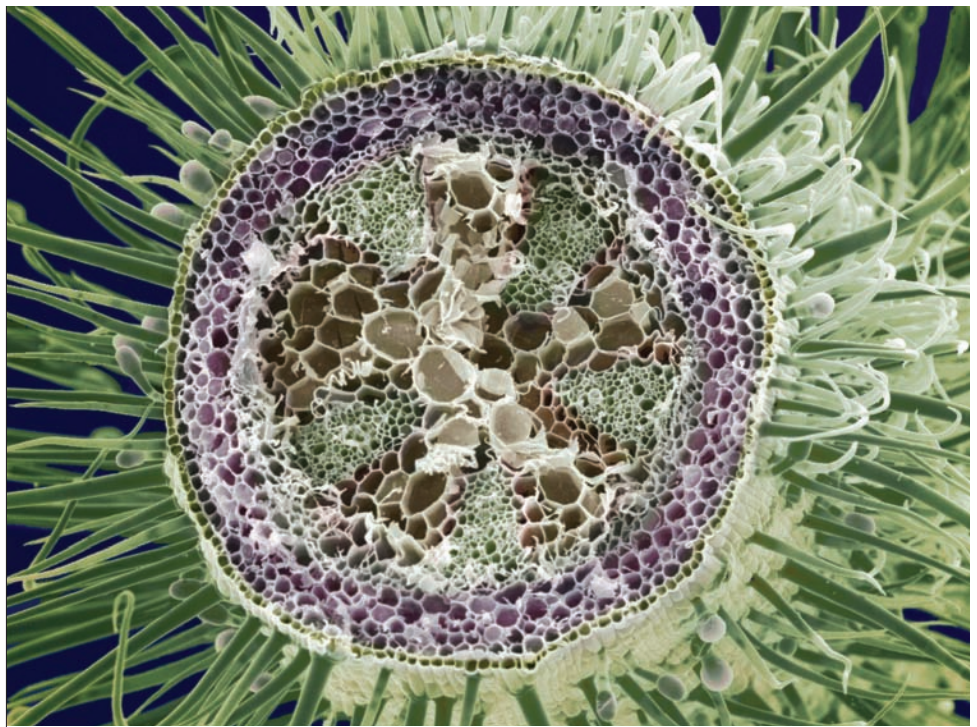


Cross section of the stem of a geranium (*Pelargonium*) showing parenchyma (pink) wrapping around vessels that transport water and nutrients in plants. In this false-color SEM, large-diameter vessels (xylem) that carry water and minerals appear whitish and bundles of smaller vessels (phloem), which transport sugars, appear pale green.

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## STUDY PLAN

### 32.1 Principles of Water and Solute Movement in Plants

Both passive and active mechanisms move substances into and out of plant cells

Osmosis governs water movement in plants

### 32.2 Transport in Roots

Water travels to the root xylem by three pathways

Roots take up ions by active transport

### 32.3 Transport of Water and Minerals in the Xylem

The mechanical properties of water have key roles in its transport

Leaf anatomy contributes to cohesion–tension forces

In the tallest trees, the cohesion–tension mechanism may reach its physical limit

Root pressure contributes to upward water movement in some plants

Stomata regulate the loss of water by transpiration

In dry climates, plants exhibit various adaptations for conserving water

### 32.4 Transport of Organic Substances in the Phloem

Organic compounds are stored and transported in different forms

Organic solutes move by translocation

Phloem sap moves from source to sink under pressure

## 32 Transport in Plants

### WHY IT MATTERS

The coast redwood, *Sequoia sempervirens* (Figure 32.1), takes life to extremes. Redwood trees can live for more than 2000 years, and they can grow taller than any other organism on Earth. The tallest known specimen, located in Redwood National Park in California, soars 115.5 m, roughly 379 ft, from the dank forest floor. Botanists who have studied these giants estimate that such massive plants consume thousands of liters of water each day to survive. And that water—with its cargo of dissolved nutrients—must be transported the great distances between roots and leaves.

At first, movement of fluids and solutes 100 m or more from a mature redwood's roots to its leafy crown may seem to challenge the laws of physics. Raising water that high above ground in a pipe requires a powerful mechanical pump at the base and substantial energy to counteract the pull of gravity. You also require a pump—your heart—to move fluid over a vertical distance of less than 3 m. Yet a redwood tree has no pump. As you'll learn in this chapter, the evolutionary adaptations that move water and solutes throughout the plant body can move large volumes over great distances by harnessing the cumulative effects of seemingly weak interactions such as cohesion



Owaki-Kullala/Corbis

**Figure 32.1**

Redwoods (*Sequoia sempervirens*) such as this tree growing in coastal California have reached recorded heights of over 100 m during life spans of more than 2000 years. Such extremely tall trees exemplify the ability of plants to move water and solutes from roots to shoots over amazingly long distances.

and evaporation. Overall, plant transport mechanisms solve a fundamental biological problem—the need to acquire materials from the environment and distribute them throughout the plant body.

Our discussion begins with a brief review of the principles of water and solute movement in plants, a topic introduced in Chapter 6. Then we examine how those principles apply to the movement of water and solutes into and through a plant's vascular pipelines.

### 32.1 Principles of Water and Solute Movement in Plants

In plants, as in all organisms, the movement of water and solutes begins at the level of individual cells and relies on mechanisms such as osmosis and the operation of transport proteins in the plasma membrane. Once water and nutrients enter a plant's specialized transport systems—the vascular tissues xylem and phloem—other mechanisms carry them between various regions of the plant body in response to changing demands for those substances. Ultimately, these movements of materials result from the integrated activities of the individual cells, tissues, and organs of a single, smoothly functioning organism—the whole plant.

Plant transport mechanisms fall into two general categories—those for short-distance transport and

those for long-distance transport. Short-distance transport mechanisms move substances into and between cells across membranes, and also to and from vascular tissues. For example, water, oxygen, and minerals enter roots by crossing the cell membranes of root hairs (**Figure 32.2a**), and nutrients such as carbohydrates from photosynthesis cross plasma membranes to nourish cells of the plant body. Similarly, water and other substances move short distances to and from a plant's xylem and phloem, which are arranged in vascular bundles (**Figure 32.2b**). Long-distance transport mechanisms move substances between roots and shoot parts (**Figure 32.2c**). Thus water and dissolved minerals travel in the xylem from roots to other plant parts, and products of photosynthesis move in the phloem from the leaves and stems into roots and other structures. Carbon dioxide for photosynthesis enters photosynthetic tissues in the shoot.

We consider transport processes in the xylem and phloem later in this chapter. For the moment our focus is on mechanisms that move water and solutes into and out of specific cells in roots, leaves, and stems. Keep in mind that the plant cell wall does not prevent solutes from moving into plant cells. Most solutes can cross the wall by way of the plasmodesmata that connect adjacent cells (see Section 5.4).

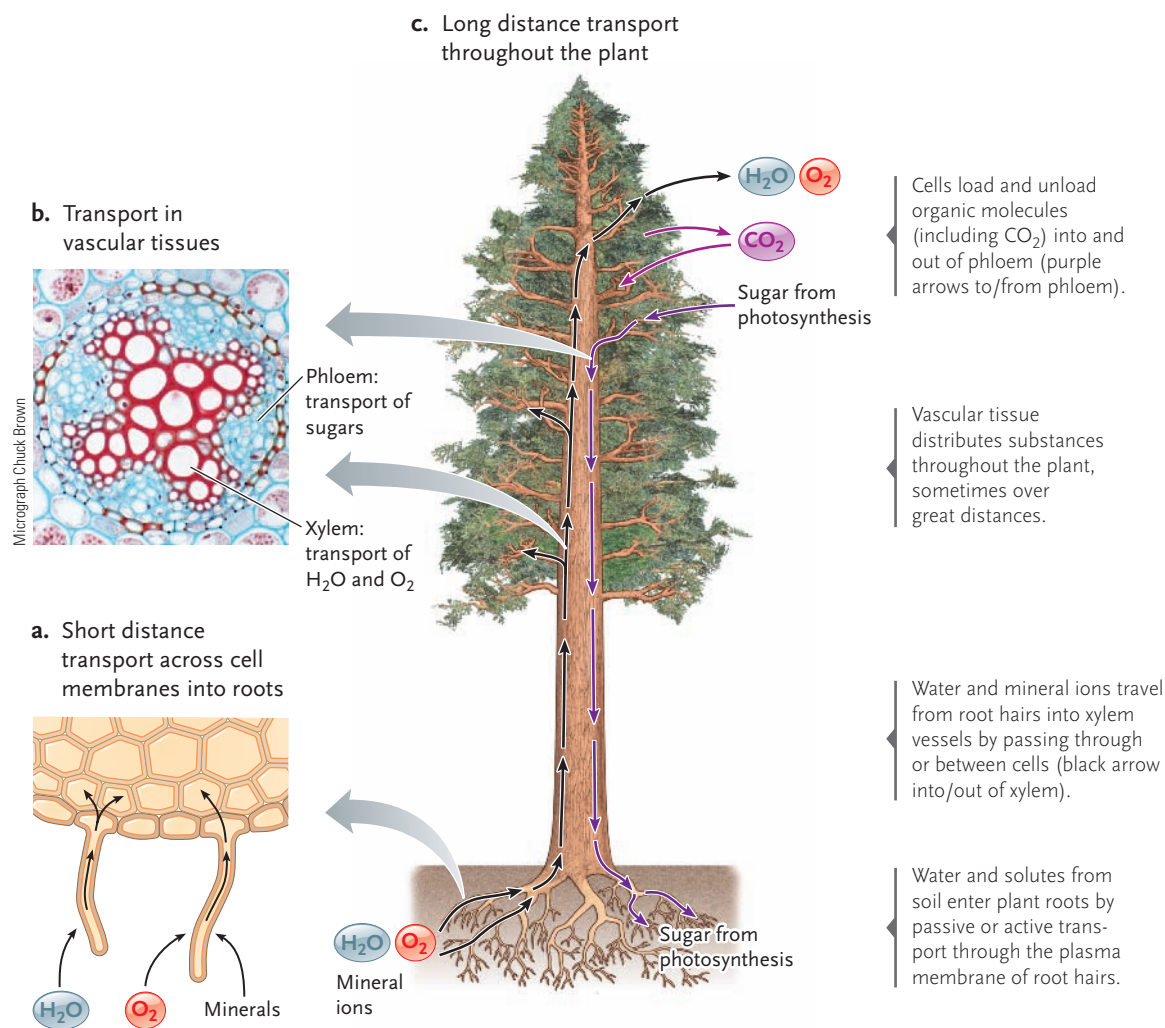
#### Both Passive and Active Mechanisms Move Substances into and out of Plant Cells

Recall from Chapter 6 that in all cells there are two general mechanisms for transporting water and solutes across the plasma membrane into and between cells. In **passive transport**, substances move down a concentration gradient or, if the substance is an ion, down an electrochemical gradient. **Active transport** requires the cell to expend energy in moving substances *against* a gradient, usually by hydrolysis of ATP.

True to its name, simple diffusion is the simplest form of passive transport: as described in Section 6.2, oxygen, carbon dioxide, water, and some other small molecules can readily diffuse across cell plasma membranes, following a concentration gradient. By contrast, in all other types of membrane transport, ions and some larger molecules cross cell membranes assisted by carriers collectively called **transport proteins**, which are embedded in the membrane.

Passive transport of substances down an electrochemical gradient is called *facilitated diffusion* because the transport protein involved “facilitates” the process in some way. Transport proteins called *channel proteins* are configured to form a pore in the plasma membrane. Those called *carrier proteins* change shape in a way that releases the substance to the other side of the membrane.

