

36

Resource Acquisition and Transport in Vascular Plants



▲ Figure 36.1 Plants or pebbles?

KEY CONCEPTS

- 36.1 Adaptations for acquiring resources were key steps in the evolution of vascular plants
- 36.2 Different mechanisms transport substances over short or long distances
- 36.3 Transpiration drives the transport of water and minerals from roots to shoots via the xylem
- 36.4 The rate of transpiration is regulated by stomata
- 36.5 Sugars are transported from sources to sinks via the phloem
- 36.6 The symplast is highly dynamic

OVERVIEW

Underground Plants

The Kalahari Desert of southern Africa receives only about 20 cm of precipitation a year, almost entirely during the summer, when daytime temperatures reach a scorching 35–45°C (95–113°F). Many animals escape the desert heat

by seeking shelter underground. A peculiar genus of perennial plants called stone plants (*Lithops*) has a similar, mostly subterranean lifestyle (Figure 36.1). Except for the tips of two succulent leaves that are exposed to the surface, a stone plant lives entirely below ground. Each leaf tip has a region of clear, lens-like cells that allow light to penetrate to the photosynthetic tissues underground. These adaptations enable stone plants to conserve moisture, hide from grazing tortoises, and avoid the potentially harmful temperatures and high light intensities of the desert.

The remarkable growth habit of *Lithops* reminds us that the success of plants depends largely on their ability to gather and conserve resources from their environment. Through natural selection, many plant species have become highly proficient in acquiring or conserving resources that are especially limited in their environment, but there are often trade-offs in such specializations. For example, the mostly subterranean lifestyle of stone plants reduces water loss from evaporation but inhibits photosynthesis. As a result, stone plants grow very slowly.

The first concept in this chapter examines structural features of shoot and root systems that increase their efficiency in acquiring resources. Resource acquisition, however, is not the end of the story but the beginning. Resources must be transported within the plant to where they are needed. Therefore, the rest of the chapter focuses on how water, minerals, and the products of photosynthesis (sugars) are transported in vascular plants.

CONCEPT 36.1

Adaptations for acquiring resources were key steps in the evolution of vascular plants

EVOLUTION Land plants typically inhabit two worlds—above ground, where their shoot systems acquire sunlight and CO₂, and below ground, where their root systems acquire water and minerals. Without adaptations that allow acquisition of these resources, plants could not have colonized land.

The algal ancestors of land plants absorbed water, minerals, and CO₂ directly from the water in which they lived. Transport in these algae was relatively simple because every cell was close to the source of these substances. The earliest land plants were nonvascular plants that grew photosynthetic shoots above the shallow fresh water in which they lived. These leafless shoots typically had waxy cuticles and few stomata, which allowed them to avoid excessive water loss while still permitting some exchange of CO₂ and O₂ for photosynthesis. The anchoring and absorbing functions of early land plants were assumed by the base of the stem or by threadlike rhizoids (see Figure 29.8).

As land plants evolved and increased in number, competition for light, water, and nutrients intensified. Taller plants with broad, flat appendages had an advantage in absorbing light. This increase in surface area, however, resulted in more evaporation and therefore a greater need for water. Larger shoots also required more anchorage. These needs favored the production of multicellular, branching roots. Meanwhile, as greater shoot heights further separated the top of the photosynthetic shoot from the nonphotosynthetic parts below ground, natural selection favored plants capable of efficient long-distance transport of water, minerals, and products of photosynthesis.

The evolution of vascular tissue consisting of xylem and phloem made possible the development of extensive root and shoot systems that carry out long-distance transport (see Figure 35.10). The xylem transports water and minerals from roots to shoots. The phloem transports products of photosynthesis from where they are made or stored to where they are needed. **Figure 36.2** provides an overview of resource acquisition and transport in a vascular plant.

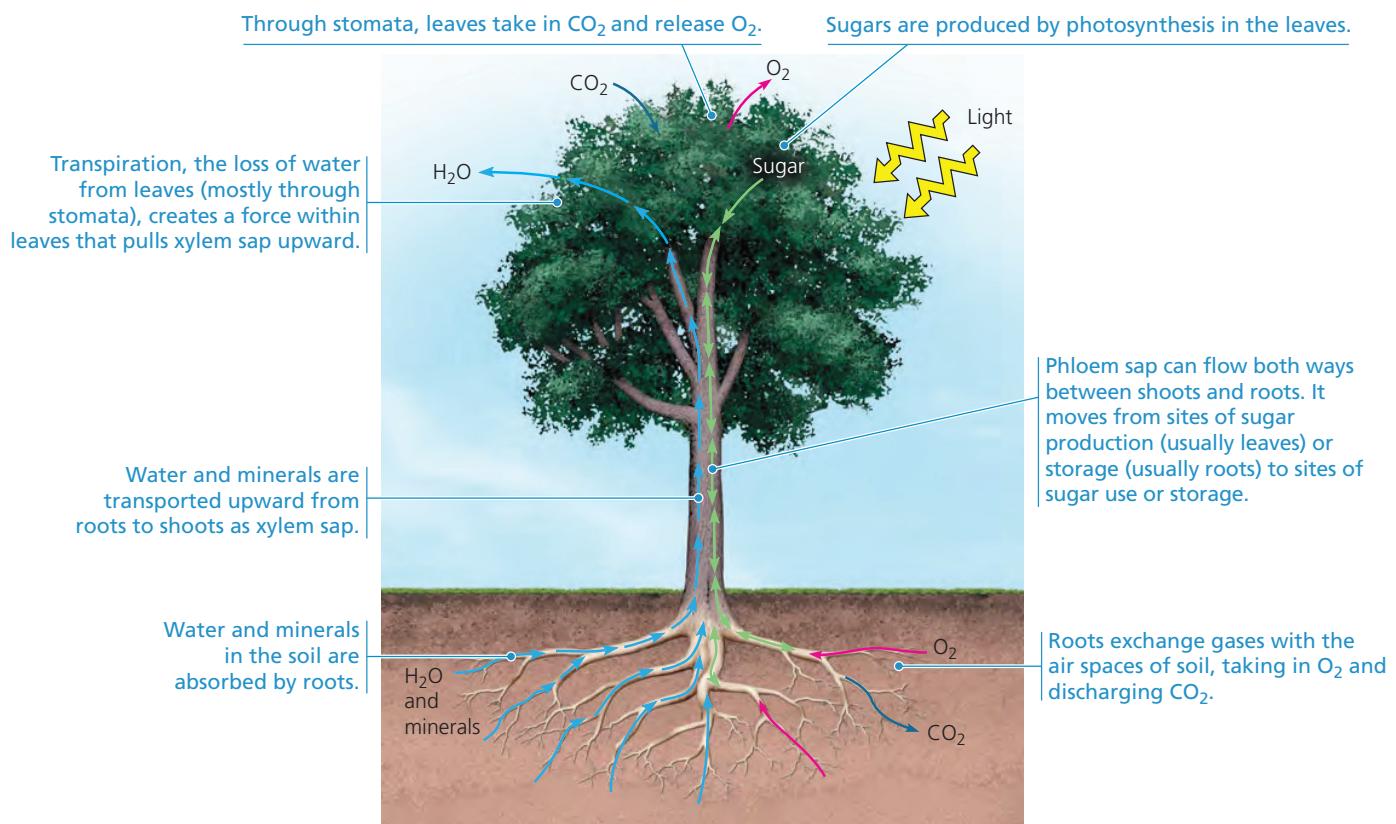
Because plant success depends on photosynthesis, evolution has resulted in many structural adaptations for efficiently acquiring light from the sun, CO₂ from the air, and water from the ground. Perhaps just as importantly, land plants must minimize the evaporative loss of water, particularly in environments where water is scarce. The adaptations

of each species represent compromises between enhancing photosynthesis and minimizing water loss in the species' particular habitat. Later in the chapter, we discuss how plants enhance CO₂ uptake and minimize water loss by regulating stomatal pores. Here, we examine how the basic architecture of shoots and roots helps plants acquire resources.

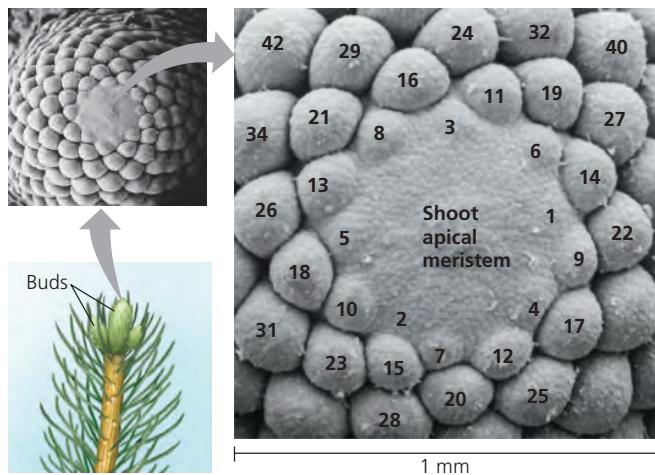
Shoot Architecture and Light Capture

In shoot systems, stems serve as supporting structures for leaves and as conduits for the transport of water and nutrients. Variations in shoot systems arise largely from the form and arrangement of leaves, the outgrowth of axillary buds, and the relative growth in stem length and thickness.

Leaf size and structure account for much of the outward diversity in plant form. Leaves range in length from the minuscule 1.3-mm leaves of the pygmy weed (*Crassula erecta*), a native of dry, sandy regions in the western United States, to the 20-m leaves of the palm *Raphia regalis*, a native of African rain forests. These species represent extreme examples of a general correlation observed between water availability and leaf size. The largest leaves are typically found in species from tropical rain forests, whereas the smallest are usually found in species from dry or very cold environments, where liquid water is scarce and evaporative loss from leaves is potentially more problematic.

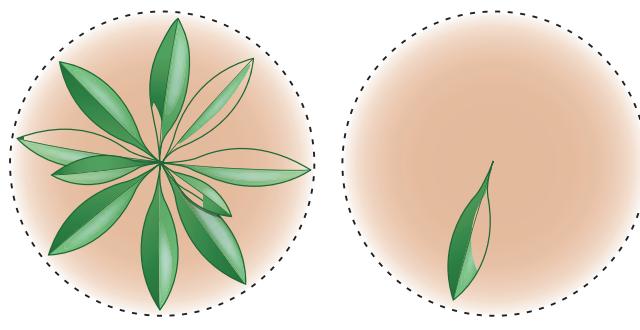


▲ **Figure 36.2** An overview of resource acquisition and transport in a vascular plant.



▲ Figure 36.3 Emerging phyllotaxy of Norway spruce. This SEM, taken from above a shoot tip, shows the pattern of emergence of leaves. The leaves are numbered, with 1 being the youngest. (Some numbered leaves are not visible in the close-up.)

? With your finger, trace the progression of leaf emergence, starting with leaf number 29. What is the pattern?



▲ Figure 36.4 Leaf area index. The leaf area index of a single plant is the ratio of the total area of the top surfaces of the leaves to the area of ground covered by the plant, as shown in this illustration of two plants viewed from the top. With many layers of leaves, a leaf area index value can easily exceed 1.

? Would a higher leaf area index always increase the amount of photosynthesis? Explain.

while also providing strong anchorage. The tallest plant species, including gymnosperms and eudicots, are typically anchored by strong taproot systems with numerous branches (see Figure 35.2). Although there are exceptions, such as palms, most monocots do not reach treelike heights because their fibrous root systems do not anchor a tall plant as strongly as a taproot system (see Figure 30.13).

Plants can rapidly adjust the architecture and physiology of their roots to exploit patches of available nutrients in the soil. The roots of many plants, for example, respond to pockets of low nitrate availability in soils by extending straight through the pockets instead of branching within them. Conversely, when encountering a pocket rich in nitrate, a root will often branch extensively there. Root cells also respond to high soil nitrate levels by synthesizing more proteins involved in nitrate transport and assimilation. Thus, not only does the plant devote more of its mass to exploiting a nitrate-rich patch; the cells also absorb nitrate more efficiently.

