37

Soil and Plant Nutrition

▲ **Figure 37.1** **A rat trap?**

KEY CONCEPTS

37.1 **Soil contains a living, complex ecosystem**
37.2 **Plants require essential elements to complete their life cycle**
37.3 **Plant nutrition often involves relationships with other organisms**

OVERVIEW

A Horrifying Discovery

In 1858, two British explorers made a grisly discovery during their ascent of Mount Kinabalu, in northern Borneo: a dead rat. What was unusual about this rat was that it was the partially digested meal of *Nepenthes rajah*, a member of a group of carnivorous plants called "pitcher plants" because their highly modified leaves resemble pitchers **(Figure 37.1)**. Each pitcher contains a slightly viscous fluid of the plant's own production, which 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. Although carnivory by pitcher plants is well documented, what sets *N. rajah* apart from other *Nepenthes* species is the size of its pitcher and the size of its prey: The pitcher of *N. rajah* holds several liters of solution, and it is one of only a few *Nepenthes* species documented as having caught mammals in the wild.

To understand the reason for this marvelous adaptation, it is necessary to consider the unproductive serpentine soil found on the slopes of Mount Kinabalu. 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 unusual 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.

Plant nutrition is the study of the chemical elements that are necessary for plant growth. As discussed in Chapter 36, plants obtain nutrients from both the atmosphere and the soil. Using sunlight as an energy source, plants produce organic nutrients by reducing carbon dioxide to sugars through the process of photosynthesis. Land plants also take up water and various mineral nutrients from the soil through their root systems. In this chapter, we discuss the basic physical properties of soils and the factors that govern soil quality. We then explore why certain inorganic nutrients are essential for plant function. Finally, we examine some nutritional adaptations that have evolved in plants, often in relationships with other organisms.

CONCEPT 37.1

Soil contains a living, complex ecosystem

The upper layers of the soil, from which plants absorb nearly all of 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 human mismanagement in just a few years. To understand why soil must be conserved and why particular plants grow where they do, it is necessary to first consider the basic physical properties of soil: its texture and composition.

Soil Texture

The texture of soil depends on the sizes of its particles. Soil particles can range from coarse sand (0.02–2 mm in diameter) to silt (0.002–0.02 mm) to microscopic clay particles (less than 0.002 mm). These different-sized particles arise ultimately from the weathering of rock. Water freezing in the crevices of rocks causes mechanical fracturing, and weak acids in the soil break rocks down chemically. When organisms penetrate the rock, they accelerate breakdown by chemical and mechanical means. Plant roots, for example, secrete acids that dissolve the rock, and their growth in fissures leads to mechanical fracturing. The mineral particles released by weathering become mixed with living organisms and **humus**, the remains of dead organisms and other organic matter, forming **topsoil**. The topsoil and other distinct soil layers are called **soil horizons** **(Figure 37.2)**. The topsoil, or A horizon, can range in depth from millimeters to meters. We focus mostly on the properties of topsoil because it is generally the most important soil layer for the growth of plants.

In the topsoil, plants are nourished by the soil solution, the water and dissolved minerals in the pores between soil particles. The pores also contain air pockets. After a heavy rainfall, water drains away from the larger spaces in the soil, but smaller spaces retain water because water molecules are attracted to the negatively charged surfaces of clay and other soil particles.

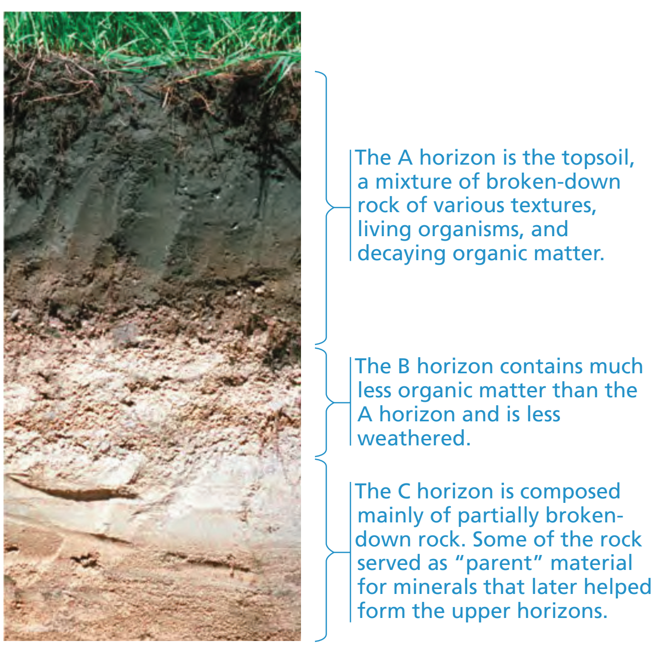
The topsoils that are the most fertile—supporting the most abundant growth—are **loams**, which are composed of roughly equal amounts of sand, silt, and clay. Loamy soils have enough small silt and clay particles to provide ample surface area for the adhesion and retention of minerals and water. Meanwhile, the large spaces between sand particles enable efficient diffusion of oxygen to the roots. Sandy soils generally don't retain enough water to support vigorous plant growth, and clayey soils tend to retain too much water. When soil does not drain adequately, the air is replaced by water, and the roots suffocate from lack of oxygen. Typically, the most fertile topsoils have pores that are about half water and half air, providing a good balance between aeration, drainage, and water storage capacity. The physical properties of soils can be adjusted by adding soil amendments, such as peat moss, compost, manure, or sand.

Topsoil Composition

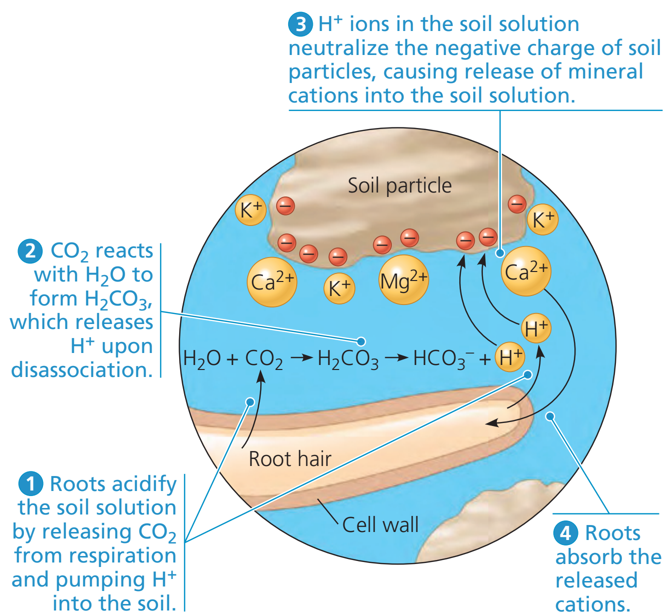
A soil's composition encompasses its inorganic (mineral) and organic chemical components. The organic components include the many life-forms that inhabit the soil.

Inorganic Components

The surface charges of soil particles determine their ability to bind many nutrients. Most soil particles are negatively charged. Positively charged ions (cations)—such as potassium (K^+), calcium (Ca^{2+}), and magnesium (Mg^{2+})—adhere to these particles and are therefore not easily lost by *leaching*, the percolation of water through the soil. Roots, however, do not absorb mineral cations directly from soil particles; they absorb them from the soil solution. Mineral cations enter the soil solution by **cation exchange**, a process in which cations are displaced from soil particles by other cations, particularly H^+ **(Figure 37.3)**. Therefore, a soil's capacity to exchange cations is determined by the number of cation adhesion sites



▲ **Figure 37.2 Soil horizons.**



▲ **Figure 37.3 Cation exchange in soil.**

? *Which are more likely to be leached from the soil by heavy rains—cations or anions? Explain.*

and by the soil's pH. Soils with higher capacities generally have a larger reserve of mineral nutrients.

Negatively charged ions (anions)—such as the plant nutrients nitrate (NO_3^-), phosphate ($H_2PO_4^-$), and sulfate (SO_4^{2-})—do not bind to the negatively charged soil particles and are therefore easily released. During heavy rain or irrigation, they are leached into the groundwater, making them unavailable for uptake by roots.

Organic Components

The major organic component of topsoil is humus, which consists of organic material produced by the decomposition of dead organisms, feces, fallen leaves, and other organic matter by bacteria and fungi. Humus prevents clay particles from packing together and forms a crumbly soil that retains water but is still porous enough to aerate roots adequately. Humus also increases the soil's capacity to exchange cations and serves as a reservoir of mineral nutrients that return gradually to the soil as microorganisms decompose the organic matter.