In active transport, membrane transport proteins use energy to move substances against a concentration gradient or an electrochemical gradient. As you may



**Figure 32.2**  
Overview of transport routes in plants.

recall from Section 6.4, an electrochemical gradient exists across cell membranes when the concentrations of various ions differ inside or outside the cell. The differences in ion concentration result in a difference in electrical charge across the plasma membrane. In plant cells the cytoplasm is slightly more negative than the fluid outside the cell. This charge difference is measured as an electrical voltage called the **membrane potential**. The word “potential” refers to the fact that the movement of ions across a membrane is a potential source of energy—that is, such ion movements can perform cellular work.

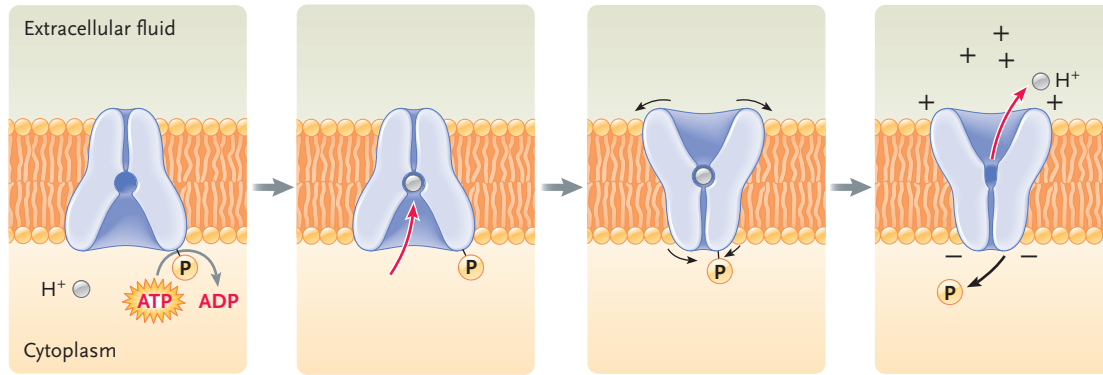
ATP provides the energy for active transport of substances into and out of plant cells. Hydrogen ions (protons), which tend to be more concentrated outside the cell than in the negatively charged cytoplasm, play a central role in the process. First, a proton pump pushes H<sup>+</sup> across the plasma membrane against its electrochemical gradient, from the inside to the outside of the cell (**Figure 32.3a**). As protons accumulate outside the cell, the electrochemical gradient becomes steeper and significant potential energy is available. Crucial solutes such as cations (positively charged ions) often are more concentrated in the extracellular fluid. One result of the increased charge difference cre-

ated by proton pumping is that cations move into the cell through their membrane channels (**Figure 32.3b**). These cations include mineral ions that have essential roles in plant cell metabolism.

The H<sup>+</sup> gradient also powers *secondary active transport*, a process in which a concentration gradient of an ion is used as the energy source for active transport of another substance. The two secondary mechanisms—*symport* and *antiport*—actively transport ions, sugars, and amino acids into and out of plant cells against their concentration gradient. In *symport*, the potential energy released as H<sup>+</sup> follows its gradient into the cell is coupled to the simultaneous uptake of another ion or molecule (**Figure 32.3c**). In this way, plant cells can take up metabolically important anions such as nitrate (NO<sub>3</sub><sup>-</sup>) and potassium (K<sup>+</sup>). Nearly all organic substances that enter plant cells move in by symport as well.

In *antiport*, the energy released as H<sup>+</sup> diffuses into the cell powers the active transport of a second molecule, such as Ca<sup>2+</sup>, in the opposite direction, *out of* the cell (**Figure 32.3d**). One of antiport’s key functions is to remove excess Na<sup>+</sup>, which readily moves into plant cells by facilitated diffusion through channel proteins. If the Na<sup>+</sup> were not eliminated, it would quickly build up to toxic levels.

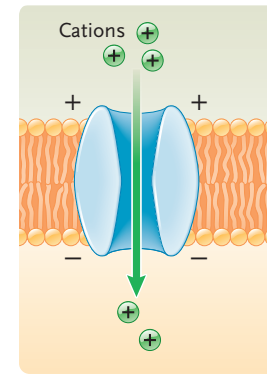
**a. H<sup>+</sup> pumped against its electrochemical gradient**



ATP energy pumps hydrogen ions (H<sup>+</sup>) out of the cytoplasm, creating an H<sup>+</sup> gradient.

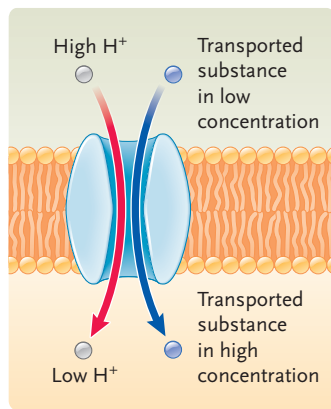
The concentration of H<sup>+</sup> becomes higher outside the membrane than inside. Inward diffusion of H<sup>+</sup> in response to the gradient becomes a source of energy for transporting other ions and neutral molecules such as sugar into the plant cell.

**b. Uptake of cations**



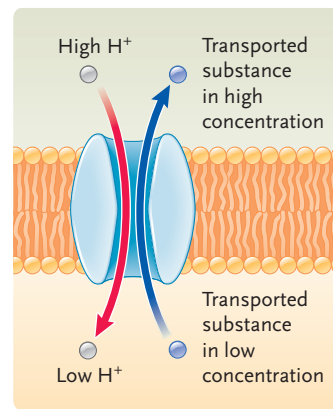
Some cations, such as NH<sub>4</sub><sup>+</sup>, enter the cell through selective channel proteins, following the electrochemical gradient created by H<sup>+</sup> pumping.

**c. Symport**



In symport, the inward diffusion of H<sup>+</sup> is coupled with the simultaneous active transport of another substance into the cell.

**d. Antiport**



In antiport, H<sup>+</sup> moving into the cell powers the movement of another solute in the opposite direction.

**Figure 32.3**  
Ion transport across the plasma membrane.

Both passive and active transport are selective transport mechanisms that transport specific substances. Two factors govern this specificity. One is the size of the interior channel, which allows only molecules in a particular size range to pass through. The other factor is the distribution of charges along the inside of the channel. A channel that permits cations such as Na<sup>+</sup> to pass through easily may completely bar anions such as Cl<sup>-</sup> and vice versa.

Relatively speaking, only small amounts of mineral ions and other solutes move into and out of plant cells. As we see next, H<sub>2</sub>O is another matter. Throughout a plant's life large volumes of water enter and exit its cells and tissues by way of osmosis.

### Osmosis Governs Water Movement in Plants

One of the most important aspects of plant physiology is how water moves into and through plant cells and tissues. Inside a plant's tubelike vascular tissues,

large amounts of water or any other fluid travel by **bulk flow**—the group movement of molecules in response to a difference in pressure between two locations, like water in a closed plumbing system gushing from an open faucet. For example, the dilute solution of water and ions that flows in the xylem, called **xylem sap**, moves by bulk flow from roots to shoot parts. The solution is pulled upward through the plant body in a process that relies on the cohesion of water molecules and that we will consider more fully later in this chapter. Individual cells, however, gain and lose water by **osmosis**, the passive movement of water across a selectively permeable membrane in response to solute concentration gradients, a pressure gradient, or both (see Section 6.3). The driving force for osmosis is energy stored in the water itself. This potential energy, called **water potential**, is symbolized by the Greek letter  $\psi$ . By convention, pure water has a  $\psi$  value of zero. Two factors that strongly influence this value in living plants are the presence of solutes and physical pressure.

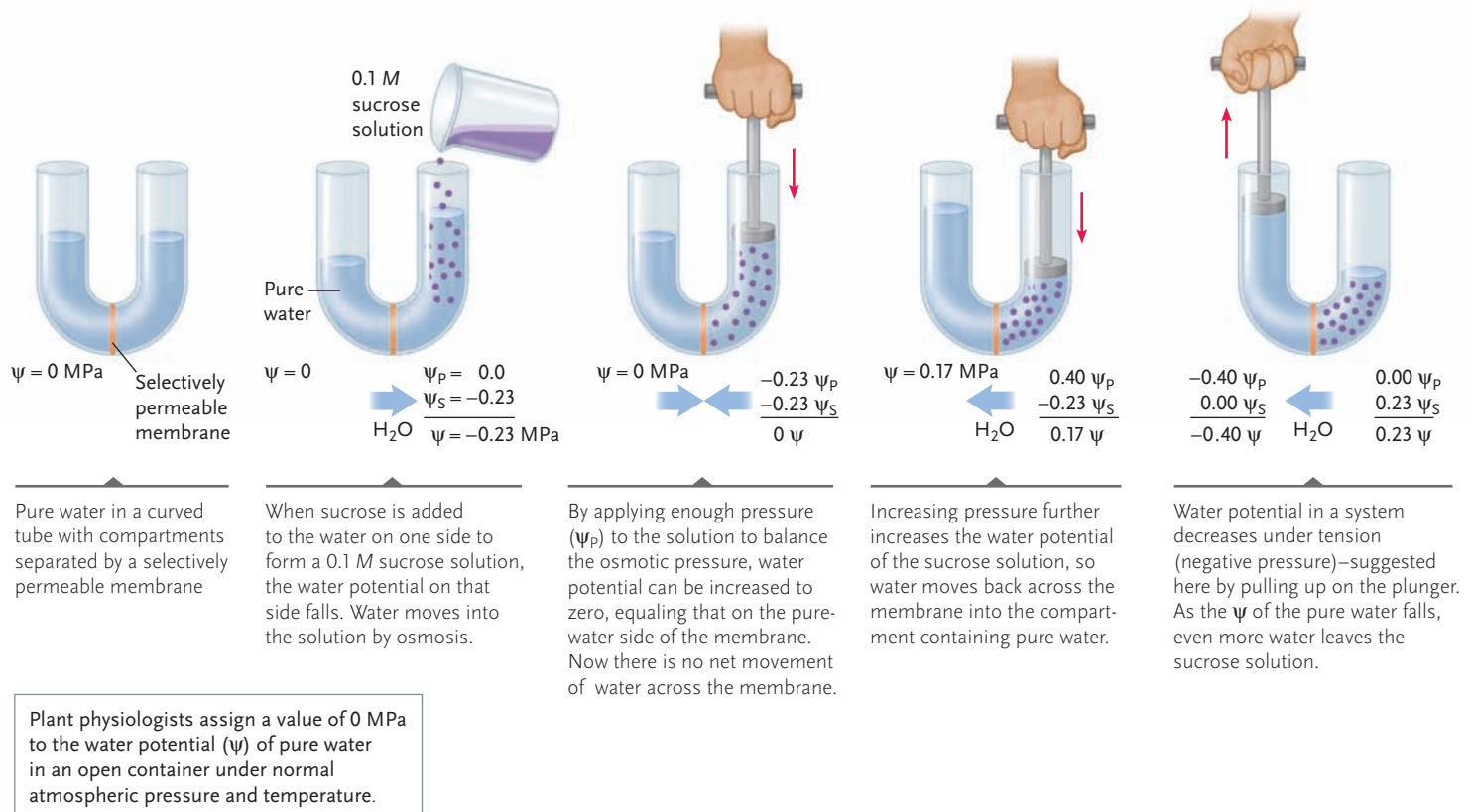
The effect of dissolved solutes on water's tendency to move across a membrane is called *solute potential*, symbolized by  $\psi_s$ . In practical terms, water potential is higher where there are more water molecules in a solution relative to the number of solute molecules. Likewise, the water potential is *lower* in a solution with relatively more solutes. The relationship between water potential and solute potential is vital to understanding transport phenomena in plants because water tends to move by osmosis from regions where water potential is higher to regions where it is lower. Solute molecules are usually more concentrated inside plant cells than in the fluid surrounding them. This means the water potential is higher outside plant cells than inside them, so water tends to enter the cells by osmosis. This in fact is the mechanism that draws soil water into a plant's roots.

