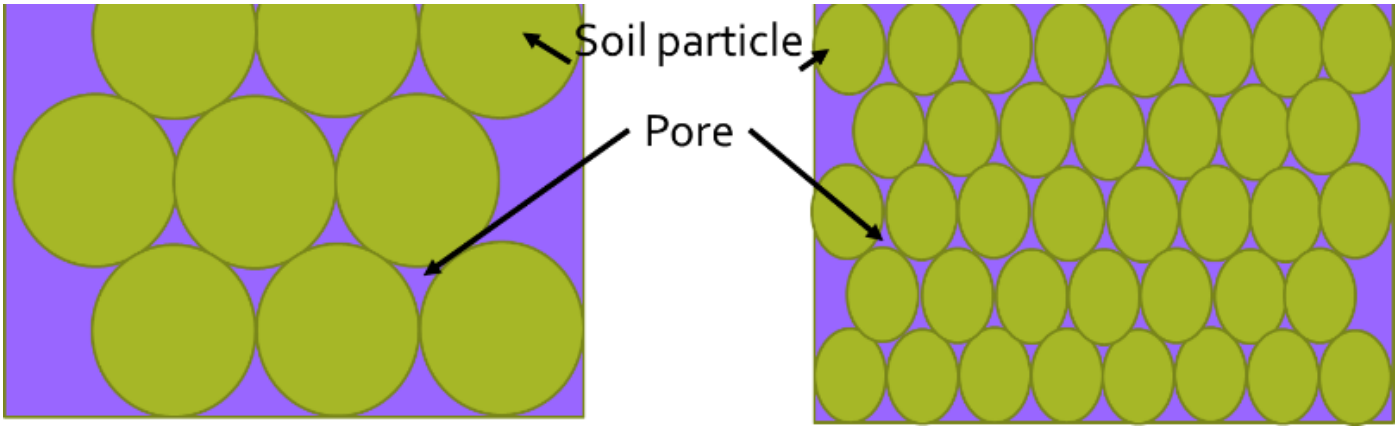


Figure 7-12. Left - Larger particles leads to large pore spaces. Smaller particles produce smaller pore spaces. For a visual comparison, think of a giant tube. If you fill the tube with basketballs, the pore spaces created would be larger than your fist. If you fill the same tube with marbles, the spaces would be about size of a radish seed (~2mm). (Stephanie Harvey. 2019. CC-BY-NC)

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7.1.4: Soil Horizons and Profiles

Depending on geological history, climate and land usage, soils can be very different in different locations and at different depths. In a given area, a soil profile can be determined based on the soil layers or horizons. Soil scientists, who are also called pedologists, look at the layers by digging pits. A profile can provide insight into the history of an area and about its potential for future land usage.

Soil horizons differ in a number of easily seen soil properties such as color, texture, structure, and thickness. Other properties are less visible. Properties, such as chemical and mineral content, consistency, and reaction require special laboratory tests. All these properties are used to define types of soil horizons.

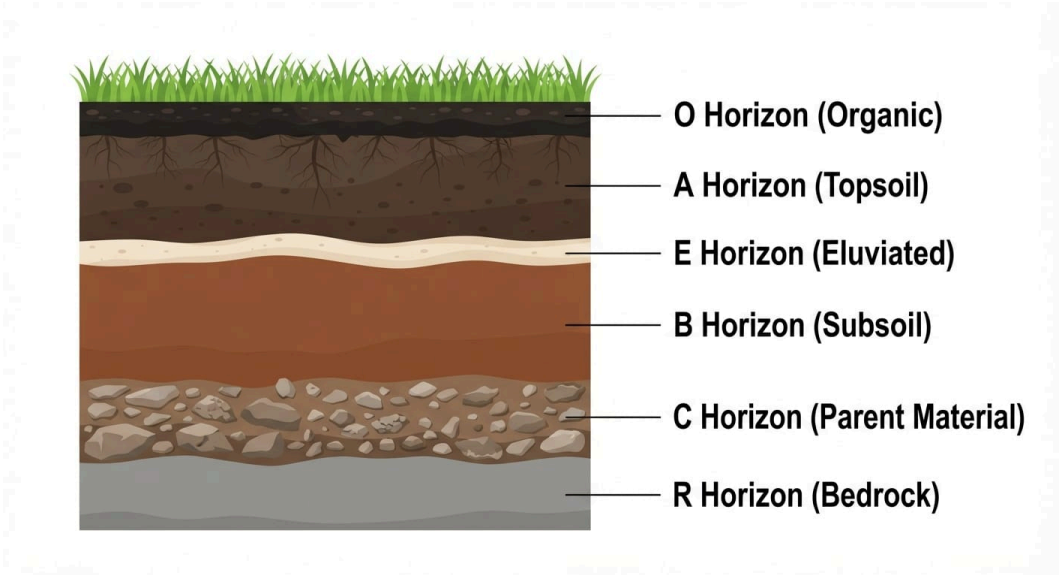


Figure 7-13. Diagram showing the basic soil horizons from the surface down to bedrock. Most soils have three major horizons -- the surface horizon (A), the subsoil (B), and the substratum (C). Some soils have an organic horizon (O) on the surface, but this horizon can also be buried. The master horizon, E, is used for subsurface horizons that have a significant loss of minerals (eluviation). Hard bedrock, which is not soil, uses the letter R. (Image generated by Google Gemini. Prompted by Stephanie Harvey. Google, November 13, 2026).

Soil scientists use the capital letters **O**, **A**, **B**, **C**, and **E** to identify the master horizons, and lowercase letters for distinctions of these horizons (Figure 7-13). Most soils have three major horizons -- the surface horizon (**A**), the subsoil (**B**), and the substratum (**C**). Some soils have an organic horizon (**O**) on the surface, but this horizon can also be buried. The master horizon, **E**, is used for subsurface horizons that have a significant loss of minerals (eluviation). Hard bedrock, which is not soil, uses the letter **R**.

Not every soil contains every horizon and depth of each horizon varies between different soils.

O Horizon (Figure 7-14) represents the layer of accumulated organic matter such as leaves, grass twigs in various states of decomposition. In the O horizon, most organic material can still be matched to it source based on physical characteristics. In general, the layer color is dark and represents a zone of significant biological activity.

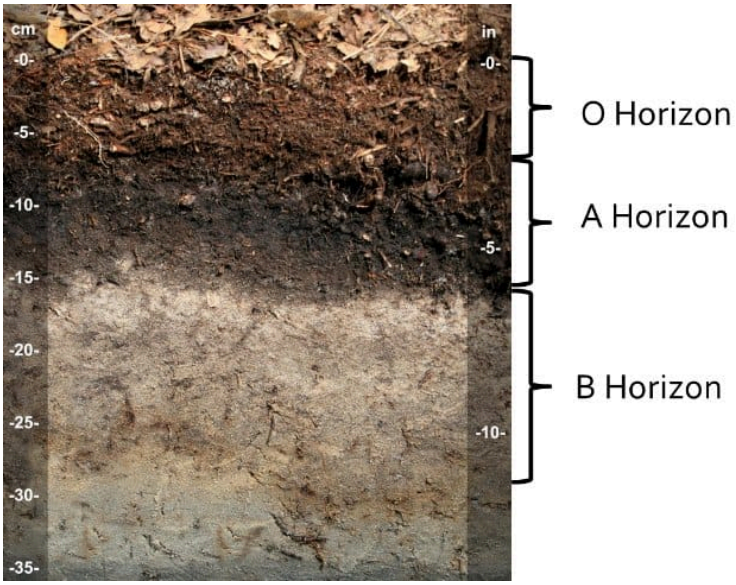


Figure 7-14. Soil with distinct O, A and B horizons. O shows partially decomposed plant parts. A is darker with fully decomposed organic material. B is very light in color with very little organic material. (John A. Kelley, USDA Natural Resources Conservation. 2009. Accessed 2019)

The A horizon has organic matter incorporated with the mineral soil. Decomposition is advanced enough that identification of organic sources cannot be achieved by the naked eye. This layer is general dark in color and often referred to as the topsoil. A is a surface horizon, and as such is also known as the zone in which most biological activity occurs. Soil organisms such as earthworms, potworms, arthropods, nematodes, fungi, and many species of bacteria and archaea are concentrated here, often in close association with plant roots. Thus, the A horizon may be referred to as the biomantle.

B Horizon is the zone of illuviation or deposition. Accumulation of materials “washed” from horizons above. This material is commonly clay, humus, sesquioxides, or a mixture of the three. Variable in color from red and yellow to brown and gray. The brownish or reddish tones are due to the iron oxides.

The C Horizon is dominated by unconsolidated material that has been affected a little by the soil formation process (Figure 7-15). There is no biotic activity and climate effects are minimal. Colors vary based on the parental material. This soft bedrock is described as paralithic. R is bedrock and is strongly cemented with no weather effect. It is described as lithic.

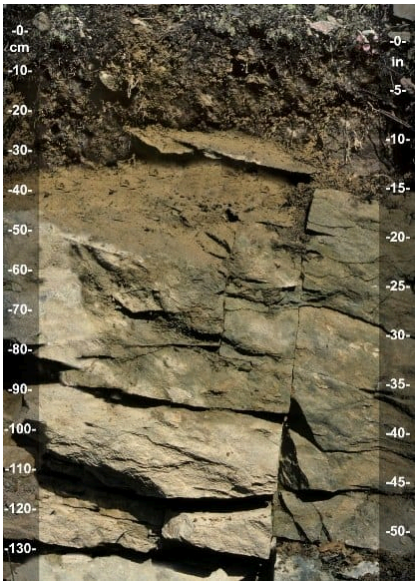


Figure 7-15. The bedrock (R horizon) is not part of the soil profile. It is strongly cemented together. Photo by John A. Kelley, USDA Natural Resources Conservation. 2009. Accessed 2019.

Example of a Soil Profile

Distinct profiles are given names and Figure 7-16 shows a profile called Bama. It is found in Alabama, as you might have guessed, and it is Alabama state soil profile. Georgia's is the "Tift" profile. I selected the Bama profile because the horizons are clearer than with the Tift profile. The appearance of the profile is as follows: Surface layer: dark brown fine sandy loam (A). Subsurface layer: pale brown fine sandy loam (E). Subsoil: red clay loam and sandy clay loam (B)

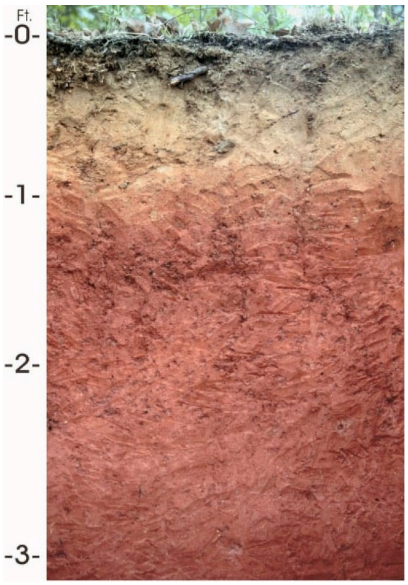


Figure 7-16. Bama Soil Profile. This is Alabama state profile. At surface layer we have a dark brown fine sandy loam; Subsurface layer is pale brown fine sandly loam. Subsoil is a red clay loam and sandy clay loam. By USDA Public Domain, https://commons.wikimedia.org/w/inde...?curid=1341623

"The Bama series consists of very deep, well drained, moderately permeable soils on high stream or marine terraces. These soils formed in thick beds of loamy sediments. Near the "type" location, the average annual air temperature is about 67 degrees F, and the average annual precipitation is about 63 inches. Taxonomic class: Fine-loamy" (For more information: Link to BAMA [soilseries.sc.egov.usda.gov])

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7.1.5: Soil pH

As mentioned in the previous section, the physical properties of soil can impact plant growth. The chemical properties of soil can also impact growth in multiple ways. The chemical composition of the soil will determine what minerals are present. However, the presence of the minerals does not mean that they are available to the plants. Other factors such as soil pH and soil CEC can determine what is actually available to the plants.

In Figure 7-17, Zea *mays* or corn is grown in two different soil pH. The smaller plants to the left of the image are in acidic soil where the greener and taller plants are in a soil that has been limed to adjust the pH up. Soil pH can impact nutrient availability and thus plant growth.



Figure 7-17. Rows of corn in a field: plants in acid soil on the left are short and yellowish, while plants in limed soil on the right are taller and greener. By Alandmanson - Own work, CC BY-SA 4.0, Link to Source [commons.wikimedia.org]

Before we look at how soil pH impacts nutrient availability let us first look at pH itself. The pH scale is a logarithmic expression of the concentrations of hydrogen ions in a solution. Because it is a log scale, pH goes from 0 to 14 with seven being neutral. The lower the number the more acidic and the more hydrogen protons there are. The higher the pH the more basic or alkaline the soil is and thus the fewer hydrogen protons.

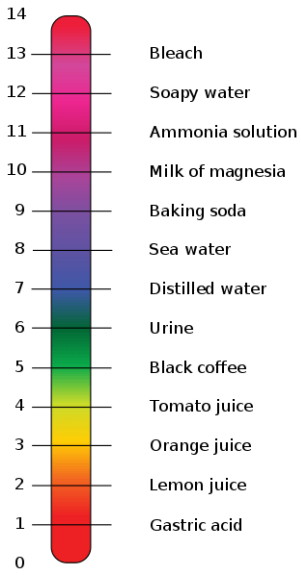


Figure 7-18. The pH scale ranges from 0 to 14. Some solutions with different pHs are shown. pH scale diagram showing a vertical bar ranging from 0 to 14 with common substances labeled at their approximate pH values. The scale is organized from most acidic (bottom) to most alkaline (top): gastric acid at pH 1, lemon juice at pH 2, orange juice at pH 3, tomato juice at pH 4, black coffee at pH 5, urine at pH 6, distilled water at pH 7 (neutral), sea water at pH 8, baking soda at pH 9, milk of magnesia at pH 10, ammonia solution at pH 11, soapy water at pH 12, and bleach at pH 13. Values below 7 are acidic, 7 is neutral, and values above 7 are alkaline or basic. (By Edward Stevens - Own work, CC BY 3.0; curid=9869144)

The scale of Figure 7-18, provides some common everyday items at their standard pH. At pH of one (1), there are gastric acids. Gastric acid is the acid in your stomach that helps break down food. If we move up our pH scale will notice that tomato juice has a pH of four (4) urine pH of six (6) and again our distilled water which is neutral at a pH of seven (7). At pH is above seven substances are said to be basic or alkaline. Milk of magnesia, for example, is often used as an antacid because it is basic nature. Notice that bleach has a pH of 13. People often associate low pH solutions – acids - with being dangerous however a high pH such as 12, 13 or 14 can be just as damaging as a low pH. It can cause severe chemical burns and even death.

The pH of the soil affects the availability of nutrients. The graph (Figure 7-19) depicts the essential nutrients that plants need for growth and their availability at different soil pHs. Along the bottom of the graph (x-axis) is the pH scale from 4.0 to 10.0. Each essential element is shown as a band. The wider the band the more available it is while the narrower the band the more difficult it is for the plants to extract from the soil.

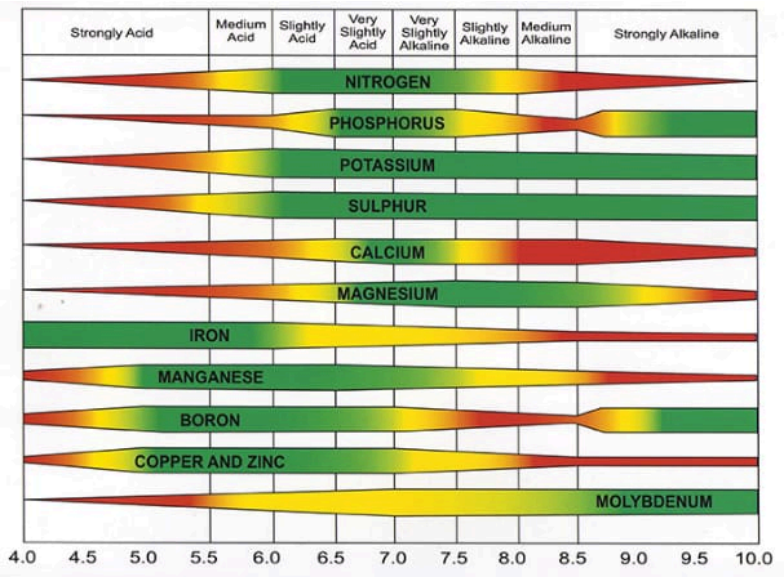


Figure 7-19. Soil pH affects availability of plant nutrients. Green (wider) ribbons indicate greater availability. Long description: Chart showing the effect of soil pH on plant nutrient availability. The horizontal axis shows pH values from 4.0 (strongly acidic) to 10.0 (strongly alkaline), with categories labeled as strongly acid, medium acid, slightly acid, very slightly acid, neutral (around pH 7.0), very slightly alkaline, slightly alkaline, medium alkaline, and strongly alkaline. Thirteen essential plant nutrients are listed vertically, each represented by a horizontal band that widens where the nutrient is more available and narrows where availability is limited. Nitrogen availability is optimal between pH 6.0-8.0. Phosphorus shows best availability between pH 6.0-7.5. Potassium availability is broad, ranging from pH 6.0-9.5. Sulphur is most available between pH 6.0-9.5. Calcium availability increases from pH 6.5-8.5 and beyond. Magnesium is most available above pH 6.5. Iron availability decreases sharply above pH 6.5, being most available in acidic conditions (pH 4.0-6.5). Manganese is most available in acidic conditions (pH 4.5-6.5). Boron shows relatively consistent availability across pH ranges with optimal availability between pH 5.0-7.0. Copper and zinc are most available in slightly acidic to neutral conditions (pH 5.0-7.0). Molybdenum is most available in alkaline conditions (pH 7.0-10.0). The chart demonstrates that most nutrients achieve optimal availability in slightly acidic to neutral pH ranges (6.0-7.5). (Link to source [www.growmarkfs.com])

At pH 7 most of the nutrients are fairly available particularly nitrogen, phosphorus, and potassium, the three primary macronutrients. However, if you look at iron, manganese, and boron you will notice that at pH 7 there is limited availability. The availability increases with shifts into more acidic conditions. In contrast molybdenum, and to some extent calcium, availability increases as the soil becomes more alkaline. At pH of 7.5 to 8, they are more available than at neutral or at more acidic pHs.

Soil pH can also impact pathogens and other diseases of crops. Blossom-end rot for example is typically seen when the soil pH is somewhat acidic. It is partly due to the low availability of calcium which causes the cell walls to be soft and vulnerable for fungal attack. In other cases, the pathogen itself flourishes in either higher or low pH soils.

Soil pH can be adjusted using amendments and selective fertilizers. It is typically easier to raise the pH than to lower it. For acidic soils, the pH can be raised by adding materials such as calcium or limestone. This is typically referred to as liming a field. For alkaline soils, the pH can be lowered by adding sulfur or sulfur compounds. The effect is not as immediate nor as extreme. Shifting a soil toward a more acidic pH may take several years. These types of adjustments to pH are typically done prior to planting and are done over a significant area.

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7.1.6: Soil Cation Exchange Capacity

Chemical analysis of the soil can determine what nutrients are present in the soil. Deficiencies can then be addressed with fertilizers. However, the presence of nutrients may not reflect its availability to the plants. To determine nutrient availability the **cation exchange capacity** (CEC) of the soil must be known. A soil's cation exchange capacity describes the ability of the soil to hold and release positively charged nutrients such that they are available for the plant (Figure 7-20). Soil particles, like silica, have negative charges along the surface. The nutrients that are present as positive charged ions - cations - are attracted to the negative charge. Elements such as calcium, magnesium, sodium, and potassium are held to the soil particles and in order for the plants to make use of them they must be released.

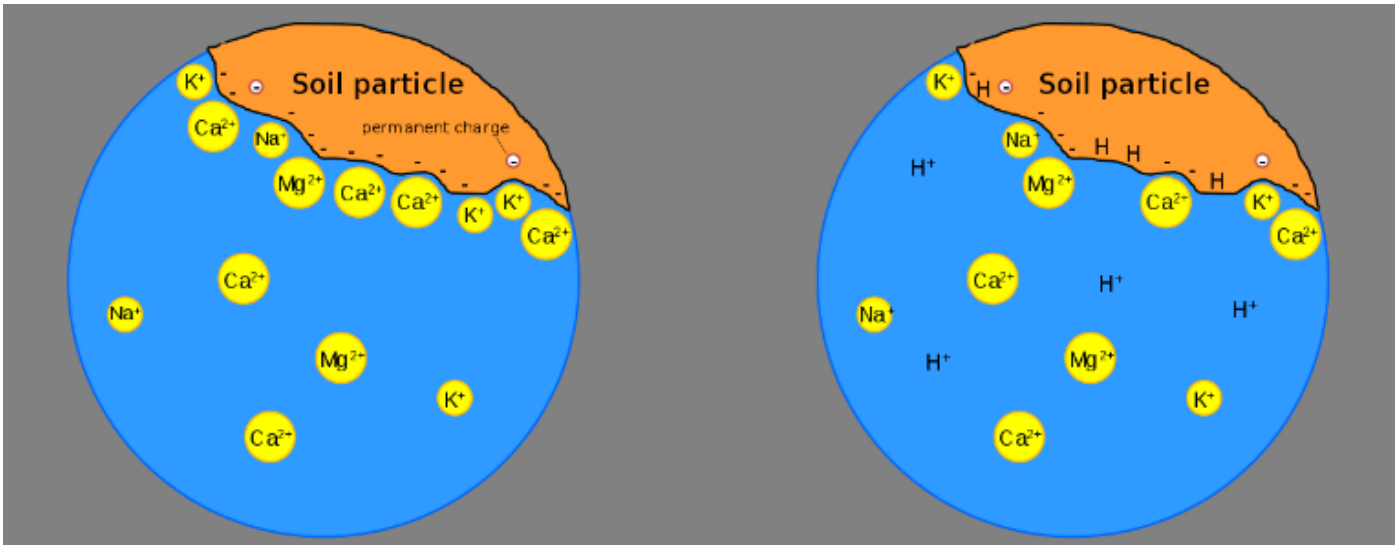


Figure 7-20. Diagram show the negative charges on soil particles that hold positively charged ion (left) and then the release of the cations after acidification of the soil water. (By Kyle MoJo & Kazem Zamanian, CC BY-SA 4.0, curid=62073921 (modified by S. Harvey 2019))

Plant root tips pump hydrogen protons into the soil solution. Hydrogen protons displace the nutrient cations. With the cations in the soil water plants can take them up for use in their growth processes. How tightly the soil particles hold these cations will determine how easily the plant can strip them from the soil particles and thus use them for their own purposes. The negative charges on the silica components do not hold anions (negatively charged ions). Nutrients that exist as anions are more easily leached from the soil than their cation counter parts. Thus, the CEC has little effect on some of the primary plant nutrients such as nitrogen (nitrate NO_3^-).

Soils can be tested for nutrients, the CEC (availability) and soil pH. Your local extension service can provide these tests. To collect soil for such tests you should take multiple samples in a W pattern across the area. Next, bulk the samples together. "Bulking" means to add the individual samples together and make one master sample. The third step is to allow the sample to now air dry. Once it is dry remove all large organic matter, large roots, stems, leaves and any rocks that are present. The sample is now ready to submit for testing.

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7.2: THE BIOTIC NATURE OF SOILS

Soil is a dynamic medium that includes biotic factors that impact plant growth. These impacts can be positive or negative depending on the nature of the organisms. These biotic or living components can be classified as microscopic inhabitants and macroscopic inhabitants of the soil.



Small mounds of soil left by emerging solitary bees. (Stephanie Harvey 2024 CC-BY-NC)

7.2.1: Microscopic Inhabitants

7.2.2: Macroscopic Inhabitants

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7.2.1: Microscopic Inhabitants

The soil is teeming with microscopic lifeforms that play critical roles in plant health and growth. The most abundant of these tiny soil dwellers are bacteria and fungi. While invisible to the naked eye, the presence and activity of these microorganisms have an enormous influence on the ability of plants to take up nutrients from the soil.

There are billions of bacteria in each gram of fertile soil. These single-celled organisms assist with plant growth in a variety of ways. Certain bacteria transform atmospheric nitrogen into ammonium and nitrate compounds that plants rely on for proteins and nucleic acid production. This process, known as nitrogen fixation, makes the key nutrient nitrogen available for plant absorption. Other types of bacteria solubilize phosphorous, immobilize toxic heavy metals, and produce plant growth-promoting hormones. Exudates and waste products of bacteria also contribute to the development of soil structure conducive to air and water movement.

Alongside bacteria are ubiquitous soil fungi, forming a network of thin filaments or hyphae. The hardy hyphae extend the reach of plant roots and aid in nutrient and water uptake. Fungi also secret enzymes and acids that decompose dead organic matter, recycling nutrients back into the soil system. The mutualistic relationship between plant roots and mycorrhizal fungi is particularly vital (Figure 7-21). These fungi colonize root cells, increasing the surface area for absorption of water and nutrients, notably less mobile nutrients like phosphorus and zinc. In exchange, the plants provide fungi with carbohydrates.

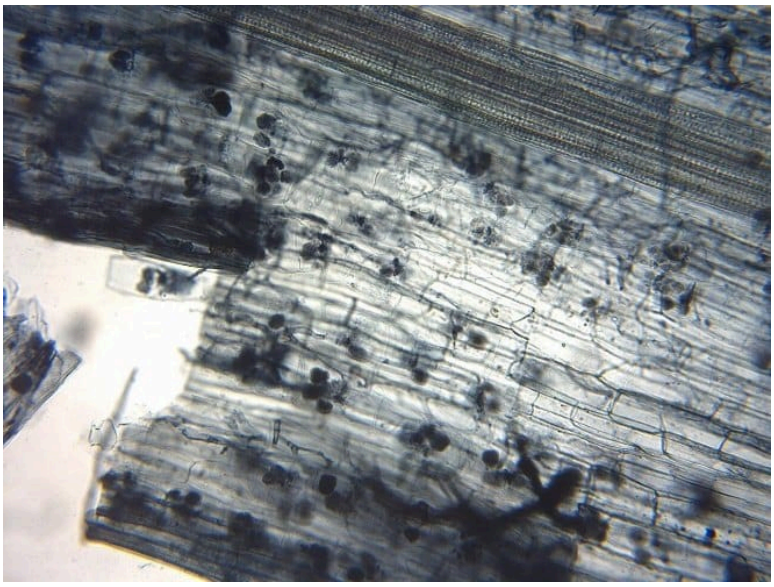


Figure 7-21. Arbuscular mycorrhiza seen under microscope. Flax root cortical cells containing paired arbuscules. (By Msturmel - MS Turmel, University of Manitoba, Plant Science Department, Public Domain; curid=7553044)

Of course, while most microbes in soil are beneficial or benign to plants, there are also disease-causing pathogens and parasites (Figure 7-22). These include fungi, bacteria, nematodes, oomycetes, and viruses. Well-known soilborne phytopathogens are species of *Fusarium*, *Verticillium*, and *Rhizoctonia* fungi which trigger wilts and rots, and *Agrobacterium* bacteria responsible for crown gall disease. Plant-parasitic nematodes penetrate and damage root tissues, providing entry points for other pathogens. Destructive species include root knot, cyst, lesion, and citrus nematodes. Damping-off diseases are caused by *Phytophthora* and *Pythium* oomycetes infecting seeds or seedlings. Viruses like tobacco mosaic virus can persist in soil for years, transferred between plants by nematodes.



Figure 7-22. *Verticillium dahliae* infected sunflowers. (photo by Howard F. Schwartz, Colorado State University, Bugwood.org)

Pathogens are regular soil residents, but their harmful effects on plants are typically held in check by the much larger mass and activity of beneficial microorganisms. Invisible to our eyes, soil bacteria and fungi have an ever-present, interconnected role in soil ecology, soil fertility, nutrient cycles, and plant growth. The beneficial microorganisms fix nutrients into plant-accessible forms, build soil structure, enhance root systems, unlock bound nutrients from organic matter through decomposition and help minimize the pathogen exposure. In essence, healthy, vigorous populations of soil microbes translate into active plant growth and bountiful crop production above ground. Disturbing these microbial communities through chemical inputs, lack of plant diversity, and excessive tillage can starve plants by limiting their access to benefits provided by bacteria and fungi flourishing in the soil. Imbalances favoring the pathogens arise when soils are nutritionally depleted or exposed to extensive chemical inputs and disturbance.

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7.2.2: Macroscopic Inhabitants

The soil environment houses not only microscopic life but also an abundance of larger organisms that affect soil properties and plant growth. Macroscopic organisms range from barely visible nematodes and tiny mites to more conspicuous earthworms, ants, and moles. Although not always noticed, they contribute to nutrient transformations, soil development, and plant health in crucial ways.

The slim nematodes, microscopic roundworms, are among the most abundant soil animals. While some nematodes are parasitic to plants, most species feed on bacteria, fungi, and protozoa, regulating soil microbial activity and releasing excess nutrients. Nematodes enhance soil porosity and mixing as they move through the soil. Other microscopic soil fauna like springtails, mites, and protozoa grind up and decompose organic materials, making nutrients available through mineralization.

Earthworms arguably have the most noticeable impact on soils (Figure 7-23). They drag organic residues down into the soil profile through their permanent burrows while tilling and aerating the soil. The deep burrows created by earthworms facilitate water infiltration and root growth. Their feeding and castings mineralize essential nutrients like nitrogen and phosphorus. Earthworm mucus and castings contain growth hormones and nutrients that can stimulate plant growth.



Figure 7-23. Closeup of an earthworm in garden soil. (GFDL 1.2, https://commons.wikimedia.org/w/inde...?curid=3474224)

Ants fill several ecological roles in the soil system. Ant burrowing assists with aeration and water movement while their nests concentrate nutrients. Certain species of ants protect plants from herbivorous insects and disperse seeds. Other larger soil macrofauna like ground beetles, termites, and millipedes contribute to breaking up organic matter. Their movement, burrowing, and feeding habits improve soil porosity, fertility, and plant growth.

On a broader scale, the activities of digging mammals like gophers, moles, and prairie dogs markedly restructure soils through displacement and mixing (Figure 7-24). Their extensive burrowing systems loosen and circulate air and water in soil. Old tunnels made by these animals become pathways for roots. Their excavated mounds bury surface litter and organic matter, distributing nutrients deeper into the soil. Over time, the complex maze of macro pores and mounded soil material create landscape level soil diversity.



Figure 7-24. Molehill created by burrowing. (By Karelj - Own work, Public Domain, https://commons.wikimedia.org/w/inde...?curid=2464250)

The air, water, and nutrient benefits furnished by the visible soil macrofauna amplify plant growth both directly and indirectly. While the burrowing, feeding, digesting, and casting activities of these larger organisms can damage some individual plants, on balance they enhance soil fertility and structure. These improvements foster productive plant communities on the whole.

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7.3: End of Chapter Review

Chapter Summary

- Soil is a complex medium composed of mineral matter, organic matter, air, and water that provides physical support and nutrients for plant growth.
- Soil formation through weathering and biological activity is a gradual process dependent on factors like climate, parent material, topography, and time.
- Key physical properties like soil texture and structure impact drainage, aeration, and nutrient retention capacities. Loams balance adequate drainage with sufficient water and nutrient holding abilities.
- Soil chemical factors like pH and cation exchange capacity determine actual nutrient availability for plant uptake. Soil testing helps identify deficiencies.
- Microscopic organisms like bacteria and fungi fix nitrogen, decompose organic matter to release nutrients, and establish symbioses with plant roots.
- Larger soil macrofauna including earthworms, ants, and digging mammals alter soil properties through burrowing activities and localized nutrient recycling.
- While essential to soil fertility and plant productivity, soil biotic communities and processes can be disrupted through chemical inputs, physical disturbance, and lack of diversity.
- Together the interdependent abiotic and biotic soil components and processes promote plant anchorage, water availability, nutrient supply, and overall ecosystem function.

Key Terms

- Aggregates
- Bacteria
- Bedrock
- Cation exchange capacity (CEC)
- Clay
- Earthworms
- Ecosystem function
- Fungi
- Horizon
- Macrofauna
- Microbial communities
- Mineral matter
- Mycorrhizae
- Nematodes
- Nitrogen fixation
- Nutrient cycling
- Nutrient supply
- Organic matter
- pH
- Physical disturbance
- Plant anchorage
- Pore space
- Sand
- Silt
- Structure
- Subsoil
- Texture
- Topsoil
- Water availability
- Weathering

Self-Review

1. What are the four main components that make up soil?
2. How do the processes of physical, chemical, and biological weathering contribute to soil formation?
3. What are the three main soil particle sizes that determine texture?
4. How does soil texture impact drainage, nutrient leaching, and compaction?
5. What is soil structure and how do aggregates affect pore spaces?
6. Briefly describe the major soil horizons.
7. How does soil pH affect nutrient availability?
8. What is cation exchange capacity and why is it important?
9. What roles do bacteria play in the soil ecosystem?
10. How do mycorrhizal fungi interact symbiotically with plant roots?
11. What impacts do earthworms have on the physical properties of soil?
12. How do nematodes and other microscopic fauna contribute to soil nutrient cycles?
13. What effects can digging mammals have on soil over time?
14. Why are healthy microbial communities essential for soil fertility and plant productivity?
15. What human actions can disrupt soil biotic components and processes?

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8: ESSENTIAL NUTIRENTS

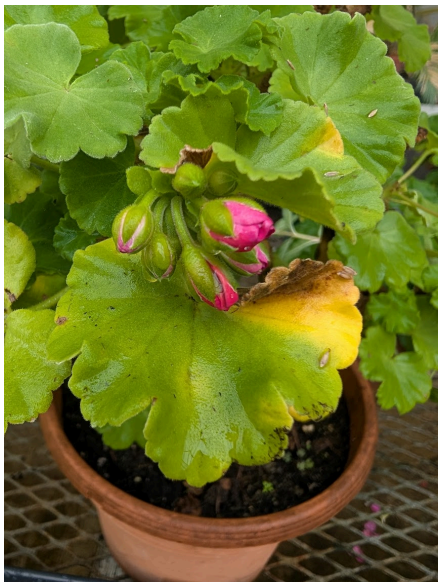


Figure 8-1. Geranium with leaf yellow and necrotic at margin. (Stephanie Harvey. 2026).

Plants are photosynthetic organisms and have very minimal requirements for survival. With light as a source of energy, they need water and some nutrients to survive. These required nutrients, referred to as essential elements, are taken from the environment via soil or air. Since carbon dioxide, water and oxygen are readily available from the environment, the need for elements of oxygen, hydrogen and carbon are chiefly ignored. If oxygen, hydrogen, or carbon are the most limiting factors to plant growth then there is something much more serious going on in the environment (Figure 8-1). In this chapter we will look at various aspects of the nutritional requirements for plants - their essential nutrients.

8.1: Elemental Analysis

8.2: Hydroponics and the Essential Nutrients

8.3: Nutrient Deficiencies

8.4: Essential Nutrients and Symptoms of Deficiencies

8.4.1: Nitrogen

8.4.2: Phosphorus

8.4.3: Potassium

8.4.4: Calcium

8.4.5: Magnesium

8.4.6: Sulfur

8.4.7: Iron and Other Micronutrients

8.5: Fertilizers and Amendments

8.5.1: Synthetic and Organic Fertilizers

8.5.2: Soil Amendments

8.6: Application Methods for Fertilizers

8.7: End of Chapter Review

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8.1: Elemental Analysis

For a nutrient to be considered “essential,” the lack of it must results in abnormal growth, failure of the plant to complete its life cycle or premature death (Figure 8-1). Additionally, to classify as an essential element, the nutrient cannot be replaceable by any other nutrient or element. The essential nutrients must influence growth or metabolism directly as opposed to indirect impact via control of pests or diseases.

One way to determine what minerals are needed for plant growth is to analyze the minerals that are found within the plant tissue. There are multiple mechanisms for determining the minerals in plants. Figure 8-2 (left) shows a digital handheld instrument that determines nitrogen levels in plant sap. Other single nutrient meters are available.



Figure 8-2. Handheld meter for nitrate (left) and ICP-MS (right) used for broad-spectrum elemental analysis. (Image from: Link to source [nutri-tech.com.au]; Analytical instrument- ICP-MS from Varian. (By Karelj - Own work, Public Domain; curid=1358929)

To get a more complex analysis an instrument such as an ICP - inductively coupled plasma- spectrophotometer can be used (Figure 8-2, right). An example of such can be seen in the image to the right. An ICP can analyze tissue and determine the concentrations of many elements. The device is sensitive enough to detect minerals at the level of parts per billion. Samples must be handled using different techniques depending on the analysis used: dry ashing and wet digestion, or Kjeldahl digestions.

- Atomic absorption spectroscopy (AAS) - This technique uses the absorption of light to measure the concentration of elemental nutrients like calcium, magnesium, iron, zinc, copper, and manganese. Samples are digested and atomized before being passed through a flame. The amount of light absorbed at specific wavelengths is proportional to the concentration of the element in the sample.
- Inductively coupled plasma optical emission spectrometry (ICP-OES) - Similar to AAS but uses an inductively coupled plasma to excite the sample atoms. Capable of detecting more than 30 elements simultaneously. Samples must be acid digested before analysis.
- Kjeldahl method - Commonly used to determine total nitrogen content in plants. The sample is digested in sulfuric acid, which converts nitrogen to ammonia. The amount of ammonia is then determined by titration and used to calculate total N.
- Titrimetric methods - Acid-base titrations can be used to determine nutrients like calcium, magnesium, potassium. The plant extract is titrated with a standard solution, allowing calculation of the nutrient's concentration.
- Colorimetric methods - Photometric analysis of colored compounds produced by specific reactions with some nutrients. For example, phosphorus forms a blue color after reaction with ammonium molybdate and ascorbic acid. Intensity of color determines concentration.
- Enzymatic methods - Use of enzymes to break down compounds and allow quantification of specific nutrients like nitrate, ammonia, urea, or amino acids. The products are then measured using spectrophotometric methods.

A common method of sample preparation is dry ashing. The plant tissue samples are dried and then placed in a muffle furnace.

The muffle furnace burns off all organic material leaving behind the minerals that can be and then analyzed using an ICP or an AA -atomic absorption - instrument. Wet digestion can be used for some analysis. It involves the use of solvents to break down the plant tissue this allows accessibility to the minerals for determination.

While these analytical techniques can determine the minerals found in the plant tissue, it can be misleading in terms of what the plant actually needs for growth and development. Some plants tend to hyper accumulate elements including those they do not need. This can lead to overestimation of plant's needs. Tom

In fact, plants can actually become dangerous for human consumption due to the levels hyper-accumulated. Carrots,for example, can accumulate lead (Pd), cadmium (Cd) and arsenic (As). If harvested from historic industrial site, Pd ans As levels can exceed international safety limits. Lettuce is typically classified as high-risk vegetable for Cd because the leaves have high transpiration rates and water-soluble metals like Cd move rapidly into edible structures. In heavily contaminated soils *Nicotiana glauca*, a plant sometimes used medicinally, can accumulate levels nearing 100 mg/kg dry weight. World Health Organization (WHO) recommendations are 1.0 mk/kg dry weight.

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8.2: Hydroponics and the Essential Nutrients

To avoid this over estimation, **hydroponics** was used to isolate each essential nutrient and to verify the concentrations needed for plant growth. Hydroponics is a system in which nutrients are dissolved in water. Plants are then grown in the resulting solution. The plants can then be closely observed for signs of deficiencies in their tissues can be analyzed for mineral content.

In Figure 8-3, sunflower plants are growing in solutions that contain uranium and radium. Neither of these are essential elements but it nicely demonstrates how a hydroponic system could be used for determination of nutrient need. Here, however, the plants are being investigated for their ability to remove these elements from the soil as a form of bioremediation.



Figure 8-3. Sunflowers in solutions that contain uranium and radium. (P. Blanco Rodríguez, F Vera Tomé, María Pérez-Fernández, María Pérez-Fernández & J C Lozano. 2006. Science of The Total Environment 361 (1-3): 1-7. DOI: 10.1016/j.scitotenv.2005.08.)

Based on hydroponics studies, a list of essential nutrients has been developed (Table 8-2). As refining techniques improved to limit contaminants in the chemicals used, the list was modified to include even trace level requirements. The essential nutrients were divided into 2 categories based on the level of the nutrients needed by the plants: Macronutrients are needed in higher concentrations and are typically reported as percent of the plant biomass. **Micronutrients** are needed at lower concentrations and are typically reported as parts per million and parts per billion.

