35

Transport in Plants

About 40 years ago the biologist Per Scholander was studying water movement to the top of an 80-meter Douglas fir. To collect samples rapidly from the treetop, he hired a sharpshooter, who aimed a high-powered rifle at a twig high in the tree and fired. From high above, a twig fluttered to the ground, and Scholander quickly inserted it into an instrument for measuring tension in the xylem sap. As we will soon see, Scholander's measurements increased our understanding of how water and minerals reach the tops of tall trees.

The water and minerals in a plant's xylem must be transported to the entire shoot system, all the way to the highest leaves and apical buds. Carbohydrates produced in all the leaves, including the highest, must be translocated to all the living nonphotosynthetic parts of the plant. Before we consider the mechanisms underlying these processes, we should consider two questions: How much water is transported? And how high can water be transported?

In answer to the first question, consider the following example: A single maple tree 15 meters tall was estimated to have some 177,000 leaves, with a total leaf surface area of 675 square meters—half again the area of a basketball court. During a summer day, that tree lost 220 liters of water *per hour* to the atmosphere by evaporation from the leaves. To prevent wilting, the xylem needed to transport 220 liters of water from the roots to the leaves every hour. (By comparison, a 50-gallon drum holds 189 liters.)

The second question can be rephrased: How tall are the tallest trees? The tallest gymnosperms, the coast redwoods—*Sequoia sempervirens*—exceed 110 meters in height, as do the tallest angiosperms, the Australian *Eucalyptus regnans*. Any successful explanation of water transport in the xylem must account for transport to these great heights.

In this chapter we consider the uptake and transport of water and minerals by plants, the control of evaporative water loss through the stomata, and the translocation of substances in the phloem.

A Long Way to the Top
Water and minerals must defy gravity and climb over 80 meters to reach the top branches of these Douglas firs (*Pseudotsuga menziesii*).

Uptake and Transport of Water and Minerals

Terrestrial plants obtain both water and mineral nutrients from the soil, usually by way of their roots. You already know that water is one of the ingredients required for carbohydrate production by photosynthesis in the leaves. Water is also essential for transporting solutes, for cooling the plant, and for developing the internal pressure that supports the plant body.

How do leaves high in a tree obtain water from the soil? What are the mechanisms by which water and mineral ions enter the plant body through the roots and ascend as sap in the xylem? Because neither water nor minerals can move through the plant into the xylem without crossing at least one plasma membrane, we focus first on osmosis. Then we examine the uptake of mineral ions, and follow the pathway by which both water and minerals move through the root to gain entry to the xylem.

Water moves through a membrane by osmosis

Osmosis, the movement of water through a membrane in accordance with the laws of diffusion, was described in Chapter 5. The **solute potential** (osmotic potential) of a solution is a measure of the effect of dissolved solutes on the osmotic behavior of the solution. The greater the solute concentration of a solution, the more negative its solute potential, and the greater the tendency of water to move into it from another solution of lower solute concentration (and less negative solute potential). For osmosis to occur, the two solutions must be separated by a membrane permeable to water but relatively impermeable to the solute. Recall, too, that osmosis is a passive process—energy is not required.

Unlike animal cells, plant cells are surrounded by a relatively rigid cell wall. As water enters a plant cell, the entry of more water is increasingly resisted by an opposing **pressure potential** (turgor pressure), owing to the rigidity of the wall. As more and more water enters, the pressure potential becomes greater and greater.

Pressure potential is a hydraulic pressure analogous to the air pressure in an automobile tire; it is a real pressure that can be measured with a pressure gauge. Cells with walls do not burst when placed in pure water; instead, water enters by osmosis until the pressure potential exactly balances the solute potential. At this point, the cell is *turgid*; that is, it has a high pressure potential.

The overall tendency of a solution to take up water from pure water, across a membrane, is called its **water potential**, represented as ψ, the Greek letter psi (Figure 35.1). The water potential is simply the sum of the (negative) solute potential (ψ_s) and the (usually positive) pressure potential (ψ_p):

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

For pure water under no applied pressure, all three of these parameters are zero.

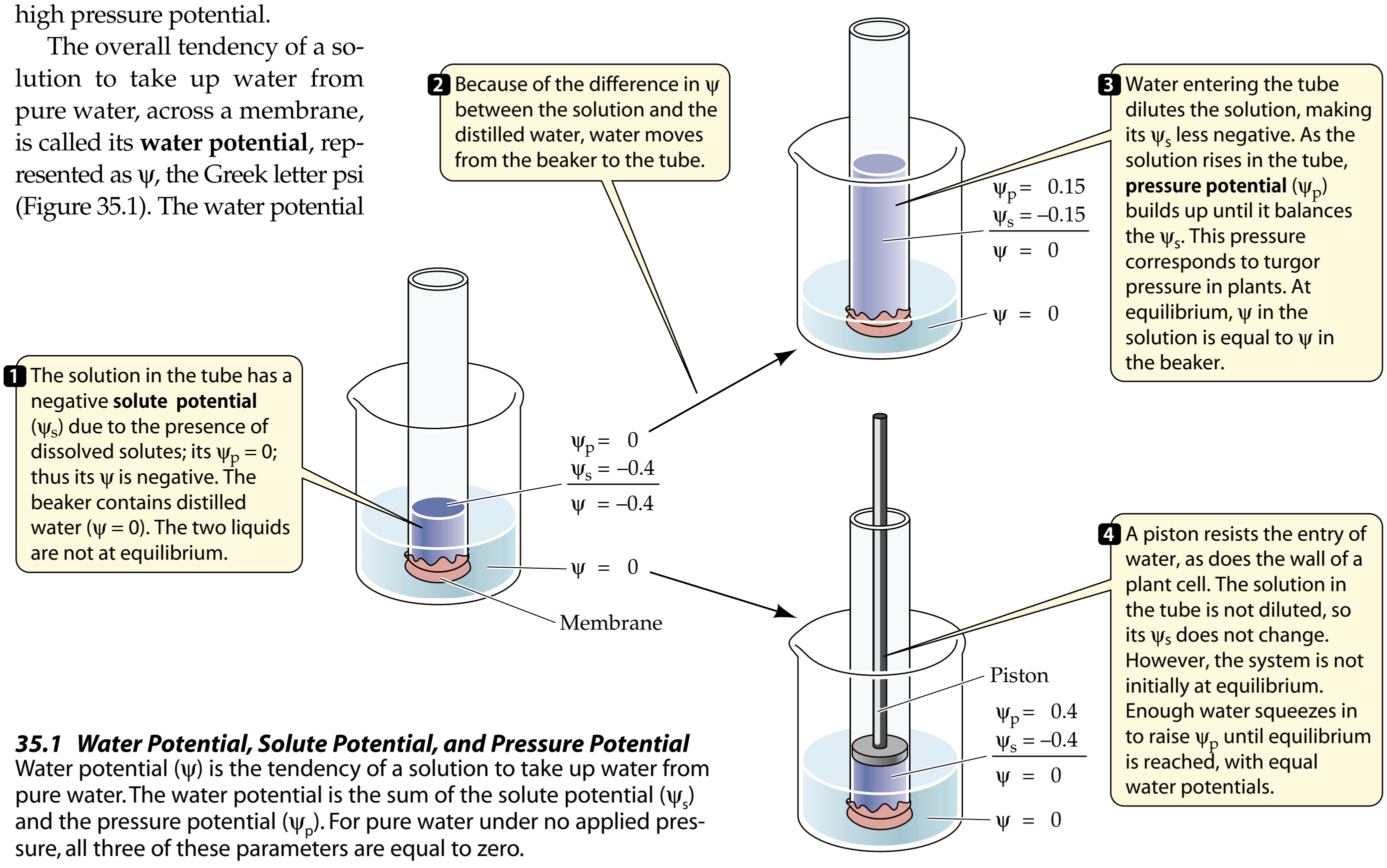
We can measure solute potential, pressure potential, and water potential in *megapascals* (MPa), a unit of pressure. (Atmospheric pressure is about 0.1 MPa, or 14.7 pounds per square inch; typical pressure in an automobile tire is about 0.2 MPa.)

