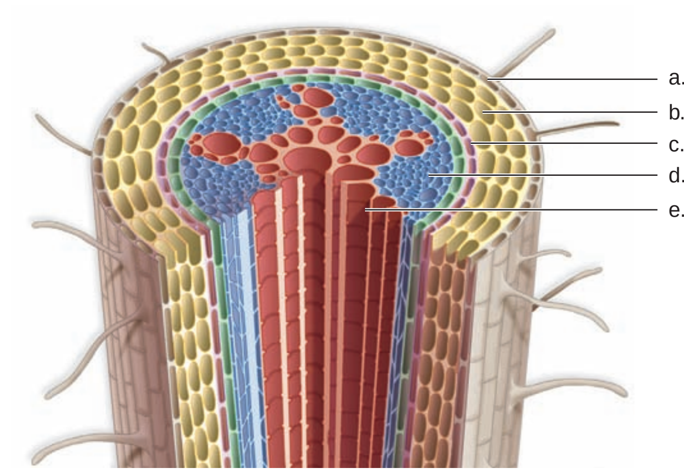
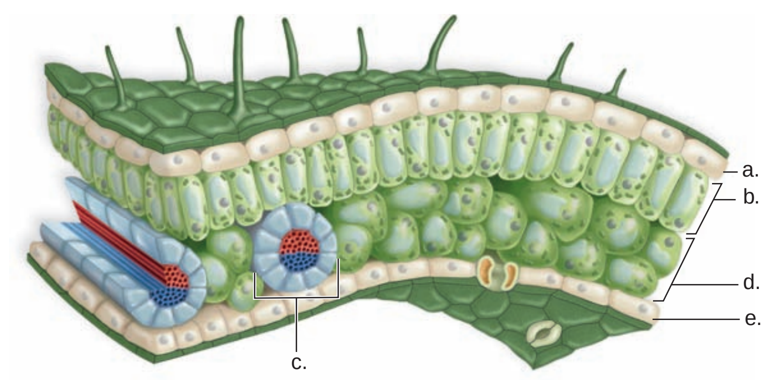
9. The Casparian strip is found
   a. between all epidermal cells.
   b. between xylem and phloem cells.
   c. on four sides of endodermal cells.
   d. within the secondary wall of parenchyma cells.
   e. in both endodermis and pericycle.
10. Which of these is a stem?
    a. taproot of carrots
    b. stolon of strawberry plants
    c. spine of cactuses
    d. prop roots
    e. Both b and c are correct.
11. Meristem tissue that gives rise to epidermal tissue is called
    a. procambium.
    b. ground meristem.
    c. epiderm.
    d. protoderm.
    e. periderm.
12. New plant cells originate from the
    a. parenchyma.
    b. collenchyma.
    c. sclerenchyma.
    d. base of the shoot.
    e. apical meristem.
13. Ground tissue does not include
    a. collenchyma cells.
    b. sclerenchyma cells.
    c. parenchyma cells.
    d. chlorenchyma cells.
14. Evenly thickened cells that function to support mature regions of a flowering plant are called
    a. guard cells.
    b. aerenchyma cells.
    c. parenchyma cells.
    d. sclerenchyma cells.
    e. xylem cells.
15. Roots
    a. are the primary site of photosynthesis.
    b. give rise to new leaves and flowers.
    c. have a thick cuticle to protect the epidermis.
    d. absorb water and nutrients.
    e. contain spores.
16. Monocot stems have
    a. vascular bundles arranged in a ring.
    b. vascular cambium.
    c. scattered vascular bundles.
    d. a cork cambium.
    e. a distinct pith and cortex.
17. Secondary thickening of stems occurs in
    a. all angiosperms.
    b. most monocots.
    c. many eudicots.
    d. few eudicots.
18. All of these may be found in heartwood except
    a. tracheids.
    b. vessel elements.
    c. parenchyma cells.
    d. sclerenchyma cells.
    e. companion cells.
19. How are compound leaves distinguished from simple leaves?
    a. Compound leaves do not have axillary buds at the base of leaflets.
    b. Compound leaves are smaller than simple leaves.
    c. Simple leaves are usually deciduous.
    d. Compound leaves are found only in pine trees.
    e. Simple leaves are found only in gymnosperms.
20. Label this root using these terms: endodermis, phloem, xylem, cortex, and epidermis.



21. Label this leaf using these terms: leaf vein, lower epidermis, palisade mesophyll, spongy mesophyll, and upper epidermis.



thinking scientifically

1. Utilizing an electron microscope, how might you confirm that a companion cell communicates with its sieve-tube member?
2. Design an experiment that tests the hypothesis that new plants arise at the nodes of a stolon according to environmental conditions (temperature, water, and sunlight).

Biology website

The companion website for *Biology* provides a wealth of information organized and integrated by chapter. You will find practice tests, animations, videos, and much more that will complement your learning and understanding of general biology.

http://www.mhhe.com/maderbiology10

25

Flowering Plants: Nutrition and Transport

Plants have nutrient requirements just as animals do. They use carbon, hydrogen, oxygen, nitrogen, potassium, calcium, phosphorus, magnesium, and sulfur in relatively large amounts to make all the substances they need to carry out life functions. Plant leaves absorb the gas carbon dioxide and their roots take up oxygen. Water and dissolved minerals move into root hairs often covered by mycorrhizae. Plants have an amazing ability to concentrate minerals in their tissues to a much higher level than they occur in the soil. Some plants, such as those in the legume family (peanuts, clovers, beans), have roots colonized by bacteria that can convert atmospheric nitrogen to a form usable by plants.

This chapter discusses the nutrient requirements of plants and how they are absorbed and distributed within the body of a plant. Plants have no central pumping mechanism, yet materials move throughout the body of the plant. The unique properties of water account for the movement of water and minerals in xylem, while osmosis plays an essential role in phloem transport of sugars. The same mechanisms account for transport in very tall redwood trees and in dwarf gardenias.

Redwoods, *Sequoia sempervirens*.

concepts

25.1 Plant Nutrition and Soil

The ancient Greeks believed that plants were "soil-eaters" and somehow converted soil into plant material. Apparently to test this hypothesis, a seventeenth-century Dutchman named Jean-Baptiste Van Helmont planted a willow tree weighing 5 lb in a large pot containing 200 lb of soil. He watered the tree regularly for five years and then reweighed both the tree and the soil. The tree weighed 170 lb, and the soil weighed only a few ounces less than the original 200 lb. Van Helmont concluded that the increase in weight of the tree was due primarily to the addition of water.

Water is a vitally important nutrient for a plant, but Van Helmont was unaware that water and carbon dioxide (taken in at the leaves) combine in the presence of sunlight to produce carbohydrates, the chief organic matter of plants. Much of the water entering a plant evaporates at the leaves. Roots, like all plant organs, carry on cellular respiration, a process that uses oxygen and gives off carbon dioxide (Fig. 25.1).

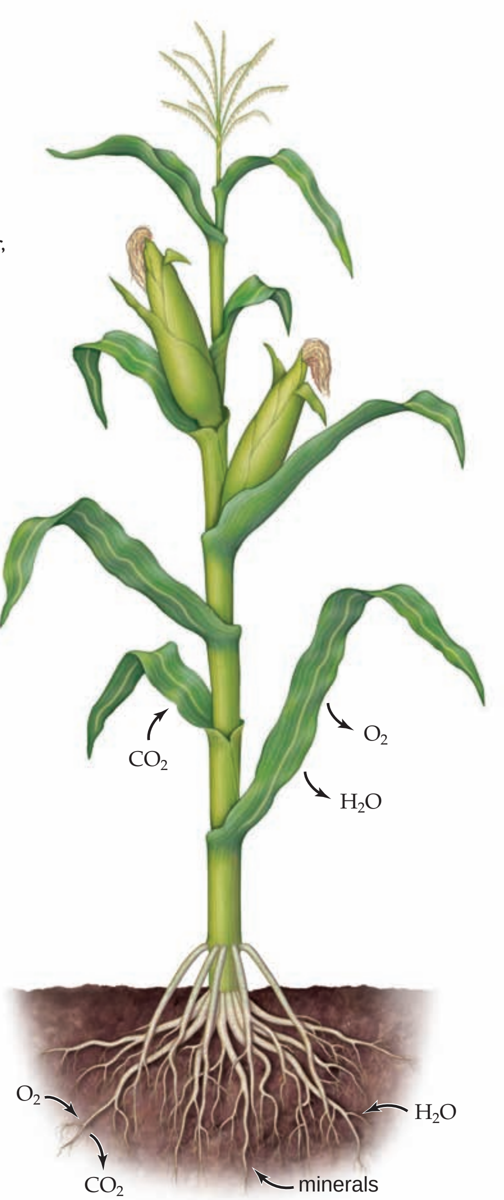


FIGURE 25.1
Overview of plant nutrition.

Carbon dioxide, which enters leaves, and water, which enters roots, are combined during photosynthesis to form carbohydrates, with the release of oxygen from the leaves. Root cells, and all other plant cells, carry on cellular respiration, which uses oxygen and gives off carbon dioxide. Aside from the elements carbon, hydrogen, and oxygen, plants require nutrients that are absorbed as minerals by the roots.

Essential Inorganic Nutrients

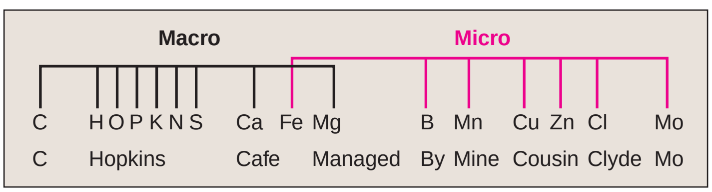
Approximately 95% of a typical plant's dry weight (weight excluding free water) is carbon, hydrogen, and oxygen. Why? Because these are the elements that are found in most organic compounds, such as carbohydrates. Carbon dioxide (CO_2) supplies carbon, and water (H_2O) supplies hydrogen and oxygen found in the organic compounds of a plant.

TABLE 25.1

Some Essential Inorganic Nutrients in Plants

Elements	*Symbol*	*Form*	*Major Functions*
Macronutrients			
Carbon Hydrogen Oxygen	C H O	CO_2 H_2O O_2	Major component of organic molecules
Phosphorus	P	$H_2PO_4^-$ HPO_4^{2-}	Part of nucleic acids, ATP, and phospholipids
Potassium	K	K^+	Cofactor for enzymes; water balance and opening of stomata
Nitrogen	N	NO_3^- NH_4^+	Part of nucleic acids, proteins, chlorophyll, and coenzymes
Sulphur	S	SO_4^{2-}	Part of amino acids, some coenzymes
Calcium	Ca	Ca^{2+}	Regulates responses to stimuli and movement of substances through plasma membrane; involved in formation and stability of cell walls
Magnesium	Mg	Mg^{2+}	Part of chlorophyll; activates a number of enzymes
Micronutrients			
Iron	Fe	Fe^{2+} Fe^{3+}	Part of cytochrome needed for cellular respiration; activates some enzymes
Boron	B	BO_3^{3-} $B_4O_7^{2-}$	Role in nucleic acid synthesis, hormone responses, and membrane function
Manganese	Mn	Mn^{2+}	Required for photosynthesis; activates some enzymes such as those of the citric acid cycle
Copper	Cu	Cu^{2+}	Part of certain enzymes, such as redox enzymes
Zinc	Zn	Zn^{2+}	Role in chlorophyll formation; activates some enzymes
Chlorine	Cl	Cl^-	Role in water-splitting step of photosynthesis and water balance
Molybdenum	Mo	MoO_4^{2-}	Cofactor for enzyme used in nitrogen metabolism

In addition to carbon, hydrogen, and oxygen, plants require certain other nutrients that are absorbed as minerals by the roots. A **mineral** is an inorganic substance usually containing two or more elements. Why are minerals from the soil needed by a plant? In plants, nitrogen is a major component of nucleic acids and proteins, magnesium is a component of chlorophyll, and iron is a building block of cytochrome molecules. The major functions of various **essential nutrients** for plants are listed in Table 25.1. A nutrient is essential if (1) it has an identifiable role, (2) no other nutrient can substitute and fulfill the same role, and (3) a deficiency of this nutrient causes a plant to die without completing its life cycle. Essential nutrients are divided into **macronutrients** and **micronutrients** according to their relative concentrations in plant tissue. The following diagram and slogan helps us remember which are the macronutrients and which are the micronutrients for plants:



Beneficial nutrients are another category of elements taken up by plants. Beneficial nutrients either are required for or enhance the growth of a particular plant. Horsetails require silicon as a mineral nutrient and sugar beets show enhanced growth in the presence of sodium. Nickel is a beneficial mineral nutrient in soybeans when root nodules are present. Aluminum is used by some ferns, and selenium, which is often fatally poisonous to livestock, is used by locoweeds.

Determination of Essential Nutrients

When a plant is burned, its nitrogen component is given off as ammonia and other gases, but most other essential minerals remain in the ash. The presence of a mineral in the ash, however, does not necessarily mean that the plant normally requires it. The preferred method for determining the mineral requirements of a plant was developed at the end of the nineteenth century by the German plant physiologists Julius von Sachs and Wilhem Knop. This method is called water culture, or **hydroponics** [Gk. *hydrias,* water, and *ponos,* hard work]. Hydroponics allows plants to grow well if they are supplied with all the nutrients they need. The investigator omits a particular mineral and observes the effect on plant growth. If growth suffers, it can be concluded that the omitted mineral is an essential nutrient (Fig. 25.2). This method has been more successful for macronutrients than for micronutrients. For studies involving the latter, the water and the mineral salts used must be absolutely pure, but purity is difficult to attain, because even instruments and glassware can introduce micronutrients. Then, too, the element in question may already be present in the seedling used in the experiment. These factors complicate the determination of essential plant micronutrients by means of hydroponics.

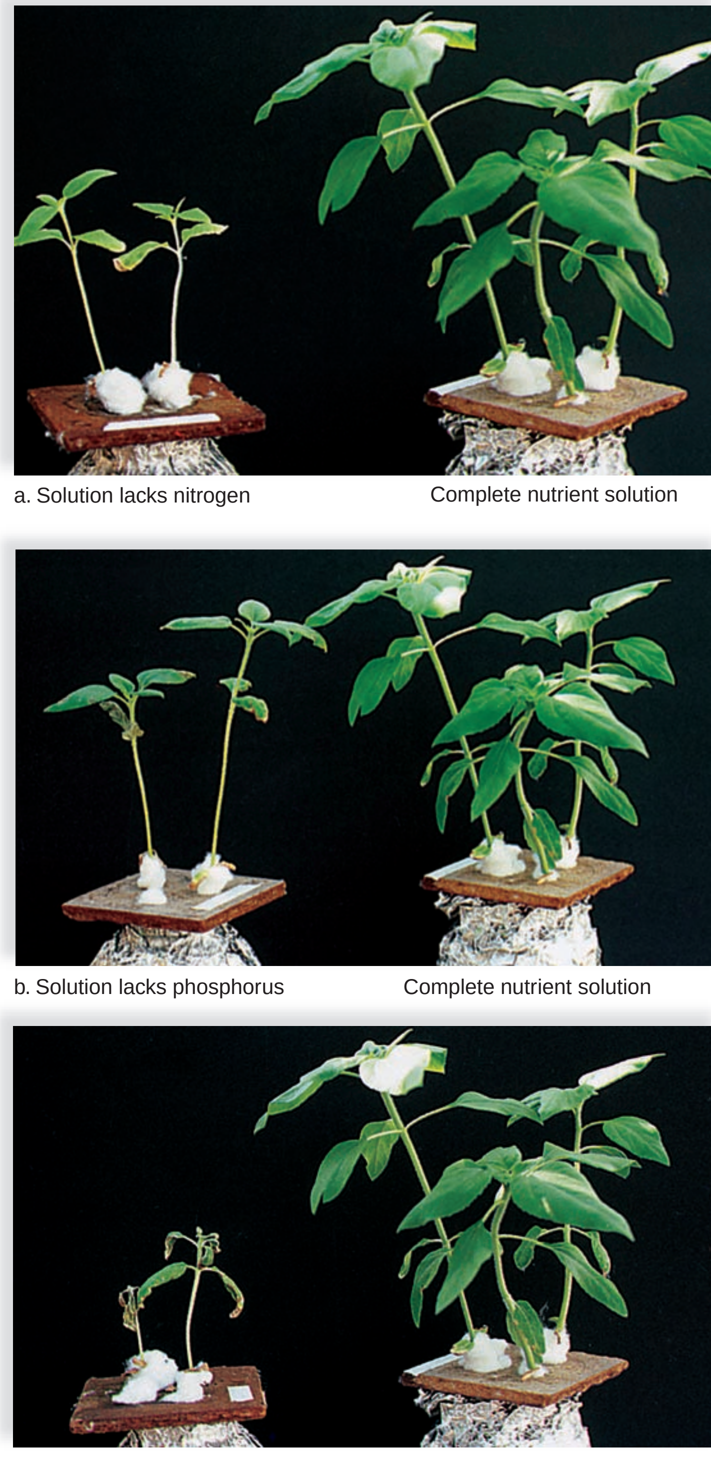


FIGURE 25.2 Nutrient deficiencies.

The nutrient cause of poor plant growth is diagnosed when plants are grown in a series of complete nutrient solutions except for the elimination of just one nutrient at a time. These experiments show that sunflower plants respond negatively to a deficiency of (**a**) nitrogen, (**b**) phosphorus, and (**c**) calcium.

Hydroponics

Hydroponics is of interest as a way to grow crops in the future. Plant pests and diseases are eliminated, and there are no weeds. Water is reused in a pipeline system and little is lost through runoff.

Soil

Plants acquire carbon when carbon dioxide diffuses into leaves through stomata. Oxygen can enter from the air, but all of the other essential nutrients are absorbed by roots from the soil. It would not be an exaggeration to say that terrestrial life is dependent on the quality of the soil and the ability of soil to provide plants with the nutrients they need.

Soil Formation

Soil formation begins with the weathering of rock in the Earth's crust. Weathering first gradually breaks down rock to rubble and then to soil particles. Some weathering mechanisms, such as the freeze-thaw cycle of ice or the grinding of rock on rock by the action of glaciers or river flow, are purely mechanical. Other forces include a chemical effect, as when acidic rain leaches (washes away) soluble components of rock or when oxygen combines with the iron of rocks.

In addition to these forces, organisms also play a role in the formation of soil. Lichens and mosses grow on pure rock and trap particles that later allow grasses, herbs, and soil animals to follow. When these die, their remains are decomposed, notably by bacteria and fungi. Decaying organic matter, called **humus,** begins to accumulate. Humus supplies nutrients to plants, and its acidity also leaches minerals from rock.

Building soil takes a long time. Under ideal conditions, depending on the type of parent material (the original rock) and the various processes at work, a centimeter of soil may develop within 15 years.