The elements of carbon, hydrogen and oxygen make up the bulk of the dry mass of plant tissues. They are macronutrients. However, since these elements are readily available and rarely contribute to deficiencies, they are often ignored when looking at plant nutrients.

Table 8-2. *List of Essential nutrients for most plants.*

Macronutrients	Micronutrients
Carbon (air)	Iron
Hydrogen (air/water)	Molybdenum
Oxygen (air/water)	Boron
Nitrogen (primary)	Copper
Phosphorus (primary)	Manganese
Potassium (primary)	Sodium
Sulfur	Zinc

Macronutrients	Micronutrients
Calcium	Nickel
Magnesium	

There are 3 primary macronutrients: nitrogen, phosphorus, and potassium. There are also 3 secondary macronutrients: sulfur, calcium, and magnesium. Most of the macronutrients are components in biological molecules such as proteins and nucleic acids. Micronutrients typically work as cofactors with enzymes. They include iron, molybdenum, boron, copper, manganese, sodium, zinc, and nickel. Some of the micronutrients are needed at such small levels they are often referred to as trace elements.

There are some nutrients that are essential to a select group of plants but are not included in our list since they are not critical to all plants. Examples of elements that are essential to a small subset of plants include aluminum, cobalt, silicon, and selenium. For example, silicon is essential in horsetails. In these plants, silicon strengthens the cell wall and without it the plant cannot support its own weight. It collapses and does not complete its life cycle.

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8.3: Nutrient Deficiencies

Previously, we discussed the essential nutrients needed by plants in general. We will look at some of them in a later section. For now, however, we will look at what happens when these nutrients are not available in the necessary amounts needed.

While analytical techniques can be used to determine deficiencies in plant tissues, the home gardener or a farmer may not have access to the equipment to run these tests nor be able to have them run at a lab. They may have to rely on symptomology. Symptoms are the physical appearance brought about by the deficiency - the limitation of a require nutrient. Understanding the symptoms seen in a plant can help us diagnose a particular deficiency. Typically, the deficiency produces a symptom link to how the nutrient is used in the plant. For example, the lack of green coloration may be due to a lack of chlorophyll production. This lack of chlorophyll production is in turn linked to the deficiency.

There are 2 main symptoms seen in plants that are suffering from deficiencies: chlorosis and necrosis (Figure 8-4). Chlorosis is the yellowing of the leaf or stem due to the lack of chlorophyll formation or chlorophyll loss. Necrosis on the other hand is the dying of tissue and can be seen as the browning of the leaf or stem tissue.



Figure 8-4. A) Lobed leaf with heavy chlorosis (yellowing) along the leaf edges. B) Leaves with necrosis (dead, brown tissue) along the leaf tips. Stephanie Harvey. 2019. CC-BY. Scot Nelson. 2015. Link to Source [www.flickr.com]

Symptom location can help define the deficient. For example: a symptom can develop as interveinal chlorosis (yellowing). This means the veins remain green but the spaces between them are yellowish. Figure 8-5 (left) shows a sweetgum leaf suffering what is most likely a magnesium deficiency. Figure 8-5 (right) shows a tomato leaflet with chlorosis at the margin of the leaf. Note the yellowing from the edge of the leaf back toward the base. In this case we are looking at the deficiency of potassium on a tomato leaf.



Figure 8-5. Sweetgum leaf (left) showing interveinal chlorosis. Tomato leaflet (right) showing chlorosis starting at distal margin accompanied by some necrosis. By Jim Conrad - JIM CONRAD'S NATURALIST NEWSLETTER. Link to Source [backyardnature.net];By Goldlocki - This is of my own making., CC BY-SA 3.0, curid=228226.

Most nutrient deficiencies produce chlorosis or necrosis, so determining the exact nutrient can be difficult. In addition to its location on the leaf, we can also look at the placement on the plant itself. The mobility of a nutrient will determine where the deficiency is seen on the plant. For mobile nutrients deficiencies show up in older leaves while for non-mobile nutrients the deficiency shows up in younger leaves and tissues.

Mobile nutrients are scoured from older tissues so that the new tissues can be the healthiest. This is an advantage since the newer tissues are the most photosynthetic productive of the tissues. The mobile nutrients within the plant include nitrogen, phosphorus, potassium, magnesium, and sulfur. If, however, a nutrient is non-mobile it will stay in the older tissues, and the deficiency will show up in the younger leaves and stems as well as fruits. Calcium, sulfur, and most of the micronutrients are immobile.

In Figure 8-6, we see blossom-end-rot on young tomato fruits. The growing tip, or bottom, of the tomato fruit is the youngest part and here we see damage occurring due to a lack of calcium. Calcium is non-mobile therefore the tips of the youngest tissue show the deficiency. The rot seen here is a secondary effect of the deficiency. The low calcium causes the tissue to be soft, allowing for the secondary infection to easily invade the tissue. Blossom-end-rot is common on Solanaceae crops, such as tomatoes, peppers, and eggplants, as well as Cucurbitaceae crops such as squash and pumpkins.



Figure 8-6. Blossom-end-rot is due to a secondary infection that attacks weak, calcium-deficient, young tissues. (Scot Nelson. 2006. Link to Source [www.flickr.com])

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8.4: ESSENTIAL NUTRIENTS AND SYMPTOMS OF DEFICIENCIES

The macronutrients of interest as far as plant deficiencies go are nitrogen, potassium, calcium magnesium, phosphorus, and sulfur as mentioned earlier. Table 8-3 gives the percentage of mass in dry tissue for each of the macronutrients. In addition, the major functions are listed as well as the form of the nutrient available for plant uptake. Note that with the exception of potassium and calcium, the other macronutrients are components of biological molecules.

Table 8-3. *Macronutrients that are essential for a typical plant.*

Element	Form available to plants	% mass (in dry tissue)	Major functions
Nitrogen	NO_3^-, NH_4^+	1.5	**Component of nucleic acids, proteins**, hormones, chlorophyll, coenzymes
Potassium	K^+	1	Cofactor that functions in protein synthesis, major solute functioning in water balance, operation of stomata.
Calcium	Ca^{2+}	0.5	Important in the formation and stability of cell walls and in maintenance of membrane structure and permeability; activates some enzymes; regulates many responses of cells to stimuli.
Magnesium	Mg^{2+}	0.2	**Component of chlorophyll;** activate many enzymes.
Phosphorus	$H_2PO_4^-$, HPO_4^{2-}	0.2	**Component of nucleic acids, phospholipids, ATP**, several coenzymes
Sulfur	SO_4^{2-}	0.1	**Component of proteins**, coenzymes.

While the macronutrients are reported as % of dry mass or parts per hundred, the micronutrients are quantified as part per million (ppm) or part per billion (ppb). Most of these nutrients play a role in enzyme activation. Table 8-4 list each micronutrient, available form ppm in dry tissues and their major function.

Table 8-4. *Micronutrients that are essential for plant growth and development.*

Element	Form available to plants	% mass (in dry tissue)	Major functions
Chlorine	Cl^-	0.01 (100 ppm)	Required for water-splitting set of photosynthesis; functions in water balance.
Iron	Fe^{3+}, Fe^{2+}	0.01 (100 ppm)	Component for cytochromes; activates some enzymes
Manganese	Mn^{2+}	0.005 (50 ppm)	Active in formation of amino acids; activates some enzymes; required for water-splitting set of photosynthesis
Boron	$H_2BO_3^-$	0.002 (20 ppm)	Cofactor in chlorophyll synthesis; maybe involved in carbohydrate transport and nucleic acid synthesis; role in cell wall function.
Zinc	Zn^{2+}	0.002 (20 ppm)	Active in formation of chlorophyll; activates some enzymes
Copper	Cu^+, Cu^{2+}	0.001 (10 ppm)	Component of many redox and lignin-biosynthetic enzymes
Nickel	Ni^{2+}	0.001 (10 ppm)	Cofactor for an enzyme functioning in nitrogen metabolism

Element	Form available to plants	% mass (in dry tissue)	Major functions
Molybdenum	MoO_4^{2-}	0.0001 (1 ppm)	Essential for symbiotic relationship with nitrogen-fixing bacteria; cofactor in nitrate reduction.

8.4.1: Nitrogen

8.4.2: Phosphorus

8.4.3: Potassium

8.4.4: Calcium

8.4.5: Magnesium

8.4.6: Sulfur

8.4.7: Iron and Other Micronutrients

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8.4.1: Nitrogen

Nitrogen is required in remarkably high amounts compared to other essential elements. It is typically the most limiting nutrient to plant growth. Nitrogen contributes to the greenness of plants, as it is a component of chlorophyll. Its availability is also critical as a component of both proteins and nucleic acids. It is an important component in fertilizers for the greening of vegetative tissues such as turf grasses and leafy vegetables.

In Figure 8-7, you can see light yellow plants demonstrating chlorosis due to a nitrogen deficiency while the greener plants do not have a deficiency. This mottled effect is common in fields where conditions can change with soil type.



Figure 8-7. Mottle color effect is due to locational nitrogen deficiency. (source unknown).

Nitrogen is plentiful in the atmosphere in the form N_2. Atmospheric nitrogen consists of 2 nitrogen atoms triple bonded to one another. In this form is unavailable for plants. The energy required to convert it to ammonia (NH_3) is significant. The process is called nitrogen fixation. Some organisms can break triple bonds. Found within the soil, there are anaerobic bacteria that have enzymes that make the conversion of into to NH_3 possible. Additionally, some bacteria such as rhizobia live in a symbiotic relationship with plants. The *Rhizobium* bacteria live in the root nodules of legumes-peas and beans are an example (Figure 8-8). In their relationship, the *Rhizobium* gets carbohydrates from the legume plant, while the legume plant gets ammonia (NH_3) from the *Rhizobium*. Additionally, the *Rhizobium* gets an environment that is anaerobic within the bean root nodules. This is critical because the enzymes responsible for nitrogen fixation require an anaerobic process.



Figure 8-8. Root nodules on legumes due to *Rhizobium* symbiosis. By Stdout - http://allthingsplants.com/plants/photo/73597/. This photo was taken by Dave Whitinger at All Things Plants. Released under the GFDL, as documented here., CC BY-SA 3.0, https://commons.wikimedia.org/w/inde...curid=19212279

The nitrogen cycle is a critical biogeochemical cycle. From the biotic perspective, Figure 8-9 shows the movement of nitrogen in its various forms through the environment. Plants can take up both nitrate (NO_3^-) and ammonium (NH_4^+). Nitrogen in the atmosphere is abundant but in the N_2 is biologically unavailable to most organisms. Nitrogen fixing bacteria living in the legumes root nodules or the nitrogen fixing soil bacteria fix nitrogen into ammonium. Some of the ammonium undergoes nitrification (NO_3^-). Both NH_4^+ and NO_3^- form are available plants. In the plants, the fixed nitrogen is incorporated into biomolecules through several metabolic processes. Primary consumers (like rabbits) eat the plant material and acquire the nitrogen they need through digestion. Secondary consumers can get their nitrogen by eating the primary consumers. Both plant material and animal material at death are broken down by decomposers. As the organic material is broken down ammonium is returned to the soil where it can be picked up by plants again or can undergo nitrification. Nitrifying bacteria convert ammonium into nitrites (NO_2^-). The nitrites can be turned into nitrates which can then be assembled again by the plants. Some of the nitrates, however, get denitrifying by denitrifying bacteria. This returns the nitrogen to atmosphere in its N_2 state.

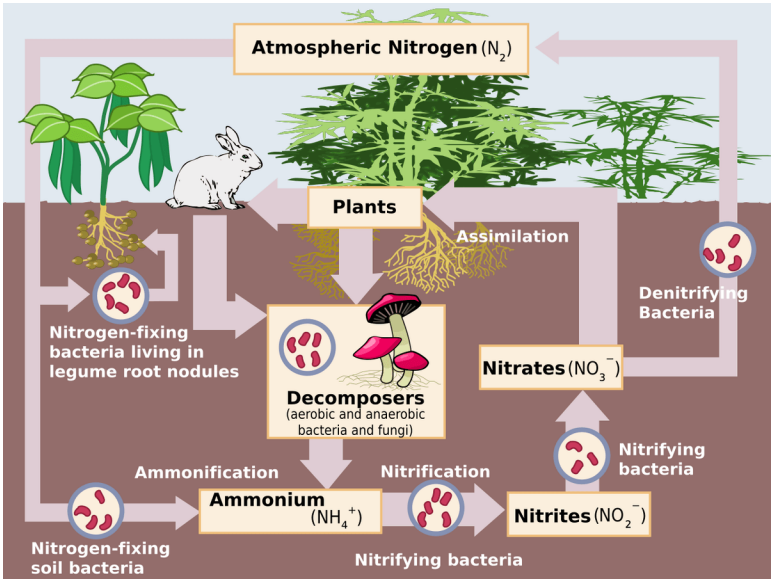


Figure 8-9. The Nitrogen Cycle. Long Description: Diagram of the nitrogen cycle showing the transformation and movement of nitrogen through the atmosphere, soil, plants, and decomposers. The cycle begins with atmospheric nitrogen (N_2) in the air above ground. Nitrogen enters the soil through two pathways: nitrogen-fixing bacteria living in legume root nodules, and nitrogen-fixing soil bacteria, both converting atmospheric nitrogen into forms plants can use. Plants assimilate nitrogen from the soil through their roots. When plants and animals die, decomposers (aerobic and anaerobic bacteria and fungi) break down organic matter, releasing nitrogen back into the soil. Through the process of ammonification, decomposers convert organic nitrogen into ammonium (NH_4^+). Nitrifying bacteria then perform nitrification in two steps: first converting ammonium to nitrites (NO_2^-), then converting nitrites to nitrates (NO_3^-). Plants primarily absorb nitrogen in the form of nitrates. Denitrifying bacteria complete the cycle by converting nitrates back into atmospheric nitrogen (N_2), which returns to the atmosphere. The diagram also shows animals (represented by a rabbit) that consume plants and contribute organic matter back to the soil when they die or produce waste. (Environmental Protection Agency [derivative work]).

Nitrate is the preferred form of nitrogen for storage and transport within the plant. However, it must be converted to ammonium before entering the metabolic processes. In the soil nitrate is an anion (negatively charged molecule) and does not absorb well due to the negative charge on the soil particles. Thus, it tends to easily leach from the soil and can move to non-target areas such as bodies of water.

Nitrogen Deficiency Symptoms

- Chlorosis - Yellowing of the leaves while the veins remain green – interveinal chlorosis - nitrogen plays a critical role in chlorophyll development and photosynthesis. **Oldest leaves exhibit deficiency symptoms** first since nitrogen is mobile and reallocated from older leaves to younger growth (Figure 8-10).
- Reduced growth - Plants exhibit stunted or reduced growth of shoots and leaves. Biomass production slows down since proteins and nucleic acids, key for growth, require nitrogen for synthesis. Yields are lower when nitrogen availability decreases.
- Leggy or spindly growth - Shoot and stem growth is excessive and disproportionate compared to slower developing, smaller leaves. This leads to tall but weak, thin plants.
- Delayed maturity - Lower nitrogen availability delays plant development and time to reach reproductive maturity as the plant limps along with restricted nutrition. This can delay flowering and fruit ripening.
- Purple leaf hues - Some plants develop red or purple pigments in the leaves when nitrogen is deficient. This is caused by accumulation of sugar-based anthocyanin pigments in plant leaves.



Figure 8-10. Nitrogen deficiencies cause a yellowing in older corn leaves, often displayed in a V pattern starting from the tip of the leaf. (University of Minnesota Extension. Accessed 12-2023)

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8.4.2: Phosphorus

Phosphorus, like nitrogen, is a component of several biomolecules. As a structural component of phospholipids, phosphorus is essential for forming cell membranes and organelle membranes. The double lipid layer of membranes regulates transport of compounds in/out of cells and organelles. Phosphorus is also found in nucleotides and nucleic acids like DNA/RNA.

Phosphorus is a key component of ATP, the main energy-transfer molecule in cells. ATP allows plants to activate energy-requiring processes like photosynthesis, nutrient transport, biosynthesis reactions, and carbohydrate metabolism. Phosphorus supports the formation of good root systems, stimulating early root formation and growth of lateral/fibrous roots. Well-developed roots lead to improved nutrient and water uptake. It also accelerates plant maturity and promotes flowering and seed production. It is vital for the formation of flowers and seeds, ultimately maximizing yields.

Additionally, phosphorus plays a critical role in energy storage and transfer. When sugars like glucose are produced during photosynthesis, phosphate groups are added to the sugar molecules in a process called phosphorylation. The resulting compounds are phosphorylated sugars like glucose-6-phosphate or fructose-6-phosphate. These phosphorylated sugars are more stable and can be stored more readily. The addition of phosphate acts as an energy "storage device" of sorts. The movement of energy-rich sugars and phospholipids throughout plants occurs primarily via the phloem. Phosphorus plays an integral role in forming these phospholipids that make up the phloem vessel membranes. Thus, it supports energy transport from sources like leaves to sinks like roots, flowers, fruits, and seeds.

In short, the many roles of phosphorus in plant bioenergetics, macromolecule synthesis, and growth processes make it indispensable for achieving high agricultural yields.

Phosphorus Deficiency Symptoms

- Reduced growth - Phosphorus deficiency causes severely stunted growth and smaller plants overall since phosphorus is integral for plant energy production and use.
- Dark foliage color - Leaves often turn a dark green or violet shade as phosphorus deficient plants accumulate sugars and starch while growth is slowed. This darker color is a result of phosphate deficiency.
- Reddish foliage - Some species develop leaves with red, brown, or purple hues due to pigment accumulation when deprived of phosphorus for growth (Figure 8-11).
- Delayed maturity - Phosphorus deprivation delays plant development stages and the time taken to reach maturity. This affects the time to first flowering and fruit ripening.
- Weak stems - Shoots and stems are typically thinner and structurally weaker. Lateral root growth is also reduced without sufficient phosphorus nutrition leading to reduced water and nutrient uptake.
- Reduced seed production - Flowering and development of viable seeds and grains diminish greatly. Germination rates also decrease without adequate phosphorus reserves being built up by the plant.



Figure 8-11. Purple hue of corn leaves due to phosphorus deficiency. (University of Minnesota Extension. Accessed 12-2023)

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8.4.3: Potassium

Potassium, while not a component of biomolecules, positively impacts many biochemical pathways related to plant growth, metabolism, water use efficiency, and pathogen defense. Deficiencies in potassium can severely stunt plant development and crop yields.

Potassium activates many enzymes involved in processes like energy metabolism, photosynthesis, starch synthesis, protein synthesis, nitrate reduction, and sugar degradation. Activating these enzymes allows these critical biochemical pathways to proceed properly. Potassium helps regulate the water content of plant cells and the opening and closing of stomata. This helps plants cope with drought better, move water and nutrients between the roots and leaves, and cool the plant through transpiration. It also facilitates the transport of nutrients like nitrate and sugars from the leaves to storage organs and growing parts of plants. It is necessary for photosynthates to be distributed efficiently through the plant via the phloem.

Potassium strengthens cell walls and makes plants more resistant to fungal and bacterial diseases. It plays a role in activating plant defense mechanisms as well. It is also an activator of many growth-related enzymes; potassium promotes the growth of meristems and canopy development. Additionally, potassium improves fruit quality and accelerates the ripening process in some fruits and vegetables.

Potassium is not a component of the biomolecules but plays an important role in plant cells. Potassium is typically present in the plant in its ionic form of K+. It is often an enzyme activator or coenzyme. Potassium also plays an important role in the regulation of the guard cells that open and close the stomata pores.

Potassium is useful in root development and often counteracts nitrogen in plants by increasing pest-, disease-, drought-, and cold-tolerance. Recommended application rates are usually based on a ratio of nitrogen to potassium. Common ratios are 2:1, 1:1, and 1:2. Potassium nitrate and potassium phosphate are common forms of potassium found in fertilizers.

Potassium Deficiency Symptoms

- Chlorosis along leaf margins - Yellowing and necrosis (browning) of the tissues along the outer edges of older, lower leaves as potassium is redirected to new growth. This marginal leaf scorching spreads inward as the deficiency worsens (Figure 8-12).
- Reduced growth rates - Stunting of shoots and younger leaves since potassium is vital for protein synthesis and cell expansion needed for rapid growth.
- Weak stems - Stems are thinner and weaker making plants more susceptible to lodging or falling over, especially for top-heavy plants.
- Poor fruit quality - Fruits are smaller in size, have lower sugar content, poor texture and perish faster after ripening due to the vital role potassium plays in translocation of photosynthates.
- Increased disease - Deficient plants are more readily attacked by fungal or bacterial pathogens as potassium contributes to plants having stronger, more rigid cell walls.



Figure 8-12. Leaf of bean plants demonstrating potassium deficiency of chlorosis and necrosis along leaf margin. (By Alandmanson - Own work, CC BY-SA 4.0, curid=61380486)

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8.4.4: Calcium

Calcium's diverse roles in structure, transport mechanisms, enzyme function, and signaling pathways allow plants to achieve optimal cellular functioning and coordinate complex responses during growth and development. Calcium facilitates selective uptake of nutrients like nitrate and potassium by root cells. It helps regulate transport proteins and passage through root cell membranes. Some enzymes involved in growth regulation and carbohydrate metabolism require calcium as an activator to function properly. This includes starch synthesizing enzymes.

As a secondary messenger, calcium conveys signals responsible for responses like gravitropism (gravity response) or fruit ripening. It facilitates protein interactions that translate stress signals into adaptive changes. Additionally, calcium is used to regulate transport of solutes and adjust osmotic potential in cells. This helps plants better maintain water balance and withstand osmotic stress.

Its largest role in plants is that calcium strengthens and provides structural support to cell walls and membranes. Pectins are polysaccharides that contribute to the gel-like nature of the cell wall matrix. Calcium forms ionic cross-links between negatively charged carboxyl groups on adjacent pectin chains. This cross-linking creates a rigid, stable cell wall structure able to withstand internal turgor pressure. Some of the pectins cross-linked by calcium contribute to the middle lamella, the "glue" that cement neighboring plant cells together. Calcium bridges help adjoining cells adhere strongly to form intact tissues.

Calcium also plays a role in regulating cell elongation. The cell wall needs to selectively loosen and tighten to enable controlled elongation and growth. This requires calcium modulation of cell wall-loosening enzymes like expansins. The strengthening and loosening of cross-links regulate wall extensibility.

The cell wall serves as the first line of defense against physical or ecological stresses. By enabling pectin cross-linking and overall structural reinforcement, calcium preserves wall integrity and prevents rupture of cells under stress pressure. This maintains integrity of cells and prevents leaky membranes or collapse under internal turgor pressure. When calcium is limited, the cell walls that form are soft and not resistant to fungal and bacterial attack. Because calcium is nonmobile these soft delicate cells are typically found in the youngest tissues of the plant.

Calcium Deficiency Symptoms

- Tip-burn - Necrotic brown spots develop on leaf tips or margins of young, rapidly expanding leaves due to inadequate calcium reaching those areas. This occurs in lettuce, cabbage, peppers, etc.
- Blossom end rot - Tomatoes, peppers, squash and watermelon show sunken black lesions on the blossom (bottom) end of developing fruits as calcium is immobile in the plant (Figure 8-13).
- Stunted root tips - Without sufficient calcium, root tips stop growing properly, roots branch excessively, and root systems remain stunted unable to adequately uptake water and nutrients.
- Weak stems - Calcium strengthens cell wall pectins. Deficiency therefore causes weak, fragile stems more prone to breaking, boring insects, and infection by fungal or bacterial pathogens entering through damaged tissues.
- Impaired fruit quality - Fruits are often misshapen and lack firmness since calcium maintains cell wall & membrane integrity important for fruit development and storage ability.



Figure 8-13. Calcium deficiency seen here as blossom end rot on grape tomato fruit. (By Siltloam - Own work, Public Domain, curid=10897152)

A calcium deficiency may not be caused by a lack of calcium in the soil. Calcium and magnesium both compete for the same uptake pathways in the plant roots. Therefore, surplus of magnesium can block the uptake of calcium and vice versa. Symptoms of calcium deficiency may also appear if water availability tends to be erratic. This may limit the uptake of calcium at certain points during plant growth. Because calcium is not mobile, influx of new calcium following rain or irrigation events does not fix the problem.

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8.4.5: Magnesium

Magnesium-facilitated reactions are essential for photosynthesis, energy metabolism, synthesizing components, and regulating transport functions within plants. Magnesium is the central atom in the chlorophyll molecule; hence it is essential for chlorophyll production and green color development. Without magnesium, plants cannot photosynthesize. Magnesium also activates many plant enzymes involved in respiration, glycolysis, RNA transcription, phosphate metabolism, carbohydrate metabolism, and protein synthesis. It allows catalytic functioning of these enzymes. It also contributes to the formation of energy storage and transfer molecules like ATP (adenosine triphosphate) and GTP as well as DNA and RNA. Multiple magnesium ions help stabilize ribosome particles and allow for efficient translation and protein production within chloroplasts and mitochondria.

Magnesium Deficiency Symptoms

- Interveinal chlorosis - Yellowing between the veins of **older leaves** while the green veins remain, caused by impaired chlorophyll production and photosynthesis (Figure 8-14). In severe cases, lower leaves turn reddish purple.
- Stunted growth - Shoots and leaves grow more slowly or are smaller than normal since magnesium is needed to activate enzymes for growth hormone & protein production.
- Necrotic spots - Small necrotic lesions surrounded by chlorotic halos appear on leaves in severe deficiency cases. These dead brown spots indicate cell death.
- Premature leaf drop - Chlorotic, contaminated leaves detach and drop early from the plant as symptoms worsen. The plant is starved of vital chlorophyll and cannot sustain growth.
- Impaired fruit set - Reproductive processes fail leading to excessive flower or fruit drop since magnesium facilitates transport of photosynthates needed for fruit development.



Figure 8-14. Magnesium deficiency symptoms leaves of young radish plants. (Stephanie Harvey 2025 CC-BY-NC)

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8.4.6: Sulfur

Sulfur is an important macronutrient for plants. Sulfur is a core component of two amino acids - cysteine and methionine. These sulfur-containing amino acids are needed to build proteins and enzymes essential for plant growth. Covalent bonds (disulfide bridges) can form between the sulfur containing R-groups of these amino acids which stabilize protein structure. Many plant enzymes also contain sulfur-based compounds that act as cofactors required for the enzyme to function properly. This includes key enzymes involved in photosynthesis and nitrogen fixation. It also plays a large role in the production of some defense compounds. Sulfur is used to biosynthesize diverse secondary sulfur compounds like alliin, glucosinolates, and thioneins - important defense molecules against pests and diseases.

Several vitamins (thiamine, biotin) and metabolites like coenzyme A and ferredoxin that facilitate metabolic processes contain sulfur as part of their chemical makeup. Additionally, sulfur balances nutrient intake and influences fatty acid or oil biosynthesis in some seed crops like canola, sunflower, peanut, and soybean.

Sulfur Deficiency Symptoms

- Overall chlorosis - Uniform yellowing of younger leaves due to lack of sulfur for synthesis of enzymes required for chlorophyll production. The yellowing is seen in the younger leaves because sulfur is not mobile in the plant (Figure 8-15).
- Reduced growth - Shoots and leaves exhibit stunted growth as sulfur is required for manufacturing diverse proteins, vitamins and plant hormones that stimulate growth.
- Spindly stems & thin leaves - Leaves and stems appear thinner and weaker without adequate sulfur to build structural proteins for plant biomass.
- Delayed maturity - Flowering, seed set, and plant maturation is delayed since sulfur compounds facilitate these reproductive transitions.
- Legume nodulation issues - In beans, peas, soybeans etc., sulfur deprivation severely decreases nitrogen-fixing root nodule formation and function. This also reduces nitrogen supply.
- Poor flavor - Sulfur compounds greatly affect flavor, so fruits and vegetables taste blander when sulfur levels are insufficient. Oilseed quality also declines.



Figure 8-15. Common bean plant demonstrating sulfur deficiency. Note chlorosis is on new leaves and uniform across leaf. (Stephanie Harvey. 2023. CC-BY-NC)

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8.4.7: Iron and Other Micronutrients

Iron is the one micronutrient we are going to study with some depth. Iron is required for chlorophyll photosynthesis and is a component of enzymes associated with energy transfer. The lack of iron can result in chlorosis or yellowing of the plant tissues. Iron is not readily available in the soil at neutral pH. For that reason's plants like blueberries and azaleas that have a high iron demand prefer acidic soil.

One of the problems with iron is it interacts with many other molecules including manganese copper and zinc. Even if it is present in the soil, it tends to not be available for the plant. To avoid this interaction, most fertilizers use chelated iron. A chelator is a molecule that holds an ion and prevents it from interacting with other compounds, however, it can be released from the chelator into the soil water for plant uptake.

Iron Deficiency Symptoms

- Interveinal chlorosis - Yellowing of leaf tissue between the veins while veins remain green. This occurs due to iron's role in chlorophyll synthesis, leading to impaired chlorophyll production between veins (Figure 8-16).
- Reduced growth rates - Shoot and root growth slows down, resulting in smaller, stunted plants. Growth depends on various iron-activated enzymes and proteins.
- Necrotic spots - In severe deficiency cases, tiny brown spots surrounded by yellow halos emerge on leaves as cells begin to die without essential iron compounds.
- Bronzing symptoms - Some species exhibit bronzing, a bronze-like metallic sheen, on the upper sides of leaves along with interveinal chlorosis on undersides. This occurs in crops like sorghum and soybeans under iron deficiency.
- Poor fruit quality - Fruits develop poor color, size, texture, and flavor since iron facilitates sugar translocation and ripening processes important for fruit development.



Figure 8-16. Gardenia leaf showing iron and manganese deficiency. (©2023 DAFWA - Accessed 12-2023)

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8.5: FERTILIZERS AND AMENDMENTS

Fertilizers influence plant growth by improving the supply of available nutrients to the plants. The primary plant nutrients that limit plant growth (production) are nitrogen, phosphorus and potassium (N, P, K) are listed on commercially available fertilizers as X – X – X. For example, in Figure 8-17, the left fertilizer is 16:16:16. This means that by weight, 16% of the material is N, 16% P and 16% K. On the other hand, the 2nd bag of fertilizer (one on the right) is labeled 46:0:0. This means if you apply 100kg of this fertilizer you would be applying 4.5 kg of nitrogen.



Figure 8-17. Granular fertilizer. On left NPK of 16:16:16 and on rights 46:0:0. (photo – IFDC photography, Nigeria; Link to Source [www.flickr.com])

A fertilizer containing all 3 major nutrients is called a complete fertilizer, whereas a product that supplies only one or 2 of them is an incomplete fertilizer. Complete fertilizers are not always necessary; if soil is deficient in nitrogen, you can save money by buying incomplete fertilizer that provides nitrogen alone, as ammonium sulfate for example.

8.5.1: Synthetic and Organic Fertilizers

8.5.2: Soil Amendments

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8.5.1: Synthetic and Organic Fertilizers

Synthetic (Inorganic) and organic fertilizers can be used to meet the nutrient demands of the crop. Synthetic fertilizers are manufactured artificially and contain minerals or synthetic chemicals. Organic fertilizers contain only plant or animal-based materials that are either a byproduct or an end product of a naturally occurring process such as manures, leaves and compost. There are pros and cons to either side of the organic/synthetic fertilizer battle.

Synthetic fertilizers are typically easy to apply. They are often granular and dry thus making them easily applied through spreader equipment or by hand. Organic fertilizers on the other hand often contain large amounts of water and therefore are very heavy. Due to both weight and how difficult it can be to portion and applied, special handling is often required.

If applying a fertilizer in response to a deficiency in an existing crop, synthetic fertilizers will provide that missing nutrient immediately. Organic fertilizers, however, must actually break down to release the nutrients so this will take time once the organic fertilizer is added to the soil. On the other hand, synthetic fertilizers are subject to leaching because of this availability while the slow release of organic fertilizers make them less susceptible to leaching. Thus, synthetic fertilizers are susceptible to runoff and therefore are more likely to enter streams, rivers, and lakes. The organic material being slow released is less likely to run off and enter our watersheds.

Since synthetic fertilizers are synthesized or come from minerals, the exact ratio of nutrients can easily be determined. With organic fertilizers the nutrient availability can change with time. This means that the application rates can be more difficult to determine with organic fertilizers as compared to synthetic fertilizers.

Because organic fertilizers are the byproduct or end-product of a naturally occurring process the energy required to produce it is very low. In many cases it is formed by recycling spent organic material. The synthetic fertilizers on the other hand require high-energy processes in order to produce them. Organic materials that are part of the organic fertilizers adding significant organic material to the soil. This can improve soil structure and water holding abilities. Synthetic fertilizers lack organic material and therefore do not improve soil structure. On the other hand, synthetic fertilizers are sterile while organic fertilizers have the potential to introduce pathogens into the soil. Another issue with organic fertilizers is its lack of appeal to neighbors and surrounding areas. Organic fertilizers can often smell and look unappealing. If you have close neighbors, they may object to the smell of manure in your garden. In contrast the inorganic fertilizers have little smell. Table 8-5 summaries some of these points.

Table 8-5. *Summary of pros and cons when making comparisons between synthetic fertilizers and organic fertilizers.*

Trait	Inorganic fertilizers	Organic fertilizers
Ease of application	Very	Can be labor intensive
Immediate access	Yes	No
Subject to leaching	Yes	No
Application rates	Known	Subject to change
Environmental impact – energy	High	Low – recycled organic material
Environmental impact – run-off	High	Low – slow release
Sterile	Yes	No
Appeal (smell & look)	Acceptable	Can be offensive
Improve soil structure	No	Yes

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8.5.2: Soil Amendments

Soil amendments are added to the soil to modify soil composition and texture (Figure 8-18). They are often referred to as soil conditioners. They may be organic in nature such as peat moss (Figure 8-18A) or inorganic such as perlite (Figure 8-18B) and vermiculite (Figure 8-18C). Amendments like compost, animal manures, wood ash, etc. directly add essential macro- & micronutrients upon decomposition, providing nutrients otherwise deficient for plants. Gypsum, lime, and sulfur amendments can alter soil pH and chemistry to convert bound nutrients like phosphorus into plant-available forms to remedy deficiencies. Sandy soils are loosened up with compost addition increasing moisture retention. Adding organic matter, biochar or gypsum binds up and improves structure of heavy clay soils facilitating better drainage and root penetration. Organic matter additions support populations of beneficial microbes and contribute negative charges in soils to retains and supply cations like potassium, ammonium, and calcium to plant roots through cation exchange processes. This buffers nutrient levels. Amendments like biochar, peat or coir have high porosity and surface area to retain more moisture while additions like sand improve water infiltration and drainage as needed to optimize growth. The specific type of amendment will vary with the needs to be addressed, size of application and amendment availability.







Figure 8-18: A) Peat moss is a dark, organic soil amendment formed from the decayed remains of plant matter, predominantly *Sphagnum* moss. (By Ragesoss - Own work, CC BY-SA 3.0; curid=4334841) B) Perlite is a lightweight, sterile, porous volcanic glass formed naturally by the hydration of obsidian. (Stephanie Harvey, 2026 CC-BY-NC) C) Vermiculite is a natural, hydrated laminar magnesium-aluminum-iron silicate. (Stephanie Harvey, 2026 CC-BY-NC)

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8.6: Application Methods for Fertilizers

The method of applying fertilizers will vary depending on the nature of the planting, the plant's individual nutritional needs, and their growth stage. For example, transplanted tomatoes, eggplants, and peppers can get a jump start with the use of the starter solution that is applied during the transplant process. Techniques and equipment can also change depending on the size of fields and plants.

One application method is referred to as **broadcasting**. Broadcasting a fertilizer refers to the spreading of fertilizers uniformly over an area. This method is often used on fields prior to planting in which case it is referred to as a **basal application**. It can also be used to apply fertilizers to establish lawns this is referred to as **top dressing**.



Figure 8-19. Push-spreader. Public Domain.

Broadcasting can be carried out using large-scale equipment, small homeowner size pieces of equipment like the ones in Figure 8-19 or simply by hand scattering. There are some disadvantages to broadcasting. The nutrients cannot be freely utilized by plant roots unless it is placed near the root tips. If roots fail to contact the nutrients only weakly stimulated growth may occur across the field. Nutrients can wash away from the soil easily and there is the risk of burning if over applied.

Although traditionally broadcasting was restricted to dry synthetic fertilizers, equipment has been developed to allow broadcasting of both solid and liquid manures on fields. In Figure 8-20 shows both a solid manure and a liquid manure spreader.



Figure 8-20. A) a solid manure spreader pulled behind a tractor throwing small chunks in a pasture. B) A tanker pulled behind a tractor spraying liquid manure on a harvested corn field. (A - By Kenneth Allen, CC BY-SA 2.0, Link to Source [commons.wikimedia.org]; B - Chesapeake Bay Program - originally posted to Flickr as Manure_Spreading, CC BY 2.0, Link to Source [commons.wikimedia.org])

Banding fertilization involves the addition of fertilizers to the side of growing plants. It is sometimes known as “side dressing” (Figure 8-21, A-B) In contrast to the broadcast method, banding places the fertilizer within the reach of the plant but not across the whole field. This helps conserve fertilizers and decreases the amount of leaching and runoff. Higher concentrations can be applied without risks. However, it requires specialized equipment for large scale applications and more time consuming since multiple passes are required.

Mobile nutrients such as magnesium can be applied using **foliar feeding** and can provide a quick growth response when needed (Figure 8-21, C). Some micronutrients such as zinc or iron often get locked into the soil because of their reactivity. In other cases, the plants may not be able to extract nutrients due to cold temperatures of the soil. In both of these cases foliar application can produce the desired results. Absorption begins within minutes after application and with most nutrients is complete within 1 to 2 days. Foliar fertilization can be a supplemental to soil fertilization at critical times in the plants grow it is not however a substitute for soil fertilization. Foliar applications can be expensive and there is an increased possibility of chemical burning to the plants.

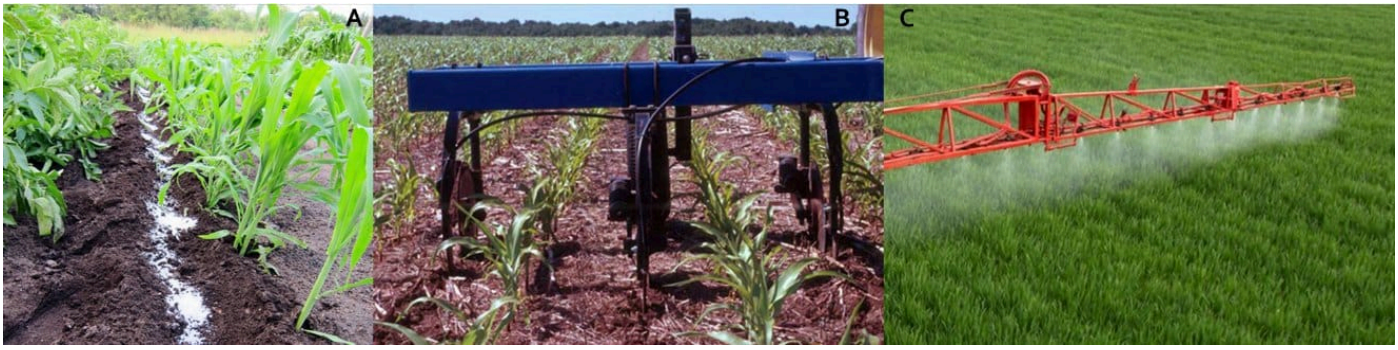


Figure 8-21. A - Banding aside corn plants. B- Equipment used for banding applications. C - Foliar applications. (A&B - Link to Source [qknowbooks.gitbooks.io] ; C - Link to Source [www.haifa-group.com])

Fertigation is the application of fertilizers within the watering system. For this to work the fertilizers must be highly soluble in water. Otherwise, undissolved components can block outlets or sprinkler heads. The combination of watering and fertilizing is ideal. Without water applied fertilizers cannot reach the roots nor can they be absorbed. There is a significant reduction in labor for this application, but the soluble fertilizers are more expense. The delivered fertilizers must be diluted to prevent burning of leaves and other tissues. Fertigation can be applied with synthetic fertilizers or with organic fertilizers. It is common to pump liquid out of manure lagoons onto crops.