In all cases in which water moves between two solutions separated by a membrane, the following rule of osmosis applies: *Water always moves across a differentially permeable membrane toward the region of more negative water potential.*

Osmotic phenomena are of great importance to plants. The structure of many plants is maintained by the pressure potential of their cells; if the pressure potential is lost, a plant *wilts*. Within living tissues, the movement of water from cell to cell by osmosis follows a gradient of *water potential*. Over longer distances, in open tubes such as xylem vessels and phloem sieve tubes, the flow of water and dissolved solutes is driven by a gradient in *pressure potential*. The movement of a solution due to a difference in pressure potential between two parts of a plant is called **bulk flow**.

Uptake of mineral ions requires transport proteins

Mineral ions, which carry electric charges, cannot move across a plasma membrane unless they are aided by trans-



1 The solution in the tube has a negative **solute potential** (ψ_s) due to the presence of dissolved solutes; its $\psi_p = 0$; thus its ψ is negative. The beaker contains distilled water ($\psi = 0$). The two liquids are not at equilibrium.

2 Because of the difference in ψ between the solution and the distilled water, water moves from the beaker to the tube.

3 Water entering the tube dilutes the solution, making its ψ_s less negative. As the solution rises in the tube, **pressure potential** (ψ_p) builds up until it balances the ψ_s. This pressure corresponds to turgor pressure in plants. At equilibrium, ψ in the solution is equal to ψ in the beaker.

4 A piston resists the entry of water, as does the wall of a plant cell. The solution in the tube is not diluted, so its ψ_s does not change. However, the system is not initially at equilibrium. Enough water squeezes in to raise ψ_p until equilibrium is reached, with equal water potentials.

35.1 Water Potential, Solute Potential, and Pressure Potential
Water potential (ψ) is the tendency of a solution to take up water from pure water. The water potential is the sum of the solute potential (ψ_s) and the pressure potential (ψ_p). For pure water under no applied pressure, all three of these parameters are equal to zero.

port proteins. (You may wish to review the description of transport proteins in Chapter 5.) When the concentration of these charged ions in the soil is greater than that in the plant, ion channels and carrier proteins can move them into the plant by facilitated diffusion.

The concentrations of some ions in the soil solution, however, are lower than those required inside the plant. Thus the plant must take up these ions against a concentration gradient. Electric potential also plays a role in this process: To move a negatively charged ion into a negatively charged region is to move it against an electrical gradient. The combination of concentration and electrical gradients is called an *electrochemical gradient*. Uptake against an electrochemical gradient is active transport, an energy-requiring process, depending on cellular respiration for ATP. Active transport, of course, requires specific carrier proteins.

Unlike animals, plants do not have a sodium–potassium pump for active transport. Rather, plants have a **proton pump**, which uses energy obtained from ATP to move protons out of the cell against a proton concentration gradient (Figure 35.2*a*). Because protons (H^+) are positively charged, their accumulation on one side of a membrane has two results:

- The region outside the membrane becomes positively charged with respect to the region inside.
- A proton concentration gradient develops.

Each of these results has consequences for the movement of other ions. Because of the charge difference across the membrane, the movement of positively charged ions, such as potassium (K^+), into the cell through their membrane channels is enhanced. These positive ions move into the now more negatively charged interior of the cell by facilitated diffusion (Figure 35.2*b*). In addition, the proton concentration gradient can be harnessed to drive secondary active transport, in which negatively charged ions such as chloride (Cl^-)are moved into the cell against an electrochemical gradient by a symport protein that couples their movement with that of H^+ (Figure 35.2*c*). In sum, there is vigorous traffic of ions across plant membranes.

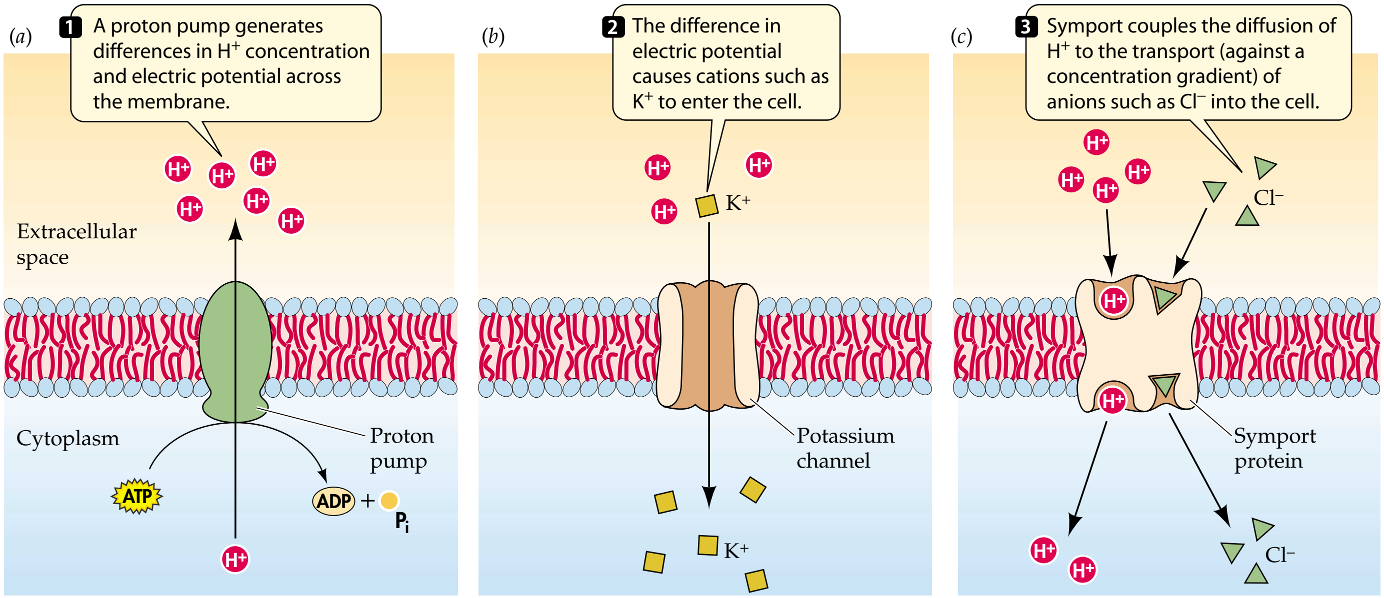
The proton pump and the coordinated activities of other membrane transport proteins cause the interior of a plant cell to be strongly negative with respect to the exterior. Such a difference in charge across a membrane is called a *membrane potential*. Biologists can measure the membrane potential of a plant cell with microelectrodes, just as they can measure similar charge differences in neurons (nerve cells) and other animal cells. Most plant cells have a membrane potential of at least –120 millivolts, and they maintain it at this level. The membrane potential difference affects the movements of mineral ions into and out of cells.

