Evaporation of water in a leaf creates negative pressure or tension in the xylem, which literally pulls water up the stem from the roots. The strong pressure gradient between leaves and the atmosphere cannot be explained by evaporation alone. As water diffuses from the xylem of tiny, branching veins in a leaf, it forms a thin film along mesophyll cell walls. If the surface of the air–water interface is fairly smooth (flat), the water potential is higher than if the surface becomes rippled.

The driving force for transpiration is the humidity gradient from 100% relative humidity inside the leaf to much less than 100% relative humidity outside the stomata. Molecules diffusing from the xylem replace evaporating water molecules. As the rate of evaporation increases, diffusion cannot replace all the water molecules. The film is pulled back into the cell walls and becomes rippled rather than smooth. The change increases the pull on the column of water in the xylem, and concurrently increases the rate of transpiration.

Vessels and tracheids accommodate bulk flow

Water has an inherent **tensile strength** that arises from the cohesion of its molecules, their tendency to form hydrogen bonds with one another (see chapter 2). These two factors are the basis of the cohesion–tension theory of the bulk flow of water in the xylem. The tensile strength of a column of water varies inversely with the diameter of the column; that is, the smaller the diameter of the column, the greater the tensile strength. Because plant tracheids and vessels are tiny in diameter, the cohesive force of water is stronger than the pull of gravity. The water molecules also adhere to the sides of the tracheid or xylem vessels, further stabilizing the long column of water.

Given that a narrower column of water has greater tensile strength, it is intriguing that vessels, having diameters that are larger than tracheids, are found in so many plants. The difference in diameter has a larger effect on the mass of water in the column than on the tensile strength of the column. The volume of liquid moving in a column per second is proportional to r^4, where r is the radius of the column, at constant pressure. A twofold increase in radius would result in a 16-fold increase in the volume of liquid moving through the column. Given equal cross-sectional areas of xylem, a plant with larger-diameter vessels can move more water up its stems than a plant with narrower tracheids.

Inquiry question

? **If a mutation increased the radius of a xylem vessel threefold, how would the movement of water through the plant be affected?**

The effect of cavitation

Tensile strength depends on the continuity of the water column; air bubbles introduced into the column when a vessel is broken or cut would cause the continuity and the cohesion to fail. A gas-filled bubble can expand and block the tracheid or vessel, a process called **cavitation**. Cavitation stops water transport and can lead to dehydration and death of part or all of a plant (figure 38.10).

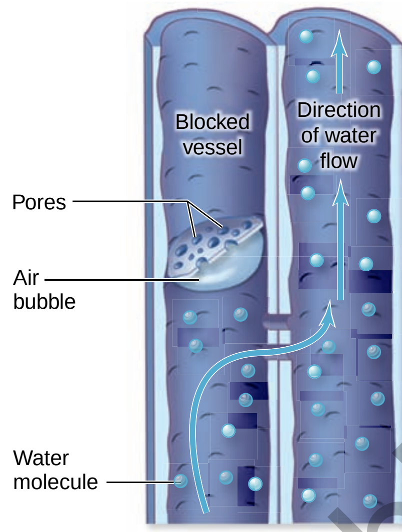


Figure 38.10 Cavitation. An air bubble can break the tensile strength of the water column. Bubbles are larger than pits and can block transport to the next tracheid or vessel. Water drains to surrounding tracheids or vessels.

Anatomical adaptations can compensate for the problem of cavitation, including the presence of alternative pathways that can be used if one path is blocked. Individual tracheids and vessel members are connected to other tracheids or vessels by pits in their walls, and air bubbles are generally larger than these openings. In this way, bubbles cannot pass through the pits to further block transport. Freezing or deformation of cells can also cause small bubbles of air to form within xylem cells, especially with seasonal temperature changes. Cavitation is one reason older xylem often stops conducting water.

Mineral transport

Tracheids and vessels are essential for the bulk transport of minerals. Ultimately, the minerals that are actively transported into the roots are removed and relocated through the xylem to other metabolically active parts of the plant. Phosphorus, potassium, nitrogen, and sometimes iron may be abundant in the xylem during certain seasons. In many plants, this pattern of ionic concentration helps conserve these essential nutrients, which may move from mature deciduous parts such as leaves and twigs to areas of active growth, namely meristem regions.

Keep in mind that minerals that are relocated via the xylem must move with the generally upward flow through the xylem. Not all minerals can reenter the xylem conduit once they leave. Calcium, an essential nutrient, cannot be transported elsewhere once it has been deposited in a particular plant part. But some other nutrients can be transported in the phloem.

Learning Outcomes Review 38.3

Guttation occurs when root pressure is high but transpiration is low. It commonly occurs at night in temperate climates when the air is cool and the humidity is high. Water's high tensile strength results from the cohesiveness of water molecules for each other and adhesiveness to the walls of cells in the xylem; both of these are effects of hydrogen bonding. Cavitation, which stops water movement, results from a bubble in the water transport system that breaks cohesion.

- ***What controls the rate of transpiration when the humidity is low?***
- ***What happens to minerals once they leave the xylem?***

38.4 The Rate of Transpiration

Learning Outcomes

1. *Explain the process by which guard cells regulate the opening of stomata.*
2. *Name the two conflicting requirements that influence opening and closing of stomata.*

More than 90% of the water taken in by the roots of a plant is ultimately lost to the atmosphere. Water moves from the tips of veins into mesophyll cells, and from the surface of these cells it evaporates into pockets of air in the leaf. As discussed in chapter 36, these intercellular spaces are in contact with the air outside the leaf by way of the stomata.

Stomata open and close to balance H_2O and CO_2 needs

Water is essential for plant metabolism, but it is continuously being lost to the atmosphere. At the same time, photosynthesis requires a supply of CO_2 entering the chlorenchyma cells from the atmosphere. Plants therefore face two somewhat conflicting requirements: the need to minimize the loss of water to the atmosphere and the need to admit carbon dioxide. Structural features such as stomata and the cuticle have evolved in response to one or both of these requirements.

The rate of transpiration depends on weather conditions, including humidity and the time of day. As stated earlier, transpiration from the leaves decreases at night, when stomata are closed and the vapor pressure gradient between the leaf and the atmosphere is less. During the day, sunlight increases the temperature of the leaf, while transpiration cools the leaf through evaporative cooling.

On a short-term basis, closing the stomata can control water loss. This occurs in many plants when they are subjected to water stress. But the stomata must be open at least part of the time so that CO_2 can enter. As CO_2 enters the intercellular spaces, it dissolves in water before entering the plant's cells where it is used in photosynthesis. The gas dissolves mainly in water on the walls of the intercellular spaces below the stomata. The continuous stream of water that reaches the leaves from the roots keeps these walls moist.

Turgor pressure in guard cells causes stomata to open and close

The two sausage-shaped guard cells on each side of a stoma stand out from other epidermal cells not only because of their shape, but also because they are the only epidermal cells containing chloroplasts. Their distinctive wall construction, which is thicker on the inside and thinner elsewhere, results in a bulging out and bowing when they become turgid.

You can make a model of this for yourself by taking two elongated balloons, tying the closed ends together, and inflating both balloons slightly. When you hold the two open ends together, there should be very little space between the two balloons. Now wrap duct tape around both balloons as shown in figure 38.11 (without releasing any air) and inflate each one a bit more. Hold the open ends together again. You should now be holding a roughly doughnut-shaped pair of "guard cells" with a "stoma" in the middle. Real guard cells rely on the influx and efflux of water, rather than air, to open and shut.

Turgor in guard cells results from the active uptake of potassium (K^+), chloride (Cl^-), and malate. As solute concentration increases, water potential decreases in the guard cells, and water enters osmotically. As a result, these cells accumulate water and become turgid, opening the stomata (figure 38.12). The energy required to move the ions across the guard cell membranes comes from the ATP-driven H^+ pump shown in figure 38.1.

The guard cells of many plant species regularly become turgid in the morning, when photosynthesis occurs, and lose turgor in the evening, regardless of the availability of water. During the course of a day, sucrose accumulates in the photosynthetic guard cells. The active pumping of sucrose out of guard cells in the evening may lead to loss of turgor and close the guard cell.

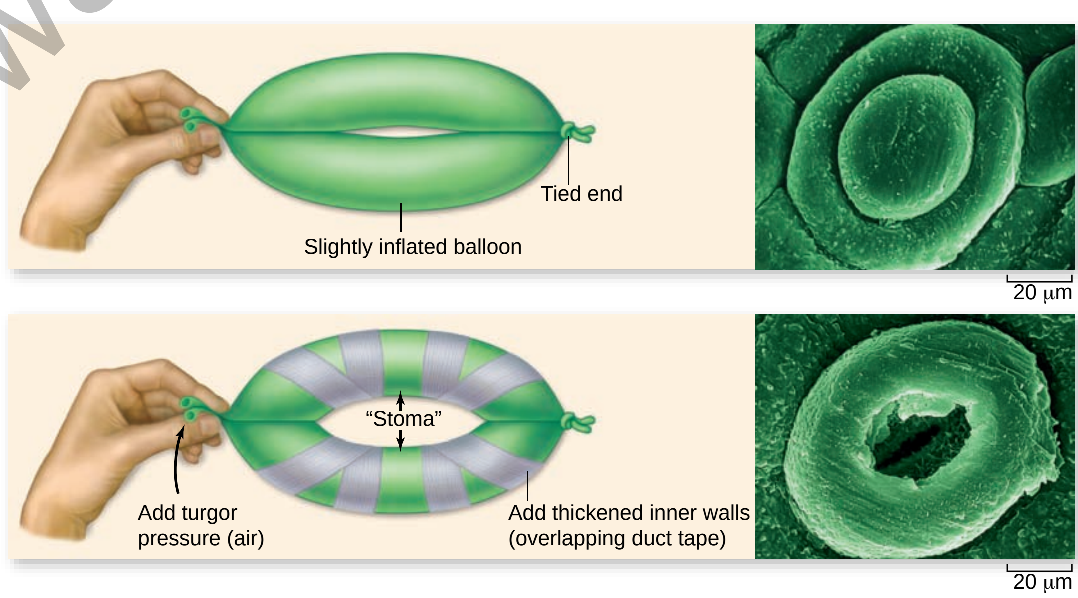


Figure 38.11 Unequal cell wall thickenings on guard cells result in the opening of stomata when the guard cells expand.

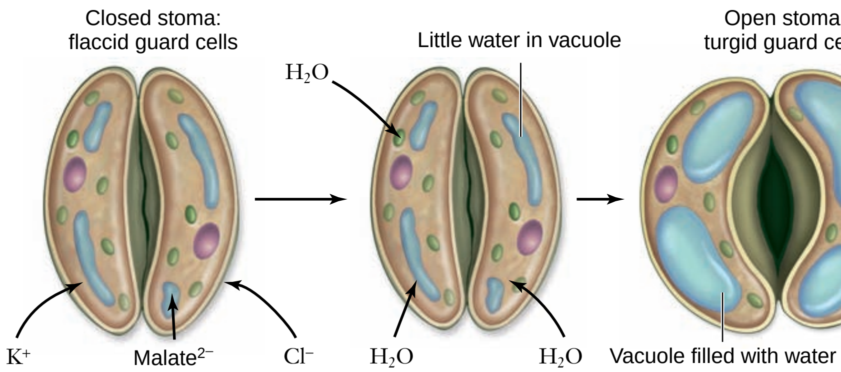


Figure 38.12 How a stoma opens. When H+ ions are pumped from guard cells, K+ and Cl- ions move in, and the guard cell turgor pressure increases as water enters by osmosis. The increased turgor pressure causes the guard cells to bulge, with the thick walls on the inner side causing each guard cell to bow outward, thereby opening the stoma.

Environmental factors affect transpiration rates

Transpiration rates increase with temperature and wind velocity because water molecules evaporate more quickly. As humidity increases, the water potential difference between the leaf and the atmosphere decreases, but even at 95% relative humidity in the atmosphere, the vapor pressure gradient can sustain full transpiration. On a catastrophic level, when a whole plant wilts because insufficient water is available, the guard cells may lose turgor, and as a result, the stomata may close. Fluctuations in transpiration rate are tempered by opening or closing stomata.

Experimental evidence has indicated that several pathways regulate stomatal opening and closing. **Abscisic acid (ABA),** a plant hormone discussed in chapter 41, plays a primary role in allowing K^+ to pass rapidly out of guard cells, causing the stomata to close in response to drought. ABA binds to receptor sites in the plasma membranes of guard cells, triggering a signaling pathway that opens K^+, Cl^-, and malate ion channels. Turgor pressure decreases as water loss follows, and the guard cells close (figure 38.13).

CO_2 concentration, light, and temperature also affect stomatal opening. When CO_2 concentrations are high, the guard cells of many plant species are triggered to decrease the stomatal opening. Additional CO_2 is not needed at such times, and water is conserved when the guard cells are closed.

Blue light regulates stomatal opening. This helps increase turgor to open the stomata when sunlight increases the evaporative cooling demands. K^+ transport against a concentration gradient is promoted by light. Blue light in particular triggers proton (H^+) transport, creating a proton gradient that drives the opening of K^+ channels.

The stomata may close when the temperature exceeds 30° to 34°C and water relations are unfavorable. To ensure sufficient gas exchange, these stomata open when it is dark and the temperature has dropped. Some plants are able to collect CO_2 at night in a modified form to be utilized in photosynthesis during daylight hours. In chapter 9, you learned about Crassulacean acid metabolism (CAM), which occurs in succulent plants such as cacti. In this process, stomata open and CO_2 is taken in at night and stored in organic compounds. These compounds are decarboxylated during the day, providing a source of CO_2 for fixation when stomata are closed. CAM plants are able to conserve water in dry environments.

Learning Outcomes Review 38.4

When guard cells of the stomata actively take up ions, their water potential decreases and they take up water by osmosis. When they become turgid they change shape, creating an opening in the stoma. Stomata close when a plant is under water stress, but they open when carbon dioxide is needed and transpiration does not cause excess water loss. Transpiration rates increase with high wind velocity, high temperatures, and low humidity.

- ***Why is it critical that carbon dioxide dissolve in water upon entering plants?***

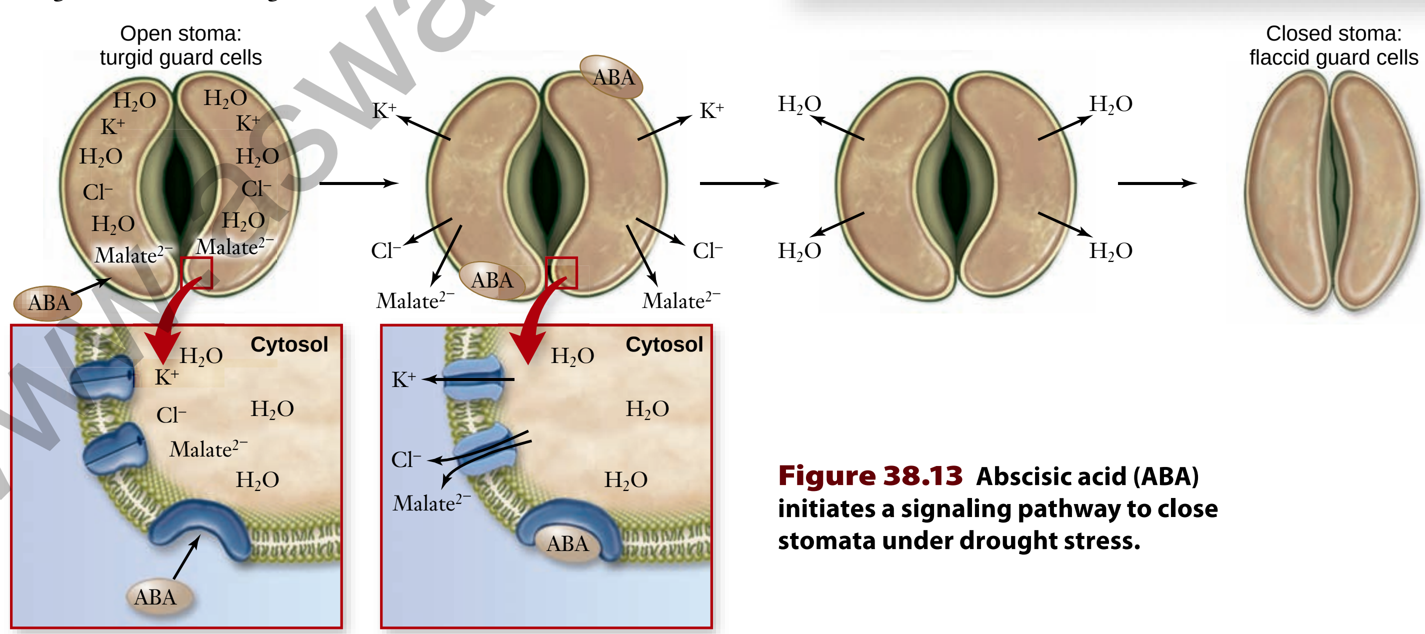


Figure 38.13 Abscisic acid (ABA) initiates a signaling pathway to close stomata under drought stress.

