39

Nutrition and Transport in Plants

FIGURE 39.1
A carnivorous plant. Most plants absorb water and essential nutrients from the soil, but carnivorous plants are able to obtain some nutrients directly from small animals.

Concept Outline

39.1 Plants require a variety of nutrients in addition to the direct products of photosynthesis.

Plant Nutrients. Plants require a few macronutrients in large amounts and several micronutrients in trace amounts.

Soil. Plant growth is significantly influenced by the nature of the soil.

39.2 Some plants have novel strategies for obtaining nutrients.

Nutritional Adaptations. Venus flytraps and other carnivorous plants lure and capture insects and then digest them to obtain energy and nutrients. Some plants entice bacteria to produce organic nitrogen for them. These bacteria may be free-living or form a symbiotic relationship with a host plant. About 90% of all vascular plants rely on fungal associations to gather essential nutrients, especially phosphorus.

39.3 Water and minerals move upward through the xylem.

Overview of Water and Mineral Movement through Plants. The bulk movement of water and dissolved minerals is the result of movement between cells, across cell membranes, and through tubes of xylem.

Water and Mineral Absorption. Water and minerals enter the plant through the roots.

Water and Mineral Movement. A combination of the properties of water, structure of xylem, and transpiration of water through the leaves results in the passive movement of water to incredible heights. Water leaves the plant through openings in the leaves called stomata. Too much water is harmful to a plant, although many plants have adaptations that make them tolerant of flooding.

39.4 Dissolved sugars and hormones are transported in the phloem.

Phloem Transport Is Bidirectional. Sucrose and hormones can move from shoot to root or root to shoot in the phloem. Phloem transport requires energy to load and unload sieve tubes.

Vast energy inputs are required for the ongoing construction of a plant such as described in chapter 38. In this chapter, we address two major questions: (1) what inputs, besides energy from the sun, does a plant need to survive? and (2) how do all parts of the complex plant body share the essentials of life? Plants, like animals, need various nutrients to remain alive and healthy. 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 through photosynthesis and from the soil, although some take a more direct approach (figure 39.1). Carbohydrates produced in leaves must be carried throughout the plant, and minerals and water absorbed from the ground must be transported up to the leaves and other parts of the plant. As discussed in chapter 38, these two types of transport take place in specialized tissues, xylem and phloem.

39.1 Plants require a variety of nutrients in addition to the direct products of photosynthesis.

Plant Nutrients

The major source of plant nutrition is the fixation of atmospheric CO_2 into simple sugar using the energy of the sun. CO_2 enters through the stomata. O_2 is a product of photosynthesis and atmospheric component that also moves through the stomata. It is used in cellular respiration to release energy from the chemical bonds in the sugar to support growth and maintenance in the plant. However, CO_2 and light energy are not sufficient for the synthesis of all the molecules a plant needs. Plants require a number of inorganic nutrients (table 39.1). Some of these are macronutrients, which the plants need in relatively large amounts, and others are micronutrients, which are required in trace amounts. There are nine macronutrients: carbon, hydrogen, and oxygen—the three elements found in all organic compounds—as well as nitrogen (essential for amino acids), potassium, calcium, phosphorus, magnesium (the center of the chlorophyll molecule), and sulfur. Each of these nutrients approaches or, as in the case with carbon, may greatly exceed 1% of the dry weight of a healthy plant. The seven micronutrient elements—iron, chlorine, copper, manganese, zinc, molybdenum, and boron—constitute from less than one to several hundred parts per million in most plants (figure 39.2). 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.

Nutritional requirements are assessed in hydroponic cultures; the plants roots are suspended in aerated water containing nutrients. The solutions contain all the necessary nutrients in the right proportions but with certain known or suspected nutrients left out. The plants are then

Table 39.1 Essential Nutrients in Plants

Elements	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^{++})	0.2–3.5	Component of cell walls, maintenance of membrane structure and permeability, activates some enzymes
Magnesium	(Mg^{++})	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	($SO_4^=$)	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^{++}, Fe^{+++})	25–300	Chlorophyll synthesis, cytochromes, nitrogenase
Manganese	(Mn^{++})	15–800	Activator of certain enzymes
Zinc	(Zn^{++})	15–100	Activator of many enzymes, active in formation of chlorophyll
Boron	(BO_3^- or $B_4O_7^=$)	5–75	Possibly involved in carbohydrate transport, nucleic acid synthesis
Copper	(Cu^{++})	4–30	Activator or component of certain enzymes
Molybdenum	($MoO_4^=$)	0.1–5	Nitrogen fixation, nitrate reduction

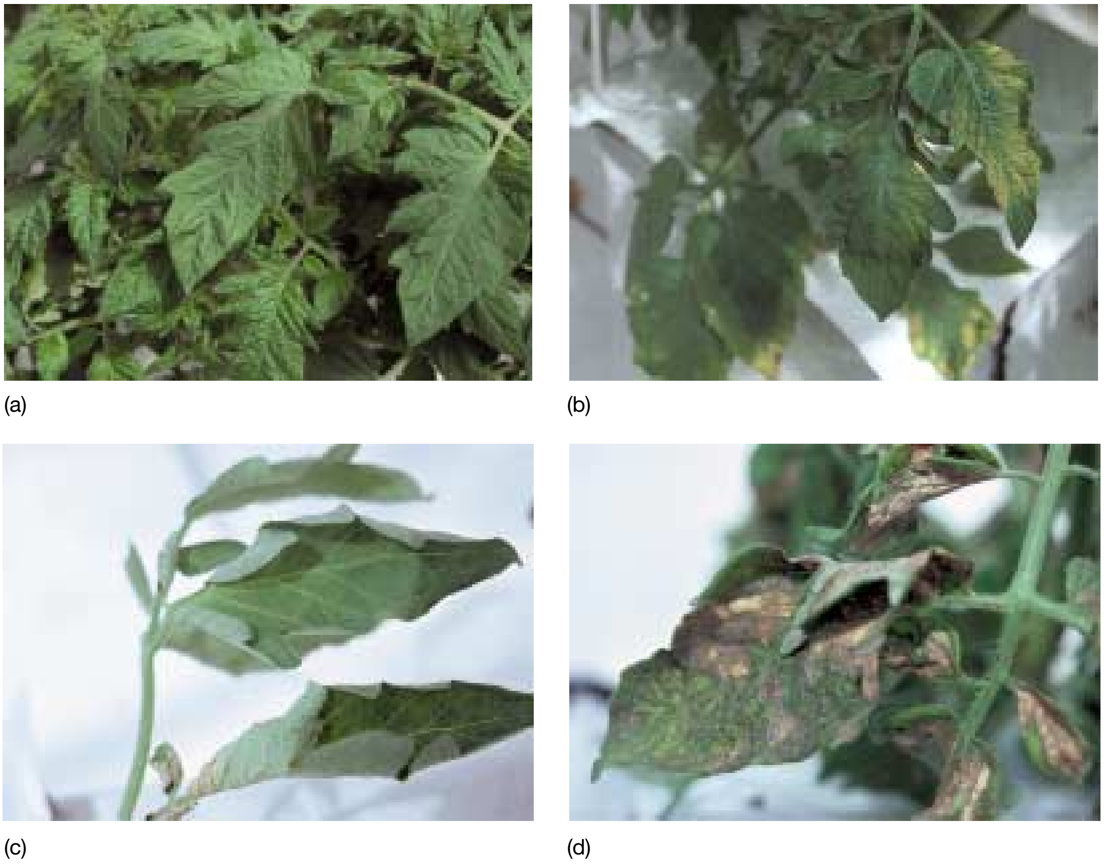


FIGURE 39.2
Mineral deficiencies in plants. (*a*) Leaves of a healthy Marglobe tomato (*Lycopersicon esculentum*) plant. (*b*) Chlorine-deficient plant with necrotic leaves (leaves with patches of dead tissue). (*c*) Copper-deficient plant with blue-green, curled leaves. (*d*) Zinc-deficient plant with small, necrotic leaves. (f) Manganese-deficient plant with chlorosis (yellowing) between the veins. The agricultural implications of deficiencies such as these are obvious; a trained observer can determine the nutrient deficiencies that are affecting a plant simply by inspecting it.

allowed to grow and are studied for the presence of abnormal symptoms that might indicate a need for the missing element (figure 39.3). However, the water or vessels used often contain enough micronutrients to allow the plants to grow normally, even though these substances were not added deliberately to the solutions. To give an idea of how small the quantities of micronutrients may be, the standard dose of molybdenum added to seriously deficient soils in Australia amounts to about 34 grams (about one handful) per hectare, once every 10 years! Most plants grow satisfactorily in hydroponic culture, and the method, although expensive, is occasionally practical for commercial purposes. Analytical chemistry has made it much easier to take plant material and test for levels of different molecules. One application has been the investigation of elevated levels of CO_2 (a result of global warming) on plant growth. With increasing levels of CO_2, the leaves of some plants increase in size, but the amount of nitrogen decreases relative to carbon. This decreases the nutritional value of the leaves to herbivores.