Topsoil is home to an astonishing number and variety of organisms. A teaspoon of topsoil has about 5 billion bacteria, which cohabit with fungi, algae and other protists, insects, earthworms, nematodes, and plant roots. The activities of all these organisms affect the soil's physical and chemical properties. Earthworms, for example, consume organic matter and derive their nutrition from the bacteria and fungi growing on this material. They excrete wastes and move large amounts of material to the soil surface. In addition, they move organic matter into deeper layers of the soil. In effect, earthworms mix and clump the soil particles, allowing for better gaseous diffusion and retention of water. Plant roots also affect soil texture and composition. For example, by binding the soil, they reduce erosion, and by excreting acids, they lower soil pH.

Soil Conservation and Sustainable Agriculture

Ancient farmers recognized that yields on a particular plot of land decreased over the years. Moving to uncultivated areas, they observed the same pattern of reduced yields over time. Eventually, they realized that fertilization could make soil a renewable resource that enabled crops to be cultivated season after season at a fixed location. This sedentary agriculture facilitated a new way of life. Humans began to build permanent dwellings—the first villages. They also stored food for use between harvests, and food surpluses enabled some members of these early communities to specialize in nonfarming occupations. In short, soil management, by fertilization and other practices, helped prepare the way for modern societies.

Unfortunately, soil mismanagement has been a recurrent problem throughout human history, as exemplified by the American Dust Bowl, 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 had been covered by hardy grasses that held the soil in place in spite of recurring droughts and torrential rains. But in the late 1800s and early 1900s, many homesteaders settled in the region, planting wheat and raising cattle. These land uses left the soil exposed to erosion by winds. 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 **(Figure 37.4)**. In one of the worst dust storms, clouds of dust blew eastward to Chicago, where soil fell like snow, and even reached the Atlantic coast. Hundreds of thousands of people in the Dust Bowl region were forced to abandon their homes and land, a plight immortalized in John Steinbeck's novel *The Grapes of Wrath*.

▲ **Figure 37.4 A massive dust storm in the American Dust Bowl during the 1930s.**

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. As the world's population continues to grow, the demand for food increases. Because soil quality is a major determinant of crop yield, the need to manage soil resources prudently has never been greater.

We'll now discuss how farmers irrigate and modify soil in order to maintain good crop yields. The goal is **sustainable agriculture**, a commitment embracing a variety of farming methods that are conservation minded, environmentally safe, and profitable. We will also examine problems and solutions relating to soil degradation.

Irrigation

Because water is often the limiting factor in plant growth, perhaps no technology has increased crop yield as much as irrigation. However, irrigation is a huge drain on freshwater resources. Globally, about 75% of all freshwater use is devoted to agriculture. Many rivers in arid regions have been reduced

▲ **Figure 37.5 Sudden land subsidence.** Overuse of groundwater for irrigation triggered formation of this sinkhole in Florida.

to trickles by the diversion of water for irrigation. The primary source of irrigation water, however, is not surface waters, such as rivers and lakes, but underground water reserves called *aquifers*. In some parts of the world, the rate of water removal is exceeding the natural refilling of the aquifers. The result is *land subsidence*, a gradual settling or sudden sinking of Earth's surface **(Figure 37.5)**. Land subsidence alters drainage patterns, causes damage to human-made structures, contributes to loss of underground springs, and increases the risk of flooding.

Irrigation, particularly from groundwater, can also lead to soil *salinization*—the addition of salts to the soil that make it too salty for cultivating plants. Salts dissolved in irrigation water accumulate in the soil as the water evaporates, making the water potential of the soil solution more negative. The water potential gradient from soil to roots is reduced, diminishing water uptake (see Chapter 36).

Many forms of irrigation, such as the flooding of fields, are wasteful because much of the water evaporates. To use water efficiently, farmers must understand the water-holding capacity of their soil, the water needs of their crops, and the appropriate irrigation technology. One popular technology is *drip irrigation*, the slow release of water to soil and plants from perforated plastic tubing placed directly at the root zone. Because drip irrigation requires less water and reduces salinization, it is used in many arid agricultural regions.

Fertilization

In natural ecosystems, mineral nutrients are usually recycled by the excretion of animal wastes and the decomposition of humus. Agriculture, however, is unnatural. The lettuce you eat, for example, contains minerals extracted from a farmer's field. As you excrete wastes, these minerals are deposited far from their original source. Over many harvests, the farmer's field will eventually become depleted of nutrients. Nutrient depletion is a major cause of global soil degradation. Farmers must reverse nutrient depletion by **fertilization**, the addition of mineral nutrients to the soil.

Today, most farmers in industrialized nations use fertilizers containing minerals that are either mined or prepared by energy-intensive processes. These fertilizers are usually enriched in nitrogen (N), phosphorus (P), and potassium (K)—the nutrients most commonly deficient in depleted soils. You may have seen fertilizers labeled with a three-number code, called the N-P-K ratio. A fertilizer marked "15-10-5," for instance, is 15% N (as ammonium or nitrate), 10% P (as phosphate), and 5% K (as the mineral potash).

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 the inorganic nutrients that roots can absorb. Whether from organic fertilizer or a chemical factory, the minerals a plant extracts are in the same form. However, organic fertilizers release them gradually, whereas minerals in commercial fertilizers are immediately available but may not be retained by the soil for long. Minerals not absorbed by roots are often leached from the soil by rainwater or irrigation. To make matters worse, mineral runoff into lakes may lead to explosions in algal populations that can deplete oxygen levels and decimate fish populations.

Adjusting Soil pH

Soil pH is an important factor that influences mineral availability by its effect on 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. Most plants prefer slightly acidic soil because the high H^+ concentrations can displace positively charged minerals from soil particles, making them more available for absorption. Adjusting soil pH for optimal crop growth is tricky because a change in H^+ concentration may make one mineral more available but another less available. At pH 8, for instance, plants can absorb calcium, but iron is almost unavailable. The soil pH should be matched to a crop's mineral needs. If the soil is too alkaline, adding sulfate will lower the pH. Soil that is too acidic can be adjusted by adding lime (calcium carbonate or calcium hydroxide).

When the soil pH dips to 5 or lower, toxic aluminum ions (Al^{3+}) become more soluble and are absorbed by roots, stunting root growth and preventing the uptake of calcium, a needed plant nutrient. Some plants can cope with high Al^{3+} levels by secreting organic anions that bind Al^{3+} and render it harmless. However, low soil pH and Al^{3+} toxicity continue to pose serious problems, especially in tropical regions, where the pressure of producing food for a growing population is often most acute.

Controlling Erosion

As happened most dramatically in the Dust Bowl, water and wind erosion can remove considerable amounts of topsoil.

▲ **Figure 37.6 Contour tillage.** These crops are planted in rows that go around, rather than up and down, the hills. Contour tillage helps slow water runoff and topsoil erosion after heavy rains.

Erosion is a major cause of soil degradation because soil nutrients are carried away by wind and streams. To limit erosion, farmers plant rows of trees as windbreaks, terrace hillside crops, and cultivate crops in a contour pattern (**Figure 37.6**). 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 traditional plowing, the entire field is tilled, or turned over. This practice helps control weeds but disrupts the meshwork of roots that holds the soil in place, leading to increased surface runoff and erosion. In no-till agriculture, a special plow creates narrow furrows for seeds and fertilizer. In this way, the field can be seeded with minimal disturbance to the soil, while also requiring less fertilizer.

Phytoremediation

Some land areas are unfit for cultivation because toxic heavy metals or organic pollutants have contaminated the soil or groundwater. Traditionally, soil remediation, the detoxification of contaminated soils, has focused on nonbiological technologies, such as removing and storing contaminated soil in landfills, but these techniques are very costly and often disrupt the landscape. **Phytoremediation** is a nondestructive biotechnology that harnesses 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. Such plants show promise for cleaning up areas contaminated by smelters, mining operations, or nuclear testing. Phytoremediation is a type of bioremediation, which also includes the use of prokaryotes and protists to detoxify polluted sites (see Chapters 27 and 55).

We have discussed the importance of soil conservation for sustainable agriculture. Mineral nutrients contribute greatly to soil fertility, but which minerals are most important, and why do plants need them? These are the topics of the next section.

CONCEPT CHECK 37.1

1. Explain how the phrase "too much of a good thing" can apply to watering and fertilizing plants.
2. Some lawn mowers collect clippings for easy disposal. What is a drawback of this practice with respect to plant nutrition?
3. **WHAT IF?** How would adding clay to loamy soil affect the soil's capacity to exchange cations and retain water? Explain.
4. **MAKE CONNECTIONS** Note three ways in which the properties of water contribute to soil formation. See pages 47–51 of Concept 3.2.