38.5 Water-Stress Responses

Learning Outcomes

1. *List three drought adaptations in plants.*
2. *Describe the negative effects of flooding on plant growth.*
3. *Outline three ways in which a plant may deal with a salty environment.*

Because plants cannot simply move on when water availability or salt concentrations change, adaptations have evolved to allow plants to cope with environmental fluctuations, including drought, flooding, and changing salinity.

Plant adaptations to drought include strategies to limit water loss

Many mechanisms for controlling the rate of water loss have evolved in plants. Regulating the opening and closing of stomata provides an immediate response. Morphological adaptations provide longer term solutions to drought periods. For example, for some plants dormancy occurs during dry times of the year; another mechanism involves loss of leaves, limiting transpiration. Deciduous plants are common in areas that periodically experience severe drought. In a broad sense, annual plants conserve water when conditions are unfavorable simply by going into "dormancy" as seeds.

Thick, hard leaves often with relatively few stomata—and frequently with stomata only on the lower side of the leaf—lose water far more slowly than large, pliable leaves with abundant stomata. Leaves covered with masses of wooly-looking trichomes (hairs) reflect more sunlight and thereby reduce the heat load on the leaf and the demand for transpiration for evaporative cooling.

Plants in arid or semiarid habitats often have their stomata in crypts or pits in the leaf surface (figure 38.14). Within these depressions, the water surface tensions are altered, reducing the rate of water loss.

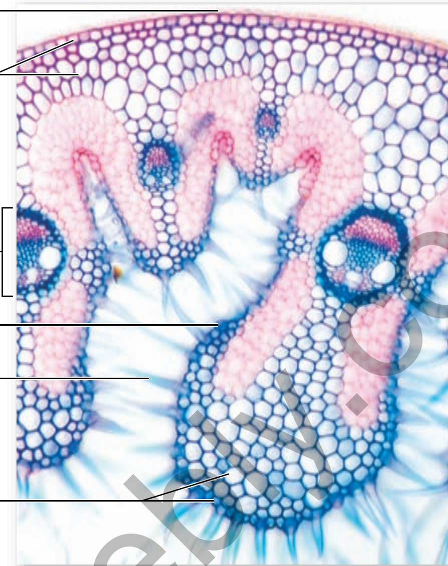


Figure 38.14 Anatomical protection from drought in leaves. Deeply embedded stomata, extensive trichomes, and multiple layers of epidermis minimize water loss in this leaf, shown in cross section.

Plant responses to flooding include short-term hormonal changes and long-term adaptations

Plants can also receive too much water, in which case they ultimately "drown." Flooding rapidly depletes available oxygen in the soil and interferes with the transport of minerals and carbohydrates in the roots. Abnormal growth often results. Hormone levels change in flooded plants; ethylene, a hormone associated with suppression of root elongation, increases, while gibberellins and cytokinins, which enhance growth of new roots, usually decrease (see chapter 41). Hormonal changes contribute to the abnormal growth patterns.

Oxygen deprivation is among the most significant problems because it leads to decreased cellular respiration. Standing water has much less oxygen than moving water. Generally, standing-water flooding is more harmful to a plant (riptides excluded). Flooding that occurs when a plant is dormant is much less harmful than flooding when it is growing actively.

Physical changes that occur in the roots as a result of oxygen deprivation may halt the flow of water through the plant. Paradoxically, even though the roots of a plant may be standing in water, its leaves may be drying out. Plants can respond to flooded conditions by forming larger lenticels (which facilitate gas exchange) and adventitious roots that reach above flood level for gas exchange.

Whereas some plants survive occasional flooding, others have adapted to living in fresh water. One of the most frequent adaptations among plants to growing in water is the formation of **aerenchyma,** loose parenchymal tissue with large air spaces in it (figure 38.15). Aerenchyma is very prominent in water lilies and many other aquatic plants. Oxygen may be transported from the parts of the plant above water to those below by way of passages in the aerenchyma. This supply of oxygen allows oxidative respiration to take place even in the submerged portions of the plant.

Some plants normally form aerenchyma, whereas others, subject to periodic flooding, can form it when necessary. In corn, increased ethylene due to flooding induces aerenchyma formation.

Plant adaptations to high salt concentration include elimination methods

The algal ancestors of plants adapted to a freshwater environment from a saltwater environment before the "move" onto land. This adaptation involved a major change in controlling salt balance.

Growth in salt water

Plants such as mangroves that grow in areas normally flooded with salt water must not only provide a supply of oxygen to their submerged parts, but also control their salt balance. The salt must be excluded, actively secreted, or diluted as it enters. The black mangrove *(Avicennia germinans)* has long, spongy, air-filled roots that emerge above the mud. These roots, called

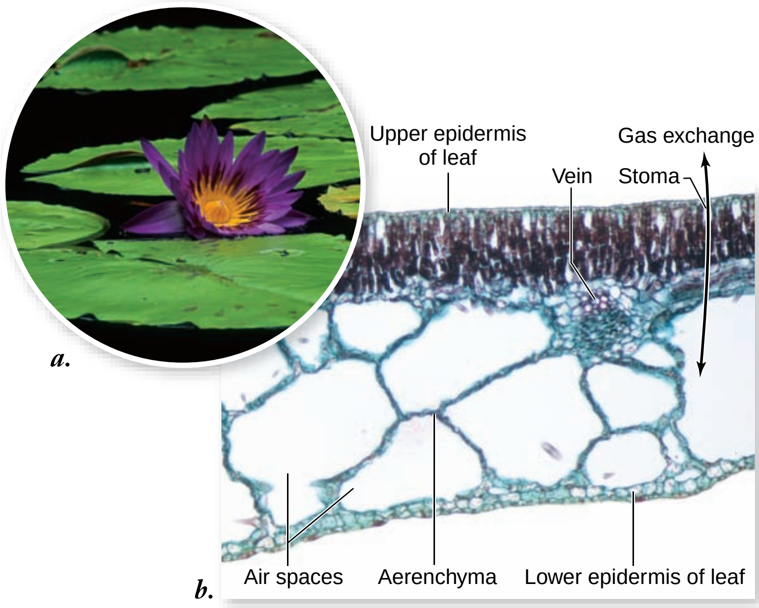


Figure 38.15 Aerenchyma. This tissue facilitates gas exchange in aquatic plants. ***a.*** Water lilies float on the surface of ponds, collecting oxygen and then transporting it to submerged portions of the plant. ***b.*** Large air spaces in the leaves of the water lily add buoyancy. The specialized parenchyma tissue that forms these open spaces is called aerenchyma. Gas exchange occurs through stomata found only on the upper surface of the leaf.

pneumatophores (see chapter 36), have large lenticels on their above-water portions through which oxygen enters; it is then transported to the submerged roots (figure 38.16). In addition, the succulent leaves of some mangrove species contain large quantities of water, which dilute the salt that reaches them. Many plants that grow in such conditions also either secrete large quantities of salt or block salt uptake at the root level.

Growth in saline soil

Soil salinity is increasing, often caused by salt accumulation from irrigation. Currently 23% of the world's cultivated land has high levels of saline that reduce crop yield. The low water potential of saline soils results in water-stressed crops. Some plants, called **halophytes** (salt lovers), can tolerate soils with high salt concentrations. Mechanisms for salt tolerance are being studied with the goal of breeding more salt-tolerant plants. Some halophytes produce high concentrations of organic molecules within their roots to alter the water potential gradient between the soil and the root so that water flows into the root.

Learning Outcomes Review 38.5

Adaptations to drought include dormancy, leaf loss, leaves that minimize water loss, and stomata that lie in depressions. When plants are exposed to flooding, oxygen deprivation leads to lower cellular respiration rates, impedance of mineral and carbohydrate transport, and changes in hormone levels. If a plant is exposed to a salty environment, it may exclude the salt from uptake, secrete it after it has been taken up, or dilute it.

- ***Why are flooded plants in danger of oxygen deprivation when photosynthesis produces oxygen?***

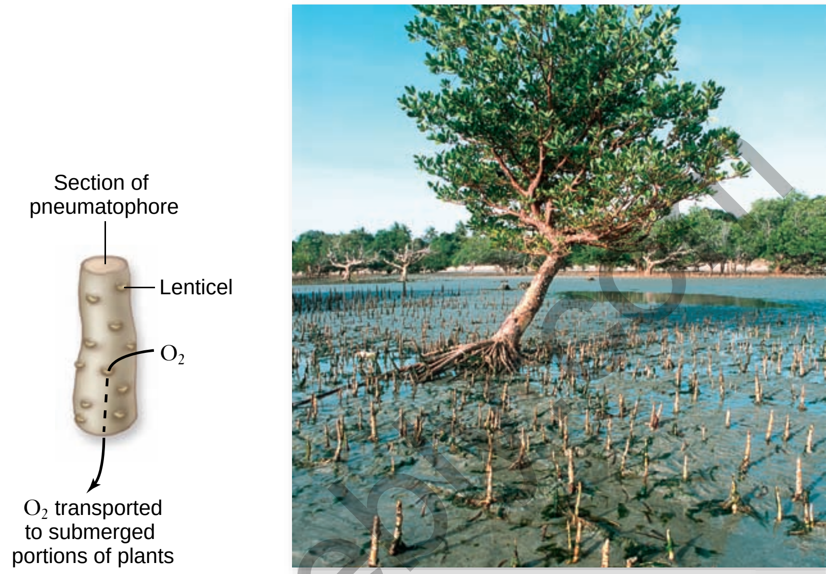


Figure 38.16 How mangroves get oxygen to their submerged parts. The black mangrove *(Avicennia germinans)* grows in areas that are commonly flooded, and much of each plant is usually submerged. However, modified roots called pneumatophores supply the submerged portions of the plant with oxygen because these roots emerge above the water and have large lenticels. Oxygen diffuses into the roots through the lenticels, passes into the abundant aerenchyma, and moves to the rest of the plant.

38.6 *Phloem Transport*

Learning Outcomes

1. ***Define translocation.***
2. ***List the substances found in plant sap.***
3. ***Explain the pressure-flow hypothesis.***

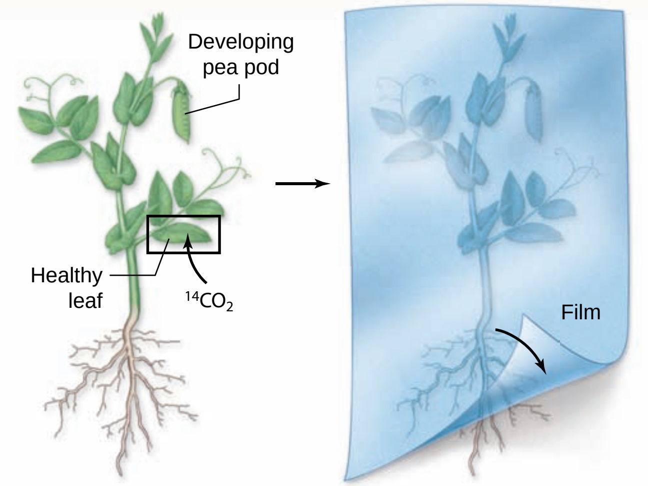
Most carbohydrates manufactured in leaves and other green parts are distributed through the phloem to the rest of the plant. This process, known as translocation, provides suitable carbohydrate building blocks for the roots and other actively growing regions of the plant. Carbohydrates concentrated in storage organs such as tubers, often in the form of starch, are also converted into transportable molecules, such as sucrose, and moved through the phloem. In this section we discuss the ways by which carbohydrate- and nutrient-rich fluid, termed **sap,** is moved through the plant body.

Organic molecules are transported up and down the plant

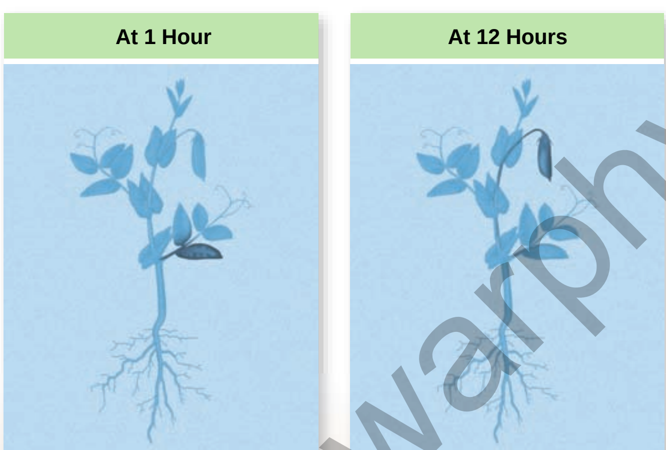
The movement of sugars and other substances can be followed in phloem using radioactive labels (figure 38.17). Radioactive carbon dioxide ($^{14}CO_2$) can be incorporated into glucose as a result of photosynthesis. Glucose molecules are used to make the disaccharide sucrose, which is transported in the phloem. Such studies have shown that sucrose moves both up and down in the phloem.

SCIENTIFIC THINKING

Hypothesis: *As pea embryos develop in a pod, sugars will be transported through the phloem to the developing embryos.*
Prediction: *Radioactively labeled sugars will accumulate in developing pea embryos.*
Test: *Expose a healthy pea leaf to radioactive carbon dioxide ($^{14}CO_2$). Place photographic film over the entire plant at 1 and 12 hours after treatment and develop film.*



Result: *After 1 hour the radioactivity is concentrated near the application site. After 12 hours the radioactivity is concentrated in the developing embryo.*



Conclusion: *The $^{14}CO_2$ is incorporated into sugars during photosynthesis and transported to the developing embryo in the pod.*
Further Experiments: *Carrots take two years to flower. During the first season an underground root, the 'carrot', develops and sugars are stored to be used for reproduction the next year. How could you test the hypothesis that sugars are transported to the developing storage root during the first season of growth for a carrot plant?*

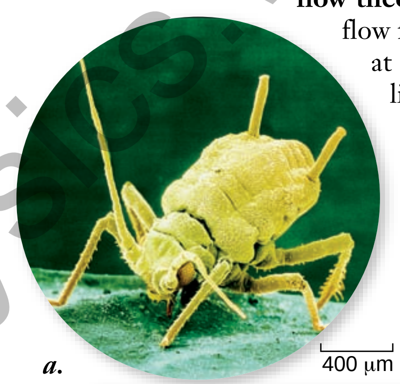
Figure 38.17 Sucrose flow in phloem during fruit development.

Aphids, a group of insects that extract plant sap for food, have been valuable tools in understanding translocation. Aphids thrust their stylets (piercing mouthparts) into phloem cells of leaves and stems to obtain the abundant sugars there. When a feeding aphid is removed by cutting its stylet, the liquid from the phloem continues to flow through the detached mouthpart and is thus available in pure form for analysis (figure 38.18). The liquid in the phloem, when evaporated, contains 10 to 25% of dry-weight matter, almost all of which is sucrose. Using aphids to obtain the critical samples and radioactive tracers to mark them, plant biologists have demonstrated that substances in phloem can move remarkably fast, as much as 50 to 100 cm/h.