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8.7: End of Chapter Review

Chapter Summary

- Discusses analytical techniques like atomic absorption spectroscopy, ICP-OES, Kjeldahl method to determine mineral levels in plant tissues.
- Explains use of hydroponics to isolate each nutrient and verify essential concentrations.
- Covers nutrient deficiency symptoms - chlorosis, necrosis, relation to nutrient mobility.
- Outlines roles of major nutrients like N, P, K, Ca, Mg, S in key plant processes
- Categorizes macronutrients and micronutrients with their functions.
- Compare synthetic and organic fertilizers on factors like nutrient release rate, environmental impact, and soil health.
- Mentions distinct types of soil amendments to adjust soil conditions.
- Describe fertilizer application techniques - broadcasting, banding, foliar sprays, fertigation.

Key Terms

- Banding
- Basal application
- Broadcasting
- Chlorosis
- Complete fertilizer
- Denitrification
- Essential Nutrients
- Fertigation
- Foliar feeding
- Hydroponics
- Immobile nutrients
- Incomplete fertilizer
- Macronutrients
- Micronutrients
- Mobile nutrients
- Necrosis
- Nitrification
- Nitrogen fixation
- Organic fertilizers
- Side dressing
- Synthetic fertilizers
- Top dressing

Self-Review

1. What are the criteria used to determine if a mineral nutrient is "essential" for plant growth?
2. What are the main analytical methods used to analyze the mineral content in plant tissues?
3. What is the difference between macronutrients and micronutrients? Give 3 examples of each.
4. What causes the deficiency symptoms of chlorosis and necrosis to occur in plants?
5. How does the mobility or immobility of a nutrient effect where deficiency symptoms show up on the plant?
6. What roles does nitrogen play in plant growth and metabolism?
7. Describe three visible deficiency symptoms of phosphorus deprivation in plants.
8. Why is potassium important for a plant's water balance and disease resistance?
9. What causes blossom-end rot in tomato, pepper, and squash plants?
10. How does magnesium facilitate chlorophyll production and photosynthesis?
11. What causes sulfur deficiency to result in poor flavor of fruits and vegetables?
12. Why do some acid-loving plants have high iron demand?

13. What is the difference between complete fertilizer and incomplete fertilizer?
14. Compare the pros and cons of synthetic versus organic fertilizers.
15. What role do soil amendments play in plant nutrition and growth?

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9: PLANT PROPAGATION



Newly germinated seedlings in growing cubes. (Stephanie Harvey. 2026. CC-BY-NC)

Propagation includes various methods of creating new plants or new combinations of plants. Horticulturists and farmers having taking advantage of both sexual and asexual reproductive strategies that plants use to produce new plants. We will delve into traditional methods of propagation such as seed and cuttings, as well as some more modern techniques.

9.1: Propagation by Seed

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9.1.2: Saving Seed

9.1.3: Seed Treatments and Storage

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9.2.1: Cuttings from Woody Plants

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9.1: PROPAGATION BY SEED

There are numerous reasons to decide to grow a plant or crop from seed. Seeds (Figure 9-1) evolved as a means for plants to reproduce and disperse. The basic seed consist of a multi-cellular embryo, a nutritive food source and a protective layer (seed coat). They are a self-contained unit that needs little to begin the development of a new individual.

From a grower's perspective there are good reasons to use them to produce the crops/plants you desire. One of the biggest benefits to using seeds is that it is relatively cheap (in comparison to other propagates). Plants often produces many seeds in a growing season. A single dandelion head (*Taraxacum officinale*) consists of 150-200 seeds and a plant can produce up 10 heads each year while living for 10 years. Thus, a single plant can produce 15,000 to 20,000 seed during its lifetime. Some plants are less prolific while other are significantly more prolific. A single female pigweed (*Amaranthus palmeri*) can produce 600,000 seed in a single season.

The seeds dormant at maturity and relatively dry. The dormant nature of the seed allows it to remain viable for extended periods of time. Research on longevity has demonstrated germination in seed over 100 years old. In one study 200-year-old barley grains (*Hordeum* sp) were found to be viable. In their dormant and desiccated state, storage of seeds for later easy. Their small size and small mass also make storage easy.



Figure 9-1. Assortment of seeds. (Stephanie G. Harvey. CC-BY-NC)

If you are look for specific characteristics in your plants, there is a wider selection of varieties available as seeds as compared to the typical transplants at a garden center. If you want to grow interesting tomatoes - green, orange, purple or yellow stripped tomatoes - numerous varieties are available as seeds (Figure 9-2). You can also find seeds for rare and unusual plants. Just be careful of bringing in potential invasive.



Figure 9-2. Tomatoes of several varieties and colors, some cut in half, ranging from red and yellow to green and deep purple. (Marco Verch. 2020. CC-BY. Link to Source [flickr.com])

It is possible to save seed from the fruit of one season to use to propagate plants for the next season. There are some issues with hybrid plants but there are a lot of plants where you can use this technique and eliminate the expense of purchasing seed.

9.1.1: Seed Sources

9.1.2: Saving Seed

9.1.3: Seed Treatments and Storage

9.1.4: Sowing Seeds

9.1.5: Starting Transplants Indoors

9.1.6: Transplanting

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9.1.1: Seed Sources

Now days there are many sources for purchasing seeds – garden center, agricultural suppliers, mail-order, discount stores and online. However, there are several things one needs to consider before purchasing seed. Not all seeds are equal and sometimes what seems like a bargain is not. Failure to handle the seed properly can lead to non-viable seeds - ones that don't germinate. When you are looking to buy seeds, you want to look for reputable sources. Companies that sell seeds to growers are probably the most reliable due to the economics riding on the success of the crop. This may be local source (in Americus, Farmers' Seed & Feed Services) or through online or mail order catalogs. Other sources, such as nurseries and garden centers, friends that save seeds, collections from the wild or your own garden can be just as good but may have more relaxed quality control.

Seed quality is a critical concern when purchasing seeds. Many factors impact seed quality. Exposure to high temperatures, such as being stored in a non-climate-controlled warehouse, can negatively impact viability. Sanitation during and after seed harvest can also impact seed quality. Exposure of the seed to pathogens, such as fungi and bacteria can lower seed viability or lower the survival rate of seedlings post-germination. Seed contamination with weed seed is another concern. The hitch-hiking seeds lead to new weed problems in gardens and fields. A number of our invasive plant species arrived in the US via seed source contamination.

The age of a seed will have an impact of the seed's quality. Seeds become less viable as they age. While some seeds can be viable for 50 plus years (some of the grains and pseudocereals) other have very short shelf-lives. In general, larger seeds and seed with high oil content tend to have shorter viability windows. So, be aware of older seeds. If you are buying prepackaged seeds the year should stamped on to the package. Saving extra seeds not planted one season for use in the next is may not be the best option.

The storage and handling of seeds is important. While not very active – the seed is said to be dormant- the embryo is alive. A seed is more resilient than a plant in most cases but can be impacted by environmental conditions. Exposure to heat, cold, desiccation and chemicals can kill the embryo. If the embryo is dead the seed will not germinate. Heat is commonly used to kill weed seeds in soil. While steam is used on large scales production, a microwave can be used for small home batches of soil (Figure 9-3). Extreme cold can also be used to kill. Storage of soils at minus 80^{o} Celsius is a sterilization technique used when moving soil across borders because it kills most biota (living things), including seeds.



Figure 9-3. Microwave used to kill weed-seeds prior to sowing. (Msscacti. 2007. Link to Source [flickr.com]).

If you have older seeds or perhaps could not pass up on the 10 packs for $1.00 at the discount store, you should conduct a germination test prior to sowing (planting) the seed to check their viability. Start by randomly selecting 10 seeds from the seed package. Soak the seeds for 8-10 hrs and then place them in a dish on damp paper towels (Figure 9-4). Monitor the seeds for the next few days to weeks keeping the paper towels damp. Note when the first seed germinates and continue to follow until no more are germinating. If only 8 out of 10 germinated, then your germination rate or viability rate is 80%. Knowing the germination rate,

you can sow enough seeds to compensate. For example, if you want 12 pepper plants and your germination rate is 80%, you need to sow 15 seeds to compensate for the reduced viability. If your germination rate was 50%, you would want to sow at least 24 seeds.

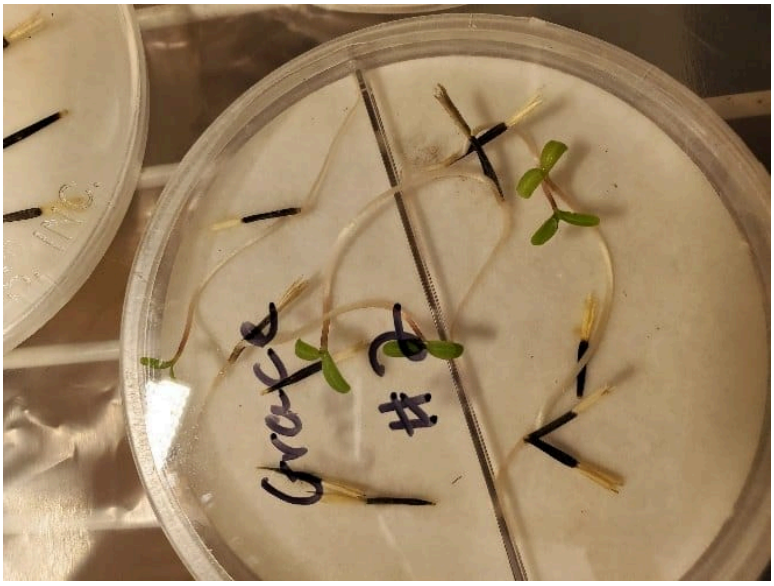


Figure 9-4. Germination test with 50% germination rate. Petri dish lined with paper holding seeds; about half have sprouted roots and small green seedlings, while the rest show no growth. (Stephanie Harvey. 2021. CC-BY-NC)

Some seeds may need more attention to ensure germinate and one away to see if your seeds need "special" attention is to look at the seed package. The seed package contains a lot of valuable information (Figure 9-5). It should have a "Sell by" or packed for date stamped on the package. If you purchase seed and there is no information about when it was packed, you should be concerned. The package should also contain the point of origin and the lot number. Both of these pieces of information can be helpful if you need to track the seed back to its original source. The seed packets also include a lot of practical information for the sowing of the seeds. Some of the things typically given on seed package include instructions for propagation – depth to plant seeds, spacing between seeds/plants, days to the emergence of seedlings and days to harvest/bloom. They can provide a calendar as to when to plant based average soil temperatures for a region. This is typically shown in map format. So, for southwest Georgia, these seeds could go in the ground Jan-April and Aug-Nov. A new addition to the package information is a QR code (blurred in Figure 9-5 for copyright purposes). By scanning a QR code, it can lead you to a website with more information about these plants/seeds.



Figure 9-5. The back of a seed pack can provide critical information. Long Description: The back of a seed packet with planting information, including a color-coded map of direct-sow dates by region, planting depth, spacing, and days to harvest. An arrow points to the stamp reading "Packed for 2015, sell by 11/15." (Stephanie Harvey. 2022. CC-BY-NC)

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9.1.2: Saving Seed

Saving seed from your own garden can be rewarding. You know exactly how the variety performs in your garden, so you don't have to guess about planting conditions. If there is enough light, for example. However, there are some challenges that must be addressed. We can't save seeds from all plants. The most obvious example is seed fruit such as seedless watermelons. If there are no seeds, you can't save them. If you are planting hybrids (plants that are result of cross between two different species or cultivars) the seeds produced by hybrids are often sterile. Those that are viable are unlikely to produce a plant with the same set of characteristics as the original hybrid. Thus, if you want that hybrid you will need to purchase the seeds each year. Other thinks to consider are when to harvest, how to store and will pre-germination treatments be needed.

For the seeds to be viable the fruit will need to have reached maturity. Unfortunately determining that point can be difficulty, particularly since we often harvest and consume fruits at significantly immature stages. For example, cucumbers are consumed while the seeds are very immature. This is why the seeds are so soft. As the cucumber matures the seeds get larger and the seed coat toughens up. You need to know the nature of the plant and it fruits. As we learned earlier in this class, fruits can be fleshy or dry at maturity. Fruits can also be **dehiscent** or **indehiscent**. These factors can present problems for seed collection and saving. If the fruit is dehiscent, it is easy to tell when the seeds are mature because the fruit will open to release the seed. However, you need to collect the seeds before they drop to the ground so the timing can be tricky. If the seeds hit the ground they can pick up pathogens that can impact seed and seedling viability. Indehiscent don't open and you can't see the seeds to determine maturity so you have to look for other clues.

The left image of Figure 9-6 shows open legumes of soybeans. Legumes are dry, dehiscent fruits but we often eat them while still immature. To save seeds, some pods will need to left behind to mature but they will need to be harvested before they shatter (open and drop their seeds). The tomato (Figure 9-6, right) is a flesh, indehiscent fruit. To collect these seeds, you need to leave the fruit to mature (ripen). Then, in the case of tomatoes, the fruit has to go through a souring stage. The seeds need to be exposed to this acidity to be viable. It is effectively a form a scarification, a type of seed prepping.



Figure 9-6. Soybean pods dehiscing to release seeds (left); Tomato fruit is a fleshy, non-dehiscent fruit. (Left - Public Domain, Link to Source [commons.wikimedia.org]; Right - CC BY-SA 3.0, Link to Source [commons.wikimedia.org])

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9.1.3: Seed Treatments and Storage

The seeds of some plants require being prepping before they will germinate. For some, seeds must be exposed to chilling or cold temperatures for a period of time before they will germinate. This process is called **stratification**. This is an evolutionary adaptation that helps ensure that the seeds will have the best conditions for germination and for the survival of the seeding. If a seed produced in late summer were to germinate just before a freeze occurred, the young tender tissues are unlikely to survive. Therefore, it is an evolutionary advantage that the seeds remain dormant until they have been exposed to cold temperatures for a period of time. Then, as the soil warms up in spring, germination is triggered. Plants that have evolved in areas with extremely long, cold winters need longer exposure times to cold to germinate in the spring, while plants that evolve in areas with milder, shorter winters have evolved to need less exposure. Seeds of tropical plants don't require stratification. The need for stratification can be a problem if you move a plant out of its region. A short-winter-evolved plant may germinate at the first warm weather when in fact spring is still months away.

Another prepping process that may need to occur with some seeds is **scarification**. This process changes something about the seed coat (chemically or physically) that will allow germination to proceed. The seed coat often plays a major role in preventing a seed from germination. One method for this is by preventing water uptake (**imbibition**) by the seed. For the seed to imbibe water, the seed coat needs to change. This can be done through mechanical and chemical scarring of the seed coat. In the soil, a new seed's coat would stop water uptake, but after some time in the soil, the seed coat gets physical abraded and becomes more porous. This can be achieved artificially by roughing the seed with sandpaper or tumbling it with coarse sand. In some cases, like with our tomato, chemical scarification can achieve the same goal. As the tomato fruit sours around the seeds, the acid levels increase. This process weakens the seed coat and allow the seed to imbibe and germinate. Fire can also act as a scarifying agent in fire-adapted species. In other cases, dormancy hormones impact the viability of some seeds. Environmental cues change the hormone balance and allow germination to occur.

For farmers it is often important that seed germinate uniformly across the field. This synchronized germination is not a natural phenomenon but a trait bred into crops to facilitate uniform harvests. For example, if you are going to harvest soybean with a combine, all the legumes on all the plants need to be mature at the same time or else you will lose part of the crop to shattering and some will not have mature seeds. To help insure quick and uniform germination, seeds can be **primed**. In priming seeds are allowed to slowly uptake water. At a point prior to triggering of germination, the process is stopped, and the seeds are shipped to a grower. In Figure 9-7 you can see the effect of priming seed compared to raw seeds (no priming) on germination. Priming solution can also be used that provide a nutrient infusion for the young seedling.

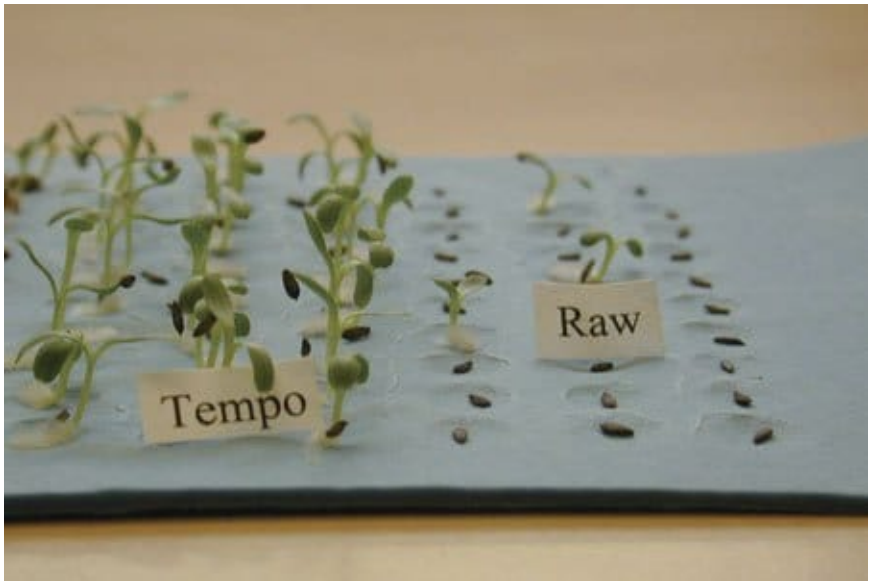


Figure 9-7. Tempo Seed Priming© versus raw seed germination. Long Description: Seedlings on a germination blotter: seeds labeled Tempo (primed) have produced many green seedlings, while seeds labeled Raw have barely begun to sprout. (Link to Source [germains.com])

Another change that can made to seeds prior to sowing is **encapsulation**. There can be many benefits to encapsulation. One is that very small seeds can be made larger. This can allow easier handling for mechanical sowing or hand-sowing. The seeds

can be coated in various layers to help improve the seedlings chance of survival. Figure 9-8 demonstrates various coats that can be applied to a seed – fungicides, insecticides, fertilizers, growth promoters, beneficial bacteria and protective layers. These can increase self-life of the seed and improved germination and seedling success rate. Of course, this comes with a cost. Encapsulated seed are significantly more expensive that non-encapsulated seed. But, for some crops in problems fields, that expense may be offset by increased yields.

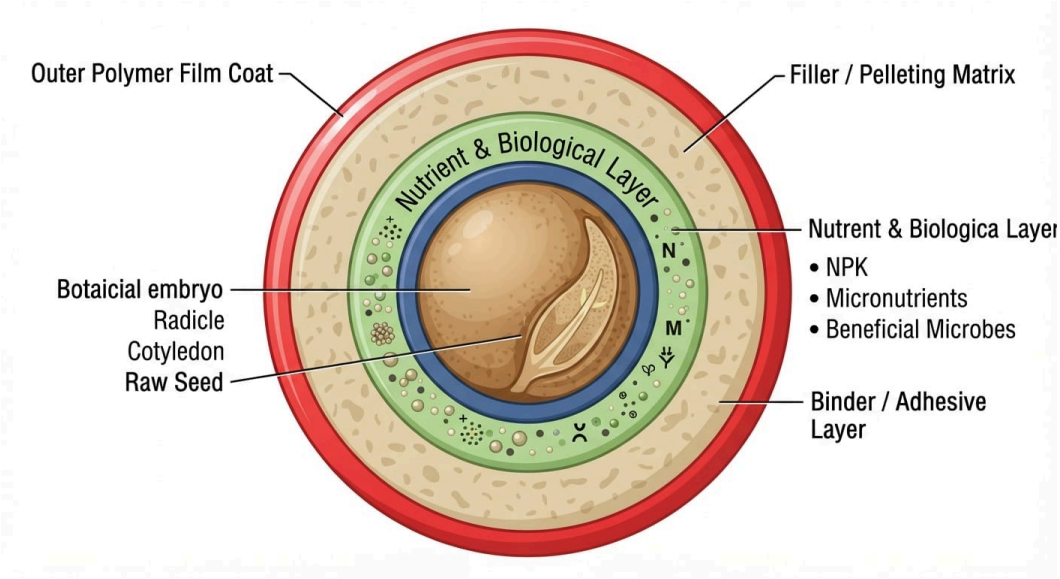


Figure 9-8. Layering of chemicals as part of the encapsulation process. (Google. (2026). *Google Gemini* (Nov 14 version) Prompt by Stephanie Harvey[AI-generated image of encapsulated seed coat layers]. https://gemini.google.com/)

To maintain seed viability as long as possible, seeds should be stored in a cool, dry location. The temperature should not get below freezing with 4 to 8^{o} C being ideal. Excess moisture needs to be avoided. It can stimulate germinate or encourage growth of pathogens, such as fungi and bacteria, on the seeds. Figure 9-9 is an image of the Svalbard Global Seed Vault located in Norway on a remote Arctic island. You can achieve the same thing, granted to a significantly smaller degree, by placing seeds in a tightly closed bag or container and placing them in a refrigerator drawer. You can do this to save left-over seeds from this year's sowing or to save seeds from your garden until next spring. Even with ideal conditions, some viability will be lost. Conduct a germination test to determine how viable each seed type is prior to sowing.



Figure 9-9. Svalbard Global Seed Vault. (By Miksu - Own work, CC BY-SA 3.0, Link to Source [commons.wikimedia.org])

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9.1.4: Sowing Seeds

Sowing is the placing of seeds into a media such that they will germinate and develop into seedlings. Seeds are dormant embryos with an attached, limited nutritive source and a protective seed coat. To maximize crop yields we need to make sure the conditions for the seed is as perfect as possible. The ideal conditions for germination will vary with species. Table 9-1 provides a list of some common crops, their species, growing season and ideal soil temperatures for germination. There are several crops listed under the classification of "**cool-season**" crops. This means they will germinate in cooler soil temperatures and thrive under cooler weather conditions. Some examples include broccoli, cabbage, cauliflower, carrots, and lettuce. Their ideal soil temperatures range from 40 to 56 degrees F. The "**warm-season**" crops prefer soil temperatures above 65 and ranging to 75^{O}F. They include crops such as beans, pepper and tomatoes. Notice that sweet corn is classified as a warm-season crop but has a "cool" season soil temperature. This discrepancy is due years of selective breeding for corn seed that is tolerant of the cooler soil temps. However, optimum growth is still closer to the "warm" temperatures. The only example given of a "hot-season" crop is watermelon; their ideal soil temperature is between 70- and 80-degree F. Soil temperature is often the determining factor as to when a field/garden can be planted.

Table 9-1. *Some common crops with their species, seasonality and preferred soil temperatures (F^{O}) for germination.*

Crop	Species	Season	Soil temp (°F)
Broccoli, cabbage, cauliflower	*Brassica oleracea*	Cool	55–65
Beans	*Phaseolus* spp.	Warm	65–75
Carrot	*Daucus carota*	Cool	45–55
Corn, sweet	*Zea mays*	Warm	50–60
Lettuce	*Lactuca sativa*	Cool	40–65
Onion	*Allium cepa*	Cool	40–50
Peppers	*Capsicum annuum*	Warm	65–75
Tomatoes	*Lypersicum esculentum*	Warm	65–75
Watermelon	*Citrullus lanatus*	Hot	70–80

In addition to soil temperature, seeds of different crops will have different ideal planting depths, plant spacing and preferred soil texture. These factors will affect how and when seeds are planted. They may also impact your method of sowing. **Direct-seeding method** (as called direct-sowing method) is when the seed are placed in the ground where they will germinate and develop as seedlings and ultimately to mature plants. The second the development of transplants that will be moved methods involves the starting seeds indoor to be transplanted later. **Transplants** are created by starting seeds indoors. You sow the seeds into containers where they will germinate and develop into young seedlings but then will be removed from the container and placed in the garden or field. There benefits to each method depending on the crop, climate and your circumstances.

Direct-Seeding: There are both advantages and disadvantages to direct-seeding. One major advantage is the mechanical planting option. Seeds can be planted using a drain drill that will allow for set spacing and minimal "hands-on" contact with seeds. This is important for large agronomic crops such as wheat, corn, soybeans and cotton. Soils in the field or garden need to be prepared before seeding. Of particular importance is the tillage because the seeds need to make good contact with the soil to ensure they can extract water adequately. In a poorly tilled field, seed can fall into spaced between soil aggregates (or clumps). In this larger pore spaces, the seed may have access to the water needed for germination. For some crops, direct-seeding is beneficial because the plants don't tolerate transplanting well. Plants that form large taproots, for example carrots and turnips, fare better with direct-planting. One of the major disadvantages is that you are subject to the whims of weather. Soil temperatures need to be within the ideal range for the crop to be sown and moisture levels before and after sowing can impact germination/survivorship. Field conditions may prevent sowing such that maturity/harvest dates are later. If your growing season is short and the time to maturation/harvest is long, this could be problematic. Or the crop might make but you miss the market window for the crop. For example, watermelon harvest needs to begin before July 4th to maximize profits because after the July 4th prices drop significantly.

The methods of direct-seeding can vary dramatically depending on the area to cover and the precision in which the seeds need to be placed. The simplest method would be to **hand-broadcast** which involves hand scattering of seeds. This works well for small areas and with crops where the seed placement is close to the surface and plant density is not a problem. For larger scale application, tow-behind broadcasters work well. The disadvantage is that with the random placement of the seeds, re-entry into the crop is problematic – no rows. Additionally, for crops that need space for growth, overcrowding can lead to lower yields.

For better control of seed placement – hand-drilling, walk-behind seeders or sophisticated **air-seeders** (**grain drills)** can be used. Obviously, if you are planting each seed by hand you can control the separation and depth of the placement. Similarly, devices such as walk-behind seeders can allow you to control spacing and depth of seed placement using mechanized settings. For large field application air-seeder control the delivery of the seed while the drill component controls the depth of placement. This precision allows for highly precise planting densities and allow for re-entry via the establishment of uniformed rows. In Figure 9-10 (left) an air-seeder can be seen in the foreground (red) sitting in a field that has been harvest. The sowing precision is clearly visible as the remaining stubble clearly defines where the rows lay.





Figure 9-10. In the foreground (left image) is a red air-seeder/drill combination sitting in a harvested field. Image to right is of seedling growing in plastic cups. (Left - By Rfagnou - Own work, CC BY-SA 4.0, Link to Source [commons.wikimedia.org]); Right - Link to Source [images.app.goo.gl])

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9.1.5: Starting Transplants Indoors

Transplants: If your growing season is on the short side or you crave early production, you can sometimes get a jump on the growing season by starting your seed indoor (Figure 9-10-right). By providing artificial conditions for seed germination, you can start this process while outside temperatures are unsuitable. While this sounds ideal, it does have some disadvantages. It requires indoor spaces with adequate lighting and temperature control. This may mean building a greenhouse or cold-frame or giving up some of your living space. The process requires some hands-on techniques for seeding the small containers (there are some automated system for large scale production) and may require an intermediate transplant to a larger container prior to transplanting in the garden or field. The transplant process is stressful on the seedlings due to damage to root hairs and dramatic change in environmental conditions. To minimize plant loss, transplants need to undergo what is known as "**hardening-off**". In this process plants are placed outside to acclimate to the environment. Initial exposure times are short but then are lengthened gradually until at two weeks they are being left outdoors the entire day and night. This staged exposure triggers thickening of stems, increased root production and solar tolerance. Thus, the main drawback is the increase level of manual labor. Additionally, as mentioned earlier, some plants, like dill, don't do well when transplanted so losses can be high.

What you choose to germinate your seed is up to you. Traditional flats, plastic or Styrofoam - as seen in Figure 9-11, allow for high concentrations of plants in limited space. They are also easy to handle throughout the growing and during transplant process. The individual wells prevent root from adjacent plants from becoming entwined. You can use a seed medium - a fine mixture of soil specifically produced for seed germination – or simple potting soil. Another option is peat pellets. Purchased as a compressed disk, when water is added it expand to 4-5 times its original height (Figure 9-12). Once expanded just plant seed. These are great in that they store well prior to use, however they tend to buckle, once wet, and not very stable. With a tall seedling it is easily tipped. Also, excessive handling of peat bundle can induce structural failure. If used, it is best to place them in a sturdy tray to facilitate future handling. Non-commercial products can also be used – paper cups, egg cartons, or folded newspaper cups. Really anything that can hold the soil and tolerate some level of dampness while maintaining their integrity can work.



Figure 9-11. Styrofoam seedling tray. (By Aris Papachristou. 2004., CC BY-SA 3.0, Link to Source [commons.wikimedia.org])

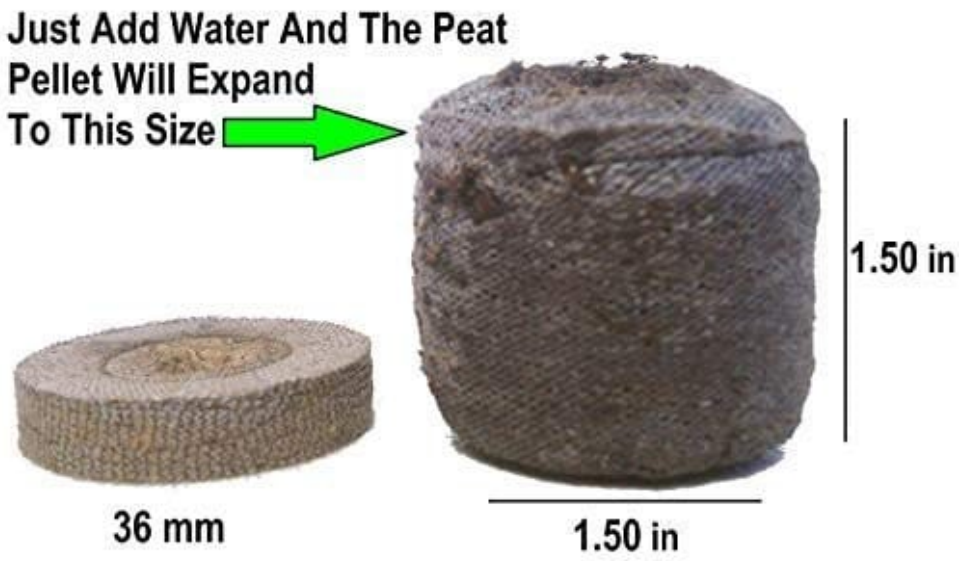


Figure 9-12. Standard peat pellets that expand when soaked. Long Description: A flat, dry peat pellet beside an expanded pellet about 1.5 inches tall and wide, with the label "Just add water and the peat pellet will expand to this size." (image from www.Walmart.com)

The benefit to starting seeds indoors is the ability to control the environment. Your ability to control the elements will depend greatly on where you place the seeded pots for germination. If you are placing them inside your home, what is idea for the plant may not be idea for you. If you are using a greenhouse or other isolated area more control may be obtainable. Since germination is often tightly linked to soil temperature, seedling heating mats can provide the soil warming some plants desire (Figure 9-13 left). These pads are similar to a heating pad but are sealed against water and are safe to use in damp condition.



Figure 9-13. Seedling heating mats help keep trays of soil warm (left); Watering system on timer with fine spray. (image sources unknown)

Once the seeds begin the germination process it is critical that they have adequate (but not too much) water. Automated watering systems that produce a fine spray are ideal (Figure 9-13 right). If that is not an option, creating a tent using plastic sheeting or a plastic bag will help retain the moisture and minimize the time spent watering. Supplemental lighting may also be helpful. Low light levels will cause excessive expansion of the internodes leading to weak, "leggy" plants. Depending on the type of light source it may also contribute to warming the space.

As mentioned in the first segment of this chapter, seed packets have a lot of information for the grower – when to plant, how much space to allow and depth. But what if you don't have that information? You can, of course, attempt to look it up online. This is probably a good move these days. However, if you can't find anything there is a good "rule of thumb" to use for sowing depth. For a seed or bulb, **don't plant any deeper than twice the width of the seed or bulb**. Figure 9-14 show this with bulbs – the large the bulb the deeper it can be planted. The science behind this general rule is that the size of the seed (or bulb) mirrors the energy available for the germinating embryo. A tiny seed has very little stored energy, so the seedling must quickly emerge and start photosynthesizing. Larger seeds or bulbs have more resources and thus can fuel the growth of the seedling until it reaches

the surface.

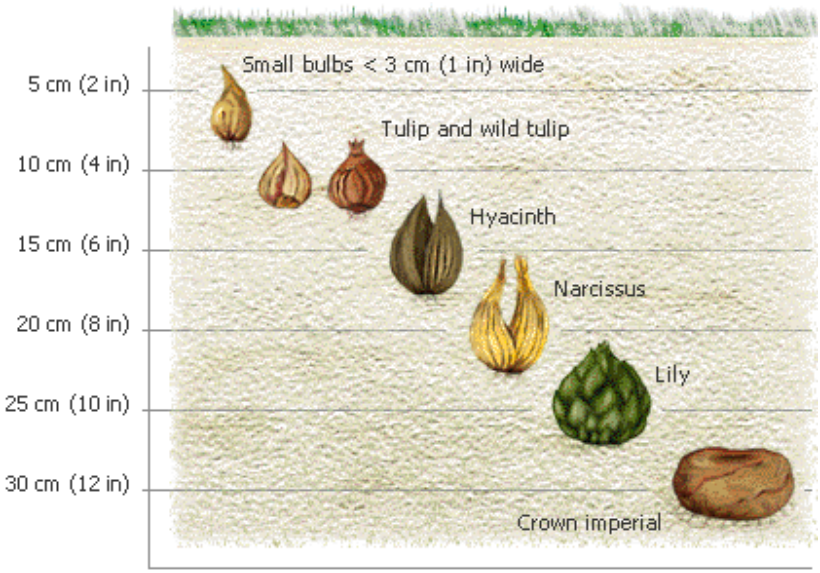


Figure 9-14. Estimated planting depth for different sized bulbs. Long Description: Chart of planting depths for bulbs, from about 2 inches (5 cm) to 12 inches (30 cm). Larger bulbs are planted deeper: small bulbs under 1 inch wide are shallowest, followed by tulips, hyacinths, narcissus, and lilies, with crown imperial deepest. (source unknown).

Once the seeds have been planted and all the conditions you can control have been controlled, watch for the appearance of the seedling. Germination begins with the uptake of water – a process called **imbibition**. This uptake reverses some of the changes that occurs as the seed entered dormancy like the loss of water, slowed metabolic activity and suspension of cell growth. This "renewal" triggers embryo growth and ultimately leads to the production of a seedling. Germinations ends with the emergence of the first true leaf – which is not always the first photosynthetic part of the plant. A light fertilizer solution can be applied a couple weeks after germination to stimulate plant growth. Plants grow rapidly when kept at the optimal temperature, light, water and nutrient levels so plants should be closely monitored so adjustments can be made as needed.

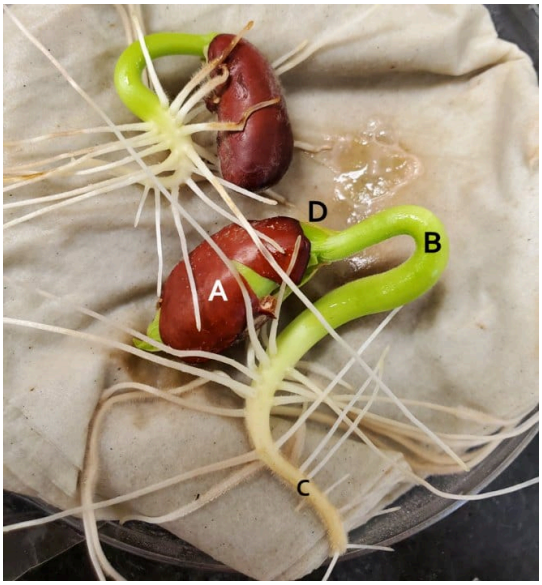


Figure 9-15. Bean seeds germinating. A-slitting seed coat; B-hypocotyl hook; C-radicle with secondary roots; D- green cotyledons just starting to emerge from seed coat. (Stephanie Harvey. 2021. CC-BY-NC)

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9.1.6: Transplanting

Transplanting refers to moving of a plant from one location to another, but is often used to specifically refer to the moving of indoor-started seedlings into the garden or field. This is traumatic process for young seedlings and care must be given during the process. Plants should not be planted outdoors until air temperatures are sufficiently warm to support active growth. However, even if outdoor conditions are good for planting, the dramatic shift in environmental conditions can induce significant stress. To minimize this transitional stress, seedlings should be "hardened off" before planting. This process should be started about two weeks before expected planting date. First the young seedlings should be placed outside for several hours only, and then returned indoors. This is repeated 2-3 days followed by longer and longer exposure times. Finally, the last few days before planting the seedlings should be left completely outside. This allow time for physiological changes to occur that increase the seedlings likelihood of surviving. The leaf surface surfaces become tougher and more water-proofing is added to the leaf surfaces to prevent water loss. The stems stiffen and thicken to support the plant. Sunlight tolerance increases with increased chlorophyll (for greater photosynthetic activity) and carotenoids (protective pigments).

Preparation of the planting hole is important for encouraging proper root growth. The transplant hole should be wider but no deeper than the root ball or tray cell it has grown in. Backfill the hole with native soil or amended soil to cover the roots and firmed gently to set the transplant at the same depth it was growing previously. This should be done with minimum disturbance to the root ball. Some plants, like tomato plants, can be planted deeper if desired because the stems will produce adventitious roots to help with water and nutrient uptake. Space between plants will vary with species and cultivar. Small, fast-growing varieties can be planted closely together while plants that will grow larger will require proper spacing for future development. Tomato plant are typically planted 18 inches apart while basil plants can be planted 6-8 inches apart. A starter fertilizer solution can be applied at planting using water-soluble formulations or root-stimulating granular products worked into the backfill soil.

Regardless of the care taken when transplanting seedlings, some damage to the root system is unavoidable. The root hairs are responsible for most of the water and nutrient uptake by a plants root system. These delicate structures are simple extensions of epidermal cells and are easily destroyed. It is there for critical that regular irrigation occur during the establishment period as the root systems expands and the root hairs are replaced. For most crops this is about a two-week period. The use of organic mulch around transplants helps suppress weeds, conserve moisture and regulate soil temperatures. Placing protective floating row covers over transplants shields them from pests.

The threat of frost damage to cold-sensitive plants is a concern when transplanting early in the season. Spring night temperatures can be difficult to predict. If you have already put your transplants in the ground and then need to protect them for the cold, there are several options available. Fabrics (like bedsheets), paper or plastic sheeting can provide some level of protection from the cold atmospheric temperatures. The addition of soil mounds, walls of compost or grass clippings around transplants can hold heat and provide insulation. Commercial products like "low-tunnels", "hot kaps" domes, cloches, and water teepees can purchase for use as well (Figure 9-16). Since water has a high thermal capacity filling plastic milk jugs or larger containers with hot water and placing them among the transplants will release warmth overnight. While these methods will provide so limited degrees of protection, transplant date selection based on the expected end of frost occurrence is more reliable for avoiding cold damage.

Using established transplants is helpful for ensuring plants have ample time to mature the desired amount before the end of the season. Starting seeds indoors allows earlier planting dates and monitoring growing conditions can encourage strong seedlings ready to withstand the transition outdoors. Careful attention to hardening off, proper planting procedures and frost protection where needed leads to higher success rates for establishing transplants in the landscape or garden.



Figure 9-16. Commercially available products such as low tunnels, cloches and water teepees (from left to right) can provide protection for frost. Long Description: Three frost-protection products: a white fabric low tunnel over a raised bed, a clear plastic cloche over a young plant, and red water-filled teepees around young tomato plants.(Link to Source [gardeners.com]

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9.2: VEGETATIVE PROPAGATION

While seeds are a common mechanism for propagating plants, it is not always the most effective propagule. A **propagule** is any plant material used for the purpose of plant propagation. Many plants reproduce using asexual techniques and we can take advantages of these methods to create propagules when seeds are not possible or simply less effective for plant production.

There are advantages and disadvantages to asexual reproduction. With **sexual reproduction** in plants a pollen and an ovum source are required. While some plants are bisexual other are not and can't reproduce without a partner. If seeds are successfully produced, the new plants develop independently from very small embryos. There are a lot of potential barriers to survival: can the seedling uptake enough water? are the nutrients adequate? is the sunlight adequate? will something eat it before it is mature? **Vegetative (asexual) reproduction** allows a single individual to produce clonal offspring (Figure 9-17). The advantage is that the "parent plant" can continue to support the propagule as it develops – providing photosynthates and water while leaves and roots are produced. This support often produces significantly larger offspring that have established roots and leaves. The new plants (once separated from the parent they are considered xplants) are **clones** of the parent – that is they are genetically identical. This can be an advantage if the environment is stable and the parent plant is well suited for its environment. One of the downsides is asexual reproduction minimizes genetic diversity so if something changes in the environment there is little genetic flexibility available within the population due to the lack of genetic recombination. From a horticulturalist prospective, asexual reproduction can be very useful. If you like the characteristics of the "parent" the vegetative propagules will have then same characteristics.