The plant macronutrients carbon, oxygen, and hydrogen constitute about 94% of a plant's dry weight; the other macronutrients—nitrogen, potassium, calcium, phosphorus, magnesium, and sulfur—each approach or exceed 1% of a plant's dry weight.

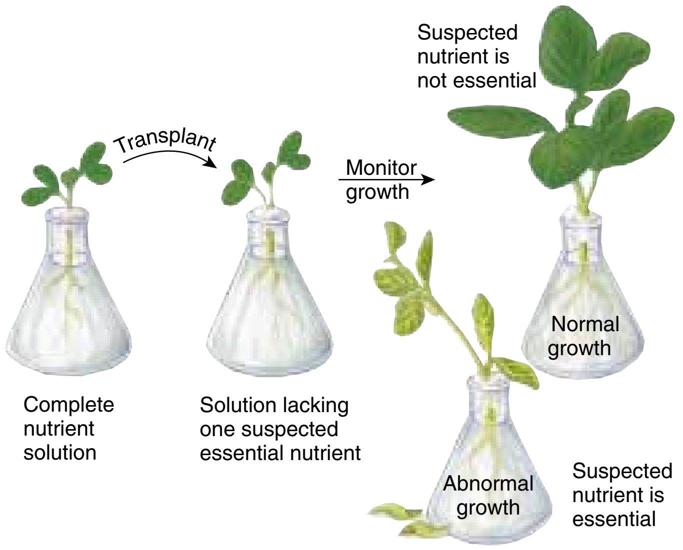


FIGURE 39.3
Identifying nutritional requirements of plants. A seedling is first grown in a complete nutrient solution. The seedling is then transplanted to solution that lacks one suspected essential nutrient. The growth of the seedling is then studied for the presence of abnormal symptoms, such as discolored leaves and stunted growth. 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 lacking nutrient is essential for growth.

Soil

Plant growth is affected by soil composition. 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, and various other forms of mineral and organic matter; pore spaces containing water and air occur between the particles. The mineral fraction of soils varies according to the composition of the rocks. The crust includes about 92 naturally occurring elements; table 2.1 in chapter 2 lists the most common of these elements and their percentage of the earth's crust by weight. Most elements are combined as 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. About 5 metric tons of carbon is tied up in the organisms that are present in the soil under a hectare (0.06 mile^2) of wheat land in England, an amount that approximately equals the weight of 100 sheep!

Most roots are found in **topsoil** (figure 39.4), which is a mixture of mineral particles of varying size (most less than 2 mm thick), living organisms, and **humus.** Humus consists of partly decayed organic material. 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.

About half of the total soil volume is occupied by spaces or pores, which may be filled with air or water, depending on moisture conditions. Some of the soil water, because of its properties described below, is unavailable to plants. Due to gravity, some of the water that reaches a given soil will drain through it immediately. Another fraction of the water is held in small soil pores, which are generally less than about 50 micrometers in diameter. This water is readily available to plants. When it is depleted through evaporation or root uptake, the plant will wilt and eventually die unless more water is added to the soil.

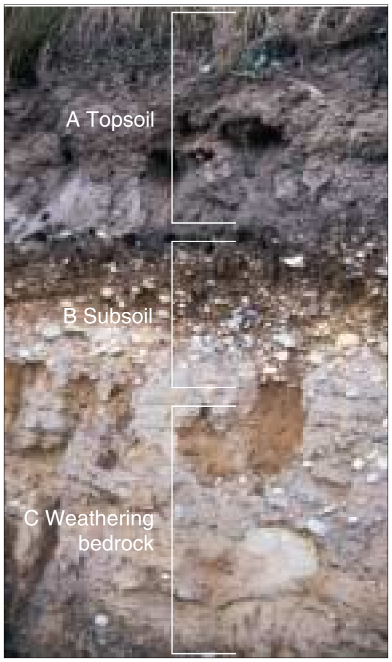


FIGURE 39.4
Most roots occur in topsoil. The uppermost layer in soil is called topsoil, and it contains organic matter, such as roots, small animals, and humus, and mineral particles of various sizes. Subsoil lies underneath the topsoil and contains larger mineral particles and relatively little organic matter. Beneath the subsoil are layers of bedrock, the raw material from which soil is formed over time and weathering.

Cultivation

In natural communities, nutrients are recycled and made available to organisms on a continuous basis. When these communities are replaced by cultivated crops, the situation changes drastically: the soil is much more exposed to erosion and the loss of nutrients. For this reason, cultivated crops and garden plants usually must be supplied with additional mineral nutrients.

One solution to this is **crop rotation**. For example, a farmer might grow corn in a field one year and soybeans the next year. Both crops remove nutrients from the soil, but the plants have different nutritional requirements, and therefore the soil does not lose the same nutrients two years in a row. Soybean plants even add nitrogen compounds to the soil, released by nitrogen-fixing bacteria growing in nodules on their roots. Sometimes farmers allow a field to lie fallow—that is, they do not grow a crop in the field for a year or two. This allows natural processes to rebuild the field's store of nutrients.

Other farming practices that help maintain soil fertility involve plowing under plant material left in fields. You can do the same thing in a lawn or garden by leaving grass clippings and dead leaves. Decomposers in the soil do the rest, turning the plant material into humus.

Fertilizers are also used to replace nutrients lost in cultivated fields. The most important mineral nutrients that need to be added to soils are nitrogen (N), phosphorus (P), and potassium (K). All of these elements are needed in large quantities (see table 39.1) and are the most likely to become deficient in the soil. Both chemical and organic fertilizers are often added in large quantities and can be significant sources of pollution in certain situations (see chapter 30). Organic fertilizers were widely used long before chemical fertilizers were available. Substances such as manure or the remains of dead animals have traditionally been applied to crops, and plants are often plowed under to increase the soil's fertility. There is no basis for believing that organic fertilizers supply any element to plants that inorganic fertilizers cannot provide and they can. However, organic fertilizers build up the humus content of the soil, which often enhances its water- and nutrient-retaining properties. For this reason, nutrient availability to plants at different times of the year may be improved, under certain circumstances, with organic fertilizers.

Soils contain organic matter and various minerals and nutrients. Farming practices like crop rotation, plowing crops under, and fertilization are often necessary to maintain soil fertility.

39.2 Some plants have novel strategies for obtaining nutrients.

Nutritional Adaptations

Carnivorous Plants

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 directly, such plants obtain adequate nitrogen supplies and thus are able to grow in these seemingly unfavorable environments. Carnivorous plants have modified leaves adapted to lure and trap insects and other small animals (figure 39.5). The plants digest their prey with enzymes secreted from various types of glands.

The Venus flytrap *(Dionaea muscipula)*, which grows in the bogs of coastal North and South Carolina, has three sensitive hairs on each side of each leaf, which, when touched, trigger the two halves of the leaf to snap together (see figure 39.1). Once the Venus flytrap enfolds a prey item within a leaf, enzymes secreted from the leaf surfaces digest the prey. These flytraps actually shut and open by a growth mechanism. They have a limited number of times they can open and close as a result. In the sundews, the glandular trichomes secrete both sticky mucilage, which traps small animals, and digestive enzymes. Unlike Venus flytraps they do not close rapidly and it is possible that the two share a common ancestor.

Pitcher plants attract insects by the bright, flowerlike colors within their pitcher-shaped leaves and perhaps also by sugar-rich secretions. Once inside the pitchers, insects slide down into the cavity of the leaf, which is filled with water and digestive enzymes.