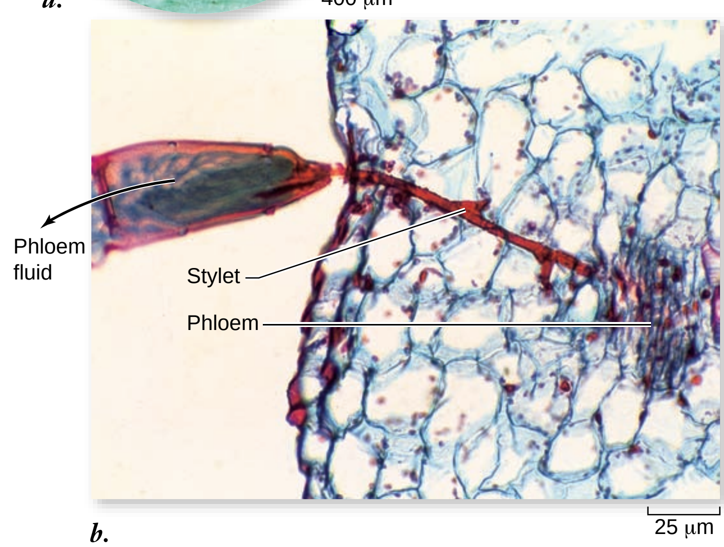
Phloem also transports plant hormones, and as will be explored in chapter 41, environmental signals can result in the rapid translocation of hormones in the plant. Recent evidence also indicates that mRNA can move through the phloem, providing a previously unknown mechanism for long-distance communication among cells. In addition, phloem carries other molecules, such as a variety of sugars, amino acids, organic acids, proteins, and ions.

Turgor pressure differences drive phloem transport

The most widely accepted model of how carbohydrates in solution move through the phloem has been called the **pressure–flow theory.** Dissolved carbohydrates flow from a *source* and are released at a *sink*, where they are utilized. Carbohydrate sources include photosynthetic tissues, such as the mesophyll of leaves. Food-storage tissues, such as the cortex of roots, can be either sources



a.



b.

Figure 38.18 Feeding on phloem. ***a.*** Aphids, including this individual shown on the edge of a leaf, feed on the food-rich contents of the phloem, which they extract through ***(b)*** their piercing mouthparts, called stylets. When an aphid is separated from its stylet and the cut stylet is left in the plant, the phloem fluid oozes out of it and can then be collected and analyzed.

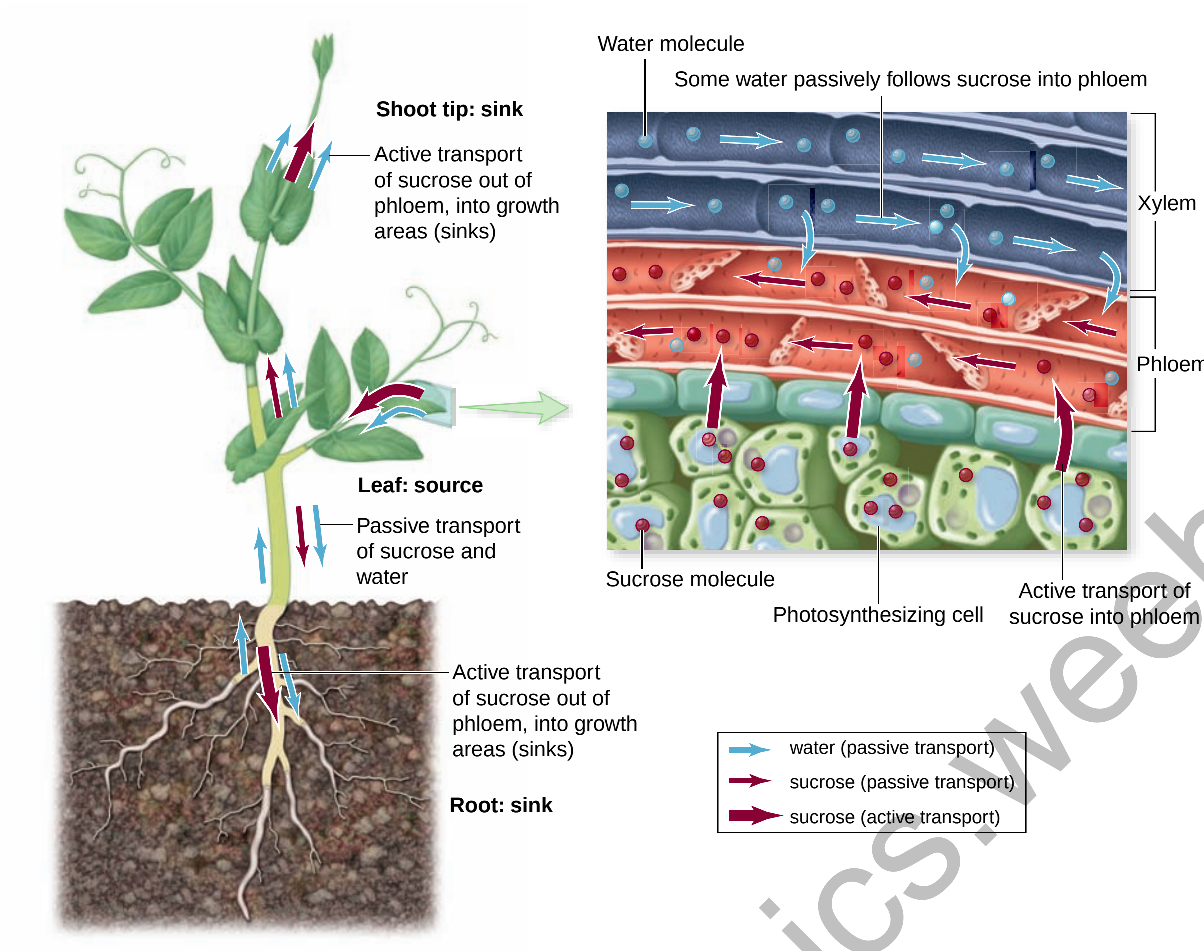


Figure 38.19
Diagram of mass flow. In this diagram, *red* dots represent sucrose molecules and *blue* dots symbolize water molecules. After moving from the mesophyll cells of a leaf or another part of the plant into the conducting cells of the phloem, the sucrose molecules are transported to other parts of the plant by mass flow and unloaded where they are required.

or sinks. Sinks also occur at the growing tips of roots and stems and in developing fruits. Also, because sources and sinks can change through time as needs change, the direction of phloem flow can change.

In a process known as **phloem loading,** carbohydrates (mostly sucrose) enter the sieve tubes in the smallest veins at the source. Some sucrose travels from mesophyll cells to the companion and sieve cells via the symplast (see figure 38.8). Much of the sucrose arrives at the sieve cell through apoplastic transport and is moved across the membrane via a sucrose and H^+ symporter (see chapter 5). This energy-requiring step is driven by a proton pump (see figure 38.1). Companion cells and parenchyma cells adjacent to the sieve tubes provide the ATP energy to drive this transport. Unlike vessels and tracheids, sieve cells must be alive to participate in active transport.

Bulk flow occurs in the sieve tubes without additional energy requirements. Because of the difference between the water potential in the sieve tubes and in the nearby xylem cells, water flows into the sieve tubes by osmosis. Turgor pressure in the sieve tubes thus increases, and this pressure drives the fluid throughout the plant's system of sieve tubes. At the sink, sucrose and hormones are actively removed from the sieve tubes, and water follows by osmosis. The turgor pressure at the sink drops, causing a mass flow from the stronger pressure at the source to the weaker pressure at the sink (figure 38.19). Most of the water at the sink then diffuses back into the xylem, where it may either be recirculated or lost through transpiration.

Transport of sucrose and other carbohydrates within sieve tubes does not require energy. But the pressure needed to drive the movement is created through energy-dependent loading and unloading of these substances from the sieve tubes.

Learning Outcomes Review 38.6

Translocation is the movement of dissolved carbohydrates and other substances from one part of the plant to another through the phloem. Sap in the phloem contains sucrose and other sugars, hormones, mRNA, amino acids, organic acids, proteins, and ions. According to the pressure-flow hypothesis, carbohydrates are loaded into sieve tubes, creating a difference in water potential. As a result, water enters the tubes and creates pressure to move fluid through the phloem.

- ***What is the key difference between the fluid in xylem and the fluid in phloem?***

Chapter Review

38.1 Transport Mechanisms (see figure 38.2)

Local changes result in long-distance movement of materials.

Properties of water, osmosis, and cellular activities predict the directions of water movement.

Water potential regulates movement of water through the plant (see figures 38.3 and 38.4).

The major force for water transport in a plant is the pulling of water by transpiration. Cohesion, adhesion, and osmosis all contribute to water movement.

Water potential is the sum of pressure potential and solute potential. Water moves from an area of high water potential to an area of low water potential.

Aquaporins enhance osmosis (see figure 38.5).

Aquaporins are water channels in plasma membranes that allow water to move across the membrane more quickly.

38.2 Water and Mineral Absorption

Root hairs and mycorrhizal fungi can increase the surface area for absorption of water and minerals.

Three transport routes exist through cells.

The apoplast route is through cell walls and spaces between cells. The symplast route is through the cytoplasm and between cells via plasmodesmata. The transmembrane route is also through the cytoplasm, but across membranes, where entry and exit of substances can be controlled.

Transport through the endodermis is selective.

Casparian strips in the endoderm force water and nutrients to move across the cell membranes, allowing selective flow of water and nutrients to the xylem.

38.3 Xylem Transport

Root pressure is present even when transpiration is low or not occurring.

Root pressure results from the active transport of ions into the root cells, which causes water to move in through osmosis. Guttation occurs when water is forced out of a plant as a result of high root pressure.

Water has a high tensile strength due to its cohesive and adhesive properties, which are related to hydrogen bonding.

A water potential gradient from roots to shoots enables transport.

Water moves into plants when the soil water potential is greater than that of roots. Evaporation of water from leaves creates a negative water potential that pulls water upward through the xylem.

Vessels and tracheids accommodate bulk flow.

The volume of water that can be transported by a xylem vessel or tracheid is a function of its diameter. As diameter decreases, tensile strength increases; however, a larger volume of water can be transported through a tube with a larger radius.

Cavitation occurs when a gas bubble forms in a water column and water movement ceases.

38.4 The Rate of Transpiration

Stomata open and close to balance H_2O and CO_2 needs.

More than 90% of the water absorbed by the roots is lost by evaporation through stomata. Stomata must open to take up carbon dioxide for photosynthesis and to allow evaporation for transpiration and cooling for the leaf (see figure 39.12).

Turgor pressure in guard cells causes stomata to open and close.

Stomata open when the turgor pressure of guard cells increases due to the uptake of ions. The turgid guard cells change shape and create an opening between them. Stomata close when guard cells lose turgor pressure and become flaccid.

Environmental factors affect transpiration rates.

Transpiration rates increase as temperature and wind velocity increase and as humidity decreases. Stomata close at high temperatures or when carbon dioxide concentrations increase.

38.5 Water-Stress Responses

Plant adaptations to drought include strategies to limit water loss.

Plant adaptations to minimize water loss include closing stomata, becoming dormant, altering leaf characteristics to minimize water loss, and losing leaves.

Plant responses to flooding include short-term hormonal changes and long-term adaptations.

Flooding reduces oxygen availability for cellular respiration, results in abnormal growth, and reduces the efficiency of transport mechanisms.

Plants adapted to wet environments exhibit a variety of strategies, including lenticels, adventitious roots such as pneumatophores, and aerenchyma tissue to ensure oxygen for submerged parts.

Plant adaptations to high salt concentration include elimination methods.

Plants found in saline waters may exclude, secrete, or dilute salts that have been taken up.

Halophytes can take up water from saline soils by decreasing the water potential of their roots with high concentrations of organic molecules.

39.6 Phloem Transport

Organic molecules are transported up and down the plant.

Movement of organic nutrients from leaves to other parts of the plant through the phloem is called translocation.

The sap that moves through phloem contains sugars, plant hormones, mRNA, and other substances. Carbohydrates must be actively transported into the sieve tubes.

Turgor pressure differences drive phloem transport.

At the carbohydrate source, such as a photosynthetic leaf, active transport of sugars into the phloem causes a reduction in water potential.

As water moves into the phloem, turgor pressure drives the contents to a sink, such as a nonphotosynthetic tissue, where the sugar is unloaded.

Review Questions

UNDERSTAND

1. Which of the following is an active transport mechanism?
   a. Proton pump
   b. Ion channel
   c. Symport
   d. Osmosis
2. The water potential of a plant cell is the
   a. sum of the membrane potential and gravity.
   b. difference between membrane potential and gravity.
   c. sum of the pressure potential and solute potential.
   d. difference between pressure potential and solute potential.
3. Hydrogen bonding between water molecules results in
   a. submersion.
   b. adhesion.
   c. evaporation.
   d. cohesion.
4. Water movement through cell walls is
   a. apoplastic.
   b. symplastic.
   c. both a and b
   d. neither a nor b
5. Casparian strips are found in the root
   a. cortex.
   b. dermal tissue.
   c. endodermis.
   d. xylem.
6. The formation of an air bubble is the xylem is called
   a. agitation.
   b. cohesion.
   c. adhesion.
   d. cavitation.
7. Guttation is most likely to be observed on
   a. cold winter day.
   b. cool summer night.
   c. warm sunny day.
   d. warm cloudy day.
8. Stomata open when guard cells
   a. take up potassium.
   b. lose potassium.
   c. take up sugars.
   d. lose sugars.
9. Which of the following is not an adaptation to a high saline environment?
   a. Secretion of salts
   b. Lowering of root water potential
   c. Exclusion of salt
   d. Production of pneumatophores
10. A plant must expend energy to drive
    a. transpiration.
    b. translocation.
    c. both transpiration and translocation.
    d. neither transpiration nor translocation.

APPLY

1. Which of the following statements is inaccurate?
   a. Water moves to areas of low water potential.
   b. Xylem transports materials up the plant while phloem transports materials down the plant.
   c. Water movement in the xylem is largely due to the cohesive and adhesive properties of water.
   d. Water movement across membranes is often due to differences in solute concentrations.
2. If you could override the control mechanisms that open stomata and force them to remain closed, what would you expect to happen to the plant?
   a. Sugar synthesis would likely slow down.
   b. Water transport would likely slow down.
   c. Both a and b could be the result of keeping stomata closed.
   d. Neither a nor b would be the result of keeping stomata closed.
3. What will happen if a cell with a solute potential of –0.4 MPa and a pressure potential of 0.2 MPa is placed in a chamber filled with pure water that is pressurized with 0.5 MPa?
   a. Water will flow out of the cell.
   b. Water will flow into the cell.
   c. The cell will be crushed.
   d. The cell will explode.
4. If you were able to remove the aquaporins from cell membranes, which of the following would be the likely consequence?
   a. Water would no longer move across membranes.
   b. Plants would no longer be able to control the direction of water movement across membranes.
   c. The potassium symport would no longer function.
   d. Turgor pressor would increase.
5. What would be the consequence of removing the Casparian strip?
   a. Water and mineral nutrients would not be able to reach the xylem.
   b. There would be less selectivity as to what passed into the xylem.
   c. Water and mineral nutrients would be lost from the xylem back into the soil.
   d. Water and mineral nutrients would no longer be able to pass through the cell walls of the endodermis.

SYNTHESIZE

1. If you fertilize your houseplant too often, you may find that it looks wilted even when the soil is wet. Explain what has happened in terms of water potential.
2. How could you detect a plant with a mutation in a gene for an important aquaporin protein?
3. Contrast water transport mechanisms in plants with those in animals.
4. Measurements of tree trunk diameters indicate that the trunk shrinks during the day, with shrinkage occurring in the upper part of the trunk before it occurs in the lower part. Explain how these observations support the hypothesis that water is pulled through the trunk as a result of transpiration.
5. A carrot is a biennial plant. In the first year of growth, the seed germinates and produces a plant with a thick storage root. In the second year, a shoot emerges from the storage root and produces a flower stalk. Following fertilization, seeds are formed to start the life cycle again. Draw a carrot plant during the spring, summer, and fall of the two years of its life cycle and indicate the carbohydrate sources and sinks in each season.

ONLINE RESOURCE

www.ravenbiology.com

connect BIOLOGY

Understand, Apply, and Synthesize—enhance your study with animations that bring concepts to life and practice tests to assess your understanding. Your instructor may also recommend the interactive eBook, individualized learning tools, and more.

Chapter 39

Plant Nutrition and Soils

Chapter Outline

Introduction

Vast energy inputs are required for the building and ongoing growth of a plant. In this chapter, you'll learn what inputs, besides energy from the Sun, a plant needs to survive. Plants, like animals, need various nutrients to remain healthy. The lack of an important nutrient may slow a plant's growth or make the plant more susceptible to disease or even death. Plants acquire these nutrients mainly through photosynthesis and from the soil. In addition to contributing nutrients, the soil hosts bacteria and fungi that aid plants in obtaining nutrients in a usable form. Getting sufficient nitrogen is particularly problematic because plants cannot directly convert atmospheric nitrogen into amino acids. A few plants are able to capture animals and secrete digestive juices to make nitrogen available for absorption.

