Chapter 37

Soil and Plant Nutrition

Lecture Outline

Overview: A Horrifying Discovery

- The carnivorous plant *Nepenthes rajah* belongs to a class of carnivorous plants called "pitcher plants" because their highly modified leaves resemble pitchers.
    - Each pitcher contains slightly viscous fluid that is used to drown prey.
    - Along the upper lip of the trap is a slick waxy coating that makes the escape of its prey virtually impossible.
    - Above the lip is a lid that in many species keeps rain from diluting the viscous fluid within the pitcher.
    - The lower part of the trap contains glands that absorb nutrients from the captured prey.
- *N. rajah* is unique for the size of its pitcher and the size of its prey: The pitcher of *N. rajah* holds several liters of solution, and it is only one of a few *Nepenthes* species that can catch mammals in the wild.
- *N. rajah* grows on unproductive serpentine soil.
    - Serpentine soils are notoriously poor soils derived from Earth's molten magma: they typically have a high metal content but contain low amounts of nutrient elements such as calcium, potassium, and phosphorus.
    - The carnivorous habit of *N. rajah* is an adaptation that allows the plant to supplement its meager mineral rations from the soil with minerals released from its digested prey.
- Plants obtain water and nutrients from the atmosphere and from the soil through their root systems.
- Using sunlight as an energy source for photosynthesis, plants produce organic nutrients by reducing CO_2 to sugars.
- Land plants also take up water and various mineral nutrients from the soil through their root systems.

Concept 37.1 Soil contains a living complex ecosystem

- The upper layers of soil, from which plants absorb the water and minerals they require, contain a wide range of living organisms that interact with each other and with the physical environment.
- This complex ecosystem may take centuries to form but can be destroyed by mismanagement within a few years.

Soil texture and composition are key environmental factors in terrestrial ecosystems.

- The basic physical properties of soil—its texture and composition—determine why plants grow where they do.
- Soil has its origin in the weathering of solid rock.
    - Water that seeps into crevices and freezes in winter fractures rock. Acids dissolved in soil water also help break down rock chemically.
    - Organisms, including lichens, fungi, bacteria, mosses, and the roots of vascular plants, accelerate the breakdown of rock by secreting acids and expanding their roots in fissures.
- The texture of soil depends on the size of its particles, which are classified in a range from coarse sand (2–0.02 mm) to silt (0.02–0.002 mm) to microscopic clay particles (smaller than 0.002 mm).
- The mineral particles released by weathering become mixed with living articles and **humus**, the remains of partially decayed organic material, forming **topsoil**.
- Topsoil and other distinct soil layers are called **soil horizons**.
    - Topsoil, or the A horizon, can range from millimeters to meters in depth.
    - Topsoil is the richest horizon in organic material and is thus the most important for plant growth.
- In the topsoil, plants are nourished by the soil solution, the water and dissolved minerals in the pores between soil particles.
    - The pores contain air pockets.
    - After a heavy rainfall, water drains away from the larger spaces of the soil, but the smaller spaces retain water because water molecules are attracted to the negatively charged surfaces of clay and other soil particles.
- The most fertile topsoils are **loams**, made up of roughly equal amounts of sand, silt, and clay.
    - Loamy soils have enough fine particles to provide a large surface area for retaining minerals and water, which adhere to the particles.
    - Loams also have enough coarse particles to provide air spaces that supply oxygen to the root for cellular respiration.
- Sandy soils tend not to retain enough water to support vigorous plant growth, whereas clayey soils tend to retain too much water.
- Inadequate drainage can have a dramatic impact on the survival of many plants.
    - Plants can suffocate if air spaces are replaced by water.
- Fertile topsoils have pore spaces that are about half water and half air, thus balancing aeration, drainage, and water storage capacity.
- The physical properties of soils can be adjusted by adding peat moss, compost, manure, or sand.

A soil's composition includes its inorganic (mineral) and organic components.

- The surface charges of soil particles determine their ability to bind plant nutrients.
- Most soil particles are negatively charged.
- Positively charged ions (cations), such as potassium (K^+), calcium (Ca^{2+}), and magnesium (Mg^{2+}), adhere by electrical attraction to the negatively charged surfaces of soil particles.
    - This adherence prevents the *leaching* of mineral nutrients as water percolates through the soil.