Figure 9-17. Pingao (Ficinia spiralis) spreads by forming stolons in the sand producing clonal offspring via asexual reproduction. (By Arne Hückelheim - Own work, CC BY-SA 3.0, Link to Source [commons.wikimedia.org])

Some plants produce horizontal stems from their base. These stems may run along the top of the soil (stolons; Figure 9-18) or may be just under it (in which case they are called rhizomes). At points along the stem, adventitious roots develop. Remember that adventitious roots are those that develop from non-root tissue (in this case stem tissue). Hormones produced by these new roots, stimulate the production of new leaves along the stem. After establishment of the roots and new leaves, the connective stolon can die away leaving independent new plants behind.



Figure 9-18. 'Lipstick' hybrid strawberry (Comarum palustre × Fragaria × ananassa) along stolons. (By Dr U at English Wikipedia - Transferred from en.wikipedia to Commons., Public Domain, Link to Source [commons.wikimedia.org]).

Tubers, like those formed by potato (*Solanum tuberosum*), are modified stolons that hold food reserves and a few buds (the "eyes"). The tubers are an over-wintering structure. Winter kills back the above ground structure, but the underground tubers survive. Come spring, the buds will develop into new shoots and then produce adventitious roots. Because a single plant can have numerous tubers, a number new plants can emerge. Note the distinct lack of roots on the tubers. Tubers are often used for cultivation by cutting them into pieces so that each segment has at least one "eye." These are then planted into the soil to produce a new plant. This is the preferred method for potato propagation over seeds.



Figure 9-19. Amaryllis bulb with bulblets. (Link to Source [images.app.goo.gl])

Bulbs and corms are both reproductive and overwintering structures for some plant. Most of the plant stays below ground throughout the year but sends up leaves in spring and summer to photosynthesis. The stem and storage tissue remain below ground protected from cold weather and herbivory. A **bulb** consists of a condense stem, often referred to as a "**stem disk**" and fleshy leaves. In spring, stored reserves power the production of new photosynthetic leaves that emerge above the soil surface. In contrast a **corm** is a subterranean fleshy stem surrounded by dry, brittle leaves, but works similarly to a bulb. Small bulbs – called bulbil or bulblets- can form from edge of the stem disk of the larger bulb (Figure 9-19). When separated from the older bulb they can propagate new plants. Likewise, small cormels or cormlets can for from the base of the corm.

There are other ways that plants use vegetative propagation to produce propagules. Some plants produce short shoots that arise from an axillary bud near the base of the stem that gives rise to a daughter plants at its apex. This is known as an offshoot (Figure 9-20).



Figure 9-20. Palm with two offshoots. (Link to Source [images.app.goo.gl])

An interesting method of vegetative propagation is seen in the plant commonly known as Mother-of-thousands (***Bryophyllum daigremontianum)*** *(Figure 9-21)***.** Their leaves are really phylloclades – flatten stems that function as leaves. At margins of the phylloclade are spoon-shaped spurs which bear plantlets. Many of these plantlets form roots while still attached to phylloclade.



Figure 9-21. Mother-of-thousands (*Bryophyllum daigremontianum*) with plantlets. (Stephanie Harvey. 2023. CC-BY-NC.)

9.2.1: Cuttings from Woody Plants

9.2.2: Cuttings from Herbaceouse Plants

9.2.3: Layering

9.2.4: Propagation Using Storage Organs

9.2.5: Propagating Bulbs, Corms, Tubers and Rhizomes

9.2.6: Crown Division

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9.2.1: Cuttings from Woody Plants

Many plants produce vegetative propagules to maximize their reproductive potential. In the absence of a sexual partner they can still produce “offspring”. We can harvest these propagules and use them to create plants for human usage. We can also use the innate cloning ability to force the creations of propagules. Techniques allow the creation of propagules from vegetative organs including leaves, stem and storage organs.

Cuttings: Cutting is a propagation method that takes advantage of plants’ ability to generate adventitious roots and other tissues. In cutting, a portion of a plant is removed from a “parent” plant and then triggered to produce new root and shoot material. Cutting techniques are typically divided into two groups – cuttings from herbaceous plants and cuttings from woody plants. In the segment we will discuss several techniques for each type of plant. With all cuttings it is critical to maintain the **“shoot-root” orientation**. If the tip end is planted down, the x-plant is likely to rot instead or root. Remember – *the difference between ROT and ROOT is the O – orientation*.

Woody plants are defined as those that produced 2^{nd} growth in the form of 2^{nd} xylem. They are typically perennials that live many years and thus survive winters. Example of woody plants would include trees and shrubs. The type of cutting used with woody plants is based on when the cutting is taken and the physiological state of the cutting at the time of removal from the parent. The three types are named after the state of the woody cutting: softwood cuttings, semi-hardwood cuttings and hardwood cuttings.

Softwood cuttings are cuttings taken in spring after a new flush of growth. The cutting should be about 4 to 6 inches long, from the new growth. The cuttings lacks roots and can quickly desiccate especially since they will have leaves. Since the leaves are the primary site of water loss, some trimming down of their size can be helpful (Figure 9-22). You don’t want to remove all the leaves since energy from photosynthesis is need for the new growth. However, removing 40-50% of a large leaf will reduce water loss. Cuttings should ideally be placed in a mist bed. If a mist bed is not available, you can create a tent to trap moisture but be careful not to let too much heat get trapped or else the cutting can be killed. Application of a rooting hormone to the cut surface can help speed up the formation of adventitious roots but is not necessary for many plants. Because of the rapid growth occurring in the tissues in the spring, softwood cuttings should have significant root growth within 3 to 4 weeks.

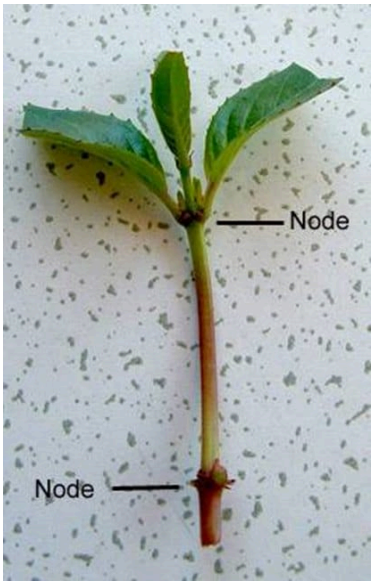


Figure 9-22. Softwood cutting with the large leaves trimmed to reduce water loss. (Source Unknown).

Semi-hardwood cuttings are taken in the Summer from the current season’s growth. Because of the reduces activity of the tissues it typically takes 6-12 weeks to produce roots. The process is very similar to that with the softwood. Reducing the leaf area will help reduce water loss and a misting bed should be used. A rooting hormone can be useful particular with species that are slow to root.

Hardwood cuttings are taken in fall or winter after the plant has gone dormant. Since there are no leaves, misting is not required. Because of the lower tissue activity, a rooting hormone may be useful. While simpler that the other two since there is no misting

needed, it does take significantly longer – over 12 weeks. Cutting also be should be longer than what is taken for the other two methods. Stems should be longer than 6 inches. Additionally, they can heeled-in (placed into a mound of dirt) to allow a **callus** to form first. A callus is a cluster of undifferentiated cells that can then be triggered to form root through application of hormones.



Figure 9-23. Hardwood cutting are taken when the plant is dormant. (Gmihail - Sopstveno delo, CC BY-SA 3.0 Link to Source [commons.wikimedia.org]).

Root cuttings are a special type of hardwood cutting. As the name would imply, root cutting are taken from an existing plant's root system. The root should be cut in the plant's dormant season. A 3-6 inch sections should be removed from a health roots. At the end near the base of the plant (proximal), make a straight cut across the root. On the distal end (further away from the plant stem, make the lower cut diagonally. The two different cuts serve two purposes. First, they help you maintain the polarity of the cutting. Secondly, they diagonal cut provides more surface area for water uptake while the straight cut at the top has less surface area for water loss. When you place your cutting in the media remember the diagonal cut goes down into the media.

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9.2.2: Cuttings from Herbaceouse Plants

Cuttings from herbaceous plants are typically easier to root than wood stems since there is more active tissue in the herbaceous plant parts. In general, you only need to apply rooting hormones on the most stubborn of species. Since all herbaceous plants are active (not dormant) with leaves, desiccations is a risk. Herbaceous cutting can be taken from multiple organs.

Stem cutting are taken from stems. They should be 4-6 inches long and include a shoot tip along with some leaves. The lower leaves should be removed such that only 1-2 leaves remain. As with the softwood and semi-hardwood cuttings, if the leaves are very large their area should be reduced via trimming. The lowest node is where the root development with take place so make sure it is firmly inserted into the media. If leaves touch the media, try to trim or remove them so they don't. If the leaves touch the wet media they are more like to rot and potentially compromise the cutting. Rooting media can be as simple as water, or wet sand to vermiculite, perlite, or peat moss. Mostly the medium has to provide water but also allow oxygen to the newly forming roots.

Some plants respond well to leaf cutting. In leaf cutting a leaf with part of the stem or even just part of the leaf can be used to create new propagules. With some plants, rooting hormones can be helpful just to speed up the process. In these cases, the removed part does not contribute significantly to the new plantlet. In Figure 9-24-A the thick leaves of Mother-in-law's tongue can be cut into 2-3 inches long segments. Roots will form first and then a new plant arises from the base of the cut, after roots and a new rhizome has been established. Likewise, with African violets (Figure 9-24-B), the new plant emerges from the base of the petiole to the leaf blade. As was mentioned in the earlier in this section, it important to maintain polarity of the cuttings. For leaves like the African violet, this is easy to determine. However, a section from the middle of the Mother-in-law's tongue leaf look about the same regardless of orientation. If placed upside down in the medium, it might eventually produce a new plant, but only after roots form at the "top"and then grow down in the media. Many cuttings placed upside down will just rot.

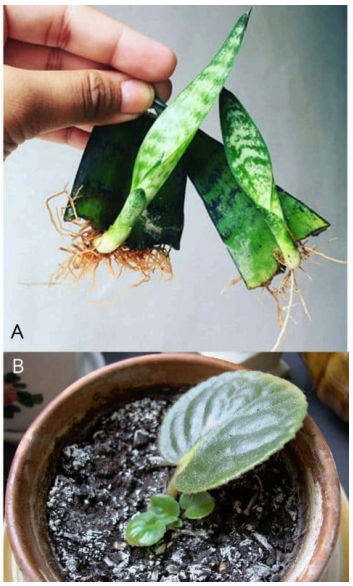


Figure 9-24. Rooted cuttings from leaves. Long Description: A) Snake plant leaf cuttings held in a hand, with new roots and shoots growing from their bases. B) A leaf cutting in a pot with a small new plantlet at its base. (Link to Source [images.app.goo.gl] Link to Source [images.app.goo.gl]

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9.2.3: Layering

Layering is another propagation technique. It involved the productions of adventitious roots and removal of plantlet from a “mother” plant. The critical different between layering and cutting however, is that the production of adventitious roots it triggered first and then once there is enough root development is the explant cutaway from the supporting plant. There are several variations of layering techniques but we will focus on ground layering and air layering.

The first step in **ground layering** is to bring a branch of a tree or shrub into contact with the soil (Figure 9-25). This will need to be a new branch since it will still need to be flexible. Once you have located one that will work, you will need to abrade the bark on the part that will rest on the soil. You can carefully scrape away the bark using a knife or box cutter. Don’t go too deep. You only want to remove down to the cambial layer. Dusting the abraded area with rooting hormone will speed up the formation of roots. Position the branch so the abraded surface touches the soil. Then, using a u-shaped landscape pin or use a brick or other object, secure it to the ground. One way to increase soil contact it to bury the section under a pile of soil. A ground layering is typically started in early spring and is only cut away from the parent plant once they both have entered dormancy. The newly explant can be replanted in a desired location.

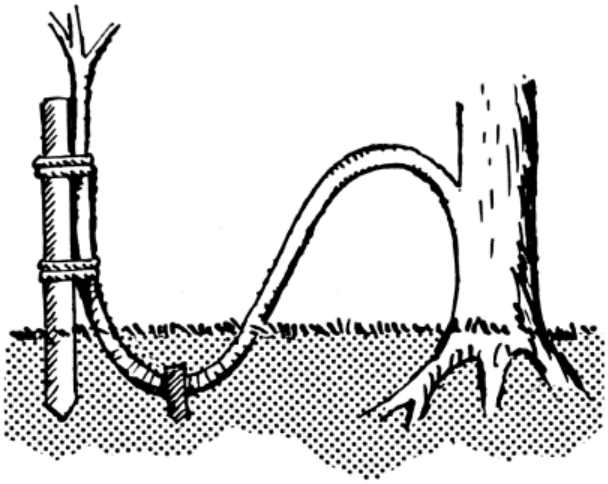


Figure 9-25. Diagram demonstrating ground layering. Long Description: Line drawing of ground layering: a branch is bent down from the parent plant and buried in the soil where roots form, with its tip tied upright to a stake. (Pearson Scott Foresman - Public Domain, Link to Source [commons.wikimedia.org])

Instead of bring the branch down to the soil, in **air layering** the “rooting media” or soil is brought to the branch. A branch is selected and a region along its length is wounded by an upward 4 cm long cut and held open with a toothpick or similar, or a strip of bark is removed (Figure 9-26-AB). The wound is then surrounded with a lump water-retaining sphagnum moss or a cloth (Figure 9-26-C.) Then a moisture barrier such as plastic film tied or taped to the branch to prevent moisture loss or ingress of too much water as from rain (Figure 9-26-D). While clear plastic is a great covering b/c you can see when the roots have formed, is can also act like a greenhouse and introduce too much heat. A sunshield of aluminum foil is easy to wrap round the bundle to reflect the sun’s light. It can also be easily removed to check progress. When sufficient roots have grown from the wound, the stem is removed from the parent plant and planted, taking care to shield it from too much sun and to protect it from drying out until the new roots take hold.



Figure 9-26. Air layering. Long Description: Four photos of air layering: A) plastic wrapped around a wounded branch, B) the plastic tied below the wound, C) the plastic filled with moist rooting medium, and D) the bundle tied closed above. By Mihailo Grbic - Faculty of Forestry, Belgrade, CC BY-SA 3.0 rs, Link to Source [commons.wikimedia.org].

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9.2.4: Propagation Using Storage Organs

As discussed earlier in this chapter some species use asexual reproduction associated with storage organs. This natural process can be slow and produce only a few propagules. For some plants it happens very rarely or not at all. Unfortunately, many other propagation techniques don't work well with the types of plant that produce bulb and corms. Humans have developed techniques to increase the rate of propagule production from storage organs for horticultural purposes.

Before we discuss how to propagate from bulbs and corms, we need to know about their anatomy. For a mental reference, think about an onion bulb you might purchase from the grocery store. The outer, paper layers are referred to as the **tunic** and they are protective in nature (Figure 9-27). Below the tunic are the **scales**. These are fleshy leaves that are storage structures that stockpile energy molecules during the growing season and then provide for the plant throughout the winter. These are also the part of the bulb that we consume. Come spring, the reserves are used to support the growth of the new bud that will send leaves (and flowering shoots) above ground. At the base of the bulb is the **basal plate** or **stem disk**. This is that rather fibrous, tough structure that we typically cutaway when preparing onions to eat. It is compressed stem of the plant from which the buds and scales are produced. It also gives rise to the **adventitious roots** see below the bulb. For propagation, we are mostly concerned with the basal plate.

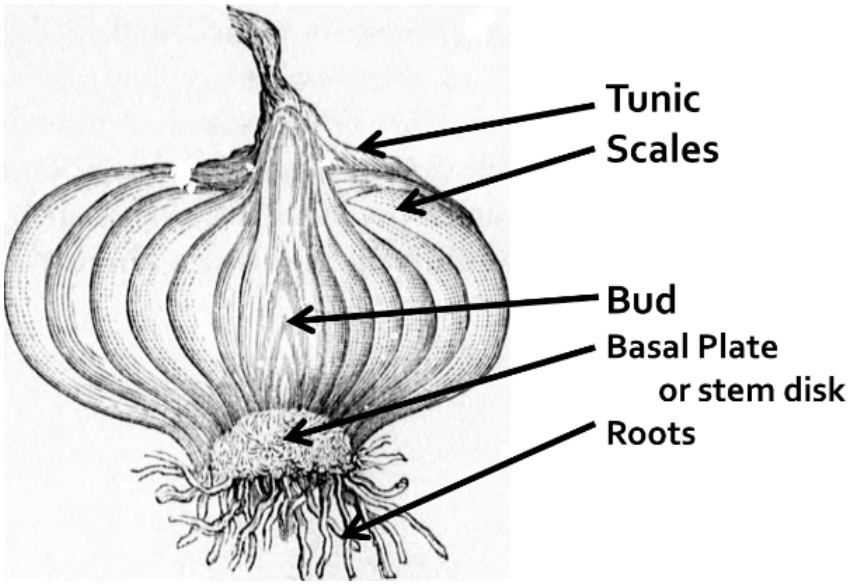


Figure 9-27. Anatomy of a Bulb. Long Description: Labeled drawing of a bulb cut lengthwise showing the papery tunic, fleshy scales, central bud, basal plate (stem disk), and roots. (Public Domain. Modified by S. Harvey 2019).

Corms are very similar to bulb and share similar characteristic. Depending on the time of year you see the corm, it can look quite different. This image is of a corm in early spring so we only see the corm from last year and at this point still flush with nutrients to fuel the spring growth (Figure 9-28). The corm is covered in papery leaf bases. It is sometimes called a tunic. At the base of the corm are adventitious roots and thicker **contractile roots** which work to position the corm at the correct depth. At the top of the corm are two buds. These have already broken dormancy and are in the process of emerging from the soil and producing leaves and flowering shoots. As the spring/summer progresses, the corm seen here will wither and a new corm will develop above it. High energy molecules produced from photosynthesis will be stockpiled here to overwinter and provide for next year growth.

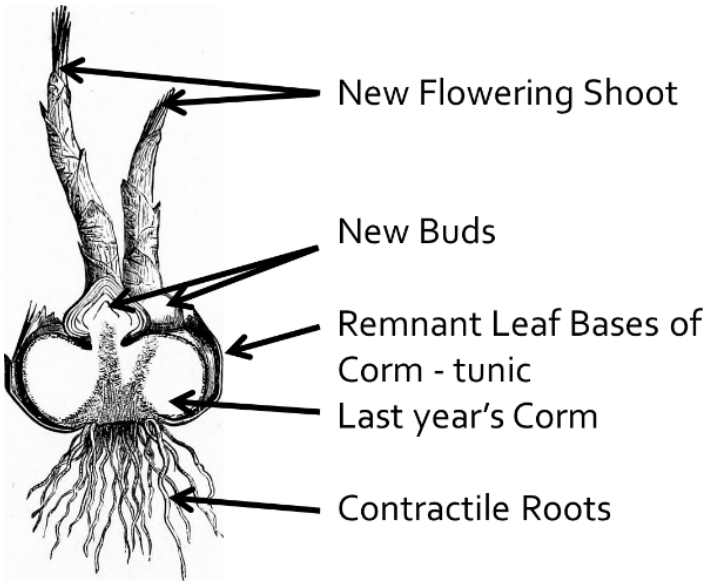


Figure 9-28. Anatomy of a Corm. Long Description: Labeled drawing of a corm showing new flowering shoots, new buds, remnant leaf bases forming the tunic, last yearâ€™s shriveled corm, and contractile roots. (Morphart Vector - ID 218089766; Modified by S. Harvey 2019).

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9.2.5: Propagating Bulbs, Corms, Tubers and Rhizomes

Propagation of bulbs includes a variety of techniques: scaling, scooping and scoring. All of these techniques share the following work habits. 1) These techniques are used when bulbs are dormant. 2) The first step is to clean and dry the bulb. 3) Bulbs are then inspected to make sure they are healthy. 4) to maintain the health of the bulbs all equipment and work surfaces should be sterilized. 4) Following the procedure, fungicides should be applied to all cut tissues. It should be noted that plants using bulbs and corms for overwintering are perennials and it can take several years before new bulbs reach maturity and flower.

Scaling: Scaling is used on bulbs that are loosely bunched together, thus the scales can be removed by hand. Bulbs such as lilies and some fritillaries can be propagated by scaling. Once the shoot growth (above ground growth) has naturally died down for the winter, the bulb should be lifted, cleaned and dried. A number of outer scales can then be simply snapped off. They should be removed as close to the basal plate as possible. A small amount of the basal plate is need for successful propagation. Any unhealthy or damaged scales should be discarded. The parent bulb should be re-planted immediately. If the goal is to maximize the number of propagules, the parental bulb can be used in its entirety.

All removed scales and the parent bulb should be treated with a fungicide to prevent any infections while healing and growing. The removed scales should be place it in a plastic bag with a moist mixture of half perlite and half peat/coir or vermiculite. The plant tissues will need oxygen as they grow, so this can be supplied by inflating the bag by blowing air into it. Seal the bag (label it!) and then store it in a dark location at around 68^{O}F.

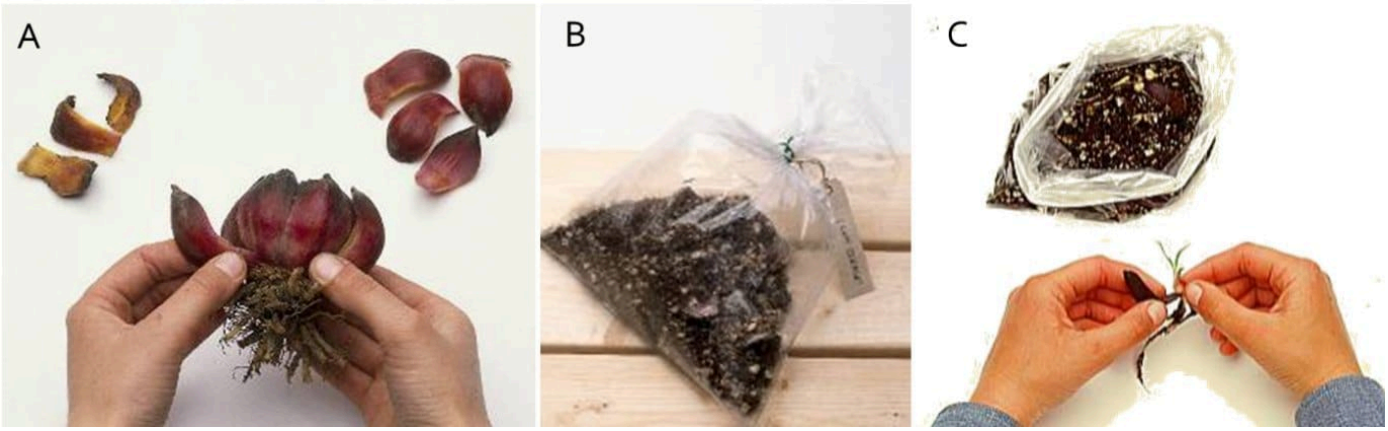


Figure 9-29. Scaling to produce propagules. A. removal of outer scales. B. Scales sealed in labeled bag with moist medium. C. Months later new tiny bulblets can be removed (withered scale removed) and planted. (Link to Source [dkimages.com])

After a few months, tiny bulbs ('**bulblet**s') will have formed at the base of the scales. Individual bulblets can be potted in a loose mixed medium consisting of half loam-based potting soil and half sand. Prior to planting removed the scale but not if it is attached to the newly formed roots of the bulblet. Place the potted bulblets in a cool, shady place over the summer and move to a warm location such as a cold frame for the winter. Each spring they should be repotted, until they reach flowering size, at which point they can be planted out in a garden. This processed takes about three to five years for the bulblets to reach maturity.

Scooping: For more traditional bulbs like that of onions or hyacinths, scooping can be used to force the creation of bulblets. This requires the use of a sterilized scalpel or a teaspoon with a sharpened edge. The center of the basal plate is scooped out leaving only the outer rim intact. Since any open wound is susceptible to fungal attach, the cut surface should be treated with a fungicide. Scooped bulbs should be placed in a moist sand tray with the scooped area facing upwards and stored in a warm, dark place. The sand should be kept moist but not saturated. After 12 weeks new bulblets should have formed on the scooped area. Detach them when they are large enough to handle and pot them as if they were seeds. This technique can produce 30 plus bulblets. It will take about 5 yrs for them to reach a good size (mature) and flower.



Figure 9-30. Scooping to induce bulblet formation. (Link to Source [propg.ifas.ufl.edu])

Scoring: This technique follows the same process as scooping but instead of removing all the inside of the basal plate, cuts are made across it or thin wedges of basal plate and bulb tissues are removed in a cross formation (Figure 9-31). Bulbs should be dusted with a fungicide and the allowed to dry in sand for about a week. They can then be placed in a dark, warm space with high humidity. The new bulblets form at the base of the exposed leaf scales. This procedure produces about 12-25 bulblets in about 12-14 weeks. It usually takes scored bulblets 3 years to reach maturity and flower.



Figure 9-31. Scoring of a bulb to induce bulblet production. (Link to Source [propg.ifas.ufl.edu])

Sectioning: Corm and some bulbs can be used to propagate plants using the sectioning technique. In this method the entire structure, bulb or corm, is cut into wedges as evenly as possible. For bulbs, it is important that part of the basal disk be included with each sectional cut. For corms, each segment must contain part of the corm's stem. Since this technique creates significant cut surface area, fungicides can best be applied using the "shake and coat" method. Place section in a bag with the fungicide and then shake until all segments are coated with the fungicide. Once treated, the sections are placed and seal in a bag with damp potting soil/sand mixture and store in a dark, warm location for approximately 12 weeks. The new **cormels** (miniature corms) or bulblets can be removed and planted. It will take several years for them to reach maturity and flower.

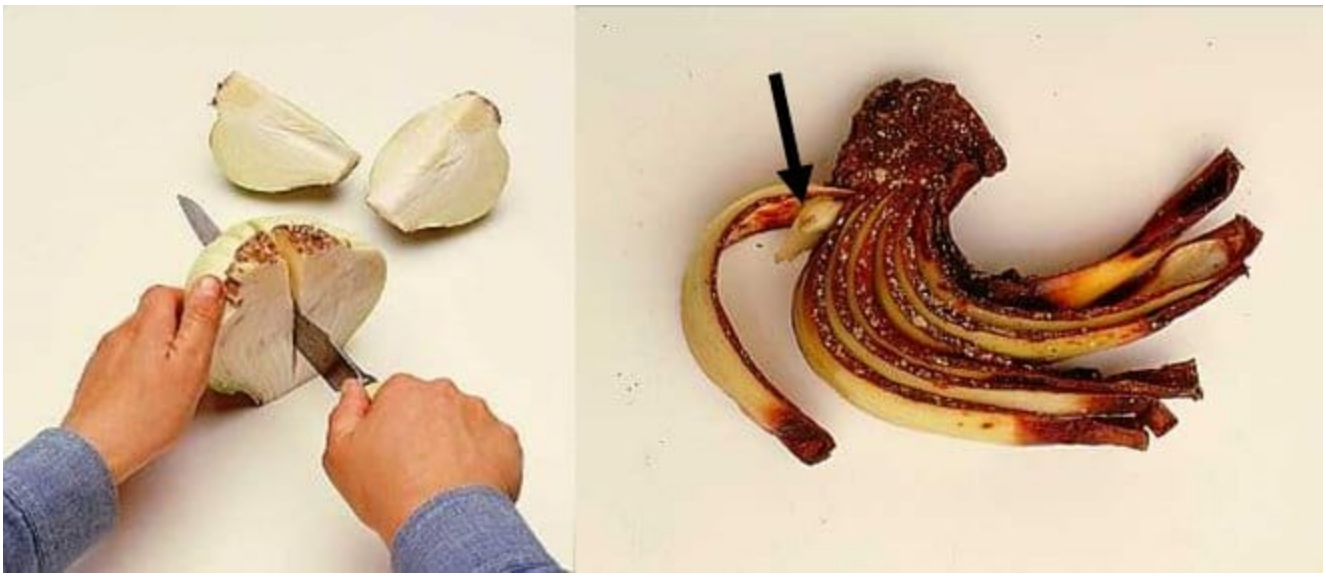


Figure 9-32. Sectioning to induce formation of bulblets or cormels. Arrow indicates new bulblet forming a leaf base. Long Description: Left: a bulb being cut into wedge-shaped sections with a knife. Right: a single section with an arrow pointing to a new bulblet forming at the base of a leaf.(Source unknown).

Sectioning can be used with tuber and rhizome to produce propagules. Both tubers and rhizomes are modified stems and, as such, they have nodes that contain meristematic tissue. When cut into sections such that each piece has one or more nodes, the pieces can potentially develop into new plants. What are called “seed” potatoes are tubers cuts into segments such that each section contains one or more eyes. Potato tuber eyes are nodes. When purchased pre-cut they are often coated with a fungicide to prevent pathogens that might cause damage or death.



Figure 9-33. Iris rhizomes. Rhizomes can be sectioned to create new propagules. (By Jamain - Own work, CC BY-SA 3.0, Link to Source [commons.wikimedia.org])

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9.2.6: Crown Division

Crown division is a common and effective means of propagating many herbaceous perennial plants. It involves dividing the crown of an established plant into multiple sections, with each section containing a portion of the original root system and one or more growth buds. Crown division takes advantage of the natural tendency of many perennials to spread via underground stems or stolons. By dividing these crown sections and replanting, new individual plants are created that are genetic clones of the original plant.

Crown division is typically done in early spring before new growth has emerged, or in fall after flowering finishes. The plant is dug up and excess soil is removed to expose the crown and roots (Figure 9-34). The crown is then divided into sections using a sharp knife or pruners, ensuring that each section contains viable roots and buds. Two to six sections can generally be obtained, depending on the size and growth habit of the plant. It is important to make clean cuts rather than tearing the roots. The resulting divisions are then replanted in prepared soil at the same depth as previously grown, and watered well.



Figure 9-34. Crown division of Asparagus. (Link to Source [propg.ifas.ufl.edu])

Within a season, the divided crowns will re-establish themselves as individual plants. Crown division is advantageous because it results in mature plants that will flower and fully develop within the first year, unlike growing plants from seed or bulblet/cormel formation.

Many herbaceous perennials are well-suited to crown division and will readily re-grow when divided. Some examples include:

- Daylilies - fleshy divisions are separated with a knife, ensuring a portion of crown and roots.
- Hosta - divisions with 3-5 leaves and plenty of roots recover quickly.
- Ornamental grasses - most grasses can be divided in spring or fall.
- Peonies - divisions should have 3-5 eyes or growth buds.
- Russian sage - sections of root clusters will regrow readily.

Crown division allows the creation of an endless supply of the desired plant. However, equally important is that the dividing of overcrowded plants. It restores the plant's vigor and contributes to the continuing beauty of the garden. The technique of crown division is an indispensable part of perennial garden maintenance.

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9.3: GRAFTING

Grafting is a horticultural technique used to join parts from two or more plants together in such a way that they will unite and continue to grow as a single plant. Grafting itself does not produce propagules as such. However, to does produce individual plants with a specific combination of characteristics. Typically, the upper part of one plant (the scion) is grafted onto the root system (rootstock) of another plant (Figure 9-35). The scion contains the desired aboveground growth characteristics such as flowers, leaves, and fruits, while the rootstock provides the root system and some desirable adaptive traits. Grafts made between members of the same species will usually work. But in the case of some of the highly breed horticultural and ornamental crops, enough genetic difference can cause problems that lead to graft failure. So, if rootstock A is not compatible with scion Z, a transition section tissue that is compatible with both A and Z and be inserted between the two. Grafting allows horticulturists to propagate plants with specific qualities predictably and efficiently. However, grafting requires hands-on labor, so the advantages must be significant to make it worthwhile.

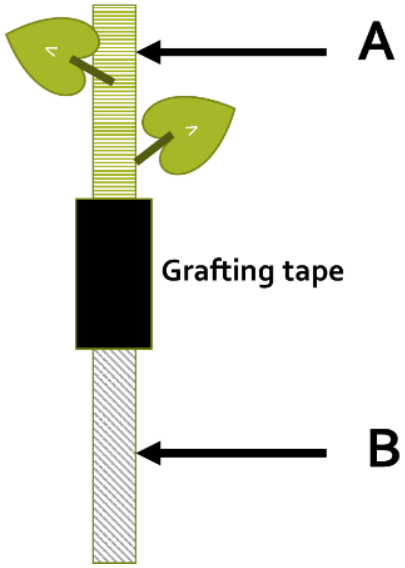


Figure 9-35. Diagram of grafting. A) scion; B)rootstock. Long Description: Diagram of a graft: the leafy scion (A) above is joined to the rootstock (B) below, with grafting tape wrapped around the union. (Stephanie Harvey. 2019. CC-BY-NC.)

9.3.1: Advantages of Grafting

9.3.2: Methods of Grafting

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9.3.1: Advantages of Grafting

There are a lot of reasons or advantages for grafting plants. Manipulation of the scion and rootstock can change growth characteristics such as size, yield, ripening time etc. Grafted fruit trees are **precocious**. This means that the trees start reproducing at a significantly younger age than normal. With the trees will producing fruit sooner, the time from planting to payout is shorter. These trees are often **prolific** as well - yielding significantly heavier yields than non-grafted varieties. Many of the rootstocks available result in **dwarfing** of the trees. This allows the trees to be planted at higher densities thus more production per acre. It also makes for easier harvest. With shorter, trimmer trees fruit can be harvested without use of tall orchard ladders. Dwarfing increases harvesting speed and worker safety.

If in a natural population there are plants with desirable traits such as hardiness or disease/pest resistance, traditional breeding would require 100's of thousand crosses to move all the desirable traits into a single cultivar while editing out less-desirable traits. With grafting you don't have to get everything from a single individual's genetic makeup. Instead you can choose a rootstock that has improved hardiness and resistance to soilborne pest and not worry about how the fruit looks or taste because it will only be used as a rootstock. Then you can select a scion with the flower, fruits and resistance to leaf molds and not worry about how susceptible it is to soil pathogens. Grafting can replace portions killed by weather, disease, pests or injury.

Grafting can also be used to "fix" problems. One issue that can crop up in apples is pollen incompatibility. A specific variety of apples may not be able to self-fertilize and without fertilization there would be no fruit. Large-scale growers plant multiple varieties with compatible pollen close enough so that cross-pollination can occur. In smaller orchards or home gardens, being able to graft some compatible pollen-producing branches on to the desired fruit trees can save space. In the quest for bright, juicier, larger fruit hybrids are frequently created. However, the period from seed production to maturity can be long. By grafting a young juvenile sapling onto an established rootstock, fruit will be produced quicker allow further breeding consideration.

Grafting can also solve issues when cultivars become less desirable or just don't produce like advertised. A lot of money goes into establishing an orchard and if the variety turns out to be a dud (does not sell or does not produce) you can effectively change the cultivar by top-working the plants. This allow the well-established root system to be used to support new growth of a new cultivar – hopefully a more favored one. The new scion wood will transition quickly to maturity and production.

Grafting can also allow for mixing of cultivars on a single rootstock. This can be for visual interest or food diversity. Since closely related cultivars typically graft well, floral displays can be altered. Likewise, several types of apples might be grafted onto a single trunk. When taken to the extreme, as seen in this art piece by Sam Van Aken (Figure 9-36), 40 different fruit types were grafted onto a single trunk. Different varieties of peaches, apricots, almonds and nectarines used to produce this beautiful mosaic flush of blooms. Even more incredible are the varieties of fruit produced later in the season.



Figure 9-36. Known as "Sam Van Aken's Tree of 40 Fruit" this tree has scion wood from multiple Prunus species grafted on to a single trunk (root stock). (Link to Source [www.cnn.com])

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9.3.2: Methods of Grafting

There are many grafting techniques used in horticulture. There use varies with the purpose of the grafting. The most common types of grafting are described in this section.

Bud grafting: Both T-budding and Chip-budding are grafting techniques that involve taking a single bud from the desired scion plant and inserting it into the side of the selected rootstock. In T-budding (Figure 9-37), a T-shaped cut is made in the bark of the rootstock and the bud slid just under the bark so the cambial tissues touch. Some grafters prefer to invert the T to prevent the potential of water becoming trapped behind the bark. The bud is then wrapped and sealed to encourage it to unite with the rootstock. As the bud grows, it will form the desired stem and variety of the scion plant. Bud grafting allows propagation of new plants using very limited amounts of scion material onto easily germinated rootstock. It is commonly used for woody plants like roses and fruit trees.



Figure 9-37. T-shaped incision with a bud for the selected scion wood in place (left). Scion bud has broken dormancy and the rootsock above the bud has been removed (right). (By User Chrizz on sv.wikipedia - sv:Användare:Chrizz, CC BY-SA 3.0, Link to Source [commons.wikimedia.org] ;Link to Source [images.app.goo.gl])

Cleft grafting: Cleft grafting is often used when the rootstock is larger than the scion wood. It requires that the rootstock be split down the center to form a cleft (Figure 9-38). This is typically done by cutting the top of the rootstock at an angle and splitting it with a grafting knife. The smaller scion is cut to form a wedge shape at the bottom and then inserted into the cleft so the cambium layers of scion and stock meet. The union is wrapped tightly to encourage the scion and stock to fuse together. As the scion grows, the wrap is loosened and eventually removed. Cleft grafting provides close contact between the scion and stock so they can unite easily. This technique can be used to top-work an established tree for purposes of cultivar change or rejuvenation of older trees.

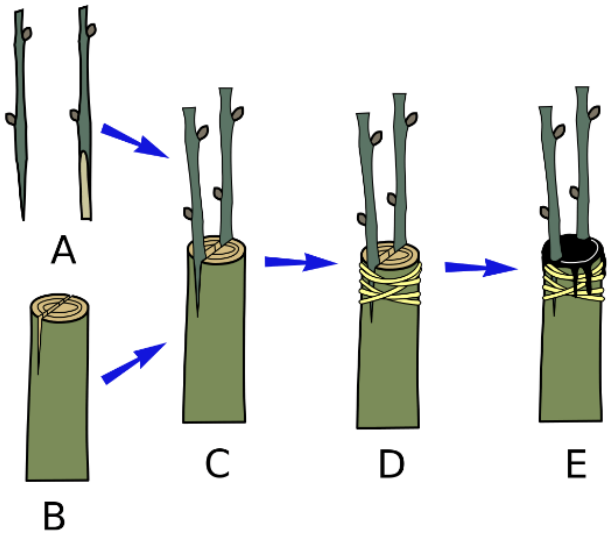


Figure 9-38. Cleft grafting. A-Scion is cut to form a wedge. B-Rootstock is split to form a cleft. C-Scion are insert such that the cambium layers of the scion and rootstock meet. D-Union is wrapped tightly. E. Wound area sealed to prevent desiccation and pathogen entry. (By Giancarlodessi - Own work, CC BY-SA 3.0, Link to Source [commons.wikimedia.org])

Whip grafting: For any graft to be successful, the cambium layers must match up. The cambium is the source of all future vascular tissue in the stem. For nutrients to continue to flow, the vascular tissues of the two components have to align. Whip grafting is used join scion and rootstocks of similar diameter using a slanted cut. The slant increases the contact area between the two pieces and thus increases the chance for cambial alignment. The most difficult version of a whip graft is called the whip and tongue. It creates a slanted "z" for added strength and surface area. While it is difficult to master it is the most successful of the whip styles. To create such as graft (Figure 9-39, *left*), first cut the rootstock and scion at complementary angles, then create the flap on the scion by notching and removing the outer bark. In the root stock, make a nearly vertical cut that match up with the flap on the scion. Once the cuts are complete, slide the scion wood into the matching notch as seen in this image. The grafted area needs to be supported and protected from desiccation. To accomplish this grafting tape – or other types of stretchy tape (electrical for example) is wrapped around the joint. When healed, the union is smooth and strong (*right*). Whip grafting is commonly used for grafting young rootstock and scion material that are the same diameter. It allows rapid grafting and is used for many fruit and ornamental trees.

