Lush azaleas *(Rhododendron)* and a stately Southern live oak *(Quercus virginiana)* draped with the unusual flowering plant called Spanish moss *(Tillandsia usneoides)*. The roots of shrubs, trees, and most other plants take up water and minerals from soil, but Spanish moss is an epiphyte—it lives independently on other plants and obtains nutrients via absorptive hairs on its leaves and stems.

© Ellen McKnight/Alamy

33 Plant Nutrition

STUDY PLAN

WHY IT MATTERS

Tropical rainforests are remarkable for many reasons, but for biologists the key one may be that they are the most biologically diverse ecosystems on Earth. In addition to containing countless thousands of species of animals, fungi, protists, and prokaryotes, these amazingly lush domains are dense with broadleaved, evergreen trees, some of which soar 40 or 50 m skyward. With rain a near-daily event, it may not seem surprising that the trees' foliage is a luxuriant deep green **(Figure 33.1).** Yet tropical rainforests are demanding places for plants to survive, in large part because the soil is chronically deficient in nutrients, the chemical elements necessary for plant metabolism. This nutrient scarcity is a direct outcome of the incessant rain and the high acidity of tropical rainforest soil. There is ample moisture in the upper layer of soil, but in acid soil mineral nutrients vital to plant metabolism, such as potassium, calcium, magnesium, and phosphorus, are subject to **leaching**—being washed into deeper soil levels that are not as accessible to plant roots. In addition, in the warm, moist environment of a tropical rainforest, bacteria and fungi speedily decompose fallen leaves and other organic remains. Just as rapidly, established trees and vines

Gerry Ellis/The Wildlife Collection

Figure 33.1
A lush tropical rain forest growing in Southeast Asia.

take up any nutrients these decomposers have released, leaving few or none to enrich the soil. As falling rain dissolves some atmospheric CO_2, it creates carbonic acid—a type of "acid rain" that exacerbates the leaching problem even more.

Such poor soil and the near perpetual twilight at the forest floor make it extremely difficult for small shrubs and herbaceous plants to survive there. Nearly all such plants climb upward as vines using the tree trunks for mechanical support, or they live attached to the upper branches of taller species, where they can absorb needed minerals from falling dust or from the surfaces of other plants. These intricate adaptations to their particular environment allow the plants to secure energy and raw materials and to utilize both for growth and development.

Tropical rainforests are not unique in posing nutritional challenges for plants. In fact, plants rarely have ready access to a full complement of necessary resources. In a rainforest, the carbon, hydrogen, and oxygen plants need for photosynthesis are relatively easy to come by: plants there usually get enough carbon from the CO_2 in air, and their roots can take up enough water to gain the necessary hydrogen and oxygen. But soils in other environments are frequently dry, making water a limited resource, and almost nowhere in nature do soils hold lavish amounts of dissolved minerals such as nitrogen, calcium, and others that are vital for a plant's survival. In response to the challenge of obtaining nutrients, plants have evolved the range of structural and physiological adaptations that we consider in this chapter.

33.1 Plant Nutritional Requirements

No organism grows normally when deprived of a chemical element essential for its metabolism. In the latter half of the nineteenth century, plant physiologists exploited rapid advances in chemistry to probe both the chemical composition of plants and the essential nutrients plants need to survive. Because plants require some nutrients in only trace amounts, in recent times researchers have brought to bear sophisticated methods in their studies of plant nutrition.

Plants Require Macronutrients and Micronutrients for Their Metabolism

By weight, the tissues of most plants are more than 90% water. Early researchers could obtain a rough idea of the composition of a plant's dry weight by burning the plant and then analyzing the ash. This method typically yielded a long list of elements, but the results were flawed. Chemical reactions during burning can dissipate quantities of some important elements, such as nitrogen. Also, plants take up a variety of ions that they don't use; depending on the minerals present in the soil where a plant grows, a plant's tissues can contain nonnutritive elements such as gold, lead, arsenic, and uranium.

Studying Plant Nutrition Using Hydroponics. In 1860, German plant physiologist Julius von Sachs pioneered an experimental method for identifying the minerals

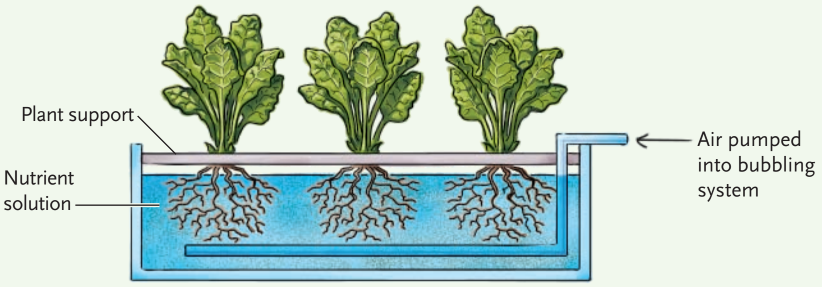
Figure 33.2 Research Method

Hydroponic Culture

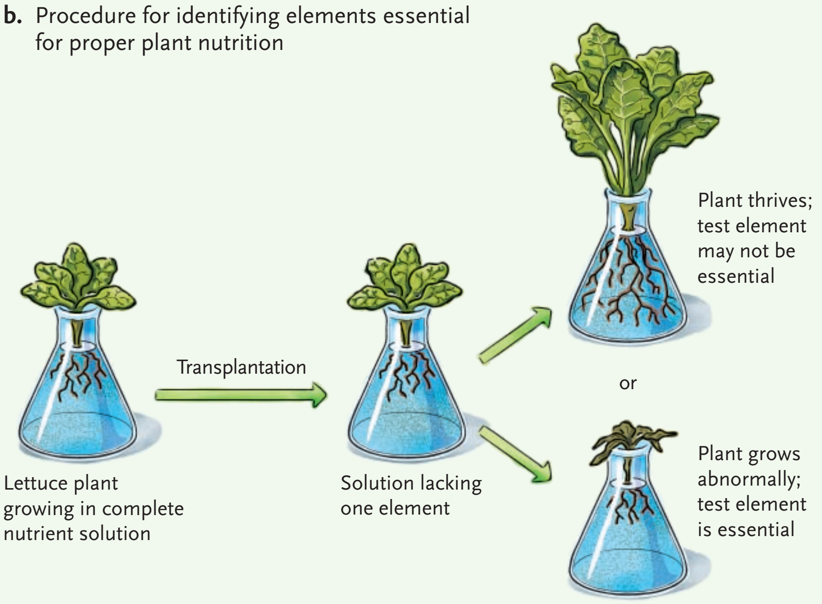
PURPOSE: In studies of plant nutritional requirements, using hydroponic culture allows a researcher to manipulate and precisely define the types and amounts of specific nutrients that are available to test plants.

PROTOCOL: In a typical hydroponic apparatus, many plants are grown in a single solution containing pure water and a defined mix of mineral nutrients. The solution is replaced or refreshed as needed and is aerated with a bubbling system:

a. Basic components of a hydroponic apparatus



b. Procedure for identifying elements essential for proper plant nutrition



A "complete" solution contains all the known and suspected essential plant nutrients. An "incomplete" solution contains all but one of the same nutrients, in the same amounts. For experiments, researchers first grow plants in a complete solution, then transplant some of the plants to an incomplete solution.

INTERPRETING THE RESULTS: Normal growth of test plants suggests that the missing nutrient is not essential, while abnormal growth is evidence that the missing nutrient may be essential.

absorbed into plant tissues that are essential for plant growth. Sachs carefully measured amounts of compounds containing specific minerals and mixed them in different combinations with pure water. He then grew plants in the solutions, a method called now **hydroponic culture** (*hydro* = water; *ponos* = work). By eliminating one element at a time and observing the results, Sachs deduced a list of six essential plant nutrients, in descending order of the amount required: nitrogen, potassium, calcium, magnesium, phosphorus, and sulfur.

Sachs's innovative research paved the way for decades of increasingly sophisticated studies of plant nutrition. In the spirit of his work, one basic experimental method involves growing a plant in a solution containing a complete spectrum of known and possible essential nutrients **(Figure 33.2a).** The healthy plant is then transferred to a solution that is identical, except that it lacks one element having an unknown nutritional role **(Figure 33.2b).** Abnormal growth of the plant in this solution is evidence that the missing element is essential. If the plant grows normally, the missing element may not be essential; however, only further experimentation can confirm this hypothesis.

In a typical modern hydroponic apparatus, the nutrient solution is refreshed regularly, and air is bubbled into it to supply oxygen to the roots. Without sufficient oxygen for respiration, the plants' roots do not absorb nutrients efficiently. (The same effect occurs in poorly aerated soil.) Variations of this technique are used on a commercial scale to grow some vegetables, such as lettuce and tomatoes.