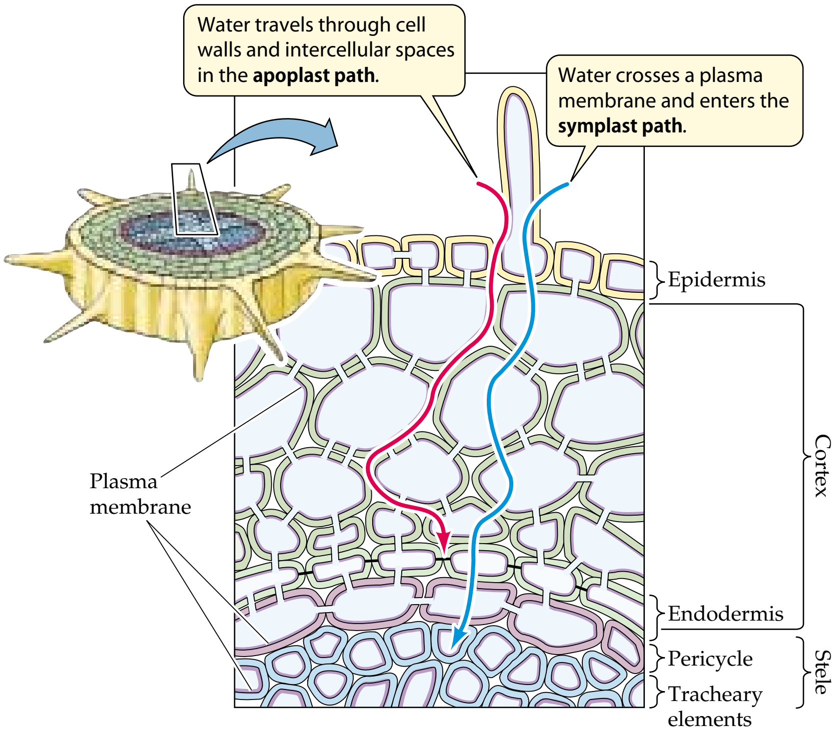
Water and ions pass to the xylem by way of the apoplast and symplast

Mineral ions enter and move through plants in various ways. Where bulk flow of water is occurring, dissolved minerals are carried along in the stream. Where water is moving more slowly, minerals move by diffusion. At certain points, where plasma membranes are being crossed, some mineral ions are moved by active transport. One such point is the surface of a root hair, where mineral ions first enter the cells of the plant. Later, within the stele, the ions must cross a plasma membrane before entering the lifeless cells of the xylem.

The movement of ions across membranes can also result in the movement of water. Water moves into a root because the root has a more negative water potential than does the

35.2 The Proton Pump and Its Effects
The buildup of hydrogen ions transported across the plasma membrane by the proton pump (*a*) triggers the movement of both cations (*b*) and anions (*c*) into the cell.





Water travels through cell walls and intercellular spaces in the **apoplast path**.

Water crosses a plasma membrane and enters the **symplast path**.

35.3 Apoplast and Symplast The plant cell walls and intercellular spaces constitute the apoplast. The symplast comprises the living cells, which are connected by plasmodesmata. To enter the symplast, water and solutes must pass through a plasma membrane. No such selective barrier limits movement through the apoplast.

soil solution. Water moves from the cortex of the root into the stele (which is where the vascular tissues are located) because the stele has a more negative water potential than does the cortex.

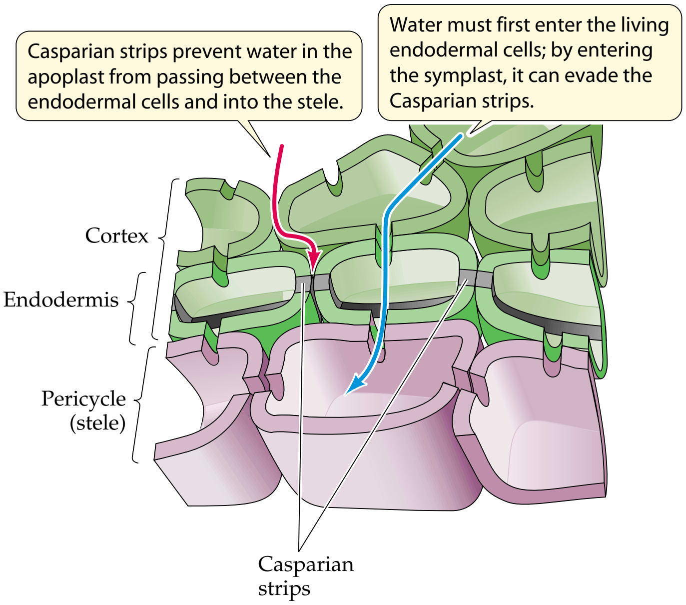
Water and minerals from the soil may pass through the dermal and ground tissues to the stele via two pathways: the apoplast and the symplast. Plant cells are surrounded by cell walls that lie outside the plasma membrane, and intercellular spaces (spaces between cells) are common in many tissues. The walls and intercellular spaces together constitute the **apoplast** (from the Greek for "away from living material"). The apoplast is a continuous meshwork through which water and dissolved substances can flow or diffuse without ever having to cross a membrane (Figure 35.3). Movement of materials through the apoplast is thus unregulated.

The remainder of the plant body is the **symplast** (from the Greek for "together with living material"). The symplast is the portion of the plant body enclosed by membranes—the continuous cytoplasm of the living cells, connected by plasmodesmata (see Figure 35.3). The selectively permeable plasma membranes of the cells control access to the symplast, so movement of water and dissolved substances into the symplast is tightly regulated.

Water and minerals can pass from the soil solution through the apoplast as far as the endodermis, the innermost layer of the cortex. The endodermis is distinguished from the rest of the ground tissue by the presence of **Casparian strips**. These waxy, suberin-containing structures impregnate the endodermal cell wall and form a belt surrounding the endodermal cells. The Casparian strips act as a gasket that prevents water and ions from moving between the cells (Figure 35.4).

The Casparian strips of the endodermis thus completely separate the apoplast of the cortex from the apoplast of the stele. They do not obstruct the outer or inner faces of the endodermal cells. Accordingly, water and ions can enter the stele only by way of the symplast—that is, by entering and passing through the cytoplasm of the endodermal cells. Thus transport proteins in the membranes of these cells determine which mineral ions pass into the stele, and at what rates. This is one of several ways in which plants regulate their chemical composition and ensure an appropriate balance of their constituents. This balance is essential to plant life.

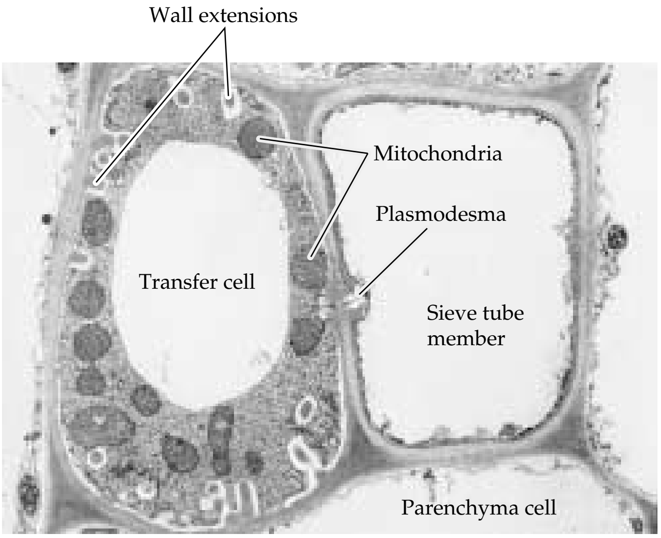
Once they have passed the endodermal barrier, water and minerals leave the symplast. Parenchyma cells in the pericycle or xylem help mineral ions move back into the apoplast. Some of these parenchyma cells, called **transfer cells**, are structurally modified for transporting mineral ions from their cytoplasm (part of the symplast) into their cell walls (part of the apoplast). The wall that receives the transported ions has many knobby extensions projecting into the transfer cell, increasing the surface area of the plasma membrane, the



Casparian strips prevent water in the apoplast from passing between the endodermal cells and into the stele.

Water must first enter the living endodermal cells; by entering the symplast, it can evade the Casparian strips.

35.4 Casparian Strips
Suberin-impregnated Casparian strips prevent water and ions from moving between the endodermal cells.



35.5 A Transfer Cell
Three walls of this transfer cell in a pea leaf have knobby extensions that face the cells from which the transfer cell imports solutes. This transfer cell exports the solutes to the neighboring sieve tube member.

number of transport proteins, and thus the rate of transport (Figure 35.5).