For suggested answers, see Appendix A.

CONCEPT 37.2

Plants require essential elements to complete their life cycle

Watch a large plant grow from a tiny seed, and you cannot help wondering where all the mass comes from. Aristotle hypothesized that plants "ate" soil because they were seen to arise from the ground. In the 1640s, Jan Baptista van Helmont tested the hypothesis that plants grow by consuming soil. He planted a small willow in a pot that contained 90.9 kg of soil. After five years, the plant weighed 76.8 kg, but only 0.06 kg of soil had disappeared from the pot. He concluded that the willow had grown mainly from the water added. A century later, the English physiologist Stephen Hales, armed with knowledge from advances in physics and chemistry that air is a substance with mass, postulated that plants are nourished mostly by air.

There is some truth to all three hypotheses because soil, water, and air all contribute to plant growth. The water content of a plant can be measured by comparing the plant's mass before and after drying. Typically, 80–90% of a plant's fresh mass is water. We can also analyze the chemical composition of the dry residue. Inorganic substances generally account for about 4% of the dry mass. Thus, inorganic nutrients from the soil, although essential for plant survival, contribute very little to the plant's mass. Some 96% of the dry mass consists of organic compounds produced by photosynthesis. The carbon and most of the oxygen atoms in these compounds come from CO_2 assimilated from the air, while water supplies most of the hydrogen atoms and some oxygen atoms (see Figure 10.5). Most of the organic material of plants is carbohydrate, including the cellulose of cell walls. Thus, the components of carbohydrates—carbon, oxygen, and hydrogen—are the most abundant elements in a dried plant. Because many macromolecules contain nitrogen, sulfur, or phosphorus, these elements are also relatively abundant in plants.

Macronutrients and Micronutrients

The inorganic substances in plants contain more than 50 chemical elements. In studying the chemical composition of plants, we must distinguish elements that are essential from those that are merely present in the plant. A chemical element is considered an **essential element** only if it is required for a plant to complete its life cycle and produce another generation.

To determine which chemical elements are essential, researchers use **hydroponic culture**, in which plants are grown in mineral solutions instead of soil **(Figure 37.7)**. Such studies have helped identify 17 essential elements needed by all plants **(Table 37.1)**. Hydroponic culture is also used on a small scale to grow some greenhouse crops.

Nine of the essential elements are called **macronutrients** because plants require them in relatively large amounts. Six of these are the major components of organic compounds forming a plant's structure: 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, chlorophyll, and other important organic molecules.

The remaining eight essential elements are known as **micronutrients** because plants need them in only tiny quantities. They are chlorine, iron, manganese, boron, zinc, copper, nickel, and molybdenum. In some cases, sodium may be a ninth essential micronutrient: Plants that use the C_4 and CAM pathways of photosynthesis (see Chapter 10) require sodium ions to regenerate phosphophenolpyruvate, which is the CO_2 acceptor in these two types of carbon fixation.

Micronutrients function in plants mainly as cofactors, nonprotein helpers in enzymatic reactions (see Chapter 8). Iron, for example, is a metallic component of cytochromes, the proteins in the electron transport chains of chloroplasts and mitochondria. It is because micronutrients generally play catalytic roles that plants need only tiny quantities. The requirement for molybdenum, for instance, is so modest that there is only one atom of this rare element for every 60 million atoms of hydrogen in dried plant material. Yet a deficiency of molybdenum or any other micronutrient can weaken or kill a plant.

▼ **Figure 37.7** **RESEARCH METHOD**

Hydroponic Culture

APPLICATION In hydroponic culture, plants are grown in mineral solutions without soil. One use of hydroponic culture is to identify essential elements in plants.

TECHNIQUE Plant roots are bathed in aerated solutions of known mineral composition. Aerating the water provides the roots with oxygen for cellular respiration. (Note: The flasks would normally be opaque to prevent algal growth.) A mineral, such as potassium, can be omitted to test whether it is essential.

Control: Solution containing all minerals

Experimental: Solution without potassium

RESULTS If the omitted mineral is essential, mineral deficiency symptoms occur, such as stunted growth and discolored leaves. By definition, the plant would not be able to complete its life cycle. Deficiencies of different elements may have different symptoms, which can aid in diagnosing mineral deficiencies in soil.

Symptoms of Mineral Deficiency

The symptoms of a deficiency depend partly on the mineral's function as a nutrient. For example, a deficiency of magnesium, a component of chlorophyll, causes *chlorosis*, yellowing of the leaves. In some cases, the relationship between a mineral deficiency and its symptoms is less direct. For instance, iron deficiency can cause chlorosis even though chlorophyll contains no iron, because iron ions are required as a cofactor in one of the enzymatic steps of chlorophyll synthesis.

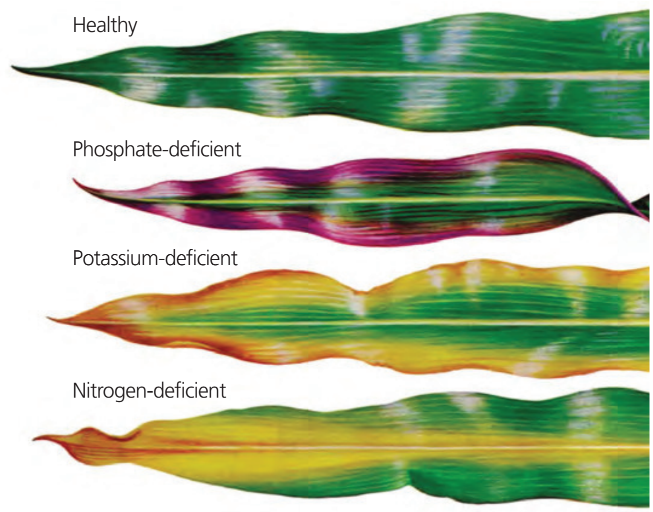
Mineral deficiency symptoms depend not only on the role of the nutrient but also on its mobility within the plant. If a nutrient moves about freely, symptoms appear first in older organs because young, growing tissues are a greater sink for nutrients that are in short supply. For example, magnesium is relatively mobile and is shunted preferentially to young leaves. Therefore, a plant deficient in magnesium first shows signs of chlorosis in its older leaves. The mechanism for preferential routing is the source-to-sink translocation in phloem, as minerals move along with sugars to the growing tissues (see Figure 36.18). In contrast, a deficiency of a mineral that is relatively immobile affects young parts of the plant first. Older tissues may have adequate amounts that they retain during periods of short supply. For example, iron does not move freely within a plant, and an iron deficiency causes yellowing of young leaves before any effect on older leaves is visible. The mineral requirements of a plant may also change with the time of the year and the age of the plant. Young seedlings, for example, rarely show mineral deficiency symptoms because their mineral requirements are met largely by minerals released from stored reserves in the seed itself.

Table 37.1 Essential Elements in Plants

Element	Form Primarily Absorbed by Plants	% Mass in Dry Tissue	Major Functions
Macronutrients			
Carbon	CO_2	45%	Major component of plant's organic compounds
Oxygen	CO_2	45%	Major component of plant's organic compounds
Hydrogen	H_2O	6%	Major component of plant's organic compounds
Nitrogen	NO_3^-, NH_4^+	1.5%	Component of nucleic acids, proteins, hormones, chlorophyll, coenzymes
Potassium	K^+	1.0%	Cofactor that functions in protein synthesis; major solute functioning in water balance; operation of stomata
Calcium	Ca^{2+}	0.5%	Important in 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; cofactor and activator of 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
Micronutrients			
Chlorine	Cl^-	0.01%	Required for water-splitting step of photosynthesis; functions in water balance
Iron	Fe^{3+}, Fe^{2+}	0.01%	Component of cytochromes; cofactor of some enzymes; needed for photosynthesis
Manganese	Mn^{2+}	0.005%	Active in formation of amino acids; activates some enzymes; required for water-splitting step of photosynthesis
Boron	$H_2BO_3^-$	0.002%	Cofactor in chlorophyll synthesis; may be involved in carbohydrate transport and nucleic acid synthesis; role in cell wall function
Zinc	Zn^{2+}	0.002%	Active in formation of chlorophyll; cofactor of some enzymes; needed for DNA transcription
Copper	Cu^+, Cu^{2+}	0.001%	Component of many redox and lignin-biosynthetic enzymes
Nickel	Ni^{2+}	0.001%	Cofactor for an enzyme functioning in nitrogen metabolism
Molybdenum	MoO_4^{2-}	0.0001%	Essential for mutualistic relationship with nitrogen-fixing bacteria; cofactor in nitrate reduction

MAKE CONNECTIONS *Three of the mineral requirements for humans in Table 41.2, on page 878, come from plants but are not essential for plant survival. What are those minerals, and how can plants be a source when they don't need them to complete their life cycle?*

Deficiencies of phosphorus, potassium, and especially nitrogen are most common. Micronutrient shortages are less common and tend to occur in certain geographic regions because of differences in soil composition. The symptoms of a mineral deficiency may vary between species but are often distinctive enough for a plant physiologist or farmer to diagnose the cause **(Figure 37.8)**. One way to confirm a diagnosis is to analyze the mineral content of the plant or soil. The amount of a micronutrient needed to correct a deficiency is usually quite small. For example, a zinc deficiency in fruit trees can usually be cured by hammering a few zinc nails into each tree trunk. Moderation is important because overdoses of many nutrients can be detrimental or toxic to plants. Too much nitrogen, for example, can lead to excessive vine growth in tomato plants at the expense of good fruit production.