The osmotic movement of water into a plant cell cannot continue indefinitely, however, because eventually physical pressure counterbalances it. The wall around a plant cell strictly limits how much the cell can expand. Accordingly, as water moves into plant cells, the pressure inside them increases. This pressure, called **turgor pressure**, rises until it is high enough to prevent more water from entering a cell by osmosis. In effect, when osmotic water movement stops, turgor pressure has increased the water potential inside the

cell until it equals the potential of the water outside the cell. The physical pressure required to halt osmotic water movement across a membrane is termed a solution's *pressure potential* and is symbolized as  $\psi_p$ .

By convention, plant physiologists measure water potential in units of pressure called **megapascals** (MPa). They use standard atmospheric pressure as a baseline, assigning it a value of zero. Accordingly, the water potential of pure water at standard atmospheric pressure is expressed as 0 MPa. This notation can be used to describe the changing effects under different conditions of solute potential and pressure potential (**Figure 32.4**). Adding pressure increases the MPa while adding solutes reduces it (because the relative concentration of water is lower), and water will flow from a solution of higher MPa to a solution of lower MPa. With these principles in mind, consider now how they operate in living plant cells.

Recall from Section 5.4 that a large **central vacuole** occupies most of the volume of a mature plant cell. The central vacuole, which is surrounded by a vacuolar membrane, or **tonoplast**, contains a dilute solution of sugars, proteins, other organic molecules, and salts. The cell cytoplasm is confined to a thin layer between the tonoplast and the plasma membrane. A major role of the central vacuole is to maintain turgor pressure in



**Figure 32.4**

The relationship between osmosis and water potential. If the water potential is higher on one side of a selectively permeable membrane, water will cross the membrane to the area of lower water potential. This diagram shows pure water on one side of a selectively permeable membrane and a simple sucrose solution on the other side. In an organism, however, the selectively permeable membranes of cells are rarely if ever in contact with pure water.



## INSIGHTS FROM THE MOLECULAR REVOLUTION

### A Plant Water Channel Gives Oocytes a Drink

Water moves into or out of the central vacuole of plant cells to compensate for gains or losses of water in the surrounding cytoplasm. Does this water simply diffuse through the lipid part of the tonoplast, or does it move through an aquaporin? Christophe Maurel and his colleagues at the University of California, San Diego, sought to answer this question. They were encouraged by the discovery of aquaporins in the plasma membranes of red blood cells and by the fact that a closely related protein called TIP (tonoplastintrinsic protein) occurs in the tonoplast.

To find out whether TIP functions as the water channel of tonoplasts, the team began by isolating the gene that encodes TIP in *Arabidopsis thaliana* plants. For the later experiments they selected animal cells (oocytes of the frog *Xenopus laevis*) to ensure no other proteins made in plant cells could affect the outcome.

Next they cloned the coding sequence of the TIP gene, inserting it into a bacterial plasmid cloning vector. The vector contained a promoter that allowed in vitro transcription of a cloned coding sequence. In addition, the research team had added to it DNA sequences for 5' and 3' UTRs (untranslated regions; see Section 15.3) that function in the processing of the coding sequence in the mRNA transcripts of a *Xenopus* gene. The TIP coding sequence was inserted between the DNA for the UTRs, which ensured that the *Xenopus* oocytes could efficiently translate mRNAs transcribed from the TIP sequence clone. That is, the test-tube transcription of the engineered TIP clone produced mRNAs in a form that could readily be translated into TIP proteins inside *Xenopus* cells.

The test-tube TIP mRNA molecules were then injected into mature *Xenopus* oocytes, which are normally only

slightly permeable to water. After 2 to 3 days in an isotonic medium, the oocytes were transferred to a hypotonic medium. They swelled and ruptured within 6 minutes. Control oocytes that were not injected with the TIP mRNA, or that were injected only with distilled water, swelled only slightly during the same interval and did not burst when placed in a hypotonic medium. These results supported the conclusion that the TIP protein forms an aquaporin when inserted into a membrane. In this system, the TIP proteins inserted into the oocyte plasma membrane, since animal cells do not have tonoplasts. In its normal location in the tonoplast of plant cells, TIP evidently allows water to move readily in either direction, compensating for water movement between the thin layer of cytoplasm and the extracellular space.

the cell. Many solutes that enter a plant cell are actively transported from the cytoplasm into the central vacuole through channels in the tonoplast. As the solutes accumulate, water follows by osmosis.

The plant cell's relatively small amount of cytoplasm must compensate fairly quickly for water gains or losses caused by changes in osmotic flow. If the medium around a plant cell becomes hypertonic (has a high solute concentration), for example, water flows rapidly out of the cell. Water from the central vacuole replaces it, entering the cytoplasm through water-conducting channel proteins called **aquaporins**. Experiments that identified this channel are the topic of this chapter's *Insights from the Molecular Revolution*.

The water mechanics we have been discussing have major implications for land plants. For instance, the drooping of leaves and stems called **wilting** occurs when environmental conditions cause a plant to lose more water than it gains. Conditions that lead to wilting include dry soil, in which case the water potential in the soil falls below that in the plant. Then the turgor pressure inside the cells falls, and the protoplast shrinks away from the cell wall (**Figure 32.5a**). By contrast, as long as the  $\psi$  of soil is higher than that in root epidermal cells, water will follow the  $\psi$  gradient and enter root cells, making them turgid, or firm (**Figure 32.5b**). As we see in the next section, water and solutes entering roots may move through the plant body by several routes.

## STUDY BREAK

1. Explain the role(s) of a gradient of protons in moving substances across a plant cell's plasma membrane.
2. How do symport and antiport differ? Give examples of key substances each mechanism transports.
3. What is "water potential," and why is it important with respect to plant cells?

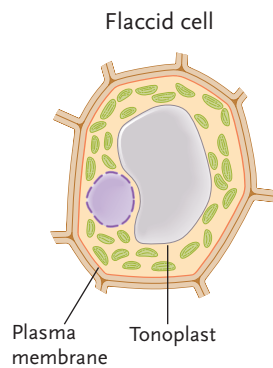
## 32.2 Transport in Roots

Soil around roots provides a plant's water and minerals, but roots don't simply "soak up" these essential substances. Instead, water and minerals that enter roots first travel laterally through the root cortex to the root xylem. Only then do they begin their journey upward to stems, leaves, and other tissues.

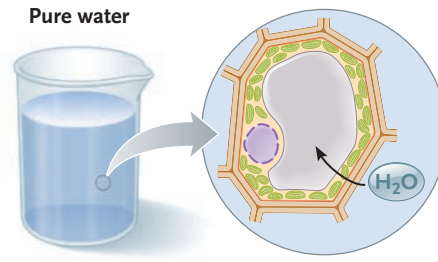
### Water Travels to the Root Xylem by Three Pathways

Soil water always enters a root through the root epidermis. Once inside a root, however, water may take one of three routes into the root xylem, traveling either through living cells or in nonliving areas of the root (**Figure 32.6**).

The experimenter begins with flaccid plant cells at atmospheric pressure and temperature. The cells contain enough water to prevent the plasma membrane from shrinking away from the cell wall, but lack turgor.



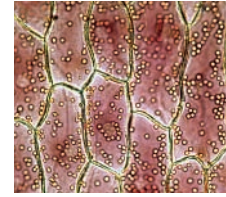
**a.** A flaccid cell is placed in distilled water, which has a water potential of zero—much greater than the negative water potential inside the cell. The cell gains water by osmosis and swells until it is turgid. The cell wall prevents it from taking in more water and bursting.



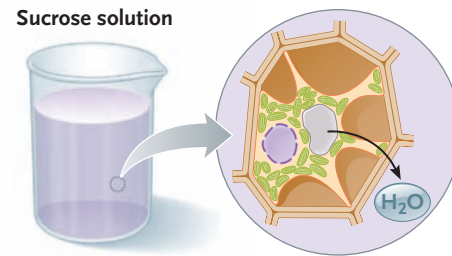
**Pure water**  
 Distilled water  
 $\psi_p = 0 \text{ MPa}$   
 $\psi_s = 0 \text{ MPa}$   
 $\psi = 0 \text{ MPa}$

**Turgid cell at equilibrium with its environment**  
 $\psi_p = 0.7 \text{ MPa}$   
 $\psi_s = -0.7 \text{ MPa}$   
 $\psi = 0.0 \text{ MPa}$

Turgid cells from an iris petal (*Iris*)



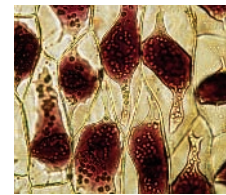
**b.** A flaccid cell is placed in a sucrose solution. The water potential inside the cell is much greater than that in the solute-rich solution, and the cell loses water until the vacuole shrinks and the protoplast shrinks away from the cell wall. This outcome of the experiment is called plasmolysis.



**Sucrose solution**  
 0.4 M sucrose  
 $\psi_p = 0.0 \text{ MPa}$   
 $\psi_s = -0.9 \text{ MPa}$   
 $\psi = -0.9 \text{ MPa}$

**Plasmolyzed cell at equilibrium with its environment**  
 $\psi_p = 0.0 \text{ MPa}$   
 $\psi_s = -0.9 \text{ MPa}$   
 $\psi = -0.9 \text{ MPa}$

Plasmolyzed cells from a wilted iris petal



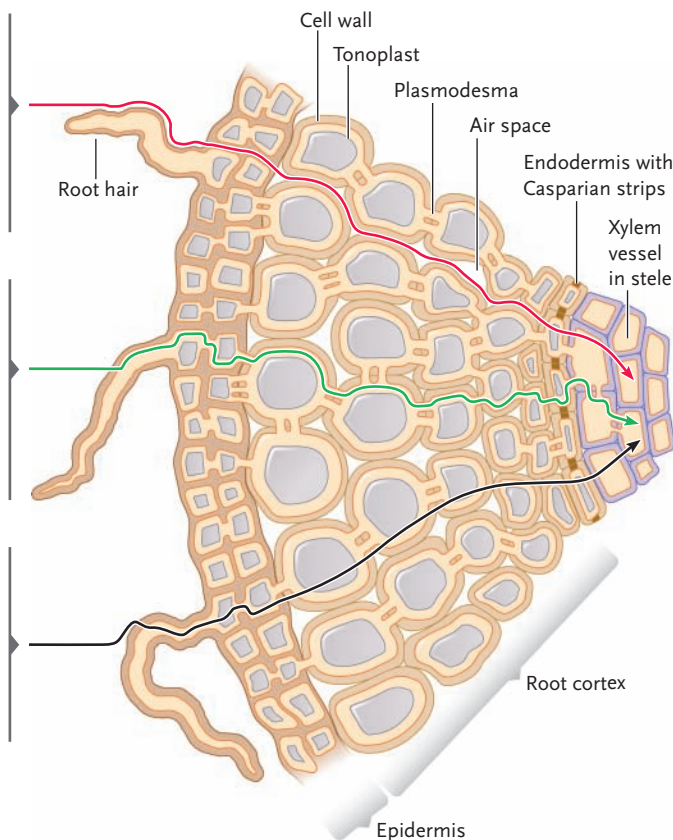
**Figure 32.5**

An experiment to test the effects of different osmotic environments on plant cells. Notice that in both (a) and (b) the final condition is the same: the water potential of the plant cell and its environment become equal. (Micrographs: © Claude Nuridsany and Marie Perennou/Science Photo Library/Photo Researchers, Inc.)

In the **apoplastic pathway** (red), water moves through nonliving regions—the continuous network of adjoining cell walls and tissue air spaces. However, when it reaches the endodermis, it passes through one layer of living cells.