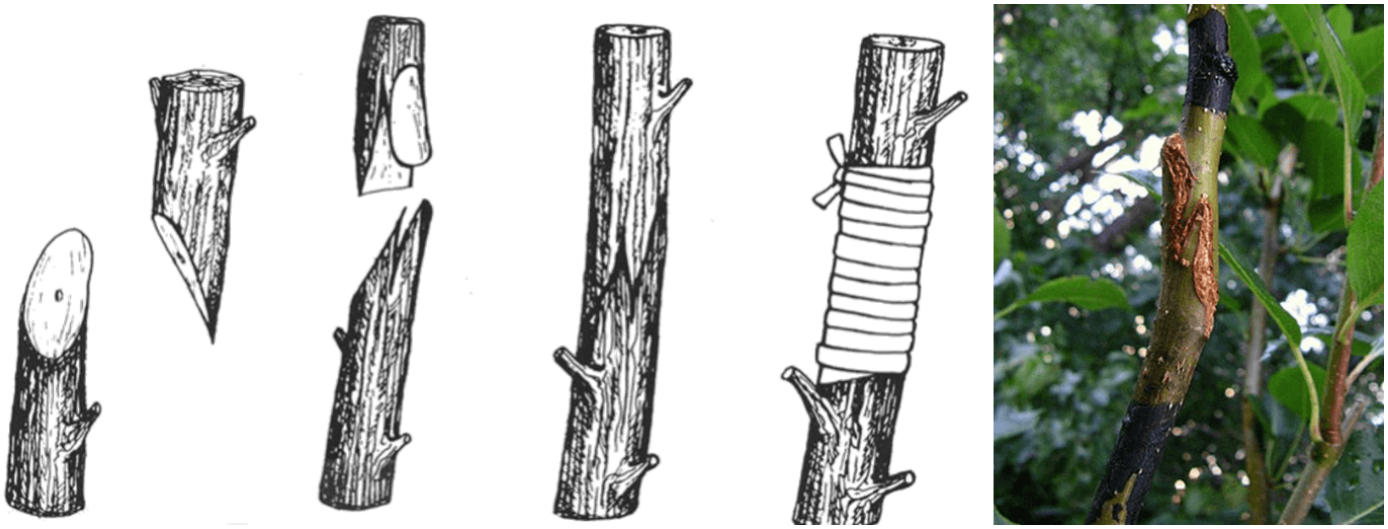


Figure 9-39. Whip grafting (left). A successful whip graft (right). Long Description: Line drawings of whip grafting showing matching angled cuts on the scion and rootstock, which are fitted together and wrapped. At right, a photo of a healed whip graft on a young tree. (By Chris Hibbard - I (Chris Hibbard, acct: chrishibbard7) created this work entirely by myself., GFDL, Link to Source [commons.wikimedia.org])

Bridge grafting: Bridge grafting is a technique used to repair trees by grafting scion material above and below the damaged area of the trunk. The bridge grafts help transport nutrients and water past the damaged area so the tree can recover. Bridge grafting

can restore growth to a tree section that would likely have died from significant damage without grafting.

In Figure 9-40, the diagram on left shows an example of how this works. A young tree was girdled by mice. Item B shows that tree's trunk after the wound has be cleaned and the bark along the margin of wound trimmed back to healthy wood. Item C show the scion wood with tapered end ready for insertion. Item D shows a cut-away, with scions inserted beneath the health bark ("w" mark insertion point). Item E show the multiple scions in place and ready for waxing. The wax seals pathogens and water that might lead to rot. The scions act like hoses to allow the flow of water from the roots to the shoots and the flow of nutrients in both directions. The scions, as living wood, grow with the tree and eventually their bark merges with that of the original tree (Figure 9-40, *right*).

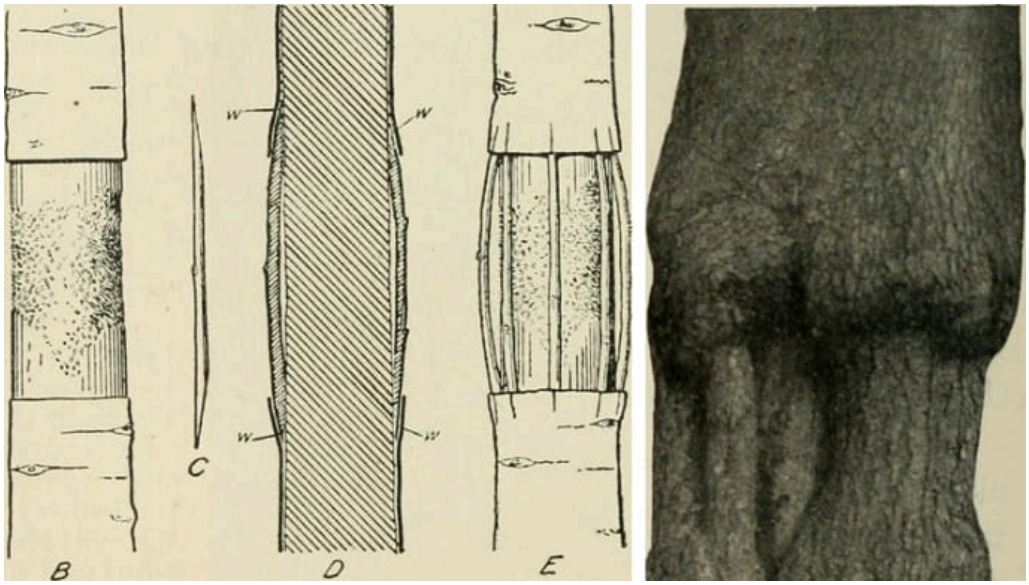


Figure 9-40. Diagram showing technique for using bridge-grafting to repair a girdled tree (left). Tree with old bridge graft repair (right). Long Description: Left: diagram of a bridge graft, with scion pieces inserted under the bark above and below a girdled band of trunk. Right: an old tree trunk with bulging, healed bridge grafts spanning a damaged area. (Left – J. of the Dept of Agric. South Africa, 1920; archived at Link to Source [www.flickr.com]; Right -Maine, Dept of Agriculture. 1903-1940); archived at Link to Source [www.flickr.com])

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9.4: End of Chapter Review

The ability to reproduce plants is fundamental to horticulture and agriculture. Propagation utilizes plants' innate capacity for both sexual and asexual reproduction. Humans have developed techniques that take advantage of natural reproductive processes and optimize them for our purposes. Whether growing food, ornamental plants, or environmental restoration, careful use of propagation allows the reliable perpetuation of species and cultivars with desirable qualities. Both ancient and modern practices enable efficient reproduction on scales from the home gardener to industrial agriculture. Continued innovation promises propagation techniques that are even more accessible, productive, and sustainable. Our skill at propagation helps fulfill human needs today and provides hope for meeting the challenges of tomorrow.

Chapter Summary

- Propagation refers to creating new plants, either from seeds (sexual reproduction) or vegetatively (asexual reproduction).
- Propagation by seed takes advantage of seeds' ability to produce new plants. Benefits include lower cost, wider variety availability, and ability to save seeds. Important considerations are seed sources, quality, storage, pretreatments like stratification and scarification, and proper sowing techniques.
- Vegetative propagation uses plant parts like stems, leaves, or storage organs to produce clones of the parent plant. Methods include cuttings, layering, division, and grafting. These maintain desired traits and allow quicker maturity than seed propagation.
- For woody plants, softwood, semi-hardwood, and hardwood stem cuttings are taken at different times based on growth stage. Herbaceous cuttings can come from stems, leaves, etc. Layering involves encouraging root growth before separating the new plant.
- Bulbs, corms, tubers and rhizomes can be divided into sections with meristem tissue to generate new propagules. Crown division splits the crown of perennials into sections with roots and buds.
- Grafting joins the top growth (scion) of one plant onto the root system (rootstock) of another. This combines desired aboveground traits with adaptive root traits. Methods include budding, cleft, whip, and bridge grafting.
- Careful use of propagation techniques allows efficient reproduction of plants with particular qualities. Both sexual and asexual methods are important for horticulture and agriculture.

Key Terms

- Adventitious roots
- Asexual reproduction
- Bulb
- Cambium
- Crown division
- Cutting
- Grafting
- Layering
- Propagation
- Propagule
- Rhizome
- Rootstock
- Scion
- Sexual reproduction
- Tuber
- Vegetative reproduction

Self-Review

1. What are the main advantages of propagating plants from seed?
2. How can you test the viability of older seeds before planting them?
3. What does stratification and scarification do to prepare seeds for germination?

4. What are some differences between direct seeding and using transplants?
5. What is hardening off and why is it important?
6. How do vegetative propagation techniques produce new plants asexually?
7. What are the differences between softwood, semi-hardwood, and hardwood cuttings?
8. When is the best time to take stem cuttings from herbaceous plants?
9. What are the steps involved in air layering?
10. How can bulbs and corms be propagated by sectioning or scoring?
11. What is an important consideration when dividing perennial crowns?
12. What are some reasons grafting is used in horticulture?
13. How does T-budding allow new plants to be grown?
14. What is whip grafting and when might it be used?
15. What is the purpose of bridge grafting on damaged trees?

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10: PRODUCTION SYSTEMS



Sod farm in Sumter County, Georgia. (Stephanie Harvey. 2025. CC-BY-NC)

Agriculture is fundamental to human civilization, providing food, fiber, fuel, and other goods. Over thousands of years, humans have developed various methods and technologies for cultivating crops and livestock. This chapter examines four major types of agricultural production systems: traditional methods, greenhouse, plasticulture and hydroponics.

10.1: Traditional Agricultural Methods

10.1.1: Subsistence Agriculture

10.1.2: Home Gardening

10.1.3: Semi-Intensive Mixed Commercial

10.1.4: High intensive Commercial Agriculture

10.1.5: Cultural Techniques in Traditional Agriculture

10.2: Plasticulture

10.2.1: Plastic Mulch Films

10.2.2: Polythene Greenhouses

10.2.3: Other Uses of Plastics in Production Systems

10.3: Hydroponics

10.3.1: Bag and Deep Water Culture

10.3.2: Ebb & Flow and Nutrient Film Techniques

10.3.3: Benefits and Limitations to Hydroponics

10.4: Other Cropping Systems

10.4.1: Raised Bed Gardening

10.4.2: Straw Bale Culture

10.4.3: Permaculture

10.5: End of Chapter Review

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10.1: TRADITIONAL AGRICULTURAL METHODS

Since the origins of agriculture 10,000+ years ago, traditional techniques have formed the foundation of crop production. Traditional crop farming utilizes techniques like seed selection, tillage, irrigation, crop rotation, and pest control. Within this method there are four categories that are typically recognized based upon the degree of market integration and specialization: subsistence, home garden, semi-intensive (mixed commercial) and very intensive commercial productions. These categories include end targets for produce, operational size, and investments in terms of chemicals and equipment.



Edge of Corn Field with Central Pivot Irrigation. (Stephanie Harvey. 2026 CC-BY-NC)

10.1.1: Subsistence Agriculture

10.1.2: Home Gardening

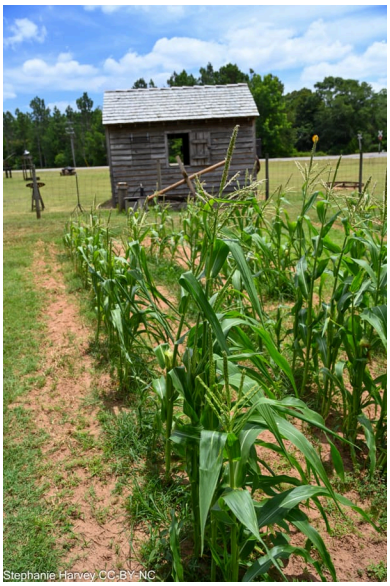
10.1.3: Semi-Intensive Mixed Commercial

10.1.4: High intensive Commercial Agriculture

10.1.5: Cultural Techniques in Traditional Agriculture

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10.1.1: Subsistence Agriculture



Corn growing in small family farm as part of the Jimmy Carter Boyhood Farm, in Plains, Georgia. (Stephanie Harvey. 2024. CC-BY-NC)

Subsistence agriculture is one of the oldest and most prevalent farming systems worldwide. It is found mainly in developing regions like sub-Saharan Africa, parts of Asia and Latin America. Subsistence farms aim first and foremost to feed the farmer's household and provide fodder for dairy and work animals. Some products may be bartered to obtain items they cannot produce, but very little if any monetary exchange occurs.

Typically, subsistence farming operations are small 1-2-hectare plots that focus on production of a set of traditional crops. Staple grains like rice, wheat, or maize provide the main caloric intake. The selected crops grow well in their environment with minimal external additions. Farmers supplement with vegetables, fruits, pulses, and livestock if space allows. Fields may be prepared with hand tools like hoes or ploughs pulled by animals. Seeds are saved, selected, and replanted each season. Organic waste provides the primary fertilizer. Pests are managed by crop rotation, natural pesticides, and manual removal.

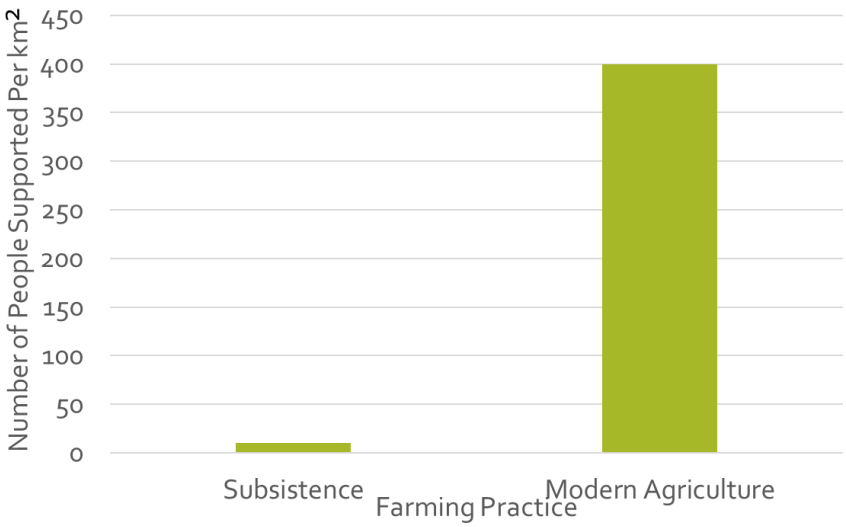


Figure 10-1. Approximate number of people supported per square kilometer under subsistence farming versus modern agriculture. Subsistence value based on densities reported for fallow farming systems (Pingali & Binswanger, 1984, after Boserup, 1981); modern value calculated from global cropland area (FAO, 2025) and world population. Long Description: Bar graph with the number of people supported per km-squared of farmland on Y-axis. The X-axis compares subsistence and modern agriculture. Subsistence agriculture supports 10 people per km-squared. Modern agriculture supports about 400 people per km-squared.

Subsistence farming is highly labor-intensive. Entire households engage in daily tasks like tilling, planting, weeding, and harvesting. Yields per hectare tend to be low due to limited mechanization and nutrient inputs (Figure 10-1). But subsistence models are resilient, diverse, and well-adapted to local conditions. Many subsistence farmers still rely on traditional practices that sustained their ancestors for generations.

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10.1.2: Home Gardening

Home gardens represent small-scale agriculture occurring near family dwellings. These integrated multi-crop systems are found across Latin America, Africa, Asia, and the Pacific. Home gardens typically combine vegetables, fruits, herbs, spices, and medicinal plants with livestock raising and aquaculture. Their purpose is to supplement the food sources and to some extent family income. Crops grown are often higher value horticultural crops. These gardens are not meant to provide all the food needed by a family group but to contribute to the family's diet and income. It provides both financial security and aids in survival through lean times.

Plots average around 0.5 hectares but may expand right next to the home or extend for several kilometers. Soil fertility is enhanced using compost, manure, and nitrogen-fixing plants. Diversified cropping provides food year-round while minimizing pests. Livestock like chickens, small ruminants, cattle, and fish provide additional protein. Home gardens satisfy household nutritional needs and generate supplemental income through sales at local markets. In India, home gardens enhance family incomes on average as much as 20-30% (Figure 10-2).



Figure 10-2. Local market sales can enhance family income. (By Kalamazadkhan - Own work, CC BY-SA 3.0, Link to Source [commons.wikimedia.org]).

This integrated approach maximizes production from limited land. The diversity of crops and livestock promotes ecological resilience against weather, pests, and diseases. Home gardens also conserve genetic resources and traditional knowledge. Women often manage home gardens, providing food security and autonomy. But like subsistence systems, home gardens have low mechanization and potential for expanded commercial production.

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10.1.3: Semi-Intensive Mixed Commercial

As smallholder farmers gain access to markets, many shift toward semi-intensive commercial production. These mixed systems combine subsistence crops with high-value cash crops for sale. Farm sizes may remain under 2 hectares but are intentionally managed to generate income.

Family labor continues providing much of the workforce. Some mechanized tools like two-wheeled tractors may supplement hand tools for plowing and harvesting. While staple grains are still grown for subsistence, a portion of land is allocated to cash crops like fruits, vegetables, teas, or flowers. Livestock production expands into small-scale aquaculture, poultry, sheep, and dairy.

Farmers purchase some commercial inputs like fertilizers, pesticides, feed supplements, or propagules. Yields increase from both semi-intensive techniques and genetic improvements. Farmers sell produce through cooperatives, contracts, or local vendors. Additional income allows investments in education, healthcare and expanded production. Mixed systems thus bridge subsistence activities with market participation.

However, smallholder commercial agriculture remains limited by land constraints, financial barriers, and inaccessible distribution networks. Farmers may struggle to consistently produce surplus crops that meet market standards. Semi-intensive systems are also vulnerable to volatile market prices. Most use traditional techniques that require extensive physical labor for land preparation, planting, weeding, and harvesting. Yields tend to be lower compared to modern industrialized farming. But many smallholder farmers worldwide still utilize traditional methods due to their low cost and independence from external inputs.

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10.1.4: High intensive Commercial Agriculture

As agriculture becomes fully commercialized, systems transition toward specialized large-scale production of high-value commodities. High-intensive commercial agriculture present maximize efficiency in terms of cost of land and labor. Large intensive farms exceed 50-100 hectares on average. They specialize in productions of only a few crops at high densities. Major crops include **cereals** like maize, wheat and rice grown for national and global markets. Vegetable, fruit, and nut crops require advanced irrigation systems and year-round labor. The system requires more equipment to minimize time and labor from seeding to harvest. There needs to be multiple supporting industries for these types of systems to work, and farmers need to understand economics and their target consumers.

Here is an example of what is meant by "support industries". Cereal crops are typical of large-scale agricultural practices (Figure 10-3). These systems rely heavily on industrial methods and must have supportive industries as mentioned previously. For example, the grower will need to purchase large quantities of high-yielding seed. This goes beyond the ability to “save-seeds” as is seen in both subsistence and home garden systems. To synchronize harvest, planting needs to be synchronized. For large acreage this requires equipment such as grain drills as the seeds for an entire field need to be sowed within a short window or else the crop will mature at different times. Irrigation systems are typically employed to ensure crop success even when the weather is not cooperating. There is too much financially riding on the crops to leave water to chance. The system requires chemical inputs such as fertilizers, herbicides, and pesticides to yield greatest quantities, at the highest quality. When harvesting a day or two delay can significantly impact yields in some crops. Use of combines for harvest necessitates that the crops mature at the same time as mentioned earlier. And lastly, once the harvest is made, it has to be stored, transported and disseminated to buyers. Based on all this you can surmise that the support industries include – farming production equipment, agro-chemical industry, storage facilities such as cold rooms, controlled atmospheric storage and grain silos, transportation to markets and distribution centers to handle selling large volumes.



Figure 10-3. High-intensive production of cereal crops is common. (By Dag Endresen, CC BY 3.0, Link to Source [commons.wikimedia.org])

Mechanization is extensive across the production chain. Gasoline/diesel tractors and implements allow large-scale tillage, planting, and chemical application. Automated drip irrigation and climate control optimizes growing conditions. Harvesting equipment and grain conveyors reduce labor needs. Genetically engineered crops also increase yields. Farm employees provide most of the arduous manual labor. These highly specialized operations supply agricultural commodities to downstream distribution, processing, and retail networks.

Intensive systems are extremely productive (Figure 10-1), generating surpluses for national and international markets. However, they require substantial capital investments in land, equipment, supplies and labor. Input costs and product prices fluctuate significantly. Intensive production can damage long-term soil health and pollute groundwater. And specialized large-scale farms depend heavily on petroleum, finance, and export markets, making them vulnerable to changing costs and demand.

Intensive production systems typically operate in **monoculture**. That is the production of a single cultivar on large acreage. While it makes for efficient farming production – sowing, fertilizing, harvest, and marketing – it can also lead to problems. In such circumstances, there is low biodiversity. This means that the plants are all competing for the same group of nutrients uniformly. Additionally, it can lead to increase levels of disease and pest due to the reoccurring presence of a host crop. Synthetic fertilizers and pesticides sustain monoculture production despite depleted soils and resistant pests.

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10.1.5: Cultural Techniques in Traditional Agriculture

Crop Rotation

There are records back in the 16th century describing the benefit of **crop rotation**. This practice helps ameliorate some of the issues associated with monoculture. The practice involves swapping crops in a field through 3- or 4-season rotations. Obviously, the grower wants to plant crops that will increase his/her revenues but continue growth of a cash crop will lead to diminished returns as soil fertility drops and pest and disease occurrences increase. Several considerations must be considered when determining what the rotation will be. A preliminary assessment of crop interrelationships can be found in how each crop: (1) contributes to soil organic matter (SOM) content, (2) provides for pest management, (3) manages deficient or excess nutrients, (4) how it contributes to or controls for soil erosion, (5) interbreeds with other crops to produce hybrid offspring, and (6) impacts surrounding food webs and field ecosystems.

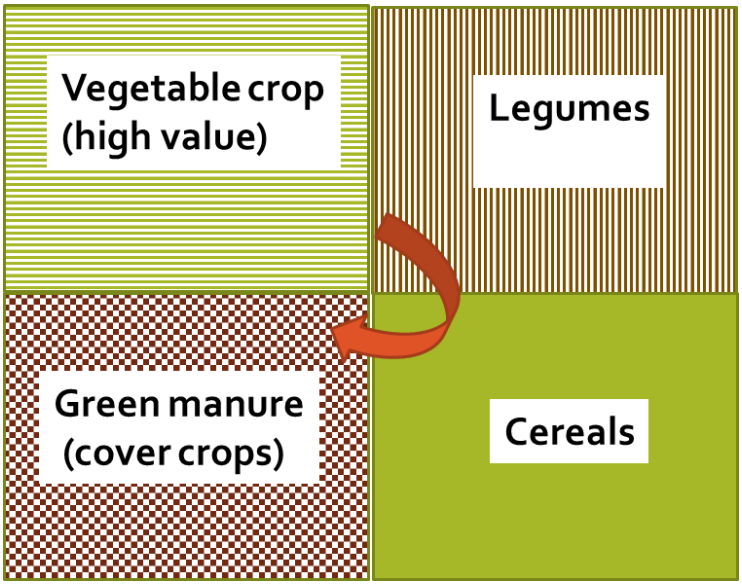


Figure 10-4. Diagram showing a crop rotation plan. Long Description: A diagram of a crop rotation through four fields that comprise a square. Upper left field has vegetable (high value) crop while upper right has a legume crop. Lower right has cereals and lower left is a green manure (cover crop). Rotation is clockwise. (Stephanie Harvey. 2019. CC-BY-NC).

A typical rotation (Figure 10-4) involves high value crop, followed by a legume crop (replenishes nitrogen). This is then followed by a cereal crop and finally a cover crop (ideally green mature). **Green manures** are grown as covers where they prevent erosion when land is not cropped. Then prior to planting the next crop, the cover is plowed into the field to increase organic matter and general nutrient levels.

Intercropping

It is critical for a grower to maximize yield per unit area. With some crop, such as perennial tree crops, a significant amount of space is required to support the health of the trees. While the tree crop is young (and perhaps not producing yet) there is lost income and potential for soil erosion if there is no ground cover between the trees. Intercropping can help with this issue. It is the production of multiple crops in the same area at the same time. In Figure 10-5, *Tagetes erecta* (Aztec marigold) is a planted understory to the coconut trees. This maximizes utilization of growing area and can keep workers in jobs off-peak seasons.



Figure 10-5. Tagetes erecta (Aztec marigold) is planted understory to the coconut trees. (Ezhuttukari. CC BY-SA 3.0, Link to Source [commons.wikimedia.org])

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10.2: PLASTICULTURE

Plasticulture is a modern approach to crop farming that utilizes plastic materials to improve conditions. Some of the main plasticulture techniques include plastic mulch, drip irrigation, insect netting, and greenhouse shelters. The term is often extended to include nursery pots and silage bags. However, it is most often used in reference to the covering of soil with plastics films.

10.2.1: Plastic Mulch Films

10.2.2: Polythene Greenhouses

10.2.3: Other Uses of Plastics in Production Systems

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10.2.1: Plastic Mulch Films

The standard practice for use of **plastic mulch films** includes the formation of a raised bed (Figure 10-6). Soil is formed into a hill that sits slightly above the surrounding field. Plastic is pulled over the bed tightly and held in place with soil sealing the edges. As the plastic is laid, a drip irrigation tube is also placed under the plastic. The position of it is determined by how the plants are inserted into the formed bed. Transplants can then be placed into the bed in a single row with the tubing on one side. If planting a double-row on the hill, the tubing can be placed between the plants. The configuration will depend on the crop. The soil bed provides room for the roots to grow, and the irrigation tube provides a water source.

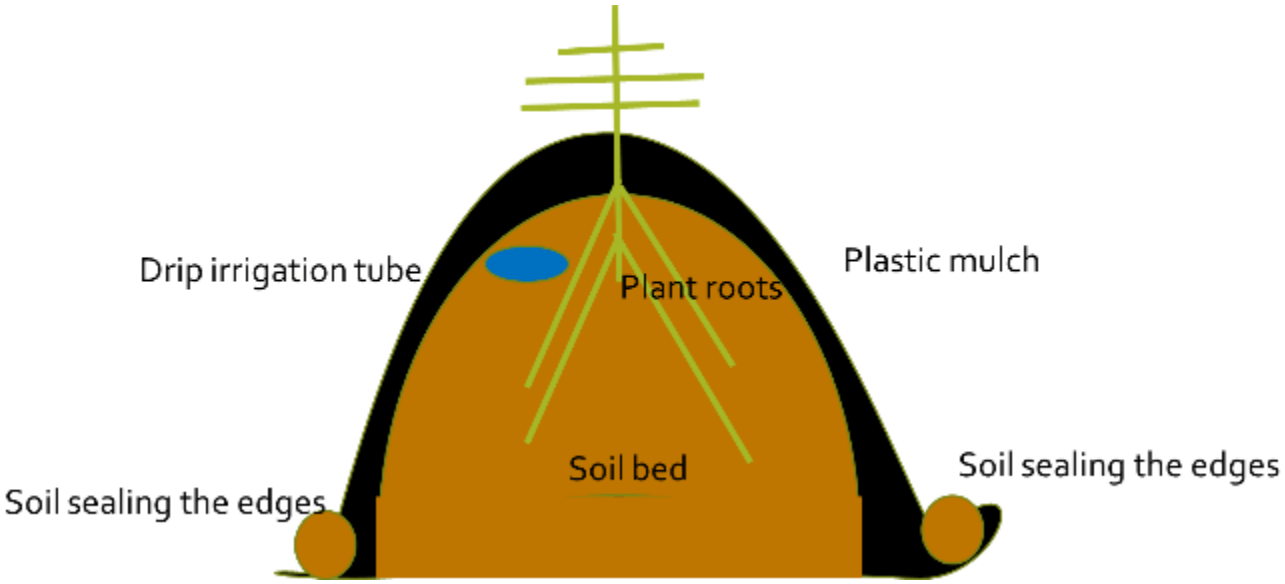


Figure 10-6. Diagram showing the relationship between soil, plant, *irrigation,* and plastic film. Long Description: Diagram showing how plastic mulch film is used. Soil is mounded. Plastic mulch film is stretched over mound with a drip irrigation tube placed just under and slightly to one side of mound. Plants are then inserted along the top of the mound. (Stephanie Harvey. 2019. CC-BY-NC)



Figure 10-7. Plastic film over the soil *protects* strawberry fruit from pathogens. Long Description: A field of strawberries growing in plastic mulch film beds. Ripening berries can be seen lying on the plastic covering rather than soil. (By Bn100 - Own work, Public Domain, Link to Source [commons.wikimedia.org])

There are many benefits to using plastic mulch. One benefit is that it speeds up the warming of the soil in early spring, thus bringing the soil temperatures up to those optimal for the crop's growth. This warmth can minimize the time from sowing to

harvest. Hilling the soil also has the benefit of improving drainage. Spring rainfall can delay planting when fields are too wet. The raised nature of the hills allows it to dry more quickly. The plastic cover also helps to minimizing evaporation during the growing season. Water released by the drip tubes is trapped under the plastic and is more available for plants. The mulch also helps with minimizing erosion in fields following heavy tillage. The plastic also helps maintain crop sanitation. The barrier created between the soil and delicate fruits, such as strawberries (Figure 10-7), can limit exposure to soilborne pathogens. It also keeps the fruit cleaner which is appealing for fresh market production.

A significant amount of research has been completed on the use of both clear and pigmented films and has found some benefits and disadvantages (Figure 10-8). The most common films are black. They stop light penetration and prevent weed growth since most weed-seeds germinate when exposed to sunlight. It also does not overheat the soil, which under high light intensities is important. Clear films transmit light so the soil heats up quickly in the spring but weed can germinate below the plastic. Additionally, at the high solar intensity of summer, temperatures can get high enough under the clear films to damage roots. There is some research that suggests some colored plastics can enhance ripening for specific crops. For example, red plastic has been shown to increase fruit color in tomatoes.



Figure 10-8. Different colors of plastic mulch are used. (cc-by-sa/2.0 - © Stephen Middlemiss - geograph.org.uk/p/3955031; Link to Source [www.harrisseeds.com]

The use of plastic films as row covers requires some specialized equipment (Figure 10-9). The equipment, pulled behind a tractor, performs several jobs at the same time. A series of blades form a bed by pushing soil to the center. As it moves along, plastic is pulled tightly over the bed. Two rear blades seal the edges of the plastic to keep it taut and minimize encroachment. Near the front of the attachment (not seen in Figure 10-9) is a roll of drip tape that is laid under the plastic as well. When complete the two ends are covered and the drip-tape attached to an irrigation system.



Figure 10-9. Equipment for creating raised, plastic mulched beds. Rain-Flo Model 2670 Series ii Raised Bed Mulch Layer. (Link to Source [www.rainfloirrigation.com])

Once the beds are made, transplants (plugs) can be inserted. This can be done by hand, cutting holes in the plastic and then inserting the plug. For larger fields, a **water wheel transplanter** can be used for setting plugs through plastic mulch (Figure 10-10). This tractor attachment has a metal planting wheel with spikes. As the tractor moves over the hill the spikes on the planting wheel pierce the mulch (plastic) and fill the hole with water (with a starter fertilizer) from an onboard tank. Operators riding close to the row can then hand set the plants into holes at the proper depth. Depending on the crop transplanted wheels with different arrangements of spikes can be used to control planting distance.

The benefits of plasticulture include increased yields, improved crop quality, extended growing seasons and more efficient water usage. It is cost prohibitive to use it on all crops and it is typically reserved for high value horticultural crops that, for various reasons, benefit from it use. Additionally, plasticulture has major drawbacks as well. Plastic mulch and other materials are derived from petroleum. They must eventually be removed and discarded, leading to environmental pollution. The high costs of installation and plastic disposal may make plasticulture prohibitive for smallholder farmers. Critics also argue that plasticulture makes agriculture more reliant on fossil fuels. There has been some effort to recycle the plastic and research into production of biodegradable plastics from non-petroleum sources.



Figure 10-10. Water Wheel Transplanter with a wheel that creates a double row of closely spaced plants. Long Description: Tractor pulling a water wheel transplanter. Four people, seated on attached seats, insert transplants into holes created through the plastic film. (screen capture from Link to Source [www.facebook.com])

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10.2.2: Polythene Greenhouses



Figure 10-11. Polythene greenhouses (polytunnels) at a commercial nursery. (By Derek Harper, CC BY-SA 2.0, Link to Source [commons.wikimedia.org])

Polythene plastic sheeting greenhouses (polytunnels) are a common sight in modern agriculture (Figure 10-11). Polythene, also known as polyethylene plastic, is used to cover greenhouse frames made of wood or metal. The plastic sheeting allows sunlight to penetrate while trapping heat and providing insulation. This allows farmers to control the growing environment and grow crops year-round, even in colder climates.

Polythene greenhouses are relatively inexpensive and simple to construct. The frame is typically made using lumber, steel pipes, or aluminum. The frame sections are joined together to form the desired greenhouse shape - often an arched roof shape to maximize sunlight exposure. The frame is anchored securely to the ground. A layer of polythene plastic sheeting is spread over the greenhouse frame and attached with clips, tape, or cord. The plastic sheeting comes in large rolls in thicknesses ranging from 80 to 250 microns. Thicker plastic is more durable and insulating. An additional layer of plastic may be added for increased insulation and in colder climates air is pumped between the layers for added insulation.

Ventilation is important in greenhouses to allow air flow. Vents and fans are usually installed in polythene greenhouses to regulate temperature and air circulation. Automated vents, fans, and climate control systems are sometimes added in more high-tech greenhouses. Doors and end walls may be left open or closed depending on the weather and crop needs. Roll-up sidewalls allow the greenhouse space to be opened up fully when weather permits. Shadecloth or whitewash may be applied to the plastic sheeting to reduce heat on hot sunny days.

Polythene plastic greenhouses allow growers to control and optimize the plant growing environment. Key advantages of polythene greenhouses include:

- Temperature Control - The enclosed space warms up during the day while preventing heat loss at night, allowing crops to grow in colder months.
- Protection from Weather - Plastic sheeting protects plants from frost, wind, rain, and hail damage. Crops stay cleaner and drier.
- Improved Growth Rates - The favorable growing conditions lead to faster plant growth and potentially higher yields.
- Extended Growing Season - Growing seasons can be extended into cooler months, allowing for multiple harvests per year.
- Protection from Pests - Enclosing crops provides protection from insect pests, rodents, and birds. However, greenhouse hygiene is important to prevent build-up of pathogens.
- Reduced Water Use - Evaporation is reduced compared to open field agriculture, resulting in lower water demands. Drip irrigation is often used.

Polythene greenhouses are used globally to grow vegetables, fruits, flowers, and other crops. They allow crop production in spaces and climates that would otherwise be unsuitable for agriculture. With optimal growing conditions, polythene greenhouses can improve yields and provide local supply of fresh produce. However, they do require investment in construction and maintenance. The polythene ages and becomes opaquer over time. This reduces solar input and lowers growth and productivity. Plastic sheeting is more susceptible to physical damage as well. Hail, high winds, and heavy snows can easily compromise the structure. Other materials such as glass or polycarbonate sheets can be used for greenhouses. They are more expensive but can lower long-term maintenance cost.

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10.2.3: Other Uses of Plastics in Production Systems

Floating row covers are lightweight, spun, or woven plastic, polyester or polypropylene materials that form sheets. These fabrics are permeable to light, water, and air. These can be placed over plants to exclude pest (Figure 10-12a). To prevent infestations, covers should be installed at planting. Pests that emerge from the soil, however, can be trapped in with the plants, so care must be taken not to use them in fields where these types of pest are prevalent.

Covers can also extend the growing season. Depending on the weight of the covering used, gains between 2 and 8 degrees can be achieved. This can provide frost protection or warm the local environment sufficiently to harvest certain crops a week or two early. When combined with other cultural practices (for example, planting on a south-facing slope) the potential for early planting and harvesting can be profitable.



Figure 10-12a. Floating row cover protects lettuce plants. (Link to Source [hort.extension.wisc.edu])

Floating row covers can be laid directly over low-growing, flexible crops. Just be sure to leave enough slack when covering rows so the cover can expand as the crop grows. You have to bury the edges completely if you are using floating row cover for pest exclusion. If you are not using it to keep bugs out, you may use anything with weight to hold down the edges. For some crops it may be necessary to support the cover material on hoops. PVC pipes are easy to bend and stick in the soil to create a framework over which to drape the row cover. Since the cover modifies the climate, it is important to remove covers gradually to harden off the crop. A cloudy day works great for the final removal. Fabrics can be stored and reused. If left in direct sunlight, fabric will degrade overtime due to UV exposure.

Silage bag are heavy-duty, multi-layer polyethylene tubes used to store and ferment livestock feed, grain and other agricultural byproducts in an airtight environment. This protects the nutritional value and minimizes dry matter loss over conventional storage. The exterior of the bags are typical white to reflect sunlight and keep internal temperature stable, while the interior is black to block light and maintain dark conditions (Figure 10-12b).



Figure 10-12b: Individual bales wrapped in specialized polyethylene bale bags long field edge in Norway. (Stephanie Harvey. 2025 CC-BY-NC)

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10.3: HYDROPONICS

Hydroponics is the method of growing plants without soil, using mineral nutrient solutions in water. The roots are suspended in the nutrient solution which provides all the elements required for plant growth. Hydroponics is considered a subset of soilless culture, which may use mediums such as perlite, gravel, mineral wool, and coconut coir to provide mechanical support. Due to high infrastructure costs, hydroponics tends to be most economically viable for high value vegetable and ornamental crops. The premium prices of produce like tomatoes, cucumbers, lettuce, herbs, and flowers can offset the production expenses. Hydroponics has gained popularity as a viable system for commercial crop production as well as for hobbyists.

While plants normally grow in soil, it has been demonstrated since the 17th century that plants can grow normally when their roots are immersed in a nutrient solution. The first scientific study of nutrient film technique, a hydroponic method, was published in 1929 by William Frederick Gericke of the University of California at Berkeley. Gericke coined the term hydroponics, from Greek words meaning "water working." In the 1950's-60's, NASA and the U.S. Army helped popularize hydroponics by using it to grow fresh vegetables for astronauts and troops stationed on un-farmable islands. By the 1970's hydroponics had emerged as a viable commercial farming method, with large greenhouse farms established in Holland, Spain, Israel, Australia, and North America. While hydroponics is not suitable for many major field crops, it has become a specialized technique for producing high-value vegetable and ornamental crops.

10.3.1: Bag and Deep Water Culture

10.3.2: Ebb & Flow and Nutrient Film Techniques

10.3.3: Benefits and Limitations to Hydroponics

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10.3.1: Bag and Deep Water Culture

There are two main types of hydroponic systems: liquid systems which use no medium, and aggregate systems which use an inert medium to provide mechanical support. Common media include perlite, vermiculite, coco coir, gravel, sand, peat, and sawdust. These media help buffer the plant roots from dramatic shifts in pH and nutrient concentrations in the solution. The inert media provide anchorage and moisture retention while allowing oxygen diffusion to the roots. Systems can also be categorized as either open systems or closed systems. In open systems, once the nutrient solution is delivered to the plant roots, it is not reused. In closed system, surplus nutrient solution is recovered, recycled, and periodically replenished.

Bag culture is a type of aggregated hydroponics that uses a plastic bag or sack as the growing container (Figure 10-13). The bag is filled with an inert porous growing medium like perlite, vermiculite, coconut coir, pine bark or even shredded Styrofoam. The nutrient solution is delivered into the bag and allowed to wick through the medium to the plant roots.



Figure 10-13. Indeterminate cherry-tomato plants grown in bag culture. (Link to Source [risehydroponics.in])

There are several advantages to bag culture hydroponics. The bags are lightweight compared to other containers, making handling and transport simpler. The bags allow the entire root system to be moved. Plants can be shifted to follow the sunlight, to adjust spacing with growth or for pest/disease control. Bags come in a range of sizes from 1 gallon to over 100 gallons to fit different horticultural needs. These plastic bags are an inexpensive container option compared to pots or troughs. The medium can be reused too. Aeration is critical for root health. Depending on the medium used in the bag, this type of hydroponic can provide good aeration. For plant that do not handle “wet feet” (root submerged in water), this is a viable technique. With readily available nutrients, algae growth can be a problem in hydroponic system. The opaque bags prevent light from reaching the nutrient solution, inhibiting algae growth.