Researchers have uncovered a fascinating physiological mechanism that reduces competition within the root system of a plant. Cuttings from the stolons of buffalo grass (*Buchloe dactyloides*) develop fewer and shorter roots in the presence of cuttings from the same plant than they do in the presence of cuttings from another buffalo grass plant. Although the mechanism underlying this ability to distinguish self from nonself is unknown, avoiding competition between roots of the same plant for the same limited pool of resources certainly seems beneficial.

The evolution of mutualistic associations between roots and fungi called **mycorrhizae** (Figure 36.5) was a critical step in the successful colonization of land by vascular plants, especially given the poorly developed soils available at that time. About 80% of extant land plant species form

mycorrhizal associations. Mycorrhizal hyphae endow the fungus and plant roots with an enormous surface area for absorbing water and minerals, particularly phosphate. The role of mycorrhizae in plant nutrition will be examined more fully in Chapter 37.

Once acquired, resources must be transported to other parts of the plant that need them. In the next section, we examine the processes and pathways that enable resources such as water, minerals, and sugars to be transported throughout the plant.

CONCEPT CHECK 36.1

1. Why is long-distance transport important for vascular plants?
2. What architectural features influence self-shading?
3. Some plants can detect increased levels of light reflected from leaves of encroaching neighbors. This detection elicits stem elongation, production of erect leaves, and reduced lateral branching. How do these responses help the plant compete?
4. **WHAT IF?** If you prune a plant's shoot tips, what will be the short-term effect on the plant's branching and leaf area index?
5. **MAKE CONNECTIONS** Explain how fungal hyphae provide more surface area for nutrient absorption. See pp. 637–638 of Concept 31.1.

For suggested answers, see Appendix A.

CONCEPT 36.2

Different mechanisms transport substances over short or long distances

Given the diversity of substances that move through plants and the great range of distances and barriers over which such substances must be transported, it is not surprising that plants employ a variety of transport processes. Before examining these processes, however, we will look at the two major pathways of transport: the apoplast and the symplast.

The Apoplast and Symplast: Transport Continuums

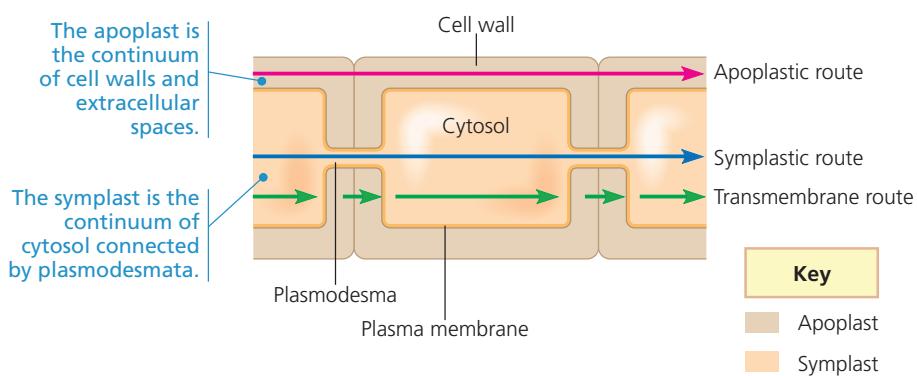
Plant tissues may be viewed as having two major compartments—the apoplast and the symplast. The **apoplast** consists of everything external to the plasma membranes of living cells and includes cell walls, extracellular spaces, and the interior of dead cells such as vessel elements and tracheids (see Figure 35.10). The **symplast** consists of the entire mass of cytosol of all the living cells in a plant, as well as the plasmodesmata, the cytoplasmic channels that interconnect them.



▲ **Figure 36.5 A mycorrhiza, a mutualistic association of fungus and roots.** The fine fungal hyphae provide an extensive surface area for the absorption of water and minerals.

► **Figure 36.6 Cell compartments and routes for short-distance transport.**

Some substances may use more than one transport route.



The compartmental structure of plants provides three routes for transport within a plant tissue or organ: the apoplastic, symplastic, and transmembrane routes (Figure 36.6). In the *apoplastic route*, water and solutes (dissolved chemicals) move along the continuum of cell walls and extracellular spaces. In the *symplastic route*, water and solutes move along the continuum of cytosol. This route requires substances to cross a plasma membrane once, when they first enter the plant. After entering one cell, substances can move from cell to cell via plasmodesmata. In the *transmembrane route*, water and solutes move out of one cell, across the cell wall, and into the neighboring cell, which may pass them to the next cell in the same way. The transmembrane route requires repeated crossings of plasma membranes as substances exit one cell and enter the next. These three routes are not mutually exclusive, and some substances may use more than one route to varying degrees.

Short-Distance Transport of Solutes Across Plasma Membranes

In plants, as in any organism, the selective permeability of the plasma membrane controls the short-distance movement of substances into and out of cells (see Chapter 7). Both active and passive transport mechanisms occur in plants, and plant cell membranes are equipped with the same general types of pumps and transport proteins (channel proteins, carrier proteins, and cotransporters) that function in other cells. In this section, we focus on some ways that plants differ from animals in solute transport across plasma membranes.

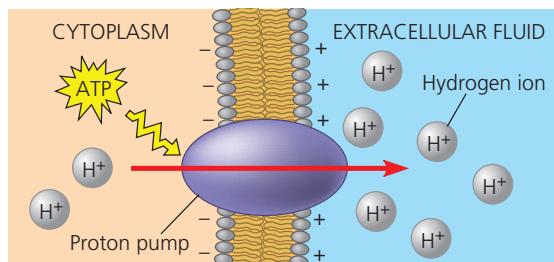
Hydrogen ions (H^+), rather than sodium ions (Na^+), play the primary role in basic transport processes in plant cells. For example, in plant cells the membrane potential (the voltage across the membrane) is established mainly through the pumping of H^+ by proton pumps (Figure 36.7a), rather than the pumping of Na^+ by sodium-potassium pumps. Also, H^+ is most often cotransported in plants, whereas Na^+ is typically cotransported in animals. During cotransport,

plant cells use the energy in the H^+ gradient and membrane potential to drive the active transport of many different solutes. For instance, cotransport with H^+ is responsible for absorption of neutral solutes, such as the sugar sucrose, by phloem cells and other plant cells. An H^+ /sucrose cotransporter couples movement of sucrose against its concentration gradient with movement of H^+ down its electrochemical gradient (Figure 36.7b). Cotransport with H^+ also facilitates movement of ions, as in the uptake of nitrate (NO_3^-) by root cells (Figure 36.7c).

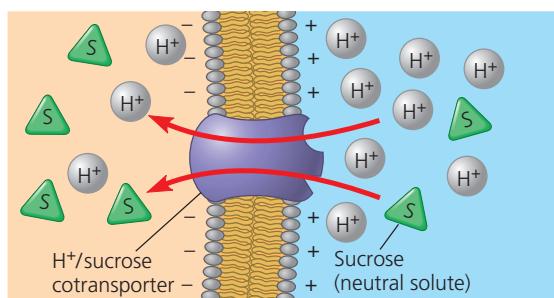
The membranes of plant cells also have ion channels that allow only certain ions to pass (Figure 36.7d). As in animal cells, most channels are gated, opening or closing in response to stimuli such as chemicals, pressure, or voltage. Later in this chapter, we discuss how K^+ ion channels in guard cells function in opening and closing stomata. Ion channels are also involved in producing electrical signals analogous to the action potentials of animals (see Chapter 48). However, these signals are 1,000 times slower and employ Ca^{2+} -activated anion channels rather than the Na^+ ion channels used by animal cells.

Short-Distance Transport of Water Across Plasma Membranes

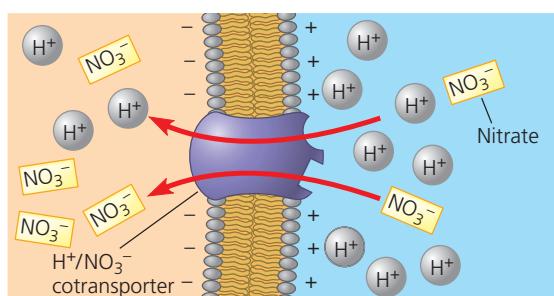
The absorption or loss of water by a cell occurs by **osmosis**, the diffusion of free water—water that is not bound to solutes or surfaces—across a membrane (see Figure 7.14). The physical property that predicts the direction in which water will flow is called **water potential**, a quantity that includes the effects of solute concentration and physical pressure. Free water moves from regions of higher water potential to regions of lower water potential if there is no barrier to its flow. For example, if a plant cell is immersed in a solution that has a higher water potential than the cell, water will move into the cell. As it moves, water can perform work, such as cell expansion. The word *potential* in the term *water potential* refers to water's potential energy—



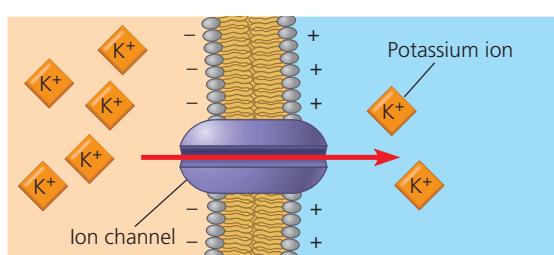
(a) H⁺ and membrane potential. The plasma membranes of plant cells use ATP-dependent proton pumps to pump H⁺ out of the cell. These pumps contribute to the membrane potential and the establishment of a pH gradient across the membrane. These two forms of potential energy can drive the transport of solutes.



(b) H⁺ and cotransport of neutral solutes. Neutral solutes such as sugars can be loaded into plant cells by cotransport with H⁺ ions. H⁺/sucrose cotransporters, for example, play a key role in loading sugar into the phloem prior to its transport throughout the plant.



(c) H⁺ and cotransport of ions. Cotransport mechanisms involving H⁺ also participate in regulating ion fluxes into and out of cells. For example, H⁺/NO₃⁻ cotransporters in the plasma membranes of root cells are important for the uptake of NO₃⁻ by plant roots.



(d) Ion channels. Plant ion channels open and close in response to voltage, stretching of the membrane, and chemical factors. When open, ion channels allow specific ions to diffuse across membranes. For example, a K⁺ ion channel is involved in the release of K⁺ from guard cells when stomata close.

▲ **Figure 36.7 Solute transport across plant cell plasma membranes.**

? Assume that a plant cell has all four of the plasma membrane transport proteins shown above. Assume also that you have specific inhibitors for each of the four transport proteins. Then predict what effect the individual application of each inhibitor would have on the cell's membrane potential.

water's capacity to perform work when it moves from a region of higher water potential to a region of lower water potential.

Water potential is abbreviated by the Greek letter ψ (psi, pronounced "sigh"). Plant biologists measure ψ in a unit of pressure called a **megapascal** (abbreviated MPa). By definition, the ψ of pure water in a container open to the atmosphere under standard conditions (at sea level and at room temperature) is 0 MPa. One MPa is equal to about 10 times atmospheric pressure at sea level. The internal pressure of a

living plant cell due to the osmotic uptake of water is approximately 0.5 MPa, about twice the air pressure inside an inflated car tire.

How Solutes and Pressure Affect Water Potential

Both solute concentration and physical pressure can affect water potential, as expressed in the *water potential equation*:

$$\psi = \psi_s + \psi_p$$

where ψ is the water potential, ψ_s is the solute potential (osmotic potential), and ψ_p is the pressure potential. The **solute potential** (ψ_s) of a solution is directly proportional to its molarity. Solute potential is also called *osmotic potential* because solutes affect the direction of osmosis. The solutes in plants are typically mineral ions and sugars. By definition, the ψ_s of pure water is 0. When solutes are added, they bind water molecules. As a result, there are fewer free water molecules, reducing the capacity of the water to move and do work. In this way, an increase in solutes has a negative effect on water potential, which is why the ψ_s of a solution is always expressed as a negative number. For example, a 0.1 M solution of a sugar has a ψ_s of -0.23 MPa. As the solute concentration increases, ψ_s becomes more negative.