In the **symplastic pathway** (green), water passes into and through living cells. After being taken up into root hairs water diffuses through the cytoplasm and passes from one living cell to the next through plasmodesmata.

In the **transmembrane pathway** (black), water that enters the cytoplasm moves between living cells by diffusing across cell membranes, including the plasma membrane and perhaps the tonoplast.



**Figure 32.6**

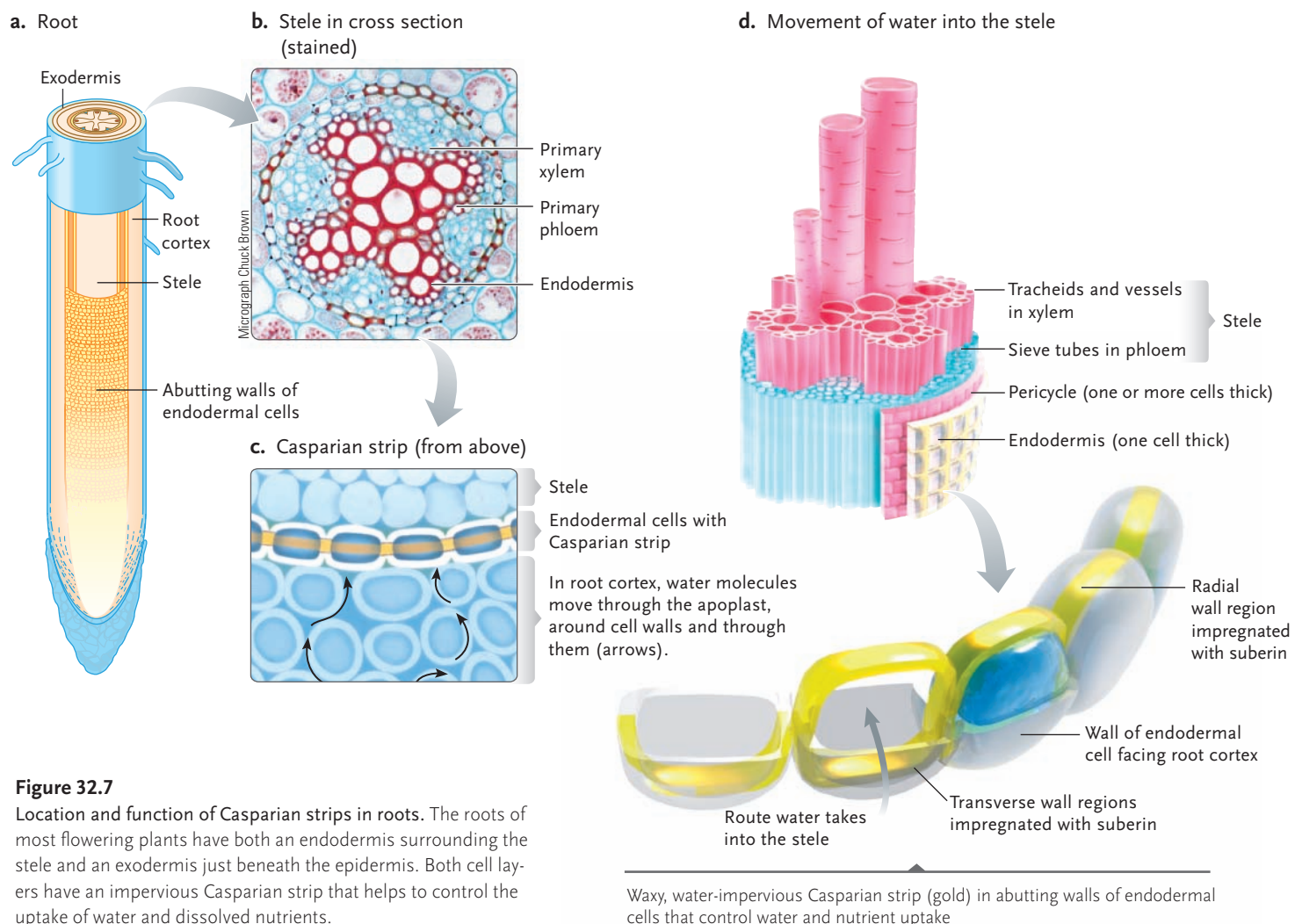
Pathways for the movement of water into roots. Ions also enter roots via these three pathways, but must be actively transported into cells when they reach the Casparian strips of the endodermis. In this way, only certain solutes in soil water are allowed to enter the stele.

Nonliving regions of a plant such as the continuous network of adjoining cell walls and air spaces in root tissue are called the *apoplast*. Thus water follows an **apoplastic pathway** when it moves through the apoplast of roots, a route that does not cross cell membranes. Botanists refer to a plant's living parts as the *symplast*, and water moving through roots in the **symplastic pathway** moves from cell to cell through the open channels of plasmodesmata. Water also can enter root cells across the cell plasma membranes, a **transmembrane pathway**. Water crosses the tonoplast of the central vacuole in this way as well.

When water enters a root, some diffuses into epidermal cells, entering the symplast. But a great deal of the water taken up by plant roots moves into the apoplast, moving along through cell walls and intercellular spaces. This apoplastic water (and any solutes dissolved in it) travels rapidly inward until it encounters the endodermis, the sheetlike single layer of cells that separates the root cortex from the stele. Cells in the root cortex generally have air spaces between them (which helps aerate the tissue), but endodermal cells are tightly packed (**Figure 32.7a**). Each one also has a beltlike **Casparian strip** in its radial and transverse walls, positioned somewhat like a ribbon of packing tape around a rectangular package

(**Figure 32.7b–c**). The strip is impregnated with suberin, a waxy substance impermeable to water. Thus the Casparian strip blocks the apoplastic pathway at the endodermis, preventing water and solutes in the apoplast from automatically passing on into the stele. Instead, if molecules are to move into the stele, they must detour across the plasma membranes of endodermal cells, entering the cells (and the symplast) where the wall is not blanketed by a Casparian strip (**Figure 32.7d**). From there water and solutes can pass through plasmodesmata to cells in the outer layer of the stele (the pericycle), then on into the xylem.

Although water molecules can easily cross an endodermal cell's plasma membrane, the semipermeable membrane allows only a subset of the solutes in soil water to cross. Undesirable solutes may be barred, while desirable ones may move into the cell by facilitated diffusion or active transport. Conversely, the endodermis prevents needed substances in the xylem from leaking out, back into the root cortex. In this way the endodermis provides important control over which substances enter and leave a plant's vascular tissue. The roots of most flowering plants also have a second layer of cells with Casparian strips just inside the root



**Figure 32.7**

Location and function of Casparian strips in roots. The roots of most flowering plants have both an endodermis surrounding the stele and an exodermis just beneath the epidermis. Both cell layers have an impervious Casparian strip that helps to control the uptake of water and dissolved nutrients.



epidermis. This layer, the exodermis, functions like the endodermis.

### Roots Take Up Ions by Active Transport

Mineral ions in soil water also enter roots through the epidermis. Some enter the apoplast along with water, but most ions important for plant nutrition tend to be much more concentrated in roots than in the surrounding soil, so they cannot follow a concentration gradient into root epidermal cells. Instead the epidermal cells actively transport ions inward—that is, ions enter the symplast immediately. They travel to the xylem via the symplastic or transmembrane pathways. Other ions can still move inward following the apoplastic pathway until they reach the Casparian strip of the endodermis. If they are to contribute to the plant's nutrition, however, they must be actively transported from the exodermis into cells of the root cortex and, as just described, from the endodermis into the stele. In short, mechanisms that control which solutes will be absorbed by root cells ultimately determine which solutes will be distributed through the plant.

Once an ion reaches the stele, it diffuses from cell to cell until it is “loaded” into the xylem. Experiments to determine whether the loading is passive (by diffusion) or active have been inconclusive, so the details of this final step are not entirely clear. Because the xylem's conducting elements are not living, water and ions in effect reenter the apoplastic pathway when they reach either tracheids or vessels. Once in the xylem, water can move laterally to and from tissues or travel upward in the conducting elements. Minerals are distributed to living cells and taken up by active transport. The following section examines how this “distribution of the wealth” takes place.

### STUDY BREAK

1. Explain two key differences in how the apoplastic and symplastic pathways route substances laterally in roots.
2. How does an ion enter a root hair and then move to the xylem?

## 32.3 Transport of Water and Minerals in the Xylem

We return now to the question that opened this chapter: How does the solution of water and minerals called xylem sap move—100 m or more in the tallest trees—from roots to stems, then into leaves? Xylem sap is mostly water, and we know that it moves upward by bulk flow through the tracheids and vessels in xylem. Yet because mature xylem cells are dead, they cannot

expend energy to move water into and through the plant shoot. Instead, the driving force for the upward movement of xylem sap from root to shoot is sunlight, which causes water to evaporate from leaves and other aerial parts of land plants. Experiments show that only a small fraction of the water in xylem sap is used in a plant's growth and metabolism. The rest evaporates into the air in a phenomenon called **transpiration**. As described next, transpiration drives the ascent of sap.

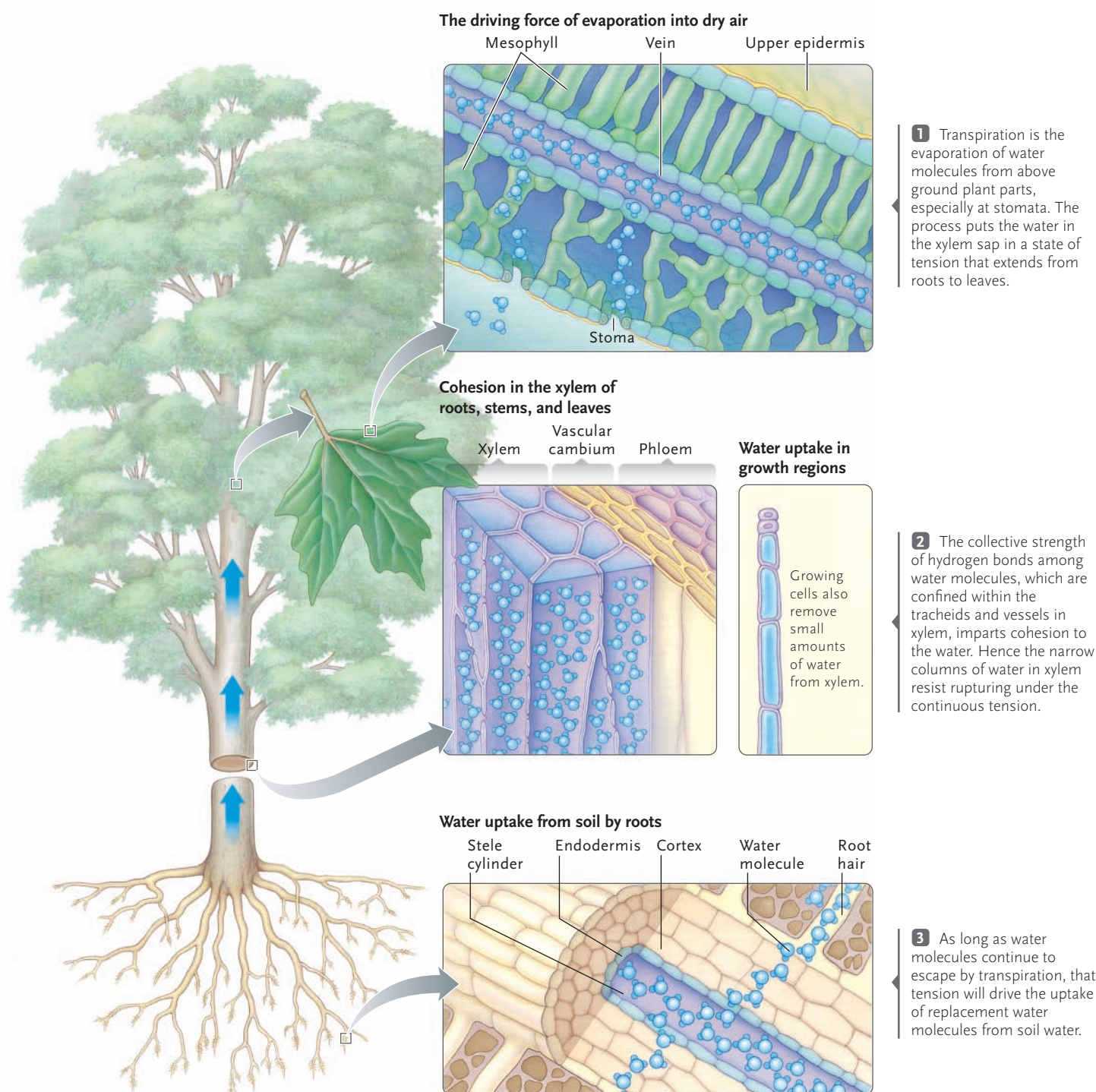
### The Mechanical Properties of Water Have Key Roles in Its Transport