Bag culture systems require good drainage holes at the bottom of the bags. Drip irrigation or periodic flooding/drainage works well for wetting the medium. While other materials can be used for bags, the plastic helps retain moisture between irrigations and can withstand repeated wetting and pressure from the root ball. Since the nutrients are not recycled, less monitoring of the nutrient solution pH and **electrical conductivity (EC)** is needed. Each batch is freshly mixed so there is no concern of depletion. Overall, bag culture offers a flexible, low-tech, low-cost hydroponic method suitable for small and large-scale producers.

Deep water culture (DWC) is one of the most popular hydroponic techniques used by home and commercial growers. Also known as the reservoir method, DWC is a liquid, closed system that involves suspending plant roots directly into a container of oxygenated nutrient solution (Figure 10-14).



Figure 10-14. Deep water culture hydroponics with leaf lettuces. Long Description: Deep water culture raft supporting leaf lettuce plants. Raft has been lifted from float tank to show root growth beneath raft. (By Neitram - Own work, CC BY-SA 4.0, Link to Source [commons.wikimedia.org])

The central component of DWC systems is the reservoir, which is filled with the nutrient solution. Common containers used include plastic buckets, tubs, or trays of various dimensions. The reservoir should be opaque to block light and reduce algae growth. Plant pots or slots for net pots (net pots are containers pre-punched with small slits all over the sides and bottom) are incorporated in the reservoir lid or cover. This allows the roots to be submerged in the nutrient solution below while the shoot system is supported above. Clay pebbles, perlite, or vermiculite can be used as medium in the net pots (if so, system it technically aggregate).

A key aspect of DWC is oxygenation of the nutrients. One or more air pumps continuously provide air flow through air stones placed at the bottom of the reservoir. The rising bubbles oxygenate the solution and create circulation, providing excellent conditions for root development. The water level is maintained within a suitable range by adding fresh nutrient solution, normally on a weekly basis. The old solution can be drained and refreshed to avoid excessive salt buildup. The pH and EC (dissolved salts) of the solution must be monitored to ensure the nutrients remain optimal.

With direct root immersion and oxygenation, DWC allows rapid growth rates. The system facilitates easy root inspection and maintenance. Drawbacks include increased disease risk if hygiene is not maintained. Additionally, plants are sensitive to “wet feet” preform poorly in this system.

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10.3.2: Ebb & Flow and Nutrient Film Techniques

Ebb and flow, also known as flood and drain, is a closed hydroponic technique that uses intermittent flooding of the roots with nutrient solution. The system consists of a growing tray or table, reservoir, water pump, and timer. The reservoir stores the nutrient solution, while the pump is used to pump solution from the reservoir up to the elevated grow tray. The grow tray contains a medium like gravel, perlite, or rockwool to support the plants. Clay pebbles are a common choice as they provide excellent drainage. The tray is fitted with a stand or legs to hold it above the reservoir.

A timer controls the water pump, turning it on for brief periods to flood the upper tray with nutrient solution. The solution level rises up and submerges the lower portion of the medium and roots – the “flow.” After a set time, the pump shuts off, allowing the solution to drain back down into the reservoir- the “ebb.” This flood/drain cycle is repeated multiple times per day, typically for 15-30 minutes of flooding followed by 1-2 hours of draining. The wet-dry intervals promote ample oxygen availability for the roots between flood events.

The reservoir size is calculated to hold sufficient nutrient solution volume to completely saturate the grow tray during floods. The recycling reduces water usage and waste compared to open systems. The solution is monitored for pH, EC, and nutrient levels. As nutrient are depleted by the plants, the solution must be refreshed. This requires a good technical understanding of pH and EC.

Ebb and flow hydroponics provide a simple, scalable system that can accommodate various growing configurations. With proper management, it allows efficient delivery of water, nutrients, and oxygen to the plant roots.

NFT (nutrient film technique) is one of the most common hydroponic techniques used commercially. It involves channeling a thin film of nutrient solution along troughs or pipes in which the plant roots are suspended (Figure 10-15). The main components of NFT systems include a reservoir, submersible pump, piping network, and growing channels. The reservoir stores the nutrient solution which is pumped into the piping network.

The piping lines feed into multiple growing channels made of plastic or PVC. The channels are tilted at a slight angle, usually 1-3 degrees, to facilitate flow. Nutrient solution from the top of the channel flows down along the bottom in a thin film just a few millimeters deep before draining back into the reservoir.

Plants are placed in holes cut into the top of the channels or into slots for net pots. This positions the plant roots and crown within the channel while the shoot system grows above. The roots dangle into the flowing nutrient film, absorbing water and nutrients. The thin film provides a constant supply of water, nutrients, and oxygen to the roots. The solution is oxygenated in the reservoir before recirculating through the system. Additionally, since not all of the root mass is submerged, the exposed roots can extract oxygen from the air. Flow rates are adjusted to maintain the optimal nutrient film depth, typically with multiple cycles per day.



Figure 10-15. Kale grown in NFT system at Georgia Southwestern State University. Photo By: Stephanie Harvey. 2025. CC-BY-NC.

NFT systems provide excellent aeration and are relatively easy to monitor and maintain compared to other hydroponic methods. They are commonly used for lettuce, herbs, tomatoes, and other vegetables in commercial greenhouses. Overall, NFT provides a scalable, efficient hydroponic technique.

Other hydroponic techniques include:

- Wick system - uses capillary action in fibrous media like vermiculite to deliver nutrients passively to the roots.
- Drip system - nutrient solution is actively dripped onto roots via drip lines and a timer-controlled pump.
- Aeroponics - roots are misted with nutrient solution from spray nozzles.

Each system has advantages and drawbacks relating to aeration, humidity, pH shifts, ease of monitoring, and other factors that influence their suitability to different crops. The addition of environmental control systems can help maintain optimal temperature, light, humidity, and CO_2 levels.

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10.3.3: Benefits and Limitations to Hydroponics

There are a number of potential benefits that make hydroponics an attractive cropping system. With the ability to optimize the nutrients and growing conditions for a specific crop (or variety), improved growth rates and yields can be achieved. Waste of water and nutrients is limited even in open systems. For systems that recycle water and nutrients there is even less waste. After several season of planting directly in the soil, growers begin to see declines in growth and productivity due to soilborne pathogen. Instead of moving the greenhouse to a new location, they can go soilless to avoid the pathogens. Hydroponics allows for the growth of plants in areas unsuitable for traditional farming. Likewise, greenhouse hydroponics can allow for year-round production in any climate. Access to water and power is technically all that is needed. Additionally, some of the labor is reduced. Planting, weeding, harvesting can be simpler with no soil tillage needed.

With the ability to precisely control the root environment, hydroponics facilitates highly efficient and intensive crop production. Yields per unit area can be 10-25 times higher than conventional agriculture. With enclosed greenhouses, multiple crops per year are feasible. The premium yields and quality achieve higher prices for hydroponic produce.

While promising, hydroponics also comes with some limitations. In general, mother nature is cheaper. The capital outlay for equipment â€“ greenhouses, hydroponic systems, and environment controls â€“ can be high and there are ongoing energy and equipment maintenance cost. These systems rely on energy and equipment so power and equipment failures can disrupt growth or even lead to death. Additional hydroponics is not feasible for many field crops and grains.

Disease prevention and nutrient management are critical. Introduction to a pathogen in system or greenhouse can be devastating. Many of the same conditions that optimize plant growth also optimize growth of pathogens. Miscalculations when compounding the nutrient solution are unforgiving. There is little or no buffering. The highly artificial growing environment leaves little margin for error. Experienced management and monitoring are essential to maintain healthy growth.

While still a niche, hydroponics is becoming an increasingly important contributor to greenhouse vegetable production. The global hydroponics market is forecast to grow steadily at a compound annual growth rate of over 9% from 2022-2027. Hydroponics is most extensively used for tomatoes, cucumbers, peppers, lettuce, spinach, herbs, and microgreens. Hydroponics is also commonly used for flowers, potted ornamentals, and cannabis production. Larger commercial hydroponic farms utilize greenhouses over 10,000 m^2, often with fully automated control systems. Smaller hydroponic growers can be successful starting in spaces under 100 m^2. Indoor vertical farming using multi-level hydroponics is also gaining interest for urban food production (Figure 10-16).



Figure 10-16. Vertical cropping system. (By Valcenteu - Own work, CC BY-SA 3.0, Link to Source [commons.wikimedia.org])

As hydroponic technologies and knowledge improve, adoption rates are expected to increase, especially in regions with scarce farming land and water. However, hydroponics is unlikely to fully replace conventional soil agriculture for staple crops on a broad scale. It will continue serving a supplemental role in producing fresh specialty vegetables, fruits, and ornamentals.

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10.4: OTHER CROPPING SYSTEMS



Spring planting in straw bale culture. (Stephanie Harvey. 2026. CC-BY-NC)

10.4.1: Raised Bed Gardening

10.4.2: Straw Bale Culture

10.4.3: Permaculture

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10.4.1: Raised Bed Gardening

Raised bed gardening involves growing plants in mounded soil beds that are higher than the surrounding soil (Figure 10-17). Raised beds are typically contained by a frame or border made of wood, stone, or concrete blocks to keep the soil in place. They are an increasingly popular gardening method due to a number of benefits. By elevating the plant roots above ground level, raised beds allow for better drainage both downward through the soil and away from the plants. This prevents waterlogging issues. The loose, mounded soil heats up quicker in spring allowing for earlier planting. The frames also act as heat sinks absorbing warmth from sunlight.



Figure 10-17. Raised bed garden. (Local Food Initiative. Link to Source [flickr.com])

The compact form makes weeding, pruning, harvesting and other tasks simpler without having to tread over expansive garden areas. The elevated height makes gardening possible for those with mobility constraints. Beds can also be designed vertically on fences or walls. Generally, less stooping and bending are needed. Raised beds allow amendment with fresh brought-in topsoil, compost and fertilizers tailored to plant needs. Soil quality and nutrition are optimized. Beds are commonly 3-4 feet wide to facilitate access from both sides, with walkways in between. More plants can be grown per square foot compared to traditional row gardens. Additionally, separating plants from surrounding soil disrupts some pest/disease cycles and can deter fungi and root rot.

Raised beds do require proper construction and annual filling with new soil or compost. Irrigation systems like drip lines or soaker hoses are ideal. Overall, raised bed gardening is a flexible option that enhances productivity and ergonomics.

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10.4.2: Straw Bale Culture



Figure 10-18. Straw bale *culture at Georgia Southwestern State University. Photo: Stephanie Harvey. 2025. CC-BY-NC.*

Straw bale gardening involves using straw bales as the growing medium to cultivate plants and vegetables (Figure 10-18). The concept was pioneered in the 1980s by Joel Karsten as a low-cost gardening method suitable for limited space. The technique involves setting up straw bales on a well-draining surface, then conditioning them by adding nitrogen fertilizer and watering over a period of 10-14 days. This facilitates microbiological activity and decomposition within the bale, generating heat and converting the straw into a suitable growing medium.

Once conditioned, the bales are ready for planting. For vegetables and annuals, holes are cut into the top surface of the bale and filled with compost or potting mix to support the transplants or seeds. For larger perennial plants and shrubs, the entire bale can be used as the planting base. A typical bale provides approximately 1.2-1.5 m^2 of growing area. The bales are normally arranged in rows or a grid layout with aisles between. Drip irrigation tubing is set along the tops of bales to provide regular watering and soluble fertilizer application.

Straw bales offer good drainage and aeration for healthy root growth. As the straw breaks down, nutrients are released to feed the plants. Weeding and pest issues are minimized. At the end of the season, the bales make excellent compost or can be used as mulch.

Advantages of straw bale gardening include efficient use of space, earlier warming of root zones, and reduced weeding/pest pressure. However, regular irrigation is needed, and some find the initial conditioning process difficult. Overall, straw bale culture offers a unique and sustainable gardening method. For more information: Gardening with Straw Bales from the University of California.

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10.4.3: Permaculture

Permaculture is an ecological design system for sustainable living and agriculture. Permaculture gardens aim to create stable, resilient systems that provide human needs while regenerating the environment. The key principles of permaculture gardening include:

- Observing and cooperating with natural patterns and cycles rather than fighting them
- Using and valuing diversity of plants, animals, structures, and landscapes
- Maximizing useful connections between system components
- Utilizing renewable resources and energy whenever possible
- Applying self-regulation and accepting feedback

Permaculture gardens are carefully designed to suit the local climate and environment. Placement of elements is key. Zoning organizes components according to use frequency and needs. Structures and plants are positioned to maximize energy and resource efficiency. Integrated water collection, graywater reuse, and water-wise irrigation help conserve water. Soil health is maintained through composting, mulching, intercropping, and reduced tillage. Food forests with edible polycultures provide sustainable yields. Features like food-producing vines on fences, bees supporting pollination, and chickens grazing under fruit trees demonstrate permaculture's emphasis on beneficial relationships. Adaptive management and continual improvement are employed.

Permaculture offers an ethical, whole-systems approach to create productive and ecologically sound gardens. It aims to move away from intensive resource use towards designing regenerative human habitats. The principles can be applied in backyards or on any scale.

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10.5: End of Chapter Review

Chapter Summary

In summary, this chapter covered major production systems ranging from ancient to modern techniques. It highlighted how cultural practices, plasticulture, hydroponics, and permaculture can enhance yields, resource efficiency, and environmental sustainability in agriculture.

- Traditional agricultural methods like crop rotation, intercropping, and green manures have sustained agriculture for millennia. Subsistence farming focuses on household food needs, while home gardens supplement nutrition and income. As small farms commercialize, they shift to mixed or high-intensive systems.
- Plasticulture utilizes plastic mulch, drip irrigation, and polytunnels to optimize crop environments. Plastic mulch warms soils, reduces weeds, and conserves moisture. Polythene greenhouses allow temperature and climate control for improved growth.
- Hydroponics involves growing plants without soil, using mineral nutrient solutions. Systems like NFT, deep water culture, and ebb and flow allow precise control over nutrients, water, and root environments. Hydroponics facilitates high yields but has high infrastructure costs.
- Raised bed gardening improves drainage and soil quality. Beds are framed and filled with amended soil tailored to plant needs. Straw bale gardening uses bales as a lightweight, weed-free growing medium.
- Permaculture applies ecological principles to create sustainable food systems. Key practices include zoning, water conservation, enhancing biodiversity, and promoting beneficial connections between system components.

Key Terms

- Crop rotation
- Deep water culture
- Ebb and flow
- Electrical conductivity (EC)
- Green manures
- Hydroponics
- Intercropping
- Monoculture
- Nutrient film technique (NFT)
- Permaculture
- Plastic mulch films
- Plasticulture
- Polythene greenhouses
- Raised bed gardening
- Straw bale culture
- Subsistence agriculture

Self-Review

1. What are the main goals of subsistence agriculture?
2. How do home gardens supplement family food and income?
3. What techniques help replenish soil fertility in traditional systems?
4. What equipment is used in high-intensive commercial farming?
5. What potential issues are associated with monoculture cropping?
6. How does crop rotation benefit soil health?
7. What benefits does plastic mulch provide for crop production?
8. How do polythene greenhouses optimize plant growth environments?
9. What are the main components of a deep-water culture hydroponic system?
10. How does nutrient film technique provide nutrients and oxygen to plant roots?
11. What factors make hydroponics suitable mainly for high value specialty crops?

12. What are two key advantages of raised bed gardening?
13. How are straw bales conditioned for planting?
14. What are some key principles and practices of permaculture farming?
15. Which production system described seems most suitable for small-scale sustainable farming?

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11: PEST AND DISEASE

Plants are the producers in terrestrial food webs. The planting of crops for human consumption or for beautification of the landscape does not prevent organisms from taking advantage of a potential resource. Production loss from predators (Figure 11-1) and pathogens can be significant. Additionally, the same conditions that are ideal for the growth of the crop will be ideal for their competitor, weeds. In this chapter we will look at some of the pest and diseases that result in production problems for growers.



Figure 11-1. Banana slug chewing on leaf in Sitka, Alaska. (Stephanie Harvey. 2023. CC-BY-NC)

11.1: Weeds

11.1.1: The Nature of Weeds

11.1.2: Control of Weeds

11.1.3: Non-Chemical Control

11.1.4: Herbicides

11.2: Insect Pests

11.2.1: Insect Damage

11.2.2: Common Insect Pests

11.2.3: Control of Insect Pests

11.3: Plant Disease

11.3.1: Viruses

11.3.2: Bacteria

11.3.3: Fungi

11.4: End of Chapter Review

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11.1: WEEDS

As horticulturalists our goal is to encourage plant growth. We fertilize and water to nurture plants from seedlings to maturity, to fruit and seed production. The conditions that support crop growth are the same conditions that support non-crop growth. This makes control of weeds (unwanted plants) difficult.

The term **weed** is loosely defined as a plant growing where it is not wanted. Botanically, the term does not have a concrete definition that allows us to separate weed from non-weed. One might attribute “weed” as a state of mind since depends on the observer's standpoint. There are groups of non-cultivated plants that have characteristics that tend to make them a problem to control. These groups fall under the more concrete application of the term. For a wheat grower with a couple of hundred corn plants popping up across their wheat field, the corn is just as much a problem as the more traditional weeds.

Weeds can significantly impact a crop’s yield. One reason for this is that weeds compete with the cultivated plants for resources. There is a finite supply of nutrients in the soil and weed seeds often germinate and grow faster than the cultivated crop. They can establish root systems that deplete the soil’s nutrient reserves before the cultivated plant’s roots can get there. The same is true of water. There is only so much available and if it is divided between the plants and the weeds then the crop is going to potentially suffer from insufficient resources.



Figure 11-2. Invasive Kudzu (*Pueraria montana*) overgrowing pine trees to the extent the trees have died due to low solar input. Long Description: Kudzu covering every surface in sight. Kudzu has covered trees to the extent that the trees have died and are now just standing columns covered in Kudzu. (Kerry Britton, USDA Forest Service, Bugwood.org. CC-BY.)

Weeds can block sunlight from striking the plant (Figure 11-2). Even if the crop and weed are about the same height, it will impact solar incidence on the sides of the plants and thus lower productivity. Dense weeds can crowd around the cultivated plants and prevent adequate air circulation. While it might be possible to have a small impact on photosynthesis due to lower CO_2 levels, the real issue is with disease. Lack of air circulation amongst leaf canopies can lead to fungal pathogens and issues with some insect pest as well.

In addition to direct competition for resources, weeds can impact crops by acting as sanctuaries for pest insects including those that carry disease. The weeds provide cover for the insect populations during spraying of the fields and serve as harbors for insects from one crop cycle to the next. Many of the piercing-sucking insects, such as aphids and leafhoppers (Figure 11-3), are also vectors of disease. The presence of these insects increases the risk of introducing a virus. We will look at this in more detail later in this chapter.



Figure 11-3. Leafhopper, a piercing sucking insect that can vector diseases. (By Sarefo - Own work, CC BY-SA 4.0, Link to Source [commons.wikimedia.org])

11.1.1: The Nature of Weeds

11.1.2: Control of Weeds

11.1.3: Non-Chemical Control

11.1.4: Herbicides

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11.1.1: The Nature of Weeds

Some weeds are native to our regions while others are introduced. For the native plants, it is typically the characteristics of the species or genus that make it more likely to be classified as a weed. Additionally, selective practices – such as using the same herbicide repeatedly – has led to populations that are resistant to the popular herbicides like glyphosate (active ingredient in Roundup™). So, weeds that have historically been well controlled may become a larger problem in the future.

Other weed are exotics; non-natives that were introduced either intentionally or unintentionally. Some species were introduced as people moved into new areas. They wanted to continue to eat what they ate at "home" or were medicinal plants with which they were familiar. These then escaped cultivation and naturalized throughout the new territories. Some weeds were introduced by accident. Weed seed were often contaminates in crop seeds ship from other countries. Prior to controls on soil movement, they came in with the root balls of desired plants.



Figure 11-4. Charlock is a common field weed introduced unintentionally in crop seeds. (Stephanie Harvey. 2024. CC-BY-NC)

There are a set of traits that are common in what are typically referred to as "weedy" species (Figure 11-4). Most weeds are what we call "R" strategist. They spend a lot of their resources to produce copious amounts of seeds. This prolific production ensures that there is a significant seed pool just waiting for a chance to germinate. These seeds are also persistent – that is they can remain viable in the soil for many years. For example, a single female *Amaranth hybridus,* pigweed, can produce 100 thousand seeds and some of these can remain viable for 40-60 years. As part of the "R" strategist condition, each seed is very small and has limited resources of its own. However, their small size makes them easily distributed by wind, birds, and other animals (Figure 11-5). Weedy plants often have short lifecycles. They germinate quickly, reach maturity, flower, and seed in a short period often with 2-3 life cycles in a single growing season. This fast growth can allow them to out compete the crops for resources. Some weeds are also perennial (at least their roots system) and persist year after year.



Figure 11-5. *Cirsium horridulum* is a very weedy thistle. The floral head, a single floral head seen in the left image, can produce hundreds of individual seeds that are carried by the wind. (Stephanie Harvey. 2019& 2023. CC-BY-NC).

A common problem with introduced weeds is that the environmental checks that controlled their expansion in their native region can be lost when introduced into a new area. When a short growing season in the native region is replaced by a longer growing season, growth may be more expansive, or multiple generation can be produced in a single growing season. This can lead to exponential growth that overwhelms native plants. In its native region, cold winter temperatures might kill back a plant preventing its overall growth. In a new environment that control may not be present. The pests and diseases that limited the weed's ability to grow many not exist in the new environment. This can create problems for native species. Since plants are often the base of an ecosystem's food web replacing one plant with another may cause stress and even extinct of organisms that depend on native plants for survival.

Some examples of plants that have been intentionally introduced but now present significant control problems include – Privet (horticultural shrub; Figure 11-6) and kudzu (fast growing vine mean to control erosion along railways).



Figure 11-6. Nearly impenetrable walls of privet (*Ligustrum sinense*) blocks wildlife corridors. (John D. Byrd, Mississippi State University, Bugwood.org CC-BY)

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11.1.2: Control of Weeds

Weeds are most readily controlled when they are small – when they are easy to disrupt from the soil and need the least herbicide. Scouting fields regularly to find new weed flushes (new growth) allows timely control action. Monitoring which weeds are present and their life cycles informs the choice of management tactic. Keeping records over time helps evaluate the effectiveness of control methods. Weed control focuses on interrupting the weed's lifecycle. To be effective in control efforts some level of weed identification must be achieved. At the most basic identification is the type of lifecycle and growth habit – annual, perennial, biennial, or woody weeds.

Annual weeds complete their life cycle in one year. They germinate from seeds, grow, flower, set new seeds, and die all within a single growing season (Figure 11-7). Examples of annual weeds include crabgrass, pigweed, and foxtail. Annual weeds reproduce by seeds, so the key to controlling them is to prevent them from going to seed. Annual weeds can be further categorized as either winter annuals or summer annuals. Winter annuals germinate at cooler soil temperatures, often germinating in fall. They grow slowly through fall and overwinter, then resume rapid growth in early spring, flowers and go to seed. Summer annuals require warmer soils for germination, so they appear in late spring and into summer with late summer or fall seed production.



Figure 11-7. A common vetch, an annual weed and member of the pea family. It is very vine-like in appearance due to its tendrils that attach it to other structures for support. (Stephanie Harvey. 2021. CC-BY-NC)

Perennial weeds live for multiple years. They regrow from root systems or other plant parts like tubers or rhizomes each year. Perennial weeds include dandelions, bindweed, and nutsedge. Because they regrow from roots or other plant structures, perennial weeds are more difficult to control than annuals. Simply disturbing the top growth is often not effective. Repeated cultivation or herbicide treatments are often needed to fully kill the weed and its root system.



Figure 11-8. Brambles such as blackberries and dewberries are an example of a woody weed. Long Description: Blackberries and dewberries are woody shrubs with sharp prickles. They produce white to light pink flowers with 5 petals and many yellow stamen. (Stephanie Harvey. 2023. CC-BY-NC.)

Biennial weeds have a two-year life cycle. The first season they germinate and grow vegetatively, storing nutrients in a basal rosette or root system. The second year they flower, set seed, and die. Examples are wild carrot, burdock, and common mullein. Biennials are best managed in their first season before they flower and go to seed. **Woody** weeds (technically perennial) include tree saplings, shrubs, vines, and brambles (Figure 11-8). They have hard, woody stems and extensive root systems. Common woody weeds are tree of heaven, multiflora rose, poison ivy, and kudzu vine. Control often necessitates cutting or mowing repeatedly to deplete root reserves or the use of systemic herbicides that kill the roots.

Effective control methods are needed to reduce the weeds' establishment, growth, and reproduction. There are many cultural, chemical, mechanical, biological, and physical methods that can effectively manage weeds. Often, integrated approaches that combine tactics like rotation, competitive planting, cultivation, mulching, mowing, and bioherbicides for optimal control with minimal environmental impact.

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11.1.3: Non-Chemical Control

Cultural methods involve crop management practices that prevent weeds or reduce their competitive effects. These include crop rotation, planting competitive crop varieties, adjusting row spacing and density, and intercropping. Rotating between crops prevents any one weed from dominating. Competitive crops shade out weeds or outcompete them for resources. Close crop spacing and intercropping occupy space so weeds cannot establish. Growing a cover crops during non-production season help limit weeds in the next season by crowding the weeds out and preventing their establishment.

Cultivation uproots and buries weeds through shallow tillage. Tools like harrows, cultivators, hoes, and plows are used to physically disrupt weed growth. Timing is important, as cultivation works best on young, small weeds. Repeated cultivation controls perennials by cutting off new shoot growth and depleting root reserves. However, cultivation can damage crop roots and soil structure if done improperly or excessively.

Mulching with organic materials like straw or leaves, plastic films, or landscape fabrics blocks light. Many weed seed require light exposure to initiate germination. Thus, without light, weeds cannot emerge. Mulches also conserve soil moisture and modify soil temperature. Organic mulches add organic matter when incorporated into the soil. Inorganic plastic mulches can be effect but must be removed after the growing season. In flower beds where plants are planted and then left relatively undisturbed, landscape fabrics can be used. They allow water and air exchange while suppressing weeds around gardens and landscaping.

Mowing and cutting can control annual and perennial weeds. Ideally, well timed cutting interrupts growth cycles before seed production while repeated mowing can start roots of need energy. Close mowing gives desired plants a competitive edge. String trimmers and brush cutters help manage large areas. Hand pulling and hoeing are effective for small infestations. Heat applications can kill weeds and prevent seed germination. **Solarization** uses clear plastic sheets to trap heat and kill weeds, seeds, and soilborne pests. It is effective in gardens and small areas but has also been employed on large agricultural scale in sunny climates. Soil is kept moist, then sealed under plastic for 4-6 weeks in summer. Temperatures achieved can be up to 140°F which kill weeds and weed seeds in the top 6 inches of soil. **Flaming** (thermic control) applies intense heat to weeds using propane-fueled torches (Figure 11-9). Cell tissues expand and rupture. It controls annual weeds and suppresses perennials. Timing is targeted to seedlings and patches. Dangers include fire and propane explosion risks.



Figure 11-9. Pesticide-free thermic weed control with a weed burner on a potato field in Germany. Long Description: Tractor with thermic device to kill weeds and pathogens in soil before planting. The image around the tractor and the field that has been treated is blurred due to the heat waves generated by the treatment. (By Dirk Ingo Franke - Own work, CC BY-SA 2.0, Link to Source [commons.wikimedia.org])

Bioherbicides utilize plant pathogens like fungi and bacteria to control weeds. They provide an alternative to chemical herbicides for organic crop production. However, they are slower acting and less effective than synthetic herbicides.

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11.1.4: Herbicides

Herbicides are chemical pesticides designed to kill weeds or inhibit their growth. There are numerous types of herbicide chemistries and modes of action. Herbicides are applied in various formulations such as sprays, granules, or pellets to foliage, soil, or water. Proper application ensures herbicides selectively control weeds without harming crops, humans, or the environment.

Herbicides are categorized by mode of action - how they kill or suppress weeds biochemically. **Contact herbicides** like paraquat disrupt cells and cause plant death upon foliage contact (Figure 11-10). **Systemic herbicides** like glyphosate are absorbed then translocated throughout the plant, including roots and shoots. This provides more complete control.



Figure 11-10. Necrotic spot due to paraquat, a contact herbicide, drift. (Link to Source [plantpath.ifas.ufl.edu])

Herbicides can be broad-spectrum or selective. **Broad-spectrum** herbicide target pathways common to all plants. Glyphosate is an example of a broad-spectrum herbicide that kills all vegetation. **Selective herbicides** target specific plant processes and physiological differences between weeds and crops. For example, 2,4-D mimics plant hormones. It causes uncontrolled growth in broadleaf weeds but not in grass crops. ACCase inhibitors like sethoxydim block lipid synthesis in grasses but not broadleaf plants. This selectivity permits effective weed control within the crop.

The time of application will control what types of herbicides can be used. Some herbicides are used as pre-emergent treatments. **Pre-emergent** application provides control before weeds become established. Soil-applied herbicides like trifluralin prevent weed seed germination and root growth. They bind to soil particles and limit uptake by plant roots. **Post-emergent** foliar herbicides are applied to foliage of actively growing weeds for rapid "burndown". The use of glyphosate to control weed in a fallow field would be an example of a post-emergent application.

Various factors affect herbicide performance. Weed size and species influence susceptibility. Environmental conditions like temperature and moisture impact plant uptake and herbicide activity. Soil-applied herbicides require moisture to move into root zones. Soil properties can increase or decrease soil-applied herbicide availability and efficacy. Foliar-applied sprays must thoroughly coat leaf surfaces. Winds and rain an impact application by minimizing contact and uptake. Proper application timing, rate, and technique ensures safety and efficacy. Applying at the right weed growth stage specified on the label improves control. Split applications or tank mixes expand the weed spectrum controlled.

Safety is also a major consideration. Following label directions avoids misapplication issues like drift, runoff, and plant damage. **Drift** is when herbicides hit unintended plants. This can be a costly error. For example, DNR had to pay peach grower in Georgia a large settlement after helicopters spraying paraquat for kudzu control killed peach trees in adjacent orchards. Personal safety is also a consideration. Wear the appropriate personal safety equipment as listed on the label. Wash exposed equipment and properly discard unused material.

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11.2: INSECT PESTS

In horticulture, the interaction between insects and plants can be positive or negative. Insects such as butterflies, moths, bees, and even ants pollinate plants and obtain nectar and pollen as food rewards. Other insects use the plants as food, usually to the detriment of the plants. In this segment of Chapter 11 we will first look at what insects are and some other closely related arthropods, how they feed and the damage they can do to crops.

Arthropods, from the phylum Arthropoda, are invertebrates characterized by exoskeletons made of chitin, segmented bodies, and jointed appendages. With over 1 million described species, arthropods encompass a vast diversity of forms including insects, arachnids, crustaceans, and myriapods (Figure 11-11). Arthropods thrive in nearly every habitat and play important ecological roles such as pollinators, predators, parasites, and herbivores. Some arthropods are also economically important crop pests.

The arthropod body plan enables mobility and adaptation. The hardened exoskeleton provides attachment sites for muscles and protects delicate tissues. However, arthropods must periodically molt, shedding and replacing this rigid exoskeleton to allow growth. Segmentation of the body increases flexibility. Paired, jointed appendages like legs, mouthparts, and antennae facilitate specialized functions related to sensing, feeding, and locomotion. For simplification of our discussion, we will identify all pest arthropods as “insects.”

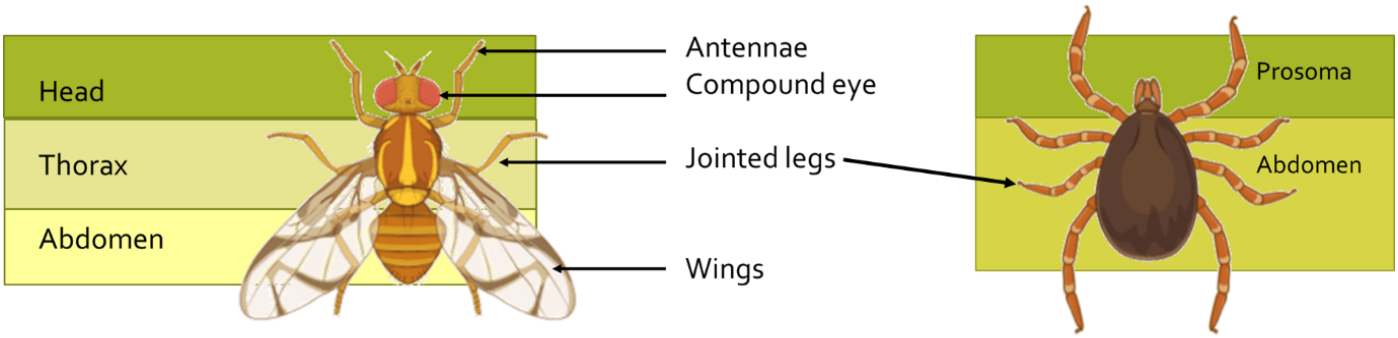


Figure 11-11. Body segment of insects (left) and arachnids (right). Long Description: Diagram comparing insects body structure with that of arachnids. A) insect has head, thorax and abdomen body segments, antennae, compound eyes, jointed legs and wings. B) arachnids have only two body segments - prosoma and abdomen. They also have jointed legs but lack the wings, antennae and don't have compound eyes. (Created in BioRender. Com By Stephanie. Harvey 2020.)

Most arthropods develop through life cycles with metamorphosis, marked by distinct changes in body form between immature and adult stages (Figure 11-12). Insects that undergo incomplete metamorphosis change gradually by undergoing a series of molts. Since insects have exoskeletons that do not stretch, they must be replaced as the insect grows. Immature insects that go through incomplete metamorphosis are called **nymphs**. Nymphs are similar in form to the adult except they do not develop wings until adulthood. Examples include grasshoppers and spiders. For insect that undergo complete metamorphosis there are four stages: egg, larva, pupa, and adult. Larvae differ dramatically from adults. Insects like butterflies undergo complete metamorphosis. Understanding the forms an insect takes through its lifecycle will help with identifying it. It also helps with control of insect pest because we need to know which stages cause the most damage and to select insecticides that will be effective on that stage. For example, in complete metamorphosis the most damaging state to the plants is that of the larva –caterpillar – when it can veraciously consume plant material.

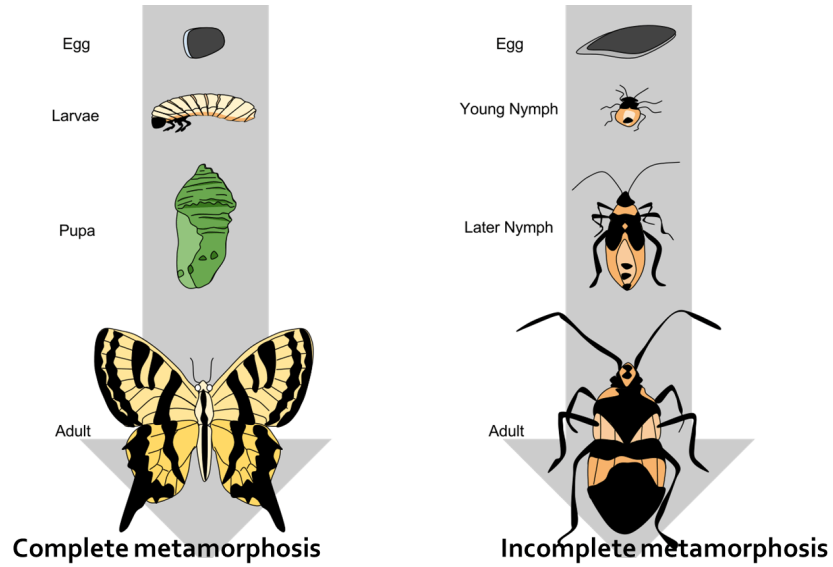


Figure 11-12. Stages of complete and incomplete metamorphosis. Long Description: Diagram comparing complete versus incomplete metamorphosis. Complete metamorphosis includes: egg, larva, pupa and adult. This is common to butterflies. Incomplete metamorphosis includes: egg, young nymph, later nymph and adult. Many beetles follow this lifecycle. In complete metamorphosis, stages between egg and adult all look very different. In incomplete, the stages look more similar with each growth stage look like a larger version of the previous. (Source unknown)

11.2.1: Insect Damage

11.2.2: Common Insect Pests

11.2.3: Control of Insect Pests

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11.2.1: Insect Damage

Among agriculturally important arthropods, insects cause the most crop damage as herbivorous pests. Chewing insects like beetles and caterpillars physically damage fruits, stems, and leaves. Piercing-sucking pests such as aphids and stink bugs extract plant fluids. Other insects mine tissues or transmit plant pathogens as vectors. Feeding reduces yields quantitatively through tissue loss and qualitatively through lost productivity.

Several factors make insects adept crop pests. Their small size allows access to protected plant parts. Short generation times and high fecundity enable rapid population growth. Physiological and behavioral adaptations amongst insects allows them to utilize diverse food sources. For example, some insects have specialized piercing mouthparts for precise extraction of sugars from phloem sap. Insects are also highly mobile which aids in dispersal and colonization.

Insect pest management relies on ecological and biological knowledge. Understanding life cycles and monitoring developmental stages informs optimal timing of control measures. Like with weed control a variety of control methods exist – cultural, mechanical, biological, and chemical. Cultural practices like crop rotation disrupt pest cycles. Use of resistant crop varieties utilize plant defenses against insects. Biological control makes use of natural predators, parasites, and pathogens. In small gardens, mechanical removal of larger pest may be feasible. When necessary, insecticides can be used to target vulnerable life stages. Effective, sustainable control is best achieved through Integrated Pest Management (IPM) which combines observation, critical threshold, and multiple control strategies.

Observation plays an important role in insect control. Some garden pests are not easy to spot. They are either well camouflaged or hide on the bottom sides of leaves. We can often spot evidence of their presence before we spot them. One thing all insects leave behind is frass. **Frass** is the excrement (poo) of the insects along with shed exoskeletons from previous molts. It can appear as just “dirt” on the leaves but often has a green tint if they insects are directly consuming the leaves. You can also pay attention to the leave surfaces. Piercing and sucking insects leave a sugary excretion called **honeydew**. This can coat the leaves and attract other pest such as molds. You may also see increased ant traffic. Some ants feed on this sugary reside and will defend the aphids from other predatory insects.

If the insects are feeding off the plant, there will be damage although again it may not be obvious. Insects that feed on plants can be categorized by their mouthparts and how they feed off the plant. The first group are those with **chewing mouthparts**. They cutaway sections of the leaf blade often leaving the major veins behind as a lacey skeleton (Figure 11-13). These would include beetles (such as the Japanese beetle), grasshoppers, grubs, and caterpillars. The second group are insects with rasping or saw-like mouthparts such as thrips and leaf-miners. They scrape way cells from the back side of the leaf and leave only the upper epidermis intact. Since the upper epidermis does not contain chloroplast, a whitish-yellow trail is left in their wake. The last group are those that have piercing-sucking mouthparts. These insects have specialized mouthparts that allow them to pierce phloem cells with amazing accuracy (we even still use them in research b/c they are better at doing this than our sophisticated equipment). The pressure of the phloem pushes the sap through the digestive track of the insect and out onto the leave as honeydew. While not doing any noticeable damage, they are siphoning off carbohydrates from the plant that thus are not being used for growth or reproduction. If the numbers are high enough, it can cause death of the plant. Some examples of piercing/sucking insects are aphids, scales, whiteflies, leafhoppers, and mites (technically arachnids).

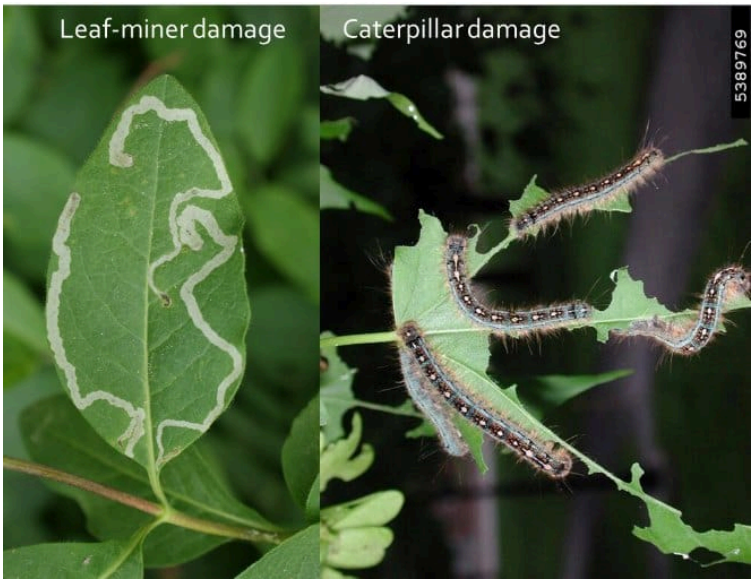


Figure 11-13. Leaf damage may be easier to spot then the insect (left) or both may be clearly evident (right). Long Description: A) Leaf with a whitish path created as a leaf miner scrapes away the softer part of the leaf but leaves upper surface intact. B) Caterpillars consuming a leaf blade, leaving only the major veins intact.(By Kenraiz Krzysztof Ziarnek - Own work, CC BY-SA 4.0, Link to Source [commons.wikimedia.org]

Insects can also cause damage to plants indirectly or in ways not associated with feeding. Some insects lay their eggs in plants. To do this they bore into the tissue leaving it vulnerable to infectious agents. Additionally, of course, once the eggs hatch, the larva will feed on the plant also.