Essential Macronutrients and Micronutrients. Hydroponics research has revealed that plants generally require 17 essential elements **(Table 33.1).** By definition, an **essential element** is necessary for normal growth and reproduction, cannot be functionally replaced by a different element, and has one or more roles in plant metabolism. With enough sunlight and the 17 essential elements, plants can synthesize all the compounds they need.

Nine of the essential elements are **macronutrients,** meaning that plants incorporate relatively large amounts

Table 33.1 Essential Plant Nutrients and Their Functions

Element	Commonly Absorbed Forms	Some Known Functions	Some Deficiency Symptoms
Macronutrients			
Carbon*	CO_2	Raw materials for photosynthesis	Rarely deficient
Hydrogen*	H_2O		No symptoms; available from water
Oxygen*	O_2, H_2O, CO_2		No symptoms; available from water and CO_2
Nitrogen	NO_3^-, NH_4^+	Component of proteins, nucleic acids, coenzymes, chlorophylls	Stunted growth; light-green older leaves; older leaves yellow and die (chlorosis)
Phosphorus	$H_2PO_4^-$, HPO_4^{2+}	Component of nucleic acids, phospholipids, ATP, several coenzymes	Purplish veins; stunted growth; fewer seeds, fruits
Potassium	K^+	Activation of enzymes; key role in maintaining water-solute balance and so influences osmosis	Reduced growth; curled, mottled, or spotted older leaves; burned leaf edges; weakened plant
Calcium	Ca^{2+}	Roles in formation and maintenance of cell walls and in membrane permeability; enzyme cofactor	Leaves deformed; terminal buds die; poor root growth
Sulfur	SO_4^{2-}	Component of most proteins, coenzyme A	Light-green or yellowed leaves; reduced growth
Magnesium	Mg^{2+}	Component of chlorophyll; activation of enzymes	Chlorosis; drooping leaves
Micronutrients			
Chlorine	Cl^-	Role in root and shoot growth, and in photosynthesis	Wilting; chlorosis; some leaves die (deficiency not seen in nature)
Iron	Fe^{2+}, Fe^{3+}	Roles in chlorophyll synthesis, electron transport; component of cytochrome	Chlorosis; yellow and green striping in grasses
Boron	H_3BO_3	Roles in germination, flowering, fruiting, cell division, nitrogen metabolism	Terminal buds, lateral branches die; leaves thicken, curl, and become brittle
Manganese	Mn^{2+}	Role in chlorophyll synthesis; coenzyme action	Dark veins, but leaves whiten and fall off
Zinc	Zn^{2+}	Role in formation of auxin, chloroplasts, and starch; enzyme component	Chlorosis; mottled or bronzed leaves; abnormal roots
Copper	Cu^+, Cu^{2+}	Component of several enzymes	Chlorosis; dead spots in leaves; stunted growth
Molybdenum	MoO_4^{2-}	Component of enzyme used in nitrogen metabolism	Pale green, rolled or cupped leaves
Nickel	Ni^{2+}	Component of enzyme required to break down urea generated during nitrogen metabolism	Dead spots on leaf tips (deficiency not seen in nature)

*Carbon, hydrogen, and nitrogen are the nonmineral plant nutrients. All others are minerals.

of them into their tissues. Three of these elements—carbon, hydrogen, and oxygen—account for about 96% of a plant's dry mass. Together, these three elements are the key components of lipids and of carbohydrates such as cellulose; with the addition of nitrogen, they form the basic building blocks of proteins and nucleic acids. Plants also use phosphorus in constructing nucleic acids, ATP, and phospholipids, and they use potassium for functions ranging from enzyme activation to mechanisms that control the opening and closing of stomata. Rounding out the list of macronutrients are calcium, sulfur, and magnesium. Carbon, hydrogen, and oxygen come from the air and water, and are the only plant nutrients that are not considered to be minerals. The other six macronutrients are minerals, inorganic substances available to plants through the soil as ions dissolved in water. Most minerals that serve as nutrients in plants are derived from the weathering of rocks and inorganic particles in the Earth's crust.

The other elements essential to plants are also minerals, and are classed as **micronutrients** because plants require them only in trace amounts. Nevertheless, they are just as vital as macronutrients to a plant's health and survival. For example, 5 metric tons of potatoes contain roughly the amount of copper in a single (copper-plated) penny—yet without it, potato plants are sickly and do not produce normal tubers.

Chlorine was identified as a micronutrient nearly a century after Sachs's experiments. The researchers who discovered its role performed hydroponic culture experiments in a California laboratory near the Pacific Ocean, where the air, like coastal air everywhere, contains sodium chloride. The investigators found that their test plants could obtain tiny but sufficient quantities of chlorine from the air, as well as from sweat (which also contains NaCl) on the researchers' own hands. Great care had to be taken to exclude chlorine from the test plants' growing environment in order to prove that it was essential.

In some cases, plant seeds contain enough of certain trace minerals to sustain the adult plant. For example, nickel (Ni^{2+}) is a component of urease, the enzyme required to hydrolyze urea. Urea is a toxic by-product of the breakdown of nitrogenous compounds, and it will kill cells if it accumulates. In the late 1980s investigators found that barley seeds contain enough nickel to sustain two complete generations of barley plants. Plants grown in the absence of nickel did not begin to show signs of nickel deficiency until the third generation.

Besides the 17 essential elements, some species of plants may require additional micronutrients. Experiments suggest that many, perhaps most, plants adapted to hot, dry conditions require sodium; many plants that photosynthesize by the C_4 pathway (see Section 9.4) appear to be in this group. A few plant species require selenium, which is also an essential micronutrient for animals. Horsetails *(Equisetum)* require silicon, and some grasses (such as wheat) may also need it. Scientists continue to discover additional micronutrients for specific plant groups.

Both micronutrients and macronutrients play vital roles in plant metabolism. Many function as cofactors or coenzymes in protein synthesis, starch synthesis, photosynthesis, and aerobic respiration. As you read in Section 32.1, some also have a role in creating solute concentration gradients across plasma membranes, which are responsible for the osmotic movement of water.

Nutrient Deficiencies Cause Abnormalities in Plant Structure and Function

Plants differ in the quantity of each nutrient they require—the amount of an essential element that is adequate for one plant species may be insufficient for another. Lettuce and other leafy plants require more nitrogen and magnesium than do other plant types, for example, and alfalfa requires significantly more potassium than do lawn grasses. An adequate amount of an essential element for one plant may even be harmful to another. For example, the amount of boron required for normal growth of sugar beets is toxic for soybeans. For these reasons, the nutrient content of soils is an important factor in determining which plants will grow well in a given location.

Plants that are deficient in one or more of the essential elements develop characteristic symptoms (Table 33.1 lists some observable symptoms of nutrient deficiencies). The symptoms give some indication of the metabolic roles the missing elements play. Deficiency symptoms typically include stunted growth, abnormal leaf color, dead spots on leaves, or abnormally formed stems **(Figure 33.3).** For instance, iron is a component of the cytochromes upon which the cellular electron transfer system depends, and it plays a role in reactions that synthesize chlorophyll. Iron deficiency causes **chlorosis,** a yellowing of plant tissues that results from a lack of chlorophyll (see Figure 33.3b). Because ionic iron (Fe^{3+}) is relatively insoluble in water, gardeners often fertilize plants with a soluble iron compound called chelated iron to stave off or cure chlorosis. Similarly, because magnesium is a necessary component of chlorophyll, a plant deficient in this element has fewer chloroplasts than normal in its leaves and other photosynthetic parts. It appears paler green than normal, and its growth is stunted because of reduced photosynthesis (see Figure 33.3c).

Plants that lack adequate nitrogen may also become chlorotic (see Figure 33.3d), with older leaves yellowing first because the nitrogen is preferentially shunted to younger, actively growing plant parts. This adaptation is not surprising, given nitrogen's central role in the synthesis of amino acids, chlorophylls, and other compounds vital to plant metabolism. With some other mineral deficiencies, young leaves are the first to

a. Plant grown using a complete growth solution
b. Iron deficiency
c. Magnesium deficiency
d. Nitrogen deficiency

e. Phosphorus deficiency
f. Potassium deficiency
g. Sulfur deficiency
h. Calcium deficiency

Figure 33.3
Leaves and stems of tomato plants showing visual symptoms of seven different mineral deficiencies. The plants were grown in the laboratory, where the experimenter could control which nutrients were available.
(Photos by E. Epstein, University of California, Davis.)

show symptoms. These kinds of observations underscore the point that plants utilize different nutrients in specific, often metabolically complex ways.