The Nutritional Function of Soil

Soil is defined as a mixture of mineral particles, decaying organic material, living organisms, air, and water, which together support the growth of plants. In a good agricultural soil, the first three components come together in such a way that there are spaces for air and water (Fig. 25.3). It's best if the soil contains particles of different sizes because only then will there be spaces for air. Roots take up oxygen from air spaces. Ideally, water clings to particles by capillary action and does not fill the spaces. That's why you shouldn't overwater your houseplants!

Mineral Particles. Mineral particles vary in size: Sand particles are the largest (0.05–2.0 mm in diameter); silt particles have an intermediate size (0.002–0.05 mm); and clay particles are the smallest (less than 0.002 mm). Soils are a mixture of these three types of particles. Because sandy soils have many large particles, they have large spaces, and the water drains readily through the particles. In contrast to sandy soils, a soil composed mostly of clay particles has small spaces that fill completely with water. Most likely, you have experienced the feel of sand and clay in your hand: Sand having no moisture flows right through your fingers, while clay clumps together in one large mass because of its water content.

Clay particles have another benefit that sand particles do not have. As Table 25.1 indicates, some minerals are negatively charged and others are positively charged. Clay particles are negative, and they can retain positively charged minerals such as calcium (Ca^{2+}) and potassium (K^+), preventing these minerals from being washed away by leaching. Plants exchange hydrogen ions for these minerals when they take them up (Fig. 25.3). If rain is acidic, its hydrogen ions displace positive mineral ions and cause them to drain away; this is one reason acid rain kills trees. Because clay particles are unable to retain negatively charged NO_3^-, the nitrogen content of soil is apt to be low. Legumes (see Fig. 1.13) are sometimes planted to replenish the nitrogen in the soil in preference to relying solely on the addition of fertilizer.

The type of soil called loam is composed of roughly one-third sand, silt, and clay particles. This combination sufficiently retains water and nutrients while still allowing the drainage necessary to provide air spaces. Some of the most productive soils are loam.

Humus. Humus, which mixes with the top layer of soil particles, increases the benefits of soil. Plants do well in soils that contain 10–20% humus.

Humus causes soil to have a loose, crumbly texture that allows water to soak in without doing away with air spaces. After a rain, the presence of humus decreases the chances of runoff. Humus swells when it absorbs water and shrinks as it dries. This action helps aerate soil.

Soil that contains humus is nutritious for plants. Humus is acidic; therefore, it retains positively charged minerals until plants take them up. When the organic matter in humus is broken down by bacteria and fungi, inorganic nutrients are returned to plants. Although soil particles are the original source of minerals in soil, recycling of nutrients, as you know, is a major characteristic of ecosystems.

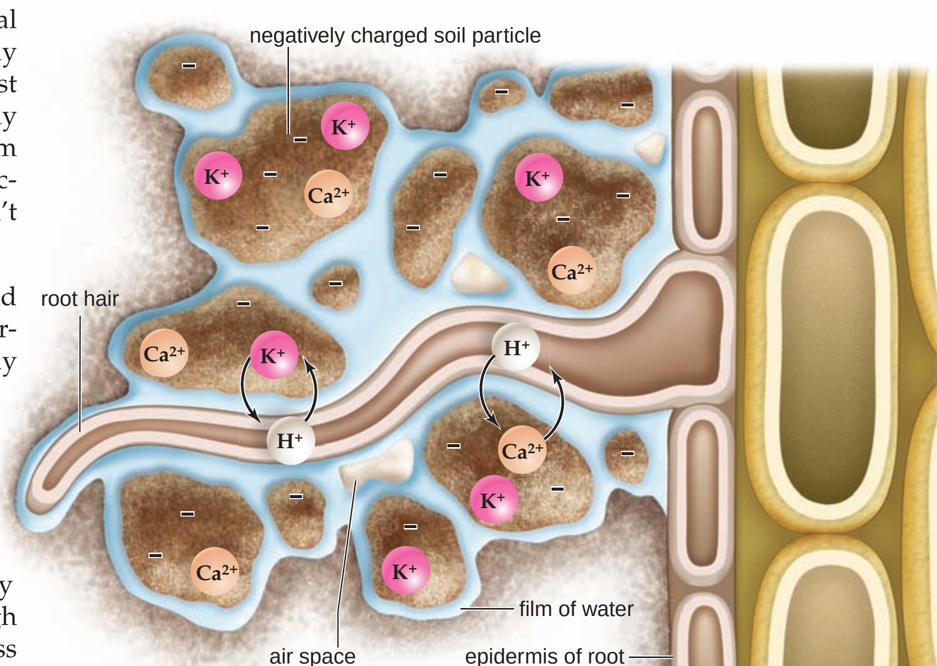


FIGURE 25.3 Absorbing minerals.

Negatively charged clay particles bind positively charged minerals such as Ca^{2+} and K^+. Plants extract these minerals by exchanging H^+ for them (see also Fig. 25.5).

Living Organisms. Small plants play a major role in the formation of soil from bare rock. Due to the process of succession (see Fig. 45.14), larger plants eventually become dominant in certain ecosystems. The roots of larger plants penetrate soil even to the cracks in bedrock. This action slowly opens up soil layers, allowing water, air, and animals to follow.

There are many different types of soil animals. The largest of them, such as toads, snakes, moles, badgers, and rabbits, disturb and mix soil by burrowing. Smaller animals like earthworms ingest fine soil particles and deposit them on the surface as worm casts. Earthworms also loosen and aerate the soil. A range of soil animals, including mites, springtails, and millipedes, help break down leaves and other plant remains by eating them. Soil-dwelling ants construct tremendous colonies with massive chambers and tunnels. These ants also loosen and aerate the soil.

The microorganisms in soil, such as protozoans, fungi, algae, and bacteria, are responsible for the final decomposition of organic remains in humus to inorganic nutrients. Recall that plants are unable to make use of atmospheric nitrogen (N_2) and that soil bacteria play an important nutrient role because they make nitrate available to plants.

Insects may improve the properties of soil, but they are also major crop pests when they feed on plant roots. Certain soil organisms, such as some roundworms, can severely impact golf course turf, for example.

Soil Profiles

A **soil profile** is a vertical section from the ground surface to the unaltered rock below. Usually, a soil profile has parallel layers known as **soil horizons.** Mature soil generally has three horizons (Fig. 25.4). The A horizon is the uppermost (or topsoil) layer that contains litter and humus, although most of the soluble chemicals may have been leached away. The B horizon has little or no organic matter but does contain the inorganic nutrients leached from the A horizon. The C horizon is a layer of weathered and shattered rock.

Because the parent material (rock) and climate (e.g., temperature and rainfall) differ in various parts of the biosphere, the soil profile varies according to the particular ecosystem. Soils formed in grasslands tend to have a deep A horizon built up from decaying grasses over many years, but because of limited rain, there has been little leaching into the B horizon. In forest soils, both the A and B horizons have enough inorganic nutrients to allow for root growth. In tropical rain forests, the A horizon is more shallow than the generalized profile, and the B horizon is deeper, signifying that leaching is more extensive. Since the topsoil of a rain forest lacks nutrients, it can only support crops for a few years.

Soil Erosion

Soil erosion occurs when water or wind carry soil away to a new location. Erosion removes about 25 billion tons of topsoil yearly, worldwide. If this rate of loss continues, some scientists predict that the Earth will lose practically all of its topsoil by the middle of the next century. Deforestation (removal of trees) and desertification (increase in deserts due to overgrazing and overfarming marginal lands) contribute to the occurrence of erosion, and so do poor farming practices in general.

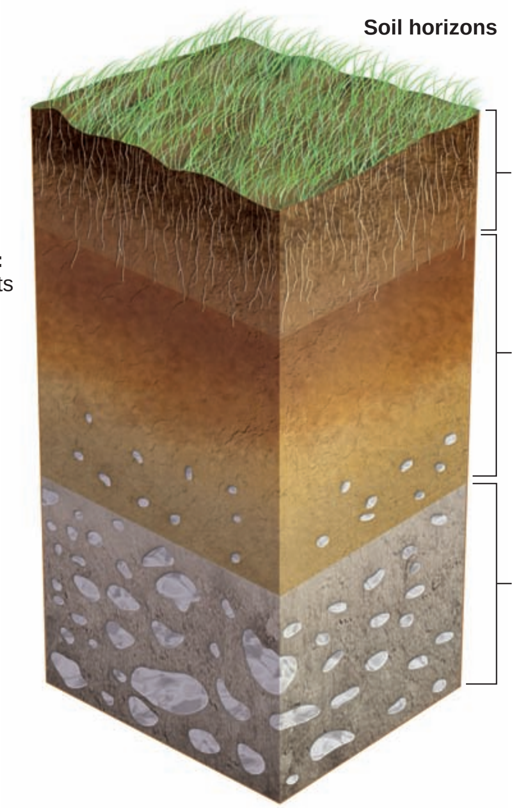


FIGURE 25.4 **Simplified soil profile.**

The top layer (A horizon) contains most of the humus; the next layer (B horizon) accumulates materials leached from the A horizon; and the lowest layer (C horizon) is composed of weathered parent material. Erosion removes the A horizon, a primary source of humus and minerals in soil.

In the United States, soil is eroding faster than it is being formed on about one-third of all cropland. Fertilizers and pesticides, carried by eroding soil into groundwater and rivers, are threatening human health. To make up for the loss of soil due to erosion, more energy is used to apply more fertilizers and pesticides to crops. Instead, it would be best to stop erosion before it occurs by following sound agricultural practices.

The coastal wetlands are losing soil at a tremendous rate. These wetlands are important as nurseries for many species of organisms, such as shrimp and redfish, and as protection against storm surge from hurricanes. In Louisiana, 24 mi^2 of wetlands are lost each year. This equates to one football field being lost every 38 minutes.

Check Your Progress 25.1

1. What element(s) in particular, aside from C, H, and O, is/are needed to form (**a**) proteins and (**b**) nucleic acids? How does a plant acquire these elements?
2. Some farmers do not remove the remains of last year's crops from agricultural lands. What are the benefits of this practice?
3. What are the benefits of humus in soil?

25.2 Water and Mineral Uptake

The pathways for water and mineral uptake and transport in a plant are the same. As Figure 25.5*a* shows, water along with minerals can enter the root of a flowering plant from the soil simply by passing between the porous cell walls. Eventually, however, the **Casparian strip,** a band of suberin and lignin bordering four sides of root endodermal cells, forces water to enter endodermal cells. Alternatively, water can enter epidermal cells at their **root hairs** and then progress through cells across the cortex and endodermis of a root by means of cytoplasmic strands within plasmodesmata (see Fig. 5.15). Regardless of the pathway, water enters root cells when they have a lower osmotic pressure than does the soil solution.

Mineral Uptake

In contrast to water, minerals are actively taken up by plant cells. Plants possess an astonishing ability to concentrate minerals—that is, to take up minerals until they are many times more concentrated in the plant than in the surrounding medium. The concentration of certain minerals in roots is as much as 10,000 times greater than in the surrounding soil. Following their uptake by root cells, minerals move into xylem and are transported into leaves by the upward movement of water. Along the way, minerals can exit xylem and enter those cells that require them. Some eventually reach leaf cells. In any case, minerals must again cross a selectively permeable plasma membrane when they exit xylem and enter living cells. By what mechanism do minerals cross plasma membranes?

Recall that plant cells absorb minerals in the ionic form: Nitrogen is absorbed as nitrate (NO_3^-), phosphorus as phosphate (HPO_4^{2-}), potassium as potassium ions (K^+), and so forth. Ions cannot cross the plasma membrane because they are unable to enter the nonpolar phase of the lipid bilayer. It has long been known that plant cells expend energy to actively take up and concentrate mineral ions. If roots are deprived of oxygen or are poisoned so that cellular respiration cannot occur, mineral ion uptake is diminished. The energy of ATP is required for mineral ion transport, but not directly (Fig. 25.5*b*). A plasma membrane pump, called a proton pump, hydrolyzes ATP and uses the energy released to transport hydrogen ions (H^+) out of the cell. This sets up an electrochemical gradient that drives positively charged ions such as K^+ through a channel protein into the cell. Negatively charged mineral ions are transported, along with H^+, by carrier proteins. Since H^+ is moving down its concentration gradient, no energy is required. Notice that this model of mineral ion transport in plant cells is based on chemiosmosis, the establishment of an electrochemical gradient to perform work.

Adaptations of Roots for Mineral Uptake

Two mutualistic relationships assist roots in obtaining mineral nutrients. Root nodules involve a mutualistic relationship with bacteria, and mycorrhizae are a mutualistic relationship with fungi.

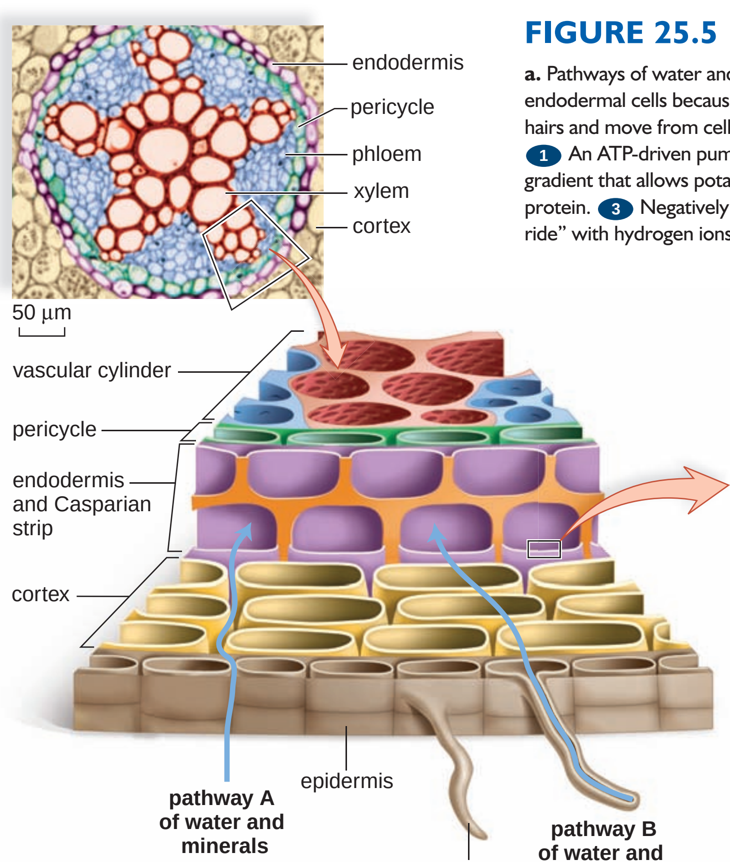
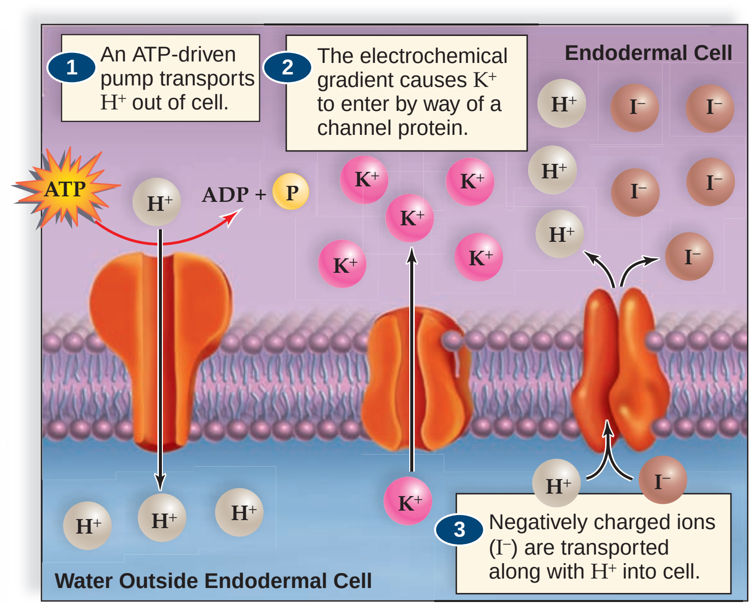


FIGURE 25.5 Water and mineral uptake.

a. Pathways of water and minerals. Water and minerals can travel via porous cell walls but then must enter endodermal cells because of the Casparian strip (pathway A). Alternatively, water and minerals can enter root hairs and move from cell to cell (pathway B). **b.** Transport of minerals across an endodermal plasma membrane. (1) An ATP-driven pump removes hydrogen ions (H^+) from the cell. (2) This establishes an electrochemical gradient that allows potassium (K^+) and other positively charged ions to cross the membrane via a channel protein. (3) Negatively charged mineral ions (I^-) can cross the membrane by way of a carrier when they "hitch a ride" with hydrogen ions (H^+), which are diffusing down their concentration gradient.



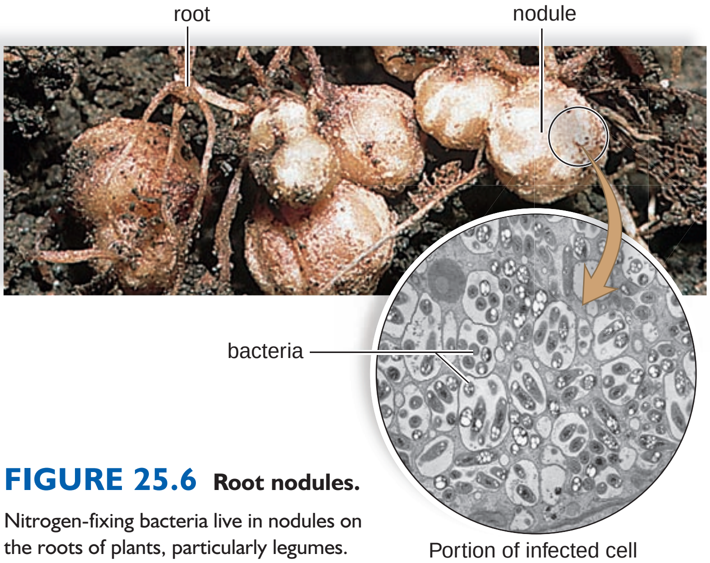


FIGURE 25.6 Root nodules.

Nitrogen-fixing bacteria live in nodules on the roots of plants, particularly legumes.

Some plants, such as members of the legume family including bean, clover, and alfalfa, have roots colonized by *Rhizobium* bacteria, which can fix atmospheric nitrogen (N_2). They break the N ≡ N bond and reduce nitrogen to NH_4^+ for incorporation into organic compounds. The bacteria live in **root nodules** [L. *nodulus,* dim. of *nodus,* knot] and are supplied with carbohydrates by the host plant (Fig. 25.6). The bacteria, in turn, furnish their host with nitrogen compounds.

The second type of mutualistic relationship, called mycorrhizae, involves fungi and almost all plant roots (Fig. 25.7). Only a small minority of plants do not have **mycorrhizae** [Gk. *mykes,* fungus, and *rhiza,* root], and these plants are most often limited as to the environment in which they can grow. The fungus increases the surface area available for mineral and water uptake and breaks down organic matter in the soil, releasing nutrients that the plant can use. In return, the root furnishes the fungus with sugars and amino acids. Plants are extremely dependent on mycorrhizae. Orchid seeds, which are quite small and contain limited nutrients, do not germinate until a mycorrhizal fungus has invaded their cells.