As mentioned before, the honeydew excreted by the piercing-sucking insects can attract other pathogens. Fungi, specifically sooty mold (Figure 11-14), can grow rampant on leaves covered in honeydew. This black layer can minimize photosynthetic ability and between that and sap removal can be very detrimental to the plants. In this image you can see the black “sooty” appearance of the leaves as well as the glossiness that is associated with the honeydew. On the stem in the background, you can see the scale insects responsible for the honeydew.

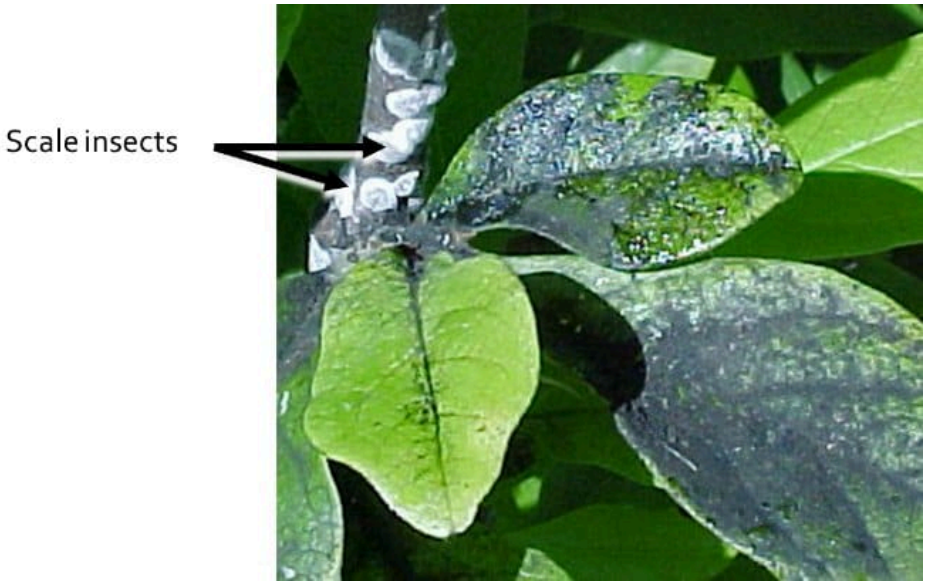


Figure 11-14. The blacken discoloration to these leaves is due to sooty mold feeding of the honeydew left behind by the scale insects. Long Description: Leaves are blackened with sooty mold due to the scale feeding on the plant. Scale insects can be seen on the stem of the plant and look like small white hills, scattered along the stem. (Unknown Source).

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11.2.2: Common Insect Pests

Aphids are small, soft-bodied insects that feed by sucking sap from stems and leaves of plants. They are pests of ornamental trees, shrubs, and flowers as well as many vegetable crops (Figure 11-15). They feed by inserting a microscopically thin mouthpart into the plant phloem and sucking the sap which is rich in sugars. As they feed, the aphids also inject saliva. This caused some plants to develop curled, hardened, or distorted growth. It is also how they can act as vectors for disease. Viruses, for example, can be transmitted from plant to plant by aphids. A single aphid would have little impact on plant vigor; however, populations of aphids can expand quickly and lead to significant losses in yields.



Figure 11-15. Aphids at various stages of development. The large, darker individuals are winged adults. The smallest white individuals are actually shed exoskeletons from molts. (Ad Sonnemans. CC BY 3.0, Link to Source [commons.wikimedia.org]

Spider-mites are a nearly microscopic pest (Figure 11-16). They are mites, so technically arachnids not insects. They have 4 sets of legs instead of 3. Spider mites are hard to spot not only b/c they are small but b/c they like the bottom side of the leaves near the apex of the plant. The environment is slightly warmer and drier at that location. Like aphids, they are piercing-sucking feeders so the damage can be difficult to spot initially. They produce golden freckles along the blade of the leaf. Eventually the entire leaf starts to go yellowish. The mites also produce a fine-silken web that can be seen when plants are heavily infested with the mites. The web catches the frass which makes the webbing more visible with time.



Figure 11-16. Left – Two-spotted spider-mites with egg. Right – leaf showing spider-mite damage as golden flecks. Long Description: A)Close up of two spider mites on a leaf surface. Mites are about 0.5 mm long. A spider mite egg is also present and is about 0.1mm in diameter. B) Leaf showing spider mite damage as golden flecks across leaf surface. Leaves look almost yellow. (By Gilles San Martin CC BY-SA 2.0, Link to Source [commons.wikimedia.org]; Stephanie Harvey. 2012 CC-BY-NC).

Caterpillars are the larvae form of butterflies and moths. They are the primary feeding stage for this group insects and do significant amounts of foliar damage (Figure 11-17). Smaller larva may remove only the most tender parts of the leaf, leaving the primary and secondary veins intact. Larger caterpillars can consume everything down to the leaf petiole. They are voracious consumers and leave large greenish fecal pellets on the foliage or under the infested plant. Common pest caterpillars are tomato hornworms, cabbage loopers, and corn earworms. Handpicking larger caterpillars, applying Bacillus thuringiensis, and encouraging natural predators like wasps and birds can protect plants from excessive defoliation by caterpillars.



Figure 11-17. Tomato hornworms on tomato plant. Long Description: Large, green tomato hornworm feeding on tomato plant. Approximately 2.5 inches long and 0.3 inches in diameter. (About the size of your ring finger.) (By Ljessee123 - Own work, CC BY-SA 4.0, Link to Source [commons.wikimedia.org])

Japanese beetles are a highly destructive insect pest in North America. They are scarab beetles with iridescent copper-colored forewings (Figure 11-18). Larvae feed on plant roots and hibernate in the soil. The beetles emerge in the spring when soil temperature warms up. Adults feed voraciously on over 300 plant species. They use pheromones to attract other beetles and overwhelm plants, skeletonizing leaves and damaging fruits. Traps, physical barriers, microbial insecticides, and neonicotinoid treatments can reduce infestations of Japanese beetles in the garden.



Figure 11-18. Feeding Japanese Beetles. (D. Gordon E. Robertson - Own work, CC BY-SA 3.0, Link to Source [commons.wikimedia.org])



Figure 11-19. Scale insects on a stem. Long Description: Scale insects on a stem. They appear oval and nearly flat, with a slight darker area toward their center. They are about 1-2 mm long. They sit flat against the stem with little if any movement. (By Gilles San Martin CC BY-SA 2.0, Link to Source [commons.wikimedia.org])

Scale insects attach themselves to stems and leaves to suck plant fluids (Figure 11-19). Severe infestations can stunt or kill plants. They vary dramatically in appearance, from very small organisms (1–2 mm) that grow beneath wax covers, to shiny pearl-like objects (about 5 mm), to animals covered with mealy wax. Adult females are almost always immobile (apart from mealybugs) and permanently attached to the plant on which they are feeding. They secrete a waxy coating for defense making them difficult to control. Horticultural oils suffocate overwintering scales. Systemic insecticides applied early in the season can reduce scale populations.

Grasshoppers have had a long relationship with humans (Figure 11-20). Swarms of locusts can have devastating effects and cause famine, having done so since Biblical times. They chew on leaves, stems, and pods of crops. They are most problematic in hot, dry conditions and swarms can devastate pasture, grains, and other crops. Row covers can exclude grasshoppers. Reducing tall vegetation around gardens can remove egg-laying sites and minimize future population. Baits and insecticide application to foliage can protect plants from severe defoliation.



Figure 11-20. Grasshopper eating the leaf of a climbing pea plant. (By Faunagalaxy - Own work, CC BY-SA 4.0, Link to Source [commons.wikimedia.org])

Stink bugs feed by sucking juices from fruits and seeds, causing ugly blemishes or distortion (Figure 11-21). They are a threat to cotton, corn, sorghum, soybeans, native and ornamental trees, shrubs, vines, weeds, and many cultivated crops. The shield-shaped adults and nymphs emit a foul odor when threatened, thus their common name. Traps, natural predators, and insecticides provide some control, but stink bugs can be difficult to manage as they are resistant to many insecticides. Removing alternate hosts weeds near the garden is recommended.



Figure 11-21. The rice stink bug is a major agricultural pest in the South US. It is straw-colored and is shield-shaped. It is about 0.5 inches long and 0.25 inches wide. (By Ilona Loser - Own work, CC BY-SA 3.0, Link to Source [commons.wikimedia.org]).

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11.2.3: Control of Insect Pests

Managing crop insect pests relies on an integrated approach combining cultural, physical, biological, and chemical control tactics. The goal is effective pest suppression with minimal environmental impact. Cultural control aims to make fields less suitable for pests. Crop rotation disrupts pest life cycles by eliminating hosts for part of the year. Maintaining sanitation through tillage or plant removal eliminates alternate hosts and overwintering sites. Planting resistant crop varieties utilize physical or chemical plant defenses against insects. Growers can adjust planting/harvest times to avoid periods of peak pest pressure. Optimizing fertilization, irrigation, and plant spacing reduces plant stress which can reduce susceptibility.

Physical and mechanical controls directly remove or exclude pests. Floating row covers and screenhouses block insect access to plants. Handpicking large insects and egg masses from plants will reduce pest populations. Traps with visual/chemical lures or vacuum devices can capture insects. Tillage destroys pest habitat and brings insects to the surface. Solarization uses solar heat under plastic sheets to kill pests in soil.

Biological controls utilize natural enemies to suppress pests. Natural predators like lady beetles and parasitic wasps attack insect pests (Figure 11-22). Diseases caused by bacteria, fungi, and viruses can be introduced to initiate epizootics. Sterile insects introduced into a field can disrupt mating and reproduction cycles. Behavior-modifying chemicals can be released to confuse insects or deter feeding and egg laying. **Companion planting** can be used where susceptible crops are interplanted with pest-repelling plants to offer protective proximity.



Figure 11-22. Tomato hornworm covered with eggs of a parasitic wasp. (Link to Source [flickr.com])

Chemical insecticides remain an important tool despite ecological concerns. Synthetic organic compounds are designed to control insects through various modes of action while exhibiting low mammalian toxicity. Two groups of powerful, broad-spectrum insecticides are organophosphates and **carbamates**. These compounds kill by over stimulating the nervous systems of the insects. While very effective, they are also very dangerous to use as they also affect the human central nervous system. Very strict guidelines are to be followed when handling, applying, and disposing of these pesticides. Unfortunately, enforcement of these guidelines is nearly impossible, leading to environmental contamination, impact on non-target species and human injury and death.

Biopesticides derived from natural sources like plants or microbes often have novel modes of action. They are usually classified into four groups. **Microbial pesticides** consist of bacteria, entomopathogenic fungi or viruses (and sometimes include the metabolites that bacteria or fungi produce). Entomopathogenic nematodes may be classed as microbial pesticides, even though they are multicellular. **Bio-derived chemicals** of which four groups are in commercial use: pyrethrum, rotenone, neem oil, and various essential oils. These are naturally occurring substances that control pests and microbial disease. Botanical oil Insecticide application is timed for maximum impact on vulnerable life stages. **Plant-incorporated protectants** (PIPs) incorporate genetic material from other species. These are genetically modified plants into which genes for protective agents are added. ***Bt*** corn is an example of this technology. Current research into new control measures includes **RNAi pesticides** (RNA interference) and nanoparticles.

An **integrated pest management** (IPM) plan combines monitoring, multiple tactics, and careful insecticide use to control pests economically and ecologically. Field scouting identifies issues early before pests reach damaging levels. Control methods are selected based on pest biology and field conditions. Insecticides are used only when warranted based on population levels exceeding economic thresholds. IPM mitigates pest resistance and negative impacts of insecticides.

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11.3: PLANT DISEASE

Plants, as the base of nearly all food webs, come under attack from many sides. As already discussed, insects consume and thus damage crops, but so do other organisms such as deer, hogs, and even other plants. They are also under attack by microscopic or near microscopic consumers – such as bacteria and fungi. Bacteria and fungi, along with viruses, cause crop diseases and can be responsible for significant crop loss. Such causative agents are referred to as pathogens (Figure 11-23).

Organisms that cause infectious diseases in plants include fungi, oomycetes, bacteria, viruses, viroids, virus-like organisms, phytoplasmas, protozoa, nematodes, and parasitic plants. Plant pathology is the scientific study of disease in plants caused by infectious organisms – pathogens. Some pathogens are opportunistic - they can be free-living in the environment and only infect under certain conditions. On the other hand, there are obligatory pathogens that require a host to complete their lifecycle.

Identification of potential infections early is critical to control and minimization of loss. To spot it we look for signs and symptoms. **Signs** are actual visible evidence of a disease pathogen. Most infectious agents are microscopic and cannot be seen with the naked eye. With fungal agents, while a solitary **hypha** (single cell-width strand) might not be visible, the collective mat of hyphae – called the **mycelium** - can become visible (Figure 11-24). The same is true of other multicellular form that the fungi can take – sporangia (spore producing structure) and other over-wintering structures such as the sclerotia. Sclerotia are the small spherical structures seen on the mycelia (yellow arrow). Bacteria signs can only be seen if there is a large enough colony. By the time, the bacterial growth is visible significant damage has already taken place.

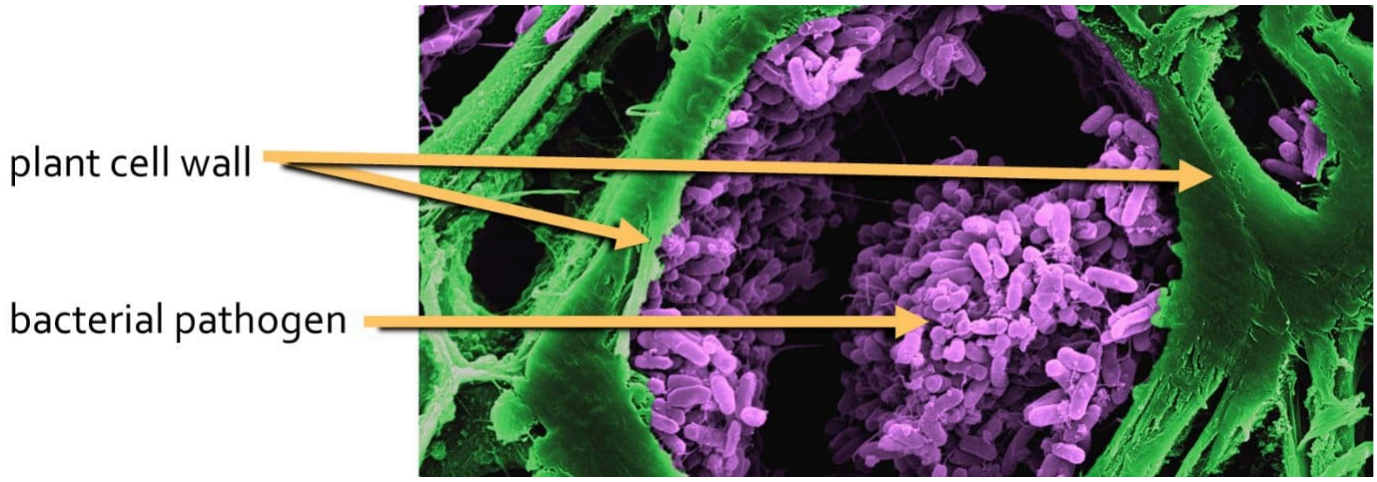


Figure 11-23. Colorized scanning electron micrograph (SEM) of infect plant tissue. Long Description: Scanning electron micrograph of plant tissue infected with bacteria. Plant cell walls are visible as scaffold-like structures. Bacteria appear as small, capsule like structures within the cell openings. Thousands of bacteria are within each plant cell. (Jeannette Rapicavoli/UC Riverside, CC BY-ND)

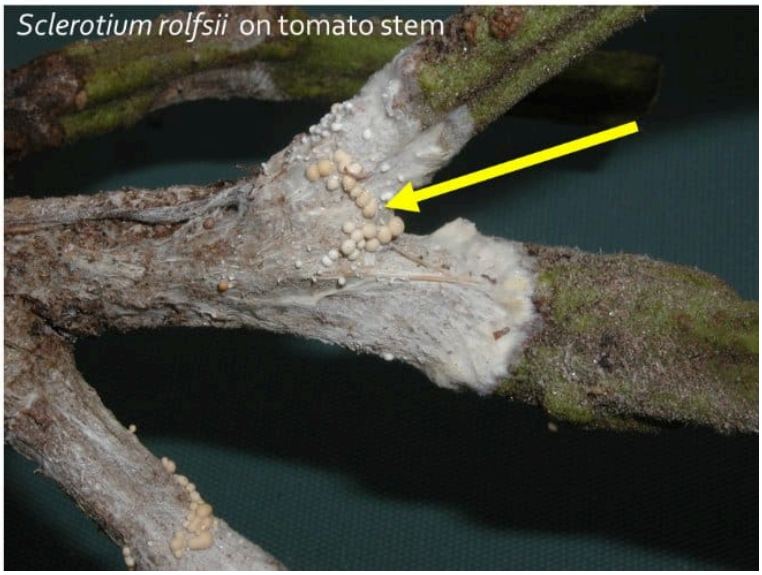


Figure 11-24. The white mycelium of *Sclerotium rolfsii* on tomato stem. Yellow arrow indicates the forming sclerotia. Long Description: Closeup of a tomato stem that is infected by the fungus Sclerotium rolfsii. A dense white fungal mass can be seen sheathing the stem. An arrow indicates some small roundish shapes (1mm) that are sclerotia. (Link to Source [gardening.stackexchange.com])

In most cases we will not see bacteria or viruses in/on plants in the field. We must rely on symptoms to help us detect and identify possible infections. The **symptoms** are changes in the plant in response to the infective agent (Figure 11-25). Symptoms are the evidence of infection, such as brown areas in the turf, yellow or brown of leaves. They can include spots on the leaves, wilt or curing of leaves. Shape, color and placement of the symptom can help with diagnosis of the infectious agent.



Figure 11-25. *Glomerella cingulate*, anthracnosa, on yam leaf. (©Sarah Simons. Accessed via Link to Source [www.cabi.org] 4.24.20)

For a plant to become infected, the infectious agent must be present. It must come in contact with the plant either through vectors (including humans) or be naturally present in the environment. Just the presence of the pathogen does not mean that disease will occur. The plant must also be susceptible. Individual pathogens have limited host ranges. For example, *Agrobacterium tumefaciens* has a host range of about 500 species but all are eudicots. Grain crops, for example, are not susceptible while tomato plants are susceptible.

Plants have defenses against pathogens so even suitable host may not become infected unless something happens to circumvent their protective mechanism. The cuticle of the plant is very well adapted for keeping pathogens out of plant cells; however, a wound can allow the pathogen an unprotected route of entry. Stomatal pores are a naturally occurring vulnerable spot due to their role in providing a route for gas exchange. Nutrient deficiencies and other stresses that lower the general health of the plant

can also make the plant more susceptible to infectious agents. For example, as mentioned when we discussed plant nutrients, a deficiency in calcium can result in weak cell walls that are prone to infection by fungal and bacterial pathogens – inducing what we commonly refer to as blossom-end-rot, as seen here on a tomato.

11.3.1: Viruses

11.3.2: Bacteria

11.3.3: Fungi

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11.3.1: Viruses

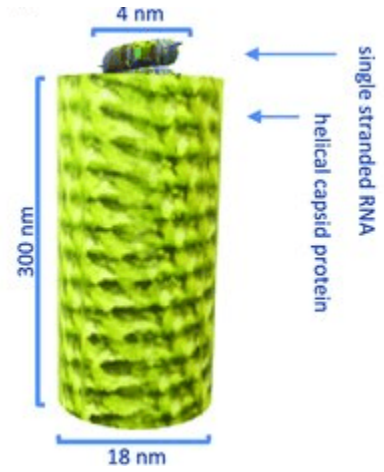


Figure 11-26. Typical plant virus consisting of single-strand RNA and proteins. Long Description: Plant virus consisting of a sheathing column of protein (capsid) and a single strand of RNA nested within the capsid. Overall size is 300 nm by 18 nm. (Carrillo-Tripp et al., 2009. CC-BY)

Plant viruses are obligatory intracellular parasites that do not have the molecular machinery to replicate without a host. A virus is not considered a living organism because it fails to meet several of the characteristics that define "life." They do not process energy, nor can they reproduce themselves. They are also acellular – meaning they lack a cellular structure that is characteristic of living organism. Most plant viruses are rod-shaped, with protein discs forming a tube surrounding the viral genome (Figure 11-26). They rarely have an envelope – a membrane like structure. The great majority have an RNA genome, which is usually small and single-stranded, but some viruses have double-stranded RNA, single-stranded DNA, or double-stranded DNA genomes. Viruses are estimated to annually cause $60 billion in lost crop yields worldwide.

Detection of viral infection depends completely on visible symptoms. Unfortunately, the symptoms displayed by plants infected with viruses vary greatly and depend on what physiological or metabolic pathways are blocked by insertion of viral nucleic acids or produced viral proteins. Common symptoms include yellow spots, necrotic spots, stunted growth, crinkling of leaf margins (Figure 11-27), abnormal growth, abnormal pigment deposition, and plant death. These symptoms should look familiar – they are nearly identical to those produced by some nutrient deficiencies. This makes virus detection difficult.



Figure 11-27. Leaf curl virus infecting a pepper plant. Long Description: Pepper plant infected with leaf curl virus. Older leaves demonstrate downward curving of margins. Younger leaves are wavy/crinkled in appearance. (Philarium, CC BY-SA 3.0, Link to Source [commons.wikimedia.org])

Most plant viruses are transmitted plant to plant via vectors. Vector transmission is often caused by piercing-sucking insects (for example, aphids and leaf hoppers), but some fungi, nematodes, and protozoa have been shown to be viral vectors. In many cases, the insect and virus are specific for virus transmission such as the beet leafhopper that transmits the curly top virus causing disease in several crop plants. Viruses have also been transmitted to a crop through contaminated seeds surfaces. While the seeds are dormant the virus cannot infect the plant tissue, but as soon as the seedling germinates it can infect the plant. Viruses can also be spread via equipment and human hands.

There is no chemical treatment for plant viruses. Heat treatments for seeds and some tissue can help prevent the spread of infections, but otherwise control is mostly through cultural practices.

- Keep vectoring pest to a minimum.
- Minimize damage to plants during cultivations since wounding increases susceptibility.
- Practice sterile technique when moving from plant to plant and location to prevent mechanical and human spreading of the potential viruses.
- When possible, purchase virus-tested and virus-free plant material so at least you start without the viruses being present. Additionally, there are some cultivars that have been bred to be resistant to some viruses.
- Most important, however, is to maintain sanitary growing conditions.

Sanitation and vector control are the best defense against viruses. If a plant looks unhealthy, you should remove it from the garden – do not compost it. Either burn it or send it to land field. Remove last year's plant residues – especially if you noticed any problems. Keep tools and equipment clean and sanitize between plants and fields.

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11.3.2: Bacteria

Bacteria are small, single-celled organism that reproduce through binary fission. They are prokaryotic cells and thus lack a nucleus or other membrane bound organelles. Most bacteria that are associated with plants are saprotrophic and do no harm to the plant itself. Some are beneficial to plant growth. However, a small number, around 100 known species, can cause disease. Phytopathogenic bacteria damage important food and fiber crops, resulting in major economic losses worldwide. Bacterial diseases are much more prevalent in subtropical and tropical regions of the world where warm temperatures allow them to flourish.

Phytopathogenic bacteria mainly enter plants through natural openings like stomata or wounds. Motility and high reproduction assist invasion and spread within plant tissues through the apoplast (the area between plant cells) of the plant and xylem. In order to be able to colonize the plant they have specific pathogenicity factors. Five main types of bacterial pathogenicity factors are known: uses of cell wall–degrading enzymes, toxins, effector proteins, phytohormones and exopolysaccharides. Enzymes like cellulases break down physical barriers. Toxins alter cell physiology or cause electrolyte leakage. Polysaccharides clog plant vascular tissues. Some bacteria inject effector proteins directly into plant cells to suppress defenses. For example, pathogens such as *Erwinia* species use cell wall–degrading enzymes to cause soft rot. *Agrobacterium* species change the level of auxins to cause tumors to form with phytohormones (Figure 11-28).



Figure 11-28. Gall (tumors) caused by *Agrobacterium tumefaciens*. (By Clemson University - USDA Cooperative Extension Slide Series, Bugwood.org - This image is Image Number 1436062 at Forestry Image CC BY-SA 3.0 us, Link to Source [commons.wikimedia.org]

Bacterial diseases have characteristic symptoms like vascular wilts, soft rots, leaf spots, scabs, and galls or tumors. Wilts cause drooping, yellowing, and death as bacteria clog water-conducting xylem. Soft rots affect fruits, tubers, and fleshy tissues, turning them mushy and slimy through cell wall-degrading enzymes. Leaf spots, often with distinct zonation, expand as bacteria multiply in the intercellular spaces. Scabs form corky, rough lesions on roots, tubers, and stems. Galls or knot-like overgrowths result from cell hyperplasia induced by bacterial toxins and hormones.

There is extremely limited chemical control of bacterial pathogens in plants. Some copper-based sprays have been effective, but resistance bacteria have arisen. The best control for bacterial diseases is to minimize factors that favor bacterial growth. Environmental factors influence bacterial plant diseases. Most bacteria prefer environments with high humidity, so try to keep humidity levels lower (when possible), limit moisture sitting on leaves (don't water late in the evening when water will sit on the leaves until then next day) and don't crowd plants so that there is poor air circulation around the plants to prevent pockets of air with high humidity. Plants transplanted in the wrong size pot (or those that have grown too large for a pot) can favor bacterial growth due to poor drainage or inadequate water holding. Any of the numerous other factors that can induce plant stress can make more favorable conditions for bacterial growth including fluctuations of water or temperature, low light intensity, deficiency, or excess application of nitrogen. Tissue injuries from wind, hail, insects, or cultural practices provide entry points.

Best practices should reduce pathogen populations and avoiding infection conditions. Good sanitation removes inoculum sources. Avoiding injury minimizes infection opportunities. Controlling irrigation can limit spread of waterborne bacteria. Promoting plant health through balanced fertilization and soil management practices will minimize disease. Implementation of crop rotation and use of resistant cultivars disrupt disease cycles. Protective chemicals include antibiotics, bactericides, and copper compounds can be used when appropriate. An integrated program combining cultural, physical, biological, and chemical tactics is most effective for controlling bacterial diseases. Understanding the nature of bacteria, their mechanisms of infection, and interactions with plants is key for effective integrated management of bacterial plant diseases.

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11.3.3: Fungi

Fungi comprise a diverse group of eukaryotic organisms that obtain nutrients by absorbing them from external sources (Figure 11-29). While many fungi form beneficial relationships with plants, some utilize plants as hosts and cause major diseases in food and fiber crops. Fungal pathogens employ novel infection strategies and diverse mechanisms to colonize, spread in, and damage plants. Managing fungal diseases is crucial for food security and requires integrated approaches based on understanding fungal biology.



Figure 11-29. Pin mold decomposing a peach. Long Description: Pin mold on a peach. Very fine hyphae growing across the surface of a peach. It has produced small, black spheres at the tips that will release spores for reproduction. (By Zephyris - Own work, CC BY-SA 3.0, Link to Source [commons.wikimedia.org]).

Fungi are unique in possessing **chitin** in their cell walls, storing carbohydrates as glycogen, and reproducing via spores. Filamentous fungi grow as multicellular structures called **hyphae** that extend through substrates. Hyphae intertwine to form **mycelia** that extract nutrients. Reproductive spores are produced in various structures; for example, rust fungi form teliospores on leaves. Spore dispersal enables rapid spread of fungi. Different spore types allow survival under adverse conditions.

Infection requires spore germination on plant surfaces and penetration through wounds or natural openings. Chemicals produced by the invading fungi, such as enzyme that degrade plant cuticle and cell walls as well as toxins and growth regulators, facilitate colonization. Some fungi form specialized feeding structures like haustoria that invaginate plant cell membranes to increase surface area for nutrient absorption and suppresses host defenses. Proliferation within plant tissues produces symptoms like wilts, blights, rusts, or smuts.

Fungal diseases reduce crop yields and quality. Pathogenic fungi can be categorized as either **biotrophic** fungal pathogens or **necrotrophic** fungal pathogens (Figure 11-30 and Figure 11-31). Biotrophic fungal pathogens colonize living plant tissue and obtain nutrients from living host cells, while necrotrophic fungal pathogens infect and kill host tissue and extract nutrients from the dead host cells. They can also be grouped according to their sign or symptom. **Vascular wilts** clog water-conducting vessels, causing leaves to wilt and, ultimately, death of the plant. **Blights** kill flower and fruit tissues. **Rusts** form reddish blister-like pustules on leaves, stems, and fruits. **Smuts** convert plant structures into black, powdery spore masses. **Rot fungi** cause fruits, bulbs, and tubers to become soft and watery. Even subtle quality losses can make products unmarketable.

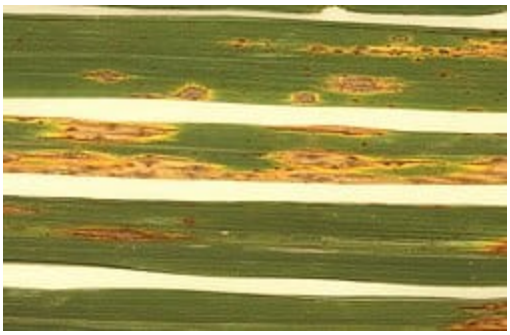


Figure 11-30. Rice blast, caused by a necrotrophic fungus. Leaf blades are shown with necrotic regions along their surface.(Public Domain, Link to Source [commons.wikimedia.org])



Figure 11-31. Powdery mildew, a biotrophic fungus. (Pollinator CC BY-SA 3.0, Link to Source [commons.wikimedia.org]).

Pathogenesis depends on complex interactions between the host, pathogen, and environment. Spores require favorable temperature, moisture, and often free water for germination and infection. Fungi thrive under humid conditions; rain and irrigation spread spores. Host susceptibility varies with age, physiology, and genetics. Resistant cultivars limit fungal colonization through physical and chemical defenses. Cultural practices also influence disease onset and spread.

Integrated pest management is essential for fungal disease suppression. As with other disease-causing agents, sanitation, crop rotation, and resistant varieties reduce inoculum levels and disrupt disease cycles. Avoiding injury to the plants limits opportunities for infections. Precision application methods optimize fungicide coverage and effectiveness. **Fungicides** are pesticides that kill or prevent the growth of fungi and their spores. Alternating fungicide modes of action helps prevent resistance. Balanced fertilization and plant health management reduce susceptibility. IPM uses predictive modeling to facilitate cultural and chemical practices that minimize crop loss.

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11.4: End of Chapter Review

In conclusion, plants face attack by diverse pathogens including insects, viruses, bacteria, and fungi. Pathogen persistence and adaptation drive ongoing crop losses and quality decreases. Sustainable plant disease management requires integrated approaches that combine cultural practices, plant resistance, biological controls, and protective chemicals based on comprehensive knowledge of pathogen biology and epidemiology. Continuing research to elucidate plant-pathogen relationships and translate findings into applied management will be crucial for securing global food production against evolving disease pressures. By implementing science-based integrated pest management programs, growers can effectively suppress multiple plant pathogens while safeguarding economic viability and ecological health.

Chapter Summary

This chapter focuses on pests and diseases that impact plant growth and crop yields. Weeds compete with crops for resources like water, nutrients, and light. Their fast growth, prolific seed production, and persistence make them challenging to control. Integrated management combines cultural practices like crop rotation, mechanical removal, mulching, and judicious herbicide use.

Insects inflict damage while feeding on plants as herbivores. Chewing and sucking insects affect leaves, stems, roots, and fruits. Their small size, rapid reproduction, and mobility enable them to spread and overwhelm plants. Biological control, physical exclusion, insecticides, and cultural practices are employed to minimize insect pest impacts.

Plant viruses depend on hosts to replicate and spread via insects, nematodes, fungi, or contaminated tools and hands. They disrupt plant processes, stunting growth and causing abnormal symptoms. Control focuses on sanitation and vector management. Bacteria also cause wilts, rots, and leaf spots in warm, humid conditions. Avoiding overwatering and tissue damage limits bacterial infection opportunities. Fungi secrete degrading enzymes and toxins to extract nutrients from living or dead plant cells. Integrated management of fungal diseases requires balancing cultural practices, resistant varieties, and fungicides to suppress spore production and dispersal while avoiding resistance.

By monitoring and understanding pest and pathogen biology, growers can implement integrated pest management programs that use cultural, biological, and chemical controls in a combined manner to effectively minimize crop losses while protecting environmental and human health.

Key Terms

- Biennial
- Biotrophic
- Broad-spectrum herbicide
- Contact herbicide
- Frass
- Fungicides
- Galls
- Honeydew
- Hypha
- Integrated Pest Management (IPM)
- Mycelium
- Necrotrophic
- Nymphs
- Perennial
- Post-emergent
- Pre-emergent
- Sclerotia
- Selective herbicide
- Signs
- Solarization

- Symptoms
- Systemic herbicide
- Vectors
- Weed

Self-Review

1. What are some common characteristics that make a plant more likely to be classified as a weed?
2. How do annual, biennial, and perennial weeds differ in their life cycles?
3. What are some examples of cultural weed control methods?
4. How do contact herbicides differ from systemic herbicides in their mode of action?
5. What is integrated pest management and what tactics does it combine?
6. How do insects with chewing mouthparts damage plants compared to those with piercing-sucking mouthparts?
7. What are the differences between incomplete and complete metamorphosis in insects?
8. Name some common insect pests and the type of damage they cause.
9. What conditions favor growth and spread of bacterial plant pathogens?
10. How do biotrophic fungal pathogens differ from necrotrophic fungal pathogens?
11. What types of structures do fungi use to infect and feed on host plants?
12. What are some visible disease signs caused by fungal pathogens?
13. How are plant viruses spread from plant to plant?
14. Why is sanitation important for controlling plant viruses and bacteria?
15. What integrated management tactics can help control insect pests?

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Answers to Chapter Self Review Questions

Chapter 1: Answers to Self-Review Questions

1. The main organs of a plant are roots, stems, leaves, and flowers.
2. The three main types of plant tissues are dermal, ground, and vascular tissues.
3. The two main steps of photosynthesis are the light-dependent reactions and the light-independent/Calvin cycle reactions.
4. Roots anchor the plant, absorb water and nutrients, and store food. Stems provide support, transport water and nutrients, and in some cases store food. Leaves are the main site of photosynthesis.
5. Plant anatomy examines the physical structure of plants while plant physiology looks at the functions and processes that allow plants to live and grow.
6. The scientific name of a plant species consists of the genus name and specific epithet.
7. Plant taxonomy studies the evolution of plants and their genetic relationships.
8. Horticulturists use techniques like seed germination, cuttings, grafting, layering, and tissue culture to propagate plants.
9. As primary producers, plants harvest sunlight, convert inorganic molecules to organic ones, produce oxygen, and form the base of most food chains.
10. Plant roots hold soil in place and plant litter protects soil from erosion. This prevents nutrient loss and runoff.
11. Humans use plants for food, medicine, textiles, lumber, paper, and fuel.
12. Cotton, flax, hemp, jute, and bamboo are major plant fibers used to make textiles.
13. Lumber keeps the wood intact while paper production involves extracting cellulose fibers by removing lignin.
14. Biodiesel is fuel made from plant/animal oils. Bioethanol is alcohol fuel made from plant carbohydrates.
15. The main categories are vegetable oils, infused/macerated oils, and essential oils.

Chapter 2: Answers to Self-Review Questions

1. Taxonomy and binomial nomenclature provide a standardized system to classify, name, and identify organisms. This allows scientists to precisely communicate about specific species.
2. In nonvascular plants the gametophyte stage is dominant and independent. In vascular plants the sporophyte is dominant, and the gametophyte is small and dependent on the sporophyte.
3. Vascular tissue allowed for the transport of water and nutrients to tall plants. Seeds and flowers allowed reproduction without external water and improved dispersal.
4. Three key adaptations were vascular tissue, stomata/cuticle, and roots.
5. The main bryophyte groups are liverworts, mosses, and hornworts.
6. Seedless vascular plants have true roots and leaves while nonvascular plants lack both. Leaves evolved as microphylls and megaphylls.
7. Heterosporous plants produce two types of spores - microspores and megaspores. This allowed the retention of the gametophyte stage on the parent plant.
8. Key adaptations of seeded plants are: reduced gametophytes, pollen, seeds, and secondary growth.
9. The four living gymnosperm groups are cycads, ginkgo, gnetophytes, and conifers.
10. Gymnosperms lack ovaries or fruits so seeds are "naked." Pollen also lacks a tubular wall.
11. Basal angiosperm features are: numerous floral parts, lack of specialized organs, simple leaves, primitive reproductive structures.
12. Magnoliids have primitive, undifferentiated floral organs, alternate phyllotaxy, and tracheids.
13. Monocot characteristics: single cotyledon, parallel leaf veins, scattered vascular bundles, trimerous flowers, fibrous roots.
14. Characteristics to distinguish monocots and eudicots include: cotyledons, leaf veins, floral organ number, and root structure.
15. Examples of co-evolution are bee orchids mimicking female bees or Rafflesia flowers smelling like rotting meat to attract fly pollinators.

Chapter 3: Answers to Self-Review Questions

1. The three main types of plant cells are parenchyma, collenchyma, and sclerenchyma. Parenchyma cells have thin, flexible walls and are usually living at maturity. They carry out most metabolic functions. Collenchyma cells have unevenly thickened walls and provide structural support. Sclerenchyma cells have thick secondary walls containing lignin and are dead at

maturity. They provide strength and support.
2. The main tissues in leaves are the upper and lower epidermis, mesophyll, and vascular bundles. The epidermis helps prevent water loss with its waxy cuticle. The mesophyll performs photosynthesis. Vascular bundles transport water, minerals, and sugars.
3. Xylem transports water and minerals from roots to shoots using dead cells. Phloem transports sugars and organic compounds between tissues bidirectionally using living cells. Xylem cells have thicker, lignified secondary cell walls while phloem cells have thinner primary walls.
4. Monocot stems have scattered vascular bundles while eudicot stems have vascular bundles arranged in a ring. This relates to the arrangement of xylem and phloem tissues within the vascular bundle.
5. The main vegetative organs are roots, stems, and leaves. Roots absorb water and minerals and anchor the plant. Stems provide structural support and connect roots to leaves. Leaves are the main site of photosynthesis.
6. Meristematic tissue contains cells that actively divide to produce new cells for growth. It is located at shoot and root tips, in vascular cambium, and in lateral meristems.
7. The four floral organs of a complete flower are sepals, petals, stamen, and carpels. Their arrangement from outermost to innermost is sepals, petals, stamen, carpels.
8. Fruits develop from the ovary after fertilization. Main types are simple, aggregate, multiple, and accessory fruits. Examples: simple - peach, aggregate - blackberry, multiple - pineapple, accessory - apple.
9. The three main parts of seeds are the embryo, food reserves, and seed coat. The embryo forms the new plant. Food reserves nourish the embryo. The seed coat protects the embryo.
10. Dormancy is broken and germination triggered when internal hormone balance changes in response to environmental cues like water, temperature, or light.
11. Stages of germination: imbibition, seed coat rupture, radicle emergence, cotyledon emergence, first true leaf.
12. A node is a point on a stem where leaves, buds, and branches are attached.
13. Alternate phyllotaxy means leaves are arranged singly at nodes, minimizing overlap of adjacent leaves. This allows maximum light exposure.
14. Adaptations to reduce water loss include waxy cuticles, stomata closure, trichomes, thicker cuticles, reduced surface area.
15. Seeds are dispersed by wind, animals externally or internally, expulsion mechanisms, and water. Examples: wind - maple samaras; animals - fleshy fruits; expulsion - peas popping out of pods.