Soils are more likely to be deficient in nitrogen, phosphorus, potassium, or some other essential mineral than to contain too much, and farmers and gardeners typically add nutrients to suit the types of plants they wish to cultivate. They may observe the deficiency symptoms of plants grown in their locale or have soil tested in a laboratory, then choose a fertilizer with the appropriate balance of nutrients to compensate for the deficiencies. Packages of commercial fertilizers use a numerical shorthand (for example, 15-30-15) to indicate the percentages of nitrogen, phosphorus, and potassium they contain.

STUDY BREAK

1. What are the two main categories of the essential elements plants need? Give several examples of each.
2. Do all plants require the same basic nutrients in the same amounts? Explain.

33.2 Soil

Soil anchors plant roots and is the main source of the inorganic nutrients plants require. It also is the source of water for most plants, and of oxygen for respiration in root cells. The physical texture of soil determines whether root systems have access to sufficient water and dissolved oxygen. These characteristics reinforce the conclusion that the physical and chemical properties of soils in different habitats have a major impact on the ability of plant species to grow, survive, and reproduce there.

The Components of a Soil and the Size of the Particles Determine Its Properties

Soil is a complex mix of mineral particles, chemical compounds, ions, decomposing organic matter, air, water, and assorted living organisms. Most soils develop from the physical or chemical weathering of rock (which also liberates mineral ions). The different kinds of soil particles range in size from sand (2.0–0.02 mm) to silt (0.02–0.002 mm) and clay (diameter less than 0.002 mm). These mineral particles usually are mixed with various organic components, including **humus**—decomposing parts of plants and animals, animal droppings, and other organic matter. Dry humus has a loose, crumbly texture. It can absorb a great deal of water and thus contributes to the capacity of soil to hold water. Organic molecules in humus are reservoirs of nutrients, including nitrogen, phosphorus, and sulfur, that are vital to living plants.

The relative proportions of the different sizes of mineral particles give soil its basic texture—gritty if the soil is largely sand, smooth if silt predominates, and dense and heavy if clay is the major component. A soil's texture in turn helps determine the number and volume of pores—air spaces—that it contains. The relative amounts of sand, silt, and clay determine whether a soil is sticky when wet, with few air spaces (mostly clay), or dries quickly and may wash or blow away (mostly sand). Clay soils are more than 30% clay, while sandy soils contain less than 20% clay or silt.

The piles of bagged humus for sale at garden centers each spring reflect the fact that the amount of humus in a soil also affects plant growth. Its plentiful organic material feeds decomposers whose metabolic activities in turn release minerals that plant roots can take up, but that is not its only value in soil. Humus helps retain soil water and, with its loose texture, helps aerate soil as well. Well-aerated soils containing roughly equal proportions of humus, sand, silt, and clay are **loams,** and they are the soils in which most plants do best.

Soil also contains living organisms. Trillions of bacteria, hundreds of millions of fungi, and several million nematodes—not to mention earthworms and insects—are present in every square meter of fertile soil. Together with the roots of living plants, these organisms have a major influence on the composition and characteristics of soil. Bacteria and fungi decompose organic matter; burrowing creatures such as earthworms aerate the soil; and when plant roots die they contribute their organic matter to the soil.

As soils develop naturally, they tend to take on a characteristic vertical profile, with a series of layers or **horizons (Figure 33.4).** Each horizon has a distinct texture and composition that varies with soil type. The top layer of surface litter—twigs and leaves, animal dung, fungi, and similar organic matter—is accordingly called the *O horizon*. The most fertile soil layer, called **topsoil,** occurs just below and forms the *A horizon*. This layer may be less than a centimeter deep on steep slopes to more than a meter deep in grasslands. It consists of humus mixed with mineral particles and usually is fairly loose; it is here that the roots of most herbaceous plants are located. Below the topsoil is the **subsoil** or *B horizon,* a layer of larger soil particles containing relatively little organic matter. Mineral ions, including those that serve as nutrients in plants, tend to accumulate in the B horizon, and mature tree roots generally extend into this layer. Under it is the *C horizon,* a layer of mineral particles and rock fragments that extends down to bedrock.

Regions where the topsoil is deep and rich in humus are ideal for agriculture; the vast grasslands of the North American Midwest and Ukraine are prime examples. Without soil management and intensive irrigation, crops

O horizon
Fallen leaves and other organic material littering the surface of mineral soil

A horizon
Topsoil, which contains some percentage of decomposed organic material and which is of variable depth; here it extends about 30 cm below the soil surface

B horizon
Subsoil; larger soil particles than the A horizon, not much organic material, but greater accumulation of minerals; here it extends about 60 cm below the A horizon

C horizon
No organic material, but partially weathered fragments and grains of rock from which soil forms; extends to underlying bedrock

Bedrock

Figure 33.4
A representative profile of soil horizons.

William Ferguson

usually cannot be grown in deserts due to the lack of rainfall and low humus in the soil. Nor can agriculture flourish for long on land cleared of a tropical rainforest, due to the soil leaching and lack of nutrients described in the chapter introduction.

The Characteristics of Soil Affect Root–Soil Interactions

In different regions, and even in different parts of a local area, the proportions of the types of soil particles can differ dramatically, with corresponding variations in the soil's suitability for plant growth.

Plants have evolved adaptations to many otherwise inhospitable soil environments, as you will see in the following section. First, however, we consider the general ways in which soil composition influences the ability of plant roots to obtain water and minerals.

Water Availability. As water flows into and through soil, gravity pulls much of the water down through the spaces between soil particles into deeper soil layers. This available water is part of the **soil solution (Figure 33.5),** a combination of water and dissolved substances that coats soil particles and partially fills pore spaces. The solution develops through ionic interactions between water molecules and soil particles. Clay particles and the organic components in soil (especially proteins) often bear negatively charged ions on their surfaces. The negative charges attract the polar water molecules, which form hydrogen bonds with the soil particles (see Section 2.4).

Unless a soil is irrigated, the amount of water in the soil solution depends largely on the amount and pattern of precipitation (rain or snow) in a region. How much of this water is actually available to plants depends on the soil's composition—the size of the air spaces in which water can accumulate and the proportions of water-attracting particles of clay and organic matter. By volume, soil is about one-half solid particles and one-half air space.

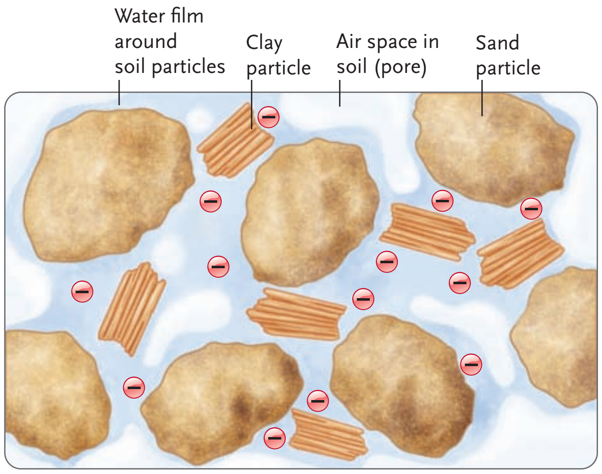


Figure 33.5
Location of the soil solution. Negatively charged ions on the surfaces of soil particles attract water molecules, which coat the particles and fill spaces between them (blue). Hydrogen bonds between water and soil components counteract the pull of gravity and help hold some water in the soil spaces.

The size of the particles in a given soil has a major effect on how well plants will grow there. Sandy soil has relatively large air spaces, so water drains rapidly below the top two soil horizons where most plant roots are located. Soils rich in clay or humus are often high in water content, but in the case of clay, ample water is not necessarily an advantage for plants. Whereas a humus-rich soil contains lots of air spaces, the closely layered particles in clay allow few air spaces—and what spaces there are tend to hold tightly the water that enters them. The lack of air spaces in clay soils also severely limits supplies of oxygen available to roots for cellular respiration, and the plant's metabolic activity suffers. Thus, few plants can grow well in clay soils, even when water content is high. (Overwatered houseplants die because their roots are similarly "smothered" by water.) Plants do not fare much better in drier clay-rich soils, because roots cannot extract the existing water and cannot easily penetrate the densely packed clay. These characteristics explain why good agricultural soils tend to be sandy or silty loams, which contain a mix of humus and coarse and fine particles.