▶ **Figure 37.8 The most common mineral deficiencies, as seen in maize leaves.** Mineral deficiency symptoms may vary in different species. In maize, phosphate-deficient plants have reddish purple margins, particularly in young leaves. Potassium-deficient maize plants exhibit "firing," or drying, along tips and margins of older leaves. Nitrogen deficiency is evident in a yellowing that starts at the tip and moves along the center (midrib) of older leaves.

Improving Plant Nutrition by Genetic Modification: Some Examples

In exploring plant nutrition so far, we have discussed how farmers use irrigation, fertilization, and other means to tailor the soil conditions to fit the needs of a crop. An opposite approach involves tailoring the plant by genetic engineering to better fit the soil conditions. Here we highlight a few examples of how genetic engineering is improving plant nutrition and fertilizer usage.

Resistance to Aluminum Toxicity

As previously discussed, aluminum in acidic soils damages roots and greatly reduces crop yields. The major mechanism of aluminum resistance is the secretion of organic acids (such as malic acid and citric acid) by roots. These acids bind to free aluminum ions and lower the levels of toxic aluminum in the soil. Luis Herrera-Estrella and colleagues (see the Unit Six interview on pages 736–737), at the National Polytechnic Institute in Mexico, altered tobacco and papaya plants by introducing a citrate synthase gene from a bacterium into the plants' genomes. The resulting overproduction of citric acid increased aluminum resistance in these two crops.

Flood Tolerance

Waterlogged soil not only deprives roots of oxygen but also can injure plants as ethanol and other toxic products of alcoholic fermentation by the plant accumulate. In Asian countries, flooding during the monsoon season often destroys rice crops. Although most varieties of rice die after being submerged for a week, some types can survive weeks of flooding. A gene called *Submergence 1A-1* (*Sub1A-1*) is the main source of submergence tolerance in flood-resistant rice. The Sub1A-1 protein regulates 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 increases the alcohol dehydrogenase levels of the plants and confers tolerance to submergence. Increasing the expression of *Sub1A-1* by genetic engineering may enhance flood tolerance in other crop species.

Smart Plants

Agricultural researchers are developing ways to maintain crop yields while reducing fertilizer use. One approach is to genetically engineer "smart" plants that signal when a nutrient deficiency is imminent—but *before* damage has occurred. One type of smart plant takes advantage of a promoter (a DNA sequence indicating where the transcription of a gene starts) that more readily binds RNA polymerase (the transcription enzyme) 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

▲ **Figure 37.9 Deficiency warnings from "smart" plants.** Some plants have been genetically modified to signal an impending nutrient deficiency before irreparable damage occurs. For example, after laboratory treatments, the research plant *Arabidopsis* develops a blue color in response to an imminent phosphate deficiency.

pigment in the leaf cells (**Figure 37.9**). When leaves of these smart plants develop a blue tinge, the farmer knows it is time to add phosphate-containing fertilizer.

So far, you have learned that soil, to support vigorous plant growth, must have an adequate supply of mineral nutrients, sufficient aeration, good water-holding capacity, low salinity, and a pH near neutrality. It must also be free of toxic concentrations of minerals and other chemicals. These physical and chemical features of soil, however, are just part of the story: We must also consider the living components of soil.

CONCEPT CHECK 37.2

1. Explain how Table 37.1 supports Stephen Hales's hypothesis.
2. Are some essential elements more important than others? Explain.
3. **WHAT IF?** If an element increases the growth rate of a plant, can it be defined as an essential element?
4. **MAKE CONNECTIONS** Based on Figure 9.18, on page 179, explain why ethanol accumulates in plant roots subjected to waterlogging.

For suggested answers, see Appendix A.

CONCEPT 37.3

Plant nutrition often involves relationships with other organisms

To this point, we have portrayed plants as exploiters of soil resources. But 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. Here we'll focus on some *mutualistic*—mutually beneficial—relationships between plants and soil bacteria or fungi. Then we'll look at some unusual plants that form nonmutualistic relationships with other plants or, in a few cases, with animals.

Soil Bacteria and Plant Nutrition

Some soil bacteria engage in mutually beneficial chemical exchanges with plant roots. Others enhance the decomposition of organic materials and increase nutrient availability. Some even live inside roots and convert nitrogen from the air.

Rhizobacteria

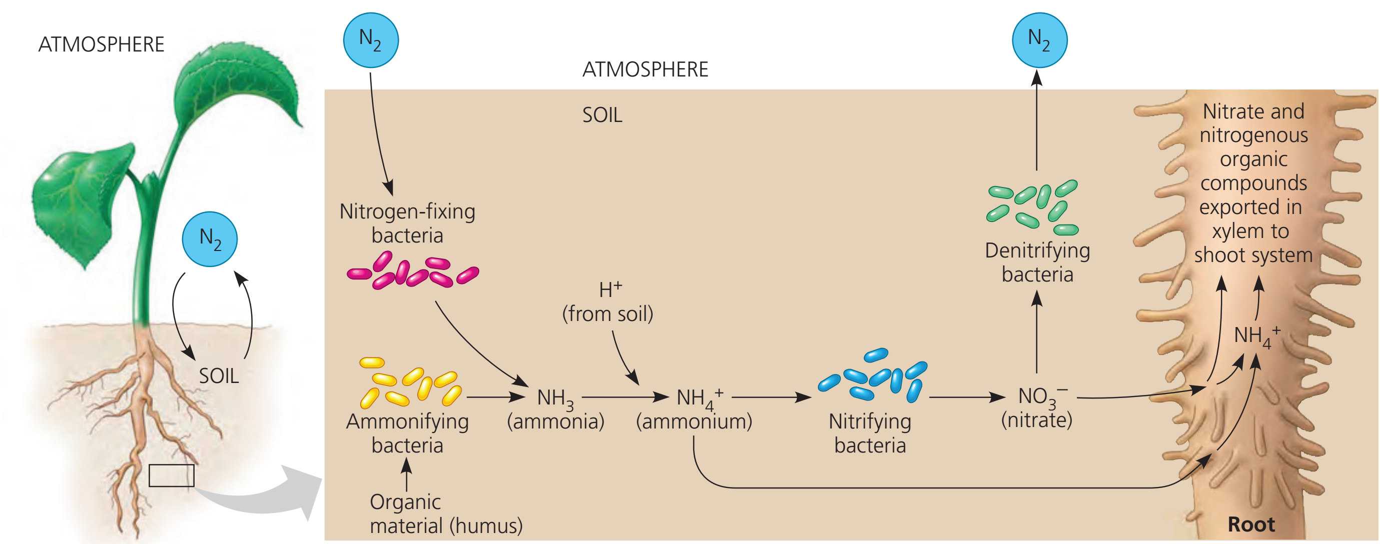
Rhizobacteria are soil bacteria with especially large populations in the **rhizosphere**, the soil layer that surrounds the plant's roots. Different soils vary greatly in the types and number of rhizobacteria they harbor. Microbial activity within a plant's rhizosphere is 10 to 100 times higher than in nearby soil because the roots secrete nutrients such as sugars, amino acids, and organic acids. Up to 20% of a plant's photosynthetic production fuels the organisms in this miniature ecosystem. 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.

Rhizobacteria known as *plant-growth-promoting rhizobacteria* enhance plant growth by a variety of mechanisms. Some produce chemicals that stimulate plant growth. Others produce antibiotics that protect roots from disease. Still others absorb toxic metals or make nutrients more available to roots. Inoculation of seeds with plant-growth-promoting rhizobacteria can increase crop yield and reduce the need for fertilizers and pesticides. How do the bacteria benefit by interacting with plants? Root secretions supply most of the energy in the rhizosphere, so bacterial adaptations that help a plant thrive and secrete nutrients also help the bacteria.