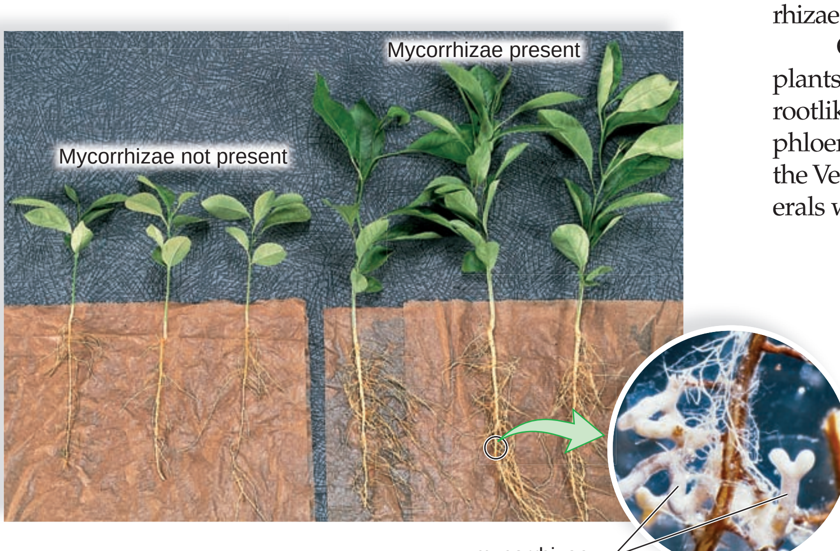
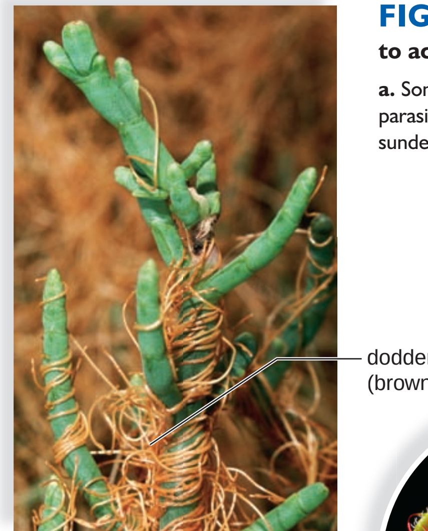
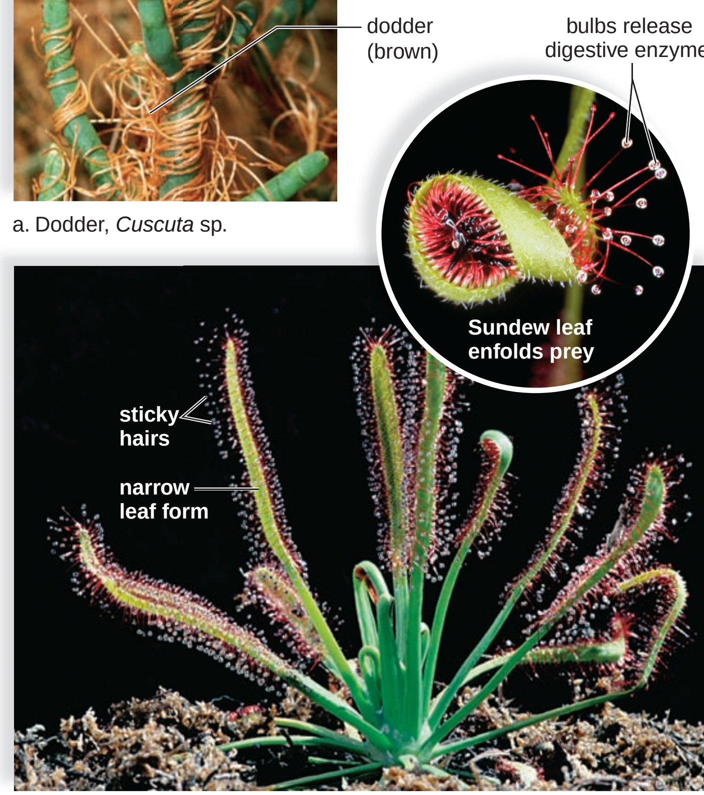


FIGURE 25.7 Mycorrhizae.

Plant growth is better when mycorrhizae are present.



a. Dodder, *Cuscuta* sp.



b. Cape sundew, *Drosera capensis*

FIGURE 25.8 Other ways to acquire nutrients.

a. Some plants, such as the dodder, are parasitic. **b.** Some plants, such as the sundew, are carnivorous.

Nonphotosynthetic plants, such as Indian pipe, use their mycorrhizae to extract nutrients from nearby trees.

Other means of acquiring nutrients also occur. Parasitic plants such as dodders, broomrapes, and pinedrops send out rootlike projections called haustoria that tap into the xylem and phloem of the host stem (Fig. 25.8*a*). Carnivorous plants such as the Venus's flytrap and sundews obtain some nitrogen and minerals when their leaves capture and digest insects (Fig. 25.8*b*).

Check Your Progress 25.2

1. Review the structure of the plasma membrane on page 460, and explain why the center of the plasma membrane is nonpolar, making it difficult for ions to cross the plasma membrane.
2. Explain the significance to plants of nitrogen-fixing bacteria in the soil.
3. Explain how both partners benefit from a mycorrhizal association.

25.3 Transport Mechanisms in Plants

Flowering plants are well adapted to living in a terrestrial environment. Their leaves, which carry on photosynthesis, are positioned to catch the rays of the sun because they are held aloft by the stem (Fig. 25.9). Carbon dioxide enters leaves at the stomata, but water, the other main requirement for photosynthesis, is absorbed by the roots. Water must be transported from the roots through the stem to the leaves.

Reviewing Xylem and Phloem Structure

Vascular plants have a transport tissue, called **xylem,** that moves water and minerals from the roots to the leaves. Xylem contains two types of conducting cells: tracheids and vessel elements. **Tracheids** are tapered at both ends. The ends overlap with those of adjacent tracheids (see Fig. 24.6). Pits located in adjacent tracheids allow water to pass from cell to cell. **Vessel elements** are long and tubular with perforation plates at each end (see Fig. 24.6). Vessel elements placed end to end form a completely hollow pipeline from the roots to the leaves. Xylem, with its strong-walled, nonliving cells, gives trees much-needed internal support.

The process of photosynthesis results in sugars, which are used as a source of energy and building blocks for other organic molecules throughout a plant. **Phloem** is the type of vascular tissue that transports organic nutrients to all parts of the plant. Roots buried in the soil cannot possibly carry on photosynthesis, but they still require a source of energy in order to carry on cellular metabolism. Vascular plants are able to transport the products of photosynthesis to regions that require them and/or that will store them for future use. In flowering plants, the conducting cells of phloem are **sieve-tube members,** each of which typically has a companion cell (see Fig. 24.7). **Companion cells** can provide proteins to sieve-tube members, which contain cytoplasm but have no nucleus. The end walls of sieve-tube members are called sieve plates because they contain numerous pores. The sieve-tube members are aligned end to end, and strands of cytoplasm within plasmodesmata extend from one cell to the other through the sieve plates. In this way, sieve-tube members form a continuous **sieve tube** for organic nutrient transport throughout the plant.

Determining Xylem and Phloem Function

Knowing that vascular plants are structured in a way that allows materials to move from one part to another does not tell us the mechanisms by which they move. Plant physiologists have performed numerous experiments to determine how water and minerals rise to the tops of very tall trees in xylem and how organic nutrients move in the opposite direction in phloem. It would be expected that these processes are mechanical in nature and based on the properties of water because water is a large part of both **xylem sap** and **phloem sap,** as the watery contents of these vessels are called. In living systems, water molecules diffuse

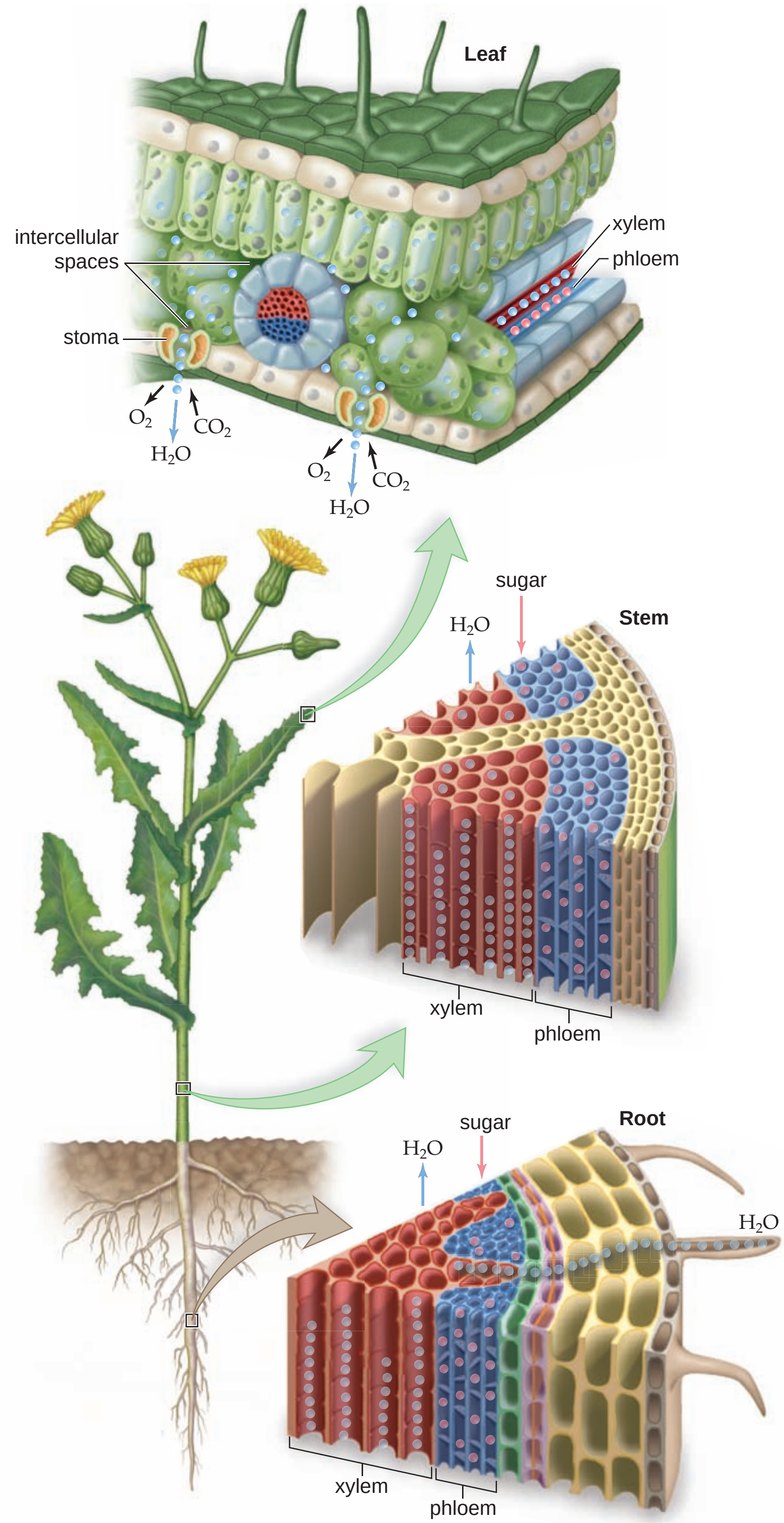


FIGURE 25.9 Plant transport system.

Vascular tissue in plants includes xylem, which transports water and minerals from the roots to the leaves, and phloem, which transports organic nutrients oftentimes in the opposite direction. Notice that xylem and phloem are continuous from the roots through the stem to the leaves, which are the vegetative organs of a plant.

science focus

The Concept of Water Potential

Potential energy is stored energy due to the position of an object. A boulder placed at the top of a hill has potential energy. When pushed, the boulder moves down the hill as potential energy is converted into kinetic (motion) energy. Once it's at the bottom of the hill, the boulder has lost much of its potential energy.

Water potential is defined as the energy of water. Just like the boulder, water at the top of a waterfall has a higher water potential than water at the bottom of the waterfall. As illustrated by this example, water moves from a region of higher potential to a region of lower water potential.

In terms of cells, two factors usually determine water potential, which in turn determines the direction in which water will move across a plasma membrane. These factors concern differences in:

1. Water pressure across a membrane
2. Solute concentration across a membrane

Pressure potential is the effect that pressure has on water potential. With regard to pressure, it is obvious that water will move across a membrane from the area of higher pressure to the area of lower pressure. The higher the water pressure, the higher the water potential. The lower the water pressure, the lower the water potential, and the more likely it is that water will flow in that direction. Pressure potential is the concept that best explains the movement of sap in xylem and phloem.

To fully explain the movement of water into plant cells, the concept of *osmotic potential* is also required. Osmotic potential takes into account the effects of solutes on the movement of water. The presence of solutes restricts the movement of water because water tends to interact with solutes. Indeed, water tends to move across a membrane from the area of lower solute concentration to the area of higher solute concentration. The lower the concentration of solutes (osmotic potential), the higher the water potential. The higher the concentration of solutes, the lower the water potential and the more likely it is that water will flow in that direction.

Not surprisingly, increasing water pressure will counter the tendency of water to enter a cell because of the presence of solutes. A common situation exists in plant cells. As water enters a plant cell by osmosis, water pressure will increase inside the cell—a plant cell has a strong cell wall that allows water pressure to build up. When will water stop entering the cell? When the pressure potential inside the cell increases and balances the osmotic potential outside the cell.

Pressure potential that increases due to the process of osmosis is often called *turgor pressure*. Turgor pressure is critical, since plants depend on it to maintain the turgidity of their bodies (Fig. 25A). The cells of a wilted plant have insufficient turgor pressure, and the plant droops as a result.

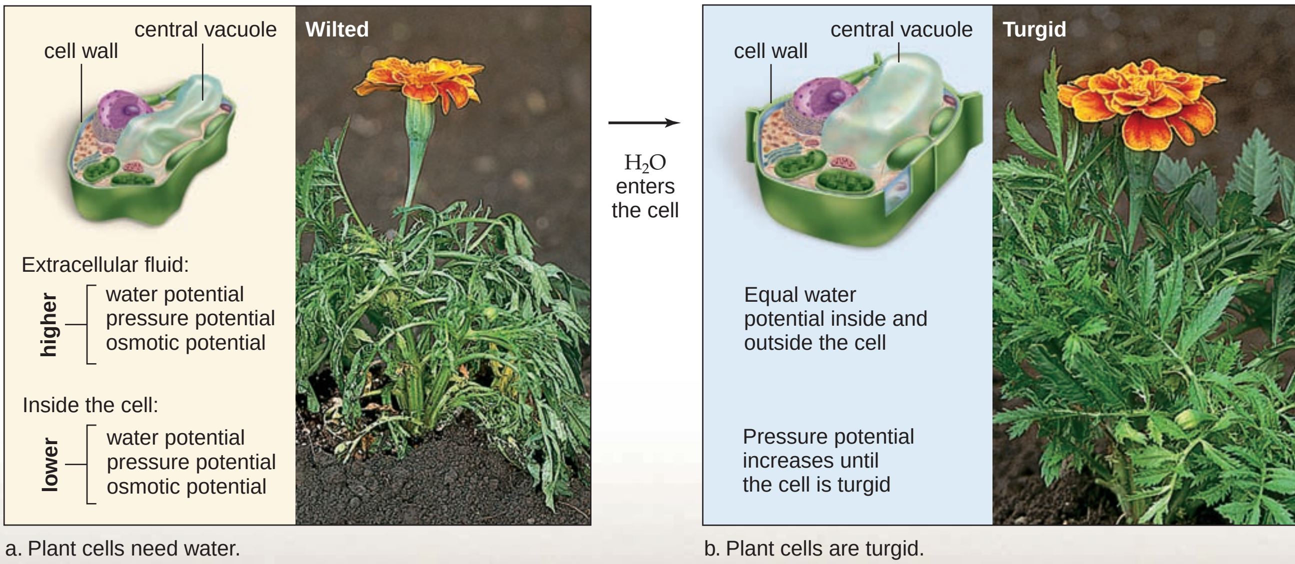


FIGURE 25A **Water potential and turgor pressure.** Water flows from an area of higher water potential to an area of lower water potential. ***a.*** The cells of a wilted plant have a lower water potential; therefore, water enters the cells. ***b.*** Equilibrium is achieved when the water potential is equal inside and outside the cell. Cells are now turgid, and the plant is no longer wilted.

freely across plasma membranes from the area of higher concentration to the area of lower concentration. Botanists favor describing the movement of water in terms of water potential: Water always flows passively from the area of higher water potential to the area of lower water potential. As can be seen in the Science Focus above, the concept of water potential has the benefit of considering water pressure in addition to osmotic pressure.

Chemical properties of water are also important in movement of xylem sap. The polarity of water molecules and the hydrogen bonding between water molecules allow water to fill xylem cells.

Water Transport

Figure 25.5 traces the path of water from the root hairs to the xylem. As you know, xylem vessels constitute an open pipeline because the vessel elements have perforation plates separating one from the other (Fig. 25.10*a*, *b*). The tracheids, which are elongated with tapered ends, form a less obvious means of transport, but water can move across the end and side walls of tracheids because of pits, or depressions, where the secondary wall does not form (Fig. 25.10*c*).

Water entering root cells creates a positive pressure called **root pressure.** Root pressure, which primarily occurs at night, tends to push xylem sap upward. Root pressure may be responsible for **guttation** [L. *gutta*, drops, spots] when drops of water are forced out of vein endings along the edges of leaves (Fig. 25.11). Although root pressure may contribute to the upward movement of water in some instances, it is not believed to be the mechanism by which water can rise to the tops of very tall trees. After an injury or pruning, especially in spring, some plants appear to "bleed" as water exudes from the site. This phenomenon is the result of root pressure.