Pressure potential (ψ_p) is the physical pressure on a solution. Unlike ψ_s , ψ_p can be positive or negative relative to atmospheric pressure. For example, the water in the hollow nonliving xylem cells (tracheids and vessel elements) of a plant is often under a

negative pressure potential (tension) of less than -2 MPa. Conversely, much like the air in a tire's inner tube, the water in living cells is usually under positive pressure due to the osmotic uptake of water. Specifically, the cell contents press the plasma membrane against the cell wall, and the cell wall then presses against the **protoplast** (the living part of the cell, which also includes the plasma membrane), producing what is called **turgor pressure**. This internal pressure is critical for plant function because it helps maintain the stiffness of plant tissues and also serves as the driving force for cell elongation.

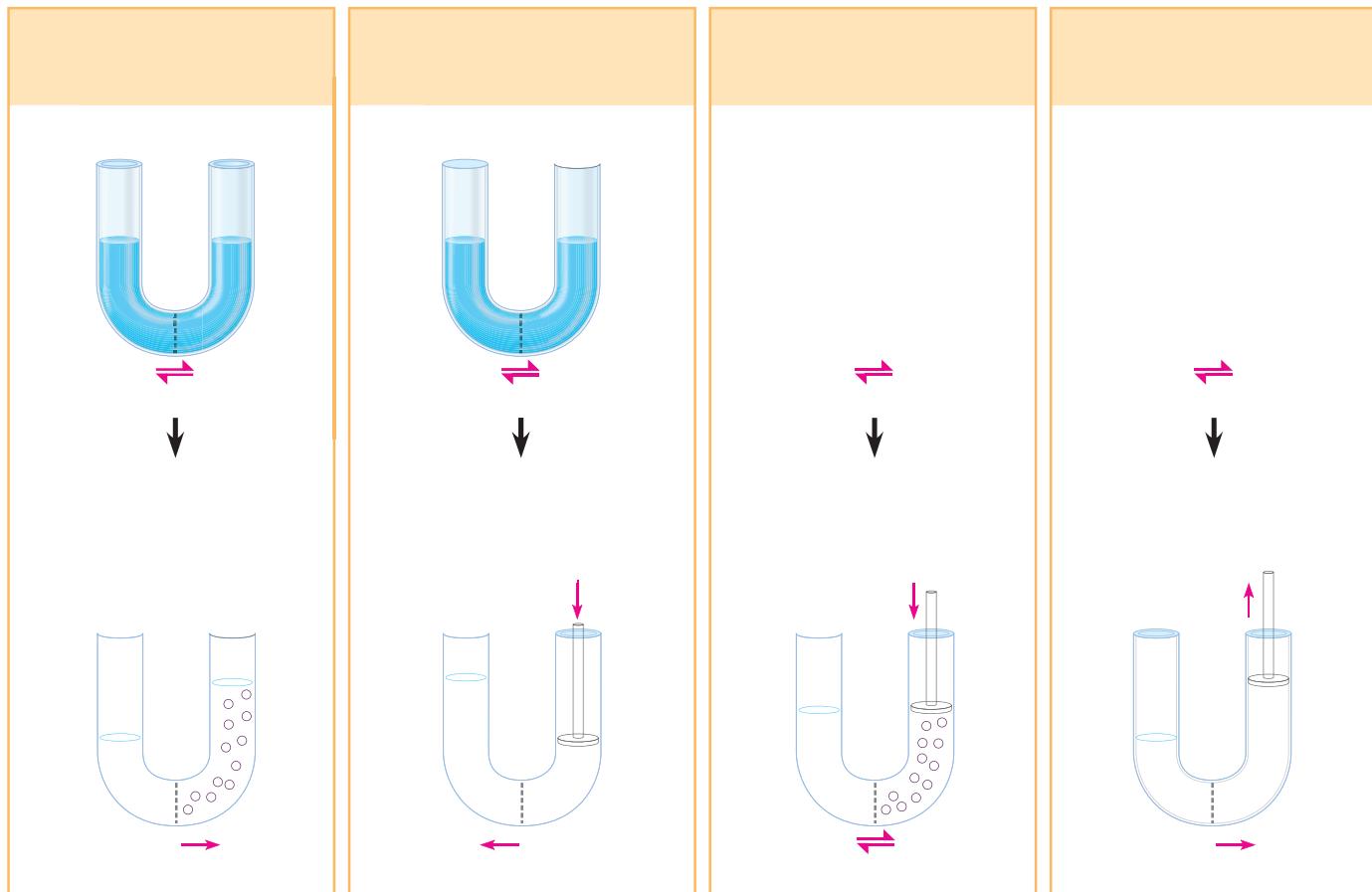
A U-shaped tube can be used to demonstrate the effects of solutes and pressure on water movement across a selectively permeable membrane (**Figure 36.8**). As you consider this model, keep in mind the key point: *Water moves from regions of higher water potential to regions of lower water potential.*

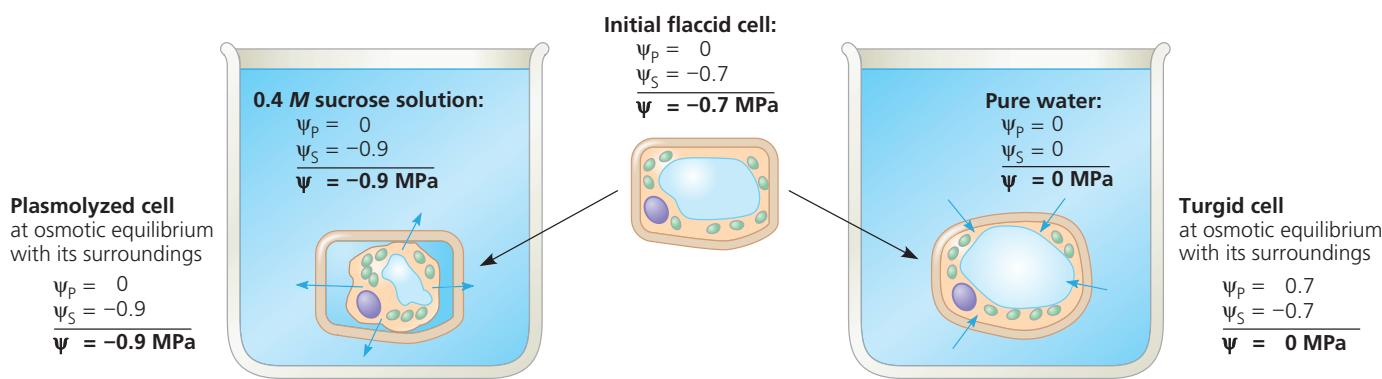
Water Movement Across Plant Cell Membranes

Now let's consider how water potential affects absorption and loss of water by a living plant cell. First, imagine a cell that is **flaccid** (limp) as a result of losing water. The cell has a ψ_p of 0 MPa. Suppose this flaccid cell is bathed in a solution of higher solute concentration (more negative solute potential) than the cell itself (**Figure 36.9a**). Since the external solution has the lower (more negative) water potential, water diffuses out of the cell. The cell's protoplast undergoes **plasmolysis**—that is, it shrinks and pulls away from the cell wall. If we place the same flaccid cell in pure water ($\psi = 0$ MPa) (**Figure 36.9b**), the cell, because it contains solutes, has a lower water potential than the water, and water enters the cell by osmosis. The contents of the cell begin to swell and press the plasma membrane against the cell wall. The partially elastic wall, exerting turgor pressure, confines the pressurized protoplast. When this pressure is enough to offset the

tendency for water to enter because of the solutes in the cell, then ψ_p and ψ_s are equal, and $\psi = 0$. This matches the water potential of the extracellular environment—in this example, 0 MPa. A dynamic equilibrium has been reached, and there is no further net movement of water.

In contrast to a flaccid cell, a walled cell with a greater solute concentration than its surroundings is **turgid**, or very firm. When turgid cells in a nonwoody tissue push against each other, the tissue is stiffened. The effects of turgor loss are seen during **wilting**, when leaves and stems droop as a result of cells losing water.





(a) Initial conditions: cellular $\psi >$ environmental ψ . The cell loses water and plasmolyzes. After plasmolysis is complete, the water potentials of the cell and its surroundings are the same.

(b) Initial conditions: cellular $\psi <$ environmental ψ . There is a net uptake of water by osmosis, causing the cell to become turgid. When this tendency for water to enter is offset by the back pressure of the elastic wall, water potentials are equal for the cell and its surroundings. (The volume change of the cell is exaggerated in this diagram.)

▲ **Figure 36.9 Water relations in plant cells.** In these experiments, flaccid cells (cells in which the protoplast contacts the cell wall but lacks turgor pressure) are placed in two environments. Blue arrows indicate initial net water movement.

Aquaporins: Facilitating Diffusion of Water

A difference in water potential determines the *direction* of water movement across membranes, but how do water molecules actually cross the membranes? Water molecules are small enough to diffuse across the phospholipid bilayer, even though the bilayer's interior is hydrophobic. However, their movement across biological membranes is too rapid to be explained by unaided diffusion. The transport of water molecules across membranes is facilitated by transport proteins called **aquaporins** (see Chapter 7). These selective channels affect the *rate* at which water moves osmotically across the membrane. Aquaporin channel proteins are highly dynamic: Their permeability is decreased by increases in cytosolic Ca^{2+} or decreases in cytosolic pH.

Long-Distance Transport: The Role of Bulk Flow

Diffusion is an effective transport mechanism over the spatial scales typically found at the cellular level. However, diffusion is much too slow to function in long-distance transport within a plant. Although diffusion from one end of a cell to the other takes just seconds, diffusion from the roots to the top of a giant redwood would take several centuries. Instead, long-distance transport occurs through **bulk flow**, the movement of liquid in response to a pressure gradient. The bulk flow of material always occurs from higher to lower pressure. Unlike osmosis, bulk flow is independent of solute concentration.

Long-distance bulk flow occurs within the tracheids and vessel elements of the xylem and within the sieve-tube elements of the phloem. The structures of these conducting cells facilitate bulk flow. As you saw in Figure 35.10, mature tracheids and vessel elements are dead cells and therefore have no cytoplasm, and the cytoplasm of sieve-tube elements is almost devoid of internal organelles. If you have ever dealt with a partially

clogged drain, you know that the volume of flow depends on the pipe's diameter. Clogs reduce the effective diameter of the drainpipe. Such experiences help us understand how the structures of plant cells specialized for bulk flow fit their function. Like the unplugging of a kitchen drain, the absence or reduction of cytoplasm in a plant's "plumbing" allows for efficient bulk flow through the xylem and phloem. Bulk flow is also enhanced by the perforation plates at the ends of vessel elements and the porous sieve plates connecting sieve-tube elements.

Diffusion, active transport, and bulk flow act in concert to transport resources throughout the whole plant. For example, bulk flow due to a pressure difference is the mechanism of long-distance transport of sugars in the phloem, but active transport of sugar at the cellular level maintains this pressure difference. In the next three sections, we examine in more detail the transport of water and minerals from roots to shoots, the control of evaporation, and the transport of sugars.

CONCEPT CHECK 36.2

- If a plant cell immersed in distilled water has a ψ_s of -0.7 MPa and a ψ of 0 MPa , what is the cell's ψ_p ? If you put it in an open beaker of solution that has a ψ of -0.4 MPa , what would be its ψ_p at equilibrium?
- How would a reduction in the number of aquaporin channels affect a plant cell's ability to adjust to new osmotic conditions?
- How would the long-distance transport of water be affected if tracheids and vessel elements were alive at maturity? Explain.
- WHAT IF?** What would happen if you put plant protoplasts in pure water? Explain.

For suggested answers, see Appendix A.

CONCEPT 36.3

Transpiration drives the transport of water and minerals from roots to shoots via the xylem

Picture yourself struggling to carry a 19-L (5-gallon) container of water weighing 19 kg (42 pounds) up several flights of stairs. Imagine doing this 40 times a day. Then consider the fact that an averaged-sized tree, despite having neither heart nor muscle, transports a similar volume of water effortlessly on a daily basis. How do trees accomplish this feat? To answer this question, we'll follow each step in the journey of water and minerals from the tips of roots to leaves.