- Positively charged mineral ions are made available to the plant when the hydrogen ions in the soil displace the mineral ions from the clay particles.
- This process, called **cation exchange**, is stimulated by the roots, which secrete H^+ and compounds that form acids in the soil solution.
    - In this process, mineral cations are displaced from soil particles by other cations, particularly H^+, and enter the soil solution, which is absorbed by root hairs.
- A soil's capacity to exchange cations is determined by the number of cation adhesion and by pH.
    - Soils with higher capacities generally have larger reserves of mineral nutrients.
- Negatively charged ions (anions), such as nitrate (NO_3^-), phosphate ($H_2PO_4^-$), and sulfate (SO_4^{2-}), are less tightly bound to soil particles and tend to leach away more quickly.
- Humus is the decomposing organic material formed by the action of bacteria and fungi on dead organisms, feces, fallen leaves, and other organic refuse.
- Humus prevents clay from packing together and builds a crumbly soil that retains water but is still porous enough for the adequate aeration of roots.
- Humus is also a reservoir of mineral nutrients that are returned to the soil by decomposition.
- Topsoil is home to an astonishing number and variety of organisms.
    - A teaspoon of topsoil has about 5 billion bacteria that cohabit with various fungi, algae and other protists, insects, earthworms, nematodes, and the roots of plants.
- The activities of these organisms affect the physical and chemical properties of soil.
    - For example, earthworms consume bacteria and fungi growing on organic material in soil.
    - Earthworms move large amounts of material to the soil surface, mixing and aggregating the soil and allowing gas diffusion and water retention.
- Plant roots bind soil and thus reduce erosion.
- Roots also affect the soil pH by releasing organic acids and reinforcing the soil against erosion.

Soil conservation is one step toward sustainable agriculture.

- Soil management, with fertilization and other practices, helped prepare the way for the establishment of modern societies in permanent settlements.
- Unfortunately, soil mismanagement has been a recurrent problem throughout human history.
- The American Dust Bowl was an ecological and human disaster that ravaged the southwestern Great Plains of the United States in the 1930s.
    - This region suffered through devastating dust storms that resulted from a prolonged drought and decades of inappropriate farming techniques.
    - Before the arrival of farmers, the Great Plains werecovered by hardy grasses that held the soil in place in spite of recurring droughts and torrential rains.
    - In the late 1800s and early 1900s, homesteaders settled in the region, planting wheat and raising cattle.
    - These land uses left the soil exposed to erosion by winds and a few years of drought made the problem worse.
    - During the 1930s, huge quantities of fertile soil were blown away in "black blizzards," rendering millions of hectares of farmland useless.

- Soil mismanagement continues to be a major problem to this day.
  - More than 30% of the world's farmland has reduced productivity stemming from poor soil conditions, such as chemical contamination, mineral deficiencies, acidity, salinity, and poor drainage.
- Farmers irrigate and modify soil to maintain good crop yields with the goal of **sustainable agriculture**, a commitment to embracing a variety of farming methods that are conservation minded, environmentally safe, and profitable.

Irrigation increases crop yields.

- Because water is often the limiting factor in plant growth, no technology has increased crop yield as much as irrigation.
  - Globally, about 75% of all freshwater use is devoted to agriculture.
- The primary source of irrigation water is underground water reserves called *aquifers*.
- In many places, the rate of water removal is exceeding the natural rate of refilling the aquifers.
  - This imbalance leads to *land subsidence*, a gradual settling or sudden sinking of the Earth's surface.
  - Land subsidence alters drainage patterns, causing damage to human-made structures, loss of underground springs, and increased risk of flooding.
- Irrigation from groundwater can also lead to soil *salinization*—the creation of soil too salty for cultivation.
  - Salts dissolved in irrigation water accumulate in soil as water evaporates, reducing the water potential of the soil solution and reducing water uptake.
- To use water efficiently, farmers must understand the water-holding capacity of their soil, the water needs of their crops, and the latest irrigation technology.
- *Drip irrigation*, the slow release of water to soil and plants through plastic tubing placed directly at the root zone, requires less water and reduces salinization.

Farmers reverse nutrient depletion by fertilization.