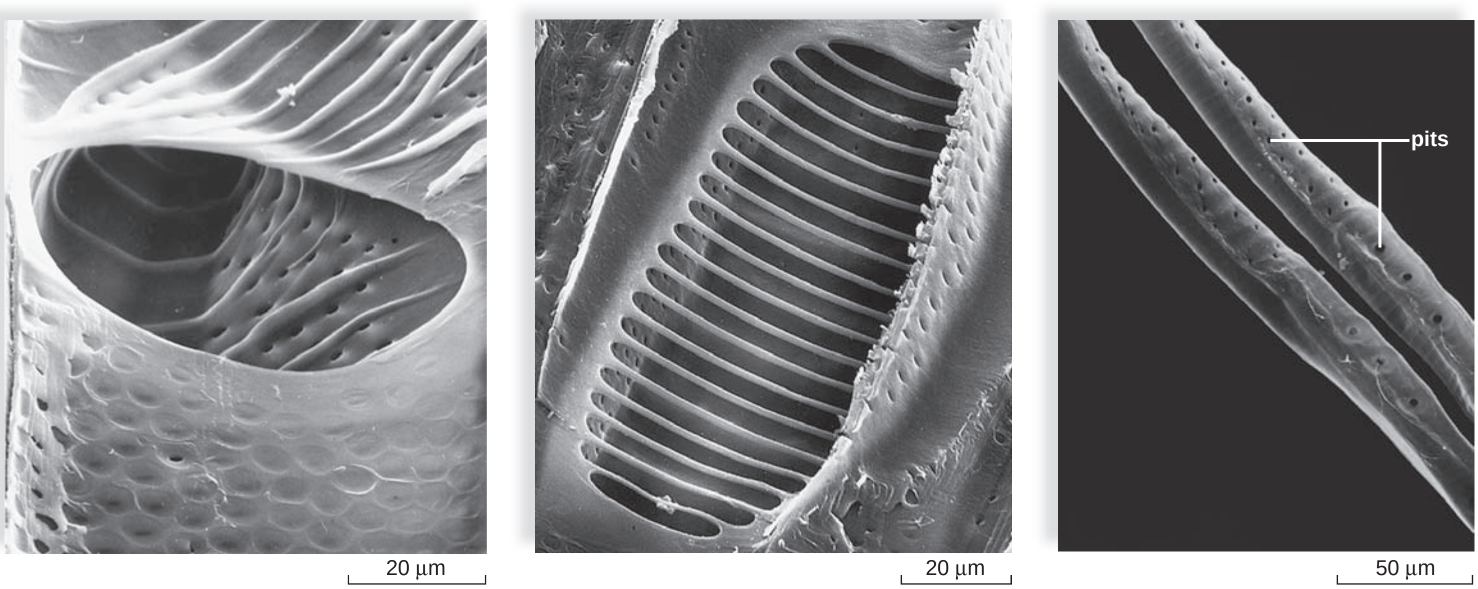
FIGURE 25.11 Guttation.

Drops of guttation water on the edges of a strawberry leaf. Guttation, which occurs at night, may be due to root pressure. Root pressure is a positive pressure potential caused by the entrance of water into root cells. Often guttation is mistaken for early morning dew.

Cohesion-Tension Model of Xylem Transport

Once water enters xylem, it must be transported to all parts of the plant. Transporting water can be a daunting task, especially for some plants, such as redwood trees, which can exceed 90 m (almost 300 ft) in height.

The **cohesion-tension model** of xylem transport, outlined in Figure 25.12 describes a mechanism for xylem transport that requires no expenditure of energy by the plant and is dependent on the properties of water. The term *cohesion* refers to the tendency of water molecules to cling together. Because of hydrogen bonding, water molecules interact with one another and form a continuous **water column** in xylem, from the leaves to the roots, that is not easily broken. In addition to cohesion, another property of water called *adhesion* plays a role in xylem transport. Adhesion refers to the ability of water, a polar molecule, to interact



a. Perforation plate with a single, large opening b. Perforation plate with a series of openings c. Tracheids

FIGURE 25.10 Conducting cells of xylem.

Water can move from vessel element to vessel element through perforation plates (**a** and **b**). Vessel elements can also exchange water with tracheids through pits. **c.** Tracheids are long, hollow cells with tapered ends. Water can move into and out of tracheids through pits only.

with the molecules making up the walls of the vessels in xylem. Adhesion gives the water column extra strength and prevents it from slipping back.

The Leaves. When the stomata of a leaf are open, the cells of the spongy layer are exposed to the air, which can be quite dry. Water then evaporates as a gas or vapor from the spongy layer into the intercellular spaces. Evaporation of water through leaf stomata is called **transpiration.** At least 90% of the water taken up by the roots is eventually lost by transpiration. This means that the total amount of water lost by a plant over a long period of time is surprisingly large. A single *Zea mays* (corn) plant loses somewhere between 135 and 200 liters of water through transpiration during a growing season. An average-sized birch tree with over 200,000 leaves will transpire up to 3,700 liters of water per day during the growing season.

The water molecules that evaporate from cells into the intercellular spaces are replaced by other water molecules from the leaf veins. Because the water molecules are cohesive, transpiration exerts a *pulling force*, or *tension*, that draws the water column through the xylem to replace the water lost by leaf cells.

Note that the loss of water by transpiration is the mechanism by which minerals are transported throughout the plant body. Also, evaporation of water moderates the temperature of leaf tissues.

There is an important consequence to the way water is transported in plants. When a plant is under water stress, the stomata close. Now the plant loses little water because the leaves are protected against water loss by the waxy **cuticle** of the upper and lower epidermis. When stomata are closed, however, carbon dioxide cannot enter the leaves, and many plants are unable to photosynthesize efficiently. Photosynthesis, therefore, requires an abundant supply of water so that stomata remain open, allowing carbon dioxide to enter.

The Stem. The tension in xylem created by evaporation of water at the leaves pulls the water column in the stem upward. Usually, the water column in the stem is continuous because of the cohesive property of water molecules. The water molecules also adhere to the sides of the vessels. What happens if the water column within xylem breaks? The water column "snaps back" down the xylem vessel away from the site of breakage, making it more difficult for conduction to occur. Next time you use a straw to drink a soda, notice that pulling the liquid upward is fairly easy, as long as there is liquid at the end of the straw. When the soda runs low and you begin to get air, it takes considerably more suction to pull up the remaining liquid. When preparing a vase of flowers, you should always cut the stems under water to preserve an unbroken water column and the life of the flowers.

The Roots. In the root, water enters xylem passively by osmosis because xylem sap always has a greater concentration of solutes than do the root cells. The water column in xylem extends from the leaves down to the root. Water is pulled upward from the roots due to the tension in xylem created by the evaporation of water at the leaves.

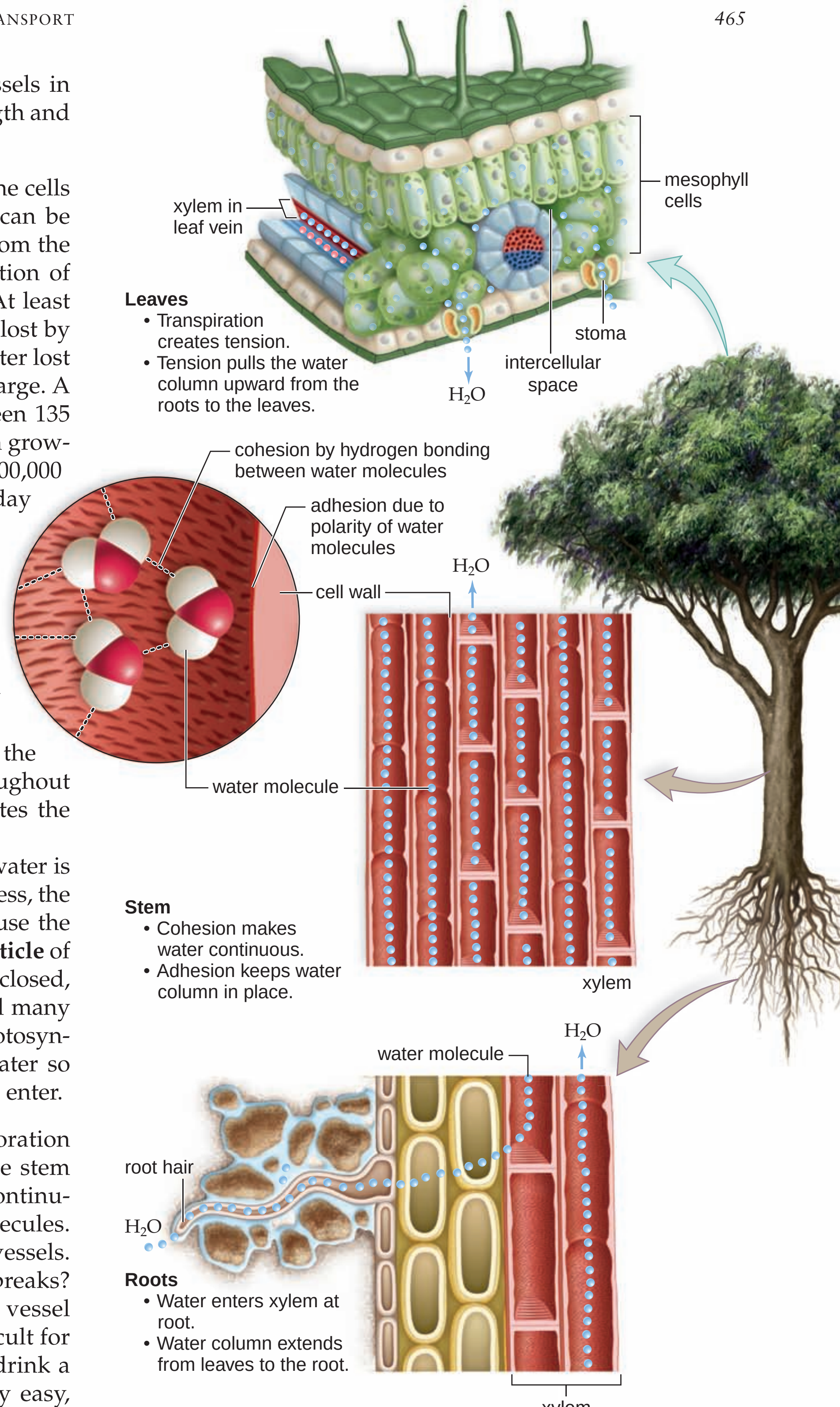


FIGURE 25.12 Cohesion-tension model of xylem transport.

Tension created by evaporation (transpiration) at the leaves pulls water along the length of the xylem—from the roots to the leaves.

Opening and Closing of Stomata

Each **stoma,** a small pore in leaf epidermis, is bordered by **guard cells.** When water enters the guard cells and turgor pressure increases, the stoma opens; when water exits the guard cells and turgor pressure decreases, the stoma closes. Notice in Figure 25.13 that the guard cells are attached to each other at their ends and that the inner walls are thicker than the outer walls. When water enters, a guard cell's radial expansion is restricted because of cellulose microfibrils in the walls, but lengthwise expansion of the outer walls is possible. When the outer walls expand lengthwise, they buckle out from the region of their attachment, and the stoma opens.

Since about 1968, it has been clear that potassium ions (K^+) accumulate within guard cells when stomata open. In other words, active transport of K^+ into guard cells causes water to follow by osmosis and stomata to open. Also interesting is the observation that hydrogen ions (H^+) accumulate outside guard cells as K^+ moves into them. A proton pump run by the hydrolysis of ATP transports H^+ to the outside of the cell. This establishes an electrochemical gradient that allows K^+ to enter by way of a channel protein (see Fig. 25.5*b*).

What regulates the opening and closing of stomata? It appears that the blue-light component of sunlight is a signal that can cause stomata to open. Evidence suggests that a flavin pigment absorbs blue light, and then this pigment sets in motion the cytoplasmic response that leads to activation of the proton pump. Similarly, there could be a receptor in the plasma membrane of guard cells that brings about inactivation of the pump when carbon dioxide (CO_2) concentration rises, as might happen when photosynthesis ceases. Abscisic acid (ABA), which is produced by cells in wilting leaves, can also cause stomata to close (see page 480). Although photosynthesis cannot occur, water is conserved.

If plants are kept in the dark, stomata open and close just about every 24 hours, just as if they were responding to the presence of sunlight in the daytime and the absence of sunlight at night. This means that some sort of internal biological clock must be keeping time. Circadian rhythms (a behavior that occurs nearly every 24 hours) and biological clocks are areas of intense investigation at this time. Other factors that influence the opening and closing of stoma include temperature, humidity, and stress.

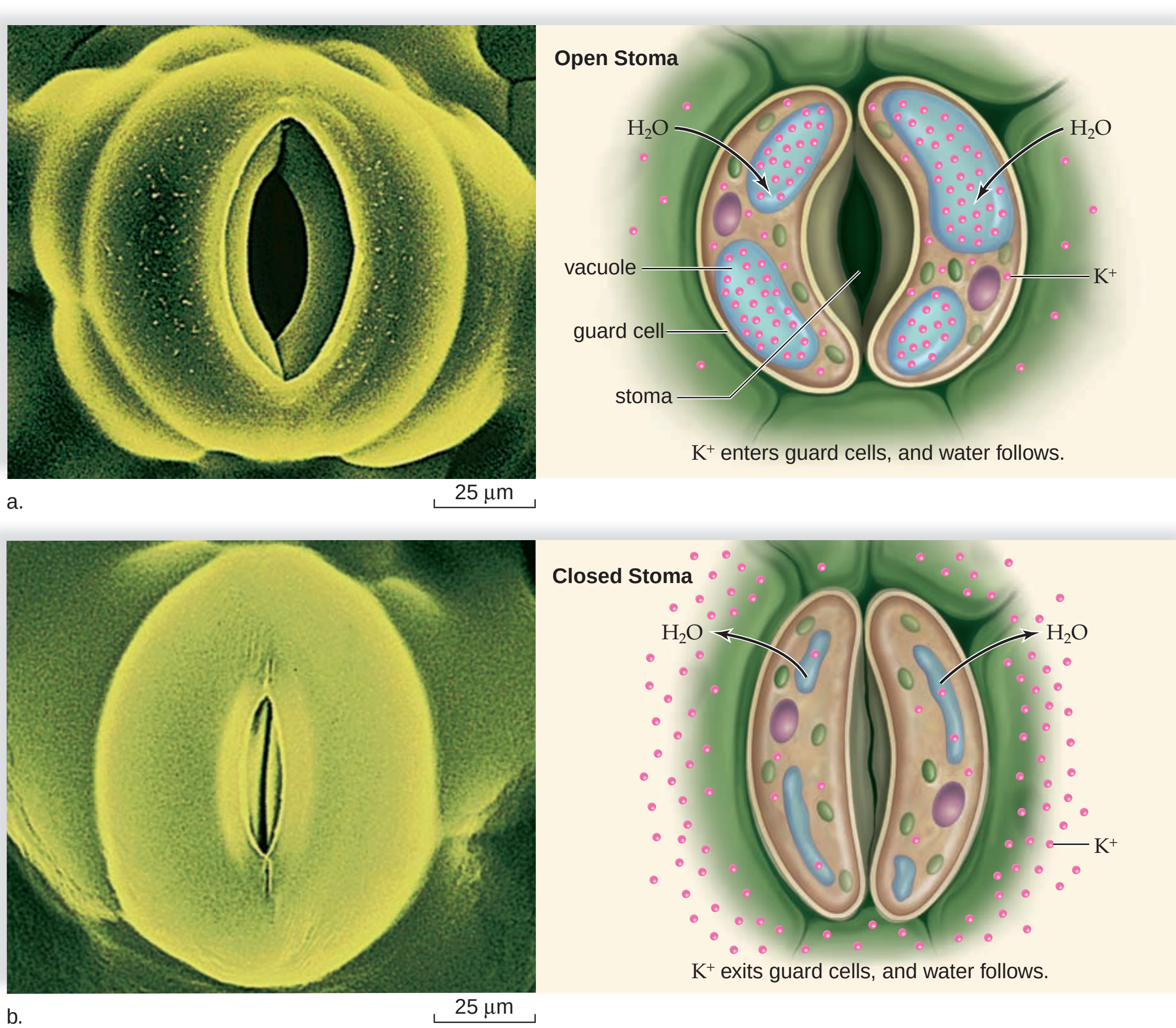


FIGURE 25.13
Opening and closing of stomata.

a. A stoma opens when turgor pressure increases in guard cells due to the entrance of K^+ followed by the entrance of water. **b.** A stoma closes when turgor pressure decreases due to the exit of K^+ followed by the exit of water.

ecology focus

Plants Can Clean Up Toxic Messes

Phytoremediation uses plants—many of them common species such as poplar, mustard, and mulberry—that have an appetite for lead, uranium, and other pollutants. These plants' genetic makeups allow them to absorb and to store, degrade, or transform substances that kill or harm other plants and animals. "It's an elegantly simple solution to pollution problems" says Louis Licht, who runs Ecolotree, an Iowa City phytoremediation company.

The idea behind phytoremediation is not new; scientists have long recognized certain plants' abilities to absorb and tolerate toxic substances. But the idea of using these plants on contaminated sites has just gained support in the last decade. Different plants work on different contaminants. The mulberry bush, for instance, is effective on industrial sludge; some grasses attack petroleum wastes; and sunflowers (together with soil additives) remove lead. The plants clean up sites in two basic ways, depending on the substance involved. If it is an organic contaminant, such as spilled oil, the plants or microbes around their roots break down the substance. The remainders can either be absorbed by the plant or left in the soil or water. For an inorganic contaminant such as cadmium or zinc, the plants absorb the substance and trap it. The plants must then be harvested and disposed of, or processed to reclaim the trapped contaminant.

Poplars Take Up Excess Nitrates

Most trees planted along the edges of farms are intended to break the wind. But a milelong stand of spindly poplars outside Amana, Iowa, is involved in phytoremediation.

The poplars act like vacuum cleaners, sucking up nitrate-laden runoff from a fertilized cornfield before this runoff reaches a nearby brook—and perhaps other waters. Nitrate runoff into the Mississippi River from Midwest farms, after all, is a major cause of the large "dead zone" of oxygen-depleted water that develops each summer in the Gulf of Mexico.

Before the trees were planted, the brook's nitrate levels were as much as ten times the amount considered safe. But then Licht, a University of Iowa graduate student, had the idea that poplars, which absorb lots of water and tolerate pollutants, could help. In 1991, Licht tested his hunch by planting the trees along a field owned by a corporate farm. The brook's nitrate levels subsequently dropped more than 90%, and the trees have thrived.

Canola Plants Take Up Selenium

Canola plants (*Brassica rapa* and *B. napa*), meanwhile, are grown in California's San Joaquin Valley to soak up excess selenium in the soil to help prevent an environmental catastrophe like the one that occurred there in the 1980s.

Back then, irrigated farming caused naturally occurring selenium to rise to the soil surface. When excess water was pumped onto the fields, some selenium would flow off into drainage ditches, eventually ending up in Kesterson National Wildlife Refuge. The selenium in ponds at the refuge accumulated in plants and fish and subsequently deformed and killed waterfowl, says Gary Bañuelos, a plant scientist with the U.S. Department of Agriculture who helped remedy the problem. He recommended that farmers add selenium-accumulating canola plants to their crop rotations (Fig. 25B). As a result, selenium levels in runoff are being managed. Although the underlying problem of excessive selenium in soils has not been solved, says Bañuelos, "this is a tool to manage mobile selenium and prevent another unlikely selenium-induced disaster."

FIGURE 25B Canola plants.
Scientist Gary Bañuelos recommended planting canola to pull selenium out of the soil.