Transfer cells also have many mitochondria that produce the ATP needed to power the active transport of mineral ions. As mineral ions move into the solution in the walls, the water potential of the wall solution (apoplast) becomes more negative; thus water moves out of the cells and into the apoplast by osmosis. Active transport of ions moves the ions directly, and water follows passively. The end result is that water and minerals end up in the xylem, where they constitute the *xylem sap*.

We have just seen that proteins regulate the movement of ions across membranes. We shall now see that even water movement itself is regulated by proteins.

Aquaporins control the rate, but not the direction, of water movement

Aquaporins are membrane channel proteins through which water can traverse a membrane without interacting with the hydrophobic environment of its phospholipid bilayer. These proteins, important in both plants and animals, allow water to move rapidly from environment to cell and from cell to cell. The permeability of some aquaporins is subject to regulation, changing the *rate* of osmosis across the membrane. However, water movement through aquaporins is always passive, so the *direction* of water movement is unchanged by alterations in aquaporin permeability.

Transport of Water and Minerals in the Xylem

So far in this chapter we've described the movement of water and minerals into plant roots and their entry into the root xylem. Now we will consider how xylem sap moves throughout the remainder of the plant. Let's first consider some early ideas about the ascent of sap and then turn to our current understanding of how it works. We'll describe the experiments that ruled out some early models as well as some evidence in support of the current model—and we'll find out what Per Scholander's sharpshooter was up to in the story that opened this chapter.

Experiments ruled out some early models of transport in the xylem

Some of the earliest attempts to explain the rise of sap in the xylem were based on a hypothetical pumping action by living cells in the stem, which pushed the sap upward. However, experiments conducted and published in 1893 by the German botanist Eduard Strasburger definitively ruled out such models.

Strasburger worked with trees about 20 meters tall. He sawed them through at their bases and plunged the cut ends into buckets containing solutions of poisons such as picric acid. The solutions rose through the trunks, as was readily evident from the progressive death of the bark higher and higher up. When the solutions reached the leaves, the leaves died, too, at which point the solutions stopped being transported (as shown by the liquid levels in the buckets, which stopped dropping).

This simple experiment established three important points:

- Living, "pumping" cells were not responsible for the upward movement of the solutions, because the solutions themselves killed all living cells with which they came in contact.
- The leaves play a crucial role in transport. As long as they were alive, solutions continued to be transported upward; when the leaves died, transport ceased.
- Transport was not caused by the roots, because the trunks had been completely separated from the roots.

Root pressure does not account for xylem transport

In spite of Strasburger's observations, some plant physiologists turned to a model of transport based on **root pressure**—pressure exerted by the root tissues that would force liquid up the xylem. The basis for root pressure is a higher solute concentration, and accordingly a more negative water potential, in the xylem sap than in the soil solution. This negative potential draws water into the stele; once there, the water has nowhere to go but up.

There is good evidence for root pressure—for example, the phenomenon of *guttation*, in which liquid water is forced out through openings in the leaves (Figure 35.6). Guttation occurs only under conditions of high atmospheric humidity and plentiful water in the soil, which occur most commonly at night. Root pressure is also the source of the sap that oozes from the cut stumps of some plants, such as *Coleus*, when their tops are removed. Root pressure, however, cannot account for the ascent of sap in trees.

Root pressure seldom exceeds 0.1–0.2 MPa (one or two times atmospheric pressure). If root pressure were driving

35.6 Guttation
Root pressure is responsible for forcing water through openings in the tips of this strawberry leaf.

sap up the xylem, we would observe a positive pressure potential in the xylem at all times. In fact, as we are about to see, the xylem sap is under tension—a negative pressure potential—when it is ascending. Furthermore, as Strasburger had already shown, materials can be transported upward in the xylem even when the roots have been removed. If the roots aren't pushing the xylem sap upward, what does cause it to rise?

The transpiration–cohesion–tension mechanism accounts for xylem transport

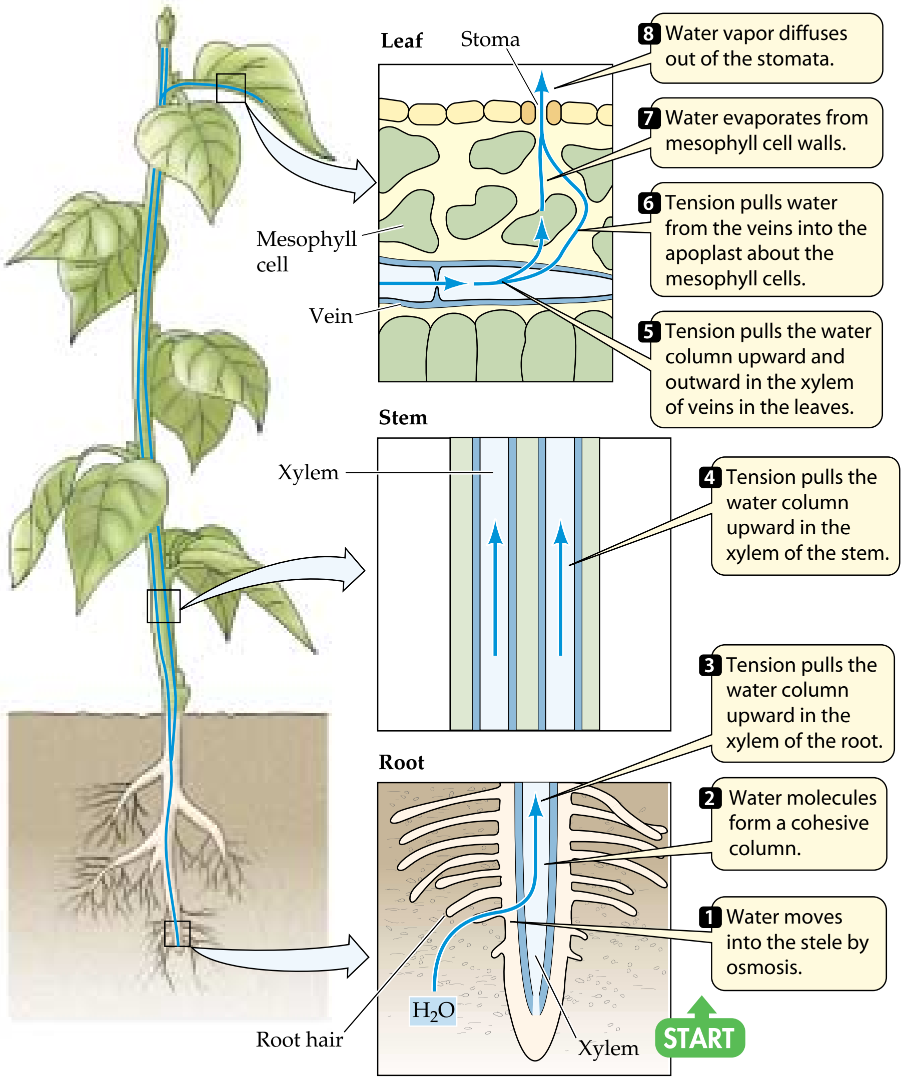
The obvious alternative to pushing is pulling: The leaves pull the xylem sap upward. **Transpiration**, the evaporative loss of water from the leaves, generates a pulling force (tension) on the water in the apoplast of the leaves. Hydrogen bonding between water molecules makes the sap in the xylem cohesive enough to withstand the tension and rise by bulk flow. Let's see how this **transpiration–cohesion–tension** mechanism works.

We'll start with transpiration. Water vapor diffuses from the intercellular spaces of the leaf, by way of the stomata, to the outside air because the water vapor concentration is greater inside the leaf than outside. Where did this water vapor come from?