- In natural ecosystems, mineral nutrients are recycled by the decomposition of dead organic material and by the excretion of animal wastes.
- In agriculture, minerals are deposited far from their original source, leading to nutrient depletion over time. Nutrient depletion is a major cause of global soil degradation.
- Farmers reverse nutrient depletion by fertilization, the addition of mineral nutrients to the soil.
  - Farmers in industrialized nations use fertilizers containing minerals that are either mined or prepared by energy-intensive processes.
  - Fertilizers are enriched in nitrogen (N), phosphorus (P), and potassium (K)—the nutrients most commonly deficient in depleted soils.
- Manure, fishmeal, and compost are called "organic" fertilizers because they are of biological origin and contain decomposing organic material.
- Before plants can use organic material, however, it must be decomposed into inorganic nutrients that roots can absorb.
- Organic fertilizers release minerals gradually, whereas minerals in commercial fertilizers are immediately available but may be leached from the soil by rainwater or irrigation.

- Mineral runoff fertilizes lakes, leading to explosions in algal populations that can deplete oxygen levels at night and decimate fish populations.

Soil pH influences mineral availability.

- Soil pH affects cation exchange and the chemical form of minerals.
- Depending on the soil pH, a particular mineral may be bound too tightly to clay particles or may be in a chemical form that the plant cannot absorb.
- Plants differ in their pH requirements.
- Most plants do best in slightly acidic soil because high H^+ concentrations displace positively charged minerals from soil particles, making them more available for absorption.
- A change in H^+ concentration may make one mineral more available but make another less available.
    - At pH 8, plants can absorb calcium, but iron is almost unavailable.
- Soil pH should be matched to a crop's mineral needs.
    - If the soil is too alkaline, adding sulfate will lower the pH, while liming (adding calcium carbonate or calcium hydroxide) will raise the pH.
- When soil pH falls to 5 or below, toxic aluminum (Al^{3+}) ions become more soluble and are absorbed by roots, stunting root growth and preventing the uptake of calcium, a needed plant nutrient.
    - Some plants secrete organic anions that bind Al^{3+} and render it harmless.

Erosion can remove considerable amounts of topsoil.

- Erosion is a major cause of soil degradation.
- Erosion can be limited by rows of trees acting as windbreaks, terraced hillside crops, and contour cultivation of crops.
    - Crops such as alfalfa and wheat provide good ground cover and protect the soil better than maize and other crops that are usually planted in more widely spaced rows.
- Erosion can also be reduced by a plowing technique called **no-till agriculture**, in which a specialized plow creates narrows furrows without disrupting the mesh of plant roots.
    - No-till farming allows the field to be seeded with minimal fertilizer and disturbance of the soil.

Phytoremediation cleans soils.

- Some areas are unfit for agriculture because toxic heavy metals or organic pollutants have contaminated the soil or groundwater.
- Phytoremediation is a nondestructive biotechnology that uses the ability of some plants to extract soil pollutants and concentrate them in portions of the plant that can be easily removed for safe disposal.
    - For example, alpine pennycress *(Thlaspi caerulescens)* can accumulate zinc in its shoots at concentrations 300 times higher than most plants can tolerate.
    - The shoots can then be harvested and the contaminating zinc removed.
- Phytoremediation may be used to clean up areas contaminated by smelters, mining operations, or nuclear testing.

Concept 37.2 Plants require essential elements to complete their life cycles

- Early ideas about plant nutrition were not entirely correct. They included:
  - Aristotle's hypothesis that plants "ate" soil.
  - van Helmont's conclusion from his experiments that plants grow mainly from water.
  - Hale's postulate that plants are nourished mostly by air.
- In fact, soil, water, and air all contribute to plant growth.
- The water content of a plant can be measured by comparing the mass of plant material before and after it is dried.
  - Typically, 80–90% of a plant's fresh mass is water.
- Inorganic nutrients from the soil generally account for about 4% of the dry mass.
- Most of a plant's dry mass is derived from CO_2 that is assimilated from the air during photosynthesis.
- More than 50 chemical elements have been identified among the inorganic substances present in plants.
  - However, not all of these 50 are **essential elements**, required for the plant to complete its life cycle and reproduce.

Plants require nine macronutrients and at least eight micronutrients.