Bladderworts, *Utricularia*, are aquatic. They sweep small animals into their bladderlike leaves by the rapid action of a springlike trapdoor, and then they digest these animals.

FIGURE 39.5
A carnivorous plant. A tropical Asian pitcher plant, *Nepenthes*. Insects enter the pitchers and are trapped and digested. Complex communities of invertebrate animals and protists inhabit the pitchers.

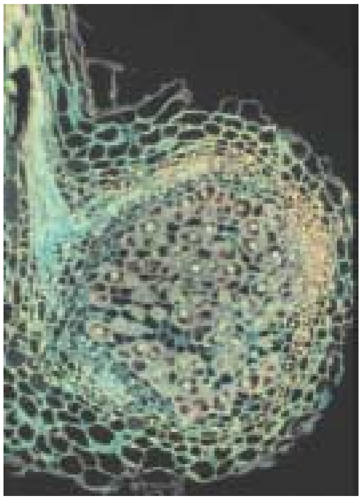


FIGURE 39.6
Nitrogen-fixing nodule. A root hair of alfalfa is invaded by *Rhizobium*, a bacterium (yellow structures) that fixes nitrogen. Through a series of exchanges of chemical signals, the plant cells divide to create a nodule for the bacteria which differentiate and begin producing ammonia.

Nitrogen-Fixing Bacteria

Plants need ammonia (NH_3) to build amino acids, but most of the nitrogen is in the atmosphere in the form of N_2. Plants lack the biochemical pathways (including the enzyme nitrogenase) necessary to convert gaseous nitrogen to ammonia, but some bacteria have this capacity. Some of these bacteria live in close association with the roots of plants. Others go through an intricate dance and end up being housed in plant tissues created especially for them called nodules (figure 39.6). Only legumes are capable of forming root nodules and there is a very specific recognition required by a bacteria species and its host. Hosting these bacteria costs the plant in terms of energy, but is well worth it when there is little ammonia in the soil. An energy conservation mechanism has evolved in the legumes so that the root hairs will not respond to bacterial signals when nitrogen levels are high.

Mycorrhizae

While symbiotic relationships with nitrogen-fixing bacteria are rare, symbiotic associations with mycorrhizal fungi are found in about 90% of the vascular plants. These fungi have been described in detail in chapter 36. In terms of plant nutrition, it is important to recognize the significant role these organisms play in enhancing phosphorus transfer to the plant. The uptake of some of the micronutrients is also enhanced. Functionally, the mycorrhizae extend the surface area of nutrient uptake substantially

Carnivorous plants obtain nutrients, especially nitrogen, directly by capturing and digesting insects and other organisms. Nitrogen can also be obtained from bacteria living in close association with the roots. Fungi help plants obtain phosphorus and other nutrients from the soil.

39.3 Water and minerals move upward through the xylem.

Overview of Water and Mineral Movement through Plants

Local Changes Result in the Long-Distance, Upward Movement of Water

Most of the nutrients and water discussed above enter the plant through the roots and move upward in the xylem. It is not unusual for a large tree to have leaves more than 10 stories off the ground (figure 39.7). Did you ever wonder how water gets from the roots to the top of a tree that high? Water moves through the spaces between the protoplasts of cells, through plasmodesmata (membrane connections between cells), through cell membranes and through the continuous tubing system in the xylem. We know that there are interconnected, water-conducting xylem elements extending throughout a plant. We also know that water first enters the roots and then moves to the xylem. After that, however, water rises through the xylem because of a combination of factors and some exits through the stomata in the leaves.

While most of our focus will be on the mechanics of water transport through xylem, the movement of water at the cellular level plays a significant role in bulk water transport in the plant as well, although over much shorter distances. You know that the Casparian strip in the root forces water to move through cells. In the case of parenchyma cells it turns out that most water also moves across membranes rather than in the intercellular spaces. For a long time, it was believed that water moved across cell membranes only by osmosis through the lipid bilayer. We now know that osmosis is enhanced by water channels called **aquaporins**. These transport channels are found in both plants and animals. In plants they exist in vacuole and plasma membranes. There at least 30 different genes coding for aquaporin-like proteins in *Arabidopsis*. Some aquaporins only appear or open during drought stress. Aquaporins allow for faster water movement between cells than osmosis. They are important not only in maintaining water balance within a cell, but in getting water between many plant cells and the xylem. The greatest distances traveled by water molecules and dissolved minerals are in the xylem.

Once water enters the xylem, it can move upward 100 m in the redwoods. Some "pushing" from the pressure of water entering the roots is involved. However, most of the force is "pulling" caused by water evaporating (**transpiration**) through the stomata on the leaves and other plant surfaces. This works because water molecules stick to themselves with hydrogen bonds (cohesion) and to the walls of the tracheid or xylem vessel (adhesion). The result is an unusually stable column of liquid reaching great heights.

FIGURE 39.7
How does water get to the top of this tree? We would expect gravity to make such a tall column of water too heavy to be maintained by capillary action. What pulls the water up?

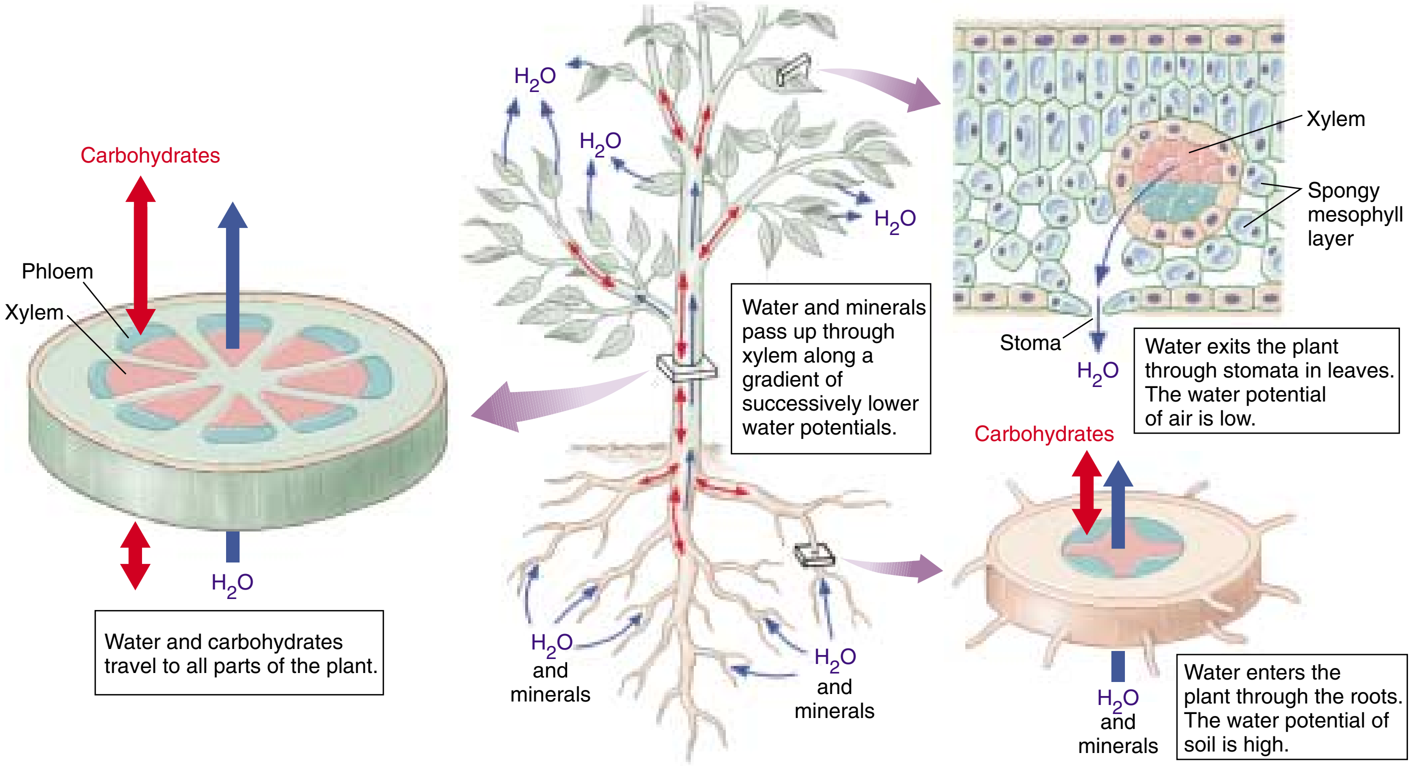


FIGURE 39.8

Water movement through a plant. This diagram illustrates the path of water and inorganic materials as they move into, through, and out of the plant body.