As you learned in Chapter 31, root hairs are specialized extensions of root epidermal cells; they directly contact the soil solution and allow roots to absorb water (and dissolved ions). The soil solution usually contains fewer dissolved solutes than does the water in the cells of plant roots. Accordingly, water tends to diffuse from wet soil into the roots, following the osmotic gradient (see Section 32.2). As roots extract water from the surrounding soil, however, the remaining water molecules are held to the negatively charged clay surfaces with ever-increasing force. Plants start to wilt when the forces that draw water into their root cells equal those holding water in soil. Under these conditions, water no longer diffuses into roots, but it continues to evaporate from leaves and to be used in photosynthesis. Plants that survive in deserts or in salty soils have adaptations that permit their roots to absorb water even when osmotic conditions in soil do not favor water movement into the plant.

Mineral Availability. Some mineral nutrients enter plant roots as cations (positively charged ions) and some as anions (negatively charged ions). Although both cations and anions may be present in soil solutions, they are not equally available to plants.

Cations such as magnesium (Mg^{2+}), calcium (Ca^{2+}), and potassium (K^{+}) cannot easily enter roots because they are attracted by the net negative charges on the surfaces of soil particles. To varying degrees, they become reversibly bound to negative ions on the surfaces. Attraction in this form is called *adsorption*. The cations are made available to plant roots through

cation exchange, a mechanism in which one cation, usually H^+, replaces a soil cation **(Figure 33.6).** There are two main sources for the hydrogen ions. Respiring root cells release carbon dioxide, which dissolves in the soil solution, yielding carbonic acid (H_2CO_3). Subsequent reactions ionize H_2CO_3 to produce bicarbonate (HCO_3^-) and hydrogen ions (H^+). Reactions involving organic acids inside roots also produce H^+, which is excreted. As H^+ enters the soil solution, it displaces adsorbed mineral cations attached to clay and humus, freeing them to move into roots. Other types of cations may also participate in this type of exchange, as shown in Figure 33.6.

By contrast, anions in the soil solution, such as nitrate (NO_3^-), sulfate (SO_4^{2-}), and phosphate (PO_4^-), are only weakly bound to soil particles, and so they generally move fairly freely into root hairs. However, because they are so weakly bound compared with cations, anions are more subject to loss from soil by leaching.

The pH of soil also affects the availability of some mineral ions. Soil pH is a function of the balance between cation exchange and other processes that raise or lower the concentration of H^+ in soil. As noted earlier, in areas that receive heavy rainfall, soils tend to become acidic (that is, they have a pH of less than 7). This acidification occurs in part because moisture promotes the rapid decay of organic material in humus; as the material decomposes, the organic acids it contains are released. Acid precipitation, which results from the release of sulfur and nitrogen oxides into the air, also contributes to soil acidification. By contrast, the soil in arid regions, where precipitation is low, often is alkaline (the pH is greater than 7).

Although most plants are not directly sensitive to soil pH, chemical reactions in very acid ($pH < 5.5$) or very alkaline ($pH > 9.5$) soils can have a major impact on whether plant roots take up various mineral cations. For example, experiments have demonstrated that in the presence of OH^- in alkaline soil, calcium and phosphate ions react to form insoluble calcium phosphates. The phosphate captured in these compounds is as unavailable to roots as if it were completely absent from the soil.

For a soil to sustain plant life over long periods, the mineral ions that plants take up must be replenished naturally or artificially. Over the long run, some mineral nutrients enter the soil from the ongoing weathering of rocks and smaller bits of minerals. In the shorter run, minerals, carbon, and some other nutrients are returned to the soil by the decomposition of organisms and their parts or wastes. Other inputs occur when airborne compounds, such as sulfur in volcanic and industrial emissions, become dissolved in rain and fall to earth. Still others, including compounds of nitrogen and phosphorus, may enter soil in fertilizers.

Although the use of commercial fertilizers maintains high crop yields, agricultural chemicals do not add humus to the soil. Their use can also cause serious problems, as when nitrogen-rich runoff from agricultural fields promotes the serious overgrowth of algae in lakes and bays. In many parts of the world, industrial pollutants such as cadmium, lead, and mercury are increasingly serious soil contaminants. The use of plants to remove such materials from soil, called *phytoremediation,* is the topic of this chapter's *Focus on Research.*

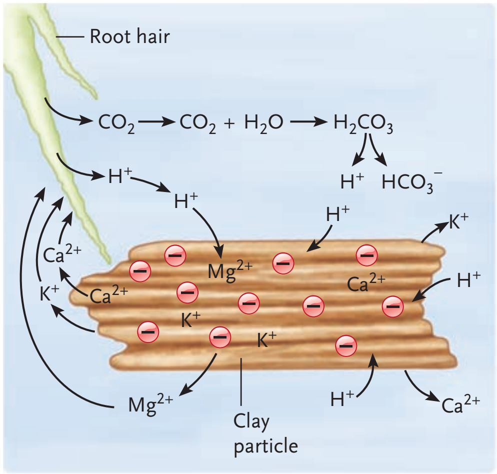


Figure 33.6
Cation exchange on the surface of a clay particle. When cations come into contact with the negatively charged surface of the particle, they become adsorbed. As one type of cation, such as H^+, becomes adsorbed, other ions are liberated and can be taken up by plant roots.

Study Break

1. Why is humus an important component of fertile soil?
2. How does the composition of a soil affect a plant's ability to take up water?
3. What factors affect a plant's ability to absorb minerals from the soil?

33.3 Obtaining and Absorbing Nutrients

Soil managed for agriculture can be plowed, precisely irrigated, and chemically adjusted to provide air, water, and nutrients in optimal quantities for a particular crop. By contrast, in natural habitats there are wide variations in soil minerals, humus, pH, the presence of other organisms, and other factors that influence the availability of essential elements. Although adequate carbon, hydrogen, and oxygen are typically available, other essential elements may not be as abundant. In particular, nitrogen, phosphorus, and potassium are often relatively scarce. The evolutionary solutions to

FOCUS ON RESEARCH

Applied Research: Plants Poised for Environmental Cleanup

For several decades researchers have been searching for efficient modes of *phytoremediation*—the use of plants to remove pollutants from the environment. A high-profile target is the highly toxic organic compound methylmercury (MeHg). This substance is present in coastal soils and wetlands contaminated by industrial wastes that contain an ionic form of the element mercury called Hg (II). Bacteria in contaminated sediments metabolize Hg(II) and generate MeHg as a metabolic by-product. Once MeHg forms, it enters the food web and eventually becomes concentrated in tissues of fishes and other animals. In humans MeHg can lead to degeneration of the nervous system and is the cause of most cases of mercury poisoning due to consuming contaminated fish.

In the 1990s a team of scientists including Scott Bizily and Richard Meagher at the University of Georgia decided to try to modify plants genetically so that they could detoxify mercury-contaminated soil and wetlands. It was already known that bacteria in contaminated sediments possess two genes, *merA* and *merB*, which encode enzymes that convert MeHg into elemental mercury (Hg)—a relatively inert substance that is much less dangerous to organisms. Both these bacterial mercury-resistance genes had already been cloned by others. After modifying the cloned genes so that they could be expressed in plants, the team used a vector (the bacterium *Rhizobium radiobacter*) to introduce each gene into several different sets of *Arabidopsis thaliana* plants (thale cress). They eventually obtained three groups of transgenic plants: some that were *merA* only, some that were *merB* only, and some that were *merA* and *merB*. In a series of experiments, seeds from each group were grown (along with wild-type controls) in five different growth media—one containing no mercury and the other four containing increasing concentrations of methylmercury. Wild-type and *merA* seeds germinated and grew only in the mercury-free growth medium. The *merB* seedlings fared somewhat better: they germinated and grew briefly even at the highest concentrations of MeHg, but soon became chlorotic and died. By contrast, seeds with the *merA*/*merB* genotype not only germinated, but the resulting seedlings grew into robust plants with healthy root and shoot systems. In later tests *merA*/*merB* plants were grown in chambers in which the chemical composition of the air was monitored. This study revealed that the doubly transgenic plants also were transpiring large amounts of Hg. The implication of these findings was clear: *A. thaliana* plants having both *merA* and *merB* genes were able to take up the toxic methylmercury with no ill effects and convert it to a harmless form. Meagher and his colleagues now are experimenting with ways of increasing the efficiency of phytoremediating enzymes when plant cells express *merA* and *merB*. They also are studying the mechanisms by which ionic mercury taken up by roots may be transported via the xylem to leaves and other shoot parts. The goal is to engineer plants that accumulate large quantities of mercury in aboveground tissues that can be harvested, leaving the living plant to continue its "work" of detoxifying a contaminated landscape.

these challenges include an array of adaptations in the structure and functioning of plant roots.