Bacteria in the Nitrogen Cycle

Plants have mutualistic relationships with several groups of bacteria that help make nitrogen more available. From a global perspective, no mineral nutrient is more limiting to plant growth than nitrogen, which is required in large amounts for synthesizing proteins and nucleic acids. The **nitrogen cycle**, discussed in Chapter 55, describes transformations of nitrogen and nitrogenous compounds in nature. Here we focus on processes leading directly to nitrogen assimilation by plants.

Unlike other soil minerals, ammonium ions (NH_4^+) and nitrate ions (NO_3^-)—the forms of nitrogen that plants can use—are not derived from the weathering of rocks. Although lightning produces small amounts of NO_3^- that get carried to the soil in rain, most soil nitrogen comes from the activity of bacteria **(Figure 37.10)**. *Ammonifying bacteria*, which are usually decomposers living in humus-rich soil, release ammonia (NH_3) by breaking down proteins and other organic compounds in humus. *Nitrogen-fixing bacteria* convert gaseous nitrogen (N_2) to NH_3 in a process we'll discuss shortly. In either case, the NH_3 produced picks up another H^+ in the soil solution to form NH_4^+. However, plants acquire nitrogen mainly in the form of NO_3^-. Soil NO_3^- is largely formed by a two-step process called *nitrification*, which consists of the oxidation of NH_3 to nitrite (NO_2^-), followed by oxidation of nitrite to nitrate (NO_3^-). Different types of *nitrifying bacteria* mediate each step. 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 as NO_3^- or organic compounds synthesized in the roots. Some soil nitrogen is lost, particularly in anaerobic soils, when denitrifying bacteria convert NO_3^- to N_2, which diffuses into the atmosphere.



▲ **Figure 37.10 The roles of soil bacteria in the nitrogen nutrition of plants.** Ammonium is made available to plants by two types of soil bacteria: those that fix atmospheric N_2 (nitrogen-fixing bacteria) and those that decompose organic material (ammonifying bacteria). Although plants absorb some ammonium from the soil, they absorb mainly nitrate, which is produced from ammonium by nitrifying bacteria. Plants reduce nitrate back to ammonium before incorporating the nitrogen into organic compounds.

Nitrogen-Fixing Bacteria: A Closer Look

Although Earth's atmosphere is 79% nitrogen, plants cannot use free gaseous nitrogen (N_2) because there is a triple bond between the two nitrogen atoms, making the molecule almost inert. For atmospheric N_2 to be of use to plants, it must be reduced to NH_3 by a process called **nitrogen fixation**. All N_2-fixing organisms are bacteria, and some that carry out this process are free-living (see Figure 37.10). One of the more important bacteria involved in N_2 fixation is the genus *Rhizobium*, which forms intimate associations with the roots of legumes (such as peas, soybeans, alfalfa, and peanuts) and markedly alters their root structure. Although *Rhizobium* can be free-living in the soil, it cannot fix N_2 in its free state, nor can legume roots fix N_2 without the bacteria.

The conversion of N_2 to NH_3 is a complicated, multistep process, but the reactants and products in nitrogen fixation can be summarized as follows:

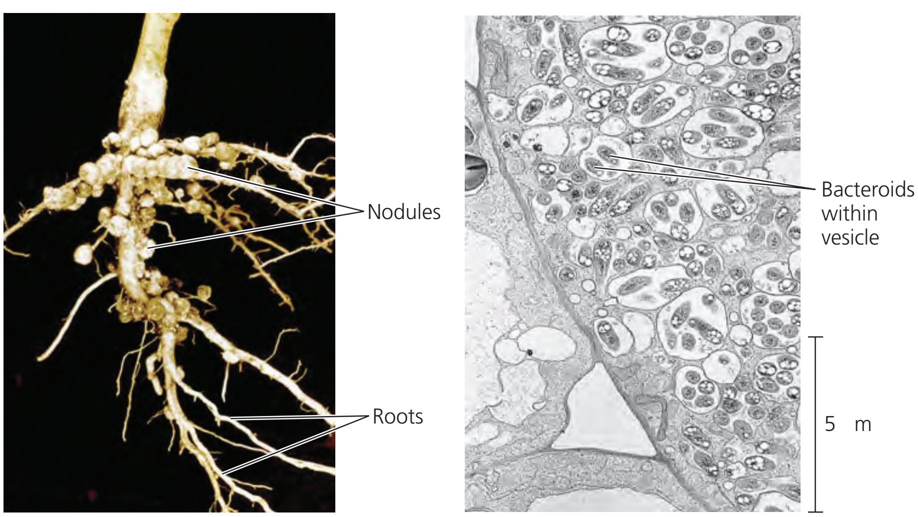
$$N_2 + 8\,e^- + 8\,H^+ + 16\,ATP \rightarrow 2\,NH_3 + H_2 + 16\,ADP + 16\,Ⓟ_i$$

The enzyme complex *nitrogenase* catalyzes the entire reaction sequence, which reduces N_2 to NH_3 by adding electrons and H^+. Because the process of nitrogen fixation requires eight ATP molecules for each NH_3 synthesized, nitrogen-fixing bacteria require a rich supply of carbohydrates from decaying material, root secretions, or (in the case of *Rhizobium*) the vascular tissue of roots.

The specialized mutualism between *Rhizobium* bacteria and legume roots involves dramatic changes in root structure. Along a legume's roots are swellings called **nodules**, composed of plant cells that have been "infected" by *Rhizobium* ("root living") bacteria **(Figure 37.11a)**. Inside each nodule, *Rhizobium* bacteria assume a form called **bacteroids**, which are contained within vesicles formed in the root cells **(Figure 37.11b)**. Legume-*Rhizobium* relationships generate more usable nitrogen for plants than all industrial fertilizers used today, and the mutualism provides the right amount of nitrogen at the right time at virtually no cost to the farmer. In addition to supplying the legume with nitrogen, this nitrogen fixation significantly reduces spending on fertilizers for subsequent crops.

The location of the bacteroids inside living, nonphotosynthetic cells is conducive to nitrogen fixation, which requires an anaerobic environment. Lignified external layers of root nodules also limit gas exchange. Some root nodules appear reddish because of a molecule called leghemoglobin (*leg-* for "legume"), an iron-containing protein that binds reversibly to oxygen (similar to the hemoglobin in human red blood cells). This protein is an oxygen "buffer," reducing the concentration of free oxygen and thereby providing an anaerobic environment for nitrogen fixation while regulating the oxygen supply for the intense cellular respiration required to produce ATP for nitrogen fixation.

Each legume species is associated with a particular strain of *Rhizobium*. **Figure 37.12** describes how a root nodule develops after bacteria enter through an "infection thread." The symbiotic relationship between a legume and nitrogen-fixing bacteria is mutualistic in that the bacteria supply the host plant with fixed nitrogen while the plant provides the bacteria with carbohydrates and other organic compounds. The root nodules use most of the ammonium produced to make