Water Potential

Plant biologists often discuss the forces that act on water within a plant in terms of **potentials.** The *turgor pressure,* which is a physical pressure that results as water enters the cell vacuoles, is referred to as **pressure potential.** Water coming through a garden hose is an example of physical pressure. There is also a potential caused by an uneven distribution of a solute on either side of a membrane, which will result in osmosis (movement of water to the side with the greater concentration of solute). By applying pressure (on the side that has the greater concentration of solute), it is possible to prevent osmosis from taking place. The smallest amount of pressure needed to stop osmosis is referred to as the **solute** (or **osmotic**) **potential** of the solution. Water will enter a cell osmotically until it is stopped by the pressure potential caused by the cell wall. The **water potential** of a plant cell is, in essence, the combination of its pressure potential and solute potential; it represents the total potential energy of the water in a plant. If two adjacent cells have different water potentials, water will move from the cell with the higher water potential to the cell with the lower water potential. Water in a plant moves along a gradient between the relatively high water potential in the soil to successively lower water potentials in the roots, stems, leaves, and atmosphere.

Water potential in a plant regulates movement of water. At the roots there is a positive water potential (except in the case of severe drought). On the surface of leaves and other organs, water loss called **transpiration** creates a negative pressure. It depends on its osmotic absorption by the roots and the negative pressures created by water loss from the leaves and other plant surfaces (figure 39.8). The negative pressure generated by transpiration is largely responsible for the upward movement of water in xylem.

Aquaporins enhance water transport at the cellular level, which ultimately affects bulk water transport. The loss of water from the leaf surface, called transpiration, literally pulls water up the stem from the roots which have the greater water potential. This works because of the strong cohesive forces between molecules of water that allow them to stay "stuck" together in a liquid column and adhesion to walls of tracheids and vessels.

Water and Mineral Absorption

Most of the water absorbed by the plant comes in through root hairs, which collectively have an enormous surface area (figure 39.8). Root hairs are almost always turgid because their solute potential is greater than that of the surrounding soil due to mineral ions being actively pumped into the cells. Because the mineral ion concentration in the soil water is usually much lower than it is in the plant, an expenditure of energy (supplied by ATP) is required for the accumulation of such ions in root cells. The plasma membranes of root hair cells contain a variety of protein transport channels, through which *proton pumps* (see page 120) transport specific ions against even large concentration gradients. Once in the roots, the ions, which are plant nutrients, are transported via the xylem throughout the plant.

The ions may follow the cell walls and the spaces between them or more often go directly through the plasma membranes and the protoplasm of adjacent cells (figure 39.9). When mineral ions pass between the cell walls, they do so nonselectively. Eventually, on their journey inward, they reach the endodermis and any further passage through the cell walls is blocked by the Casparian strips. Water and ions must pass through the plasma membranes and protoplasts of the endodermal cells to reach the xylem. However, transport through the cells of the endodermis is selective. The endodermis, with its unique structure, along with the cortex and epidermis, controls which ions reach the xylem.

Transpiration from the leaves (figure 39.10), which creates a pull on the water columns, indirectly plays a role in helping water, with its dissolved ions, enter the root cells. However, at night, when the relative humidity may approach 100%, there may be no transpiration. Under these circumstances, the negative pressure component of water potential becomes small or nonexistent.

Active transport of ions into the roots still continues to take place under these circumstances. This results in an increasingly high ion concentration with the cells, which causes more water to enter the root hair cells by osmosis. In terms of water potential, we say that active transport increases the solute potential of the roots. The result is movement of water into the plant and up the xylem columns despite the absence of transpiration. This phenomenon is called **root pressure,** which in reality is an osmotic phenomenon.

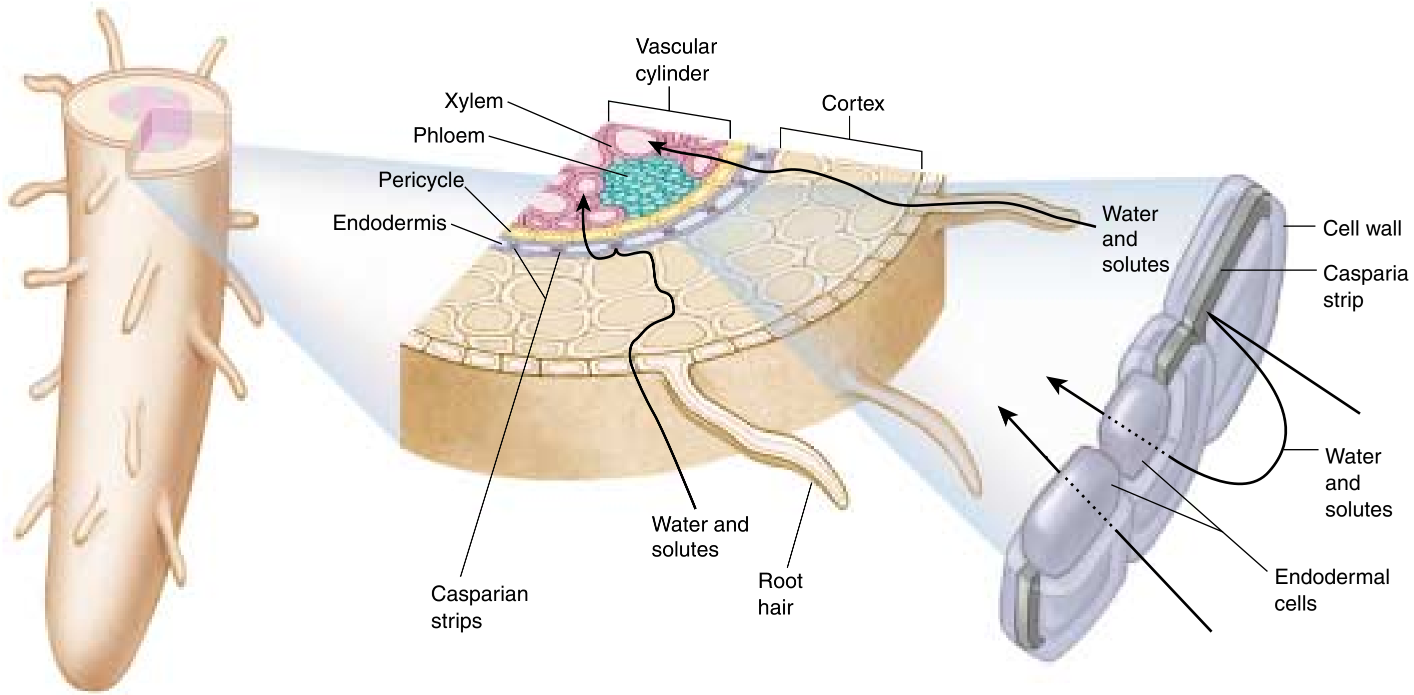


FIGURE 39.9
The pathways of mineral transport in roots. Minerals are absorbed at the surface of the root, mainly by the root hairs. In passing through the cortex, they must either follow the cell walls and the spaces between them or go directly through the plasma membranes and the protoplasts of the cells, passing from one cell to the next by way of the plasmodesmata. When they reach the endodermis, however, their further passage through the cell walls is blocked by the Casparian strips, and they must pass through the membrane and protoplast of an endodermal cell before they can reach the xylem.