Chapter 4: Answers to Self-Review Questions

1. Chloroplast
2. ATP, NADPH, O2
3. RuBisCO
4. Carbon fixation, reduction, regeneration of RuBP
5. Mitochondria
6. 2 ATP, 2 NADH, 2 pyruvate
7. 28-32
8. Transpiration cohesion-tension forces
9. Stomata
10. Guard cells
11. Phloem
12. Translocation
13. Extremely low concentrations
14. Cytokinins
15. Abscisic acid

Chapter 5: Answers to Self-Review Questions

1. PAR wavelengths range from 400-700 nm.
2. Blue and red wavelengths tend to be most effective for photosynthesis.
3. As wavelength increases, frequency and photon energy decrease. They are inversely related.
4. PPFD (µmol/m2/s) measures instantaneous light levels. DLI (mol/m2/day) measures daily light accumulation.
5. As light passes through a canopy, red light is preferentially absorbed, shifting the spectrum toward blue/green.
6. Chlorophyll a absorbs blue and red light. Chlorophyll b absorbs blue and orange light.
7. A phytochrome is a photoreceptor molecule that exists as Pr (absorbs red) and Pfr (absorbs far-red) forms.
8. Long day plants flower with short nights (<critical dark period). Short day plants need long nights to flower.

9. Phototropism involves auxin accumulating on the shaded side, causing differential growth toward light.
10. Humans can use shading, supplemental lighting, photoperiodic lighting, or sole-source lighting.
11. Shade cloths block excess sunlight before it enters a greenhouse, providing cooling.
12. Supplemental lighting boosts PPFD, photoperiodic alters daylength, and sole-source provides total light needs.
13. LEDs efficiently produce specific wavelengths. HPS lamps inefficiently produce broad orange/red spectra.
14. Incandescent lamps would be used for photoperiodic lighting because they emit high levels of red light.
15. The incandescent bulb would cost $0.324 per day to operate than the 25W LED (over $118 more per year).

Chapter 6: Answers to Self-Review Questions

1. Liquid, solid, gas
2. Hydrogen bonding
3. Stabilizes temperatures
4. Evaporation, condensation, precipitation
5. Erosion and deposition
6. Metabolism, rigidity, growth, temperature regulation
7. Sunken stomata, thick cuticle, reduced leaf surface area
8. C_4 and CAM photosynthesis
9. More water needed during growth flushes and fruit development
10. Direct deposition of moisture; fog drip
11. Dams, groundwater pumping, paving land, pollution
12. Crop type, growth stage, climate
13. Droplet size, precise targeting of water to roots
14. Timers, moisture sensors, rain detectors
15. Changing precipitation patterns could lead to drought stress in species adapted to historic norms.

Chapter 7: Answers to Self-Review Questions

1. The four main components that make up soil are mineral matter, organic matter, air, and water.
2. Physical weathering mechanically breaks down parent material. Chemical weathering alters rocks and minerals through chemical reactions. Biological weathering is caused by organisms like lichens and plant roots secreting acids.
3. The three main soil particle sizes that determine texture are sand, silt, and clay.
4. Coarse, sandy soils drain quickly leading to more nutrient leaching while fine clayey soils hold water more leading to compaction issues. Loams balance water drainage and retention.
5. Soil structure refers to the arrangement of particles into aggregates. Aggregates create both large and small pore spaces.
6. O- Organic accumulation; - A- Surface layer with organic matter incorporated; - B- Zone of illuviation and accumulation; - C- Little affected parent material; - R- Consolidated bedrock.
7. Soil pH impacts the availability of essential nutrients like N, P, K, Ca, Mg, S, Fe, and B.
8. CEC is the ability of soil to bind cations like Ca, Mg, and K and make them available for plant uptake when displaced by H+ ions.
9. Bacteria transform and fix nitrogen, solubilize phosphorus, produce plant hormones, contribute to soil structure development.
10. The fungi colonize plant roots and extend their reach, enhancing water and nutrient uptake in exchange for carbohydrates from the plant.
11. Earthworms till and aerate soil while facilitating water movement, root growth and nutrient mineralization through their burrows and castings.
12. They feed on microbes, regulating populations and releasing nutrients from their waste.
13. Over time, their burrowing systems create landscape level soil diversity through loosening, mixing, and redistributing soil components.
14. Microbes drive nutrient transformations and cycling. Disturbances to microbial communities disrupt ecosystem functions.
15. Chemical inputs, physical mixing, lack of diversity, and nutritional depletion.

Chapter 8: Answers to Self-Review Questions

1. For a mineral nutrient to be classified as "essential", its deficiency must cause abnormal growth, failure to complete the life cycle, or premature death. Also, the nutrient cannot be replaced by any other element.
2. Main methods to analyze plant mineral levels: atomic absorption spectroscopy, ICP-OES, Kjeldahl, titration, colorimetric,

enzymatic analysis.
3. Macronutrients like N, P, K are needed in higher amounts (percent dry weight). Micronutrients like Fe, B, Mo are only needed in small amounts (ppm).
4. Chlorosis is due to insufficient chlorophyll. Necrosis is tissue death/browning from severe deficiency.
5. Mobile nutrients (N, P, K) show deficiencies in old leaves since they move out of them. Immobile nutrients (Ca, Fe) deficiencies show in young tissues.
6. Nitrogen roles: component of proteins, nucleic acids, chlorophyll; needed for plant growth and metabolism.
7. Phosphorus deficiency symptoms: reduced growth, dark foliage, reddish leaves, delayed maturity, weak stems, less seed production.
8. Potassium helps regulate water balance via stomata and makes cell walls more rigid for disease resistance.
9. Blossom-end rot in fruits is caused by inadequate calcium reaching developing fruit tips.
10. Magnesium is central atom in chlorophyll, so it facilitates chlorophyll production needed for photosynthesis.
11. Sulfur compounds influence flavor profile, so sulfur deficiency causes fruits/vegetables to taste blander.
12. Acid-loving plants have higher iron demand since iron availability is low in neutral/alkaline soils.
13. A complete fertilizer contains N, P, K. An incomplete fertilizer provides only 1 or 2 of those nutrients.
14. Synthetic fertilizers - easily applied, nutrients immediately available, leachable. Organic - release nutrients slowly, less leaching, can improve soil.
15. Soil amendments adjust soil conditions like texture, drainage, and pH to improve plant nutrient availability.

Chapter 9: Answers to Self-Review Questions

1. Lower cost, wider variety availability, ability to save seeds.
2. Conduct a germination test by placing a sample of seeds on damp paper towels and monitoring germination rate.
3. Stratification exposes seeds to cold, moist conditions to break dormancy. Scarification weakens the seed coat to allow water uptake.
4. Direct seeding sows directly into the ground; transplants are started indoors and moved outside later.
5. Hardening off gradually exposes seedlings to outdoor conditions over 2 weeks to prepare for transplanting.
6. Vegetative techniques use plant parts like stems, leaves, etc. to produce clones of the parent plant.
7. Softwood cuttings are from new growth in spring. Semi-hardwood cuttings are from current season in summer. Hardwood are from dormant stems in fall/winter.
8. During active growth in spring or early summer.
9. Remove a ring of bark, wrap with moss, seal with plastic, cut off new plant after rooting.
10. Sectioning divides bulbs/corms into pieces with meristem tissue to grow new bulbs. Scoring makes cuts in basal plate.
11. Each crown section must have roots and growth buds.
12. Combine desired aboveground traits with adaptive root traits; produce dwarf trees; rejuvenate old trees.
13. A T-shaped cut is made in rootstock bark and a single bud is inserted to grow into a new variety.
14. Joining similar diameter rootstock and scion with slanted cut; used for young trees/shrubs.
15. Grafting scions above and below damage allows flow of water and nutrients to restore growth.

Chapter 10: Answers to Self-Review Questions

1. Subsistence agriculture aims to provide food for the farmer's household and livestock fodder, with minimal crops sold for profit.
2. Home gardens provide supplemental food, nutrition, and income by efficiently integrating multi-crop cultivation and livestock near family dwellings.
3. Crop rotation, intercropping, green manures, compost, and animal manure help maintain soil fertility in traditional systems.
4. High-intensive commercial farming utilizes mechanized equipment for tillage, planting, irrigation, harvesting, and materials handling.
5. Monoculture cropping can lead to declining soil fertility, increased pest/disease pressure, and vulnerability to weather extremes.
6. Crop rotation improves soil health by diversifying nutrients used by plants and disrupting pest/disease life cycles.
7. Plastic mulch warms the soil, reduces weeds/evaporation, and improves crop cleanliness and yields.
8. Polythene greenhouses allow climate control to optimize light, temperature, humidity, and air circulation for improved growth.
9. Deep water culture uses a reservoir, submersible pump, and air stones to oxygenate and circulate a nutrient solution for suspended roots.
10. Nutrient film technique channels a thin film of nutrients along sloped channels where plant roots are suspended.
11. The high infrastructure costs make hydroponics best suited for high-value vegetables, fruits, flowers, and ornamentals.

12. Raised beds improve drainage and allow tailored soil amendment for each crop's needs.
13. Straw bales are conditioned by adding nitrogen fertilizer and watering for 10-14 days before planting into the decomposing bale.
14. Permaculture principles include valuing diversity, enhancing beneficial connections, closed resource loops, and cooperating with natural cycles.
15. Permaculture or home garden systems aim for sustainably and intensively produce food on a small scale.

Chapter 11: Answers to Self-Review Questions

1. Fast growth, prolific seed production, small seeds easily dispersed, short lifecycles, adaptability.
2. Annuals complete lifecycle in one year, biennials take two years, perennials persist for multiple years via root systems
3. Crop rotation, competitive planting, cover crops, adjusting row spacing/density
4. Contact herbicides disrupt cells on foliage contact, systemic herbicides translocate throughout plant tissues.
5. IPM combines monitoring, cultural, biological, and chemical controls in a combined approach.
6. Chewing insects eat plant tissues while piercing-sucking insects extract sap fluids.
7. Incomplete metamorphosis has gradual nymph changes; complete metamorphosis has distinct larva and adult forms
8. Aphids, mites - sap feeding; caterpillars - chewing damage; beetles - skeletonizing; scales - sap feeding.
9. Warm, humid conditions; moisture sitting on leaves; overwatering; plant wounds.
10. Biotrophs colonize living tissue, necrotrophs kill host cells then feed on dead tissue.
11. Spores, hyphae, mycelium, haustoria.
12. Mycelium, sporangia, sclerotia, fungal fruiting structures.
13. Insect vectors, nematodes, fungi, contaminated tools/hands.
14. Removes inoculum sources and prevents spread via contaminated surfaces.
15. Biological control, row covers/netting, traps, cultivation, insecticides.

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GLOSSARY

A

Abscisic Acid | A phytohormone (ABA) that helps plants respond to stress, for example by closing stomata during drought, and that maintains seed and bud dormancy. It often works against growth-promoting hormones. [Chapter 4]

Absorbance spectrum | A graph showing how strongly a pigment, such as chlorophyll *a* or *b*, absorbs light at each wavelength. [Chapter 5]

Action spectrum | A graph showing the physiological activity, such as the rate of photosynthesis, produced in response to different wavelengths of light. [Chapter 5]

Adhesion | The attraction of water molecules to other substances, such as the cell walls of xylem vessels. It helps hold the water column in place so it does not slip back down. [Chapters 4, 6]

Adventitious roots | Roots that develop from non-root tissue, such as stems or leaves. [Chapter 9]

Aggregates | Clumps of soil particles bound together by organic matter, clay, and microbial products. Aggregates create soil structure and pore space. [Chapter 7]

Alternation of Generations | A plant life cycle in which a multicellular haploid stage (the gametophyte) alternates with a multicellular diploid stage (the sporophyte). [Chapter 2]

Anatomy | The study of the internal structure of plants, including their cells, tissues, and organs. [Chapter 1]

Angiosperms | Flowering plants. Seed plants whose seeds develop enclosed within an ovary that matures into a fruit. [Chapter 2]

Aquifer | An underground layer of rock, sand, or gravel that holds groundwater and from which water can be drawn by wells. [Chapter 6]

Asexual reproduction | Reproduction without seeds or the fusion of gametes, producing offspring that are genetically identical to the parent. See vegetative reproduction. [Chapter 9]

Auxins | A class of phytohormones present in all plant tissues that promote cell elongation and are involved in phototropism, apical dominance, and root formation. 2,4-D is a synthetic auxin. [Chapter 4]

B

Bacteria | Single-celled microorganisms that are the most abundant soil organisms (billions per gram of fertile soil). They decompose organic matter, cycle nutrients, and some fix nitrogen. [Chapter 7]

Banding | A fertilizer application method in which fertilizer is placed in a band near or beside the rows of plants, within reach of the roots but not across the whole field. Also called side dressing. [Chapter 8]

Basal application | Fertilizer that is broadcast over a field and worked into the soil before planting. [Chapter 8]

Bedrock | The solid rock beneath the soil horizons; hard bedrock is designated R and is not considered soil. [Chapter 7]

Biennial | A plant with a two-year life cycle that grows vegetatively the first year and flowers, sets seed, and dies the second year. [Chapter 11]

Binomial nomenclature | The two-part system for naming species, made up of the genus name followed by the specific epithet (for example, *Hydrangea quercifolia*). [Chapter 2]

Biotrophic | Describes a pathogen that colonizes living plant tissue and obtains nutrients from living host cells. [Chapter 11]

Broad-spectrum herbicide | An herbicide that targets pathways common to all plants and so kills all vegetation, such as glyphosate. [Chapter 11]

Broadcasting | Spreading fertilizer (or seed) uniformly over an entire area. [Chapter 8]

Bryophytes | A general term for the nonvascular land plants: the mosses, liverworts, and hornworts. Their life cycle is dominated by the gametophyte. [Chapter 2]

Bulb | A short underground stem surrounded by fleshy, food-storing leaves (scales), as in onions and lilies. [Chapter 9]

C

Calvin Cycle | The light-independent reactions of photosynthesis, which take place in the stroma of the chloroplast and use ATP and NADPH to fix carbon dioxide into sugars. [Chapter 4]

Cambium | A layer of meristematic tissue in stems and roots that produces new vascular tissue. In grafting, the cambium of the scion and rootstock must be aligned. [Chapter 9]

Carpels | The female reproductive organs of a flower; modified leaves that enclose the ovules. A pistil can be made of a single carpel or several

fused carpels. [Chapter 3]

Cation exchange capacity | The ability of a soil to hold and release positively charged nutrients (cations) such as potassium, calcium, and ammonium so that they are available to plants. [Chapter 7]

Cell Wall | The rigid layer, made mainly of cellulose, that surrounds a plant cell and provides structural support and protection. [Chapter 1]

Cellular Respiration | The process that breaks down glucose in the presence of oxygen to produce ATP. It takes place in the mitochondria and involves glycolysis, the Krebs cycle, the electron transport chain, and chemiosmosis. [Chapter 4]

Chemiosmosis | The final stage of cellular respiration (and of the light reactions), in which hydrogen ions flow back across a membrane through ATP synthase, powering the production of ATP. [Chapter 4]

Chlorophyll | The green, light-absorbing pigment in the thylakoid membranes of chloroplasts. It absorbs mainly red and blue light and reflects green light. [Chapter 4]

Chloroplast | The organelle in plant cells where photosynthesis takes place. Its thylakoid membranes contain the light-absorbing pigment chlorophyll. [Chapters 1, 4]

Chlorosis | Yellowing of leaf or stem tissue due to a lack of chlorophyll formation or a loss of chlorophyll; a common symptom of nutrient deficiency. [Chapter 8]

Clay | The smallest soil particles, less than 0.002 mm (2 µm) in diameter. Clay packs tightly, has small pore spaces, and holds water and nutrients well. [Chapter 7]

Co-evolution | The process by which two or more interacting species, such as flowering plants and their insect pollinators, evolve in response to each other. [Chapter 2]

Cohesion | The attraction of water molecules to one another through hydrogen bonding. It creates a strong, continuous column of water in the xylem (the basis of the cohesion-tension theory). [Chapters 4, 6]

Collenchyma cells | Plant cells that are alive at maturity and have only a primary cell wall that is unevenly thickened. They provide flexible support to growing stems and leaves. [Chapter 3]

Complete fertilizer | A fertilizer that contains all three major nutrients: nitrogen (N), phosphorus (P), and potassium (K). [Chapter 8]

Condensation | The change of water vapor into liquid water, as when clouds or dew form. It is a step in the water cycle. [Chapter 6]

Contact herbicide | An herbicide that kills only the plant tissue it touches, such as paraquat. [Chapter 11]

Cotyledons | The seed leaves of a plant embryo. They may store food or absorb it from the endosperm; monocots have one cotyledon and eudicots have two. [Chapter 3]

Crop rotation | Growing a different crop on the same land in a planned sequence over seasons or years to improve soil health and disrupt pest and disease life cycles. [Chapter 10]

Crown division | Propagating herbaceous perennials by cutting or pulling apart the crown (the base of the plant where shoots and roots meet) into sections, each with shoots and roots. [Chapter 9]

Cuticle | A waxy, non-cellular layer secreted by the epidermal cells that covers the aerial surfaces of a plant and greatly reduces water loss. [Chapters 3, 6]

Cutting | A piece of stem, leaf, or root removed from a parent plant and induced to form adventitious roots and shoots, producing a new plant. [Chapter 9]

Cytokinins | A class of phytohormones that promote cell division. They are made in actively growing tissues like roots and shoots and can move to other parts of the plant. [Chapter 4]

D

Daily light integral | The total amount of photosynthetically active light (PAR) received by plants over one day, measured in moles of light per square meter per day (mol/m^2/day). [Chapter 5]

Deep water culture | A hydroponic technique (DWC) in which plant roots hang in an oxygenated nutrient solution. [Chapter 10]

Denitrification | The conversion of nitrate in the soil to nitrogen gas by denitrifying bacteria, which returns nitrogen to the atmosphere and makes it unavailable to plants. [Chapter 8]

Deposition | The laying down of soil, sediment, or rock carried by water (or wind). Together with erosion it shapes landscapes such as the Grand Canyon. [Chapter 6]

Dermal tissue | The outer protective tissue system of the plant (the epidermis, or bark in older woody plants). It is the plant's first line of defense. [Chapter 3]

Dormancy | A resting state in which a seed (or other plant part) does not germinate or grow even when conditions are suitable. In seeds it is controlled and maintained by a balance of hormones. [Chapter 3]

Drought | A prolonged period of below-normal precipitation that results in a water shortage for plants, people, and ecosystems. [Chapter 6]

E

Earthworms | Soil macrofauna that burrow through and ingest soil and organic matter. They mix the soil, create channels for air and water, and leave nutrient-rich castings. [Chapter 7]

Ebb and flow | A closed hydroponic technique, also called flood and drain, in which the roots are periodically flooded with nutrient solution that is then drained away. [Chapter 10]

Ecology | The study of organisms and their interactions with one another and with their environment. Plant ecology focuses on plants and their environment. [Chapter 1]

Ecosystem function | The overall processes of an ecosystem, such as nutrient cycling, water regulation, and plant production, that are supported by the soil's living and non-living components. [Chapter 7]

Electrical conductivity | A measure of the dissolved salts in a nutrient solution or soil; it is used to monitor fertilizer concentration in hydroponic and container production. [Chapter 10]

Electromagnetic spectrum | The full range of electromagnetic radiation, from long radio waves to short gamma rays. Visible light (about 400–700 nm) is only a small part of it. [Chapter 5]

Electron Transport Chain | A series of electron acceptors in a membrane that pass electrons from NADH and $FADH_2$ (or from light-excited chlorophyll) along, using the energy to pump hydrogen ions across the membrane. [Chapter 4]

Endosperm | Nutritive tissue in a seed that feeds the developing embryo. In angiosperms it is formed by a second fertilization. [Chapter 3]

Epidermis | The outermost layer of cells covering the leaves, young stems, and roots of a plant. It protects the plant and contains stomata for gas exchange. [Chapter 3]

Erosion | The wearing away and removal of soil and rock by water, wind, or ice. [Chapter 6]

Essential Nutrients | The chemical elements a plant must have to complete its life cycle. They are divided into macronutrients and micronutrients. [Chapter 8]

Ethylene | A gaseous phytohormone involved in fruit ripening, senescence, and abscission. It is autocatalytic: exposure to ethylene triggers more ethylene production. [Chapter 4]

Eudicots | The largest group of flowering plants. They typically have two cotyledons, net-veined leaves, floral parts in fours or fives, vascular bundles arranged in a ring, and a taproot system. [Chapter 2]

Evaporation | The change of liquid water into water vapor. Along with transpiration it moves water from land and water surfaces into the atmosphere. [Chapter 6]

F

Fertigation | The application of fertilizers through the irrigation (watering) system. [Chapter 8]

Flower | The reproductive structure of angiosperms. A complete flower has four floral organs: sepals, petals, stamens, and carpels. [Chapters 1, 2]

Foliar feeding | Applying a fertilizer solution directly to plant leaves, where it is absorbed. It gives a quick response but supplements rather than replaces soil fertilization. [Chapter 8]

Frass | The excrement of insects, often along with shed exoskeletons; a sign of insect activity. [Chapter 11]

Fungi | Organisms that grow as networks of thin filaments (hyphae). In soil they decompose organic matter and can form beneficial mycorrhizal partnerships with roots; some are plant pathogens. [Chapter 7]

Fungicides | Pesticides that kill or prevent the growth of fungi and their spores. [Chapter 11]

G

Galls | Abnormal, knot-like overgrowths of plant tissue caused by bacteria, fungi, insects, or other organisms. [Chapter 11]

Gametophyte | The haploid, gamete-producing generation in the plant life cycle. It is dominant in bryophytes and greatly reduced in seed plants (for example, pollen grains are male gametophytes). [Chapter 2]

Genus | The taxonomic rank above species and below family. The genus name is the first part of a species' two-part scientific name. [Chapter 1]

Germination | The process by which a seed embryo resumes growth and develops into a seedling, beginning with water uptake (imbibition) and emergence of the radicle. [Chapter 3]

Gibberellins | A class of phytohormones (GAs) that promote stem elongation, seed germination, and flowering. They were first discovered in fungus-infected rice plants. [Chapter 4]

Glycolysis | The first stage of extracting usable energy from glucose. It takes place in the cytoplasm and splits glucose into two three-carbon pyruvate molecules. [Chapter 4]

Grafting | A technique that joins parts of two or more plants (usually a scion and a rootstock) so that they unite and grow as a single plant. [Chapter 9]

Green manures | Cover crops grown to protect the soil from erosion and then tilled into the soil to add organic matter and nutrients. [Chapter 10]

Ground tissue | The tissue system that makes up most of the plant body and is neither dermal, vascular, nor meristematic. It carries out photosynthesis, storage, and support. [Chapter 3]

Guard cells | The pair of specialized epidermal cells that surround each stoma. They control the size of the stomatal pore: turgid guard cells open the pore and flaccid guard cells close it. [Chapter 4]

Gymnosperm | A seed plant whose seeds are not enclosed in an ovary or fruit; they are often borne on cones. Examples include conifers, cycads, and ginkgo. [Chapter 2]

H

Honeydew | A sugary, sticky liquid excreted by piercing-sucking insects such as aphids, which often supports the growth of black sooty mold. [Chapter 11]

Horizon | A distinct layer of soil, roughly parallel to the surface, with its own color, texture, and structure. Major horizons are labeled O, A, E, B, C, and R. [Chapter 7]

Horticulture | The science and art of growing, propagating, and managing cultivated plants such as fruits, vegetables, flowers, and ornamentals. [Chapter 1]

Hydrogen bond | A relatively weak attraction between the partial positive charge of a hydrogen atom in one molecule and the partial negative charge of an atom (such as oxygen) in another. Each water molecule can form up to four. [Chapter 6]

Hydroponics | A method of growing plants without soil, with the roots supplied by mineral nutrients dissolved in water. [Chapters 8, 10]

Hypha | A single thread-like filament of a fungus. A mass of hyphae forms the mycelium. [Chapter 11]

I

Immobile nutrients | Nutrients, such as calcium, iron, sulfur, and most micronutrients, that cannot be moved from older tissues to new growth. Their deficiency symptoms appear first in young tissues. [Chapter 8]

Incandescent lamps | Lamps that produce light when electricity passes through a wire filament and heats it. They give off much of their energy as heat and are mainly used for photoperiodic lighting. [Chapter 5]

Incomplete fertilizer | A fertilizer that supplies only one or two of the three major nutrients (N, P, K). [Chapter 8]

Integrated pest management | A pest control approach that combines monitoring, multiple tactics (cultural, biological, physical, and chemical), and careful pesticide use to manage pests economically and ecologically. [Chapter 11]

Intercropping | Growing two or more crops together in the same field at the same time. [Chapter 10]

Internodes | The sections of a stem between two nodes. [Chapter 3]

Irrigation | The controlled application of water to plants or crops to supplement natural precipitation. [Chapter 6]

K

Krebs Cycle | The second stage of cellular respiration, also called the citric acid cycle. It takes place in the mitochondrial matrix and produces the electron carriers NADH and $FADH_2$, releasing carbon dioxide. [Chapter 4]

L

Layering | A propagation technique in which roots are formed on a stem while it is still attached to the parent plant (for example, ground layering and air layering). [Chapter 9]

Leaf | A vegetative organ, usually flat and green, that is the main site of photosynthesis and gas exchange in most plants. [Chapter 1]

LED lamps | Light-emitting diode lamps. They are energy-efficient, produce little heat, and can be designed to emit specific wavelengths for plant growth. [Chapter 5]

Light compensation point | The light level at which a plant's rate of photosynthesis equals its rate of respiration, so there is no net gain in carbohydrates. [Chapter 5]

Light saturation point | The light level above which further increases in light no longer increase the rate of photosynthesis. [Chapter 5]

Light-dependent reactions | The first set of photosynthesis reactions, which take place in the thylakoid membranes. They capture light energy and convert it into chemical energy (ATP and NADPH), releasing oxygen. [Chapter 4]

Light-independent reactions | The second set of photosynthesis reactions (the Calvin cycle), in which ATP, NADPH, and CO_2 are used to build carbohydrates. [Chapter 4]

M

Macrofauna | Soil animals large enough to see with the naked eye, such as earthworms, ground beetles, termites, and millipedes, that break up organic matter and improve soil structure. [Chapter 7]

Macronutrients | Essential nutrients needed by plants in relatively large amounts, such as nitrogen, phosphorus, potassium, calcium, magnesium, and sulfur. [Chapter 8]

Meristematic tissue | Tissue made of undifferentiated cells whose main function is to divide and produce new cells. It is found as apical meristems, intercalary meristems, and the vascular cambium. [Chapter 3]

Mesophyll | The photosynthetic ground tissue inside a leaf, located between the upper and lower epidermis. In many eudicots it is divided into palisade and spongy mesophyll. [Chapter 3]

Metal halide lamps | High-intensity discharge lamps (MH) that produce a broad, bluish-white spectrum that looks closer to natural sunlight than high pressure sodium lamps. [Chapter 5]

Microbial communities | The populations of bacteria, fungi, and other microorganisms living together in the soil that support soil fertility and plant growth. [Chapter 7]

Micronutrients | Essential nutrients needed by plants in only very small (trace) amounts, such as iron, manganese, zinc, copper, boron, molybdenum, and chlorine. [Chapter 8]

Mineral matter | The inorganic portion of soil (sand, silt, and clay) formed by the weathering of rocks and minerals. It makes up about 45% of the volume of a typical soil. [Chapter 7]

Mobile nutrients | Nutrients, such as nitrogen, phosphorus, potassium, and magnesium, that can be moved from older tissues to new growth. Their deficiency symptoms appear first in older, lower leaves. [Chapter 8]

Monocots | A group of flowering plants with a single cotyledon, parallel leaf veins, scattered vascular bundles, floral parts in threes, and fibrous roots. [Chapter 2]

Monoculture | Growing a single crop species over a large area, often year after year. [Chapter 10]

Mycelium | The mass of branching hyphae that forms the body of a fungus and may be visible on infected plants. [Chapter 11]

Mycorrhizae | Mutually beneficial associations between plant roots and certain fungi. The fungi help roots take up water and nutrients, especially phosphorus, in exchange for sugars. [Chapter 7]

N

Necrosis | The death of plant tissue, usually seen as browning of leaf or stem tissue. [Chapter 8]

Necrotrophic | Describes a pathogen that infects and kills host tissue and then extracts nutrients from the dead cells. [Chapter 11]

Nematodes | Microscopic roundworms that are among the most abundant soil animals. Most feed on bacteria, fungi, and protozoa, but some are plant parasites. [Chapter 7]

Nitrification | The conversion of ammonium in the soil to nitrite and then nitrate (NO_3^-) by soil bacteria. [Chapter 8]

Nitrogen fixation | The conversion of atmospheric nitrogen gas (N_2) into ammonia and related forms that plants can absorb. It is carried out by certain bacteria, often in root nodules of legumes. [Chapters 7, 8]

Nodes | The points on a stem where leaves, buds, and branches are attached. [Chapter 3]

Nutrient cycling | The movement of nutrients between living organisms, organic matter, soil, and the atmosphere as materials are taken up, decomposed, and released again. [Chapter 7]

Nutrient film technique | A hydroponic technique in which a thin film of nutrient solution flows continuously over the roots in a sloped channel. [Chapter 10]

Nutrient supply | The soil's ability to provide plants with the essential mineral nutrients they need for growth. [Chapter 7]

Nymphs | The immature stages of insects that go through incomplete metamorphosis. They resemble the adults but lack wings. [Chapter 11]

O

Organic fertilizers | Fertilizers derived from plant or animal sources, such as manure and compost. They release nutrients slowly and add organic matter to the soil but are bulky and heavy. [Chapter 8]

Organic matter | The portion of soil made of living organisms and decomposing plant and animal material. It improves soil structure, water holding, and nutrient supply. [Chapter 7]

Ovules | The structures within the ovary (or on a cone scale) that contain the female gametophyte and develop into seeds after fertilization. [Chapter 3]

P

PAR | Photosynthetically active radiation; the wavelengths of light (400–700 nm) that plants use for photosynthesis, absorbed primarily by chlorophyll. [Chapter 5]

Parenchyma cells | The most common plant cells. They are alive at maturity, have thin primary walls, and carry out most of the plant's metabolic functions, such as photosynthesis and storage. [Chapter 3]

Perennial | A plant that lives for more than two years. [Chapter 11]

Perianth | The non-reproductive parts of a flower: the calyx (sepals) and corolla (petals) together. [Chapter 3]

Permaculture | An ecological design system for sustainable living and agriculture that imitates natural ecosystems and is suited to the local climate and environment. [Chapter 10]

Petals | The often showy, colorful floral organs inside the sepals. Their primary function is to attract pollinators; together they form the corolla. [Chapter 3]

Pfr | The two interconvertible forms of phytochrome. Pr absorbs red light and converts to Pfr, the active form; Pfr absorbs far-red light (and slowly reverts in darkness) back to Pr. Their ratio controls responses such as flowering. [Chapter 5]

pH | A measure of how acidic or basic (alkaline) a soil or solution is on a scale of 0 to 14, with 7 neutral. Soil pH strongly affects nutrient availability. [Chapter 7]

Phloem | The vascular tissue that transports sugars and other products of photosynthesis throughout the plant. Its transport cells are living at maturity, and flow can move in either direction. [Chapters 2, 3]

Photomorphogenesis | The light-controlled growth and development of plants, such as the hypocotyl hook of seedlings and de-etiolation. [Chapter 5]

Photoperiodism | A plant response, such as flowering, triggered by the length of the day or, more precisely, the number of uninterrupted nighttime (dark) hours. [Chapter 5]

Photosynthesis | The process plants use to capture light energy and convert it into chemical energy stored in carbohydrates (sugars), using carbon dioxide and water and releasing oxygen. [Chapters 1, 4]

Phototropism | Growth of a plant toward (or away from) a light source. Auxin accumulates on the shaded side, causing those cells to elongate and the shoot to bend toward the light. [Chapter 5]

Physical disturbance | Disruption of the soil by actions such as excessive tillage or compaction, which can break down structure and harm soil organisms. [Chapter 7]

Physiology | The study of the biological and biochemical processes that occur within living organisms. Plant physiology includes photosynthesis, respiration, transpiration, growth, and development. [Chapter 1]

Phytochrome | A red/far-red light photoreceptor that changes its structure when irradiated, switching between the Pr and Pfr forms to regulate light responses in plants. [Chapter 5]

Phytohormones | Plant hormones; chemical signals that regulate growth and development. Unlike animal hormones, they can act on the same tissue in which they were produced. [Chapter 4]

Plant anchorage | The physical support soil provides to hold a plant's roots, and therefore the plant, firmly in place. [Chapter 7]

Plastic mulch films | Sheets of plastic laid over the soil surface, often on raised beds, to warm the soil, suppress weeds, reduce evaporation, and keep crops clean. [Chapter 10]

Plasticulture | A modern approach to crop farming that uses plastic materials, such as plastic mulch, drip irrigation, and polytunnels, to improve growing conditions. [Chapter 10]

Polythene greenhouses | Inexpensive, simple greenhouses or tunnels covered with polyethylene plastic film. [Chapter 10]

Pore space | The open spaces between soil particles that hold air and water. It is affected by soil texture and structure. [Chapter 7]

Post-emergent | Describes an herbicide applied to the foliage of weeds that have already emerged and are actively growing. [Chapter 11]

Pre-emergent | Describes an herbicide applied to the soil before weed seeds germinate or emerge. [Chapter 11]

Precipitation | Water that falls from the atmosphere to the earth's surface as rain, snow, sleet, or hail. It is seasonal and can be difficult to predict. [Chapter 6]

Propagation | Creating new plants, either from seeds (sexual propagation) or from vegetative parts (asexual propagation). [Chapter 9]

Propagule | Any plant material used to propagate a new plant, such as a seed, cutting, bulb, or tuber. [Chapter 9]

Pteridophytes | The seedless vascular plants, such as ferns, horsetails, and lycophytes. They have vascular tissue but reproduce by spores rather than seeds. [Chapter 2]

R

Raised bed gardening | Growing plants in mounded or framed soil beds that are higher than the surrounding soil. [Chapter 10]

Respiration | The process by which plants break down stored sugars to release energy in a usable form (ATP). See also cellular respiration. [Chapter 1]

Rhizome | A horizontal, modified stem that grows just below the soil surface and produces roots and shoots at its nodes. [Chapter 9]

Root | A vegetative organ, usually below ground, that anchors the plant and absorbs water and mineral nutrients from the soil. Roots may also store food. [Chapter 1]

Rootstock | The lower part of a graft, which provides the root system of the new plant. [Chapter 9]

S

Sand | The largest soil particles (0.05–2.0 mm in diameter). Sandy soils have large pore spaces, drain quickly, and hold little water or nutrients. [Chapter 7]

Scion | The upper part of a graft, a shoot or bud from the desired variety, that becomes the top of the new plant. [Chapter 9]

Sclerenchyma cells | Plant cells with thick, lignified secondary walls that are usually dead at maturity. They provide strength and support and include the transport cells of the xylem. [Chapter 3]

Sclerotia | Small, hard, compact masses of fungal hyphae that can survive harsh conditions, such as winter, and later produce new growth. [Chapter 11]

Seed | The structure that develops from a ripened, fertilized ovule in gymnosperms and angiosperms. It contains an embryo, a food supply, and a protective seed coat. [Chapter 2]

Seed coat | The protective outer covering of a seed. It develops from the maternal tissues (integuments) of the ovule. [Chapter 3]

Selective herbicide | An herbicide that kills certain plants (weeds) without harming others (the crop) by targeting physiological differences between them. [Chapter 11]

Sepals | The outermost floral organs, often green and leaf-like, that protect the flower bud. Together they form the calyx. [Chapter 3]

Sexual reproduction | Reproduction that combines pollen and egg (ovum) through fertilization to produce seeds; the offspring are genetically varied. [Chapter 9]

Side dressing | Applying fertilizer beside the rows of growing plants. See banding. [Chapter 8]

Signs | Visible evidence of the pathogen or pest itself, such as fungal mycelium, spores, insects, or frass. [Chapter 11]

Silt | Soil particles intermediate in size between sand and clay (0.002–0.05 mm). Silt feels smooth and is easily carried by water or wind. [Chapter 7]

Solarization | Covering moist soil with clear plastic sheets to trap solar heat and kill weeds, seeds, and soilborne pests. [Chapter 11]

Species | The most specific level of the taxonomic hierarchy; a group of closely related organisms that can interbreed. A species' scientific name combines the genus and the specific epithet. [Chapter 1]

Sporophyte | The diploid, spore-producing generation in the plant life cycle. It is the dominant, familiar form in vascular plants. [Chapter 2]

Stamen | The male reproductive organ of a flower, made up of an anther, where pollen is produced, supported by a filament. [Chapter 3]

Stem | A vegetative organ that supports leaves and flowers and transports water, nutrients, and sugars between the roots and the shoot. Stems are divided into nodes and internodes. [Chapter 1]

Stomata | Small pores in the epidermis, mainly of leaves, each surrounded by a pair of guard cells. They open and close to control gas exchange (CO_2 and O_2) and water loss. [Chapters 3, 4, 6]

Straw bale culture | Growing plants directly in conditioned straw bales, which decompose and release nutrients to the plants. [Chapter 10]

Structure | The way soil particles are bound together into aggregates, which determines the size and arrangement of pore spaces. [Chapter 7]

Subsistence agriculture | Farming in which the crops and livestock produced are mainly used to feed the farmer's own family, with little left over to sell. [Chapter 10]

Subsoil | The soil layer beneath the topsoil (the B horizon), where materials washed down from above accumulate. [Chapter 7]

Symptoms | Changes in a plant in response to an infecting agent or pest, such as wilting, yellowing, leaf spots, or stunting. [Chapter 11]

Synthetic fertilizers | Manufactured fertilizers that contain minerals or synthetic chemicals. They are concentrated, easy to apply, and quickly

available to plants. [Chapter 8]

Systemic herbicide | An herbicide that is absorbed and moved (translocated) throughout the plant, killing it including the roots, such as glyphosate. [Chapter 11]

T

Taxonomy | The science of identifying, classifying, and naming organisms. Plant taxonomy is the branch of botany concerned with the identification, classification, and naming of plants. [Chapters 1, 2]

Texture | The relative proportions of sand, silt, and clay particles in a soil. [Chapter 7]

Thylakoid | A flattened, sac-like membrane structure inside the chloroplast. Its membrane contains chlorophyll and is the site of the light-dependent reactions. [Chapter 4]

Top dressing | Spreading fertilizer (or another material) over the surface of established plantings, such as lawns. [Chapter 8]

Topsoil | The uppermost layer of soil (the A horizon), generally dark and rich in organic matter, where most biological activity occurs. [Chapter 7]

Transpiration | The loss of water vapor from the aerial parts of a plant, mainly through the stomata of leaves. It pulls water upward through the xylem and helps regulate the plant's water balance and temperature. [Chapters 1, 4, 6]

Tuber | A swollen, modified underground stem (a stolon) that stores food and has buds or 'eyes', as in the potato. [Chapter 9]

V

Vascular Tissue | The plant tissue system that transports water, minerals, and sugars through the plant. It consists of xylem and phloem, usually found together in vascular bundles. [Chapters 1, 2, 3]

Vectors | Organisms, such as aphids and leafhoppers, that carry and transmit a pathogen from one plant to another. [Chapter 11]

Vegetative reproduction | Asexual reproduction of a plant from vegetative parts such as stems, leaves, or roots, producing new plants genetically identical to the parent. [Chapter 9]

W

Water availability | The amount of soil water that plants are able to take up, which depends on soil texture, structure, and organic matter. [Chapter 7]

Water Cycle | The continuous circulation of water between the atmosphere, land, and oceans through evaporation, transpiration, condensation, precipitation, and runoff. [Chapter 6]

Weathering | The physical, chemical, and biological breakdown of rocks and minerals over time, which forms soil. [Chapter 7]

Weed | A plant growing where it is not wanted. [Chapter 11]

X

Xylem | The vascular tissue that transports water and dissolved minerals upward from the roots. Its transport cells are sclerenchyma cells that are dead at maturity; secondary xylem forms the wood of trees. [Chapters 2, 3]

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