Chapter 2 introduced several biologically important mechanical properties of water. Two of them interest us here. First, water molecules are strongly *cohesive*: they tend to form hydrogen bonds with one another. Second, water molecules are *adhesive*: they form hydrogen bonds with molecules of other substances, including the carbohydrates in plant cell walls. Water's cohesive and adhesive forces jointly pull water molecules into exceedingly small spaces, such as crevices in cell walls or narrow tubes such as xylem vessels in roots, stems, and leaves. In 1914, plant physiologist Henry Dixon explained the ascent of sap in terms of the relationship between transpiration and water's mechanical properties. His model of xylem transport is now called the **cohesion–tension mechanism of water transport** (Figure 32.8).

According to the cohesion–tension model, water transport begins as water evaporates from the walls of mesophyll cells inside leaves and into the intercellular spaces. This water vapor escapes by transpiration through open stomata, the minute passageways in the leaf surface. As water molecules exit the leaf, they are replaced by others from the mesophyll cell cytoplasm. The water loss gradually reduces the water potential in a transpiring cell below the water potential in the leaf xylem. Now, water from the xylem in the leaf veins follows the gradient into cells, replacing the water lost in transpiration.

In the xylem, water molecules are confined in narrow, tubular xylem cells. The water molecules form a long chain, like a string of weak magnets, held together by hydrogen bonds between individual molecules. When a water molecule moves out of a leaf vein into the mesophyll, its hydrogen bonds with the next molecule in line stretch but don't break. The stretching creates *tension*—a negative pressure gradient—in the column. Adhesion of the water column to xylem vessel walls adds to the tension. Under continuous tension from above, the entire column of water molecules in xylem is drawn upward, in a fashion somewhat analogous to the way water moves up through a drinking straw. Botanists refer to this root-to-shoot flow as the *transpiration stream*.

Transpiration continues regardless of whether evaporating water is replenished by water rapidly taken



**Figure 32.8**  
**Cohesion–tension mechanism of water transport.** Transpiration, the evaporation of water from shoot parts, creates tension on the water in xylem sap. This tension, which extends from root to leaf, pulls upward columns of water molecules that are hydrogen-bonded to one another.

up from the soil. Wilting is visible evidence that the water-potential gradient between soil and a plant's shoot parts has shifted. Remember that as soil dries out, the remaining water molecules are held ever more tightly by the soil particles. In effect, the action of soil particles reduces the water potential in the soil surrounding plant roots, and as this happens the roots take up water more slowly. However, because the water

that evaporates from the plant's leaves is no longer being fully replaced, the leaves wilt as turgor pressure drops. Reducing the water potential in soil by adding solutes such as NaCl and other salts can have the same wilting effect. When the water potential in the soil finally equals that in leaf cells, a gradient no longer exists. Then movement of water from the soil into roots and up to the leaves comes to a halt.

## Leaf Anatomy Contributes to Cohesion–Tension Forces

Leaf anatomy is key to the processes that move water upward into plants. To begin with, as much as two-thirds of a leaf's volume consists of air spaces—thus there is a large internal surface area for evaporation. Leaves also may have thousands to millions of stomata, through which water vapor can escape. Both these factors increase transpiration. Also, every square centimeter of a leaf contains thousands of tiny xylem veins, so that most leaf cells lie within half a millimeter of a vein. This close proximity readily supplies water to cells and the spaces between them, from which the water can readily evaporate.

As water evaporates from a leaf, surface tension at the interface between the water film and the air in the leaf space translates into negative pressure that draws water from the leaf veins. This tension is multiplied many times over in all of the leaves and xylem veins of a plant. It increases further as the plant's metabolically active cells take up xylem sap.

## In the Tallest Trees, the Cohesion–Tension Mechanism May Reach Its Physical Limit

A variety of experiments have tested the premises of the cohesion–tension model, and thus far the data strongly support it. For example, the model predicts that xylem sap will begin to move upward at the top of a tree early in the day when water begins to evaporate from leaves. Experiments with several different tree species have confirmed that this is the case. The experiments also showed that sap transport peaks at midday when evaporation is greatest, then tapers off in the evening as evaporative water loss slows.

Other experiments have probed the relationship between xylem transport and tree height. One team of researchers studied eight of the tallest living redwoods, including one that towers nearly 113 m above the forest floor. When the scientists measured the maximum tension exerted in the xylem sap in twigs at the tops of the trees, they discovered that it approached the known physical limit at which the bonds between water molecules in a column of water in a conifer's xylem will rupture. Based on this finding and other evidence, the team has predicted that the maximum height for a healthy redwood tree is 122 to 130 m. Therefore it is possible that the tallest redwoods alive today may grow taller still.

## Root Pressure Contributes to Upward Water Movement in Some Plants

The cohesion–tension mechanism accounts for upward water movement in tall trees. In some nonwoody plant species, however—lawn grasses, for instance—a positive pressure can develop in roots and force xy-



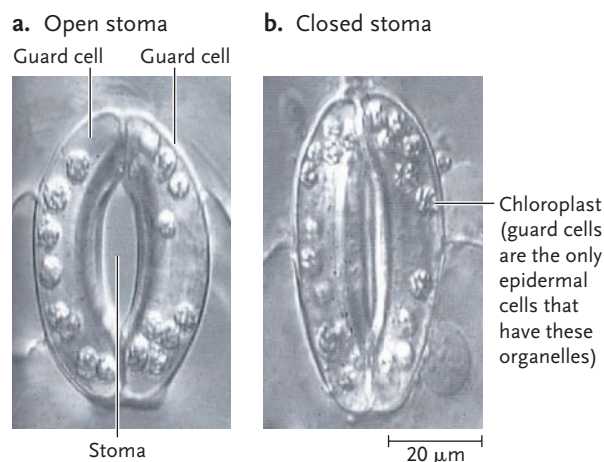
Dr. John D. Cunningham/Visuals Unlimited

**Figure 32.9**  
Guttation, caused by root pressure. The drops of water appear at the endings of xylem veins along the leaf edges of a strawberry plant (*Fragaria*).

lem sap upward. This **root pressure** operates under conditions that reduce transpiration, such as high humidity or low light. In fact, the mechanism that produces root pressure often operates at night, when solar-powered transpiration slows or stops. Then, active transport of ions into the stele sets up a water potential gradient across the endodermis. Because the Casparian strip of the endodermis tends to prevent ions from moving back into the root cortex, the water potential difference becomes quite large. It can move enough water and dissolved solutes into the xylem to produce a relatively high positive pressure. Although not sufficient to force water to the top of a very tall plant, in some smaller plant species root pressure is strong enough to force water out of leaf openings, in a process called **guttation (Figure 32.9)**. Pushed up and out of vein endings by root pressure, tiny droplets of water that look like dew in the early morning emerge from modified stomata at the margins of leaves.

## Stomata Regulate the Loss of Water by Transpiration

Three environmental conditions have major effects on the rate of transpiration: relative humidity, air temperature, and air movement. The most important is relative humidity, which is a measure of the amount of water vapor in air. The less water vapor in the air, the more evaporates from leaves (because the water potential is higher in the leaves than in the dry air). The air temperature at the leaf surface also speeds evaporation as it rises. Although evaporation does cool the leaf somewhat, the amount of water lost can double for each 10°C rise in air temperature. Air movement at the leaf surface carries water vapor away from the surface and so makes a steeper gradient. Together these factors explain why on extremely hot, dry, breezy days, the leaves of certain plants must completely replace their water each hour.

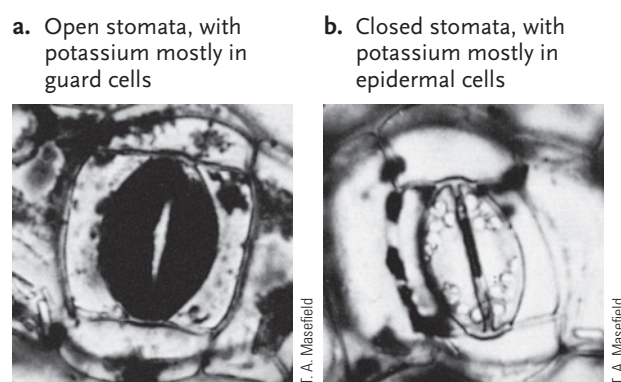


**Figure 32.10**

Guard cells and stomatal action. **(a)** An open stoma. Water entered collapsed guard cells, which swelled under turgor pressure and moved apart, thus forming the stoma in the needlelike leaf of the rock needlebush (*Hakea gibbosa*). **(b)** A closed stoma. Water exited the swollen guard cells, which collapsed against each other and closed the stoma.

Even when conditions are not so drastic, more than 90% of the water moving into a leaf can be lost through transpiration. About 2% of the water remaining in the leaf is used in photosynthesis and other activities. These measurements emphasize the need for controls over transpiration, for if water loss exceeds water uptake by roots, the resulting dehydration of plant tissues interferes with normal functioning, and the plant may wilt and die.

The cuticle-covered epidermis of leaves and stems reduces the rate of water loss from aboveground plant parts, but it also limits the rate at which CO<sub>2</sub> for photosynthesis can diffuse into the leaf. The functioning



**Figure 32.11**

Evidence for potassium accumulation in stomatal guard cells undergoing expansion. Strips from the leaf epidermis of a dayflower (*Commelina communis*) were immersed in a solution containing a stain that binds preferentially with potassium ions. **(a)** In leaf samples with open stomata, most of the potassium was concentrated in the guard cells. **(b)** In leaf samples with closed stomata, little potassium was in guard cells; most was present in adjacent epidermal cells.

of stomata also affects a plant's water balance. When stomata are open, carbon dioxide can be absorbed, but unless the relative humidity of external air is 100%, water always moves out. However, plants have evolved adaptations that balance water loss with CO<sub>2</sub> uptake. This “transpiration–photosynthesis compromise” involves the regulation of transpiration and gas exchange by opening and closing stomata as environmental conditions change.

**Opening and Closing of Stomata.** Two guard cells flank each stomatal opening (**Figure 32.10**). Their elastic walls are reinforced by cellulose microfibrils that wrap around the walls like a series of belts. The inward-facing walls are thicker and less elastic than the outer walls.