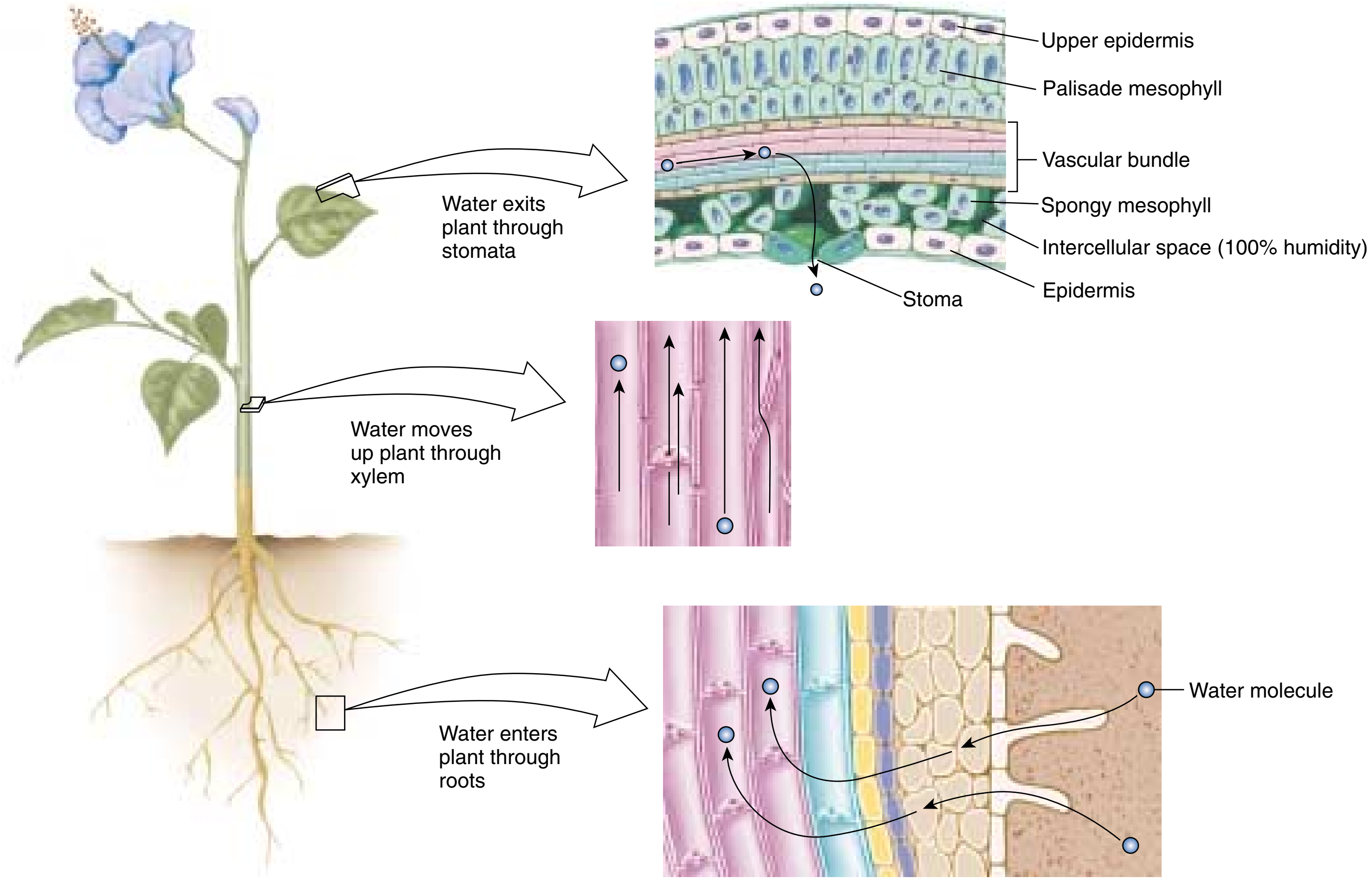


FIGURE 39.10
Transpiration. Water evaporating from the leaves through the stomata causes the movement of water upward in the xylem and the entrance of water through the roots.

Under certain circumstances, root pressure is so strong that water will ooze out of a cut plant stem for hours or even days. When root pressure is very high, it can force water up to the leaves, where it may be lost in a liquid form through a process known as **guttation** (figure 39.11). Guttation does not take place through the stomata, but instead occurs through special groups of cells located near the ends of small veins that function only in this process. Root pressure is never sufficient to push water up great distances.

Water enters the plant by osmosis. Transport of minerals (ions) across the endodermis is selective. Root pressure, which often occurs at night, is caused by the continued, active accumulation of ions in the roots at times when transpiration from the leaves is very low or absent.

FIGURE 39.11
Guttation. In herbaceous plants, water passes through specialized groups of cells at the edges of the leaves; it is visible here as small droplets around the edge of the leaf in this strawberry plant (*Fragaria ananassa*).

Water and Mineral Movement

Water and Mineral Movement through the Xylem

It is clear that root pressure is insufficient to push water to the top of a tall tree, although it can help. So, what does work? Otto Renner proposed the solution in Germany in 1911. Passage of air across leaf surfaces results in loss of water by evaporation, creating a pull at the open upper end of the "tube." Evaporation from the leaves produces a tension on the entire water column that extends all the way down to the roots. Water has an inherent tensile strength that arises from the cohesion of its molecules, their tendency to form hydrogen bonds with one another. 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 plants have transporting vessels of very narrow diameter, the cohesive forces in them are strong. The water molecules also adhere to the sides of the tracheid or xylem vessels, further stabilizing the long column of water.

The water column would fail if air bubbles were inserted (visualize a tower of blocks and then pull one out in the middle). Anatomical adaptations decrease the probability of this. Individual tracheids and vessel members are connected by one of more *pits* (cavities) in their walls. Air bubbles are generally larger than the openings, so they cannot pass through them. Furthermore, the cohesive force of water is so great that the bubbles are forced into rigid spheres that have no plasticity and therefore cannot squeeze through the openings. Deformed cells or freezing can cause small bubbles of air to form within xylem cells. Any bubbles that do form are limited to the xylem elements where they originate, and water may continue to rise in parallel columns. This is more likely to occur with seasonal temperature changes. As a result, most of the active xylem in woody plants occurs peripherally, toward the vascular cambium.

Most minerals the plant needs enter the root through active transport. Ultimately, they are removed from the roots 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, such a pattern of ionic concentration helps to conserve these essential nutrients, which may move from mature deciduous parts such as leaves and twigs to areas of active growth. 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 re-enter the xylem conduit. Calcium, an essential nutrient, cannot be transported elsewhere once it has been deposited in plant parts.

Transpiration of Water from Leaves

More than 90% of the water taken in by the roots of a plant is ultimately lost to the atmosphere through transpiration from the leaves. Water moves into the pockets of air in the leaf from the moist surfaces of the walls of the mesophyll cells. As you saw in chapter 38, these intercellular spaces are in contact with the air outside of the leaf by way of the stomata. Water that evaporates from the surfaces of the mesophyll cells leaves the stomata as vapor. This water is continuously replenished from the tips of the veinlets in the leaves.

Water is essential for plant metabolism, but is continuously being lost to the atmosphere through the stomata. Photosynthesis requires a supply of CO_2 entering the stomata from the atmosphere. This results in 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 like humidity and the time of day. After the sun sets, transpiration from the leaves decreases. The sun is the ultimate source of potential energy for water movement. The water potential that is responsible for water movement is largely the product of negative pressure generated by transpiration, which is driven by the warming effects of sunlight.

The Regulation of Transpiration Rate. On a short-term basis, closing the stomata can control water loss. This occurs in many plants when they are subjected to water stress. However, 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. 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. A plant must respond both to the need to conserve water and to the need to admit CO_2.