Absorption of Water and Minerals by Root Cells

Although all living plant cells absorb nutrients across their plasma membranes, the cells near the tips of roots are particularly important because most of the absorption of water and minerals occurs there. In this region, the epidermal cells are permeable to water, and many are differentiated into root hairs, modified cells that account for much of the absorption of water by roots (see Figure 35.3). The root hairs absorb the soil solution, which consists of water molecules and dissolved mineral ions that are not bound tightly to soil particles. The soil solution is drawn into the hydrophilic walls of epidermal cells and passes freely along the cell walls and the extracellular spaces into the root cortex. This flow enhances the exposure of the cells of the cortex to the soil solution, providing a much greater membrane surface area for absorption than the surface area of the epidermis alone. Although the soil solution usually has a low mineral concentration, active transport enables roots to accumulate essential minerals, such as K^+ , to concentrations hundreds of times greater than in the soil.

Transport of Water and Minerals into the Xylem

Water and minerals that pass from the soil into the root cortex cannot be transported to the rest of the plant until they enter the xylem of the vascular cylinder, or stele. The **endodermis**, the innermost layer of cells in the root cortex, functions as a last checkpoint for the selective passage of minerals from the cortex into the vascular cylinder (Figure 36.10). Minerals already in the symplast when they reach the endodermis continue through the plasmodesmata of endodermal cells and pass into the vascular cylinder. These minerals were already screened by the plasma membrane they had to cross to enter the symplast in the epidermis or cortex. Those minerals that reach the endodermis via the apoplast encounter a dead end that blocks their passage into the vascular cylinder. This barrier, located in the transverse and radial walls of each endodermal cell, is the **Caspary strip**, a belt made of suberin, a

waxy material impervious to water and dissolved minerals (see Figure 36.10). Thus, water and minerals cannot cross the endodermis and enter the vascular cylinder via the apoplast. The Caspary strip forces water and minerals that are passively moving through the apoplast to cross the plasma membrane of an endodermal cell before they can enter the vascular cylinder.

The endodermis, with its Caspary strip, ensures that no minerals can reach the vascular tissue of the root without crossing a selectively permeable plasma membrane. The endodermis also prevents solutes that have accumulated in the xylem from leaking back into the soil solution. The structure of the endodermis and its strategic location fit its function as an apoplastic barrier between the cortex and the vascular cylinder. The endodermis transports needed minerals from the soil into the xylem and keeps many unneeded or toxic substances out.

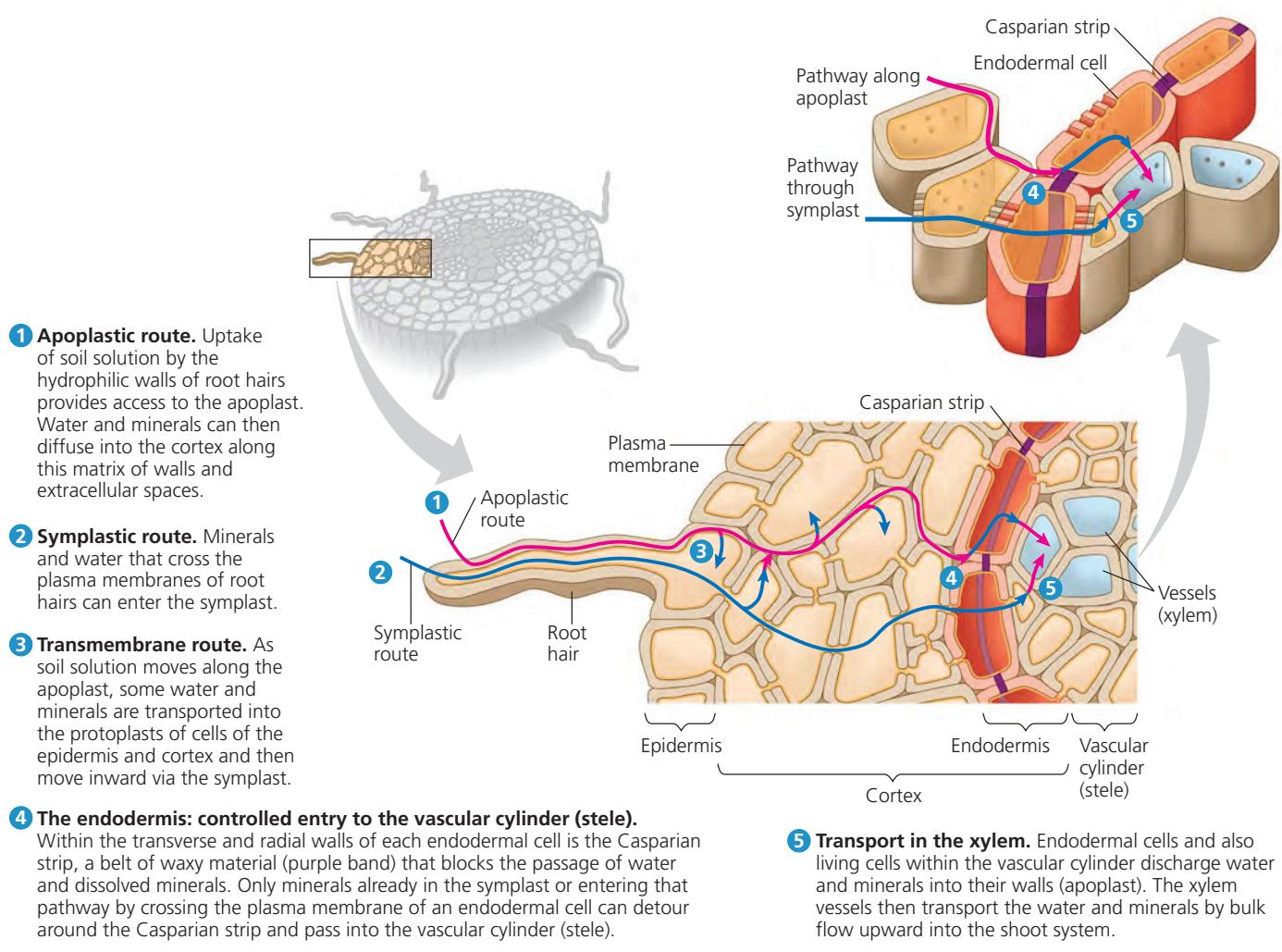
The last segment in the soil-to-xylem pathway is the passage of water and minerals into the tracheids and vessel elements of the xylem. These water-conducting cells lack protoplasts when mature and are therefore parts of the apoplast. Endodermal cells, as well as living cells within the vascular cylinder, discharge minerals from their protoplasts into their own cell walls. Both diffusion and active transport are involved in this transfer of solutes from symplast to apoplast, and the water and minerals are now free to enter the tracheids and vessel elements, where they are transported to the shoot system by bulk flow.

Bulk Flow Transport via the Xylem

Water and minerals from the soil enter the plant through the epidermis of roots, cross the root cortex, and pass into the vascular cylinder. From there the **xylem sap**, the water and dissolved minerals in the xylem, gets transported long distances by bulk flow to the veins that branch throughout each leaf. As noted earlier, bulk flow is much faster than diffusion or active transport. Peak velocities in the transport of xylem sap can range from 15 to 45 m/hr for trees with wide vessel elements. Stems and leaves depend on this efficient delivery system for their supply of water and minerals.

The process of transporting xylem sap involves the loss of an astonishing amount of water by **transpiration**, the loss of water vapor from leaves and other aerial parts of the plant. A single maize plant, for example, transpires 60 L of water (the equivalent of 170 12-ounce bottles) during a growing season. A maize crop growing at a typical density of 60,000 plants per hectare transpires almost 4 million L of water per hectare every growing season (about 400,000 gallons of water per acre per growing season). Unless the transpired water is replaced by water transported up from the roots, the leaves will wilt, and the plants will eventually die.

Xylem sap rises to heights of more than 120 m in the tallest trees. Is the sap mainly *pushed* upward from the roots, or is it mainly *pulled* upward? Let's evaluate the relative contributions of these two mechanisms.



▲ Figure 36.10 Transport of water and minerals from root hairs to the xylem.

How does the Caspary strip force water and minerals to pass through the plasma membranes of endodermal cells?

Pushing Xylem Sap: Root Pressure

At night, when there is almost no transpiration, root cells continue actively pumping mineral ions into the xylem of the vascular cylinder. Meanwhile, the Caspary strip of the endodermis prevents the ions from leaking back out into the cortex and soil. The resulting accumulation of minerals lowers the water potential within the vascular cylinder. Water flows in from the root cortex, generating **root pressure**, a push of xylem sap. The root pressure sometimes causes more water to enter the leaves than is transpired, resulting in **guttation**, the exudation of water droplets that can be seen in the morning on the tips or edges of some plant leaves (**Figure 36.11**). Guttation fluid should not be confused with dew, which is condensed atmospheric moisture.

In most plants, root pressure is a minor mechanism driving the ascent of xylem sap, at most pushing water only a few



▲ **Figure 36.11 Guttation.** Root pressure is forcing excess water from this strawberry leaf.

meters. The positive pressures produced are simply too weak to overcome the gravitational force of the water column in the xylem, particularly in tall plants. Many plants do not generate any root pressure or do so only during part of the growing season. Even in plants that display guttation, root pressure cannot keep pace with transpiration after sunrise. For the most part, xylem sap is not pushed from below by root pressure but is pulled up.

Pulling Xylem Sap: The Cohesion-Tension Hypothesis

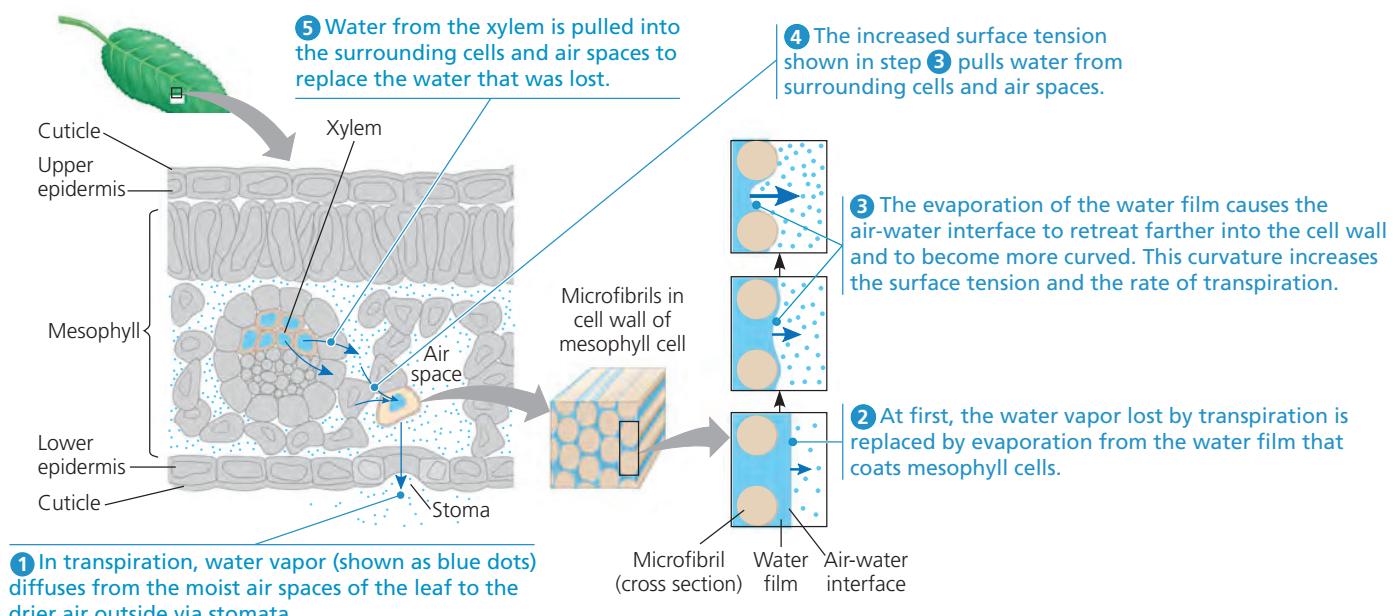
As we have seen, root pressure, which depends on the active transport of solutes by plants, is only a minor force in the ascent of xylem sap. Far from depending on the metabolic activity of cells, most of the xylem sap that rises through a tree does not even require living cells to do so. As demonstrated by Eduard Strasburger in 1891, leafy stems with their lower end immersed in toxic solutions of copper sulfate or acid will readily draw these poisons up if the stem is cut below the surface of the liquid. As the toxic solutions ascend, they kill all living cells in their path, eventually arriving in the transpiring leaves and killing the leaf cells as well. Nevertheless, as Strasburger noted, the uptake of the toxic solutions and the loss of water from the dead leaves can continue for weeks.