- Plants can be grown in **hydroponic culture** to determine which mineral elements are actually essential nutrients.
  - Plants are grown in solutions of various minerals in known concentrations.
  - If the absence of a particular mineral, such as potassium, causes a plant to appear abnormal when compared to controls grown in a complete mineral medium, then that element is essential.
- Such studies have identified 17 elements that are essential nutrients in all plants and a few other elements that are essential to certain groups of plants.
- Elements required by plants in relatively large quantities are **macronutrients**.
  - There are nine macronutrients, including the six major ingredients in organic compounds: carbon, oxygen, hydrogen, nitrogen, phosphorus, and sulfur.
  - The other three macronutrients are potassium, calcium, and magnesium.
- Of all the mineral nutrients, nitrogen contributes the most to plant growth and crop yields.
  - Plants require nitrogen as a component of proteins, nucleic acids, and chlorophyll.
- Elements that plants need in very small amounts are **micronutrients**.
  - The eight micronutrients are chlorine, iron, manganese, boron, zinc, copper, nickel, and molybdenum.
  - Plants that use C_4 and CAM pathways of photosynthesis may require sodium ions as a ninth essential nutrients to regenerate phosphophenolpyruvate.
- Most micronutrients function as cofactors, nonprotein helpers in enzymatic reactions.
  - For example, iron is a metallic component in cytochromes, proteins that function in the electron transport chains of chloroplasts and mitochondria.
  - Although the requirement for these micronutrients is modest (for example, only one atom of molybdenum for every 60 million hydrogen atoms in dry plant material), a deficiency of a micronutrient can weaken or kill a plant.

The symptoms of a mineral deficiency depend on the function and mobility of the element.

- The symptoms of a mineral deficiency depend in part on the function of that nutrient in the plant.
  - For example, a deficiency in magnesium, an ingredient of chlorophyll, causes yellowing of the leaves, or *chlorosis*.
- The relationship between a mineral deficiency and its symptoms can be less direct.
  - For example, chlorosis can also be caused by iron deficiency, even though chlorophyll contains no iron. Iron is a required cofactor in chlorophyll synthesis.
- The symptoms of mineral deficiencies also depend on the mobility of the nutrient within the plant.
- If a nutrient can move freely from one part of a plant to another, then symptoms of the deficiency will appear first in older organs.
  - Young, growing tissues are a greater sink for nutrients that are in short supply.
  - For example, a shortage of relatively mobile magnesium initially leads to chlorosis in older leaves.
- If a nutrient is relatively immobile, then a deficiency will affect young parts of the plant first.
  - Older tissue may have adequate supplies, which they can retain during periods of shortage.
  - For example, iron does not move freely within a plant. Chlorosis due to iron deficiency appears first in young leaves.
- The symptoms of a mineral deficiency are often distinctive enough for a plant physiologist or farmer to make a preliminary diagnosis of the problem.
  - This diagnosis can be confirmed by analyzing the mineral contents of plant and soil.
  - The amount of micronutrient needed to correct a deficiency is usually quite small. Care must be taken because a nutrient overdose can be toxic to plants.

Genetically engineered plants can be "tailored" to suit the soil.

- Genetic engineering is improving plant nutrition and fertilizer usage.
- Aluminum (Al) in acidic soils damages roots and greatly reduces crop yields.
  - Roots of aluminum resistant plants secrete organic acids such as malic acid and citric acid, which bind free Al^{3+} ions and lower toxic levels of aluminum in the soil.
- Luis Herrera-Estrella and his colleagues genetically introduced a bacterial citrate synthase gene into tobacco and papaya genomes.
  - The resulting overproduction of citric acid increased aluminum resistance in these crops.
- In many Asian countries, flooding during the monsoon season destroys rice crops, depriving roots of oxygen and leading to injury by the buildup of ethanol and other toxic products of alcoholic fermentation.
- A few varieties of rice can survive weeks of flooding.
- A gene called *Submergence 1A-1* (*Sub1A-1*) is the main source of submergence tolerance in the flood-resistant types of rice.
  - Sub1A-1 proteins regulate the expression of genes that are normally activated under anaerobic conditions, such as those that code for alcohol dehydrogenase, an enzyme that breaks down ethanol.
  - The heightened expression of *Sub1A-1* in flooding-intolerant varieties of rice confers tolerance to submergence and increases the alcohol dehydrogenase levels of the plants.