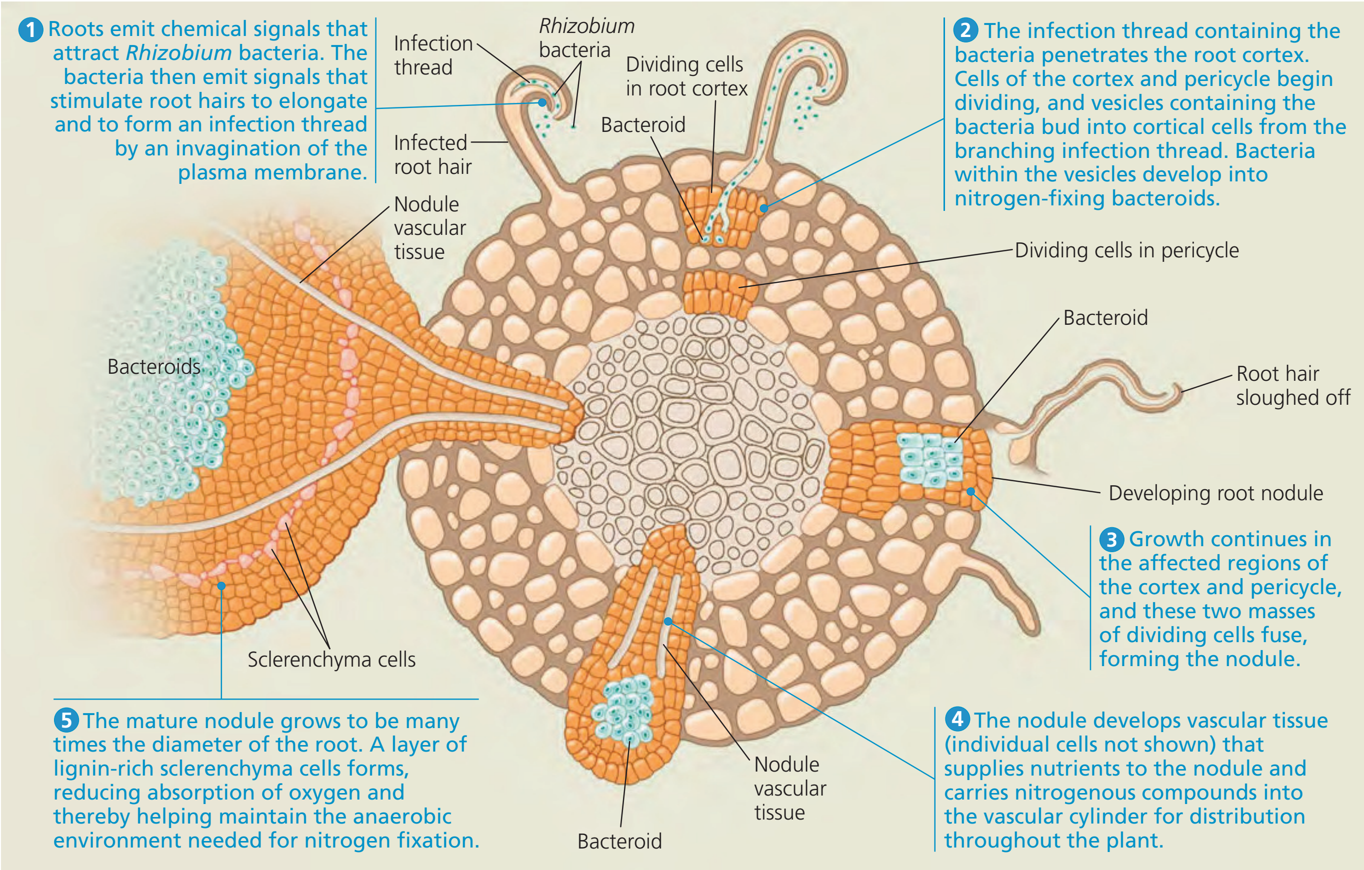


(a) Soybean root. The bumps on this soybean root are nodules containing *Rhizobium* bacteria. The bacteria fix nitrogen and obtain photosynthetic products supplied by the plant.

(b) Bacteroids in a soybean root nodule. In this TEM, a cell from a soybean root nodule is filled with bacteroids in vesicles. The cells on the left are uninfected.

◀ **Figure 37.11 Root nodules on a legume.** The coordinated activities of the legume and the *Rhizobium* bacteria depend on chemical signals between the mutualistic partners.

? *How is the relationship between legume plants and* Rhizobium *bacteria mutualistic?*



▲ **Figure 37.12 Development of a soybean root nodule.**

? *What plant tissue systems are modified by root nodule formation?*

amino acids, which are then transported up to the shoot through the xylem.

How does a legume species recognize a certain strain of *Rhizobium* among the many bacterial strains in the soil? And how does an encounter with that specific *Rhizobium* strain lead to development of a nodule? These two questions have led researchers to uncover a chemical dialogue between the bacteria and the root. Each partner responds to chemical signals from the other by expressing certain genes whose products contribute to nodule formation. By understanding the molecular biology underlying the formation of root nodules, researchers hope to learn how to induce *Rhizobium* uptake and nodule formation in crop plants that do not normally form such nitrogen-fixing mutualistic relationships.

Nitrogen Fixation and Agriculture

The agricultural benefits of mutualistic nitrogen fixation underlie most types of **crop rotation**. In this practice, a nonlegume such as maize is planted one year, and the following year alfalfa or some other legume is planted to restore the concentration of fixed nitrogen in the soil. To ensure that the legume encounters its specific *Rhizobium* strain, the seeds are exposed to bacteria before sowing. Instead of being harvested, the legume crop is often plowed under so that it will decompose as "green manure," reducing the need for manufactured fertilizers.

Many plant families besides legumes include species that benefit from mutualistic nitrogen fixation. For example, alder trees and certain tropical grasses host nitrogen-fixing actinomycete bacteria (see the gram-positive bacteria in Figure 27.17). Rice, a crop of great commercial importance, benefits indirectly from mutualistic nitrogen fixation. Rice farmers culture a free-floating aquatic fern, *Azolla*, which has mutualistic cyanobacteria that fix nitrogen. The growing rice eventually shades and kills the *Azolla*, and decomposition of this nitrogen-rich organic material increases the paddy's fertility.

Fungi and Plant Nutrition

Certain species of soil fungi also form mutualistic relationships with roots and play a major role in plant nutrition. **Mycorrhizae** ("fungus roots") are mutualistic associations of roots and fungi (see Figures 31.15 and 36.5). The host plant provides the fungus with a steady supply of sugar. Meanwhile, the fungus increases the surface area for water uptake and also supplies the plant with phosphate and other minerals absorbed from the soil. The fungi of mycorrhizae also secrete growth factors that stimulate roots to grow and branch, as well as antibiotics that help protect the plant from pathogens in the soil.

Mycorrhizae and Plant Evolution

EVOLUTION Mycorrhizae are not oddities; they are formed by most plant species. In fact, this plant-fungus mutualism might have been one of the evolutionary adaptations that helped plants initially colonize land (see Chapter 29). New fossil evidence has pushed the date for the appearance of mycorrhizae back to 460 million years ago, predating vascular plants. In early terrestrial ecosystems, the soil was probably poor in nutrients. The fungi of mycorrhizae, which are more efficient at absorbing minerals than the roots themselves, would have helped nourish the pioneering plants.

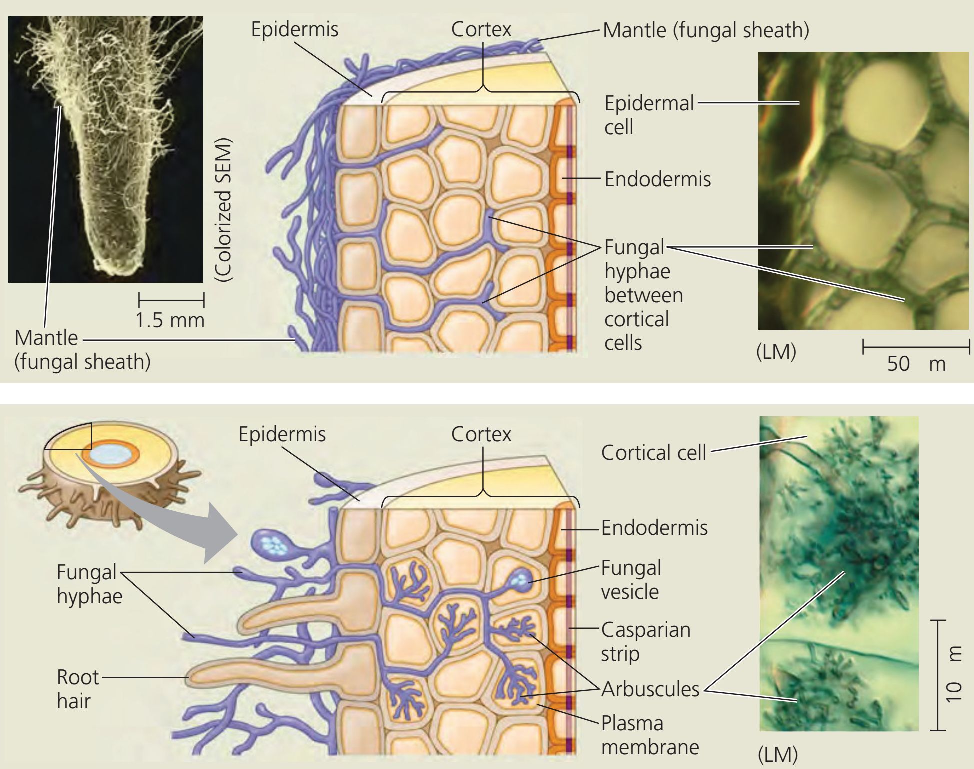
The Two Main Types of Mycorrhizae

The major mutualistic symbioses of fungi and plants are classified as either ectomycorrhizae or arbuscular mycorrhizae (sometimes called endomycorrhizae). In **ectomycorrhizae**, the mycelium (mass of branching hyphae; see Chapter 31) forms a dense sheath, or mantle, over the surface of the root **(Figure 37.13a)**. Fungal hyphae extend from the mantle into the soil, greatly increasing the surface area for water and mineral absorption. Hyphae 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 the fungus and the plant. Compared with "uninfected" roots, ectomycorrhizae are generally thicker, shorter, and more branched. They typically do not form root hairs, which would be superfluous given the extensive surface area of the fungal mycelium. About 10% of plant families have species that form ectomycorrhizae, and the vast majority of these species are woody, including members of the pine, spruce, oak, walnut, birch, willow, and eucalyptus families.