Stomata open and close because of changes in the turgor pressure of their guard cells. The sausage- or dumbbell-shaped guard cells 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 place

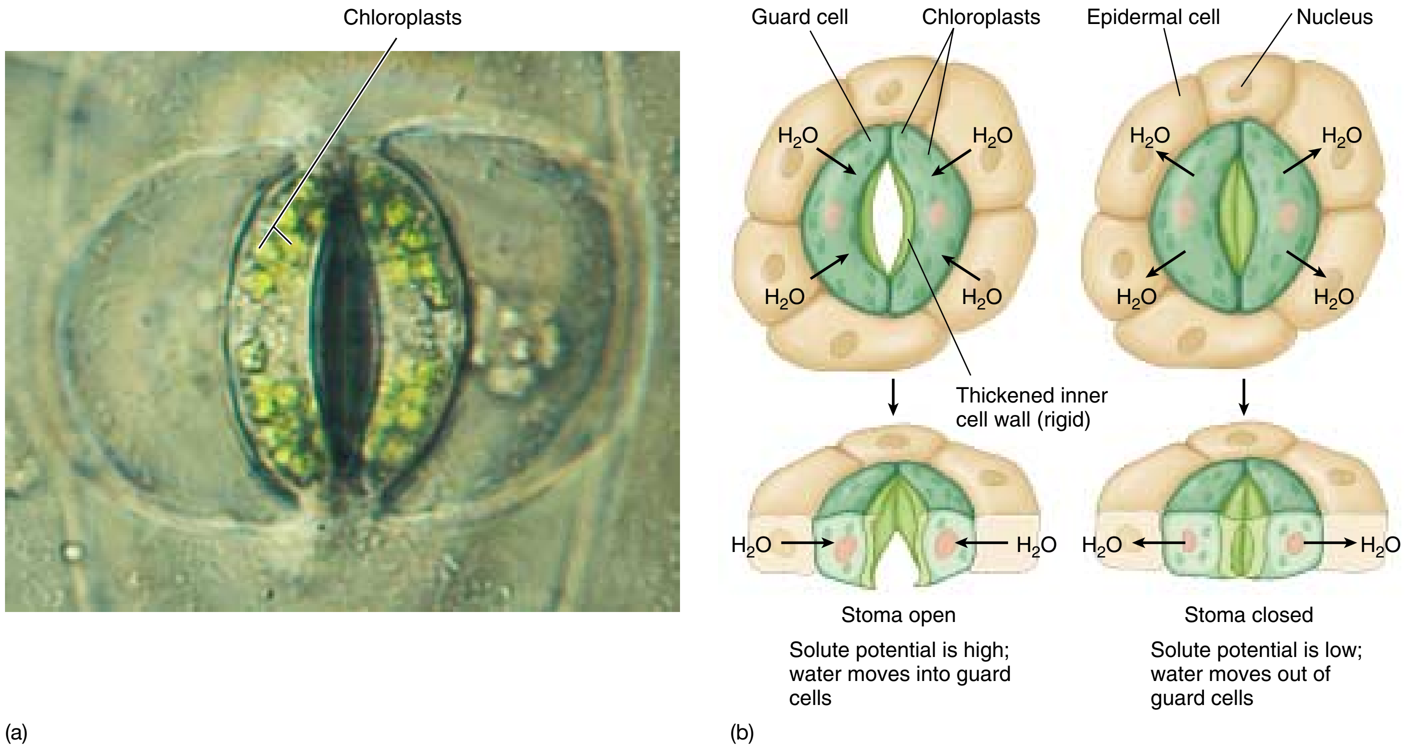


FIGURE 39.12
How a stoma opens and closes. (*a*) When potassium ions from surrounding cells are pumped into guard cells, the guard cell turgor pressure increases as water enters by osmosis. The increased turgor pressure causes the guard cells to bulge, with the thick walls on the inner side of each guard cell bowing outward, thereby opening the stoma. (*b*) When the potassium ions leave the guard cells and their solute potential becomes low, they lose water and turgor, and the stoma closes.

duct tape on the inside edge of both balloons and inflate each one a bit more. Hold the open ends together. You should now be holding a 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.

Loss of turgor in guard cells causes the uptake of potassium (K^+) ions through ATP-powered ion transport channels in their plasma membranes. This creates a solute potential within the guard cells that causes water to enter osmotically. As a result, these cells accumulate water and become turgid, opening the stomata (figure 39.12*a*). Keeping the stomata open requires a constant expenditure of ATP, and the guard cells remain turgid only as long as ions are pumped into the cells. When stomata close, sucrose, rather than K^+, leaves the cell through sucrose transporters. Water then leaves the guard cells, which lose turgor, and the stomata close (figure 39.12*b*). Why closing depends on sucrose transport out of the cell and opening on K^+ uptake is an open question. Experimental evidence is consistent with several pathways regulating stomatal opening and closing.

Photosynthesis in the guard cells apparently provides an immediate source of ATP, which drives the active transport of K^+ by way of a specific K^+ channel; this K^+ channel has now been isolated and studied. In some species, Cl^- accompanies the K^+ in and out of the guard cells, thus maintaining electrical neutrality. In most species, both Cl^- and malate^{2-} move in the opposite direction of K^+.

When a whole plant wilts because there is insufficient water available, the guard cells may also lose turgor, and as a result, the stomata may close. 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. When they are turgid, the stomata open, and CO_2 enters freely; when they are flaccid, CO_2 is largely excluded, but water loss is also retarded.

Abscisic acid, 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. This hormone is released from chloroplasts and produced in leaves. It binds to specific receptor sites in the plasma membranes of guard cells. Plants likely control the duration of stomatal opening through the integration of several stimuli, including blue light. In the next chapter, we will explore the interactions between the environment and the plant in more detail.

Other Factors Regulating Transpiration. Factors such as CO_2 concentration, light, and temperature can also affect stomatal opening. When CO_2 concentrations are high, guard cells of many plant species lose turgor, and their stomata close. Additional CO_2 is not needed at such times, and water is conserved when the guard cells are closed. The stomata also close when the temperature exceeds 30° to 34°C when transpiration would increase substantially. In the dark, stomata will open at low concentrations of CO_2. In chapter 10, we mentioned CAM photosynthesis, which occurs in some succulent like cacti. In this process, CO_2 is taken in at night and fixed during the day. CAM photosynthesis conserves water in dry environments where succulent plants grow.

Many mechanisms to regulate the rate of water loss have evolved in plants. One involves dormancy during dry times of the year; another involves loss of leaves. Deciduous plants are common in areas that periodically experience a severe drought. Plants are often deciduous in regions with severe winters, when water is locked up in ice and snow and thus unavailable to them. In a general 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. Temperatures are significantly reduced in leaves covered with masses of woolly-looking trichomes. These trichomes also increase humidity at the leaf surface. Plants in arid or semiarid habitats often have their stomata in crypts or pits in the leaf surface. Within these depressions the water vapor content of the air may be high, reducing the rate of water loss.

Plant Responses to Flooding

Plants can also receive too much water, and 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 (the only hormone that is a gas) increases, while gibberellins and cytokinins usually decrease. Hormonal changes contribute to the abnormal growth patterns.

Oxygen-deprivation is among the most significant problems. 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. One adaptive solution is that stomata of flooded plants often close to maintain leaf turgor.

FIGURE 39.13
Adaptation to flooded conditions. The "knees" of the bald cypress (*Taxodium*) form whenever it grows in wet conditions, increasing its ability to take in oxygen.

Adapting to Life in Fresh Water. Algal ancestors of plants adapted to a freshwater environment from a saltwater environment before the "move" onto land. This involved a major change in controlling salt balance. Since that time, many have "moved" back into fresh water and grow in places that are often or always flooded naturally; they have adapted to these conditions during the course of their evolution (figure 39.13). One of the most frequent adaptations among such plants is the formation of **aerenchyma,** loose parenchymal tissue with large air spaces in it (figure 39.14). 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, ethylene, which becomes abundant under the anaerobic conditions of flooding, induces aerenchyma formation. Plants also respond to flooded conditions by forming larger lenticels (which facilitate gas exchange) and additional adventitious roots.