39.1 Soils: The Substrates on Which Plants Depend

Learning Outcomes

1. *List the three main components of topsoil.*
2. *Explain how the charge of soil particles can affect the relative balance of positively and negatively charged molecules and ions in the soil water.*
3. *Describe cultivation approaches that can reduce soil erosion.*

Much of the activity that supports plant life is hidden within the soil. **Soil** is the highly weathered outer layer of the Earth's crust. It is composed of a mixture of ingredients, which may include sand, rocks of various sizes, clay, silt, humus (partially decomposed organic matter), and various other forms of mineral and organic matter. Pore spaces containing water and air occur between the particles of soil.

Soil is composed of minerals, organic matter, water, air, and organisms

The mineral fraction of soils varies according to the composition of the rocks. The Earth's crust includes about 92 naturally occurring elements (see chapter 2). Most elements are found in the form of inorganic compounds called *minerals;* most rocks consist of several different minerals.

The soil is also full of microorganisms that break down and recycle organic debris. For example, about 5 metric tons of carbon is tied up in the organisms present in the soil under a hectare of wheat land in England—an amount that approximately equals the weight of 100 sheep!

Most roots are found in **topsoil** (figure 39.1), which is a mixture of mineral particles of varying size (most less than 2 mm in diameter), living organisms, and **humus.** Topsoils are characterized by their relative amounts of sand, silt, and clay. Soil composition determines the degree of water and nutrient binding to soil particles. Sand binds molecules minimally, but clay adsorbs (binds) water and nutrients quite tightly.

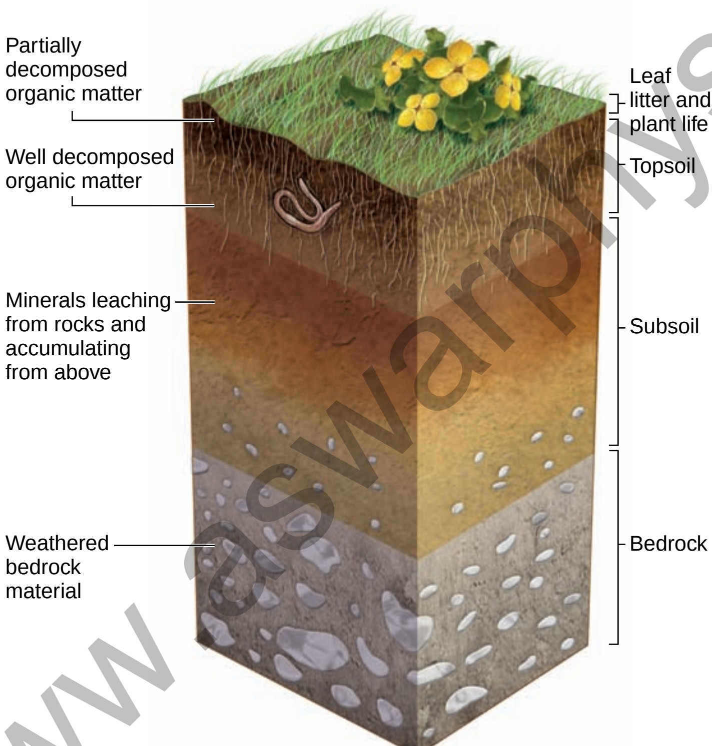


Figure 39.1 Most roots grow in the topsoil. Leaf litter and animal remains cover the uppermost layer in soil called topsoil. Topsoil contains organic matter, such as roots, small animals, humus, and mineral particles of various sizes. Subsoil lies underneath the topsoil and contains larger mineral particles and relatively little organic matter. Beneath the subsoil are layers of bedrock, the raw material from which soil is formed over time and through weathering.

Water and mineral availability is determined by soil characteristics

Only minerals that are dissolved in water in the spaces or pores among soil particles are available for uptake by roots. Both mineral and organic soil particles tend to have negative charges, so they attract positively charged molecules and ions. The negatively charged anions stay in solution, creating a charge gradient between the soil solution and the root cells, so that positive ions would normally tend to move out of the cells. Proton pumps move H^+ out of the root to form a strong membrane potential (≈ -160 mV). The strong electrochemical gradient then causes K^+ and other ions to enter via ion channels. Some ions, especially anions, use cotransporters (figure 39.2). The membrane potential maintained by the root, as well as the water potential difference inside and outside the root, affects root transport. (Water potential is described in chapter 38.)

About half of the total soil volume is occupied by pores, which may be filled with air or water, depending on moisture

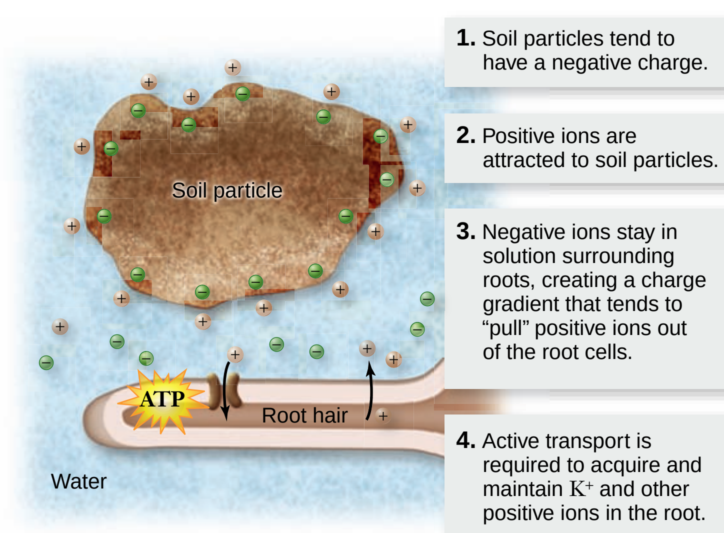


Figure 39.2 Role of soil charge in transport. Active transport is required to move positively charged ions into a root hair.

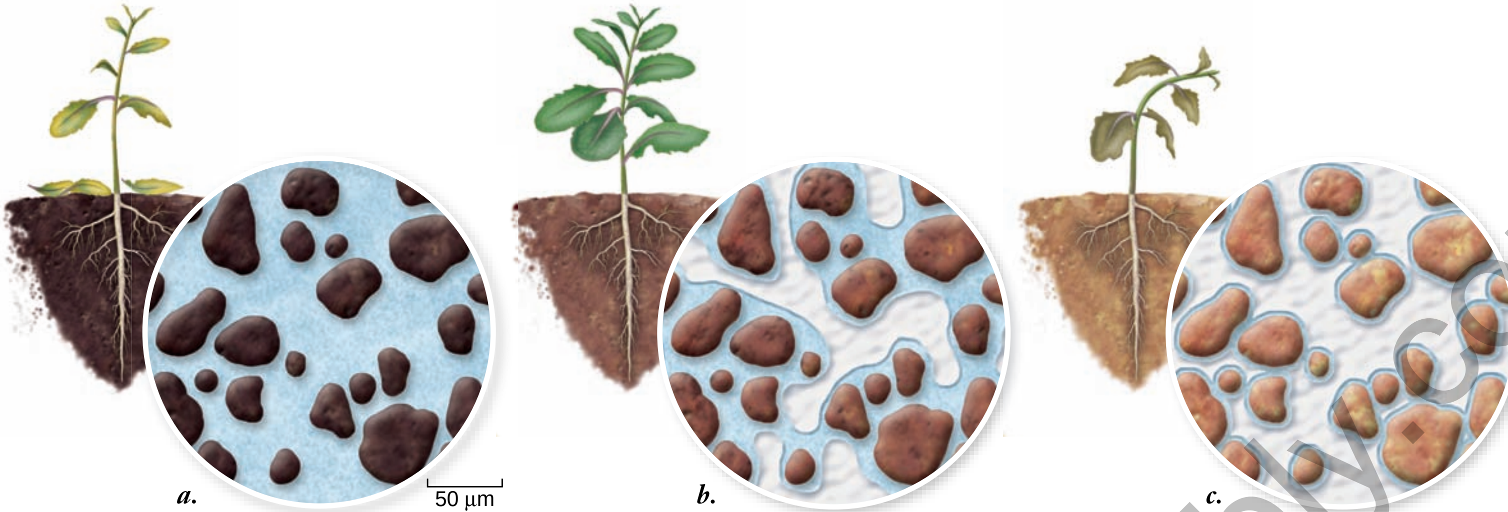


Figure 39.3 Water and air fill pores among soil particles. ***a.*** Without some space for air circulation in the soil, roots cannot respire. ***b.*** A balance of air and water in the soil is essential for root growth. ***c.*** Too little water decreases the soil water potential and prevents transpiration in plants.

conditions (figure 39.3). Some of the soil water is unavailable to plants. In sandy soil, for example, a substantial amount of water drains away immediately due to gravity. Another fraction of the water is held in small soil pores, which are generally less than about 50 μm in diameter. This water is readily available to plants. When this water is depleted through evaporation or root uptake, the plant wilts and will eventually die unless more water is added to the soil. However, as plants deplete water near the roots, the soil water potential decreases. This helps to move more water toward the roots since the soil water further away has a higher water potential.

Soils have widely varying composition, and any particular soil may provide more or fewer plant nutrients. In addition, the soil's acidity and salinity, described shortly, can affect the availability of nutrients and water.

Cultivation can result in soil loss and nutrient depletion

When topsoil is lost because of erosion or poor landscaping, both the water-holding capacity and the nutrient relationships of the soil are adversely affected. Up to 50 billion tons of topsoil have been lost from fields in the United States in a single year.

Whenever the vegetative cover of soil is disrupted, such as by plowing and harvesting, erosion by water and wind increases—sometimes dramatically, as was the case in the 1930s in the southwestern Great Plains of the United States. This region became known as the "Dust Bowl" when a combination of poor farming practices and several years of drought made the soil particularly susceptible to wind erosion (figure 39.4*a*).

New approaches to cultivation are aimed at reducing soil loss. Intercropping (mixing crops in a field), conservation tillage, and not plowing fall crop detritis under (no-till) are all erosion-prevention measures. Conservation tillage includes minimal till and even no-till approaches to farming.

Overuse of fertilizers in agriculture, lawns, and gardens can cause significant water pollution and its associated negative effects, such as overgrowth of algae in lakes (see chapter 58). Maintaining nutrient levels in the soil and preventing nutrient runoff into lakes, streams, and rivers improves crop growth and minimizes ecosystem damage.

a. b.

Figure 39.4 Soil degradation. ***a.*** Drought and poor farming practices led to wind erosion of farmland in the southwestern Great Plains of the United States in the 1930s. ***b.*** Draining marshland in Iraq resulted in a salty desert.

One approach, site-specific farming, uses variable-rate fertilizer applicators guided by a computer and the global positioning system (GPS). Variable-rate application relies on information about local soil nutrient levels, based on analysis of soil samples. Another approach, integrated nutrient management, maximizes nutritional inputs using "green manure" (such as alfalfa tilled back into the soil), animal manure, and inorganic fertilizers. Green manures and animal manure have the advantage of releasing nutrients slowly as they are broken down by decomposer organisms, so that nutrients may be utilized before leaching away. Sustainable agriculture integrates these conservation approaches.

pH and salinity affect water and mineral availability

Anything that alters water pressure differences or ionic gradient balance between soil and roots can affect the ability of plants to absorb water and nutrients. Acid soils (having low pH) and saline soils (high in salts) can present problems for plant growth.

Acid soils

The pH of a soil affects the release of minerals from weathering rock. For example, at low pH aluminum, which is toxic to many plants, is released from rocks. Furthermore, aluminum can also combine with other nutrients and make them inaccessible to plants.

Most plants grow best at a neutral pH, but about 26% of the world's arable land is acidic. In the tropical Americas, 68% of the soil is acidic. Aluminum toxicity in acid soils in Colombian fields can reduce maize (corn) yield fourfold (figure 39.5).

Breeding efforts in Colombia are producing aluminum-tolerant plants, and crop yields have increased 33%. In a few test fields, the yield increases have been as high as 70% compared with that for nontolerant plants. The ability of plants to take up toxic metals can also be employed to clean up polluted soil, a topic explored later in this chapter.

Salinity

The accumulation of salt ions, usually Na^+ and Cl^-, in soil alters water potential, leading to the loss of turgor in plants. Approximately 23% of all arable land has salinity levels that limit plant growth. Saline soil is most common in dry areas where salts are introduced through irrigation. In such areas, precipitation is insufficient to remove the salts, which gradually accumulate in the soil.

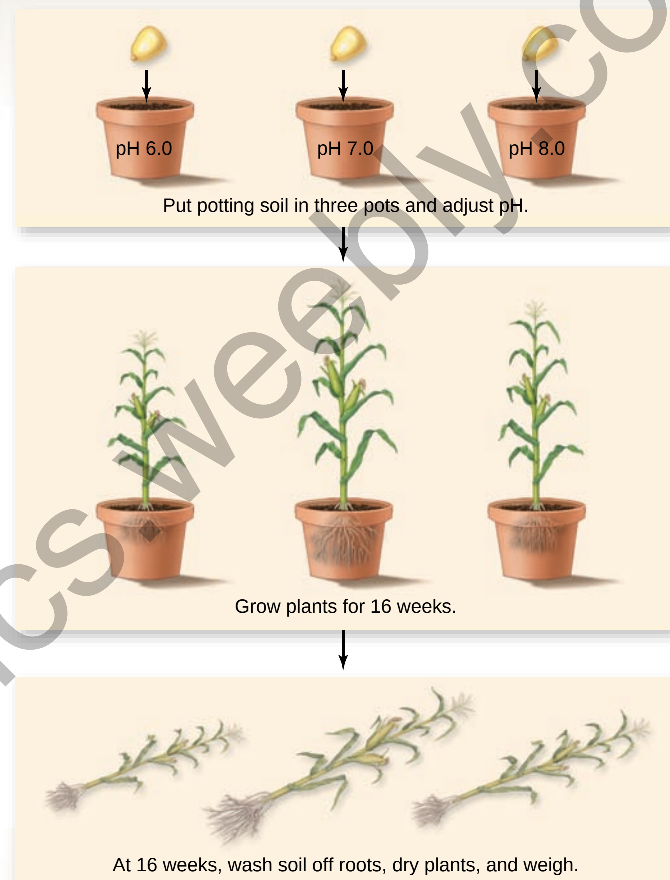
One of the more dramatic examples of soil salinity occurs in the "cradle of civilization," Mesopotamia. The region once called the Fertile Crescent for its abundant agriculture is now largely a desert. Desertification was accelerated in southern Iraq. In the 1990s, most of 20,000 km^2 of marshlands was drained by redirecting water flow with dams, turning the marshes into a salty desert (see figure 39.4*b*). The dams were destroyed later, allowing water to enter the marshlands once again. Recovery of the marshlands is not guaranteed, but in areas where the entering water has lowered the salinity there is hope.

SCIENTIFIC THINKING

Hypothesis: *Acidic or basic soils inhibit the growth of corn plants.*

Prediction: *Plants grown in soil with neutral pH will be more vigorous than those grown at high or low pH.*

Test: *Sow equal numbers of corn kernels in identical pots with soil adjusted to pH values of 6.0, 7.0, and 8.0. Allow plants to grow and, after 16 weeks, measure the biomass.*



Result: *Corn plant biomass is highest in pots with pH 7.0 soil and lowest in pH 6.0 soil.*

Conclusion: *The hypothesis is supported. Soil pH influences plant growth. Among the pH levels tested, the best for plant growth was 7.0. Acidic soil resulted in the lowest growth.*

Further Experiments: *How could you test the hypothesis that soil pH affects mineral uptake and that changes in mineral uptake were responsible for differences in plant growth?*

Figure 39.5 Soil pH affects plant growth.

Learning Outcomes Review 39.1

Topsoil is composed of mineral particles, living organisms, and humus. Roots use proton pumps to move protons (H^+) out of the root and into the soil. The result is an electrochemical gradient that causes positive mineral ions to enter the root through ion channels. The loss of topsoil by erosion can be reduced by intercropping, planting crop mixtures, conservation tillage, and no-till farming.