In contrast, **arbuscular mycorrhizae** do not have a dense mantle ensheathing the root **(Figure 37.13b)**. 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 epidermal cells and then enter the root cortex. These hyphae digest small patches of the cortical cell walls, but they do not actually pierce the plasma membrane and enter the cytoplasm. Instead, a hypha grows into a tube formed by invagination of the root cell's membrane. The process is analogous to poking a finger gently into a balloon without popping it; your finger is like the fungal hypha, and the balloon skin is like the root cell's membrane. After the fungal hyphae have penetrated in this way, some branch densely, forming structures called

(a) Ectomycorrhizae. The mantle of the fungal mycelium ensheathes the root. Fungal hyphae extend from the mantle into the soil, absorbing water and minerals, especially phosphate. Hyphae also extend into the extracellular spaces of the root cortex, providing extensive surface area for nutrient exchange between the fungus and its host plant.

(b) Arbuscular mycorrhizae (endomycorrhizae). No mantle forms around the root, but microscopic fungal hyphae extend into the root. Within the root cortex, the fungus makes extensive contact with the plant through branching of hyphae that form arbuscules, providing an enormous surface area for nutrient swapping. The hyphae penetrate the cell walls, but not the plasma membranes, of cells within the cortex.



▲ **Figure 37.13 Mycorrhizae.**

arbuscules ("little trees"), which are important sites of nutrient transfer between the fungus and the plant. Within the hyphae themselves, oval vesicles may form, possibly serving as food storage sites for the fungus. To the unaided eye, arbuscular mycorrhizae look like "normal" roots with root hairs, but a microscope reveals the enormous extent of the mutualistic relationship. Arbuscular mycorrhizae are much more common than ectomycorrhizae and are found in over 85% of plant species, including crop plants such as grains and legumes.

Agricultural and Ecological Importance of Mycorrhizae

Roots can form mycorrhizal symbioses only if exposed to the appropriate species of fungus. In most ecosystems, these fungi are present in the soil, and seedlings develop mycorrhizae. But if seeds are collected in one environment and planted in foreign soil, the plants may show signs of malnutrition (particularly phosphorus deficiency), resulting from the absence of fungal partners. Treating seeds with spores of mycorrhizal fungi can sometimes help seedlings to form mycorrhizae and improve crop yield.

Mycorrhizal associations are also important in understanding ecological relationships. Invasive exotic plants sometimes colonize areas by disrupting interactions between native organisms. For example, garlic mustard (*Alliaria petiolata*), introduced into New England from Europe during the 1800s, has invaded woodlands throughout the eastern and middle United States, suppressing tree seedlings and other native plants. Researchers at Harvard University have produced compelling evidence that 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 **(Figure 37.14)**.

Epiphytes, Parasitic Plants, and Carnivorous Plants

Almost all plant species have mutualistic symbiotic relationships with soil fungi or bacteria or both. Though rarer, there are also plant species with nutritional adaptations that use other organisms in nonmutualistic ways. **Figure 37.15**, on the next page, provides an overview of three unusual adaptations: epiphytes, parasitic plants, and carnivorous plants.

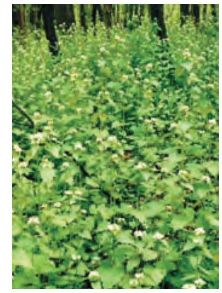
CONCEPT CHECK 37.3

1. Why is the study of the rhizosphere critical to understanding plant nutrition?
2. How do soil bacteria and mycorrhizae contribute to plant nutrition?
3. **WHAT IF?** A peanut farmer finds that the older leaves of his plant are turning yellow following a long period of wet weather. Suggest a reason why.

For suggested answers, see Appendix A.

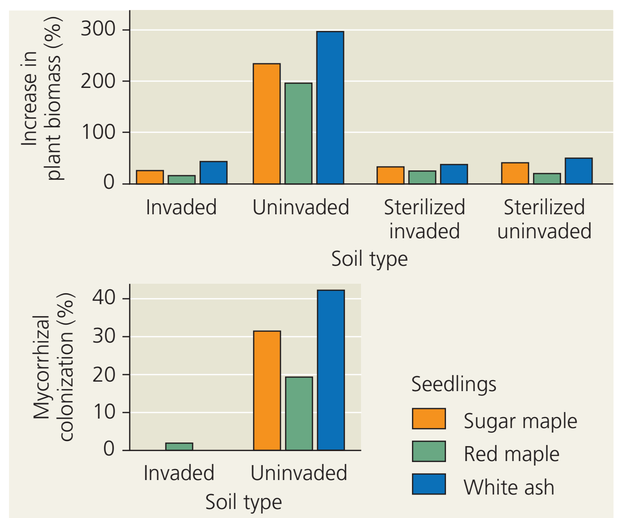
▼ Figure 37.14 **INQUIRY**

Does the invasive weed garlic mustard disrupt mutualistic associations between native tree seedlings and arbuscular mycorrhizal fungi?



EXPERIMENT Kristina Stinson, of Harvard University, and colleagues investigated the effect of invasive garlic mustard on the growth of native tree seedlings and associated mycorrhizal fungi. In one experiment, they grew seedlings of three North American trees—sugar maple, red maple, and white ash—in four different soils. Two of the soil samples were collected from a location where garlic mustard was growing, and one of these samples was sterilized. The other two soil samples were collected from a location devoid of garlic mustard, and one was then sterilized. After four months of growth, the researchers harvested the shoots and roots and determined the dried biomass. The roots were also analyzed for percent colonization by arbuscular mycorrhizal fungi.

RESULTS Native tree seedlings grew more slowly and were less able to form mycorrhizal associations when grown either in sterilized soil or in unsterilized soil collected from a location that had been invaded by garlic mustard.



CONCLUSION The data support the hypothesis that garlic mustard suppresses growth of native trees by affecting the soil in a way that disrupts mutualistic associations between the trees and arbuscular mycorrhizal fungi.

SOURCE K. A. Stinson et al., Invasive plant suppresses the growth of native tree seedlings by disrupting belowground mutualisms, *PLoS Biol* (*Public Library of Science: Biology*) 4(5): e140 (2006).

INQUIRY IN ACTION Read and analyze the original paper in *Inquiry in Action: Interpreting Scientific Papers*.

WHAT IF? What effect would applying inorganic phosphate to soil invaded by garlic mustard have on the plant's ability to outcompete native species?

▼ Figure 37.15

Exploring Unusual Nutritional Adaptations in Plants

Epiphytes

An **epiphyte** (from the Greek *epi*, upon, and *phyton*, plant) is a plant that grows on another plant. Epiphytes produce and gather their own nutrients; they do not tap into their hosts for sustenance. Usually anchored to the branches or trunks of living trees, epiphytes absorb water and minerals from rain, mostly through leaves rather than roots. Some examples are staghorn ferns, bromeliads, and many orchids, including the vanilla plant.

► **Staghorn fern**, an epiphyte

Parasitic Plants

◄ **Mistletoe**, a photosynthetic parasite

Unlike epiphytes, parasitic plants absorb water, minerals, and sometimes products of photosynthesis from their living hosts. Many species have roots that function as haustoria, nutrient-absorbing projections that tap into the host plant. Some parasitic species, such as orange-colored, spaghetti-like dodder (genus *Cuscuta*), lack chlorophyll entirely, whereas others, such as mistletoe (genus *Phoradendron*), are photosynthetic. Still others, such as Indian pipe (*Monotropa uniflora*), absorb nutrients from the hyphae of mycorrhizae associated with other plants.

▲ **Dodder**, a nonphotosynthetic parasite (orange)

▲ **Indian pipe**, a nonphotosynthetic parasite of mycorrhizae

Carnivorous Plants

Carnivorous plants are photosynthetic but supplement their mineral diet by capturing insects and other small animals. They live in acid bogs and other habitats where soils are poor in nitrogen and other minerals. Pitcher plants such as *Nepenthes* and *Sarracenia* have water-filled funnels into which prey slip and drown, eventually to be digested by enzymes (see also Figure 37.1). Sundews (genus *Drosera*) exude a sticky fluid from tentacle-like glands on highly modified leaves. Stalked glands secrete sweet mucilage that attracts and ensnares insects, and they also release digestive enzymes. Other glands then absorb the nutrient "soup." The highly modified leaves of Venus flytrap (*Dionaea muscipula*) close quickly but partially when a prey hits two trigger hairs in rapid enough succession. Smaller insects can escape, but larger ones are trapped by the teeth lining the margins of the lobes. Excitation by the prey causes the trap to narrow more and digestive enzymes to be released.