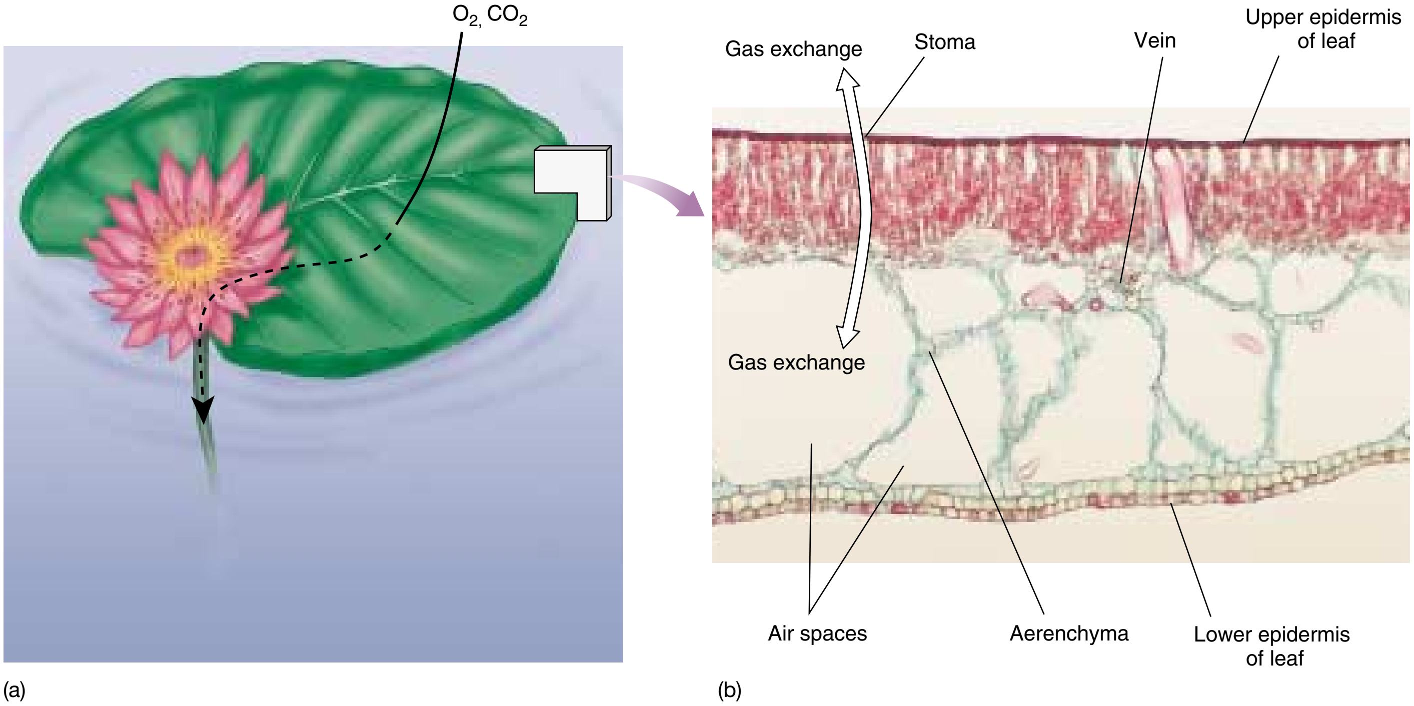


FIGURE 39.14
Aerenchyma tissue. Gas exchange in aquatic plants. (*a*) Water lilies float on the surface of ponds where oxygen is collected and transported to submerged portions of the plant. (*b*) Large air spaces in the leaves add buoyancy. The specialized parenchyma tissue that forms these open spaces is called aerenchyma. Gas exchange occurs through stomata found only on the upper surface of the leaf.

Adapting to Life in Salt Water. Plants such as mangroves that are normally flooded with salt water must not only provide a supply of oxygen for their submerged parts, but also control their salt balance. The salt must be excluded, actively secreted, or diluted as it enters. The arching silt roots of mangroves are connected to long, spongy, air-filled roots that emerge above the mud. These roots, called pneumatophores (see chapter 38), have large lenticels on their above-water portions through which oxygen enters; it is then transported to the submerged roots (figure 39.15). In addition, the succulent leaves of mangroves contain large quantities of water, which dilute the salt that reaches them. Many plants that grow in such conditions also secrete large quantities of salt.

Transpiration from leaves pulls water and minerals up the xylem. This works because of the physical properties of water and the narrow diameters of the conducting tubes. Stomata open when their guard cells become turgid. Opening and closing of stomata is osmotically regulated. Biochemical, anatomical, and morphological adaptations have evolved to reduce water loss through transpiration. Plants are harmed by excess water. However, plants can survive flooded conditions, and even thrive in them, if they can deliver oxygen to their submerged parts.

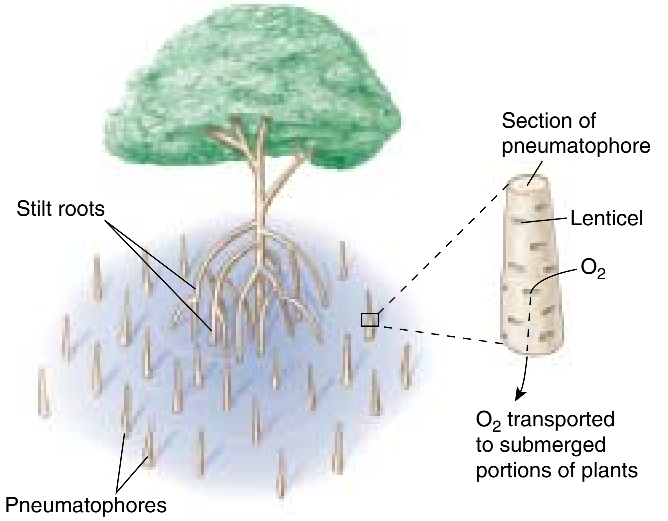


FIGURE 39.15
How mangroves get oxygen to their submerged part. Mangrove plants grow in areas that are commonly flooded, and much of each plant is usually submerged. However, modified roots called pneumatophores supply the submerged portions of the plant with oxygen because these roots emerge above the water and have large lenticels. Oxygen can enter the roots through the lenticels, pass into the abundant aerenchyma, and move to the rest of the plant.

39.4 Dissolved sugars and hormones are transported in the phloem.

Phloem Transport Is Bidirectional

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,** is responsible for the availability of suitable carbohydrate building blocks in 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. The pathway that sugars and other substances travel within the plant has been demonstrated precisely by using radioactive tracers, despite the fact that living phloem is delicate and the process of transport within it is easily disturbed. Radioactive carbon dioxide ($^{14}CO_2$) gets incorporated into glucose as a result of photosynthesis. The glucose is used to make sucrose, which is transported in the phloem. Such studies have shown that sucrose moves both up and down in the phloem.

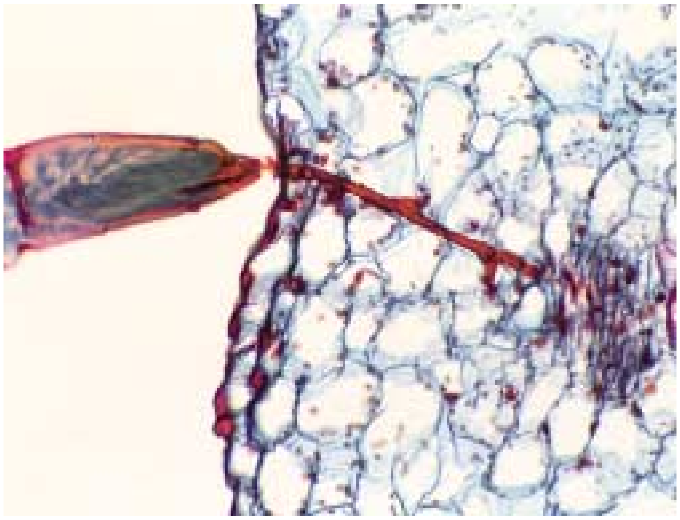
Aphids, a group of insects that extract plant sap for food, have been valuable tools in understanding translocation. Aphids thrust their *stylets* (piercing mouthparts) into phloem cells of leaves and stems to obtain abundant sugars there. When a feeding aphid is removed by cutting its stylet, the liquid from the phloem continues to flow through the detached mouthpart and is thus available in pure form for analysis (figure 39.16). The liquid in the phloem contains 10 to 25% dry matter, almost all of which is sucrose. Using aphids to obtain the critical samples and radioactive tracers to mark them, it has been demonstrated that movement of substances in phloem can be remarkably fast; rates of 50 to 100 centimeters per hour have been measured.

While the primary focus of this chapter is on nutrient and water transport, it is important to note that phloem also transports plant hormones. As we will explore in the next chapter, environmental signals can result in the rapid translocation of hormones in the plant.

Energy Requirements for Phloem Transport

The most widely accepted model of how carbohydrates in solution move through the phloem has been called the **mass-flow hypothesis, pressure flow hypothesis,** or **bulk flow hypothesis.** Experimental evidence supports much of this model. 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, and food-storage tissues, such as the cortex of roots. Sinks occur primarily at the growing tips of roots and stems and in developing fruits.