- “Smart plants” have been produced that warn a grower when a nutrient deficiency is imminent—*before* damage has occurred.
  - One type of smart plant takes advantage of a promoter that more readily binds RNA polymerase when the phosphorus content of the plant’s tissues begins to decline.
  - This promoter is linked to a “reporter” gene that leads to production of a light blue pigment in the leaf cells
- In order to support plant growth, soil must have suitable levels of mineral nutrients, good aeration, good water-holding capacity, low salinity, a pH near neutrality, and must be free of toxic concentrations of minerals and other chemicals.

Concept 37.3 Plant nutrition often involves relationships with other organisms

- Plants and soil have a two-way relationship: Dead plants provide much of the energy needed by soil-dwelling microorganisms, while secretions from living roots support a wide variety of microbes in the near-root environment.

Rhizobacteria are soil bacteria that thrive in the rhizosphere.

- The **rhizosphere** is the layer of soil that is bound to the plant’s roots.
- **Rhizobacteria** are soil bacteria with especially large populations in the rhizosphere.
  - Different soils vary greatly in the types and number of rhizobacteria they harbor.
- Microbial activity within the rhizophere is 10 to 100 times higher than in unbound soil.
  - This is because the roots secrete nutrients such as amino acids, sugars, and organic acids, releasing up to 20% of the plant’s photosynthetic production.
- As a result of diverse plant-microbe interactions, the composition of this microbial population often differs greatly from the surrounding soil and the rhizospheres of other plant species.
  - Each rhizosphere contains a unique and complex cocktail of root secretions and microbial products.
- Some rhizobacteria, known as *plant-growth–promoting rhizobacteria,* colonize roots and enhance their growth by a variety of mechanisms.
  - Some rhizobacteria produce hormones that stimulate plant growth.
  - Others produce antibiotics that protect roots from disease.
  - Some absorb toxic metals or make nutrients more available to roots.
- The inoculation of seeds with plant-growth–promoting rhizobacteria can increase crop yields and reduce the need for fertilizers and pesticides.
- What benefits do these bacteria gain by interacting with plants?
  - Root secretions supply most of the energy in the rhizosphere, and plant growth ultimately benefits the bacteria.

The metabolism of soil bacteria makes nitrogen available to plants.

- Of all the mineral nutrients, nitrogen has the greatest effect on plant growth and crop yields.
- The **nitrogen cycle** describes the transformations of nitrogen and nitrogen-containing compounds.
- Unlike other minerals, ammonium (NH_4^+) and nitrate (NO_3^-) ions do not form by weathering of rocks.

- Lightning produces small amounts of NO_3^-, but most soil nitrogen comes from the actions of soil bacteria.
  - *Ammonifying bacteria* produce NH_3 (ammonia) by breaking down nitrogen in proteins and other organic compounds in humus.
  - *Nitrogen-fixing bacteria* convert gaseous N_2 to NH_3. In soil solution, NH_3 picks up another H^+ to form NH_4^+, which plants can absorb.
- Plants acquire nitrogen mainly in the form of NO_3^-.
  - Soil NO_3^- is formed by a two-step process called *nitrification*, consisting of the oxidation of NH_3 into nitrite (NO_2^-) followed by the oxidation of nitrite into nitrate (NO_3^-).
  - Different types of *nitrifying bacteria* carry out each of these two steps.
- After the roots absorb NO_3^-, a plant enzyme reduces it back to NH_4^+, which other enzymes incorporate into amino acids and other organic compounds.
- Most plant species export nitrogen from roots to shoots via the xylem, in the form of NO_3^- or organic compounds synthesized in the roots.
- Some soil nitrogen is lost, especially in anaerobic soils, when denitrifying bacteria convert NO_3^- to N_2, which diffuses from the soil into the atmosphere.

Bacteria fix atmospheric nitrogen into usable forms.

- It is ironic that plants sometimes suffer nitrogen deficiencies because the atmosphere is 79% nitrogen (N_2).
- Plants cannot use nitrogen in the form of N_2, because the triple bond between the two nitrogen atoms makes the molecule almost inert.
- N_2 must first be converted to ammonium (NH_4^+) or nitrate (NO_3^-) by prokaryotic cells, in a process called **nitrogen fixation**.
  - All nitrogen-fixing organisms are bacteria, and some are free-living.
- Nitrogen-fixing bacteria of the genus *Rhizobium* form symbiotic associations with members of the legume family, which includes peas, soybeans, alfalfa, peanuts, and clover.
  - Although *Rhizobium* can be free living in the soil, they cannot fix N_2 in their free state, nor can legume roots fix N_2 without the bacteria.
- The reduction of N_2 to NH_3 is a complicated multistep process, catalyzed by the enzyme complex nitrogenase and simplified as:

$$N_2 + 8e^- + 8H^+ + 16ATP \rightarrow 2NH_3 + H_2 + 16ADP + 16P_i$$

- Nitrogen fixation is a very costly process, costing the bacterium eight ATP molecules for every ammonia molecule synthesized.
- Nitrogen-fixing bacteria are most abundant in soils rich in organic materials, which provide fuels for cellular respiration to support this expensive metabolic process.
- The specialized mutualism between nitrogen-fixing *Rhizobium* bacteria and legumes leads to dramatic changes in root structure.
  - A legume's roots have swellings called **nodules,** composed of plant cells that have been "infected" by nitrogen-fixing *Rhizobium* bacteria.
  - Inside the nodule, *Rhizobium* bacteria assume a form called **bacteroids**, which are contained within vesicles formed by the root cell.
- *Rhizobium* bacteria fix atmospheric N_2 into a form that can be readily used by the plant.
  - Legume-*Rhizobium* symbioses produce more usable nitrogen for plants than all industrial fertilizers, at no cost to farmers.

- Subsequent crops can also benefit from the usable nitrogen left in the soil by a legume crop.

- Nitrogen fixation requires an anaerobic environment.
  - Lignified external layers of the nodule limit gas exchange.
  - Nodules produce leghemoglobin, an iron-containing protein that binds reversibly to oxygen.
  - Leghemoglobin provides oxygen for *Rhizobium*'s intense respiration while protecting nitrogenase from free oxygen.
- Each legume is associated with a particular strain of *Rhizobium*.
  - The development of root nodules begins after bacteria enter the root through an "infection thread".
  - The bacteria penetrate the root cortex. Growth in the cortex and pericycle cells that are "infected" with bacteria in vesicles continues until the two masses of dividing cells fuse to form the nodule.
  - As the nodule continues to grow, vascular tissue connects the nodule to the xylem and phloem of the stele, providing nutrients to the nodule and carrying nitrogenous compounds to the rest of the plant.
- The symbiotic relationship between a legume and nitrogen-fixing bacteria is mutualistic, with both partners benefiting.
  - The bacteria supply the legume with fixed nitrogen.
  - Most of the ammonium produced by symbiotic nitrogen fixation is used by the nodules to make amino acids, which are then transported to the shoot and leaves via the xylem.
  - The plant provides the bacteria with carbohydrates and other organic compounds and protects the nitrogenase from free oxygen.
- The specific recognition between legume and bacteria and the development of the nodule are the result of a chemical dialogue between the bacteria and the root.
- Each partner responds to the chemical signals of the other by expressing certain genes whose products contribute to nodule formation.
- It may be possible in the future to induce *Rhizobium* uptake and nodule formation in crop plants that do not normally form such nitrogen-fixing symbioses.
- In **crop rotation**, a nonlegume crop such as corn is planted one year.
  - The following year, alfalfa or another legume is planted to restore the concentration of fixed soil nitrogen.
- Often, the legume crop is not harvested but is plowed under to decompose as "green manure."
  - To ensure the formation of nodules, the legume seeds exposed to bacteria before sowing.
- Species from many other plant families also benefit from symbiotic nitrogen fixation.
  - Alder trees and certain tropical grasses host nitrogen-fixing actinomycete bacteria.
- Rice benefits indirectly from symbiotic nitrogen fixation because it is often cultivated in paddies with the water fern *Azolla*, which has symbiotic nitrogen-fixing cyanobacteria.
  - The growing rice eventually shades and kills the *Azolla*.
  - The decomposition of the water fern adds more nitrogenous compounds to the paddy.

Mycorrhizae are symbiotic associations of roots and fungi that enhance plant nutrition.

- **Mycorrhizae** ("fungus roots") are mutualistic associations of fungi and roots.