- *In what way would alkaline soil affect plant nutrition?*

39.2 *Plant Nutrients*

Learning Outcomes

1. ***Distinguish between macronutrients and micronutrients.***
2. ***Explain how scientists determine the nutritional needs of plants.***
3. ***Describe the goal of food fortification research.***

The major source of plant nutrition is the fixation of atmospheric carbon dioxide (CO_2) into simple sugars using the energy of the Sun. CO_2 enters through the stomata; oxygen (O_2) is a waste product of photosynthesis and an atmospheric component that also moves through the stomata. Oxygen is used in cellular respiration to support growth and maintenance in the plant.

CO_2 and light energy are not sufficient, however, for the synthesis of all the molecules a plant needs. Plants require a number of inorganic nutrients as well. Some of these are **macronutrients,** which plants need in relatively large amounts, and others are **micronutrients,** required in trace amounts (table 39.1).

Plants require nine macronutrients and seven micronutrients

The nine macronutrients are carbon, oxygen, and hydrogen—the three elements found in all organic compounds—plus nitrogen (essential for amino acids), potassium, calcium, magnesium (the

TABLE 39.1 Essential Nutrients in Plants

Element	Principal Form in Which Element Is Absorbed	Approximate Percent of Dry Weight	Examples of Important Functions
MACRONUTRIENTS			
Carbon	CO_2	44	Major component of organic molecules
Oxygen	O_2, H_2O	44	Major component of organic molecules
Hydrogen	H_2O	6	Major component of organic molecules
Nitrogen	NO_3^-, NH_4^+	1–4	Component of amino acids, proteins, nucleotides, nucleic acids, chlorophyll, coenzymes, enzymes
Potassium	K^+	0.5–6	Protein synthesis, operation of stomata
Calcium	Ca^{2+}	0.2–3.5	Component of cell walls, maintenance of membrane structure and permeability; activates some enzymes
Magnesium	Mg^{2+}	0.1–0.8	Component of chlorophyll molecule, activates many enzymes
Phosphorus	$H_2PO_4^-$, HPO_4^-	0.1–0.8	Component of ADP and ATP, nucleic acids, phospholipids, several coenzymes
Sulfur	SO_4^{2-}	0.05–1	Components of some amino acids and proteins, coenzyme A
MICRONUTRIENTS (CONCENTRATIONS in ppm)			
Chlorine	Cl^-	100–10,000	Osmosis and ionic balance
Iron	Fe^{2+}, Fe^{3+}	25–300	Chlorophyll synthesis, cytochromes, nitrogenase
Manganese	Mn^{2+}	15–800	Activator of certain enzymes
Zinc	Zn^{2+}	15–100	Activator of many enzymes; active in formation of chlorophyll
Boron	BO_3^-, $B_4O_7^-$, or $H_2BO_3^-$	5–75	Possibly involved in carbohydrate transport, nucleic acid synthesis
Copper	Cu^{2} or Cu^{+}	4–30	Activator or component of certain enzymes
Molybdenum	MoO_4^-	0.1–5	Nitrogen fixation, nitrate reduction

Figure 39.6 Mineral deficiencies in plants. ***a.*** Leaves of a healthy wheat plant. ***b.*** Chlorine-deficient plants with necrotic leaves (leaves with patches of dead tissue). ***c.*** Copper-deficient plant with dry, bent leaf tips. ***d.*** Zinc-deficient plant with stunted growth and chlorosis (loss of chlorophyll) in patches on leaves. The agricultural implications of deficiencies such as these are obvious; a trained observer can determine the nutrient deficiencies affecting a plant simply by inspecting it.

center of the chlorophyll molecule), phosphorus, and sulfur. Each of these nutrients approaches or, in the case of carbon, may greatly exceed 1% of the dry weight of a healthy plant.

The seven micronutrient elements—chlorine, iron, manganese, zinc, boron, copper, and molybdenum—constitute from less than one to several hundred parts per million in most plants. A deficiency of any one can have severe effects on plant growth (figure 39.6). The macronutrients were generally discovered in the last century, but the micronutrients have been detected much more recently as technology developed to identify and work with such small quantities.

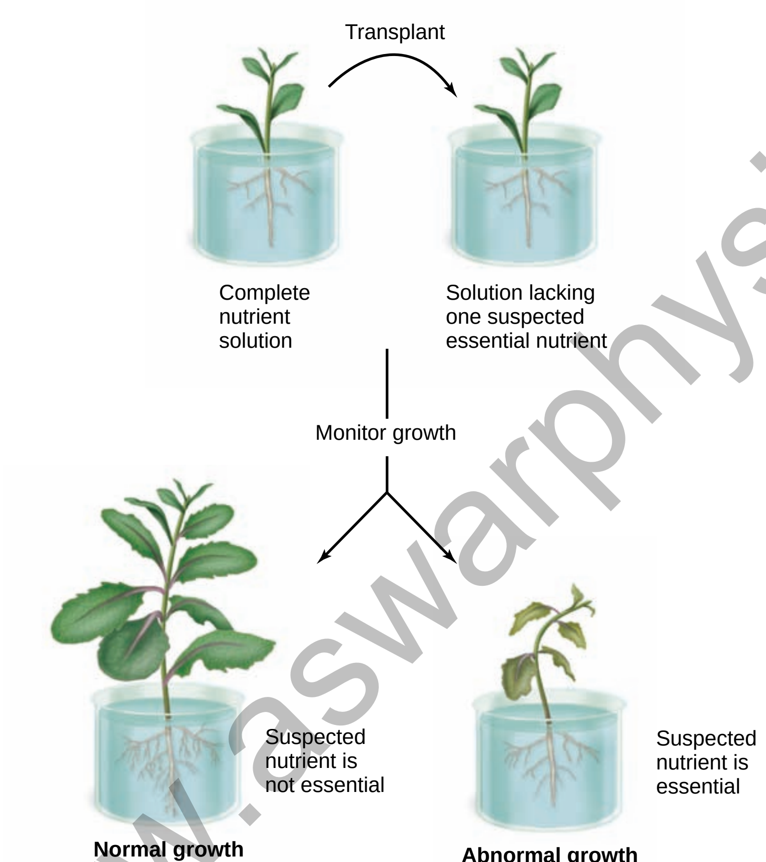


Figure 39.7 Identifying nutritional requirements of plants. A seedling is first grown in a complete nutrient solution. The seedling is then transplanted to a solution that lacks one nutrient thought to be essential. The growth of the seedling is studied for the presence of symptoms indicative of abnormal growth, such as discolored leaves or stunting. If the seedling's growth is normal, the nutrient that was left out may not be essential; if the seedling's growth is abnormal, the nutrient that is lacking is essential for growth.

Nutritional requirements are assessed by growing plants in hydroponic cultures in which the plant roots are suspended in aerated water containing nutrients. For the purposes of testing, the solutions contain all the necessary nutrients in the right proportions, but with certain known or suspected nutrients left out. The plants are then allowed to grow and are studied for altered growth patterns and leaf coloration that might indicate a need for the missing element (figure 39.7). To give an idea of how small the needed quantities of micronutrients may be, the standard dose of molybdenum added to seriously deficient soils in Australia amounts to about 34 g (about one handful) per hectare (a square 100 meters on a side—about 2.5 acres), once every 10 years!

Most plants grow satisfactorily in hydroponic cultures, if the roots are properly aerated. The method, although expensive, is occasionally practical for commercial purposes (figure 39.8). Analytical chemistry has made it much easier to test plant material for levels of different molecules.

Figure 39.8 Hydroponics. Soil provides nutrients and support, but both of these functions can be replaced in hydroponic systems. Here, tomato plants are suspended in the air, and the roots rotate through a nutrient bath.

Food security is related to crop productivity and nutrient levels

Nutrient levels and crop productivity are a significant human concern. **Food security,** avoiding starvation, is a global issue. Increasing the nutritional value of crop species, especially in developing countries, could have tremendous human health benefits.

Food fortification is an active area of research focused on ways to increase plants' uptake of minerals and the storage of minerals in roots and shoots for later human consumption. Phosphate uptake can be increased, for example, if it is more soluble in the soil. Some plants have been genetically modified to secrete citrate, an organic acid that solubilizes phosphate. As an added benefit, the citrate binds to aluminum, which can be toxic to plants and animals, and thus limits the uptake of aluminum into plants.

For other nutrients, such as iron, manganese, and zinc, plasma membrane transport is a limiting factor. Genes coding for these plasma membrane transporters have been cloned in other species and are being incorporated into crop plants. Eventually, breakfast cereals may be fortified with additional nutrients while the grains are growing in the field, as opposed to when they are processed in the factory.

Learning Outcomes Review 39.2

Plants require nine macronutrients in relatively large amounts and seven micronutrients in trace amounts. Plants are grown in controlled hydroponic solutions to determine which nutrients are required for growth. Scientists are studying ways to enhance the nutritional composition of food crops through enhancing nutrient uptake and storage. These methods of food fortification may enhance food security, the avoidance of human starvation.

- ***Why would a lack of magnesium in the soil limit food production?***

39.3 *Special Nutritional Strategies*

Learning Outcomes

1. ***Explain the significance of nitrogen-fixing bacteria for plant nutrition.***
2. ***Explain how mycorrhizal fungi benefit plants.***
3. ***Describe the benefit gained by carnivorous plants when they capture insects.***

In some species, scarce nutrients have been obtained through the evolution of mutualistic associations with other organisms, parasitism, or even predation. One example is the requirement for nitrogen: Plants need ammonia (NH_3) or nitrate (NO_3^-) to build amino acids, but most of the nitrogen in the atmosphere is in the form of gaseous nitrogen (N_2). Plants lack the biochemical pathways (including the enzyme nitrogenase) necessary to convert gaseous nitrogen to ammonia, but some bacteria have this capacity.

Figure 39.9 Nitrogen-fixing nodule. A root hair of alfalfa hosts *Rhizobium*, a bacterium that fixes nitrogen in exchange for carbohydrates.

Bacteria living in close association with roots can provide nitrogen

Symbiotic relationships have evolved between some plant groups and bacteria that can convert gaseous nitrogen. Some of these bacteria live in close association with the roots of plants. Others end up being housed in tissues the plant grows especially for this purpose, called **nodules** (figure 39.9). Legumes and a few other plants can form root nodules. Hosting these bacteria costs the plant energy, but is well worth it when the soil lacks nitrogen compounds. To conserve energy, legume root hairs do not respond to bacterial signals when nitrogen levels are high.

Nitrogen fixation is the most energetically expensive reaction known to occur in any cell. Why should it be so difficult to add H_2 to N_2? The answer lies in the strength of the triple bond in N_2. Nitrogenase requires 16 ATPs to make two molecules of NH_3. Making NH_3 without nitrogenase requires a contained system maintained at 450°C and 500 atm pressure—far beyond the maximums under which plants can survive.

Rhizobium bacteria require oxygen and carbohydrates to support their energetically expensive lifestyle as nitrogen fixers. Carbohydrates are supplied through the vascular tissue of the plant, and leghemoglobin, which is structurally similar to animal hemoglobin, is produced by the plant to regulate oxygen availability to the bacteria. Without oxygen, the bacteria die; within the bacteria, however, nitrogenase has to be isolated from oxygen, which inhibits its activity. Leghemoglobin binds oxygen and controls its availability within the nodule to optimize both nitrogenase activity and cellular respiration.

Just how do legumes and nitrogen-fixing *Rhizobium* bacteria get together (figure 39.10)? Extensive signaling between the bacterium and the legume not only lets each organism know the other is present, but also checks whether the bacterium is the correct species for the specific legume. These highly evolved symbiotic relationships depend on exact species matches. Soybean and garden peas are both legumes, but each requires its own species of symbiotic *Rhizobium*.

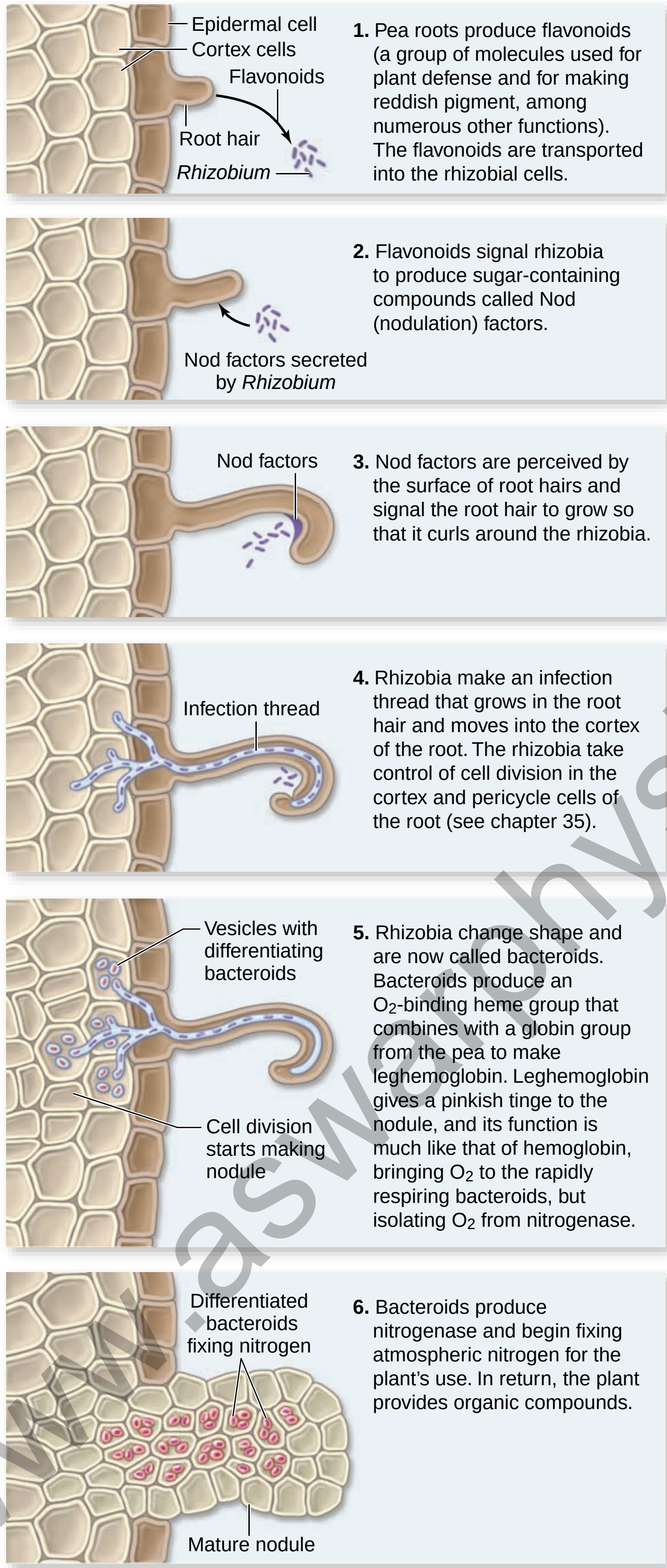


Figure 39.10 ***Rhizobium*** **induced nodule formation.**

Mycorrhizae aid a large portion of terrestrial plants

Nitrogen is not the only nutrient that is difficult for plants to obtain without assistance. Whereas symbiotic relationships with nitrogen-fixing bacteria are generally limited to some legume species, symbiotic associations with mycorrhizal fungi, described in chapter 31, are found in about 90% of vascular plants. Mycorrhizae play a significant role in enhancing phosphorus transfer to the plant, and the uptake of some of the micronutrients is also facilitated. Functionally, the mycorrhizae extend the surface area available for nutrient uptake substantially.

Fungi most likely aided early rootless plants in colonizing land. Evidence now indicates that the signaling pathways that lead to plant symbiosis with some mycorrhizae may have been exploited to bring about the *Rhizobium*–legume symbiosis.