Root Systems Allow Plants to Locate and Absorb Essential Nutrients

Immobile organisms such as plants must locate nutrients in their immediate environment, and for plants the adaptive solution to this problem is an extensive root system. Roots make up 20% to 50% of the dry weight of many plants, and even more in species growing where water or nutrients are especially scarce, such as arctic tundra. As long as a plant lives, its root system continues to grow, branching out through the surrounding soil. Roots don't necessarily grow *deeper* as a root system branches out, however. In arid regions, a shallow-but-broad root system may be better positioned to take up water from occasional rains that may never penetrate below the first few inches of soil.

A root system grows most extensively in soil where water and mineral ions are abundant. As described in Section 31.4, roots take up ions in the regions just above the root tips. Over successive growing seasons, long-lived plants such as trees can develop millions, even billions, of root tips, each one a potential absorption site.

Root hairs, the diminutive absorptive structures shown in Figure 31.10c, are another significant adaptation for the uptake of mineral ions and water. In a plant such as a mature red oak *(Quercus rubra)*, which has a vast root system, the total number of root hairs is astronomical. Even in young plants, root hairs greatly increase the root surface area available for absorbing water and ions.

Recall from Chapter 32 that plant cell membranes also have ion-specific transport proteins by which they selectively absorb ions from soil. For example, from studies of plants such as *Arabidopsis thaliana*, a weed that has become a key model organism for plant research, we know that transport channels for potassium ions (K^+) are embedded in the cell membranes of root cortical cells. Such ion transporters absorb more or less of a particular ion depending on chemical conditions in the surrounding soil.

Insights from the Molecular Revolution

Getting to the Roots of Plant Nutrition

One way that mycorrhizal fungi benefit their host plants is by increasing their phosphate uptake from soils. How do the fungi accomplish this beneficial process? A molecular answer to this question came from Maria J. Harrison and Marianne L. van Buuren at the Samuel Roberts Noble Foundation in Ardmore, Oklahoma, who were able to identify a gene in one of these fungi that encodes a phosphate transport protein.

Harrison and van Buuren began with a cDNA library prepared from a plant that had been colonized by the mycorrhizal fungus *Glomus versiforme*. They then probed the plant-derived cDNA with a gene that encodes a phosphate transporter in yeast. The goal was to determine whether any cDNA sequences were similar to the yeast gene. (Recall from Section 18.1 that a cDNA library is a cloned collection of DNA sequences derived from mRNAs isolated from a cell. Hence it represents sequences that encode proteins.) The transport protein encoded by the yeast gene is embedded in the plasma membrane, where it uses an H^+ gradient as an energy source to move phosphate ions into yeast cells by active transport (see Section 6.4).

When mixed with the plant-derived cDNA sequences, the probe did indeed pair with one of the cDNA sequences. Subsequent sequencing of the segment revealed that the cDNA coded for a protein with a structure typical of many eukaryotic and prokaryotic membrane transport proteins.

To eliminate the possibility that the probe was identifying a plant cDNA in the library rather than one from the mycorrhizal fungus, the investigators next used the identified cDNA to probe a preparation containing all the DNA of a plant that had not been colonized by *Glomus*. No pairing occurred with any of the plant DNA fragments, confirming that the cDNA represented a gene came from the fungus. Additional experiments supported this finding.

Harrison and van Buuren carried their investigation further to see whether the fungal gene actually encoded a phosphate transport protein. For this set of experiments, the investigators used a yeast mutant with a nonfunctional phosphate transporter. Because these mutant yeast cells cannot readily take in phosphate, they grow very slowly, even in a culture medium containing a high concentration of phosphate ions.

The researchers added the *Glomus* gene to the mutants under conditions that increased the likelihood that the yeast cells would take and incorporate the DNA. In response, the yeast cells began to grow rapidly and normally, indicating that they could now synthesize a functional phosphate transporter. When radioactive phosphate ions were added to the culture, the cells rapidly became labeled, confirming that they were taking up phosphate ions at a much greater rate than untreated mutants.

Harrison and van Buuren's study was the first to reveal the molecular basis of phosphate transport by the mycorrhizal fungi. More recent studies with potato plants *(Solanum tuberosum)* have identified a gene encoding a phosphate transporter protein that is expressed in parts of potato roots where mycorrhizae form. These lines of research may lead to methods for reducing the amount of phosphate fertilizers added to crop plants by identifying mycorrhizal fungi providing the most efficient phosphate uptake—or by engineering crop plants with an enhanced capacity to take in this essential nutrient.

Mycorrhizae, symbiotic associations between a fungus and the roots of a plant (see Section 28.3) also promote the uptake of water and ions—especially phosphate and nitrogen—in most species of plants. As shown in Figure 28.17, the fungal partner in the association often grows as a network of hyphal filaments around and beyond the plant's roots. Collectively, the hyphae provide a tremendous surface area for absorbing ions from a large volume of soil. As with plant roots, transport proteins shepherd ions into hyphae. Researchers have recently verified experimentally that hyphal transport proteins are encoded by the DNA of the fungus, not that of the plant (as described in *Insights from the Molecular Revolution*). Some of the plant's sugars and nitrogenous compounds nourish the fungus, and as the root grows, it uses some of the minerals that the fungus has secured. In other types of mycorrhizae, the fungus actually lives inside cells of the root cortex. Orchids, for example, depend on this type of mutualistic association. And, as will be described shortly, some other plants gain access to nitrogen by way of mutually beneficial associations with bacteria.

Nutrients Move into and through the Plant Body by Several Routes

Most mineral ions enter plant roots passively along with the water in which they are dissolved. Some enter root cells immediately. Others travel in solution *between* cells until they meet the endodermis sheathing the root's stele (see Figure 32.6). At the endodermis, the ions are actively transported into the endodermal cells and then into the xylem for transport throughout the plant.

Inside cells, most mineral ions enter vacuoles or the cell cytoplasm, where they become available for metabolic reactions. Some nutrients, such as nitrogen-containing ions, move in phloem from site to site in the plant, as dictated by growth and seasonal needs. In plants that shed their leaves in autumn, before the leaves age and fall significant amounts of nitrogen, phosphorus, potassium, and magnesium move out of them and into twigs and branches. This adaptation conserves the nutrients, which will be used in new growth the next season. Likewise, in late summer, mineral ions move to the roots and lower stem tissues of perennial range grasses that typically die back during the winter. These activities are regulated by hormonal signals, which are the topic of Chapter 35.

Plants Depend on Bacterial Metabolism to Provide Them with Usable Nitrogen

A lack of nitrogen is the single most common limit to plant growth. Air contains plenty of gaseous nitrogen—almost 80% by volume—but plants lack the enzyme necessary to break apart the three covalent bonds in each N_2 molecule ($N{\equiv}N$). Some nitrogen from the atmosphere reaches the soil in the form of nitrate, NO_3^-, and ammonium ion, NH_4^+. Plants can absorb both these inorganic nitrogen compounds, but usually there is not nearly enough of them to meet plants' ongoing needs.