In 1894, a few years after Strasburger's findings, two Irish scientists, John Joly and Henry Dixon, put forward a hypothesis that remains the leading explanation of the ascent of xylem sap. According to their **cohesion-tension hypothesis**, transpiration provides the pull for the ascent of xylem sap, and

the cohesion of water molecules transmits this pull along the entire length of the xylem from shoots to roots. Hence, xylem sap is normally under negative pressure, or tension. Since transpiration is a "pulling" process, our exploration of the rise of xylem sap by the cohesion-tension mechanism begins not with the roots but with the leaves, where the driving force for transpirational pull begins.

Transpirational Pull Stomata on a leaf's surface lead to a maze of internal air spaces that expose the mesophyll cells to the CO₂ they need for photosynthesis. The air in these spaces is saturated with water vapor because it is in contact with the moist walls of the cells. On most days, the air outside the leaf is drier; that is, it has lower water potential than the air inside the leaf. Therefore, water vapor in the air spaces of a leaf diffuses down its water potential gradient and exits the leaf via the stomata. It is this loss of water vapor by diffusion and evaporation that we call transpiration.

But how does loss of water vapor from the leaf translate into a pulling force for upward movement of water through a plant? The negative pressure potential that causes water to move up through the xylem develops at the surface of mesophyll cell walls in the leaf (**Figure 36.12**). The cell wall acts like a very thin capillary network. Water adheres to the cellulose microfibrils and other hydrophilic components of the cell wall. As water evaporates from the water film that covers the cell walls of mesophyll cells, the air-water interface retreats farther into the cell wall. Because of the high surface tension of water, the curvature of the interface induces a tension, or negative pressure potential, in the water. As more



▲ **Figure 36.12 Generation of transpirational pull.** Negative pressure (tension) at the air-water interface in the leaf is the basis of transpirational pull, which draws water out of the xylem.

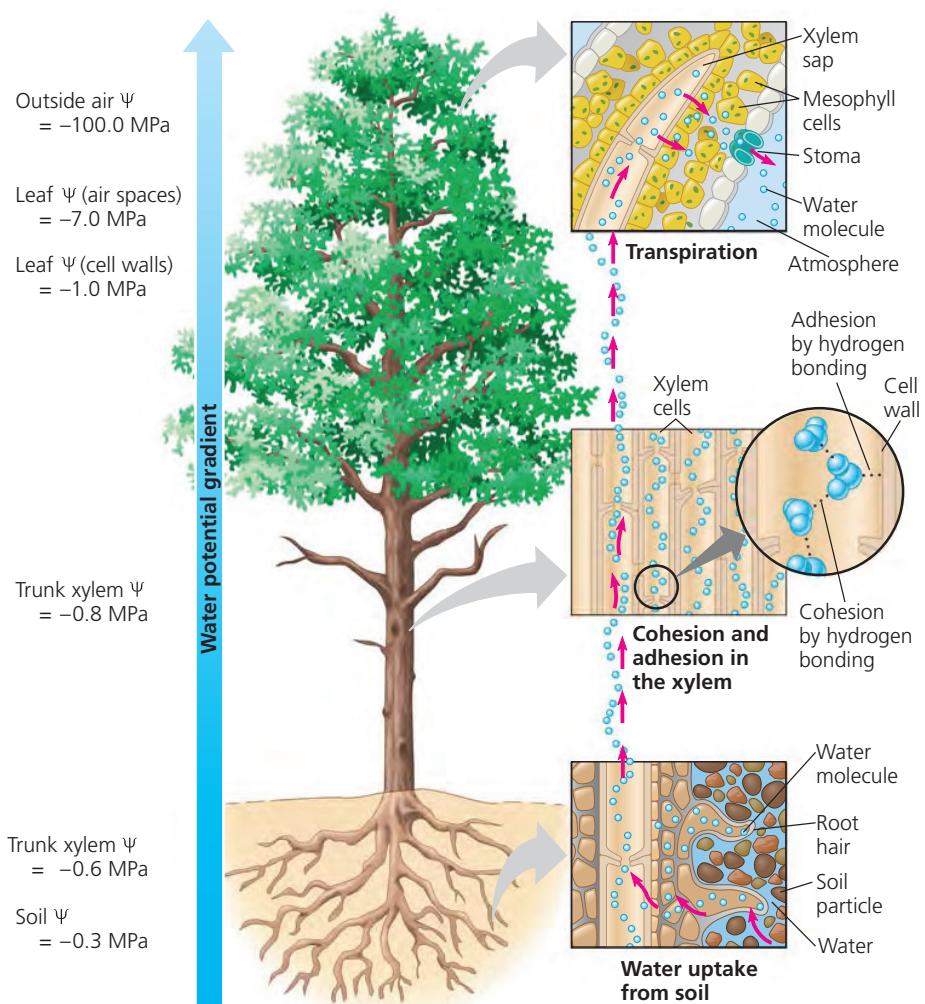
water evaporates from the cell wall, the curvature of the air-water interface increases and the pressure of the water becomes more negative. Water molecules from the more hydrated parts of the leaf are then pulled toward this area, reducing the tension. These pulling forces are transferred to the xylem because each water molecule is cohesively bound to the next by hydrogen bonds. Thus, transpirational pull depends on several of the properties of water discussed in Chapter 3: adhesion, cohesion, and surface tension.

The role of negative pressure potential in transpiration is consistent with the water potential equation because negative pressure potential (tension) *lowers* water potential (see Figure 36.8). Because water moves from areas of higher water potential to areas of lower water potential, the more negative pressure potential at the air-water interface causes water in xylem cells to be “pulled” into mesophyll cells, which lose water to the air spaces, the water diffusing out through stomata. In this way, the negative water potential of leaves provides the “pull” in transpirational pull. The transpirational pull on xylem sap is transmitted all the way from the leaves to the root tips and even into the soil solution (Figure 36.13).

Adhesion and Cohesion in the Ascent of Xylem Sap Adhesion and cohesion facilitate the transport of water by bulk flow. Adhesion is the attractive force between water molecules and other polar substances. Because both water and cellulose are polar molecules, there is a strong attraction between water molecules and the cellulose molecules in the xylem cell walls. Cohesion is the attractive force between molecules of the same substance. Water has an unusually high cohesive force due to the hydrogen bonds each water molecule can potentially make with other water molecules. It is estimated that water's cohesive force within the xylem gives it a tensile strength equivalent to that of a steel wire of similar diameter. The cohesion of water makes it possible to pull a column of xylem sap from above without the water molecules separating. Water molecules exiting the xylem in the leaf tug on adjacent water molecules, and this pull is relayed, molecule by molecule, down the entire column of water

in the xylem. Meanwhile, the strong adhesion of water molecules (again by hydrogen bonds) to the hydrophilic walls of xylem cells helps offset the downward force of gravity.

The upward pull on the sap creates tension within the vessel elements and tracheids, which are like elastic pipes. Positive pressure causes an elastic pipe to swell, whereas tension pulls the walls of the pipe inward. On a warm day, a decrease in the diameter of a tree trunk can even be measured. As transpirational pull puts the vessel elements and tracheids under tension, their thick secondary walls prevent them from collapsing, much as wire rings maintain the shape of a vacuum-cleaner hose. The tension produced by transpirational pull



▲ Figure 36.13 Ascent of xylem sap. Hydrogen bonding forms an unbroken chain of water molecules extending from leaves to the soil. The force driving the ascent of xylem sap is a gradient of water potential (ψ). For bulk flow over long distance, the ψ gradient is due mainly to a gradient of the pressure potential (ψ_P). Transpiration results in the ψ_P at the leaf end of the xylem being lower than the ψ_P at the root end. The ψ values shown at the left are a “snapshot.” They may vary during daylight, but the direction of the ψ gradient remains the same.



Visit the Study Area at www.masteringbiology.com for the BioFlix® 3-D Animation on Water Transport in Plants.

lowers water potential in the root xylem to such an extent that water flows passively from the soil, across the root cortex, and into the vascular cylinder.

Transpirational pull can extend down to the roots only through an unbroken chain of water molecules. Cavitation, the formation of a water vapor pocket, breaks the chain. It is more common in wide vessel elements than in tracheids and can occur during drought stress or when xylem sap freezes in winter. The air bubbles resulting from cavitation expand and block water channels of the xylem. The rapid expansion of air bubbles produces clicking noises that can be heard by placing sensitive microphones at the surface of the stem.

The interruption of xylem sap transport by cavitation is not always permanent. The chain of water molecules can detour around the air bubbles through pits between adjacent tracheids or vessel elements (see Figure 35.10). Moreover, root pressure enables small plants to refill blocked vessel elements. Recent evidence suggests that cavitation may even be repaired when the xylem sap is under negative pressure, although the mechanism by which this occurs is uncertain. In addition, secondary growth adds a layer of new xylem each year. Only the youngest, outermost secondary xylem layers transport water. Although the older secondary xylem no longer transports water, it does provide support for the tree (see Figure 35.22).

Xylem Sap Ascent by Bulk Flow: A Review

The cohesion-tension mechanism that transports xylem sap against gravity is an excellent example of how physical principles apply to biological processes. In the long-distance transport of water from roots to leaves by bulk flow, the movement of fluid is driven by a water potential difference at opposite ends of xylem tissue. The water potential difference is created at the leaf end of the xylem by the evaporation of water from leaf cells. Evaporation lowers the water potential at the air-water interface, thereby generating the negative pressure (tension) that pulls water through the xylem.

Bulk flow in the xylem differs from diffusion in some key ways. First, it is driven by differences in pressure potential (ψ_p); solute potential (ψ_s) is not a factor. Therefore, the water potential gradient within the xylem is essentially a pressure gradient. Also, the flow does not occur across plasma membranes of living cells, but instead within hollow, dead cells. Furthermore, it moves the entire solution together—not just water or solutes—and at much greater speed than diffusion.

The plant expends no energy to lift xylem sap by bulk flow. Instead, the absorption of sunlight drives most of transpiration by causing water to evaporate from the moist walls of mesophyll cells and by lowering the water potential in the air spaces within a leaf. Thus, the ascent of xylem sap, like the process of photosynthesis, is ultimately solar powered.

CONCEPT CHECK 36.3

- How do xylem cells facilitate long-distance transport?
- A horticulturalist notices that when *Zinnia* flowers are cut at dawn, a small drop of water collects at the surface of the stump. However, when the flowers are cut at noon, no drop is observed. Suggest an explanation.
- A scientist adds a water-soluble inhibitor of photosynthesis to roots of a transpiring plant, but photosynthesis is not reduced. Why?
- WHAT IF?** Suppose an *Arabidopsis* mutant lacking functional aquaporin proteins has a root mass three times greater than that of wild-type plants. Suggest an explanation.
- MAKE CONNECTIONS** How are the Casparyan strip and tight junctions similar? See Figure 6.32 on p. 121.

For suggested answers, see Appendix A.

CONCEPT 36.4

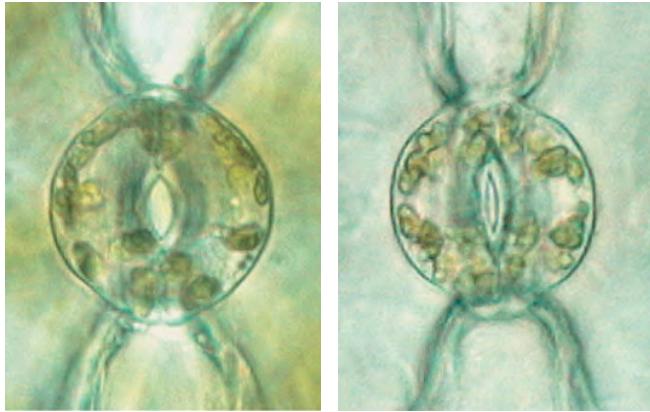
The rate of transpiration is regulated by stomata

Leaves generally have large surface areas and high surface-to-volume ratios. The large surface area enhances light absorption for photosynthesis. The high surface-to-volume ratio aids in CO₂ absorption during photosynthesis as well as in the release of O₂, a by-product of photosynthesis. Upon diffusing through the stomata, CO₂ enters a honeycomb of air spaces formed by the spongy mesophyll cells (see Figure 35.18). Because of the irregular shapes of these cells, the leaf's internal surface area may be 10 to 30 times greater than the external surface area.