As water vapor diffuses out of the leaf, more water evaporates from the moist walls of the mesophyll cells (Figure 35.7). Evaporation of water from the thin film surrounding the cell wall causes the film to shrink into the cellulose meshwork of the wall. The surface of the film curves where the water retreats into microscopic pores. The surface tension of the curved surfaces generates a **tension**—a negative pressure potential, a pull—in the film. The tension increases as more water leaves the film. This tension is what causes the bulk flow of water all the way from the roots.

The tension in the mesophyll draws water from the vessels or tracheids in the xylem of the nearest vein. The water, with its dissolved solutes, moves by bulk flow through the apoplast. The removal of water from the xylem of the veins establishes tension on the entire column of water contained within the xylem, so the column is drawn upward all the way from the roots.

The ability of water to be pulled upward through tiny tubes results from the remark-



35.7 Water Transport in Plants
Evaporation from surface cells, tension generated by the curvature of the shrinking surface film, and the cohesive nature of water molecules all account for the bulk flow of water from the soil to the atmosphere.

able cohesiveness of water—the tendency of water molecules to cohere to one another through hydrogen bonding. The narrower the tube, the greater the tension the water column can withstand without breaking. The integrity of the column is also maintained by the adhesion of water to the cell walls. In the tallest trees, such as a 100-meter redwood, the difference in pressure potential between the top and the bottom of the column may be as great as 3 MPa. The cohesiveness of water in the xylem is great enough to withstand even that great a tension.

In summary, the key elements of water transport in the xylem are:

- *Transpiration*, followed by evaporation from the moist cell walls in the leaves, resulting in…
- *tension* in the remainder of the xylem's water owing to the…
- *cohesion* of water, which pulls up more water to replace water that has been lost.

These elements require no work—no expenditure of energy—on the part of the plant. At each step between soil and atmosphere, water moves passively to a region with a more strongly negative water potential. Dry air has the most negative water potential (–95 MPa at 50% relative humidity), and the soil solution has the least negative water potential (between –0.01 and –3 MPa). Xylem sap has a water potential more negative than that of cells in the root, but less negative than that of mesophyll cells in the leaf.

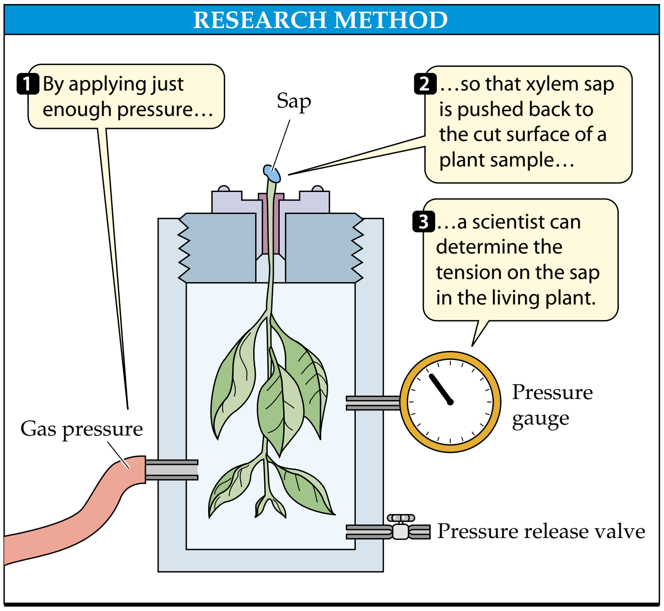
Mineral ions contained in the xylem sap rise passively with the solution as it ascends from root to leaf. In this way the nutritional needs of the shoot are met. Some of the mineral elements brought to the leaves are subsequently redistributed to other parts of the plant by way of the phloem, but the initial delivery from the roots is through the xylem.

In addition to promoting the transport of minerals, transpiration contributes to temperature regulation. As water evaporates from mesophyll cells, heat is taken up from the cells, and the leaf temperature drops. This cooling effect is important in enabling plants to live in hot environments. A farmer can hold a leaf between thumb and forefinger to estimate its temperature; if the leaf doesn't feel cool, that means that transpiration is not occurring, so it must be time to water.

A pressure bomb measures tension in the xylem sap

The transpiration–cohesion–tension model can be true only if the column of sap in the xylem is under tension (negative pressure potential). The most elegant demonstrations of this tension, and of its adequacy to account for the ascent of sap in tall trees, were performed by Per Scholander. He measured tension in stems with an instrument called a **pressure bomb**.

The principle of the pressure bomb is as follows: Consider a stem in which the xylem sap is under tension. If the stem is cut, the sap pulls away from the cut, into the stem. Now the stem is placed in a device called a pressure bomb, in which the pressure may be raised. The cut surface remains outside the bomb. As pressure is applied to the plant parts within the bomb, the xylem sap is forced back to the cut surface. When the sap first becomes visible again at the cut surface, the pressure in the bomb is recorded. This pressure is equal in magnitude but opposite in sign to the tension (negative pressure potential) originally present in the xylem (Figure 35.8).



35.8 A Pressure Bomb
The amount of tension on the sap in different types of plants can be measured with this laboratory device.

Scholander used the pressure bomb to study dozens of plant species, from diverse habitats, growing under a variety of conditions. In all cases in which xylem sap was ascending, it was found to be under tension. The tension disappeared in some of the plants at night, when transpiration ceased. In developing vines, the xylem sap was under no tension until leaves formed. Once leaves developed, transport in the xylem began, and tensions were recorded.

Suppose you wanted to measure tensions in the xylem at various heights in a large tree, to confirm that the tensions are sufficient to account for the rate at which sap is moving up the trunk. How would you obtain stem samples for measurement? Scholander used surveying instruments to determine the heights of particular twigs and then had a sharpshooter shoot the twigs from the tree with a high-powered rifle. As quickly as the twigs fell to the ground, Scholander inserted them in the pressure bomb and recorded their xylem tension. In every case, the differences in tensions at different heights were great enough to keep the xylem sap ascending.

Although transpiration provides the impetus for transport of water and minerals in the xylem, it also results in the loss of tremendous quantities of water from the plant. How do plants control this loss?

Transpiration and the Stomata

The epidermis of leaves and stems minimizes transpirational water loss by secreting a waxy cuticle, which is impermeable to water. However, the cuticle is also impermeable to carbon dioxide. This poses a problem: How can the leaf balance its need to retain water with its need to obtain carbon dioxide for photosynthesis?

Plants have evolved an elegant compromise in the form of **stomata** (singular stoma), or gaps, in the epidermis. A pair of specialized epidermal cells called **guard cells** controls the opening and closing of each stoma (Figure 35.9*a*). When the stomata are open, carbon dioxide can enter the leaf by diffusion, but water vapor is also lost in the same way. Closed stomata prevent water loss, but also exclude carbon dioxide from the leaf.

Most plants open their stomata only when the light intensity is sufficient to maintain a moderate rate of photosynthesis. At night, when darkness precludes photosynthesis, the stomata remain closed; no carbon dioxide is needed at this time, and water is conserved. Even during the day, the stomata close if water is being lost at too great a rate.

The stoma and guard cells in Figure 35.9*a* are typical of eudicots. Monocots typically have specialized epidermal cells associated with their guard cells. The principle of operation, however, is the same for both monocot and eudicot stomata. In what follows, we describe the regulation and mechanism of stomatal opening, the normal cycle of opening and closing, and the modified cycle used by some plants that live in dry or saline environments.