Mustard Plants Take Up Uranium

Phytoremediation has also helped clean up badly polluted sites, in some cases at a fraction of the usual cost. Edenspace Systems Corporation of Reston, Virginia, just concluded a phytoremediation demonstration at a Superfund site on an Army firing range in Aberdeen, Maryland. The company successfully used mustard plants to remove uranium from the firing range, at as little as 10% of the cost of traditional cleanup methods. Depending on the contaminant involved, traditional cleanup costs can run as much as $1 million per acre, experts say.

Limitations of Phytoremediation

Phytoremediation does have its limitations, however. One of them is its slow pace. Depending on the contaminant, it can take several growing seasons to clean a site—much longer than conventional methods. "We normally look at phytoremediation as a target of one to three years to clean a site," notes Edenspace's Mike Blaylock. "People won't want to wait much longer than that."

Phytoremediation is also only effective at depths that plant roots can reach, making it useless against deep-lying contamination unless the contaminated soils are excavated. Phytoremediation will not work on lead and other metals unless chemicals are added to the soil. In addition, it is possible that animals may ingest pollutants by eating the leaves of plants in some projects.

Despite its shortcomings, experts see a bright future for this technology because, for one reason, the costs are relatively small compared to those of traditional remediation technologies. Traditional methods of cleanup require much energy input and therefore have higher cost. In general, phytoremediation is a low-cost alternative to traditional methods because less energy is required for operation and maintenance. Phytoremediation is a promising solution to pollution problems but, says the EPA's Walter W. Kovalick, "it's not a panacea. It's another arrow in the quiver. It takes more than one arrow to solve most problems."

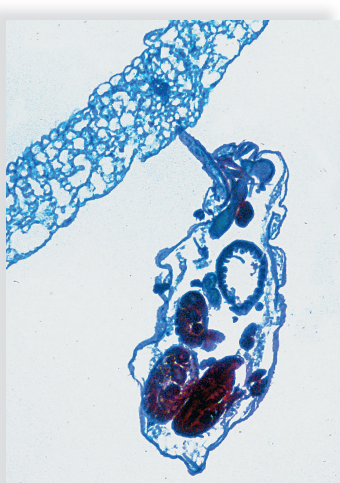
Organic Nutrient Transport

Not only do plants transport water and minerals from the roots to the leaves, but they also transport organic nutrients to the parts of plants that need them. This includes young leaves that have not yet reached their full photosynthetic potential; flowers that are in the process of making seeds and fruits; and the roots, whose location in the soil prohibits them from carrying on photosynthesis

Role of Phloem

As long ago as 1679, Marcello Malpighi suggested that bark is involved in translocating sugars from leaves to roots. He observed the results of removing a strip of bark from around a tree, a procedure called **girdling.** If a tree is girdled below the level of the majority of leaves, the bark swells just above the cut, and sugar accumulates in the swollen tissue. We know today that when a tree is girdled, the phloem is removed, but the xylem is left intact. Therefore, the results of girdling suggest that phloem is the tissue that transports sugars.

a. An aphid feeding on a plant stem



b. Aphid stylet in place

FIGURE 25.14

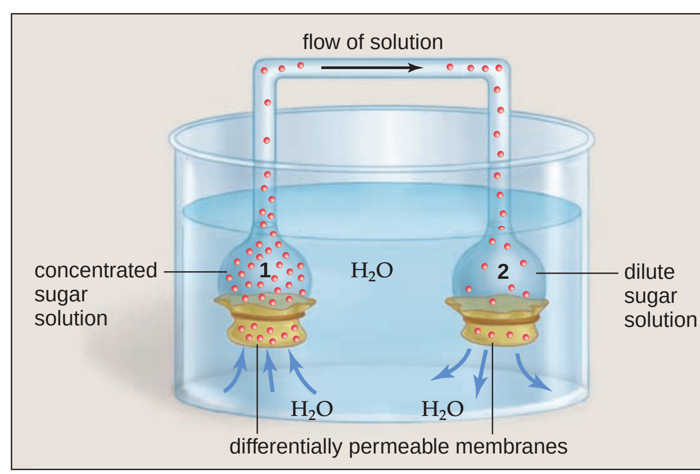
Acquiring phloem sap.

Aphids are small insects that remove nutrients from phloem by means of a needle-like mouthpart called a stylet. **a.** Excess phloem sap appears as a droplet after passing through the aphid's body. **b.** Micrograph of stylet in plant tissue. When an aphid is cut away from its stylet, phloem sap becomes available for collection and analysis.

Radioactive tracer studies with carbon 14 (^{14}C) have confirmed that phloem transports organic nutrients. When ^{14}C-labeled carbon dioxide (CO_2) is supplied to mature leaves, radioactively labeled sugar is soon found moving down the stem into the roots. It's difficult to get samples of sap from phloem without injuring the phloem, but this problem is solved by using aphids, small insects that are phloem feeders. The aphid drives its stylet, which is a sharp mouthpart that functions like a hypodermic needle, between the epidermal cells, and sap enters its body from a sieve-tube member (Fig. 25.14). If the aphid is anesthetized using ether, its body can be carefully cut away, leaving the stylet. Phloem can then be collected and analyzed by a researcher. By the use of radioactive tracers and aphids, it is known that the movement through phloem can be as fast as 60–100 cm per hour and possibly up to 300 cm per hour.

Pressure-Flow Model of Phloem Transport

The **pressure-flow model** is a current explanation for the movement of organic materials in phloem (Fig. 25.15). Consider the following experiment in which two bulbs are connected by a glass tube. The first bulb contains solute at a higher concentration than the second bulb. Each bulb is bounded by a differentially permeable membrane, and the entire apparatus is submerged in distilled water.



Distilled water flows into the first bulb because it has the higher solute concentration. The entrance of water creates a positive *pressure*, and water *flows* toward the second bulb. This flow not only drives water toward the second bulb, but it also provides enough force for water to move out through the membrane of the second bulb—even though the second bulb contains a higher concentration of solute than the distilled water.

In plants, sieve tubes are analogous to the glass tube that connects the two bulbs. Sieve tubes are composed of sieve-tube members, each of which has a companion cell. It is possible that the companion cells assist the sieve-tube members in some way. The sieve-tube members align end

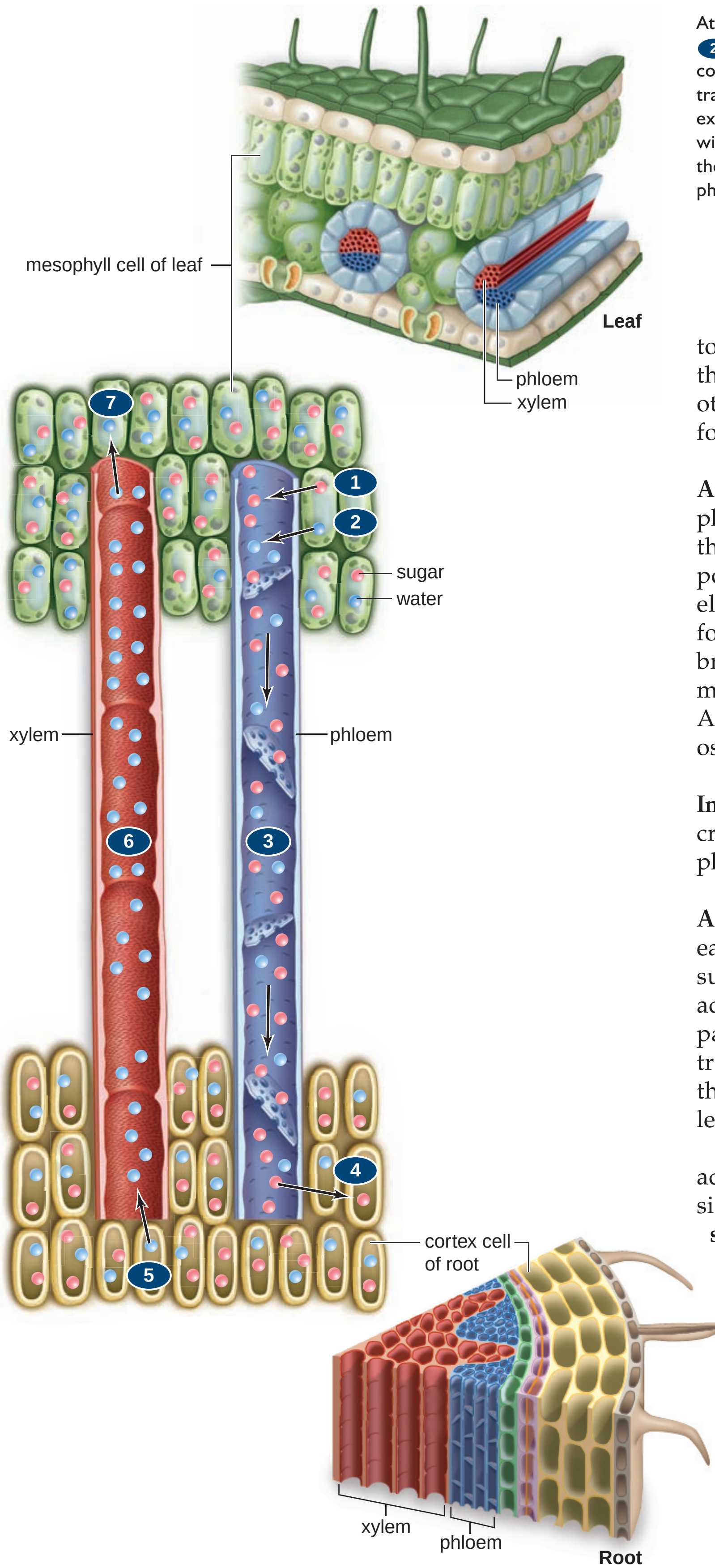


FIGURE 25.15 **Pressure-flow model of phloem transport.**

At a source, (1) sugar (pink) is actively transported into sieve tubes. (2) Water (blue) follows by osmosis. (3) A positive pressure causes phloem contents to flow from source to a sink. At a sink, (4) sugar is actively transported out of sieve tubes and cells use it for cellular respiration. Water exits by osmosis. (5) Some water returns to the xylem, where it mixes with more water absorbed from the soil. (6) Xylem transports water to the mesophyll of the leaf. (7) Most water is transpired, some is used for photosynthesis, and some reenters phloem by osmosis.

to end, and strands of plasmodesmata (cytoplasm) extend through sieve plates from one sieve-tube member to the other. Sieve tubes, therefore, form a continuous pathway for organic nutrient transport throughout a plant.

At the Source (e.g., leaves). During the growing season, photosynthesizing leaves are producing sugar. Therefore, they are a source of sugar. This sugar is actively transported into phloem. Again, transport is dependent on an electrochemical gradient established by a proton pump, a form of active transport. Sugar is carried across the membrane in conjunction with hydrogen ions (H^+), which are moving down their concentration gradient (see Fig. 25.5). After sugar enters sieve tubes, water follows passively by osmosis.

In the Stem. The buildup of water within sieve tubes creates the positive pressure that accounts for the flow of phloem contents.

At the Sink (e.g., roots). The roots (and other growth areas) are a sink for sugar, meaning that they are removing sugar and using it for cellular respiration. After sugar is actively transported out of sieve tubes, water exits phloem passively by osmosis and is taken up by xylem, which transports water to leaves, where it is used for photosynthesis. Now, phloem contents continue to flow from the leaves (source) to the roots (sink).

The pressure-flow model of phloem transport can account for any direction of flow in sieve tubes if we consider that the direction of flow is always from **source** to **sink.** For example, recently formed leaves can be a sink, and they will receive sucrose until they begin to maximally photosynthesize.

Check Your Progress 25.3

1. Explain why water is under tension in stems.
2. Explain the significance of the cohesion and adhesion properties of water to water transport.
3. Explain how sugars move from source to sink in a plant.

Connecting the Concepts

The land environment offers many advantages for plants, such as greater availability of light and carbon dioxide for photosynthesis. (Water, even if clear, filters out light, and carbon dioxide concentration and rate of diffusion is less in water.) The evolution of a transport system was critical, however, for plants to make full use of these advantages. Only if a transport system is present can plants elevate the leaves so that they are better exposed to solar energy and carbon dioxide in the air. A transport system brings water, a raw material of photosynthesis, from the roots to the leaves and also brings the products of photosynthesis down to the roots. Roots lie beneath the soil, and their cells depend on an input of organic food from the leaves to remain alive. An efficient transport system allows roots to penetrate deeply into the soil to absorb water and minerals.

The presence of a transport system also allows materials to be distributed to those parts of the plant body that are growing most rapidly. New leaves and flower buds would grow rather slowly if they had to depend on their own rate of photosynthesis, for example. Height in vascular plants, due to the presence of a transport system, has other benefits aside from elevation of leaves. It is also adaptive to have reproductive structures located where the wind can better distribute pollen and seeds. Once animal pollination came into existence, it was beneficial for flowers to be located where they are more easily seen by animals.

Clearly, plants with a transport system have a competitive edge in the terrestrial environment.

summary

25.1 Plant Nutrition and Soil

Plants need both essential and beneficial inorganic nutrients. Carbon, hydrogen, and oxygen make up 95% of a plant's dry weight. The other necessary nutrients are taken up by the roots as mineral ions. Even nitrogen (N), which is present in the atmosphere, is most often taken up as NO_3^-.

You can determine mineral requirements by hydroponics, in which plants are grown in a solution. The solution is varied by the omission of one mineral. If the plant dies, then the missing mineral must be essential for growth. If it grows poorly, than the mineral is beneficial.

Plant life is dependent on soil, which forms by the weathering of rock. Organisms contribute to the formation of humus and soil. Soil is a mixture of mineral particles, humus, living organisms, air, and water. Soil particles are of three types from the largest to the smallest: sand, silt, and clay. Loam, which contains about equal proportions of all three types, retains water but still has air spaces. Humus contributes to the texture of soil and its ability to provide inorganic nutrients to plants. Topsoil (A horizon of a soil profile) contains humus, and this is the layer that is lost by erosion, a worldwide problem.

25.2 Water and Mineral Uptake

Water, along with minerals, can enter a root by passing between the porous cell walls, until it reaches the Casparian strip, after which it passes through an endodermal cell before entering xylem. Water can also enter root hairs and then pass through the cells of the cortex and endodermis to reach xylem.

Mineral ions cross plasma membranes by a chemiosmotic mechanism. A proton pump transports H^+ out of the cell. This establishes an electrochemical gradient that causes positive ions to flow into the cells. Negative ions are carried across in conjunction with H^+, which is moving along its concentration gradient.

Plants have various adaptations that assist them in acquiring nutrients. Legumes have nodules infected with the bacterium *Rhizobium,* which makes nitrogen compounds available to these plants. Many other plants have mycorrhizae, or fungus roots. The fungus gathers nutrients from the soil, and the root provides the fungus with sugars and amino acids. Some plants have poorly developed roots. Most epiphytes live on, but do not parasitize, trees, whereas dodder and some other plants parasitize their hosts.

25.3 Transport Mechanisms in Plants

As an adaptation to life on land, plants have a vascular system that transports water and minerals from the roots to the leaves and must also transport the products of photosynthesis in the opposite direction. Vascular tissue includes xylem and phloem.

In xylem, vessels composed of vessel elements aligned end to end form an open pipeline from the roots to the leaves. Particularly at night, root pressure can build in the root. However, this does not contribute significantly to xylem transport.

The cohesion-tension model of xylem transport states that transpiration creates a tension that pulls water upward in xylem from the roots to the leaves. This means of transport works only because water molecules are cohesive with one another and adhesive with xylem walls.

Most of the water taken in by a plant is lost through stomata by transpiration. Only when there is plenty of water do stomata remain open, allowing carbon dioxide to enter the leaf and photosynthesis to occur.

Stomata open when guard cells take up water. The guard cells are anchored at their ends. They can only stretch lengthwise because microfibrils in their walls prevent lateral expansion. Therefore, guard cells buckle out when water enters. Water enters the guard cells after potassium ions (K^+) have entered. Light signals stomata to open, and a high carbon dioxide (CO_2) level may signal stomata to close. Abscisic acid produced by wilting leaves also signals for closure.

In phloem, sieve tubes composed of sieve-tube members aligned end to end form a continuous pipeline from the leaves to the roots. Sieve-tube members have sieve plates through which plasmodesmata (strands of cytoplasm) extend from one to the other. The pressure-flow model of phloem transport proposes that a positive pressure drives phloem contents in sieve tubes. Sucrose is actively transported into sieve tubes—by a chemiosmotic mechanism—at a source, and water follows by osmosis. The resulting increase in pressure creates a flow that moves water and sucrose to a sink. A sink can be at the roots or any other part of the plant that requires organic nutrients.

understanding the terms

beneficial nutrient 457
Casparian strip 460
cohesion-tension model 464
companion cell 462
cuticle 465
essential nutrient 457
girdling 468
guard cell 466

guttation 464
humus 458
hydroponics 457
macronutrient 457
micronutrient 457
mineral 457
mycorrhizae 461
phloem 462
phloem sap 462
phytoremediation 467
pressure-flow model 468
root hair 460
root nodule 461
root pressure 464
sieve tube 462
sieve-tube member 462
sink 469
soil 458
soil erosion 459
soil horizon 459
soil profile 459
source 469
stoma 466
tracheid 462
transpiration 465
vessel element 462
water column 464
water potential 463
xylem 462
xylem sap 462

Match the terms to these definitions:

a. _______________ Explanation for transport in sieve tubes of phloem.
b. _______________ Major layer of soil visible in vertical profile.
c. _______________ Plant's loss of water to the atmosphere, mainly through evaporation at leaf stomata.
d. _______________ Layer of impermeable lignin and suberin bordering four sides of root endodermal cells; causes water and minerals to enter endodermal cells before entering vascular tissue.
e. _______________ Type of plant cell that is found in pairs, with one on each side of a leaf stoma.

reviewing this chapter

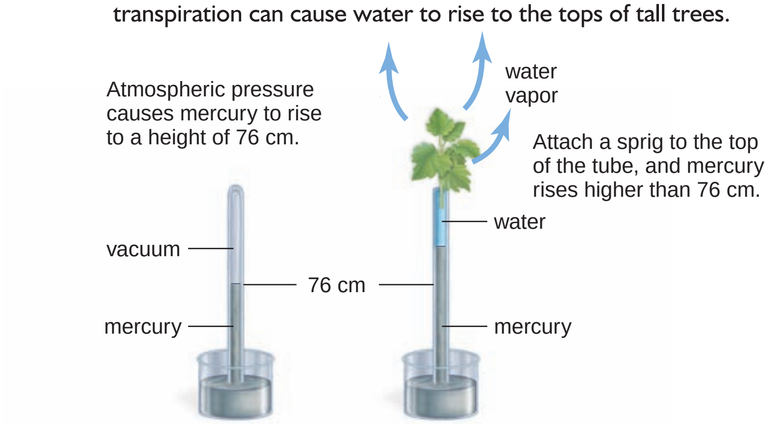
1. Name the elements that make up most of a plant's body. What are essential mineral nutrients and beneficial mineral nutrients? 456–57
2. Briefly describe the use of hydroponics to determine the mineral nutrients of a plant. 457
3. How is soil formed, and how does humus provide nutrients to plants? Describe a generalized soil profile and how a profile is affected by erosion. 458–59
4. Give two pathways by which water and minerals can cross the epidermis and cortex of a root. What feature allows endodermal cells to regulate the entrance of molecules into the vascular cylinder? 460
5. Describe the chemiosmotic mechanism by which mineral ions cross plasma membranes. 460
6. Name two symbiotic relationships that assist plants in taking up minerals and two types of plants that have other means of acquiring nutrients. 460–65
7. A vascular system is adaptive for a land existence. Explain. Describe the composition of a plant's vascular system. 462–63
8. What is root pressure, and why can't it account for the transport of water in xylem? 464
9. Describe and give evidence for the cohesion-tension model of water transport. 464–65
10. Describe the structure of stomata and explain how they can open and close. By what mechanism do guard cells take up potassium (K^+) ions? 466
11. What data are available to show that phloem transports organic compounds? Explain the pressure-flow model of phloem transport. 468–69

testing yourself

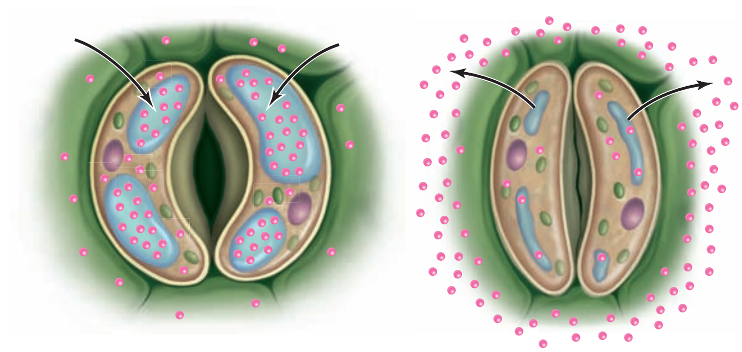
Choose the best answer for each question.