Although large surface areas and high surface-to-volume ratios increase the rate of photosynthesis, they also increase water loss by way of the stomata. Thus, a plant's tremendous requirement for water is largely a consequence of the shoot system's need for ample exchange of CO₂ and O₂ for photosynthesis. By opening and closing the stomata, guard cells help balance the plant's requirement to conserve water with its requirement for photosynthesis (Figure 36.14).

Stomata: Major Pathways for Water Loss

About 95% of the water a plant loses escapes through stomata, although these pores account for only 1–2% of the external leaf surface. The waxy cuticle limits water loss through the remaining surface of the leaf. Each stoma is flanked by a pair of guard cells. Guard cells control the diameter of the stoma by changing shape, thereby widening or narrowing the gap between the guard cell pair. Under the same environmental conditions, the amount of water lost by a leaf



▲ **Figure 36.14** An open stoma (left) and closed stoma (LMs).

depends largely on the number of stomata and the average size of their pores.

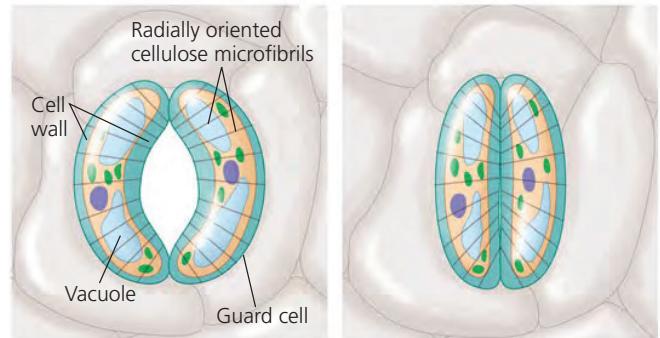
The stomatal density of a leaf, which may be as high as 20,000 per square centimeter, is under both genetic and environmental control. For example, as a result of evolution by natural selection, desert plants are genetically programmed to have lower stomatal densities than do marsh plants. Stomatal density, however, is a developmentally plastic feature of many plants. High light exposures and low CO₂ levels during leaf development lead to increased density in many species. By measuring the stomatal density of leaf fossils, scientists have gained insight into the levels of atmospheric CO₂ in past climates. A recent British survey found that stomatal density of many woodland species has decreased since 1927, when a similar survey was made. This observation is consistent with other findings that atmospheric CO₂ levels increased dramatically during the late 20th century.

Mechanisms of Stomatal Opening and Closing

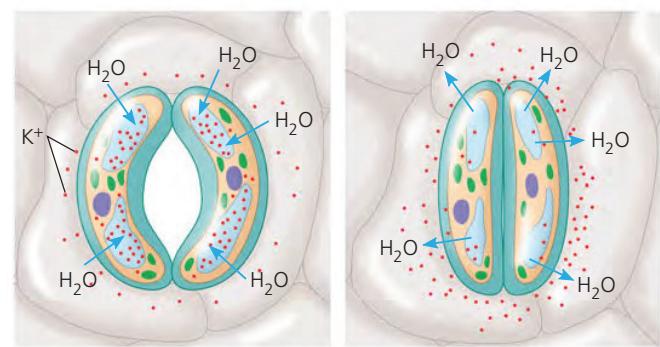
When guard cells take in water from neighboring cells by osmosis, they become more turgid. In most angiosperm species, the cell walls of guard cells are uneven in thickness, and the cellulose microfibrils are oriented in a direction that causes the guard cells to bow outward when turgid (**Figure 36.15a**). This bowing outward increases the size of the pore between the guard cells. When the cells lose water and become flaccid, they become less bowed, and the pore closes.

The changes in turgor pressure in guard cells result primarily from the reversible absorption and loss of K⁺. Stomata open when guard cells actively accumulate K⁺ from neighboring epidermal cells (**Figure 36.15b**). The flow of K⁺ across the plasma membrane of the guard cell is coupled to the generation of a membrane potential by proton pumps (see Figure 36.7a). Stomatal opening correlates with active transport of H⁺ out of the guard cell. The resulting voltage (membrane potential) drives K⁺ into the cell through specific membrane channels.

Guard cells turgid/Stoma open **Guard cells flaccid/Stoma closed**



(a) **Changes in guard cell shape and stomatal opening and closing (surface view).** Guard cells of a typical angiosperm are illustrated in their turgid (stoma open) and flaccid (stoma closed) states. The radial orientation of cellulose microfibrils in the cell walls causes the guard cells to increase more in length than width when turgor increases. Since the two guard cells are tightly joined at their tips, they bow outward when turgid, causing the stomatal pore to open.



(b) **Role of potassium in stomatal opening and closing.** The transport of K⁺ (potassium ions, symbolized here as red dots) across the plasma membrane and vacuolar membrane causes the turgor changes of guard cells. The uptake of anions, such as malate and chloride ions (not shown), also contributes to guard cell swelling.

▲ **Figure 36.15** Mechanisms of stomatal opening and closing.

The absorption of K⁺ causes the water potential to become more negative within the guard cells, and the cells become more turgid as water enters by osmosis. Because most of the K⁺ and water are stored in the vacuole, the vacuolar membrane also plays a role in regulating guard cell dynamics. Stomatal closing results from a loss of K⁺ from guard cells to neighboring cells, which leads to an osmotic loss of water. Aquaporins also help regulate the osmotic swelling and shrinking of guard cells.

Stimuli for Stomatal Opening and Closing

In general, stomata are open during the day and mostly closed at night, preventing the plant from losing water under conditions when photosynthesis cannot occur. At least three

cues contribute to stomatal opening at dawn: light, CO₂ depletion, and an internal “clock” in guard cells.

The light stimulates guard cells to accumulate K⁺ and become turgid. This response is triggered by illumination of blue-light receptors in the plasma membrane of guard cells. Activation of these receptors stimulates the activity of proton pumps in the plasma membrane of the guard cells, in turn promoting absorption of K⁺.

The stomata also open in response to depletion of CO₂ within the leaf's air spaces as a result of photosynthesis. As CO₂ concentrations decrease during the day, the stomata progressively open if sufficient water is supplied to the leaf.

A third cue, the internal “clock” in the guard cells, ensures that stomata continue their daily rhythm of opening and closing. This rhythm occurs even if a plant is kept in a dark location. All eukaryotic organisms have internal clocks that regulate cyclic processes. Cycles with intervals of approximately 24 hours are called **circadian rhythms**, which you'll learn more about in Chapter 39.

Environmental stresses, such as drought, high temperature, and wind, can cause stomata to close during the daytime. When the plant has a water deficiency, guard cells may lose turgor and close stomata. In addition, a hormone called **abscisic acid (ABA)**, produced in roots and leaves in response to water deficiency, signals guard cells to close stomata. This response reduces wilting but also restricts CO₂ absorption, thereby slowing photosynthesis. Since turgor is necessary for cell elongation, growth ceases throughout the plant. These are some reasons why droughts reduce crop yields.

Guard cells control the photosynthesis-transpiration compromise on a moment-to-moment basis by integrating a variety of internal and external stimuli. Even the passage of a cloud or a transient shaft of sunlight through a forest can affect the rate of transpiration.

Effects of Transpiration on Wilting and Leaf Temperature

As long as most stomata remain open, transpiration is greatest on a day that is sunny, warm, dry, and windy because these environmental factors increase evaporation. If transpiration cannot pull sufficient water to the leaves, the shoot becomes slightly wilted as cells lose turgor pressure. Although plants respond to such mild drought stress by rapidly closing stomata, some evaporative water loss still occurs through the cuticle. Under prolonged drought conditions, leaves can become severely wilted and irreversibly injured.

Transpiration also results in evaporative cooling, which can lower a leaf's temperature by as much as 10°C compared with the surrounding air. This cooling prevents the leaf from reaching temperatures that could denature enzymes involved in photosynthesis and other metabolic processes.

Adaptations That Reduce Evaporative Water Loss

Plants adapted to arid environments, such as the stone plants of the Kalahari Desert (see Figure 36.1), are called **xerophytes** (from the Greek *xero*, dry). **Figure 36.16** shows other examples. Dry soils are relatively unproductive because plants need a sufficient quantity of liquid water to carry out photosynthesis. However, the reason why water availability is so tied to plant productivity is not related to photosynthesis's direct need for water as a substrate but rather because freely available water allows plants to keep stomata open and take up more CO₂.

Many species of desert plants avoid drying out by completing their short life cycles during the brief rainy seasons. Rain comes infrequently in deserts, but when it arrives, the vegetation is transformed as dormant seeds of annual species quickly germinate and bloom, completing their life cycle before dry conditions return. Longer-lived species have unusual physiological or morphological adaptations that enable them to withstand the harsh desert conditions. Many xerophytes, such as cacti, have highly reduced leaves that resist excessive water loss; they carry out photosynthesis mainly in their stems. The stems of many xerophytes are fleshy because they store water for use during long dry periods. Some desert plants, such as mesquite, have roots more than 20 m long, allowing them to acquire moisture at or near the water table.

Another adaptation to arid habitats is crassulacean acid metabolism (CAM), a specialized form of photosynthesis found in succulents of the family Crassulaceae and several other families (see Figure 10.21). Because the leaves of CAM plants take in CO₂ at night, the stomata can remain closed during the day, when evaporative stresses are greater. Stomata are the most important mediators of the conflicting demands of CO₂ acquisition and water retention.

CONCEPT CHECK 36.4

- What are the stimuli that control the opening and closing of stomata?
- The pathogenic fungus *Fusicoccum amygdali* secretes a toxin called fusicoccin that activates the plasma membrane proton pumps of plant cells and leads to uncontrolled water loss. Suggest a mechanism by which the activation of proton pumps could lead to severe wilting.
- WHAT IF?** If you buy cut flowers, why might the florist recommend cutting the stems underwater and then transferring the flowers to a vase while the cut ends are still wet?
- MAKE CONNECTIONS** Explain why the evaporation of water from leaves lowers their temperature. See p. 49 of Concept 3.2.

For suggested answers, see Appendix A.

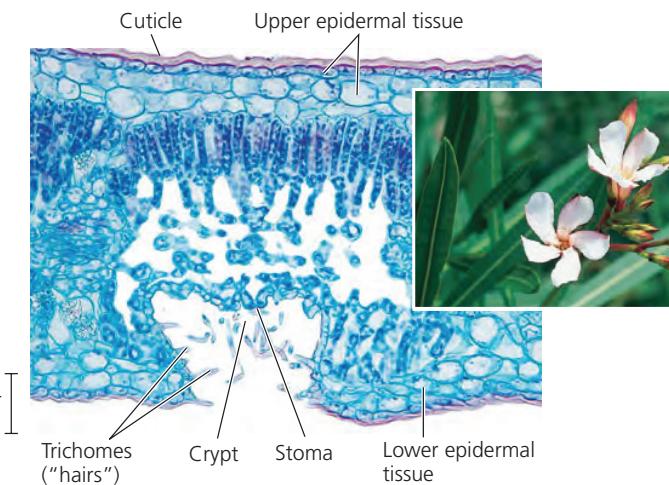
▼ Figure 36.16 Some xerophytic adaptations.

► Ocotillo (*Fouquieria splendens*) is common in the southwestern region of the United States and northern Mexico. It is leafless during most of the year, thereby avoiding excessive water loss (right). Immediately after a heavy rainfall, it produces small leaves (below and inset). As the soil dries, the leaves quickly shrivel and die.