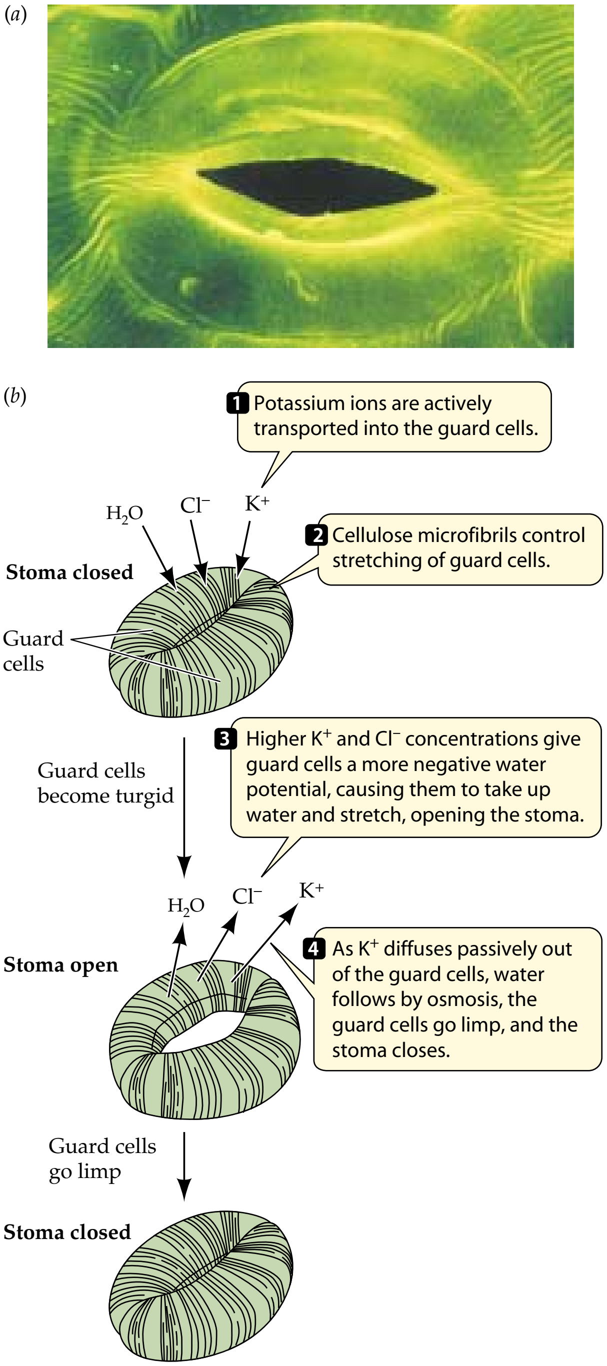
The guard cells control the size of the stomatal opening

Light causes the stomata of most plants to open, admitting carbon dioxide for photosynthesis. Another cue for stomatal opening is the level of carbon dioxide in the spaces inside the leaf. A low level favors opening of the stomata, thus allowing the uptake of more carbon dioxide.

Water stress is a common problem for plants, especially on hot, sunny, windy days. Plants have a protective response to these conditions, using the water potential of the mesophyll cells as a cue. Even when the carbon dioxide level is low and the sun is shining, if the mesophyll is too dehydrated—that is, if the water potential of the mesophyll is too negative—the mesophyll cells release a plant hormone called *abscisic acid*. Abscisic acid acts on the guard cells, causing them to close the stomata and prevent further drying of the leaf. This response reduces the rate of photosynthesis, but it protects the plant.

The increasing internal concentration of potassium ions makes the water potential of the guard cells more negative. Water enters the guard cells by osmosis, increasing their pressure potential. Their cell walls contain cellulose microfibrils that cause the cells to respond to this increase by changing their shapes so that a gap—the stoma—appears between them.

The stoma closes by the reverse process when the proton pump is no longer active. Potassium ions diffuse passively out of the guard cells, water follows by osmosis, the pressure potential decreases, and the guard cells sag together and seal off the stoma. Negatively charged chloride ions and organic ions also move out of the guard cells with the potassium ions, maintaining electrical balance and contributing to the change in the solute potential of the guard cells.



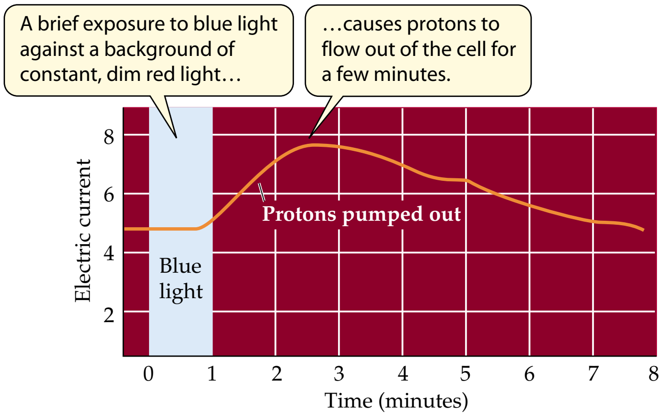
1 Potassium ions are actively transported into the guard cells.

2 Cellulose microfibrils control stretching of guard cells.

3 Higher K^+ and Cl^- concentrations give guard cells a more negative water potential, causing them to take up water and stretch, opening the stoma.

4 As K^+ diffuses passively out of the guard cells, water follows by osmosis, the guard cells go limp, and the stoma closes.

35.9 Stomata
(*a*) A scanning electron micrograph of a gaping stoma between two sausage-shaped guard cells. (*b*) Potassium ion (K^+) concentrations and water potential control the opening and closing of stomata. Negatively charged ions traveling with K^+ maintain electrical balance and contribute to the changes in osmotic potential that open and close the stomata.



A brief exposure to blue light against a background of constant, dim red light…

…causes protons to flow out of the cell for a few minutes.

35.10 Light-Induced Proton Pumping in a Guard Cell Membrane
This graph shows a trace of the tiny electric current that results from the flow of protons across the plasma membrane of a guard cell when it is exposed briefly to blue light.

What drives the opening and closing of the stomata? Certain wavelengths of blue light, absorbed by a pigment in the guard cell plasma membrane, activate a proton pump, which actively transports protons (H^+) out of the guard cells and into the surrounding epidermis (Figure 35.10). The resulting proton gradient drives the accumulation of potassium ions (K^+) (Figure 35.9*b*) in the guard cell.

Antitranspirants decrease water loss

Stomata are the referees of a compromise between the admission of CO_2 for photosynthesis and the loss of water by transpiration. Farmers would like their crops to transpire less, thus reducing the need for irrigation. Similarly, nurseries and gardeners would like to be able to reduce the amount of water lost by plants that are to be transplanted, because transplanting often damages the roots, causing the plant to wilt or die. What we need is a good **antitranspirant**: a compound that can be applied to plants, reducing water loss from the stomata without producing disastrous side effects by excessively limiting carbon dioxide uptake.

Abscisic acid and its commercial chemical analogs have been found to work as antitranspirants in small-scale tests, but their high cost has precluded commercial use. What about making plants more sensitive to their own abscisic acid? The guard cells of plants with a genetic mutation called *era* are highly sensitive to abscisic acid. These plants are resistant to wilting during drought stress.

A totally different type of antitranspirant seals off the leaves from the atmosphere for a time. Growers use a variety of compounds, most of which form polymeric films around leaves, to form a barrier to evaporation. These compounds cause undesirable side effects, however, and can be used only for relatively short periods of time. Their most common use is in the transplanting of nursery stock.

Crassulacean acid metabolism correlates with an inverted stomatal cycle

Most plants open and close their stomata on a schedule like that shown by the blue curve in Figure 35.11. The stomata are typically open for much of the day and closed at night. (They may also close during very hot days to reduce water loss.) But not all plants follow this pattern.

Many plants that live in dry areas or near the ocean have some unusual biochemical and behavioral features. One particularly surprising feature is their “backward” stomatal cycle: Their stomata are open at night and closed by day (as shown by the red curve in Figure 35.11). This behavior is part of the phenomenon of **crassulacean acid metabolism** (**CAM**), which was described in Chapter 8 (see Figure 8.21).