- The fungus benefits from a steady supply of sugar donated by the host plant.
- The fungi increase the surface area for water uptake and selectively absorb phosphate and other minerals in the soil and supply them to the plant.
  - The fungi also secrete growth factors that stimulate roots to grow and branch.
  - The fungi produce antibiotics that may help protect the plant from pathogenic bacteria and fungi in the soil.
- Almost all plant species produce mycorrhizae.
- This plant-fungus symbiosis may have been one of the evolutionary adaptations that made it possible for plants to colonize land in the first place.
  - New fossil evidence has pushed the date for the appearance of mycorrhizae back to 460 million years ago, predating vascular plants.
  - Mycorrhizal fungi are more efficient at absorbing minerals than are roots, which may have helped nourish pioneering plants in nutrient-poor soils present when terrestrial ecosystems were young.
- Mycorrhizae take two major forms: ectomycorrhizae and arbuscular.
- In **ectomycorrhizae**, the mycelium forms a dense sheath over the surface of the root.
  - Fungal hyphae extend from the mantle into the soil and also grow into the root cortex.
  - These hyphae do not penetrate the root cells but form a network in the apoplast, or extracellular space, that facilitates nutrient exchange between fungus and plant.
  - Compared with “uninfected” roots, ectomycorrhizae are generally thicker, shorter, more branched, and lacking root hairs.
- Ten percent of plant families have species that form ectomycorrhizae.
  - Ectomycorrhizae are especially common in woody plants, including trees of the pine, spruce, oak, walnut, birch, willow, and eucalyptus families.
- **Arbuscular mycorrhizae** do not have a dense mantle ensheathing the root.
  - Mycorrhizal associations start when microscopic soil hyphae respond to the presence of a root by growing toward it, establishing contact, and growing along its surface.
  - Hyphae penetrate between the epidermal cells and enter the root cortex.
  - The hyphae digest small patches of the cortical cell walls, but they do not actually enter the cytoplasm.
  - Instead, the hypha grows into a tube formed by invagination of the root cell’s membrane.
  - Some fungal hyphae within these invaginations may form dense knotlike structures called arbuscules that are important sites of nutrient transfer.
- Roots with endomycorrhizae look like “normal” roots with root hairs, but the microscopic symbiotic connections are very important.
- Endomycorrhizae are found in more than 85% of plant species, including important crop plants such as maize, wheat, and legumes.
- Roots can form mycorrhizal symbioses only if they are exposed to the appropriate fungal species.
  - In most ecosystems, these fungi are present in the soil, and seedlings develop mycorrhizae.
  - Seeds planted in foreign soil may develop into plants that show signs of malnutrition because of the absence of the plant’s fungal partners.
- Mycorrhizal associations are important in understanding ecological relationships.

- Invasive exotic plants sometimes colonize areas by disrupting the interactions between native organisms.
  - Garlic mustard *(Alliaria petiolata)* is an invasive plant in woodlands throughout the eastern and middle United States, suppressing tree seedlings and other native plants.
  - Its invasive properties may be related to an ability to slow the growth of other plant species by preventing the growth of arbuscular mycorrhizal fungi.

Epiphytes nourish themselves but grow on other plants, while parasitic plants extract nutrients from other plants.

- An epiphyte is an autotrophic plant that nourishes itself but grows on the surface of another plant, usually on the branches or trunks of trees.
- Epiphytes absorb water and minerals from rain, mostly through their leaves.
  - Examples of epiphytes are staghorn ferns, some mosses, Spanish moss, and many species of bromeliads and orchids.
- A variety of plants parasitize other plants to extract nutrients to supplement or even replace the production of organic molecules by photosynthesis by the parasitic plant.
- Many parasitic species have roots that function as haustoria, nutrient-absorbing projections that enter the host plant.
  - Mistletoe supplements its photosynthesis by using haustoria to siphon xylem sap from the vascular tissue of the host tree.
- Some parasitic plants do not perform photosynthesis at all.
  - The haustoria of dodder tap into the host's vascular tissue for water and nutrients.
  - Indian pipe obtains its nutrition indirectly via its association with fungal hyphae of the host tree's mycorrhizae.

Carnivorous plants supplement their mineral nutrition by digesting animals.

- Carnivorous plants are photosynthetic but obtain some nitrogen and minerals by killing and digesting insects and other small animals.
- Carnivorous plants live in acid bogs and other habitats where soil conditions are poor in nitrogen and other minerals.
- Various types of insect traps have evolved by the modification of leaves.
- The traps are usually equipped with glands that secrete digestive juices.
  - Examples are Venus' flytrap, pitcher plant, and sundew.