1. Which of these molecules is not a nutrient for plants?
   a. water
   b. carbon dioxide gas
   c. mineral ions
   d. nitrogen gas
   e. None of these are nutrients.
2. Which is a component of soil?
   a. mineral particles
   b. humus
   c. organisms
   d. air and water
   e. All of these are correct.
3. The Casparian strip affects
   a. how water and minerals move into the vascular cylinder.
   b. vascular tissue composition.
   c. how soil particles function.
   d. how organic nutrients move into the vascular cylinder.
   e. Both a and d are correct.
4. Which of these is not a mineral ion?
   a. NO3–
   b. Mg+
   c. CO_2
   d. Al3+
   e. All of these are correct.
5. What role do cohesion and adhesion play in xylem transport?
   a. Like transpiration, they create a tension.
   b. Like root pressure, they create a positive pressure.
   c. Like sugars, they cause water to enter xylem.
   d. They create a continuous water column in xylem.
   e. All of these are correct.
6. The pressure-flow model of phloem transport states that
   a. phloem content always flows from the leaves to the root.
   b. phloem content always flows from the root to the leaves.
   c. water flow brings sucrose from a source to a sink.
   d. water pressure creates a flow of water toward the source.
   e. Both c and d are correct.
7. Root hairs do not play a role in
   a. oxygen uptake.
   b. mineral uptake.
   c. water uptake.
   d. carbon dioxide uptake.
   e. the uptake of any of these.
8. Xylem includes all of these except
   a. companion cells.
   b. vessels.
   c. tracheids.
   d. dead tissue.
9. After sucrose enters sieve tubes,
   a. it is removed by the source.
   b. water follows passively by osmosis.
   c. it is driven by active transport to the source, which is usually the roots.
   d. stomata open so that water flows to the leaves.
   e. All of these are correct.
10. An opening in the leaf that allows gas and water exchange is called
    a. the lenticel.
    b. the hole.
    c. the stoma.
    d. the guard cell.
    e. the accessory cell.

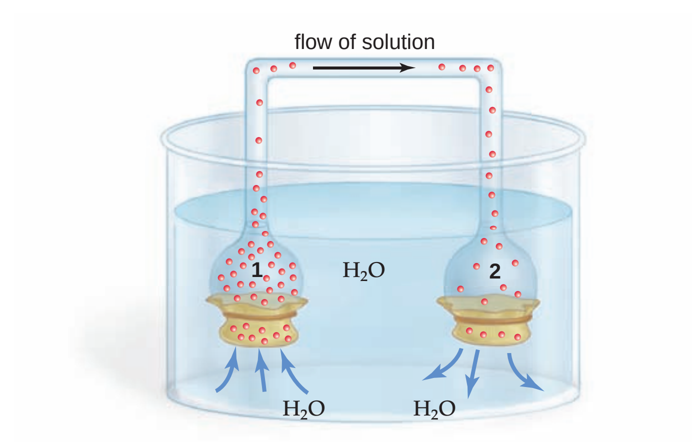
11. What main force drives absorption of water, creates tension, and draws water through the plant?
    a. adhesion
    b. cohesion
    c. tension
    d. transpiration
    e. absorption
12. A nutrient element is considered essential if
    a. plant growth increases with a reduction in the concentration of the element.
    b. plants die in the absence of the element.
    c. plants can substitute a similar element for the missing element with no ill effects.
    d. the element is a positive ion.
13. Humus
    a. supplies nutrients to plants.
    b. is basic in its pH.
    c. is found in the deepest soil horizons.
    d. is inorganic in origin.
14. Which sequence represents the size of soil particles from largest to smallest?
    a. sand, clay, silt
    b. silt, clay, sand
    c. sand, silt, clay
    d. clay, silt, sand
    e. silt, sand, clay
15. Soils rich in which type of mineral particle will have a high water-holding capacity?
    a. sand
    b. silt
    c. clay
    d. All soil particles hold water equally well.
16. Stomata are usually open
    a. at night, when the plant requires a supply of oxygen.
    b. during the day, when the plant requires a supply of carbon dioxide.
    c. day or night if there is excess water in the soil.
    d. during the day, when transpiration occurs.
    e. Both b and d are correct.
17. Why might the water column in tracheids be less susceptible to breakage than in vessels?
    a. Tracheids are more narrow, giving more opportunity for adhesion to play a role in maintaining the water column.
    b. The end walls of tracheids are more slanted than the end walls of vessel elements.
    c. Tracheids receive support from vessel elements, but not vice versa.
    d. All of these are correct.
18. Explain why this experiment supports the hypothesis that transpiration can cause water to rise to the tops of tall trees.



19. Negatively charged clay particles attract
    a. K^+.
    b. NO_3^-.
    c. Ca^+.
    d. Both a and b are correct.
    e. Both a and c are correct.
20. a. Label water (H_2O) and potassium ions (K^+) appropriately in these diagrams. b. What is the role of K^+ in the opening and closing of stomata?



21. Explain why solution flows from the left bulb to the right bulb.



thinking scientifically

1. Using hydroponics, design an experiment to determine if calcium is an essential plant nutrient. State the possible results.
2. *Welwitschia* is a genus of plant that lives in the Namib and Mossamedes deserts in Africa. Annual rainfall averages only 2.5 cm (1 inch) per year. *Welwitschia* plants contain a large number of stomata (22,000 cm^2), which remain closed most of the time. Can you suggest how a large number of stomata would be beneficial to these desert plants?

Biology website

The companion website for *Biology* provides a wealth of information organized and integrated by chapter. You will find practice tests, animations, videos, and much more that will complement your learning and understanding of general biology.

http://www.mhhe.com/maderbiology10

26

Flowering Plants: Control of Growth Responses

the observation that buttercups track the sun as it moves through the sky is a striking example of a flowering plant's ability to respond to environmental stimuli. Other responses to light can take longer than sun tracking because they involve hormones and an alteration in growth. For example, flowering plants will bend toward the light within a few hours because a hormone produced by the growing tip has moved from the sunny side to the shady side of the stem. Hormones also help flowering plants respond to stimuli in a coordinated manner. In the spring, seeds germinate and growth begins if the soil is warm enough to contain liquid water. In the fall, when temperatures drop, shoot- and root-apical growth ceases. Some plants also flower according to the season. The pigment phytochrome is instrumental in detecting the photoperiod and bringing about genetic changes, which determine whether a plant flowers or does not flower.

Plant defenses include physical barriers, chemical toxins, and even mutualistic animals. This chapter discusses the variety of ways flowering plants can respond to their environment, including other organisms.

Time-lapse photograph of a buttercup, *Ranunculus ficaria,* curving toward and tracking a source of light.

concepts

26.1 PLANT HORMONES

- Each class of plant hormones can be associated with specific responses. Even so, some responses are probably influenced by the interaction of more than one hormone. 474
- Auxins bring about a response to both light and gravity and are involved in many other growth responses as well. 475–76
- The most obvious effect of gibberellins is stem elongation between nodes, and this leads to several commercial uses of gibberellins. 476–77
- In tissue culture, the proportion of cytokinins (cause cell divisions) to auxins affects differentiation and development. 477
- Among other effects, abscisic acid helps regulate the closing of stomata, and ethylene causes fruits to ripen. 480–81

26.2 PLANT RESPONSES

- Tropisms are growth responses in plants toward or away from unidirectional stimuli, such as light and gravity. 482–83
- Plants sometimes exhibit circadian rhythms (e.g., closing of stomata) that recur approximately every 24 hours. Plant responses that are controlled by the length of daylight (photoperiod) involve the pigment phytochrome. 484–87
- Plants also respond to the biotic environment with defense mechanisms such as barriers to entry, chemical toxins, systemic mechanisms, and relationships with animals. 488–89

26.1 Plant Hormones

All organisms are capable of responding to environmental stimuli, as when you withdraw your hand from a hot stove. It is adaptive for organisms to respond to stimuli because it leads to their longevity and ultimately to the survival of the species. Flowering plants perceive and react to a variety of environmental stimuli. Some examples include light, gravity, carbon dioxide levels, pathogen infection, drought, and touch. Their responses can be short term, as when stomata open and close in response to light levels, or long term, as when they respond to gravity by the downward growth of the root and the upward growth of the stem.

Although we think of responses in terms of a plant part, the mechanism that brings about a response occurs at the cellular level. In the same manner as animal cells, researchers now know that plant cells utilize signal transduction when they respond to stimuli. Notice in Figure 26.1 that signal transduction involves:

Receptors—proteins activated by a specific signal. Receptors can be located in the plasma membrane, the cytoplasm, the nucleus, or even the endoplasmic reticulum. A receptor that responds to light has a pigment component. Fo example, phytochrome has a region that is sensitive to red light, and phototropin has a region that is sensitive to blue light.

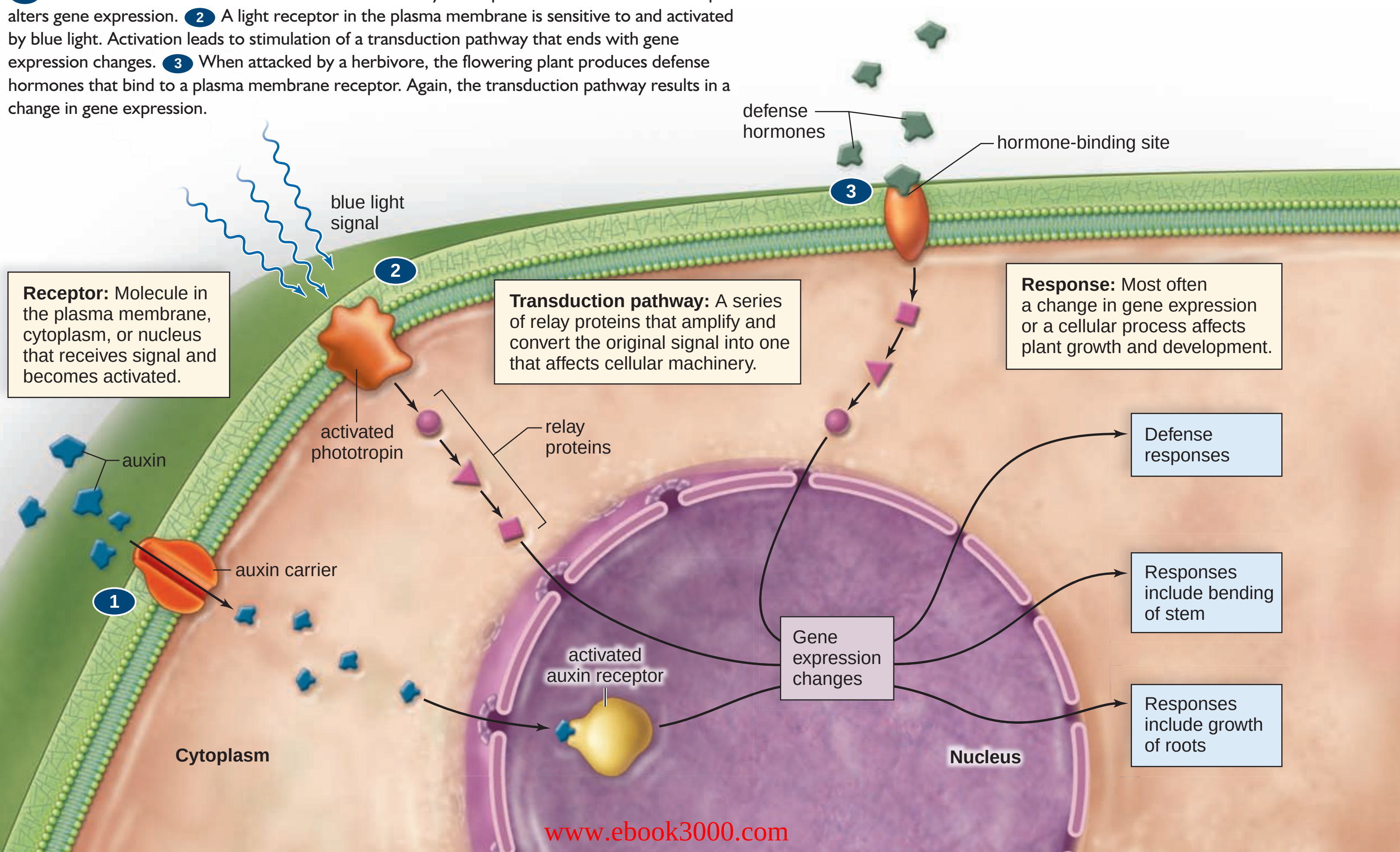
Transduction pathway—series of relay proteins or enzymes that amplify and transform the signal to one understood by the machinery of the cell. In some instances, a stimulated receptor immediately communicates with the transduction pathway, and in other instances, a second messenger, such as Ca^{2+}, initiates the response. As an analogy, consider a mother at work who wants a sitter to fix lunch for her children. The mother (the stimulus) calls home (receptor of cell), and the sitter (the second messenger) fixes lunch (activates transduction pathway).

Cellular response—occurs as a result of the transduction pathway. Very often, the response is either the transcription of particular genes or the end product of an activated metabolic pathway. The cellular response brings about the observed macroscopic response, such as stomata closing or a stem that turns toward the light.

How do hormones fit into this model for the ability of flowering plants to respond to both abiotic and biotic stimuli? Coordination between cells is required for a macroscopic response to become evident. Coordination is often dependent on plant **hormones** [Gk. *hormao,* instigate], chemical signals produced in very low concentrations and active in another part of the organism. Hormones, such as auxin, are synthesized or stored in one part of the plant, but they travel within phloem or from cell to cell in response to the appropriate stimulus.

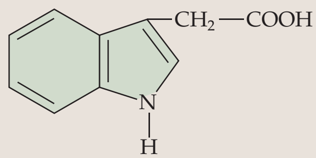
FIGURE 26.1 Signal transduction in plants.

(1) The hormone auxin enters the cell and is received by a receptor in the nucleus. This complex alters gene expression. (2) A light receptor in the plasma membrane is sensitive to and activated by blue light. Activation leads to stimulation of a transduction pathway that ends with gene expression changes. (3) When attacked by a herbivore, the flowering plant produces defense hormones that bind to a plasma membrane receptor. Again, the transduction pathway results in a change in gene expression.



Auxins

Auxins [Gk. *auximos,* promoting growth] are produced in shoot apical meristem and are found in young leaves and in flowers and fruits. The most common naturally occurring auxin is indoleacetic acid (IAA):



Structure of indoleacetic acid (IAA)

Auxins Effect Growth and Development

Auxins affect many aspects of plant growth and development. Auxins, or more simply, auxin is responsible for **apical dominance,** which occurs when the terminal bud produces new growth instead of the axillary buds. When a terminal bud is removed deliberately or accidentally, the nearest axillary buds begin to grow, and the plant branches. Therefore, pruning the top of a flowering plant generally achieves a fuller look. This removes apical dominance and causes more branching of the main body of the plant.

Auxin causes the growth of roots and fruits and prevents the loss of leaves and fruit. The application of an auxin paste to a stem cutting causes adventitious roots to develop more quickly than they would otherwise. Auxin production by seeds promotes the growth of fruit. As long as auxin is concentrated in leaves or fruits rather than in the stem, leaves and fruits do not drop off. Therefore, trees can be sprayed with auxin to keep mature fruit from falling to the ground.

Synthetic auxins are used today in a number of applications. These auxins are sprayed on plants such as tomatoes to induce the development of fruit without pollination. Thus, seedless tomatoes can be commercially developed. Synthetic auxins such as 2,4-D and 2,4,5-T have been used as herbicides to control broadleaf weeds, such as dandelions and other plants. These substances have little effect on grasses. 2,4-D is still used, but 2,4,5-T was banned in 1979 because of its detrimental effects on human and animal life. A mixture of 2,4-D and 2,4,5-T is best known as the defoliant Agent Orange, used in the Vietnam War.

Gravitropism and Phototropism. After gravity has been perceived by a flowering plant, auxin moves to the lower surface of roots and stems. Thereafter, roots curve downward and stems curve upward. Gravitropism is discussed at more length on page 482. The role of auxin in the positive phototropism of stems has been studied for quite some time. The experimental material of choice has been oat seedlings with coleoptiles intact. A **coleoptile** is a protective sheath for the young leaves of the seedling. In 1881, Charles Darwin and his son found that phototropism will not occur if the tip of the seedling is cut off or covered by a black cap. They concluded that some influence that causes curvature is transmitted from the coleoptile tip to the rest of the shoot.

In 1926, Frits W. Went cut off the tips of coleoptiles and placed them on agar (a gelatin-like material). Then he placed an agar block to one side of a tipless coleoptile and found that the shoot would curve away from that side. The bending occurred even though the seedlings were not exposed to light (Fig. 26.2). Went concluded that the agar block contained a chemical that had been produced by the coleoptile tips. This chemical, he decided, had caused the shoots to bend. He named the chemical substance auxin after the Greek word *auximos,* which means promoting growth.