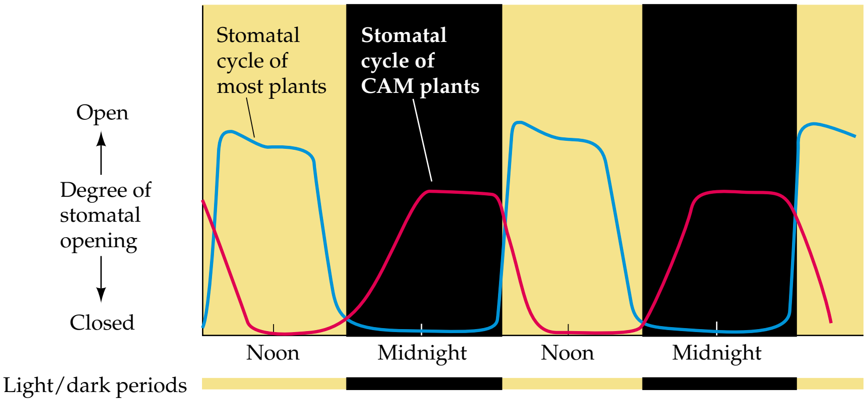
At night, while the stomata are open, carbon dioxide diffuses freely into the leaves of CAM plants and reacts in the mesophyll cells with phosphoenolpyruvic acid to produce organic acids. These acids accumulate to high concentrations. At daybreak the stomata close. Throughout the day, the organic acids are broken down to release the carbon dioxide they contain—behind closed stomata. Because the carbon dioxide cannot diffuse out of the plant, it is available for photosynthesis.

CAM is well adapted to environments where water is scarce: A leaf with its stomata open only at night—when the environment is cooler—loses much less water than does a leaf with its stomata open by day.

In both CAM and non-CAM plants, carbon dioxide is fixed and converted to the products of photosynthesis. How are these products delivered to other parts of the plant?

Translocation of Substances in the Phloem

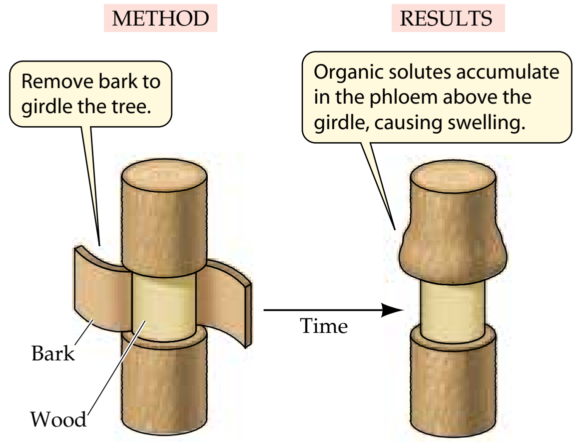
Substances in the phloem move from sources to sinks. A **source** is an organ (such as a mature leaf or a storage root) that produces (by photosynthesis or by digestion of stored



35.11 Stomatal Cycles
Most plants open their stomata during the day. CAM plants reverse this stomatal cycle: Their stomata open during the night.

EXPERIMENT

Question: Are organic solutes translocated in the xylem or in the phloem?



Conclusion: Organic solutes are translocated in the phloem, not in the xylem.

35.12 Girdling Blocks Translocation in the Phloem
By removing a ring of bark (containing the phloem), Malpighi blocked the translocation of organic solutes in a tree.

reserves) more sugars than it requires. A **sink** is an organ (such as a root, a flower, a developing tuber, or an immature leaf) that does not make enough sugar for its own growth and storage needs. Sugars (primarily sucrose), amino acids, some minerals, and a variety of other substances are translocated between sources and sinks in the phloem.

How do we know that such organic solutes are translocated in the phloem, rather than in the xylem? Just over 300 years ago, the Italian scientist Marcello Malpighi performed a classic experiment in which he removed a ring of bark (containing the phloem) from the trunk of a tree—that is, he *girdled* the tree (Figure 35.12). The bark in the region above the girdle swelled over time. We now know that the swelling resulted from the accumulation of organic solutes that came from higher up the tree and could no longer continue downward because of the disruption of the phloem. Later, the bark below the girdle died because it no longer received sugars from the leaves.

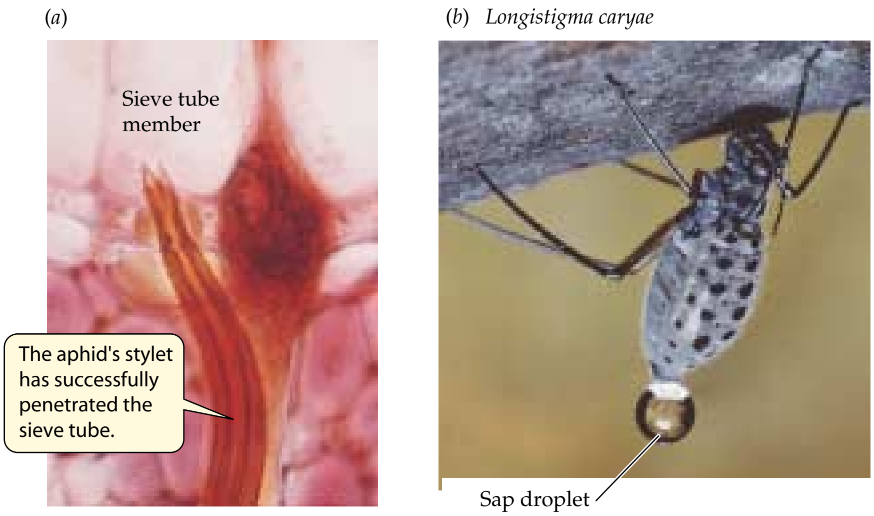
Any model to explain translocation of organic solutes must account for a few important facts:

- Translocation stops if the phloem tissue is killed by heating or other methods; thus the mechanism must be different from that of transport in the xylem.
- Translocation often proceeds in both directions—up and down the stem—simultaneously.
- Translocation is inhibited by compounds that inhibit respiration and thus limit the ATP supply in the source.

To investigate translocation, plant physiologists needed to obtain samples of pure sieve tube sap from individual sieve tube members. This difficult task was simplified when scientists discovered that a common garden pest, the aphid, feeds by drilling into a sieve tube. An aphid inserts its stylet, or feeding organ, into a stem until the stylet enters a sieve tube (Figure 35.13*a*). Within the sieve tube, the pressure is much greater than in the surrounding plant tissues, so nutritious sieve tube sap is forced up the stylet and into the aphid's digestive tract. So great is the pressure that sugary liquid is forced through the insect's body and out the anus (Figure 35.13*b*).

Plant physiologists use aphids to collect sieve tube sap. When liquid appears on the aphid's abdomen, indicating that the insect has connected with a sieve tube, the physiologist quickly freezes the aphid and cuts its body away from the stylet, which remains in the sieve tube member. For hours, sieve tube sap continues to exude from the cut stylet, where it may be collected for analysis. Chemical analysis of sieve tube sap collected in this manner reveals the contents of a single sieve tube member over time. We can also infer the rates at which different substances are translocated by measuring how long it takes for radioactive tracers administered to a leaf to appear at stylets at different distances from the leaf.

These methods have allowed us to understand how, at times, different substances might move in opposite directions in the phloem of a stem. Experiments with aphid stylets have shown that all the contents of any given sieve tube member move in the same direction. Thus, bidirectional translocation can be understood in terms of different sieve tubes conducting sap in opposite directions. Data obtained by these and other means led to the general adoption of the pressure flow model as an explanation for translocation in the phloem.



35.13 Aphids Collect Sieve Tube Sap
(*a*) Aphids feed on phloem sap drawn from the sieve tube, which they penetrate with a modified feeding organ, the stylet. (*b*) Pressure inside the sieve tube forces sap through the aphid's digestive tract, from which it can be harvested.