The opening and closing of stomata are good examples of a symport mechanism (see **Figure 32.3c**). Stomata open when potassium ions (K<sup>+</sup>) flow into the guard cells through ion channels. As a first step, an active transport pump in the plasma membrane begins pumping H<sup>+</sup> ions out of the guard cells. Recall from **Section 32.1** that H<sup>+</sup> pumped out of the cell can then follow its concentration gradient back into the cell. This inward flow of H<sup>+</sup> powers the active transport of K<sup>+</sup> into the guard cell. As a result, the K<sup>+</sup> concentration in turgid guard cells may be four to eight times higher than that in flaccid (limp) guard cells (**Figure 32.11**). Water follows inward by osmosis. As turgor pressure builds, the thick inner wall does not expand much, but the outer walls of each guard cell expand lengthwise, so the two cells bend away from each other and create a stoma (“mouth”) between them. Stomata close when the H<sup>+</sup> active transport protein stops pumping. K<sup>+</sup> flows passively out of the guard cells, and water follows by osmosis. When the water content of the guard cells dwindles, turgor pressure drops. The guard cells collapse against each other, closing the stomata.

In most plants, stomata open at first light, stay open during daylight, and close at night. Experiments have shown that guard cells respond to a number of environmental and chemical signals, any of which can induce the ion flows that open and close stomata. These signals include light, CO<sub>2</sub> concentration in the air spaces inside leaves, and the amount of water available to the plant.

**Light and CO<sub>2</sub> Concentration.** Light induces stomata to open through stimulation of blue-light receptors, probably located in the plasma membrane of guard cells. When stimulated, the receptors start the chain of events leading to stomatal opening by triggering activity of the H<sup>+</sup> pumps. Also, as photosynthesis begins in response to light, CO<sub>2</sub> concentration drops in the leaf air spaces as chloroplasts use the gas in carbohydrate production. In some way, this drop in CO<sub>2</sub>

concentration sets off the series of events increasing the flow of  $K^+$  into guard cells and furthers stomatal opening. The effects of reduced  $CO_2$  concentration have been tested by placing plants in the dark in air containing no  $CO_2$ . Even in the absence of light, as the  $CO_2$  concentration falls in leaves, guard cells swell and the stomata open.

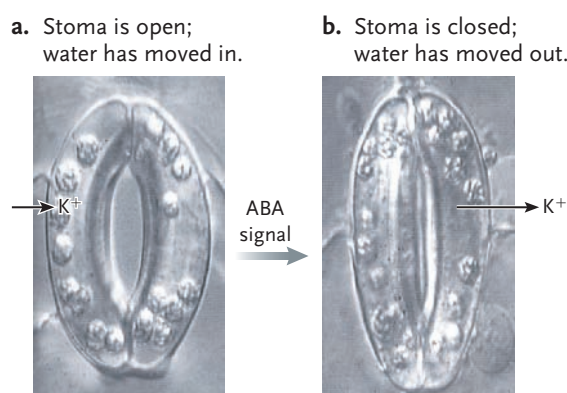
Normally, when the sun goes down, a plant's demand for  $CO_2$  drops as photosynthesis comes to a halt. Yet aerobic respiration continues to produce  $CO_2$ , which accumulates in leaves. As  $CO_2$  concentration rises, and the blue-light wavelengths that activated the  $H^+$  pumps wane,  $K^+$  is lost from the guard cells and they collapse, closing the stomata. Thus, at night transpiration is reduced and water is conserved.

**Water Stress.** As long as water is readily available to a plant's roots, the stomata remain open during daylight. However, if water loss stresses a plant, the stomata close or open only slightly, regardless of light intensity or  $CO_2$  concentration. Some simple but elegant experiments have shown that the stress-related closing of stomata depends on a hormone, abscisic acid (ABA), that is released by roots when water is unavailable. Test plants were suspended in containers so that only one-half the root system received water. Even though the roots with access to water could absorb enough water to satisfy the needs of all the plants' leaves, the stomata still closed. Tissue analysis revealed that water-stressed roots rapidly synthesize ABA. Transported through the xylem, this hormone stimulates  $K^+$  loss by guard cells, and water moves out of the cell by osmosis—so the stomata close (**Figure 32.12**). Mesophyll cells also take up ABA from the xylem and release it, with the same effects on stomata, when their turgor pressure falls due to excessive water loss. ABA can also cause stomata to close when the hormone is added experimentally to leaves.

**The Biological Clock.** Besides responding to light,  $CO_2$  concentration, and water stress, stomata apparently open and close on a regular daily schedule imposed by a biological clock. Even when plants are placed in continuous darkness, their stomata open and close (for a time) in a cycle that roughly matches the day/night cycle of Earth. Such *circadian rhythms* (*circa* = around; *dies* = day) are also common in animals, and several, including wake/sleep cycles in mammals, are known to be controlled by hormones—a topic pursued in Chapter 40.

### In Dry Climates, Plants Exhibit Various Adaptations for Conserving Water

Many plants have other evolutionary adaptations that conserve water, including modifications in structure or physiology (**Figure 32.13**). Oleanders, for example,



**Figure 32.12**

Hormonal control of stomatal closing. **(a)** When a stoma is open, high solute concentrations in the cytoplasm of both guard cells have raised the turgor pressure, keeping the cells swollen open. **(b)** In a water-stressed plant, the hormone abscisic acid (ABA) binds to receptors on the guard cell plasma membrane. Binding activates a signal transduction pathway that lowers solute concentrations inside the cells, which lowers the turgor pressure—so the stoma closes.

have stomata on the underside of the leaf at the bottom of pitlike invaginations of the leaf epidermis lined by hairlike trichomes (see **Figure 32.13b**). Sunken stomata are less exposed to drying breezes, and trichomes help retain water vapor at the pore opening, so that water evaporates from the leaf much more slowly.

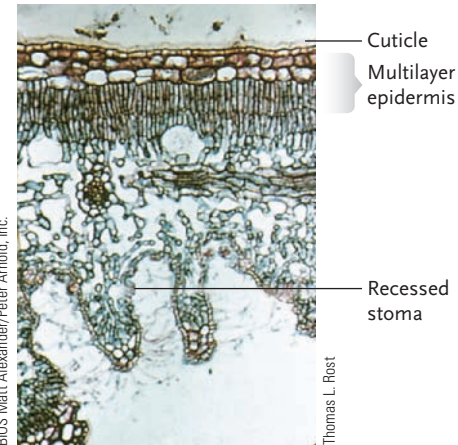
The leaves of *xerophytes*—plants adapted to hot, dry environments in which water stress can be severe—have a thickened cuticle that gives them a leathery feel and provides enhanced protection against evaporative water loss. An example is mesquite (*Prosopis*). In still other plants that inhabit arid landscapes, such as cacti, stems are thick, leaflike pads covered by sharp spines that actually are modified leaves (see **Figure 32.13c**). These structural alterations reduce the surface area for transpiration.

One intriguing variation on water-conservation mechanisms occurs in CAM plants, including cacti, orchids, and most succulents. As discussed in Section 9.4, **crassulacean acid metabolism** (CAM) is a biochemical variation of photosynthesis that was discovered in a member of the family Crassulaceae. CAM plants generally have fewer stomata than other types of plants, and their stomata follow a reversed schedule. They are closed during the day when temperatures are higher and the relative humidity is lower, and open at night. At night, the plant temporarily fixes carbon dioxide by converting it to malate, an organic acid. In the daytime, the  $CO_2$  is released from malate and diffuses into chloroplasts, so photosynthesis takes place even though a CAM plant's stomata are closed. This adaptation prevents heavy evaporative water losses during the heat of the day.

a. Oleanders



b. Oleander leaf



c. Spines (modified leaves) on a cactus stem



d. CAM plant



**Figure 32.13**

Some adaptations that enable plants to survive water stress. **(a)** Oleanders (*Nerium oleander*) are adapted to arid conditions. **(b)** As shown in the micrograph, oleander leaves have recessed stomata on their lower surface and a multilayer epidermis covered by a thick cuticle on the upper surface. **(c)** Like many other cacti, the leaves of the Graham dog cactus (*Opuntia grahamii*) are modified into spines that protrude from the underlying stem. Transpiration and photosynthesis occur in the green stems, such as the oval stem in this photograph. **(d)** *Sedum*, a CAM plant, in which the stomata open only at night.

### STUDY BREAK

1. Explain the key steps in the cohesion–tension mechanism of water transport in a plant.
2. How and when do stomata open and close? In what ways is their functioning important to a plant's ability to manage water loss?

### 32.4 Transport of Organic Substances in the Phloem

A plant's phloem is another major long-distance transport system, and a superhighway at that: it carries huge amounts of carbohydrates, lesser but vital amounts of amino acids, fatty acids, and other organic compounds,

and still other essential substances such as hormones. And unlike the xylem's unidirectional upward flow, the phloem transports substances throughout the plant to wherever they are used or stored. Organic compounds and water in the sieve tubes of phloem are under pressure and driven by concentration gradients.

### Organic Compounds Are Stored and Transported in Different Forms

Plants synthesize various kinds of organic compounds, including large amounts of carbohydrates that are stored mainly as starch. Yet regardless of where in a plant a particular compound is destined to be used or stored, starch, protein, and fat molecules cannot leave the cells in which they are formed because all are too large to cross cell membranes. They also may be too insoluble in water to be transported to other regions of the plant body. Consequently, in leaves and other plant parts, specific reactions convert organic compounds to transportable forms. For example, hydrolysis of starch liberates glucose units, which combine with fructose to form sucrose—the main form in which sugars are transported through the phloem of most plants. Proteins are broken down into amino acids, and lipids converted into fatty acids. These forms are also better able to cross cell membranes by passive or active mechanisms.

### Organic Solutes Move by Translocation

In plants, the long-distance transport of substances is called **translocation**. Botanists most often use this term to refer to the distribution of sucrose and other organic compounds by phloem, and they understand the mechanism best in flowering plants. The phloem of flowering plants contains interconnecting sieve tubes formed by living sieve tube member cells (see Figure 31.9). Sieve tubes lie end to end within vascular bundles, and they extend through all parts of the plant. Water and organic compounds, collectively called **phloem sap**, flow rapidly through large pores on the sieve tubes' end walls—another example of a structural adaptation that suits a particular function.

### Phloem Sap Moves from Source to Sink under Pressure

Over the decades, plant physiologists have proposed several mechanisms of translocation, but it was the tiny aphid, an insect that annoys gardeners, that helped demonstrate that organic compounds flow under pressure in the phloem. An aphid attacks plant leaves and stems, forcing its needlelike stylet (a mouthpart) into sieve tubes to obtain the dissolved sugars and other nutrients inside. Numerous experiments with aphids have

## Figure 32.14 Experimental Research

### Translocation Pressure

**HYPOTHESIS:** High pressure forces phloem sap to flow through sieve tubes from a source to a sink.

**EXPERIMENT:** In the late 1970s, John Wright and Donald Fisher at the University of Georgia devised an experiment to directly measure the turgor pressure in sieve tubes of weeping willow saplings (*Salix babylonica*) under nondestructive conditions, using aphids that feed on *S. babylonica* in the wild. Weeping willow saplings were grown in a greenhouse under natural conditions of light and moisture. Aphids were placed on the trees and allowed to begin feeding by inserting their stylets into sieve tubes in the normal fashion. After being anesthetized by exposure to high concentrations of carbon dioxide, the aphids' bodies were cut away and only their stylets were left embedded in the sieve tubes. A tiny pressure-measuring device called a micromanometer then was glued over the end of each stylet. The micromanometer registered the volume and pressure of phloem sap as it was exuded from the stylet over time periods ranging from 30 to 90 minutes.

a. Aphid releasing honeydew



b. Micrograph of aphid stylet in sieve tube

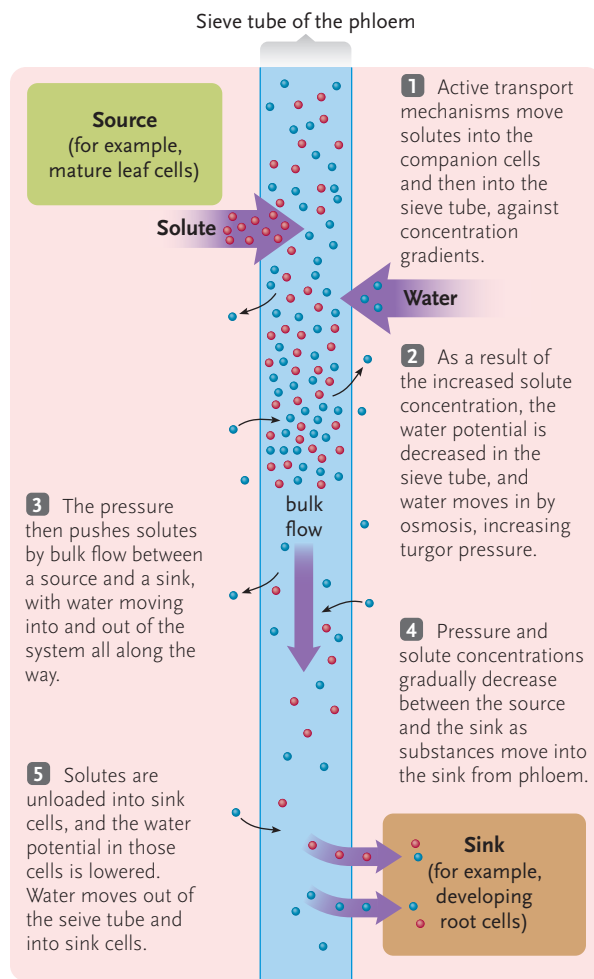


**RESULTS:** In nearly all cases, a high volume of pressurized sap flowed through the severed stylets into the micromanometer during the test periods.