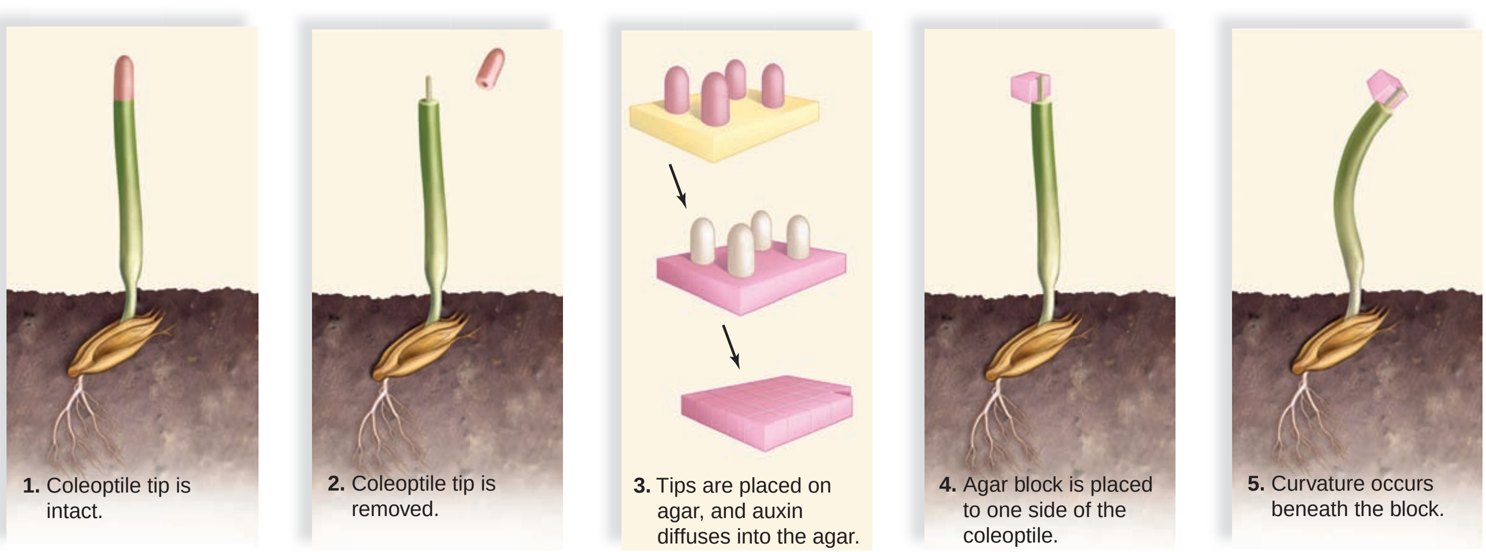
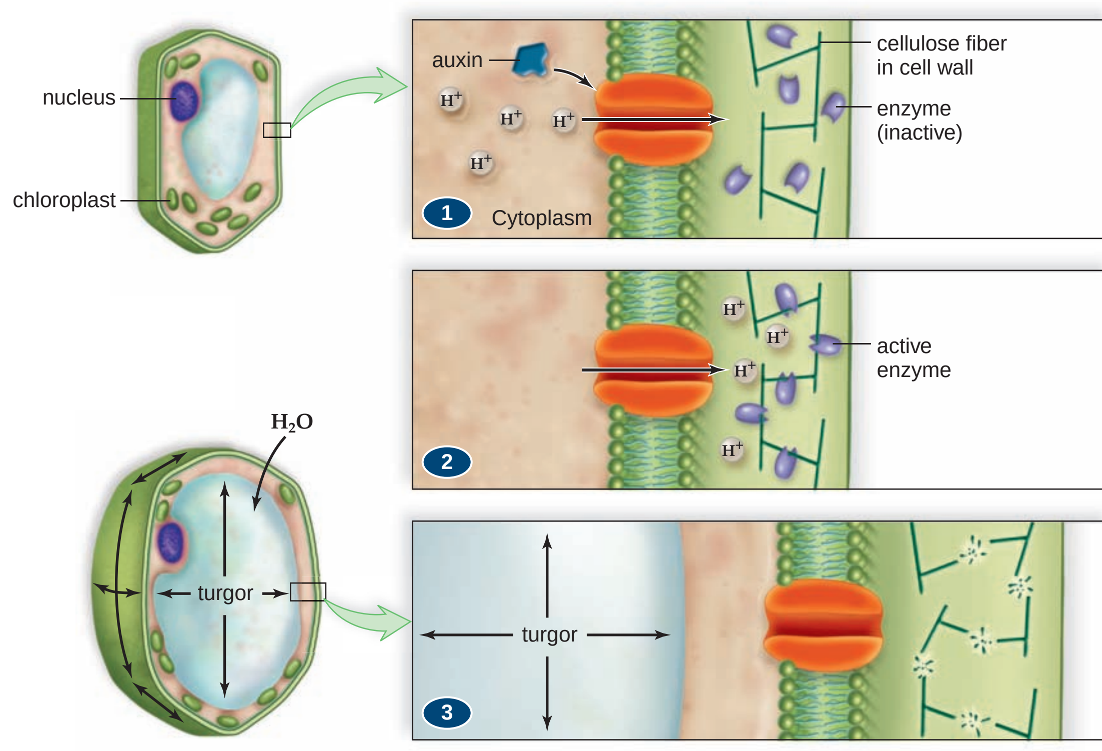


FIGURE 26.2 Auxin and phototropism.

Oat seedlings are protected by a hollow sheath called a coleoptile. After coleoptile tips are removed and placed on agar, a block of the agar to one side of the cut coleoptile can cause it to curve due to the presence of auxin (pink) in the agar. This shows that auxin causes the coleoptile to bend, as it does when exposed to a light source.

FIGURE 26.3 Expansion of the cell wall.

1 Auxin leads to activation of a proton pump and entrance of hydrogen ions in the cell wall.
2 As the pH decreases, enzymes are activated and break down cellulose fibers in the cell wall.
3 Cellulose fibers burst and the cell expands as turgor pressure inside cell increases.

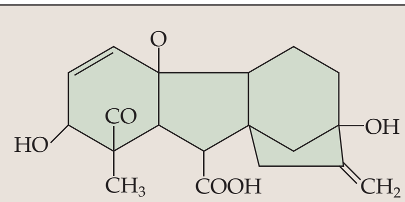


How Auxins Cause Stems to Bend

When a stem is exposed to unidirectional light, auxin moves to the shady side, where it enters the nucleus and attaches to a receptor. The complex leads to he activation of a proton (H^+) pump, and the resulting acidic conditions loosen the cell wall because hydrogen bonds are broken and cellulose fibrils are weakened by enzymatic action. The end result of these activities is elongation of the stem on the shady side so that it bends toward the light (Fig. 26.3).

Gibberellins

We know of about 70 **Gibberellins** [L. *gibbus*, bent], and they differ chemically only slightly. The most common of these is gibberellic acid, GA_3 (the subscript designation distinguishes it from other gibberellins):



Structure of gibberellic acid (GA_3)

Gibberellins Promote Stem Elongation

When gibberellins are applied externally to plants, the most obvious effect is stem elongation (Fig. 26.4*a*). Gibberellins can cause dwarf plants to grow, cabbage plants to become 2 m tall, and bush beans to become pole beans.

Gibberellins were discovered in 1926, the same year that Went performed his classic experiments with auxin. Ewiti Kurosawa, a Japanese scientist, was investigating a fungal disease of rice plants called "foolish seedling disease." The plants elongated too quickly, causing the stem to weaken and the plant to collapse. Kurosawa found that the fungus infecting the plants produced an excess of a chemical he called gibberellin, named after the fungus *Gibberella fujikuroi*. It wasn't until 1956 that gibberellic acid was isolated from a flowering plant rather than from a fungus. Sources of gibberellin in flowering plant parts are young leaves, roots, embryos, seeds, and fruits.

Commercial Uses. Commercially, gibberellins are helpful in a number of ways. Gibberellins induce the growth of plants and increase the size of flowers. Gibberellins have also been successfully used to produce larger seedless grapes. In Figure 26.4b, gibberellins caused an increase in the space between the grapes, allowing them to grow larger. **Dormancy** is a period of time when plant growth is suspended. Gibberellins can break the dormancy of buds and seeds. Thereore,

a. b.

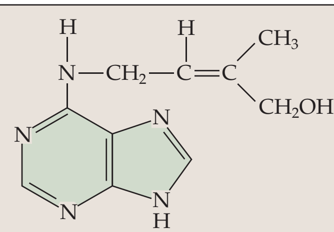
FIGURE 26.4 Gibberellins cause stem elongation.

a. The *Cyclamen* plant on the right was treated with gibberellins; the plant on the left was not treated. **b.** The grapes are larger on the right because gibberellins caused an increase in the space between the grapes, allowing them to grow larger.

application of gibberellins is one way to hasten the development of a flower bud. When Gibberellins break the dormancy of barley seeds, a large, starchy endosperm is broken down into sugars to provide energy for growth. This occurs because amylase, an enzyme that breaks down starch, makes its appearance. It would seem, then, that gibberellins are involved in a transduction pathway that leads to the production of amylase.

Cytokinins

The **cytokinins** [Gk. *kytos*, cell, and *kineo*, move] are derivatives of adenine, one of the purine bases in DNA and RNA. A naturally occurring cytokinin was not isolated until 1967. Because it came from the kernels of maize (*Zea*), it was called zeatin:



Structure of zeatin

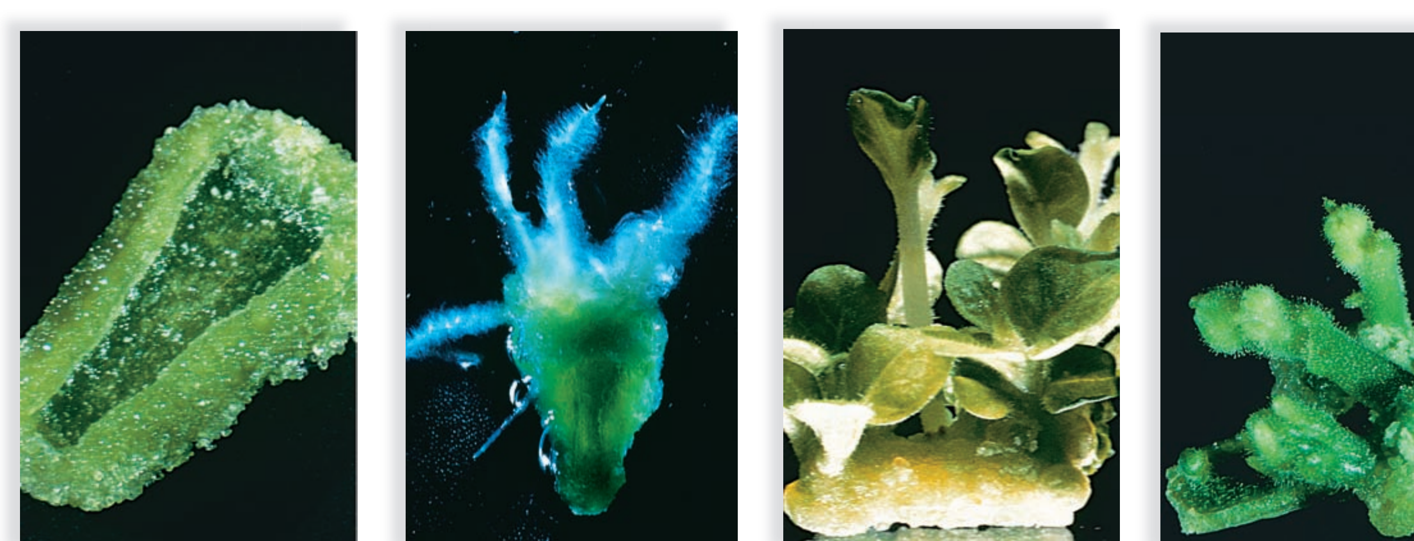
Cytokinins Promote Cell Division

Cytokinins were discovered as a result of attempts to grow plant tissue and organs in culture vessels in the 1940s. It was found that cell division occurred when coconut milk (a liquid endosperm) and yeast extract are added to the culture medium. The effective components were collectively called cytokinins because cytokinesis means cell division. Since then, cytokinins have been isolated from various seed plants, where they occur in the actively dividing tissues of roots and also in seeds and fruits. Cytokinins have been used to prolong the life of flower cuttings as well as vegetables in storage.

Plant tissue culturing is now common practice, and researchers are well aware that the ratio of auxin to cytokinin and the acidity of the culture medium determine whether the plant tissue forms an undifferentiated mass, called a callus, or differentiates to form roots, vegetative shoots, leaves, or floral shoots (Fig. 26.5). These effects illustrate that a plant hormone rarely acts alone, it is the relative concentrations of hormones and their interactions that produce an effect. Researchers have reported that chemicals they call oligosaccharins (chemical fragments released from the cell wall) are also effective in directing differentiation. They hypothesize that auxin and cytokinins are a part of a reception-transduction-response pathway, which leads to the activation of enzymes that release these fragments from the cell wall.

Cytokinins Prevent Senescence

When a plant organ, such as a leaf, loses its natural color, it is most likely undergoing an aging process called **senescence.** During senescence, large molecules within the leaf are broken down and transported to other parts of the plant. Senescence does not always affect the entire plant at once; for example, as some plants grow taller, they naturally lose their lower leaves. It has been found that senescence of leaves can be prevented by the application of cytokinins. Also, axillary buds begin to grow, despite apical dominance, when cytokinin is applied to them.



a. b. c. d.

FIGURE 26.5 Interaction of hormones.

Tissue culture experiments have revealed that auxin and cytokinin interact to affect differentiation during development. **a.** In tissue culture that has the usual amounts of these two hormones, tobacco strips develop into a callus of undifferentiated tissue. **b.** If the ratio of auxin to cytokinin is appropriate, the callus produces roots. **c.** Change the ratio, and vegetative shoots and leaves are produced. **d.** Yet another ratio causes floral shoots. It is now clear that each plant hormone rarely acts alone; it is the relative concentrations of hormones that produce an effect. The modern emphasis is to look for an interplay of hormones when a growth response is studied.

science focus

Arabidopsis Is a Model Organism

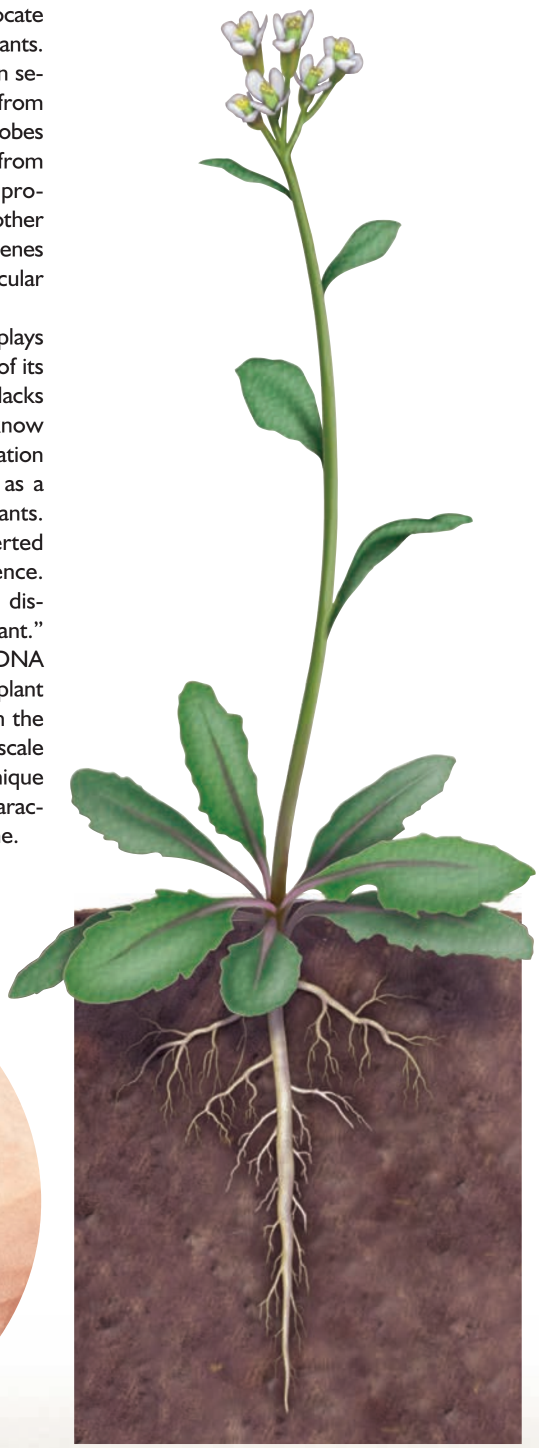
Arabidopsis thaliana is a small flowering plant related to cabbage and mustard plants (Fig. 26A). *Arabidopsis* has no commercial value—in fact, it is a weed! However, it has become a model organism for the study of plant molecular genetics, including signal transduction. Unlike crop plants used formerly, these characteristics make *Arabidopsis* a model organism.

- It is small, so many hundreds of plants can be grown in a small amount of space. *Arabidopsis* consists of a flat rosette of leaves from which grows a short flower stalk.
- Generation time is short. It only takes 5–6 weeks for plants to mature, and each one produces about 10,000 seeds!
- It normally self-pollinates, but it can easily be cross-pollinated. This feature facilitates gene mapping and the production of strains with multiple mutations.
- The number of base pairs in its DNA is relatively small: 125 million base pairs are distributed in 5 chromosomes ($2n = 10$) and 25,500 genes.

In contrast to *Arabidopsis,* crop plants, such as corn, have generation times of at least several months, and they require a great deal of field space for a large number to grow. Crop plants have much larger genomes than *Arabidopsis*. For comparison, the genome sizes for rice (*Oryza sativa*), wheat (*Triticum aestivum*), and corn (*Zea mays*) are 420 million, 16 billion, and 2.5 billion base pairs, respectively. However, crop plants have about the same number of functional genes as *Arabidopsis,* and they occur in the same sequence. Therefore, knowledge of the *Arabidopsis* genome can be used to help locate specific genes in the genomes of other plants. Now that the *Arabidopsis* genome has been sequenced, genes of interest can be cloned from the *Arabidopsis* genome and then used as probes for the isolation of the homologous genes from plants of economic value. Also, cellular processes controlled by a family of genes in other plants require only a single gene or fewer genes in *Arabidopsis.* This, too, facilitates molecular biological studies of the plant.