Carnivorous plants trap and digest animals to extract additional nutrients

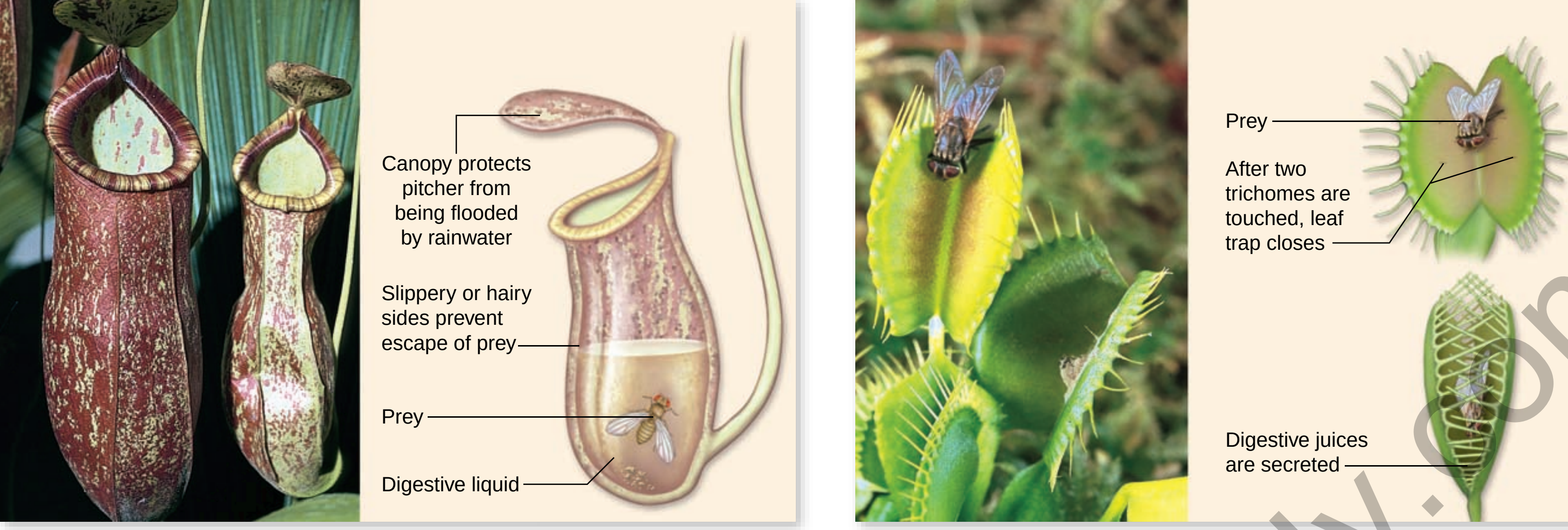
Some plants are able to obtain nitrogen directly from other organisms, just as animals do. These carnivorous plants often grow in acidic soils, such as bogs, that lack organic nitrogen. By capturing and digesting small animals, primarily insects, directly, such plants obtain adequate nitrogen supplies and are able to grow in these seemingly unfavorable environments. Carnivorous plants have modified leaves adapted for luring and trapping prey. The plants often digest their prey with enzymes secreted from specialized types of glands.

Pitcher plants (*Nepenthes* spp.) attract insects by the bright, flowerlike colors within their pitcher-shaped leaves, by scents, and perhaps also by sugar-rich secretions (figure 39.11*a*). Once inside the pitcher, insects slide down into the cavity of the leaf, which is filled with water and digestive enzymes. This passive mechanism provides pitcher plants with a steady supply of nitrogen.

The Venus flytrap *(Dionaea muscipula)* grows in the bogs of coastal North and South Carolina. Three sensitive hairs on a leaf that, when touched, trigger the two halves of the leaf to snap together in about 100 ms (figure 39.11*b*). The speed of trap closing has puzzled biologists as far back as Darwin. Turgor pressure changes can account for the movement; the speed, however, depends on the curved geometry of the leaf, which can snap between convex and concave shapes.

Once the Venus flytrap enfolds prey within a leaf, enzymes secreted from the leaf surfaces digest the prey. These flytraps use a growth mechanism to close, not just a decrease in turgor pressure. The cells on the outer leaf surface irreversibly increase in size each time the trap shuts. As a result, they can only open and close a limited number of times.

In the sundews (*Drosera* spp.), another carnivorous group, glandular trichomes secrete both sticky mucilage, which traps small animals, and digestive enzymes; they do not close rapidly (figure 39.11*c*). Venus flytraps and the sundews share a common ancestor that lacked the snap-trap mechanism characteristic of the flytrap lineage (figure 39.12).



a. *b.*

Figure 39.11 Nutritional adaptations. ***a.*** Asian pitcher plant, *Nepenthes.* Insects enter this carnivorous plant and are trapped and digested. Complex communities of invertebrate animals and protists inhabit the pitchers. ***b.*** Venus flytrap, *Dionaea.* If this fly touches two of the trichomes (hairs) on this modified leaf in a short time span, the trap will close. The plant will secrete digestive enzymes that release nitrogen compounds from the fly, which will then be absorbed by the flytrap. ***c.*** Sundew, *Drosera*, traps insects with sticky secretions and then excretes digestive enzymes to obtain nutrients from the insect's body. ***d.*** Aquatic waterwheel, *Aldrovanda.* This close relative of the Venus flytrap snaps shut to capture and digest small aquatic animals. This aquatic plant's ancestor was a land dweller.

Aldrovanda vesicular, the aquatic waterwheel, is a closer relative of the flytraps. The waterwheel is a rootless plant that uses trigger hairs and a snap-trap mechanism like that of the Venus flytrap to capture and digest small animals (figure 39.11*d*). Molecular phylogenetic studies indicate that Venus flytraps are sister species with sundews, forming a sister clade. It appears that the snap-trap mechanism evolved only once in descendants of a sundew ancestor. Therefore, the waterwheel's common ancestor must have been a terrestrial plant that made its way back into the water.

Bladderworts *(Utricularia)* are aquatic, but appear to have different origins from the waterwheel, as well as a different mechanism for trapping organisms. Small animals are swept into their bladderlike leaves by the rapid action of a springlike trapdoor; then the leaves digest these animals.

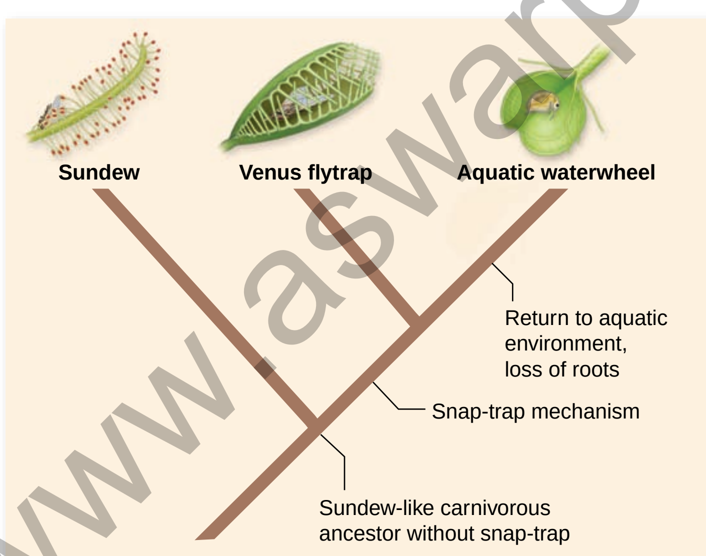


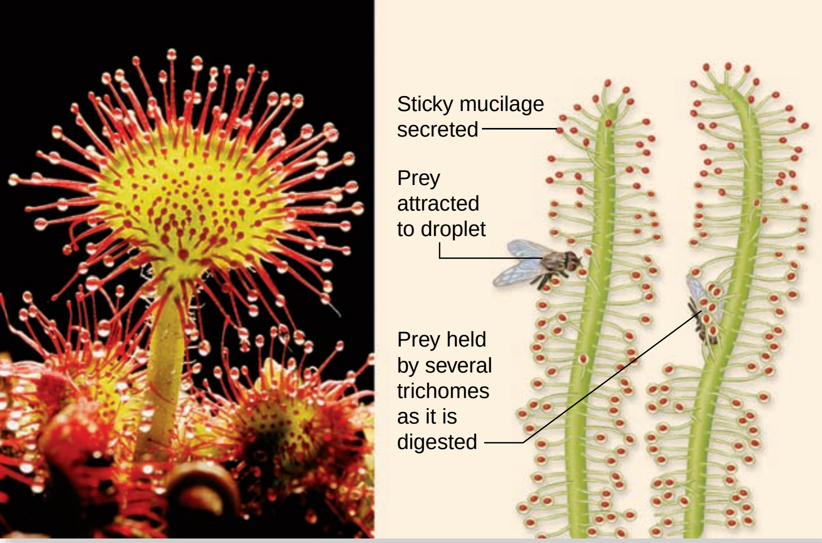
Figure 39.12 Phylogenetic relationships among carnivorous plants. The snap-trap mechanism was acquired by a common ancestor of the Venus flytrap and the aquatic waterwheel. Pitcher plants are not related to this clade.

Parasitic plants exploit resources of other plants

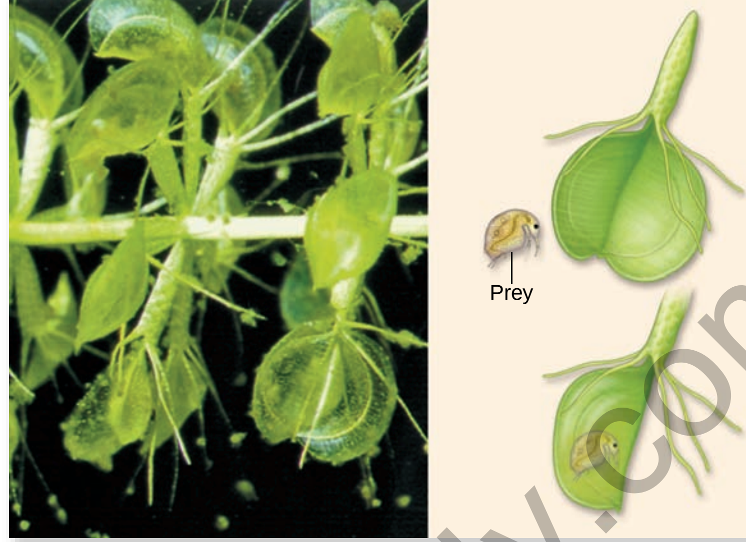
Parasitic plants come in photosynthetic and nonphotosynthetic varieties. In total, at least 3000 types of plants are known to tap into the nutrient resources of other plants. Adaptations include structures that are inserted into the vascular tissue of the host plant so that nutrients can be siphoned into the parasite. One example is dodder (*Cuscuta* spp.), which looks like brown twine wrapped around its host. Dodder lacks chlorophyll and relies totally on its host for all its nutritional needs.

Indian pipe, *Hypopitys uniflora*, also lacks chlorophyll. This parasitic plant hooks into host trees through the fungal hyphae of the host's mycorrhizae (figure 39.13). The above-ground portion of the plant consists of flowering stems.

Figure 39.13 Indian pipe, *Hypopitys uniflora.* This plant lacks chlorophyll and depends completely on nutrient transfer through the invasion of mycorrhizae and associated roots of other plants. Indian pipes are frequently found in northeastern United States forests.



c.



d.

Learning Outcomes Review 39.3

Certain types of plants, such as legumes, produce root nodules in which nitrogen-fixing bacteria grow. These bacteria provide nitrogen compounds that the plant can use for growth. Mycorrhizal fungi live in association with plant roots and are important for phosphorus uptake. Carnivorous plants typically live in low-nitrogen soils and obtain nitrogen from the insects they capture and digest.

- ***Why is nitrogen a critical macronutrient for plant growth and reproduction?***

39.4 *Carbon–Nitrogen Balance and Global Change*

Learning Outcomes

1. ***Describe the predicted effect of increased atmospheric carbon dioxide on the rate of photosynthesis in C_3 plants.***
2. ***Explain the main effect on herbivores of a higher carbon:nitrogen ratio in plants.***
3. ***Discuss why respiration rates increase with warmer temperatures.***

The Intergovernmental Panel on Climate Change (IPCC), established by the United Nations and the World Meteorological Organization, has concluded that CO_2 is probably at its highest concentration in the atmosphere in at least 20 million years. In only the last 250 years, atmospheric CO_2 has increased 31%, which correlates with increases in many human activities, including the burning of fossil fuels.

The long-term effects of elevated CO_2 are complex and are not fully understood, but are associated with increased temperatures. The IPCC predicts the average global surface temperatures will continue to increase to between 1.4°C and 5.8°C above 1990 levels, by 2100. Chapter 59 explores the causal link between elevated CO_2 and global warming. Here, we consider how increased CO_2 may alter nutrient balance within plants, specifically the carbon and nitrogen balance.

The ratio of carbon to nitrogen in a plant is important for both plant health and the health of herbivores. Altering this ratio could alter plant–pest interactions as well as affect human nutrition.

Elevated CO_2 levels can alter photosynthesis and carbon levels in plants

First, we investigate the relationship between photosynthesis and the relative concentration of atmospheric CO_2. The two questions to be addressed in this section are (1) Does elevated CO_2 increase the rate of photosynthesis? and (2) Will elevated levels of CO_2 change the ratio of carbohydrates and proteins in plants?

The rate of photosynthesis

The Calvin cycle of photosynthesis fixes atmospheric CO_2 into sugar (see chapter 8). The first step of the Calvin cycle stars the most abundant protein on Earth, ribulose 1,5-bisphosphate carboxylase/oxygenase (rubisco). The active site of this enzyme can bind either CO_2 or O_2, and it catalyzes the addition of either molecule to a five-carbon molecule, ribulose 1,5-bisphosphate (RuBP) (figure 39.14). CO_2 is used to

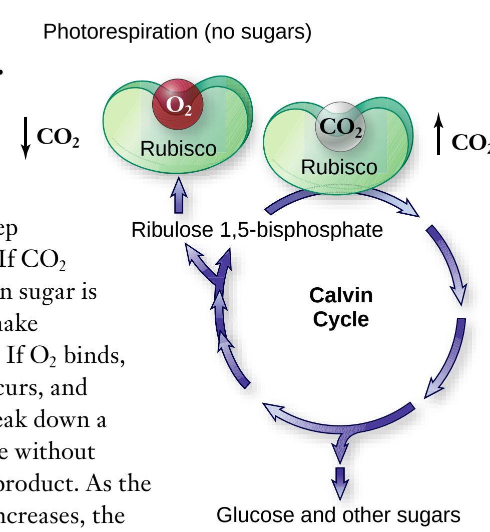
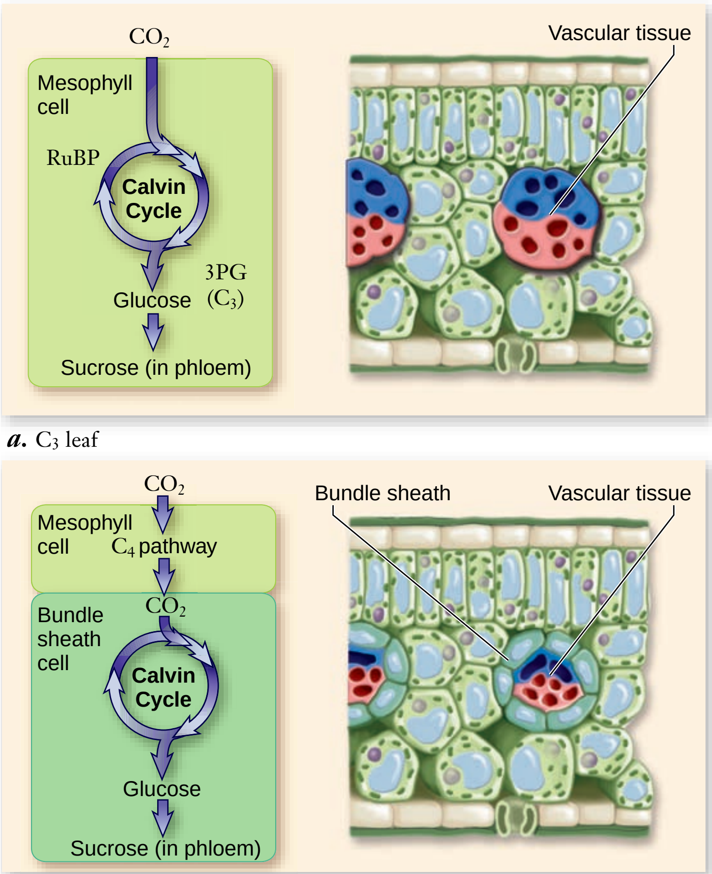


Figure 39.14 Photorespiration. CO_2 and O_2 compete for the same site on the enzyme that catalyzes the first step in the Calvin cycle. If CO_2 binds, a three-carbon sugar is produced that can make glucose and sucrose. If O_2 binds, photorespiration occurs, and energy is used to break down a five-carbon molecule without yielding any useful product. As the ratio of CO_2 to O_2 increases, the Calvin cycle can produce more sugar.