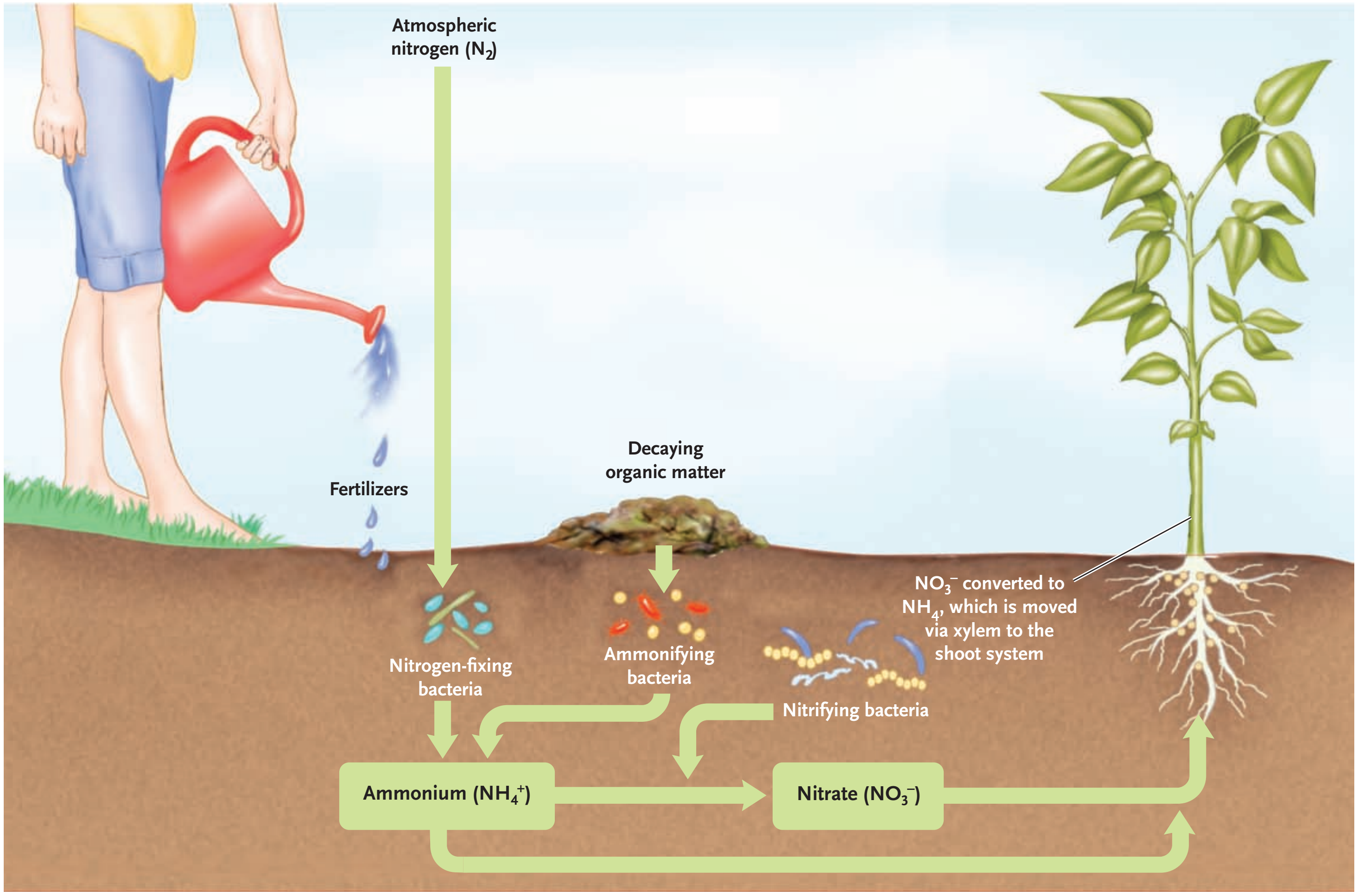
Nitrogen also enters the soil in organic compounds as dead organisms and animal wastes decompose. For example, dried blood is about 12% nitrogen by weight and chicken manure is about 5% nitrogen, but the nitrogen is bound up in complex organic molecules such as proteins, and in that form it is unavailable to plants. Instead, the main natural processes that replenish soil nitrogen and convert it to absorbable form are carried out by bacteria. These processes are described later and summarized in **Figure 33.7.** They are part of the *nitrogen cycle,* the global movement of nitrogen in its various chemical forms from the environment to organisms and back to the environment, which is described in Chapter 51.

Production and Assimilation of Ammonium and Nitrate. The incorporation of atmospheric nitrogen into compounds that plants can take up is called **nitrogen fixation.** Metabolic pathways of *nitrogen-fixing bacteria* living in the soil or in mutualistic association with plant roots add hydrogen to atmospheric N_2, producing two molecules of NH_3 (ammonia) and one H_2 for each N_2 molecule. The process requires a substantial input of ATP and is catalyzed by the enzyme nitrogenase. In a final step, H_2O and NH_3 react, forming NH_4^+ (ammonium) and OH^-.

Another bacterial process, called **ammonification,** also produces NH_4^+ when soil bacteria known as *ammonifying bacteria* break down decaying organic matter. In this way, nitrogen already incorporated into plants and other organisms is recycled.

Although plants use NH_4^+ to synthesize organic compounds, most plants absorb nitrogen in the form of nitrate, NO_3^-. Nitrate is produced in soil by **nitrification,**

Figure 33.7
How plants obtain nitrogen from soil. Many commercial nitrogen fertilizers are in the chemical form of nitrate, which plant roots readily take up, or in the form of ammonium, which nitrifying bacteria convert to nitrate.



a. Root nodules

b. Field experiment with soybeans *(Glycine max)* and *Rhizobium*

c. Bacteroids

Adrian P. Davies/Bruce Coleman

NifTAL Project, University of Hawaii, Maui

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Figure 33.8

The beneficial effect of root nodules. **(a)** Root nodules on a soybean plant *(Glycine max)*. **(b)** Soybean plants growing in nitrogen-poor soil. The plants on the right were inoculated with *Rhizobium* cells and developed root nodules. **(c)** False-color transmission electron micrograph showing membrane-bound bacteroids (red) in a root nodule cell. Membranes that enclose the bacteroids appear blue. The large yellow-green structure is the cell's nucleus.

in which NH_4^+ is oxidized to NO_3^-. Soils generally teem with *nitrifying bacteria,* which carry out this process. Because of ongoing nitrification, nitrate is far more abundant than ammonium in most soils. Usually, the only soils from which plant roots take up ammonium directly are highly acidic, such as in bogs, where the low pH is toxic to nitrifying bacteria.

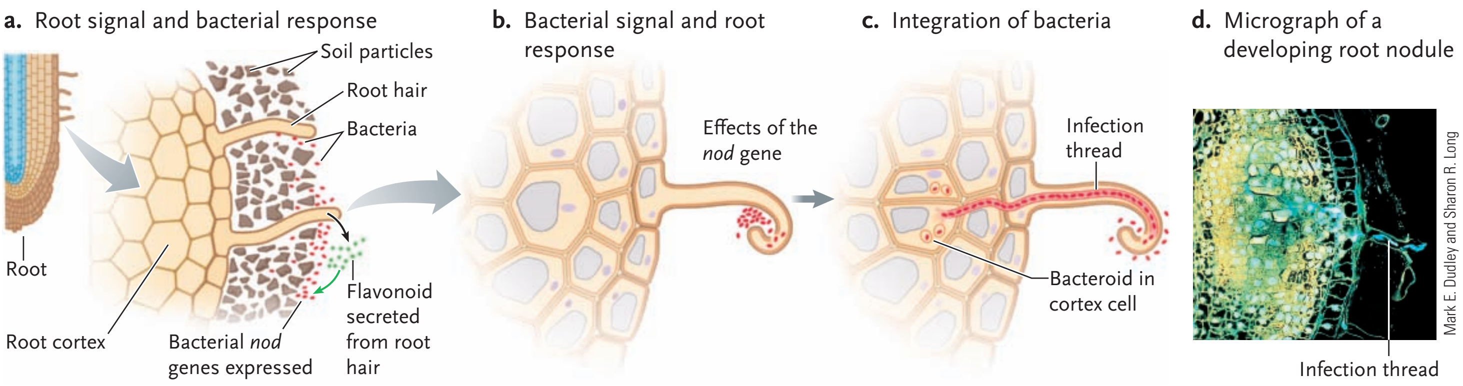
Nitrogen Assimilation. Once inside root cells, absorbed NO_3^- is converted by a multistep process back to NH_4^+. In this form, nitrogen is rapidly used to synthesize organic molecules, mainly amino acids. These molecules pass into the xylem, which transports them throughout the plant. In some plants, the nitrogen-rich precursors travel in xylem to leaves, where different organic molecules are synthesized. Those molecules travel to other plant cells in the phloem.

Nitrogen Fixation in Plant–Bacteria Associations. Although some nitrogen-fixing bacteria live free in the soil (see Figure 33.7), by far the largest percentage of nitrogen is fixed by species of *Rhizobium* and *Bradyrhizobium,* which form mutualistic associations with the roots of plants in the legume family. The host plant supplies organic molecules that the bacteria use for cellular respiration, and the bacteria supply NH_4^+ that the plant uses to produce proteins and other nitrogenous molecules. In legumes (peas, beans, clover, and alfalfa), the nitrogen-fixing bacteria reside in **root nodules**, localized swellings on roots **(Figure 33.8).** Farmers may exploit root nodules to increase soil nitrogen by rotating crops (for example, planting soybeans and corn in alternating years). When the legume crop is harvested, the root nodules and other tissues remaining in the soil enrich its nitrogen content.

Decades of research have revealed the details of how this remarkable relationship unfolds. Usually, a single species of nitrogen-fixing bacteria colonizes a single legume species, drawn to the plant's roots by chemical attractants—primarily compounds called flavonoids—that the roots secrete. Through a sequence of exchanged molecular signals, bacteria are able to penetrate a root hair and form a colony inside the root cortex.