▲ **Sundews**

◄ **Pitcher plants**

◄ **Venus flytrap**

37 CHAPTER REVIEW

SUMMARY OF KEY CONCEPTS

CONCEPT 37.1

Soil contains a living, complex ecosystem (pp. 785–789)

- Soil particles of various sizes derived from the breakdown of rock are found in soil. Soil particle size affects the availability of water, oxygen, and minerals in the soil.
- A soil's composition refers to its inorganic and organic components. **Topsoil** is a complex ecosystem teeming with bacteria, fungi, protists, animals, and the roots of plants.
- Some agricultural practices can deplete the mineral content of soil, tax water reserves, and promote erosion. The goal of soil conservation is to minimize this damage.

? *How is soil a complex ecosystem?*

CONCEPT 37.2

Plants require essential elements to complete their life cycle (pp. 789–792)

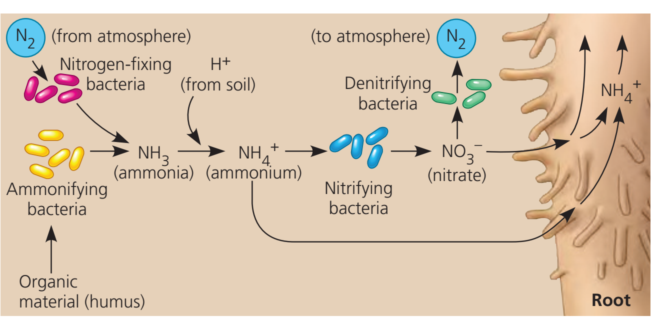
- **Macronutrients**, elements required in relatively large amounts, include carbon, oxygen, hydrogen, nitrogen, and other major ingredients of organic compounds. **Micronutrients**, elements required in very small amounts, typically have catalytic functions as cofactors of enzymes.
- Deficiency of a mobile nutrient usually affects older organs more than younger ones; the reverse is true for nutrients that are less mobile within a plant. Macronutrient deficiencies are most common, particularly deficiencies of nitrogen, phosphorus, and potassium.
- Rather than tailoring the soil to match the plant, genetic engineers are tailoring the plant to match the soil.

? *Do plants need soil to grow? Explain.*

CONCEPT 37.3

Plant nutrition often involves relationships with other organisms (pp. 792–798)

- **Rhizobacteria** derive their energy from the rhizosphere, a microbe-enriched ecosystem intimately associated with roots. Plant secretions support the energy needs of the rhizosphere. Some rhizobacteria produce antibiotics, whereas others make nutrients more available for plants. Most are free-living, but some live inside plants. Plants satisfy most of their huge needs for nitrogen from the bacterial decomposition of **humus** and the fixation of gaseous nitrogen.



Nitrogen-fixing bacteria convert atmospheric N_2 to nitrogenous minerals that plants can absorb as a nitrogen source for organic synthesis. The most efficient mutualism between plants and nitrogen-fixing bacteria occurs in the nodules formed by *Rhizobium* bacteria growing in the roots of legumes. These bacteria obtain sugar from the plant and supply the plant with fixed nitrogen. In agriculture, legume crops are rotated with other crops to restore nitrogen to the soil.

- **Mycorrhizae** are mutualistic associations of fungi and roots. The fungal hyphae of mycorrhizae absorb water and minerals, which they supply to their plant hosts.
- **Epiphytes** grow on the surfaces of other plants but acquire water and minerals from rain. Parasitic plants absorb nutrients from host plants. Carnivorous plants supplement their mineral nutrition by digesting animals.

? *Do all plants gain their energy directly from photosynthesis? Explain.*

TEST YOUR UNDERSTANDING

LEVEL 1: KNOWLEDGE/COMPREHENSION

1. Most of the mass of organic material of a plant comes from
   a. water.
   b. carbon dioxide.
   c. soil minerals.
   d. atmospheric oxygen.
   e. nitrogen.

2. Micronutrients are needed in very small amounts because
   a. most of them are mobile in the plant.
   b. most serve mainly as cofactors of enzymes.
   c. most are supplied in large enough quantities in seeds.
   d. they play only a minor role in the growth and health of the plant.
   e. only the most actively growing regions of the plants require micronutrients.

3. Mycorrhizae enhance plant nutrition mainly by
   a. absorbing water and minerals through the fungal hyphae.
   b. providing sugar to root cells, which have no chloroplasts.
   c. converting atmospheric nitrogen to ammonia.
   d. enabling the roots to parasitize neighboring plants.
   e. stimulating the development of root hairs.

4. Epiphytes are
   a. fungi that attack plants.
   b. fungi that form mutualistic associations with roots.
   c. nonphotosynthetic parasitic plants.
   d. plants that capture insects.
   e. plants that grow on other plants.

5. Some of the problems associated with intensive irrigation include all but
   a. mineral runoff.
   b. overfertilization.
   c. land subsidence.
   d. aquifer depletion.
   e. soil salinization.

LEVEL 2: APPLICATION/ANALYSIS

6. A mineral deficiency is likely to affect older leaves more than younger leaves if
   a. the mineral is a micronutrient.
   b. the mineral is very mobile within the plant.
   c. the mineral is required for chlorophyll synthesis.
   d. the mineral is a macronutrient.
   e. the older leaves are in direct sunlight.

7. We would expect the greatest difference in plant health between two groups of plants of the same species, one group with mycorrhizae and one group without mycorrhizae, in an environment
   a. where nitrogen-fixing bacteria are abundant.
   b. that has soil with poor drainage.
   c. that has hot summers and cold winters.
   d. in which the soil is relatively deficient in mineral nutrients.
   e. that is near a body of water, such as a pond or river.

8. Two groups of tomatoes were grown under laboratory conditions, one with humus added to the soil and one a control without humus. The leaves of the plants grown without humus were yellowish (less green) compared with those of the plants grown in humus-enriched soil. The best explanation for this difference is that
   a. the healthy plants used the food in the decomposing leaves of the humus for energy to make chlorophyll.
   b. the humus made the soil more loosely packed, so water penetrated more easily to the roots.
   c. the humus contained minerals such as magnesium and iron, needed for the synthesis of chlorophyll.
   d. the heat released by the decomposing leaves of the humus caused more rapid growth and chlorophyll synthesis.
   e. the healthy plants absorbed chlorophyll from the humus.

9. The specific relationship between a legume and its mutualistic *Rhizobium* strain probably depends on
   a. each legume having a chemical dialogue with a fungus.
   b. each *Rhizobium* strain having a form of nitrogenase that works only in the appropriate legume host.
   c. each legume being found where the soil has only the *Rhizobium* specific to that legume.
   d. specific recognition between the chemical signals and signal receptors of the *Rhizobium* strain and legume species.
   e. destruction of all incompatible *Rhizobium* strains by enzymes secreted from the legume's roots.

10. **DRAW IT** Draw a simple sketch of cation exchange, showing a root hair, a soil particle with anions, and a hydrogen ion displacing a mineral cation.

LEVEL 3: SYNTHESIS/EVALUATION

11. **EVOLUTION CONNECTION**
    Imagine taking the plant out of the picture in Figure 37.10. Write a paragraph explaining how soil bacteria could sustain the recycling of nitrogen *before* land plants evolved.

12. **SCIENTIFIC INQUIRY**
    Acid precipitation has an abnormally high concentration of hydrogen ions (H^+). One effect of acid precipitation is to deplete the soil of nutrients such as calcium (Ca^{2+}), potassium (K^+), and magnesium (Mg^{2+}). Suggest a hypothesis to explain how acid precipitation washes these nutrients from the soil. How might you test your hypothesis?

13. **SCIENCE, TECHNOLOGY, AND SOCIETY**
    In many countries, irrigation is depleting aquifers to such an extent that land is subsiding, harvests are decreasing, and it is becoming necessary to drill wells deeper. In many cases, the withdrawal of groundwater has now greatly surpassed the aquifers' rates of natural recharge. Discuss the possible consequences of this trend. What can society and science do to help alleviate this growing problem?

14. **WRITE ABOUT A THEME**
    Environmental Interactions The soil in which plants grow teems with organisms from every taxonomic kingdom. In a short essay (100–150 words), discuss examples of how the mutualistic interactions of plants with bacteria, fungi, and animals improve plant nutrition.

For selected answers, see Appendix A.