(a)



(a)

FIGURE 39.16
Feeding on phloem. (*a*) Aphids, like this individual of *Macrosiphon rosae* shown here on the edge of a rose leaf, feed on the food-rich contents of the phloem, which they extract through their piercing mouthparts (*b*), 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.

In a process known as *phloem loading*, carbohydrates (mostly sucrose) enter the sieve tubes in the smallest veinlets at the source. This is an energy-requiring step, as active transport is needed. Companion cells and parenchyma cells adjacent to the sieve tubes provide the ATP energy to drive this transport. Then, because of the

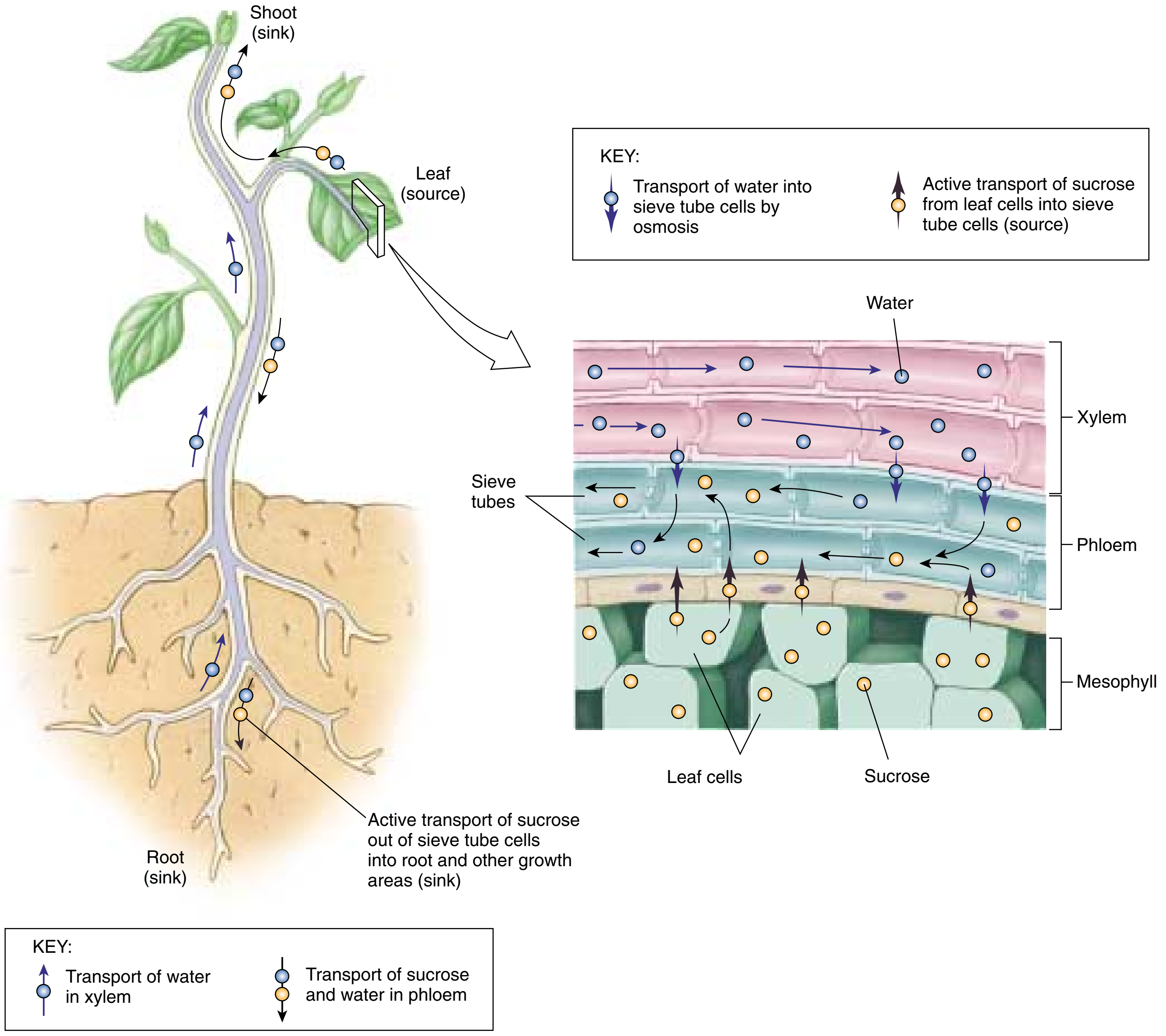


FIGURE 39.17
Diagram of mass flow. In this diagram, red dots represent sucrose molecules, and blue dots symbolize water molecules. Moving from the mesophyll cells of a leaf or another part of the plant into the conducting cells of the phloem, the sucrose molecules are then transported to other parts of the plant by mass flow and unloaded where they are required.

difference between the water potentials in the sieve tubes and in the nearby xylem cells, water flows into the sieve tubes by osmosis. Turgor pressure in the sieve tubes increases. The increased turgor pressure drives the fluid throughout the plant's system of sieve tubes. At the sink, carbohydrates are actively removed. Water moves from the sieve tubes by osmosis and the turgor pressure there drops, causing a mass flow from the higher pressure at the source to the lower pressure sink (figure 39.17). Most of the water at the sink diffuses then back into the xylem, where it may either be recirculated or lost through transpiration.

Transport of sucrose and other carbohydrates through sieve tubes does not require energy. The loading and unloading of these substances from the sieve tubes does.

Chapter 39

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Summary

Questions

Media Resources

39.1 Plants require a variety of nutrients in addition to the direct products of photosynthesis.

- Plants require a few macronutrients in large amounts and several micronutrients in trace amounts. Most of these are obtained from the soil through the roots.
- Plant growth is significantly influenced by the nature of the soil. Soils vary in terms of nutrient composition and water-holding capacity.

1. What is the difference between a macronutrient and a micronutrient? Explain how a plant would utilize each of the macronutrients.

- Nutrients
- Soil

39.2 Some plants have novel strategies for obtaining nutrients.

- Some plants entice bacteria to produce organic nitrogen for them. These bacteria may be free-living or form a symbiotic relationship with a host plant.
- About 90% of all vascular plants rely on fungal associations to gather essential nutrients.

2. The atmosphere is full of nitrogen yet it is inaccessible to most plants. Why is that? What solution has evolved in legumes?

39.3 Water and minerals move upward through the xylem.

- Water and minerals enter the plant through the roots. Energy is required for active transport.
- The bulk movement of water and minerals is the result of movement between cells, across cell membranes, and through tubes of xylem. Aquaporins are water channels that enhance osmosis.
- A combination of the properties of water, structure of xylem, and transpiration of water through the leaves results in the passive movement of water to incredible heights. The ultimate energy source for pulling water through xylem vessels and tracheids is the sun.
- Water leaves the plant through openings in the leaves called stomata. Stomata open when their guard cells are turgid and bulge, causing the thickened inner walls of these cells to bow away from the opening.
- Plants can tolerate long submersion in water, if they can deliver oxygen to their submerged tissues.

3. What is pressure potential? How does it differ from solute potential? How do these pressures cause water to rise in a plant?

4. What proportion of water that enters a plant leaves it via transpiration?

5. Why are root hairs usually turgid? Does the accumulation of minerals within a plant root require the expenditure of energy? Why or why not?

6. Under what environmental condition is water transport through the xylem reduced to near zero? How much transpiration occurs under these circumstances?

7. Does stomatal control require energy? Explain.

- Activity: Water Movement
- Uptake by Roots
- Water Movement

- Student Research: Heavy Metal Uptake

39.4 Dissolved sugars and hormones are transported in the phloem.

- Sucrose and hormones can move up and down in the phloem between sources and sinks.
- The movement of water containing dissolved sucrose and other substances in the phloem requires energy. Sucrose is loaded into the phloem near sites of synthesis, or sources, using energy supplied by the companion cells or other nearby parenchyma cells.

8. What is translocation? What is the driving force behind translocation?

9. Describe the movement of carbohydrates through a plant, beginning with the source and ending with the sink. Is this process active or passive?