► This is a close-up view of stems of old man cactus (*Cephalocereus senilis*), a Mexican desert plant. The long, white, hairlike bristles help reflect the sun.

▼ Oleander (*Nerium oleander*), shown in the inset, is commonly found in arid climates. Its leaves have a thick cuticle and multiple-layered epidermal tissue that reduce water loss. Stomata are recessed in cavities called "crypts," an adaptation that reduces the rate of transpiration by protecting the stomata from hot, dry wind. Trichomes help minimize transpiration by breaking up the flow of air, allowing the chamber of the crypt to have a higher humidity than the surrounding atmosphere (LM).



CONCEPT 36.5

Sugars are transported from sources to sinks via the phloem

You have read how water and minerals are absorbed by root cells, transported through the endodermis, released into the vessel elements and tracheids of the xylem, and carried to the tops of plants by the bulk flow driven by transpiration. However, transpiration cannot meet all the long-distance transport needs of the plant. The flow of water and minerals from soil to roots to leaves is largely in a direction opposite to the direction necessary for transporting sugars from mature leaves to lower parts of the plant, such as root tips that require large amounts of sugars for energy and growth. The transport of the products of photosynthesis, known as **translocation**, is carried out by another tissue, the phloem.

Movement from Sugar Sources to Sugar Sinks

In angiosperms, the specialized cells that are conduits for translocation are the sieve-tube elements. Arranged end to end, they form long sieve tubes (see Figure 35.10). Between these cells are sieve plates, structures that allow the flow of sap along the sieve tube.

Phloem sap, the aqueous solution that flows through sieve tubes, differs markedly from the xylem sap that is transported by tracheids and vessel elements. By far the most prevalent solute in phloem sap is sugar, typically sucrose in most species. The sucrose concentration may be as high as 30% by weight, giving the sap a syrupy thickness. Phloem sap may also contain amino acids, hormones, and minerals.

In contrast to the unidirectional transport of xylem sap from roots to leaves, phloem sap moves from sites of sugar production to sites of sugar use or storage (see Figure 36.2). A

sugar source is a plant organ that is a net producer of sugar, by photosynthesis or by breakdown of starch. A **sugar sink** is an organ that is a net consumer or depository of sugar. Growing roots, buds, stems, and fruits are sugar sinks. Although expanding leaves are sugar sinks, mature leaves, if well illuminated, are sugar sources. A storage organ, such as a tuber or a bulb, may be a source or a sink, depending on the season. When stockpiling carbohydrates in the summer, it is a sugar sink. After breaking dormancy in the spring, it is a sugar source because its starch is broken down to sugar, which is carried to the growing shoot tips.

Sinks usually receive sugar from the nearest sugar sources. The upper leaves on a branch, for example, may export sugar to the growing shoot tip, whereas the lower leaves may export sugar to the roots. A growing fruit may monopolize the sugar sources that surround it. For each sieve tube, the direction of transport depends on the locations of the sugar source and sugar sink that are connected by that tube. Therefore, neighboring sieve tubes may carry sap in opposite directions if they originate and end in different locations.

Sugar must be transported, or loaded, into sieve-tube elements before being exported to sugar sinks. In some species, it moves from mesophyll cells to sieve-tube elements via the symplast, passing through plasmodesmata. In other species, it moves by symplastic and apoplastic pathways. In maize leaves, for example, sucrose diffuses through the symplast from photosynthetic mesophyll cells into small veins. Much of it then moves into the apoplast and is accumulated by nearby sieve-tube elements, either directly or through companion cells (Figure 36.17a). In some plants, the walls of the companion cells feature many ingrowths, enhancing solute transfer between apoplast and symplast.

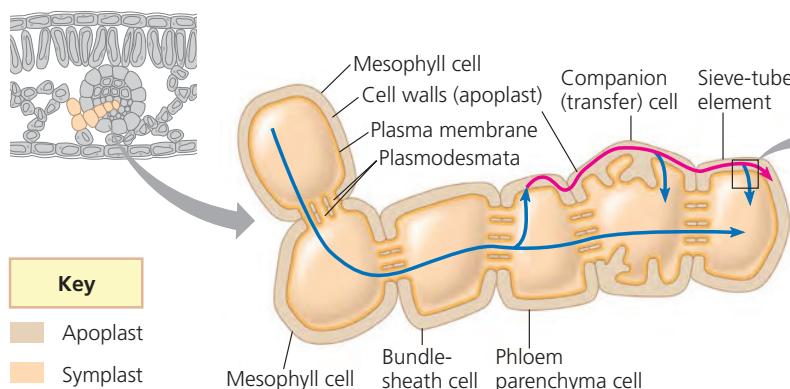
In many plants, sugar movement into the phloem requires active transport because sucrose is more concentrated in sieve-tube elements and companion cells than in mesophyll. Proton pumping and H^+ /sucrose cotransport enable sucrose to move from mesophyll cells to sieve-tube elements or companion cells (Figure 36.17b).

Sucrose is unloaded at the sink end of a sieve tube. The process varies by species and organ. However, the concentration of free sugar in the sink is always lower than in the sieve tube because the unloaded sugar is consumed during growth and metabolism of the cells of the sink or converted to insoluble polymers such as starch. As a result of this sugar concentration gradient, sugar molecules diffuse from the phloem into the sink tissues, and water follows by osmosis.

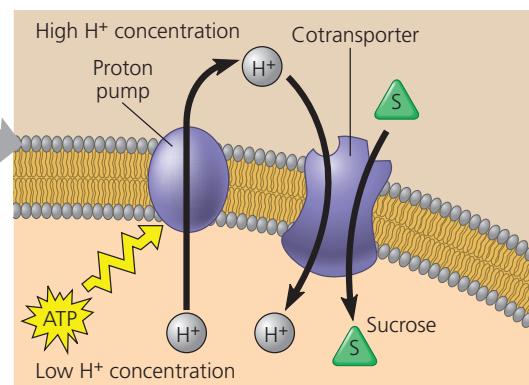
Bulk Flow by Positive Pressure: The Mechanism of Translocation in Angiosperms

Phloem sap flows from source to sink at rates as great as 1 m/hr⁻¹, much faster than diffusion or cytoplasmic streaming. Researchers have concluded that phloem sap moves through the sieve tubes of angiosperms by bulk flow driven by positive pressure, known as *pressure flow* (Figure 36.18). The building of pressure at the source and reduction of that pressure at the sink cause sap to flow from source to sink.

The pressure-flow hypothesis explains why phloem sap flows from source to sink, and experiments build a strong case for pressure flow as the mechanism of translocation in angiosperms (Figure 36.19). However, studies using electron microscopes suggest that in nonflowering vascular plants, the pores between phloem cells may be too small or obstructed to permit pressure flow.



(a) Sucrose manufactured in mesophyll cells can travel via the symplast (blue arrows) to sieve-tube elements. In some species, sucrose exits the symplast near sieve tubes and travels through the apoplast (red arrow). It is then actively accumulated from the apoplast by sieve-tube elements and their companion cells.



(b) A chemiosmotic mechanism is responsible for the active transport of sucrose into companion cells and sieve-tube elements. Proton pumps generate an H^+ gradient, which drives sucrose accumulation with the help of a cotransport protein that couples sucrose transport to the diffusion of H^+ back into the cell.

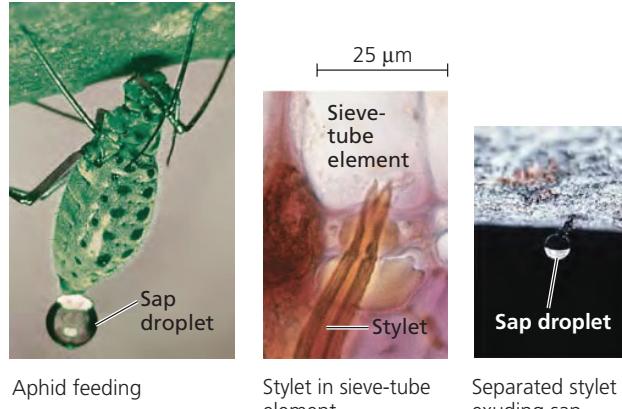
▲ Figure 36.17 Loading of sucrose into phloem.

INQUIRY

▼ Figure 36.19

Does phloem sap contain more sugar near sources than sinks?

EXPERIMENT The pressure-flow hypothesis predicts that phloem sap near sources should have a higher sugar content than phloem sap near sinks. To test this aspect of the hypothesis, researchers used aphids that feed on phloem sap. An aphid probes with a hypodermic-like mouthpart called a stylet that penetrates a sieve-tube element. As sieve-tube pressure forced out phloem sap into the stylets, the researchers separated the aphids from the stylets, which then acted as taps exuding sap for hours. Researchers measured the sugar concentration of sap from stylets at different points between a source and sink.

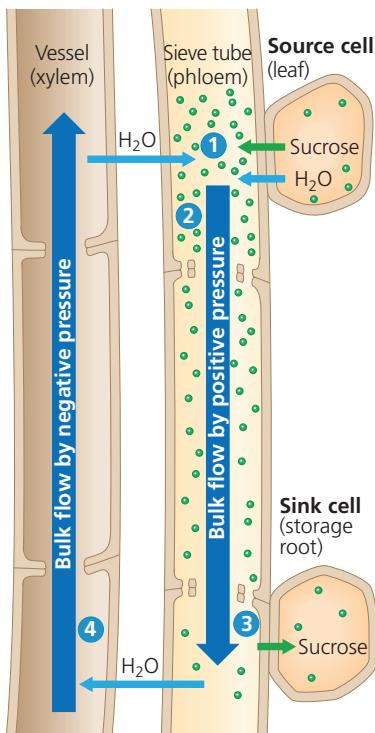


RESULTS The closer the stylet was to a sugar source, the higher its sugar concentration.

CONCLUSION The results of such experiments support the pressure-flow hypothesis, which predicts that sugar concentrations should be higher in sieve tubes closer to sugar sources.

SOURCE S. Rogers and A. J. Peel, Some evidence for the existence of turgor pressure in the sieve tubes of willow (*Salix*), *Planta* 126:259–267 (1975).

WHAT IF? Spittlebugs are xylem sap feeders that use strong muscles to pump xylem sap through their guts. Could you isolate xylem sap from the excised stylets of spittlebugs?



▲ Figure 36.18 Bulk flow by positive pressure (pressure flow) in a sieve tube.

Sinks vary in energy demands and capacity to unload sugars. Sometimes there are more sinks than can be supported by sources. In such cases, a plant might abort some flowers, seeds, or fruits—a phenomenon called *self-thinning*. Removing sinks can also be a horticulturally useful practice. For example, since large apples command a much better price than small ones, growers sometimes remove flowers or young fruits so that their trees produce fewer but larger apples.

CONCEPT CHECK 36.5

1. Compare and contrast the forces that move phloem sap and xylem sap over long distance.
2. Identify plant organs that are sugar sources, organs that are sugar sinks, and organs that might be either. Explain.
3. Why can xylem transport water and minerals using dead cells, whereas phloem requires living cells?
4. **WHAT IF?** Apple growers in Japan sometimes make a nonlethal spiral slash around the bark of trees that are destined for removal after the growing season. This practice makes the apples sweeter. Why?

For suggested answers, see Appendix A.

CONCEPT 36.6

The symplast is highly dynamic

Although we have been discussing transport in mostly physical terms, almost like the flow of solutions through pipes, plant transport is a finely tuned process. That is, the transport needs of a plant cell typically change during its development. A leaf, for example, may begin as a sugar sink but spend most of its life as a sugar source. Also, environmental changes may trigger marked responses in plant transport processes. Water stress may activate signal transduction pathways that greatly alter the membrane transport proteins governing the overall transport of water and minerals. Because the symplast is living tissue, it is largely responsible for the dynamic changes in plant transport processes.