**CONCLUSION:** The evidence supports pressure flow as the mechanism that moves phloem sap through sieve tubes.

Other experiments have confirmed that both turgor pressure and the concentration of sucrose are highest in sieve tubes closest to the sap source. Phloem sap also moves most rapidly closest to the source, where pressure is highest.

shown that in most plant species, sucrose is the main carbohydrate being translocated through the phloem. Studies also verify that the contents of sieve tubes are under high pressure, often five times as much as in an automobile tire. **Figure 32.14** explains a simple and innovative experiment that provided direct confirmation that phloem sap flows under pressure. When a live aphid feeds on phloem sap, this pressure forces the fluid through the aphid's gut and (minus nutrients absorbed) out its anus as "honeydew." If you park your car



**Figure 32.15**  
Summary of the pressure flow mechanism in the phloem of flowering plants. Organic solutes are loaded into sieve tubes at a source, such as a leaf, and move by bulk flow toward a sink, such as roots or rapidly growing stem parts.

under a tree being attacked by aphids, it might get spattered with sticky honeydew droplets, thanks to the high fluid pressure in the tree's phloem.

A great deal of what botanists know about the transport of phloem sap has come from studies of sucrose transport in flowering plants. A fundamental discovery is that in flowering plants sucrose-laden phloem sap flows from a starting location, called the *source*, to another site, called the *sink*, along gradients of decreasing solute concentration and pressure. A **source** is any region of the plant where organic substances are being loaded into the phloem's sieve tube system. A **sink** is any region where organic substances are being unloaded from the sieve tube system and used or stored. What causes sucrose and other solutes produced in leaf mesophyll to flow from a source to a sink? In flowering plants, the **pressure flow mechanism** builds up at the source end of a sieve tube system and pushes those solutes by bulk flow toward a sink, where they are removed. **Figure 32.15** summarizes this mechanism.

The site of photosynthesis in mature leaves is an example of a source. Another example is a tulip bulb. In spring, stored food is mobilized for transport upward to growing plant parts, but after the plants bloom,

the bulb becomes a sink as sugars manufactured in the tulip plant's leaves are translocated into it for storage. Young leaves, roots, and developing fruits generally start out as sinks, only to become sources when the season changes or the plant enters a new developmental phase. In general, sinks receive organic compounds from sources closest to them. Hence, the lower leaves on a rose bush may supply sucrose to roots, while leaves farther up the shoot supply the shoot tip.

Most substances carried in phloem are loaded into sieve tube members by active transport (**Figure 32.16a**). Sucrose will be our example here. In leaves, sucrose formed inside mesophyll cells is exported and eventually reaches the apoplast (adjoining cell walls and air spaces) next to a small phloem vein. Here, it is actively pumped into companion cells by symport (see **Figure 32.3**), in which  $H^+$  ions move into the cell through the same carrier that takes up the sugar molecules. From the companion cells, most sucrose crosses into the living sieve tube members through plasmodesmata. Some sucrose also is loaded into sieve tube members by symport.

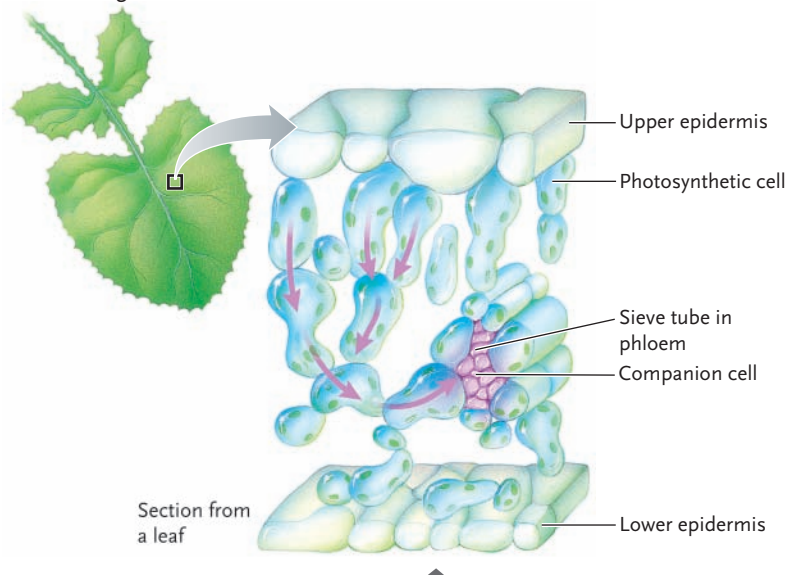
In some plants, companion cells become modified into **transfer cells** that facilitate the short-distance transport of organic solutes from the apoplast into the symplast. Transfer cells generally form when large amounts of solutes must be loaded or unloaded into the phloem, and they shunt substances through plasmodesmata to sieve tube members. As a transfer cell is forming, parts of the cell wall grow inward like pleats. This structural feature increases the surface area across which solutes can be taken up. The underlying plasma membrane, packed with transport proteins, then expands to cover the ingrowths. Transfer cells also enhance solute transport between living cells in the xylem, and they occur in glandlike tissues that secrete nectar. Botanists have discovered transfer cells in species from every taxonomic group in the plant kingdom, as well as in fungi and algae. In part because they arise from differentiated cells (instead of from meristem cells like other plant types of plant cells), researchers are working to define the molecular mechanisms that trigger their development.

When sucrose is loaded into sieve tubes its concentration rises inside the tubes. Thus the water potential falls, and water flows into the sieve tubes by osmosis. In fact, the phloem typically carries a great deal of water. As water enters sieve tubes, turgor pressure in the tubes increases, and the sucrose-rich fluid moves by bulk flow into the increasingly larger sieve tubes of larger veins. Eventually, the fluid is pushed out of the leaf into the stem and toward a sink (**Figure 32.16b**). When sucrose is unloaded at the sink, water in the tube "follows solutes," moving by osmosis into the surrounding cells (**Figure 32.16c**). Ultimately, the water enters the xylem and is recirculated.

Sieve tubes are mostly passive conduits for translocation. The system works because companion cells



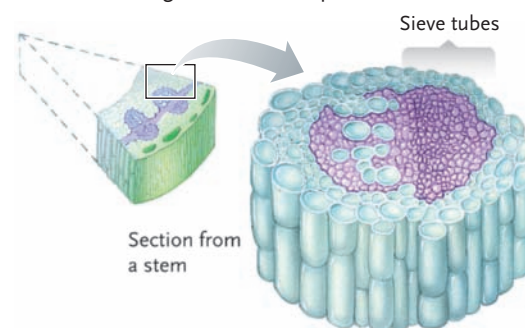
### a. Loading at a source



Section from a leaf

Photosynthetic cells in leaves are a common source of carbohydrates that must be distributed through a plant. Small, soluble forms of these compounds move from the cells into phloem (in a leaf vein).

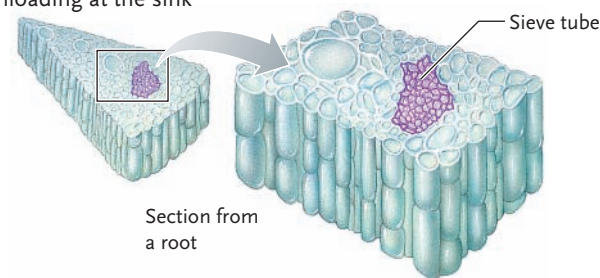
### b. Translocation along a distribution path



Section from a stem

Fluid pressure is greatest inside sieve tubes at the source. It pushes the solute-rich fluid to a sink, which is any region where cells are growing or storing food. There, the pressure is lower because cells are withdrawing solutes from the tubes and water follows the solutes.

### c. Unloading at the sink



Section from a root

Solutes are unloaded from sieve tubes into cells at the sink; water follows. Translocation continues as long as solute concentration gradients and a pressure gradient exist between the source and the sink.

**Figure 32.16**

Translocation in the tissues of *Sonchus*, commonly called sow thistle. Research on *Sonchus* provided experimental evidence for the pressure flow mechanism.

## UNANSWERED QUESTIONS

### What are plasmodesmata made of, and exactly how do they function?

Plasmodesmata, the cytoplasmic channels through plant cell walls, connect plant cells to each other. Yet two fundamental questions about plasmodesmata remain unanswered: Exactly how do plasmodesmata function, and what are their structural components?

As described in this chapter and in Chapter 5, botanists have long assumed that nutrients, water, and small molecules that serve as growth regulators move through plasmodesmata, which form part of the symplastic pathway in plant tissues. Recent studies have demonstrated that larger molecules, including viruses and important proteins involved in plant growth and development, also move from cell to cell through plasmodesmata. For example, Patricia Zambryski and K. M. Crawford at the University of California at Berkeley reported that proteins, including transcription factors, travel via plasmodesmata from the cell that produces the proteins to adjacent cells where the factors promote or inhibit the expression of particular genes.

While the normal functions of plasmodesmata in plant growth and development still are not well understood, ongoing research by Zambryski and other plant scientists has begun to shed light on the workings of these vital channels. For instance, a variety of studies of the

processes by which viruses spread through plant tissues have revealed that plasmodesmata are not simply static, open channels. Instead they are dynamic structures with the capacity to close, reopen, widen, and narrow. This capacity for structural change is not triggered by viral infection: rather, it seems that viruses simply take over the plant's natural mechanism for moving molecules from one cell to another.

Plasmodesmata were first observed using electron microscopy several decades ago, and they appear to be lined with proteins as well as membranes. Multiple biochemical approaches have failed to identify the proteins, probably because of the difficulty of purifying proteins that are associated with both a membrane and the cell wall. Genetic screens to identify plasmodesmata proteins, as well as the genes that regulate the functioning of plasmodesmata, are currently under way and may finally reveal details of plasmodesmata structure. As our understanding of the architecture of plasmodesmata and how they function grows, so will insights into the mechanisms of plant development, how plants interact with viral pathogens, and other questions as well.

Beverly McMillan

supply most of the energy that loads sucrose and other solutes at the source, and because solutes are removed at their sinks. As sucrose enters a sink, for example, its concentration in sieve tubes decreases, with a corresponding decrease in pressure. Thus for sucrose and other solutes transported in the phloem, there is always a gradient of concentration from source to sink—and a pressure gradient that keeps the solute moving along.