An association between a soybean plant *(Glycine max)* and *Bradyrhizobium japonicum* illustrates the process. In response to a specific flavonoid released by soybean roots, bacterial genes called *nod* genes (for *nodule*) begin to be expressed **(Figure 33.9a).** Products of the *nod* gene cause the tip of the root hair to curl toward the bacteria and trigger the release of bacterial enzymes that break down the root hair cell wall **(Figure 33.9b).** As bacteria enter the cell and multiply, the plasma membrane forms a tube called an **infection thread** that extends into the root cortex, allowing the bacteria to invade cortex cells **(Figure 33.9c).** The enclosed bacteria, now called **bacteroids**, enlarge and become immobile. Stimulated by still other *nod* gene products, cells of the root cortex begin to divide. This region of proliferating cortex cells forms the root nodule **(Figure 33.9d).** Typically, each cell in a root nodule contains several thousand bacteroids; the plant takes up some of the nitrogen fixed by the bacteroids, and the bacteroids utilize some compounds produced by the plant.

Inside bacteroids, N_2 is reduced to NH_4^+ (ammonium) using ATP produced by cellular respiration. The process is catalyzed by nitrogenase. Ammonium



Mark E. Dudley and Sharon R. Long

Soybean root releases a flavonoid; *Rhizobium nod* genes are expressed in response.

Products of the *nod* gene cause the root hair tip to curl; bacterial enzymes break down the cell wall.

An infection thread develops and bacterioids form as *Rhizobium* bacteria become enclosed in root cortex cells.

Figure 33.9
Root nodule formation in legumes, which interact mutualistically with the nitrogen-fixing bacteria *Rhizobium* and *Bradyrhizobium*.

is highly toxic to cells if it accumulates, however. Thus, NH_4^+ is moved out of bacteroids into the surrounding nodule cells immediately and converted to other compounds, such as the amino acids glutamine and asparagine.

One factor encoded by the bacterial *nod* genes stimulates plant nodule cells to produce a protein called **leghemoglobin** ("legume hemoglobin"). Like the hemoglobin of animal red blood cells, leghemoglobin contains a reddish, iron-containing heme group that

Unanswered Questions

Is "networking" the key to success for plants in some environments?

Key factors that influence plants' ability to take root, grow, and thrive—notably the availability of water and mineral nutrients—are belowground, in the form of mycorrhizae. As you have read in this chapter, field studies and traditional laboratory analyses established that the symbiotic associations between mycorrhizal fungi and plant roots are crucial elements in the survival of the vast majority of vascular plants. Many researchers, including Peter Kennedy and his colleagues at the University of California at Berkeley, also have wondered about possible broader impacts of mycorrhizal associations, such as the extent of their role, if any, in determining the diversity of plant species in different ecological settings and in determining the particular combinations of species that occur. Now Kennedy and others are harnessing molecular tools to shed light on new kinds of questions about interactions among plants and mycorrhizal fungi.

Researchers' ability to define and amplify fungal DNA sequences has revealed the existence of common mycorrhizal networks (CMNs), in which roots of individual plants of the same or different species all form mycorrhizae with the same individual fungus. This discovery has raised several questions: Do mineral ions or other resources pass between plants in a CMN? Several studies indicate that the answer is yes, but much more research is needed to refine scientific understanding of these interchanges. Does a CMN moderate the effects of competition among plants of different species? Does formation of a CMN improve the survival chances of seedlings, and so help shape the distribution of specific plant species in a given area? Kennedy and his coworkers are exploring these and other questions with respect to CMNs involving two tree species that grow in mixed forests near San Francisco, California—the coast Douglas fir *(Pseudotsuga menziesii)*, a gymnosperm, and the tanbark oak *(Lithocarpus densiflora)*, an angiosperm.

Research efforts by Kennedy and others are examining competition among different species of mycorrhizal fungi, which differ markedly in their resistance to drought and their capacity to take up nutrients. Among other objectives, these studies aim to determine if, or to what extent, the ability of a given plant species to withstand water stress or to gain access to soil nutrients depends on the particular species of fungus with which it forms mycorrhizae. And do the benefits of mycorrhizae increase or decline as environmental conditions change? Answers to such questions will add a new dimension to our understanding of plant nutrition, as well as to our appreciation of what has been called "possibly the most important form of symbiosis in nature."

Beverly McMillan

a. Cobra lily *(Darlingtonia californica)*

b. Dodder *(Cuscuta)*

c. Snow plant *(Sarcodes sanguinea)*

d. Lady-of-the-night orchid *(Brassavola nodosa)*

David Cavagnaro/Peter Arnold, Inc.

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Beverly McMillan

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Figure 33.10
Some plants with unusual adaptations for obtaining nutrients. **(a)** Cobra lily *(Darlingtonia californica)*, a carnivorous plant. The patterns formed by light shining through the plant's pitcherlike leaves are thought to confuse insects that have entered the pitcher, making an exit more difficult. **(b)** A parasitic dodder, one of the more than 150 *Cuscuta* species. Dodders have slender yellow to orange stems that twine around the host plant before producing haustorial roots that absorb nutrients and water from the host's xylem and phloem. **(c)** Snow plant *(Sarcodes sanguinea)*, which pops up in the deep humus of shady conifer forests after snow has melted in spring. This species lacks chlorophyll and does not photosynthesize. Instead its roots intertwine with hyphae of soil fungi that also form associations with the roots of nearby conifers. Radiocarbon studies have shown that the fungi take up sugars and other nutrients from the trees and pass a portion of this food on to the snow plant. **(d)** The lady-of-the-night orchid *(Brassavola nodosa)*, a tropical epiphyte.

binds oxygen. Its color gives root nodules a pinkish cast (see Figure 33.8). Leghemoglobin picks up oxygen at the cell surface and shuttles it inward to the bacteroids. This method of oxygen delivery is vital, because nitrogenase, the enzyme responsible for nitrogen fixation, is irreversibly inhibited by excess O_2. Leghemoglobin delivers just enough oxygen to maintain bacteroid respiration without shutting down the action of nitrogenase.

Some Plants Obtain Scarce Nutrients in Other Ways

The cobra lily (*Darlingtonia californica;* **Figure 33.10a**) is one of a curious group of plants that obtain nitrogen and other nutrients by trapping and digesting animals. Although such plants are said to be carnivorous (meat eaters), in fact they do not ingest food and digest it, as carnivorous animals do. Rather, they have become adapted to survive in nutrient-deficient environments through elaborate mechanisms for extracellular digestion and absorption. The cobra lily's leaves form a "pitcher" that is partly filled with digestive enzymes. Insects lured in by attractive odors often wander deeper into the pitcher, encountering downward-pointing leaf hairs that have a slick, waxy coating and speed the insect's descent into the pool of enzymes.

Dodders **(Figure 33.10b)** and thousands of other species of flowering plants are parasites that obtain some or all of their nutrients from the tissues of other plants. Parasitic species develop **haustorial roots** (similar to the haustoria of fungi described in Chapter 28) that penetrate deep into the host plant and tap into its vascular tissues. Although some parasitic plants, like mistletoe, contain chlorophyll and thus can photosynthesize, dodders and other nonphotosynthesizers rob the host of sugars as well as water and minerals.

The snow plant *(Sarcodes sanguinea)* shows a variation on this theme. As its deep red color suggests **(Figure 33.10c),** it lacks chlorophyll, but it doesn't have haustorial roots. Instead, the snow plant's roots take up nutrients from mycorrhizae they "share" with the roots of nearby conifers.

Epiphytes, such as the tropical orchid pictured in **Figure 33.10d,** are not parasitic even though they grow on other plants. Some trap falling debris and rainwater among their leaves, while their roots (including mycorrhizae, in the case of the orchid) invade the moist leaf litter and absorb nutrients from it as the litter decomposes. In temperate forests, many mosses and lichens are epiphytes.

These and other strategies plants have evolved for obtaining nutrients and water are only part of the survival equation, however. Plants use nutrients not only for growth and maintenance, but also, of course, for building structures such as pollen, flowers, and seeds used in reproduction—our topic in Chapter 34.

STUDY BREAK

1. What is a mycorrhiza, and why are mycorrhizal associations so vital to many plants?
2. Distinguish between nitrogen fixation, ammonification, and nitrification.
3. Summarize the mechanism by which associations with bacteria supply nitrogen to plants such as legumes.

Review

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33.1 Plant Nutritional Requirements

- Plants require carbon, hydrogen, oxygen, nitrogen, and 13 other essential nutrients (Table 33.1). With enough sunlight and these nutrients, plants can synthesize all the compounds they need.
- Nine essential elements are macronutrients, required in relatively large amounts. Four of these elements—carbon, hydrogen, oxygen, and nitrogen—are the main building blocks in the synthesis of carbohydrates, lipids, proteins, and nucleic acids. The essential macronutrients dissolved in the soil solution are nitrogen, potassium, calcium, magnesium, phosphorus, and sulfur.
- Micronutrients are required in only minuscule amounts, but they too are essential. The ones identified to date are chlorine, iron, boron, manganese, zinc, copper, molybdenum, and nickel.
- Each plant species requires specific nutrients in specific amounts. Typical deficiency symptoms are stunted growth, yellowing or other abnormal changes in leaf color, dead spots on leaves, or abnormally formed stems (Figure 33.3).
- Most mineral ions enter plant roots dissolved in water. Inside cells, most mineral ions enter vacuoles or the cell cytoplasm, where they become available for metabolic reactions. Some elements, such as nitrogen and potassium, can move from site to site in phloem as the plant grows.