a. C_3 leaf

b. C_4 leaf (Kranz anatomy)

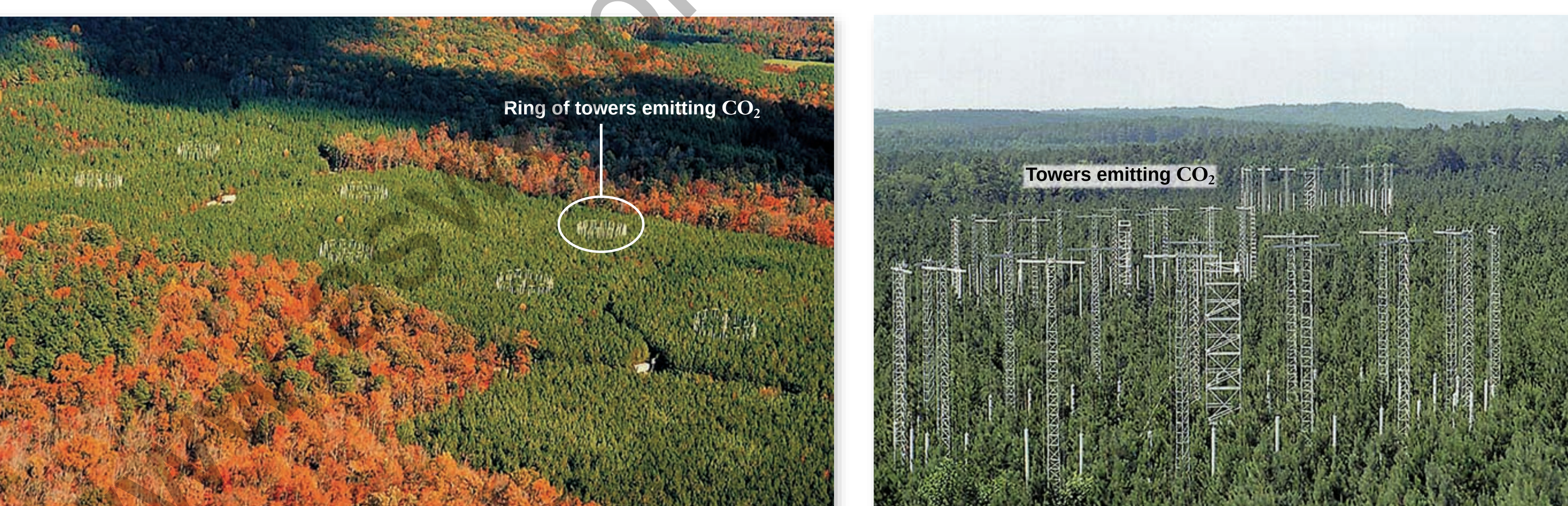
Figure 39.15 C_4 plants reduce photorespiration by limiting the Calvin cycle to cells surrounding the vascular tissue, where O_2 levels are reduced. ***a.*** C_3 photosynthesis occurs in the mesophyll cells. ***b.*** C_4 photosynthesis uses an extra biochemical pathway to shuttle carbon deep within the leaf.

produce a three-carbon sugar that can in turn be used to synthesize glucose and sucrose; in contrast, O_2 is used in photorespiration, which results in neither nutrient nor energy storage. Photorespiration is a wasteful process.

You may recall that C_4 plants have evolved a novel anatomical and biochemical strategy to reduce photorespiration (figure 39.15). CO_2 does not enter the Calvin cycle until it has been transported via another pathway to cells surrounding the vascular tissue. Here the level of CO_2 is increased relative to O_2 levels, and thus CO_2 has less competition for rubisco's binding site.

In C_3 plants, as the relative amount of CO_2 increases, the Calvin cycle becomes more efficient. Thus, it is reasonable to hypothesize that the global increase in CO_2 should lead to increased photosynthesis and increased plant growth. Assuming that nutrient availability in the soil remains the same, the more rapidly growing plants should have lower levels of nitrogen-containing compounds, such as proteins, and also lower levels of minerals obtained from the soil. The ratio of carbon to nitrogen should increase. Long-term studies of plants grown under elevated CO_2 confirm this prediction.

The optimal way to determine how CO_2 concentrations affect plant nutrition is to grow plants in an environment in which CO_2 levels can be precisely controlled. Experiments with potted plants in growth chambers are one approach, but far more information can be obtained in natural areas enriched with CO_2, called Free Air CO_2 Enrichment (FACE) studies. For example, the Duke Experimental Forest has rings of towers that release CO_2 toward the center of the ring (figure 39.16). These rings are 30 m in diameter and allow studies to be conducted at the ecosystem level. Such facilities allow for long-term studies of the effects of altered atmospheric conditions on ecosystems.



a. ***b.***

Figure 39.16 Experimentally elevating CO_2. CO_2 rings in the Duke Experimental Forest FACE site provide ecosystem-level comparisons of plants grown in ambient and elevated CO_2 environments. ***a.*** Each ring is 30 m in diameter. ***b.*** Towers surrounding the rings blow CO_2 inward under closely monitored conditions.

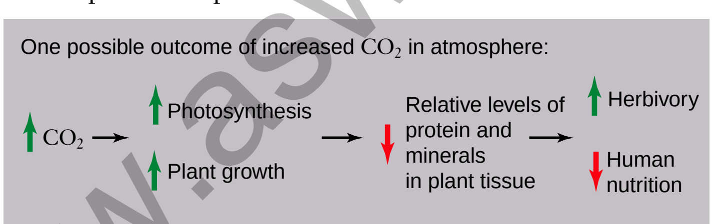
Extensive studies have yielded complex results. Potatoes grown in a European facility had a 40% higher photosynthetic rate when the concentration of CO_2 was approximately doubled. Potted plants often show an initial increase in photosynthesis, followed by a decrease over time that is associated with lower levels of rubisco production. Different species of plants in a Florida oak-shrub system showed different responses to elevated CO_2 levels, while over three years in the Duke Experimental Forest, plants achieved more biomass in the CO_2 enclosures than outside the enclosures, if the soil contained sufficient nitrogen availability to support enhanced growth. C_3 plants show a greater increase in biomass than C_4 plants, and nitrogen fixing legumes, especially soybean, had larger increases in biomass than plants depending on nitrogen from the soil. In general, increased CO_2 corresponds to some increase in biomass, but also to an increase in the carbon:nitrogen ratio.

The ratio of proteins and carbohydrates

You learned earlier in this chapter that nitrogen availability limits plant growth. As CO_2 levels increase, relatively less nitrogen and other macronutrients are found in leaves. Legumes, because of their nitrogen-fixing ability, have less of a decrease in nitrogen under elevated CO_2 conditions. In that event, herbivores need to eat more biomass to obtain adequate nutrients, particularly protein. This situation would be of significant concern in agriculture, and it could affect human health. Insect infestations could be more devastating if each herbivore consumed more biomass. Protein deficiencies in human diets could result from decreased nitrogen in crops.

The relative decreases in nitrogen in some plants is greater than would be predicted by an increase in CO_2 fixation alone. The additional decrease in nitrogen incorporation into proteins has been accounted for by a decrease in photorespiration in plants using NO_3^- as their primary nitrogen source, but not in plants using ammonia. It is possible that energy-wasting photorespiration may actually be necessary for nitrogen to be incorporated into proteins in some plants.

This example illustrates how interdependent the biochemical pathways are that regulate carbon and nitrogen levels. Although global change is an ecosystem-level problem, predictions about long-term effects hinge on understanding the physiological complexities of plant nutrition—an area of active research.



Elevated temperature can affect respiration and carbon levels in plants

As much as half of all the carbohydrates produced from photosynthesis each day can be used in plant respiration that same day. The amount of carbohydrate available for respiration may be affected by atmospheric CO_2 and photosynthesis, as just discussed. Furthermore, the anticipated rise in temperature over the next century may affect the rate of respiration in other ways. Altered respiration rates can affect overall nutrient balance and plant growth.

Inquiry question

? Why is plant respiration affected by both short-term and long-term temperature changes?

Biologists have known for a long time that respiration rates are temperature-sensitive in a broad range of plant species. Why does respiration rate change with temperature? One important factor is the effect of temperature on enzyme activity (see chapter 3). This effect is particularly important at very low temperatures and also very high temperatures that lead to protein denaturation.

Many responses of respiration rate to temperature change may be short-term, rather than long-term. Growing evidence indicates that respiration rate acclimates to a temperature increase over time, especially in leaves and roots that develop after the temperature shift. Over a long period at an elevated temperature, a plant could end up respiring at the same rate at which it had previously respired at a lower temperature.

Learning Outcomes Review 39.4

As atmospheric carbon dioxide increases, the rate of photosynthesis and the carbon:nitrogen ratio in plants are expected to increase as long as available soil nutrients do not change. A higher than normal carbon:nitrogen ratio would require herbivores to eat more biomass to meet their protein needs, which could, in turn, affect human health. As temperature increases, enzyme activity increases, accelerating the rate of respiration and breakdown of carbohydrates.

- ***What strategies could help keep the carbon:nitrogen ratio in crop plants lower?***

39.5 *Phytoremediation*

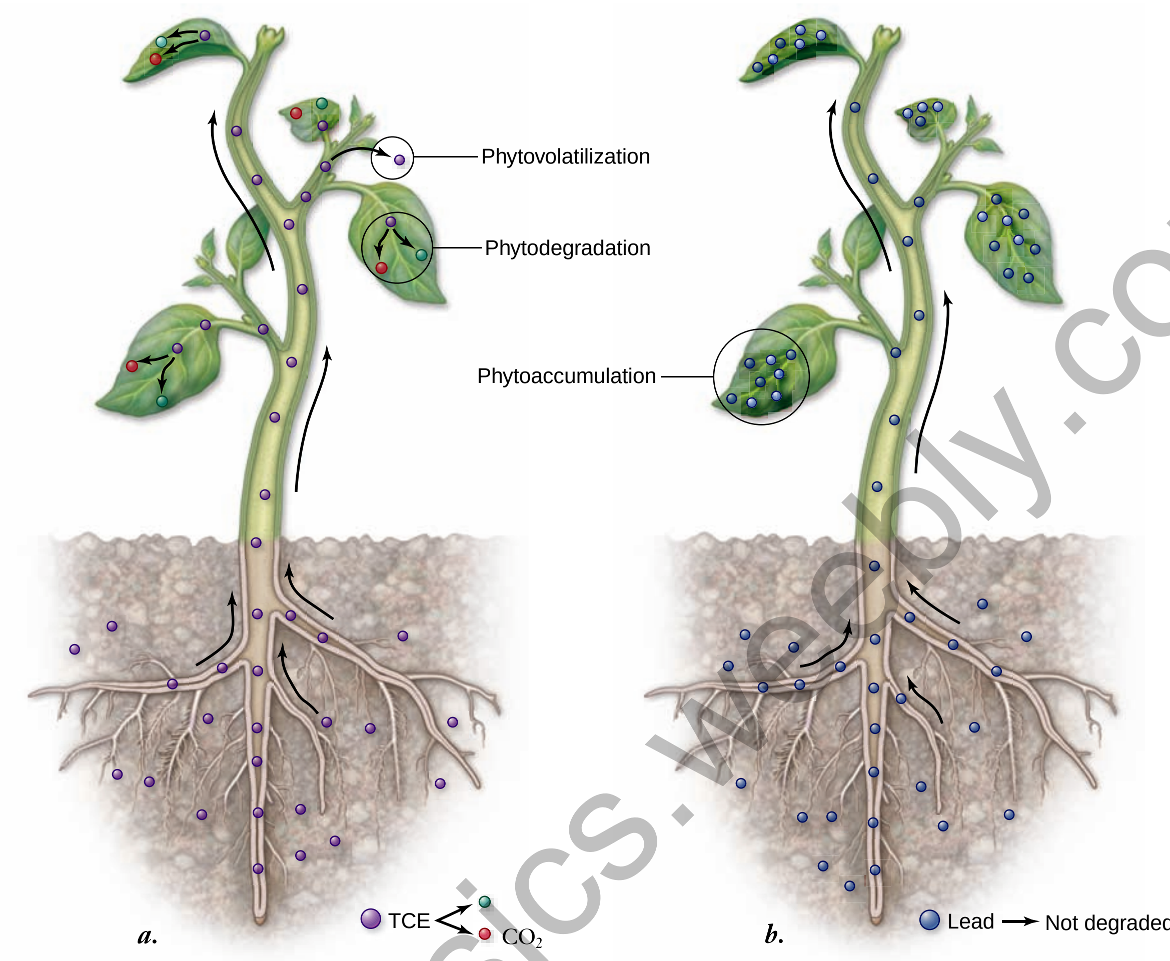
Learning Outcomes

1. ***Define phytoremediation.***
2. ***Explain how poplar trees have been used for phytoremediation.***
3. ***Describe an advantage and a disadvantage of phytoremediation.***

Some root cell membrane channels and transporters lack absolute specificity and can take up heavy metals like aluminum and other toxins. Although in most cases uptake of toxins is lethal or growth-limiting, some plants have evolved the ability to sequester or release these compounds into the atmosphere. These plants have potential for **phytoremediation,** the use of plants to concentrate or breakdown pollutants (figure 39.17).

Phytoremediation can work in a number of ways with both aquatic and soil pollutants. Plants may secrete a substance from

Figure 39.17
Phytoremediation. Plants can use the same mechanisms to remove both nutrients and toxins from the soil. ***a.*** TCE (trichloroethylene) can be taken up by plants and degraded into CO_2 and chlorine before being released into the atmosphere. This process is called *phytodegradation.* Some of the TCE moves so rapidly through the xylem that it is not degraded before it is released through the stomata as a gas in a process called *phytovolatilization.* ***b.*** Other toxins, including heavy metals such as lead, can be taken up by plants, but not degraded. Such *phytoaccumulation* is particularly effective in removing toxins if they are stored in the shoot, where they can more easily be harvested.



their roots that breaks down the contaminant. More often, the harmful chemical enters the roots and is preferably transported to the shoot system, making it easier to remove the chemical from the site. Some substances are simply stored by the plant; later, the plant material is harvested, dried, and removed to a storage site.

For example, after the nuclear reactor disaster at Chernobyl in northern Ukraine, sunflowers effectively removed radioactive cesium from nearby lakes. The plants were floated in foam supports on the surface of the lakes and later collected. Because up to 85% of the weight of herbaceous plants can be water, drying down phytoremediators can restrict toxins like radioactive cesium to a small area.

In this section, we will explore several examples of soil phytoremediation.

Trichloroethylene may be removed by poplar trees

Trichloroethylene (TCE) is a volatile solvent that has been widely used as spot remover in the dry-cleaning industry, for degreasing engine turbines, as an ingredient in paints and cosmetics, and even as an anesthetic in human and veterinary medicine. Unfortunately, TCE is also a confirmed carcinogen, and chronic exposure can damage the liver.

In 1980, the Environmental Protection Agency (EPA) established a Superfund to clean up contamination in the United States. Forty percent of all sites funded by the Superfund include TCE contamination. How can we clean up 1900 hectares of soil in a Marine Corps Air Station in Orange County, California, that contain TCE once used to clean fighter jets? Landfills can isolate, but not eliminate, this volatile substance. Burning eliminates it from the site, but may release harmful substances into the atmosphere. A promising approach is to use plants to remove TCE from the soil.

Plants may take up a toxin from soil, allowing the toxin to be removed and concentrated elsewhere; but an even more successful strategy is for the plant to break down the contaminant into nontoxic by-products. Poplar trees (genus *Populus*) may provide just such a solution for TCE-contaminated sites (figure 39.18). Poplars naturally take up TCE from the soil and metabolize it into CO_2 and chlorine.

Other plant species can break down TCE as well, but poplars have the advantage of size and rapid transpiration. A five-year-old poplar can move between 100 and 200 L of water from its roots out through its leaves in a day. A plant that transpires less would not be able to remove as much TCE in a day.

Figure 39.18
Phytoremediation for TCE. The U.S. Air Force is testing phytoremediation technology to clean up TCE at a former Air Force base in Fort Worth, Texas.