The creation of *Arabidopsis* mutants plays a significant role in discovering what each of its genes do. For example, if a mutant plant lacks stomata (openings in leaves), then we know that the affected gene influences the formation of stomata. Transformation has emerged as a powerful way to create *Arabidopsis* mutants. The transforming DNA often gets inserted directly within a particular gene sequence. This usually destroys the function of the disrupted gene, resulting in a "knockout mutant." Furthermore, the piece of transformed DNA (T-DNA) that is inserted in the disrupted plant gene can serve as a flag for tracking down the gene by molecular biology methods. Large-scale projects using this T-DNA insertion technique are under way to mutate, identify, and characterize every gene in the *Arabidopsis* genome.

a. *Arabidopsis thaliana*



b. *Arabidopsis thaliana (enlarged drawing)*

FIGURE 26A Overall appearance of *Arabidopsis thaliana*.
Many investigators have turned to this weed as an experimental material to study the actions of genes, including those that control growth and development. **a.** *Photograph of actual plant.* **b.** *Enlarged drawing.*

Researchers have discovered three classes of genes that are essential to normal floral pattern formation. These are homeotic genes because they cause sepals, petals, stamens, or carpels to appear in place of one another (Fig. 26B, *top*). Triple mutants that lack all three types of genetic activities have flowers that consist entirely of leaves arranged in whorls. And a mutation of a regulatory gene results in flowers that have three whorls of petals. These floral-organ-identity genes appear to be regulated by transcription factors that are expressed and required for extended periods.

The application of *Arabidopsis* genetics to other plants has been shown. For example, one of the mutant genes that alters the development of flowers has been cloned and reintroduced into tobacco plants, where, as expected, it caused sepals and stamens to appear where petals would ordinarily be. The investigators commented that knowledge about the development of flowers in *Arabidopsis* can have far-ranging applications. It will undoubtedly lead someday to more productive crops.

A study of the *Arabidopsis* genome will undoubtedly promote plant molecular genetics in general. And because *Arabidopsis* has been found to be a model organism, its genetics is expected to apply to humans, just as Mendel's laws were discovered by working with pea plants. It's far easier to study signal transduction in *Arabidopsis* cells than in human cells.

FIGURE 26B *Arabidopsis* mutants.
Creation of flower mutants (top) and other types of mutants has led to a knowledge of how signal transduction occurs in plant cells. A modern investigator makes use of a computer to analyze data.

Arabidopsis flower

Mutated flower

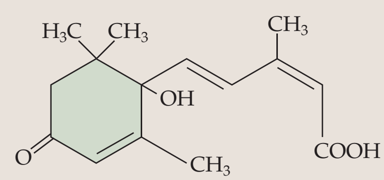
Mutated flower

A flat of *Arabidopsis*

Lab

Abscisic Acid

Abscisic acid (ABA) is produced by any "green tissue" (that contains chloroplasts). ABA is also produced in monocot endosperm and roots, where it is derived from carotenoid pigments:



Structure of abscisic acid (ABA)

Abscisic acid is sometimes called the stress hormone because it initiates and maintains seed and bud dormancy and brings about the closure of stomata. It was once believed that ABA functioned in **abscission**, the dropping of leaves, fruits, and flowers from a plant. But although the external application of ABA promotes abscission, this hormone is no longer believed to function naturally in this process. Instead, the hormone ethylene seems to bring about abscission.

ABA Promotes Dormancy

Recall that dormancy is a period of low metabolic activity and arrested growth. Dormancy occurs when a plant organ readies itself for adverse conditions by ceasing to grow (even though conditions at the time may be favorable for growth). For example, it is believed that ABA moves from leaves to vegetative buds in the fall, and thereafter these buds are converted to winter buds. A winter bud is covered by thick, hardened scales (Fig. 26.6). A reduction in the level of ABA and an increase in the level of gibberellins are believed to break seed and bud dormancy. Then seeds germinate, and buds send forth leaves. In Figure 26.7, corn kernels have begun to germinate on the developing cob because this maize mutant is deficient in ABA. Abscisic acid is needed to maintain the dormancy of seeds.

FIGURE 26.6
Dormancy and winter buds.
Abscisic acid promotes the formation of winter buds.

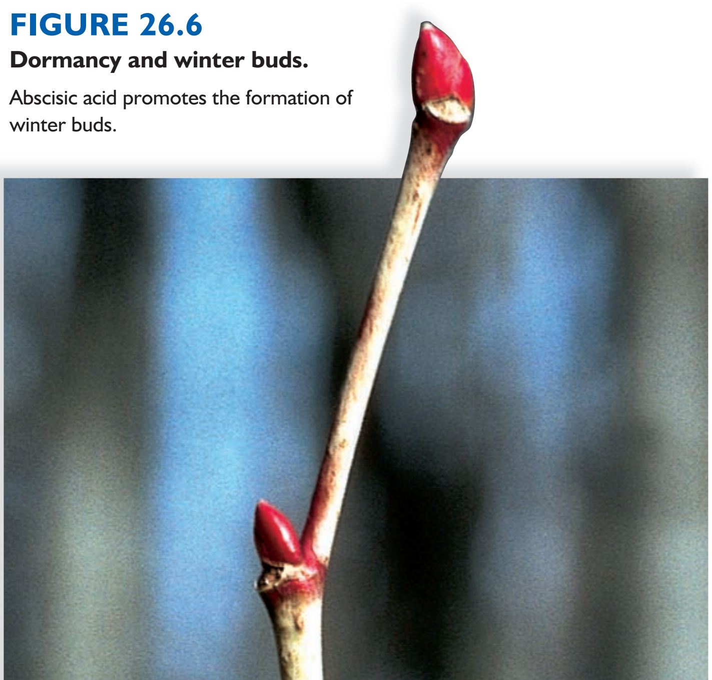


FIGURE 26.7 Dormancy and germination.
Corn kernels start to germinate on the cob (see arrows) due to low abscisic acid.

ABA Closes Stomata

The reception of abscisic acid brings about the closing of stomata when a plant is under water stress, as described in Figure 26.8. Investigators have also found that ABA induces rapid depolymerization of actin filaments and formation of a new type of actin that is randomly oriented throughout the cell. This change in actin organization may also be part of the transduction pathways involved in stomata closure.

Ethylene

Ethylene ($H_2C = CH_2$) is a gas formed from the amino acid methionine. This hormone is involved in abscission and the ripening of fruits.

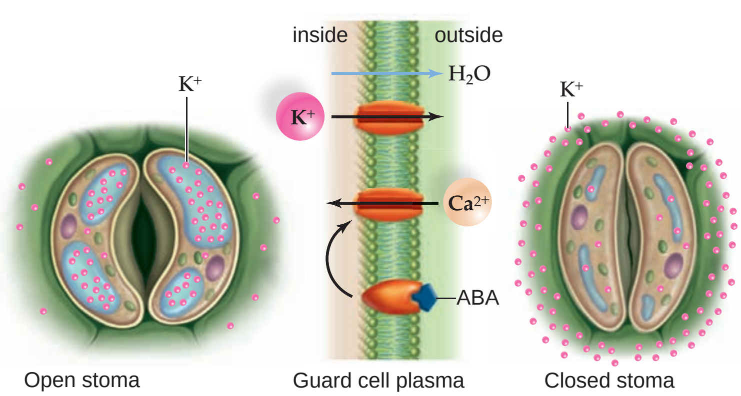


FIGURE 26.8 Abscisic acid promotes closure of stomata.
The stoma is open (*left*). When ABA (the first messenger) binds to its receptor in the guard cell plasma membrane, the second messenger (Ca^{2+}) enters (*middle*). Now, K^+ channels open, and K^+ exits the guard cells. After K^+ exits, so does water. The stoma closes (*right*).

Ethylene Causes Abscission

The absence of auxin, and perhaps gibberellin, probably initiates abscission. But once abscission has begun, ethylene stimulates certain enzymes, such as cellulase, which helps cause leaf, fruit, or flower drop. In Figure 26.9, a ripe apple, which gives off ethylene, is under the bell jar on the right, but not under the bell jar on the left. As a result, only the holly plant on the right loses it leaves.

Ethylene Ripens Fruit

In the early 1900s, it was common practice to prepare citrus fruits for market by placing them in a room with a kerosene stove. Only later did researchers realize that an incomplete combustion product of kerosene, namely ethylene, ripens fruit. It does so by increasing the activity of enzymes that soften fruits. For example, it stimulates the production of cellulase, which weakens plant cell walls. It also promotes the activity of enzymes that produce the flavor and smell of ripened fruits. And it breaks down chlorophyll, inducing the color changes associated with fruit ripening.

Ethylene moves freely through a plant by diffusion, and because it is a gas, ethylene also moves freely through the air. That is why a barrel of ripening apples can induce ripening of a bunch of bananas some distance away. Ethylene is released at the site of a plant wound due to physical damage or infection (which is why one rotten apple spoils the whole bushel).

The use of ethylene in agriculture is extensive. It is used to hasten the ripening of green fruits, such as melons and honeydews, and is also applied to citrus fruits to attain pleasing colors before marketing. Normally, tomatoes ripen on the vine because the plants produce ethylene. Today, tomato plants can be genetically modified to not produce ethylene. This facilitates shipping because green tomatoes are not subject to as much damage (Fig. 26.10). Once the tomatoes have arrived at their destination, they can be exposed to ethylene so that they ripen.

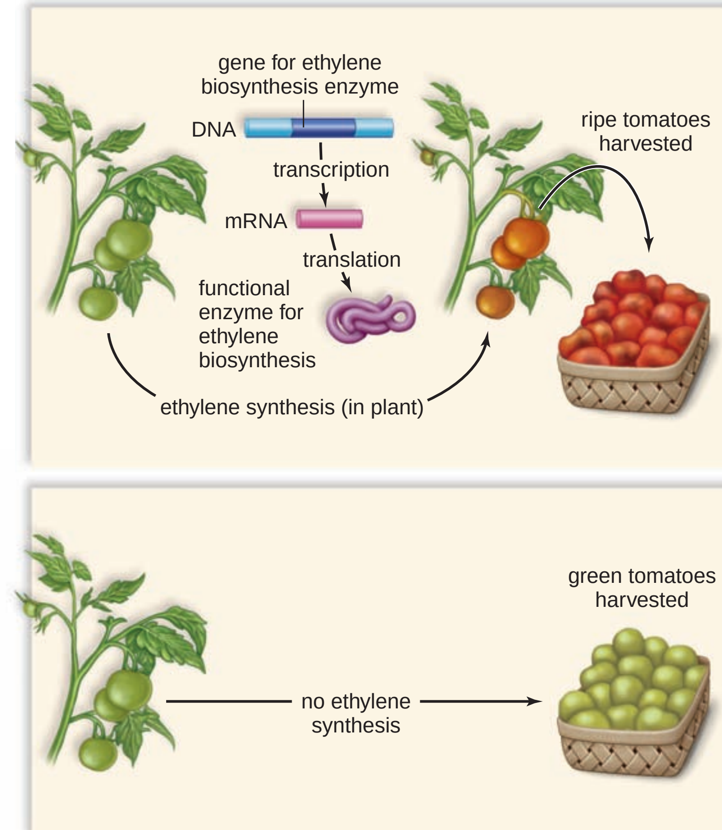


FIGURE 26.10 Ethylene and fruit ripening.

Wild-type tomatoes (*above*) ripen on the vine after producing ethylene. Tomatoes (*below*) are genetically modified to produce no ethylene and stay green for shipping.

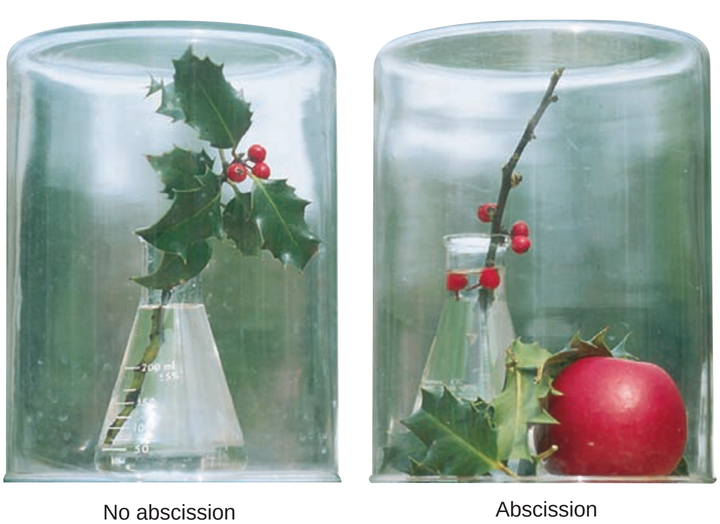


FIGURE 26.9 Ethylene and abscission.

Normally, there is no abscission when a holly twig is placed under a glass jar for a week. When an ethylene-producing ripe apple is also under the jar, abscission of the holly leaves occurs.

Other Effects of Ethylene

Ethylene is involved in axillary bud inhibition. Auxin, transported down from the apical meristem of the stem, stimulates the production of ethylene, and this hormone suppresses axillary bud development. Ethylene also suppresses stem and root elongation, even in the presence of other hormones.

This completes our discussion of plant hormones. The next part of the chapter explores plant responses to environmental stimuli.

Check Your Progress 26.1

1. In general, how do hormones assist in bringing about responses to stimuli?
2. If you wanted to increase the size of a plant organ, you might apply gibberellins and cytokinins. Explain.
3. **a.** Why is abscisic acid sometimes referred to as an inhibitory hormone? **b.** What hormone has the opposite effect of ABA on seed and bud dormancy?

26.2 Plant Responses

Animals often quickly respond to a stimulus by an appropriate behavior. Presented with a nipple, a newborn automatically begins sucking. While animals are apt to change their location, plants, which are rooted in one place, change their growth pattern in response to a stimulus. The events in a tree's life, and even the history of the Earth's climate, can be determined by studying the growth pattern of tree rings!

Tropisms

Growth toward or away from a unidirectional stimulus is called a **tropism** [Gk. *tropos,* turning]. Unidirectional means that the stimulus is coming from only one direction instead of multiple directions. Growth toward a stimulus is called a positive tropism, and growth away from a stimulus is called a negative tropism. Tropisms are due to differential growth—one side of an organ elongates faster than the other, and the result is a curving toward or away from the stimulus. A number of tropisms have been observed in plants. The three best-known tropisms are gravitropism (gravity), phototropism (light), and thigmotropism (touch).

> Gravitropism: a movement in response to gravity
> Phototropism: a movement in response to a light stimulus
> Thigmotropism: a movement in response to touch

Several other tropisms include chemotropism (chemicals), traumotropism (trauma), skototropism (darkness), and aerotropism (oxygen).

What mechanism permits flowering plants to respond to stimuli? When humans respond to light, the stimulus is first received by a pigment in the retina at the back of the eyes, and then nerve impulses are generated that go to the brain. Only then do humans perform an appropriate behavior. As shown in Figure 26.1, the first step toward a response is *reception* of the stimulus. The next step is *transduction,* meaning that the stimulus has been changed into a form that is meaningful to the organism. (In our example, the light stimulus was changed to nerve impulses.) Finally, there is a *response* by the organism to light. Animals and plants go through this same sequence of events when they respond to a stimulus.

Gravitropism

As is expected from our previous discussion on page 475, when an upright plant is placed on its side, the stem displays negative **gravitropism** [L. *gravis,* heavy; Gk. *tropos,* turning] because it grows upward, opposite the pull of gravity (Fig. 26.11*a*). Again, Charles Darwin and his son were among the first to say that roots, in contrast to stems, show positive gravitropism (Fig. 26.11*b*). Further, they discovered that if the root cap is removed, roots no longer respond to gravity. Later investigators came up with an explanation. Root cap cells contain sensors called **statoliths,** which are starch grains located within amyloplasts, a type of plastid (Fig. 26.11*c*). Due to gravity, the amyloplasts settle to a lower

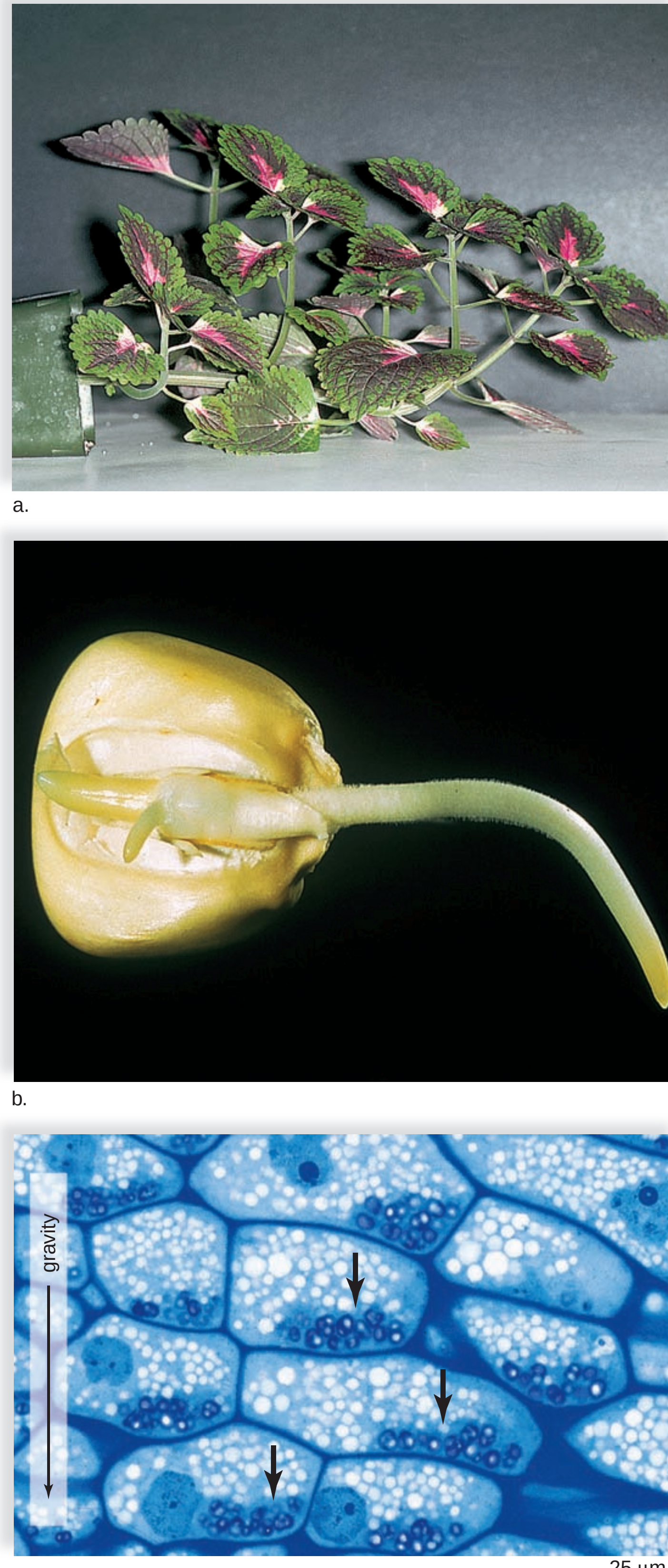


FIGURE 26.11 Gravitropism.

a. Negative gravitropism of the stem of a *Coleus* plant 24 hours after the plant was placed on its side. **b.** Positive gravitropism of a root emerging from a corn kernel. **c.** Sedimentation of statoliths (see arrows), which are amyloplasts containing starch granules, is thought to explain how roots perceive gravity.