As noted previously, phloem sap moving through a plant carries a wide variety of substances, including hormones, amino acids, organic acids, and agricultural chemicals. The phloem also transports organic nitrogen compounds and mineral ions that are removed from dying leaves and stored for reuse in root tissue.

The transport functions of xylem and phloem are closely integrated with phenomena discussed later in this unit—reproduction and embryonic development, and the hormone-based regulation of plant growth.

### STUDY BREAK

1. Compare and contrast translocation and transpiration.
2. Using sucrose as your example, summarize how a substance moves from a source into sieve tubes and then is unloaded at a sink. What is this mechanism called, and why?

## Review

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### 32.1 Principles of Water and Solute Movement in Plants

- Plants have mechanisms for moving water and solutes (1) into and out of cells, (2) laterally from cell to cell, and (3) long-distance from the root to shoot or vice versa (Figure 32.2).
- Both passive and active mechanisms move substances into and out of plant cells. Solute generally are transported by carriers (facilitated diffusion), either passively down a concentration or electrochemical gradient (in the case of ions), or actively against a gradient, which requires cellular energy. An  $H^+$  gradient creates the membrane potential that drives the cross-membrane transport of many ions or molecules (Figure 32.3).
- Most organic substances enter plant cells by symport, in which the energy of the  $H^+$  gradient is coupled with uptake of a different solute. Some substances cross the plant cell membrane by antiport, in which energy of the  $H^+$  gradient powers movement of a second solute out of cells.
- Water crosses plant cell membranes by osmosis, which is driven by water potential ( $\psi$ ). Water tends to move osmotically from regions where water potential is higher to regions where it is lower.
- Water potential reflects a balance between turgor pressure and solute potential. Water potential is measured in megapascals (MPa) (Figures 32.4 and 32.5).
- Water and solutes also move into and out of the cell's central vacuole, transported from the cytoplasm across the tonoplast. Aquaporins across the tonoplast enhance water movement. Water in the central vacuole is vital for maintaining turgor pressure inside a plant cell.
- Bulk flow of fluid occurs when pressure at one point in a system changes with respect to another point in the system.

### 32.2 Transport in Roots

- Water and mineral ions entering roots travel laterally through the root cortex to the root xylem, following one or more of three major routes: the apoplastic pathway, the symplastic pathway, and the transmembrane pathway (Figure 32.6).

- In the apoplastic pathway, water diffuses into roots between the walls of root epidermal cells. By contrast, water and solutes absorbed by roots can enter either the symplastic or transmembrane pathway, both of which pass through cells.
- Casparian strips form a barrier that forces water and solutes in the apoplastic pathway to pass through cells in order to enter the stele. When an ion reaches the stele, it diffuses from cell to cell to reach the xylem (Figure 32.7). Roots of many flowering plants have a second layer of cells with Casparian strips (exodermis) just inside the root epidermis.

[Animation: Water absorption](#)

[Animation: Root functioning](#)

### 32.3 Transport of Water and Minerals in the Xylem

- In the conducting cells of xylem, tension generated by transpiration extends down from leaves to roots. By the cohesion-tension mechanism of water transport, water molecules are pulled upward by tension created as water exits a plant's leaves (Figure 32.8).
- In tall trees, negative pressure generated in the shoot drives bulk flow of xylem sap. In some plants, notably herbaceous species, positive pressure sometimes develops in roots and can force xylem sap upward (Figure 32.9).
- Transpiration and carbon dioxide uptake occur mostly through stomata. Environmental factors such as relative humidity, air temperature, and air movement at the leaf surface affect the transpiration rate.
- Most plants lose water and take up carbon dioxide during the day, when stomata are open. At night, when stomata close, plants conserve water and the inward movement of carbon dioxide falls.
- Stomata open in response to falling levels of carbon dioxide in leaves and also to incoming light wavelengths that activate photoreceptors in guard cells.
- Activation of photoreceptors triggers active transport of  $K^+$  into guard cells. Simultaneous entry of anions such as  $Cl^-$  and synthesis of negatively charged organic acids increase the solute concentration, lowering the water potential so that water enters by osmosis. As turgor pressure builds, guard cells swell and draw apart, producing the stomatal opening (Figure 32.10).
- Guard cells close when light wavelengths used for photosynthesis wane. The stomata of water-stressed plants close re-

ardless of light or CO<sub>2</sub> needs, possibly under the influence of the plant hormone ABA. The leaves of species native to arid environments typically have adaptations (such as an especially thick cuticle) that enhance the plant's ability to conserve water (Figures 32.12 and 32.13).

**Animation: Stomata**

**Animation: Transpiration**

**Animation: Interdependent processes**

## 32.4 Transport of Organic Substances in the Phloem

- In flowering plants, phloem sap is translocated in sieve tube members. Differences in pressure between source and sink

regions drive the flow. Sources include mature leaves; sinks include growing tissues and storage regions (such as the tubers of a potato) (Figures 32.14 and 32.15).

- In leaves, the sugar sucrose is actively transported into companion cells adjacent to sieve tube members, then loaded into the sieve tubes through plasmodesmata.
- In some plants, transfer cells take up materials and pass them to sieve tube members. Transfer cells in xylem enhance the transport of solutes between tissues.
- As the sucrose concentration increases in the sieve tubes, water potential decreases. The resulting influx of water causes pressure to build up inside the sieve tubes, so the sucrose-laden fluid flows in bulk toward the sink, where sucrose and water are unloaded and distributed among surrounding cells and tissues (Figure 32.16).

## Questions

### Self-Test Questions

- Antiport transport mechanisms:
  - move dissolved materials by osmosis.
  - transport molecules in the opposite direction of H<sup>+</sup> transported by proton pumps.
  - transport molecules in the same direction as H<sup>+</sup> is pumped.
  - are not affected by the size of molecules to be transported.
  - are not affected by the charge of molecules to be transported.
- All the following have roles in transporting materials between plant cells except:
  - the stele.
  - symport.
  - the cell membrane.
  - stomata.
  - transport proteins.
- Turgor pressure is best expressed as the:
  - movement of water into a cell by osmosis.
  - driving force for osmotic movement of water ( $\psi$ ).
  - group movement of large numbers of molecules due to a difference in pressure between two locations.
  - equivalent of water potential.
  - pressure exerted by fluid inside a plant cell against the cell wall.
- Water potential is:
  - the driving force for the osmotic movement of water into plant cells.
  - higher in a solution that has more solute molecules relative to water molecules.
  - a measure of the physical pressure required to halt osmotic water movement across a membrane.
  - a measure of the combined effects of a solution's pressure potential and its solute potential.
  - the functional equivalent of turgor pressure.
- To regulate the flow of water and minerals in the root, the:
  - Casparian strip of endodermal cells blocks the apoplastic pathway, forcing water and solutes to cross cell plasma membranes in order to pass into the stele.
  - apoplastic pathway is expanded, allowing a greater variety of substances to move into the stele.
  - symplastic pathway is modified in ways that make plasma membranes of root cortex cells more permeable to water and solutes.
  - symplastic pathway shuts down entirely so that substances can move only through the apoplast.
- transmembrane pathway augments transport via the apoplast, shunting substances around cells.
- An indoor gardener leaving for vacation completely wraps a potted plant with clear plastic. Temperature and light are left at low intensities. The effect of this strategy is to:
  - halt photosynthesis.
  - reduce transpiration.
  - cause guard cells to shrink and stomata to open.
  - destroy cohesion of water molecules in the xylem.
  - increase evaporation from leaf mesophyll cells.
- Stomata open when:
  - water has moved out of the leaf by osmosis.
  - K<sup>+</sup> flows out of guard cells.
  - turgor pressure in the guard cells lessens.
  - the H<sup>+</sup> active transport protein stops pumping.
  - outward flow of H<sup>+</sup> sets up a concentration gradient that moves K<sup>+</sup> in via symport.
- A factor that contributes to the movement of water up a plant stem is:
  - active transport of water into the root hairs.
  - an increase in the water potential in the leaf's mesophyll layer.
  - cohesion of water molecules in stem and leaf xylem.
  - evaporation of water molecules from the walls of cells in root epidermis and cortex and in the stele.
  - absorption of raindrops on a leaf's epidermis.
- In translocation of sucrose-rich phloem sap:
  - the sap flows toward a source as pressure builds up at a sink.
  - crassulacean acid metabolism reduces the rate of photosynthesis.
  - companion cells use energy to load solutes at a source and the solutes then follow their concentration gradients to sinks.
  - sucrose diffuses into companion cells while H<sup>+</sup> simultaneously leaves the cells by a different route.
  - companion cells pump sucrose into sieve tube members.
- In Vermont in early spring, miles of leafless maple trees have buckets hanging from "spigots" tapped into them to capture the fluid raw material for making maple syrup. This fluid flows into the buckets because:
  - the tap drains phloem sap stored in the heartwood.
  - phloem sap is moving from its source in maple tree roots to its sink in the developing leaf buds.

- c. phloem sap is moving from where it was synthesized to the closest sink.
- d. bulk flow results as phloem sap is actively transported from smaller to larger veins.
- e. phloem sap is diverted into the tap from transfer cells.

### Questions for Discussion

1. Many popular houseplants are native to tropical rain forests. Among other characteristics, many nonwoody species have extraordinarily broad-bladed leaves, some so ample that indigenous people use them as umbrellas. What environmental conditions might make a broad leaf adaptive in tropical regions, and why?
2. Insects such as aphids that prey on plants by feeding on phloem sap generally attack only young shoot parts. Other than the relative ease of piercing less mature tissues, suggest a reason why it may be more adaptive for these animals to focus their feeding effort on younger leaves and stems.
3. So-called systemic insecticides often are mixed with water and applied to the soil in which a plant grows. The chemicals are effective against sucking insects no matter which plant tissue the insects attack, but often don't work as well against chewing insects. Propose a reason for this difference.
4. Concerns about global warming and the greenhouse effect (see Chapter 51) center on rising levels of greenhouse gases, including atmospheric carbon dioxide. Plants use CO<sub>2</sub> for photosynthesis, and laboratory studies suggest that increased CO<sub>2</sub> levels could cause a rise in photosynthetic activity. However, as one environmentalist noted, "What plants do in environmental chambers may not happen in nature, where there are many other interacting variables." Strictly from the standpoint of physiological effects, what are some possible ramifications of a rapid doubling of atmospheric CO<sub>2</sub> on plants in temperate environments? In arid environments?

### Experimental Analysis

In an experiment designed to explore possible links between ion uptake by roots and loading of ions into the xylem, a length of root was suspended through an impermeable barrier that separated two compartments—the root tip in one compartment and the cut end of the root in the other. Initially the solutions in the two compartments were identical, except that a known quantity of a radioactive tracer (representing an ion) was added to the one in which the root tip was suspended. The experimenters could then measure the relationship between ion uptake in the root and loading of the ion into the root xylem under different chemical conditions (such as the addition of a hormone or protein synthesis inhibitor). The research has provided evidence that ion uptake in the root is independent of loading of the ion into xylem. How does the experimental design support this kind of testing?

### Evolution Link

A variety of structural features of land plants reflect the conflicting demands for conserving water and taking in carbon dioxide for photosynthesis. Identify at least four fundamental structural adaptations that help resolve this dilemma and explain how each one contributes to a land plant's survival.

### How Would You Vote?

Phytoremediation using genetically engineered plants can increase the efficiency with which a contaminated site is cleaned up. Do you support planting genetically engineered plants for such projects? Go to [www.thomsonedu.com/login](http://www.thomsonedu.com/login) to investigate both sides of the issue and then vote.