33.2 Soil

- Soil is composed of sand, silt, and clay particles, usually held together by humus and other organic components. Humus absorbs a great deal of water, and so contributes to the water-holding capacity of soil.
- The relative proportions of various soil mineral particles and humus give soil its basic texture and structure. The best agricultural soils are loams that contain clay, sand, silt, and humus in roughly equal proportions. Topsoil is the most fertile soil layer (Figure 33.4).
- Due to charge differences between soil particles and water molecules, soil particles are thinly coated by the soil solution, a mixture of water and solutes (Figure 33.5). From this solution root hairs and other root epidermal cells absorb water and solutes.
- The amount of water available to plant roots depends mainly on the relative proportions of different soil components. Water moves quickly through sandy soils, while soils rich in clay and humus tend to hold the most water.
- Cations become adsorbed on the negatively charged surfaces of soil particles, potentially limiting their uptake by roots. Cation exchange, in which mineral cations are replaced by H^+, helps make these nutrients available to plants (Figure 33.6). Anions are more weakly bound to soil particles; they move more readily into root hairs but also are more apt to leach out of topsoil. In nature, the soil solution surrounding plant roots generally contains only tiny amounts of essential mineral ions

Animation: Soil profile

33.3 Obtaining and Absorbing Nutrients

- Numerous adaptations help plants solve the problems of obtaining and absorbing essential nutrients. Root systems penetrate the soil towards nutrients and water. Millions or billions of root hairs increase the root's absorptive surface. Ion-specific transporters in root cortical cells adjust the plant's uptake of particular ions. Mycorrhizal associations between fungi and plant roots enhance the absorption of nutrients, particularly phosphorus.
- Nitrogen usually is the scarcest nutrient in soil, and much of the usable soil nitrogen is produced by nitrogen-fixing bacteria. Nitrogen fixation reduces atmospheric N_2 to NH_4^+ (ammonium) in a reaction that requires the enzyme nitrogenase as a catalyst. Nitrifying bacteria rapidly convert NH_4^+ to nitrate, the form in which the roots of most plants absorb nitrogen (Figure 33.7).
- In legumes and a few other species, nitrogen-fixing bacteria reside in root nodules in a mutualistic association (Figure 33.8).
- Bacteria enclosed in a root nodule (bacteroids) reduce N_2 to NH_4^+ (Figure 33.9). The toxic NH_4^+ is moved out of the bacteroids and converted to nitrogen-rich, nontoxic compounds such as amino acids. In plants that do not form root nodules, the ni-

trate directly absorbed by roots is reduced to ammonium, which then is converted to nontoxic forms.

- In many plant species, root cells synthesize amino acids and other organic nitrogenous compounds, and these molecules are transported in xylem throughout the plant. In some plants, the nitrogen-rich precursors travel in xylem to leaves, where different organic molecules are synthesized. Those molecules then travel to other plant cells in phloem.
- A few plant species have evolved alternative mechanisms for obtaining some or all of their nutrients (Figure 33.10). So-called carnivorous plants typically produce insect-attracting secretions that contain enzymes which digest the animal's tissues. The plant then absorbs the released nutrients.
- Some plant species parasitize other plants. The parasite may or may not contain chlorophyll and carry out photosynthesis; species that do not photosynthesize obtain all of their nutrition from the host. Epiphytes grow on other plants but obtain nutrients independently.

Animation: Uptake of nutrients by plants

Questions

Self-Test Questions

1. Which best describes a micronutrient?
   a. It makes up 96% of the plant's dry mass.
   b. It cannot be replaced artificially.
   c. It is early on the periodic chart compared with macronutrients.
   d. It is required in large amounts during sunlight hours.
   e. It is an essential element.
2. Nutrient runoff from fertilizing lush lawns often causes "algal blooms" in nearby lakes, making swimming impossible. The fertilizer components most likely to have caused the blooms are:
   a. iron, magnesium, and nitrogen.
   b. nitrogen, phosphorus, and sulfur.
   c. nitrogen, potassium, and phosphorus.
   d. selenium, magnesium, and potassium.
   e. nitrogen, magnesium, and nickel.
3. Which of the following is/are *not* among the ideal soil conditions for growing crops?
   a. extremely large air spaces
   b. sandy or silty loam
   c. blend of sand and clay
   d. thick top soil
   e. less than 5% humus
4. Which of the following processes contributes to the uptake of mineral ions by plant roots?
   a. chlorosis
   b. osmosis
   c. anion exchange
   d. cation exchange
   e. growth of root hairs
5. Which of the following does *not* influence soil pH?
   a. rainfall
   b. hydroponic growth
   c. release of sulfur and nitrogen oxides into the air
   d. decomposition of organisms
   e. weathering of rock
6. Which of the following is a process that helps plants utilize nitrogen?
   a. nitrogen-fixing bacteria synthesizing nitrate
   b. ammonifying bacteria using ammonium to produce nitrate
   c. nitrifying bacteria converting NH_4^+ to NO_3^-
   d. the absorption of NH_4^+ by root hairs
   e. the absorption of atmospheric N_2 into the xylem
7. The *nod* genes in the bacteria in soybean nodules allow the bacteria to fix nitrogen. Which of the following is *not* a step in this process?
   a. The products of *nod* genes cause cells of the root cortex to divide and become the root nodule in which bacteroids fix nitrogen for the plant.
   b. In the cortex cells bacteria enlarge and become immobile, forming bacteroids.
   c. Bacteria enter the root hair cell and multiply, causing the cell plasma membrane to form an infection thread that extends into the root cortex.
   d. Roots release flavonoid, which turns on the expression of bacterial *nod* genes. Products of *nod* genes cause the tip of the root hair to curl toward the bacteria.
   e. Root hairs trigger release of bacterial enzymes that break down root hair cell walls.
   f. All of the above are steps in the process.
8. Carnivorous plants are deficient in:
   a. oxygen.
   b. phosphorus.
   c. potassium.
   d. nitrogen.
   e. carbon.
9. Haustorial roots are characteristic of plants that are:
   a. parasites.
   b. epiphytes.
   c. nitrate fixers.
   d. leghemoglobin users.
   e. carnivorous.
10. Identify the correct match of a nutrient with its function.
    a. chlorine: component of several enzymes
    b. potassium: component of nucleic acids
    c. phosphorus: component of most proteins
    d. manganese: role in shoot and root growth
    e. calcium: maintenance of cell walls and membrane permeability

Questions for Discussion

1. If you want to study factors that affect plant nutrition in nature, what would be the advantages and disadvantages of using a hydroponic culture method?
2. Gardeners often add a humus-rich "soil conditioner" to garden plots before they plant. Adding the conditioner helps aerate the soil, and the decomposing organic materials in humus provide nutrients. If the plot is for annual plants, it often must be reconditioned year after year, even though the gardener faithfully pulls weeds, fertilizes seedlings, applies chemicals to curtail disease-causing soil microbes, and immediately tosses out the mature plants (along with any plant debris) when they have finished bearing. Suggest some reasons why reconditioning is necessary in this scenario, and some strategies that could help limit the need for it.
3. One effect of acid rain is to dissolve rock, liberating minerals into soil. Accordingly, can a case be made that acid rain confers environmental benefits as well as doing harm? What are some other factors, especially with regard to plant adaptations for gaining nutrients, that bear on this question?
4. Using Table 33.1 as a guide, describe some of the known roles of nitrogen, phosphorus, and potassium in plant function. What are some of the signs that a plant suffers a deficiency in those elements?

Experimental Analysis

A plant in your garden is undersized and develops chlorotic leaves even though you fertilize it with a mixture that contains nitrogen, potassium, and phosphorus. After determining that the plant receives enough sunlight for photosynthesis, you next decide to test whether its mineral nutrition is adequate. What specific hypothesis will your experiment test? How will your experimental design test the hypothesis?

Evolution Link

This chapter's *Focus on Research* discusses phytoremediation, the use of plants to remove environmental pollutants such as heavy metals. Some plant species are "hyperaccumulaters" that take up arsenic and other metallic contaminants and sequester such toxins in shoot parts. How might this activity confer a selective advantage?