Although removing TCE with poplar trees sounds like the perfect solution, this method has some limitations. Not all the TCE is metabolized, and given the rapid rate of transpiration in the poplar, some of the TCE enters the atmosphere via the leaves. Once in the air, TCE has a half-life of 9 hours (half of it will break down into smaller molecules every 9 hours). Clearly, more risk assessment is needed before poplars are planted on every TCE-containing Superfund site.

The TCE that remains in the plant is metabolized quickly, and it is possible that the wood could be used after remediation is complete. It has been suggested that any remaining TCE would be eliminated if the wood were processed to make paper. Genetically modified poplars have been shown to metabolize about four times as much TCE as nonmodified poplars, so perhaps greater metabolic rates can be obtained.

As with any phytoremediation plan, it is critically necessary to estimate how much of a contaminant can be removed from a site by plants, and arriving at this estimate can be difficult. Possible risks, particularly when genetic modification is involved, must be weighed against the dangers posed by the contaminant.

Trinitrotoluene can be removed in limited amounts

In addition to volatile chemicals such as TCE, phytoremediation also holds promise for dealing with other environmental contaminants, including the explosive trinitrotoluene (TNT) and heavy metals. TNT is a solid, yellow material that was used widely in grenades and bombs until 1980. Contamination is found around factories that made TNT.

In some places, there is enough TNT in the soil to detonate, and thus incineration is not a viable option for removing TNT from most sites. Another issue is that TNT can seep into the groundwater; this is a matter of concern because TNT is carcinogenic and associated with liver disease.

TNT tends to stay near the top of the soil and to wash away quickly. Bean *(Phaseolus vulgaris)*, poplar, and the aquatic parrot feather *(Myriophyllum spicatum)* can take up and degrade low levels of TNT, but at higher concentrations, TNT is toxic to these plants.

Heavy metals can be successfully removed at lower cost

Heavy metals, including arsenic, cadmium, and lead, persist in soils and are toxic to animals in even small quantities. Many plants are also susceptible to heavy-metal toxicity, but species near mines have evolved strategies to partition certain heavy metals from the rest of the plant (see figure 39.17*b*).

Four hundred species of plants have been identified that have the ability to hyperaccumulate toxic metals from the soil. For example, *Brassica juncea* (a relative of broccoli and mustard plants) is especially effective at hyperaccumulating lead in the shoots of the plant. Unfortunately, *B. juncea* is a small, slow-growing plant, and eventually it becomes saturated with lead.

How would lead or cadmium travel from the soil into the leaves of a plant? There are some hints that root cell membranes may contain metal transporters that load the metal in the soil into the xylem. Citrate, mentioned earlier, can increase the rate of metal transport in xylem. The metals are sequestered inside vacuoles in the leaves. Trichomes, which are modified leaf epidermal cells, can sequester both lead and cadmium.

These hyperaccumulating plants are not a panacea for metal-contaminated soil because of concern that animals might move into the site and graze on lead- or cadmium-enriched plants. Harvesting and consolidating dried plant material is not a simple matter, but still phytoremediation is a promising technique. Estimated costs for phytoremediation are 50 to 80% lower than cleanup strategies that involve digging and dumping the contaminated soil elsewhere.

Phytoremediation may be a solution to the contamination resulting from a 1998 accident at the Aznalcóllar mine in Spain. A dam that contained the sludge from the mining operation broke, releasing 5 million cubic meters of sludge, composed of arsenic, cadmium, lead, and zinc, over 4300 hectares of land (figure 39.19). Much of the sludge was physically removed

Figure 39.19 Aznalcóllar mine spill. ***a.*** When the dike of a holding lagoon for mine waste broke, 5 million cubic meters of black sludge containing heavy metals was released into a national park and the Guadiamar River. ***b.*** Large amounts of sludge were removed mechanically. ***c.*** Phytoremediation appears to be a promising solution for treating the remaining heavy metals.

and dumped into an open mine pit. Phytoremediation solutions are being sought for the remaining contaminated soil.

Since the original spill, three plant species with the potential to hyperaccumulate some of the metals have begun growing in the area. These plants are fairly large and can accumulate a substantial amount of metal. They offer the advantage of being native species, thus reducing the dangers associated with introducing a nonnative, potentially invasive species to clean up the spill.

Learning Outcomes Review 39.5

Phytoremediation is the use of plants to concentrate or break down pollutants. Poplar trees can take up the soil contaminant trichloroethylene and break it down into nontoxic by-products. Compared with the alternative of removing contaminated soil, phytoremediation is less costly. A disadvantage is that animals could be harmed if they graze in an area where plants have taken up high levels of toxic compounds.

- *How could animals be protected from ingesting plants used for phytoremediation?*

Chapter Review

39.1 Soils: The Substrates on Which Plants Depend

Soil is composed of minerals, organic matter, water, air, and organisms.

Topsoil is a mixture of mineral particles, living organisms, and humus, which is partially decayed organic material. Microorganisms in the soil are important for nutrient recycling.

Water and mineral availability is determined by soil characteristics.

Minerals and organic soil particles are typically negatively charged so they draw positively charged ions away from the roots. Therefore, active transport of positively charged ions into the roots is required. Proton pumps in roots pump out H^+, creating an electrochemical gradient that draws mineral ions into the roots.

Approximately one-half the soil volume is made up of pores filled with air or water. Water added to the soil may drain through or be held in the pores, where it is available for root uptake.

Cultivation can result in soil loss and nutrient depletion.

Loss of topsoil through soil erosion results in reduced water-holding capacity and nutrient availability. Cultivation practices have been developed to reduce soil erosion.

Overuse of fertilizers, pesticides, and herbicides causes water pollution.

pH and salinity affect water and mineral availability.

Acidic soils release minerals, such as aluminum, at levels that are toxic to plants.

Saline soils alter water potential, leading to a loss of water and turgor in plants. Saline soils are common where irrigation is practiced.

39.2 Plant Nutrients

Plants require nine macronutrients and seven micronutrients.

The nine macronutrients required by plants are carbon, oxygen, hydrogen, nitrogen, potassium, calcium, magnesium, phosphorus, and sulfur. The eight micronutrients are chlorine, iron, manganese, zinc, boron, copper, molybdenum, and nickel.

Food security is related to crop productivity and nutrient levels.

Plant breeding efforts to increase nutrient levels in food crops aim to provide health benefits and improve food security.

39.3 Special Nutritional Strategies

Bacteria living in close association with roots can provide nitrogen.

Some plants, such as legumes, have a symbiotic relationship with nitrogen-fixing bacteria to obtain the nitrogen needed for protein synthesis. In exchange, the plants provide carbohydrates to the bacteria.

Mycorrhizae aid a large portion of terrestrial plants.

More than 90% of plants live in symbiotic association with mycorrhizal fungi. By extending the surface area of the root system, these fungi facilitate the uptake of phosphorus and micronutrients.

Carnivorous plants trap and digest animals to extract additional nutrients.

Some plants that live in acidic, nitrogen-poor environments obtain mineral nutrients by capturing and digesting small animals such as insects.

Parasitic plants exploit resources of other plants.

Some parasitic plants produce chlorophyll, while others do not. They tap into host plants to obtain nutrients, including carbohydrates.

39.4 Carbon–Nitrogen Balance and Global Change

Elevated CO_2 levels can alter photosynthesis and carbon levels in plants.

As CO_2 concentrations increase, the rate of photosynthesis increases and consequently biomass increases; however, the plant tissue that is produced is high in carbon relative to nitrogen, with a shift toward more carbohydrate and less protein.

As nutritional value decreases, more plant matter must be consumed to obtain the same amount of nutrients; the result is greater plant loss by herbivory.

Elevated temperature can affect respiration and carbon levels in plants.

The rate of enzyme reactions increases with ambient temperatures, increasing respiration. Because respiration breaks down carbohydrates, higher temperatures could cause additional changes in plant nutrient balance.

39.5 Phytoremediation

Phytoremediation utilizes plants to remove toxic contaminants from soil or water.

Trichloroethylene may be removed by poplar trees.

Poplar trees have been used to remove trichloroethylene from the soil and convert it to nontoxic carbon dioxide and chlorine compounds.

Trinitrotoluene can be removed in limited amounts.

Some plants can take up low levels of trinitrotoluene (TNT) in the soil and degrade it. However, high levels are toxic to the plants.

Heavy metals can be successfully removed at lower cost.

Plants may accumulate high levels of contaminants in their shoots and store them there. The plants can be harvested and removed. If animals feed on these plants, however, they may be exposed to high concentrations of toxic compounds.

Phytoremediation is less expensive than removing contaminated soils.

Review Questions

UNDERSTAND

1. Which of the following is not found in topsoil?
   a. Humus
   b. Bedrock
   c. Bacteria
   d. Air
2. Mineral soil particles are typically
   a. negatively charged.
   b. positively charged.
   c. neutral.
3. What proportion of the soil volume is occupied by air and water?
   a. 10%
   b. 25%
   c. 50%
   d. 75%
   e. 90%
4. Which of the following is a micronutrient?
   a. Nitrogen
   b. Calcium
   c. Phosphorus
   d. Iron
5. The nodules of legume roots contain nitrogen-fixing
   a. bacteria.
   b. fungi.
   c. algae.
   d. plants.
6. Photorespiration occurs when
   a. glucose interacts with carbon dioxide.
   b. rubisco binds with oxygen.
   c. RuBP is converted to a sugar.
   d. the Sun provides energy for the breakdown of sugar.
7. In a C_4 plant, the Calvin cycle occurs in
   a. the epidermis.
   b. vascular tissue.
   c. bundle sheath cells.
   d. mesophyll cells.
8. One potential problem with using poplars to remove TCE from soils is that
   a. some TCE enters the atmosphere via the transpiration stream.
   b. poplar trees grow slowly.
   c. most TCE will wash away from the soil before it is removed.
   d. TCE interferes with chlorophyll production.

APPLY

1. You are performing an experiment to determine the nutrient requirements for a newly discovered plant and find that for some reason your plants die if you leave boron out of the growth medium but do fine with as low as 5 ppm in solution. This suggests that boron is
   a. an essential macronutrient.
   b. a nonessential micronutrient.
   c. an essential micronutrient.
   d. a nonessential macronutrient.
2. If you wanted to conduct an experiment to determine the effects of varying levels of macronutrients on plant growth and did so in your small greenhouse at home, which of the following macronutrients would be the most difficult to regulate?
   a. Carbon
   b. Nitrogen
   c. Potassium
   d. Phosphorus
3. Which of the following would decrease nitrogen availability for a pea plant?
   a. Inability of the plant to produce flavonoids
   b. Formation of Nod factors
   c. Presence of oxygen in the soil
   d. Production of leghemoglobin
4. Which of the following might you do to increase nutrient uptake by crop plants?
   a. Decrease the solubility of nutrients
   b. Create nutrients as positive ions
   c. Frequently plow the soil
   d. Genetically modify plants to increase the density of plasma membrane transporters in root cells
5. If you were to eat one ton (1000 kg) of potatoes, calculate approximately how much of the following minerals would you eat?
   a. Copper between 4–30 ppm
   b. Zinc between 15–100 ppm
   c. Potassium between 0.5 and 6%
   d. Iron between 25–300 ppm

SYNTHESIZE

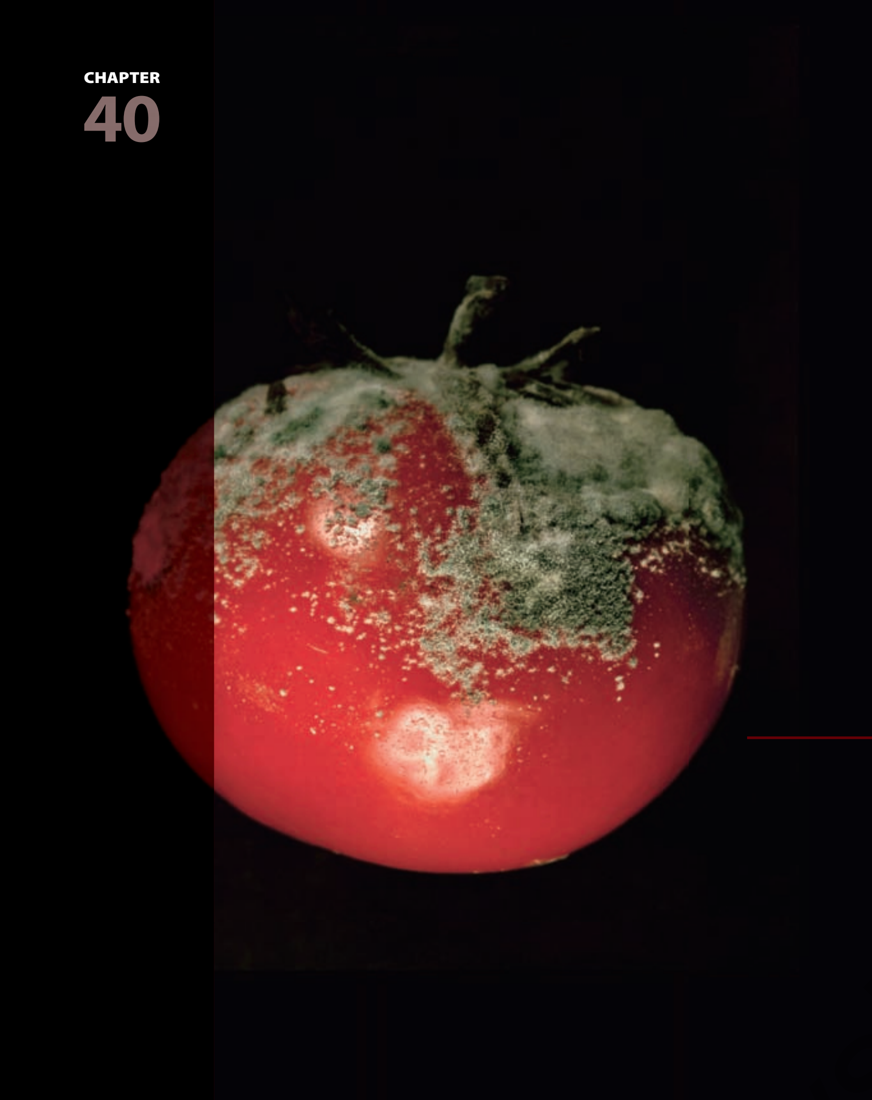
1. A common farming practice involves fumigating the soil to kill harmful fungi. Fumigants may not be selective, though, so they may kill most microorganisms in the soil. What short-term and long-term effects might fumigation have on the soil?
2. Describe an experiment to determine the amount of boron needed for the normal growth of tomato seedlings.
3. Growers of commercial crops in greenhouses often use supplemental carbon dioxide to enhance plant growth. What other inputs do you suppose they must provide to maximize plant growth?

ONLINE RESOURCE

www.ravenbiology.com

Understand, Apply, and Synthesize—enhance your study with animations that bring concepts to life and practice tests to assess your understanding. Your instructor may also recommend the interactive eBook, individualized learning tools, and more.

CHAPTER
40



Chapter 40

Plant Defense Responses

Chapter Outline

Introduction

Plants are constantly under attack by viruses, bacteria, fungi, animals, and even other plants. An amazing array of defense mechanisms has evolved to block or temper an invasion. Many plant–pest relationships undergo coevolution, with the plant winning sometimes and the pest winning with a new offensive adaptation at other times. The first line of plant defense is thick cell walls covered with a strong cuticle. Bark, thorns, and even trichomes can deter a hungry insect. When that first line of defense fails, a chemical arsenal of toxins is waiting. Many of these molecules have no effect on the plant. Some are modified by microbes in the intestine of an herbivore into a poisonous compound. Maintaining a toxin arsenal is energy-intensive; so, an alternative means of defense uses induced responses to protect and prevent future attacks.

40.1 Physical Defenses

Learning Outcomes

1. *Identify the compounds produced by the epidermis to protect against invasion.*
2. *Outline the steps taken by a fungus to invade a plant leaf.*
3. *Describe two beneficial associations between plants and microorganisms.*

There are no tornado shelters for trees. Storms and changing environmental conditions can be life-threatening to plants. Structurally, trees can often withstand high winds and the weight of ice and snow, but there are limits. Winds can uproot a tree, or snap the main shoot off a small plant. Axillary buds give many plants a second chance as they grow out and replace the lost shoot (figure 40.1).

Although abiotic factors such as weather constitute genuine threats to a plant, even greater daily threats exist in the form of viruses, bacteria, fungi, animals, and other plants. These enemies can tap into the nutrient resources of plants or use