Changes in Plasmodesmata

Plasmodesmata are highly dynamic components of the symplast. Mostly on the basis of static images from electron microscopy, biologists formerly thought of plasmodesmata as unchanging pore-like structures. Recently, however, new techniques have revealed that plasmodesmata are highly dynamic structures that can change in permeability and number. They can open or close rapidly in response to changes in turgor pressure, cytosolic Ca^{2+} levels, or cytosolic pH. Although some form during cytokinesis, they can also form much later. Moreover, loss of function is common during differentiation. For example, as a leaf matures from a sink to a source, its plasmodesmata either close or are eliminated, causing phloem unloading to cease.

Early studies by plant physiologists and pathologists came to differing conclusions regarding pore sizes of plasmodesmata. Physiologists injected fluorescent probes of different molecular sizes into cells and recorded whether the molecules passed into adjacent cells. Based on these observations, they concluded that the pore sizes were approximately 2.5 nm—too small for macromolecules such as proteins to pass. In contrast, pathologists provided electron micrographs showing evidence of the passage of virus particles with diameters of 10 nm or greater (**Figure 36.20**). One hypothesis to explain these discordant findings was that viruses dilate plasmodesmata.

Subsequently, it was learned that plant viruses produce *viral movement proteins* that cause plasmodesmata to dilate, enabling viral RNA to pass between cells. More recent evidence shows that plant cells themselves regulate plasmodesmata as part of a communication network. Viruses subvert this network by mimicking the cell's regulators of plasmodesmata.

A high degree of cytosolic interconnectedness exists only within certain groups of cells and tissues, known as *sympathetic domains*. Informational molecules, such as proteins and RNAs, coordinate development between cells within each sympathetic domain. If sympathetic communication is disrupted, development can be grossly affected.



▲ **Figure 36.20** Virus particles moving cell to cell through a plasmodesma connecting turnip leaf cells (TEM).

Phloem: An Information Superhighway

In addition to transporting sugars, the phloem is a “superhighway” for the transport of macromolecules and viruses. This transport is systemic (throughout the body), affecting many or all of the plant’s systems or organs. Macromolecules translocated through the phloem include proteins and various types of RNA that enter the sieve tubes through plasmodesmata. Although they are often likened to the gap junctions between animal cells, plasmodesmata are unique in their ability to traffic proteins and RNA.

Systemic communication through the phloem helps integrate the functions of the whole plant. One classic example is the delivery of a flower-inducing signal from leaves to vegetative meristems. Another is a defensive response to localized infection, in which signals traveling through the phloem activate defense genes in noninfected tissues.

Electrical Signaling in the Phloem

Rapid, long-distance electrical signaling through the phloem is another dynamic feature of the symplast. Electrical signaling has been studied extensively in plants that have rapid leaf movements, such as the sensitive plant (*Mimosa pudica*) and Venus flytrap (*Dionaea muscipula*). However, its role in other species is less clear. Some studies have revealed that a stimulus in one part of a plant can trigger an electrical signal in the phloem that affects another part, where it may elicit a change in gene transcription, respiration, photosynthesis, phloem unloading, or hormonal levels. Thus, the phloem can serve a nerve-like function, allowing for swift electrical communication between widely separated organs.

The coordinated transport of materials and information is central to plant survival. Plants acquire only so many resources in the course of their lifetimes. Ultimately, the successful acquisition of resources and their optimal distribution are the most critical determinants of whether the plant will compete successfully.

CONCEPT CHECK 36.6

1. How do plasmodesmata differ from gap junctions?
2. Nerve-like signals in animals are thousands of times faster than their plant counterparts. Suggest a behavioral reason for the difference.
3. **WHAT IF?** Suppose plants were genetically modified to be unresponsive to viral movement proteins. Would this be a good way to prevent the spread of infection? Explain.

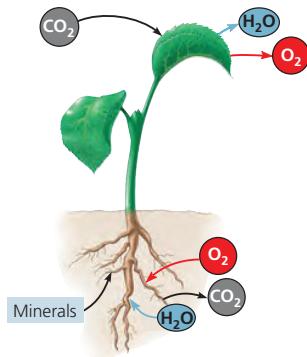
For suggested answers, see Appendix A.

36 CHAPTER REVIEW

SUMMARY OF KEY CONCEPTS

CONCEPT 36.1

Adaptations for acquiring resources were key steps in the evolution of vascular plants (pp. 764–767)



- Leaves typically function in gathering sunlight and CO_2 . Stems serve as supporting structures for leaves and as conduits for the long-distance transport of water and nutrients. Roots mine the soil for water and minerals and anchor the whole plant. **Mycorrhizae** are mutualistic associations formed between roots and certain soil fungi that aid in the absorption of minerals and water.
- Natural selection has produced plant architectures that optimize resource acquisition in the ecological niche in which the plant species naturally exists.

?

How did the evolution of xylem and phloem contribute to the successful colonization of land by vascular plants?

CONCEPT 36.2

Different mechanisms transport substances over short or long distances (pp. 767–771)

- The selective permeability of the plasma membrane controls the movement of substances into and out of cells. Both active and passive transport mechanisms occur in plants.
- Plant tissues have two major compartments: the **apoplast** (everything outside the cells' plasma membranes) and the **symplast** (the cytosol and connecting plasmodesmata).
- The direction of water movement depends on the **water potential**, a quantity incorporating solute concentration and physical pressure. The osmotic uptake of water by plant cells and the resulting internal pressure that builds up make plant cells **turgid**.
- Long-distance transport occurs through **bulk flow**, the movement of liquid in response to a pressure gradient. Bulk flow occurs within the tracheids and vessel elements of the xylem and within the sieve-tube elements of the phloem.

?

Is xylem sap usually pulled or pushed up the plant?

CONCEPT 36.3

Transpiration drives the transport of water and minerals from roots to shoots via the xylem (pp. 772–776)

- Water and minerals from the soil enter the plant through the epidermis of roots, cross the root cortex, and then pass into the

vascular cylinder by way of the selectively permeable cells of the **endodermis**. From the vascular cylinder, the **xylem sap** is transported long distances by bulk flow to the veins that branch throughout each leaf.

- The **cohesion-tension hypothesis** proposes that the movement of xylem sap is driven by a water potential difference created at the leaf end of the xylem by the evaporation of water from leaf cells. Evaporation lowers the water potential at the air-water interface, thereby generating the negative pressure that pulls water through the xylem.

?

Why is the ability of water molecules to form hydrogen bonds important for the movement of xylem sap?

CONCEPT 36.4

The rate of transpiration is regulated by stomata (pp. 776–778)

- Transpiration** is the loss of water vapor from plants. **Wilting** occurs when the water lost by transpiration is not replaced by absorption from roots.
- Stomata are the major pathway for water loss from plants. Guard cells widen or narrow the stomatal pores. When guard cells take up K^+ , the pore widens. The opening and closing of stomata is controlled by light, CO_2 , the drought hormone **abscisic acid**, and a **circadian rhythm**.
- Reduced leaves and CAM photosynthesis are examples of adaptations to arid environments.

?

Why are stomata necessary?

CONCEPT 36.5

Sugars are transported from sources to sinks via the phloem (pp. 779–781)

- Mature leaves are the main **sugar sources**, although storage organs can be seasonal sources. Growing organs such as roots, stems, and fruits are the main **sugar sinks**.
- Phloem loading depends on the active transport of sucrose. Sucrose is cotransported with H^+ , which diffuses down a gradient generated by proton pumps. Loading of sugar at the source and unloading at the sink maintain a pressure difference that keeps sap flowing through a sieve tube.

?

Why is phloem transport considered an active process?

CONCEPT 36.6

The symplast is highly dynamic (pp. 781–782)

- Plasmodesmata** can change in permeability and number. When dilated, they provide a passageway for the symplastic transport of proteins, RNAs, and other macromolecules over long distances. The phloem also conducts nerve-like electrical signals that help integrate whole-plant function.

?

By what mechanisms is symplastic communication regulated?

TEST YOUR UNDERSTANDING

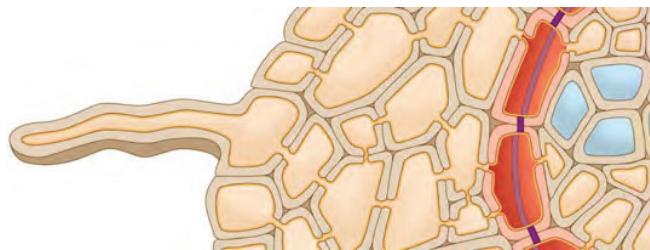
LEVEL 1: KNOWLEDGE/COMPREHENSION

1. The symplast transports all of the following *except*
 - a. sugars.
 - b. mRNA.
 - c. DNA.
 - d. proteins.
 - e. viruses.
2. Which of the following is an adaptation that enhances the uptake of water and minerals by roots?
 - a. mycorrhizae
 - b. cavitation
 - c. active uptake by vessel elements
 - d. rhythmic contractions by cortical cells
 - e. pumping through plasmodesmata
3. Which structure or compartment is part of the symplast?
 - a. the interior of a vessel element
 - b. the interior of a sieve tube
 - c. the cell wall of a mesophyll cell
 - d. an extracellular air space
 - e. the cell wall of a root hair
4. Movement of phloem sap from a source to a sink
 - a. occurs through the apoplast of sieve-tube elements.
 - b. depends ultimately on the activity of proton pumps.
 - c. depends on tension, or negative pressure potential.
 - d. depends on pumping water into sieve tubes at the source.
 - e. results mainly from diffusion.

LEVEL 2: APPLICATION/ANALYSIS

5. Photosynthesis ceases when leaves wilt, mainly because
 - a. the chlorophyll in wilting leaves is degraded.
 - b. flaccid mesophyll cells are incapable of photosynthesis.
 - c. stomata close, preventing CO₂ from entering the leaf.
 - d. photolysis, the water-splitting step of photosynthesis, cannot occur when there is a water deficiency.
 - e. accumulation of CO₂ in the leaf inhibits enzymes.
6. What would enhance water uptake by a plant cell?
 - a. decreasing the ψ of the surrounding solution
 - b. increasing the pressure exerted by the cell wall
 - c. the loss of solutes from the cell
 - d. increasing the ψ of the cytoplasm
 - e. positive pressure on the surrounding solution
7. A plant cell with a ψ_s of -0.65 MPa maintains a constant volume when bathed in a solution that has a ψ_s of -0.30 MPa and is in an open container. The cell has a
 - a. ψ_p of +0.65 MPa.
 - b. ψ of -0.65 MPa.
 - c. ψ_p of +0.35 MPa.
 - d. ψ_p of +0.30 MPa.
 - e. ψ of 0 MPa.
8. Compared with a cell with few aquaporin proteins in its membrane, a cell containing many aquaporin proteins will
 - a. have a faster rate of osmosis.
 - b. have a lower water potential.
 - c. have a higher water potential.
 - d. have a faster rate of active transport.
 - e. accumulate water by active transport.
9. Which of the following would tend to increase transpiration?
 - a. a rainstorm
 - b. sunken stomata
 - c. a thicker cuticle
 - d. higher stomatal density
 - e. spiny leaves

10. **DRAW IT** Trace the uptake of water and minerals from root hairs to the endodermis in a root, following a symplastic route and an apoplastic route. Label the routes on the diagram below.



LEVEL 3: SYNTHESIS/EVALUATION

11. EVOLUTION CONNECTION

Large brown algae called kelps can grow as tall as 25 m. Kelps consist of a holdfast anchored to the ocean floor, blades that float at the surface and collect light, and a long stalk connecting the blades to the holdfast (see Figure 28.15). Specialized cells in the stalk, although nonvascular, can transport sugar. Suggest a reason why these structures analogous to sieve-tube elements might have evolved in kelps.

12. SCIENTIFIC INQUIRY

Cotton plants wilt within a few hours of flooding their roots. The flooding leads to low-oxygen conditions, increases in cytosolic Ca²⁺, and decreases in cytosolic pH. Suggest a hypothesis to explain how flooding leads to wilting.

13. WRITE ABOUT A THEME

Structure and Function Natural selection has led to changes in the architecture of plants that enable them to photosynthesize more efficiently in the ecological niches they occupy. In a short essay (100–150 words), explain how shoot architecture enhances photosynthesis.

For selected answers, see Appendix A.

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Activities Transport of Xylem Sap • Translocation of Phloem Sap • Solute Transport in Plants

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