The pressure flow model appears to account for phloem translocation

The tonoplast breaks down during sieve tube member development, allowing the contents of the central vacuole to combine with much of the cytosol to form the sieve tube sap (see Chapter 34). The sap flows under pressure through the sieve tubes. It moves from one sieve tube member to the next by bulk flow through the sieve plates, without crossing a membrane.

Two steps in sieve tube sap flow require metabolic energy:

- Transport of sucrose and other solutes into the sieve tubes (**loading**) at sources
- Removal (**unloading**) of the solutes where the sieve tubes enter sinks

According to the **pressure flow model** of translocation in the phloem, sucrose is actively transported into sieve tube members at sources, giving these cells a much greater sucrose concentration than surrounding cells. Water therefore enters the sieve tube members by osmosis. The entry of this water causes a greater pressure potential at the source end, so the entire fluid content of the sieve tube is pushed toward the sink end of the tube—that is, the sap moves by bulk flow (Figure 35.14).

The pressure flow model of translocation in the phloem is contrasted with the transpiration–cohesion–tension model of xylem transport in Table 35.1.

Testing the pressure flow model

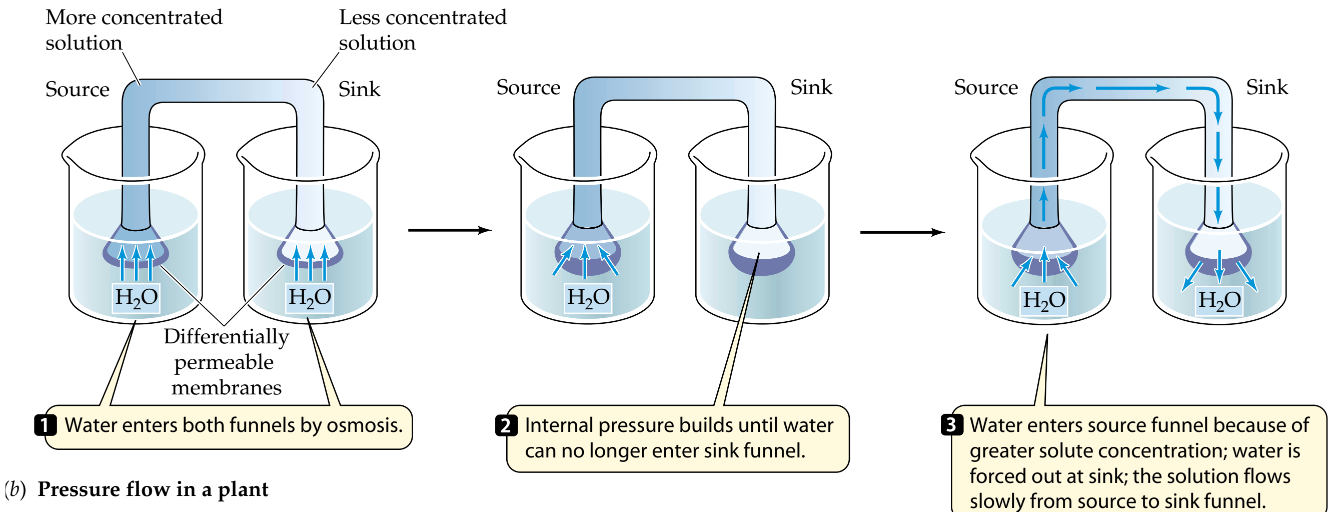
The pressure flow model was first proposed more than half a century ago, but some of its features are still debated. Other mechanisms have been proposed to account for translocation in sieve tubes. Some have been disproved, and none of the rest have been supported by a weight of evidence comparable to that for the pressure flow model, which must meet two requirements:

- The sieve plates must be open, so that bulk flow from one sieve tube member to the next is possible.
- There must be an effective method for loading sucrose and other solutes into the phloem in source tissues and removing them in sink tissues.

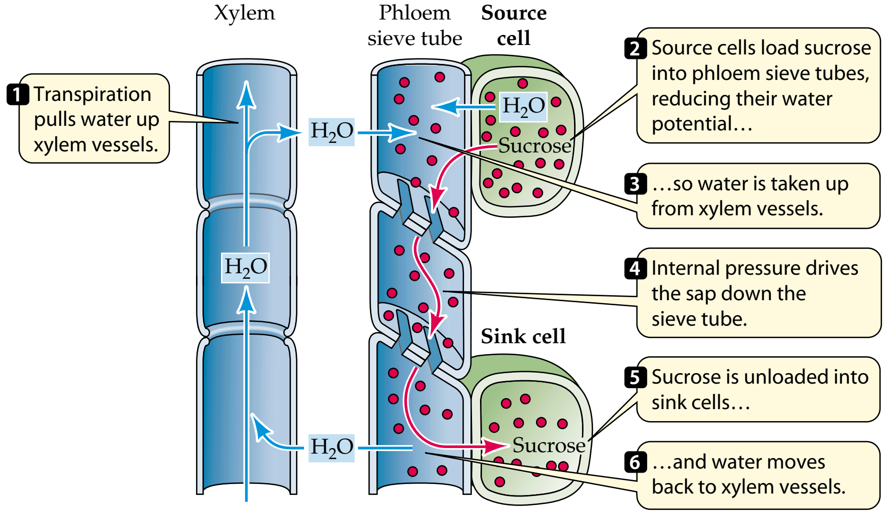
Let us see whether these requirements are met.

ARE THE SIEVE PLATES CLOGGED OR OPEN? Early electron microscopic studies of phloem samples cut from plants produced results that seemed to contradict the pressure flow

(*a*) **The pressure flow model**



(*b*) **Pressure flow in a plant**



35.14 The Pressure Flow Model (*a*) This demonstration of the pressure flow model shows how pressure potential and water potential combine to drive the bulk flow of sugars and other solutes from a source to a sink. (*b*) Sap may flow through sieve tubes in this manner.

35.1 Mechanisms of Bulk Flow in Plant Vascular Tissues

	XYLEM	PHLOEM
Source of bulk flow	Transpiration from leaves	Active transport of sucrose at source
Site of bulk flow	Dead vessel elements and tracheids	Living sieve tube members
Pressure potential in sap	Negative (pull from top)	Positive (push from source)

model. The pores in the sieve plates always appeared to be plugged with masses of a fibrous protein, suggesting that sieve tube sap could not flow freely. But what is the function of that fibrous protein?

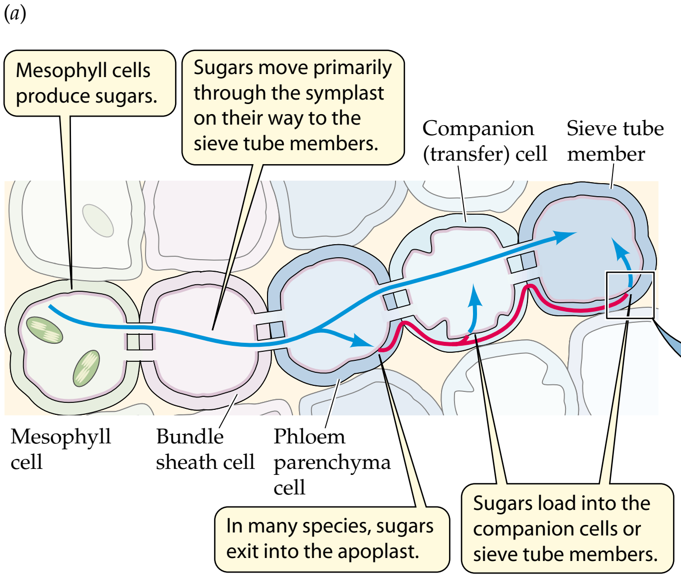
One possibility is that this protein is usually distributed more or less at random throughout the sieve tube members until the sieve tube is damaged; then the sudden surge of sap toward the cut surface carries the protein into the pores, blocking them and preventing the loss of valuable nutrients. In other words, perhaps the protein does *not* block the pores unless the phloem is damaged. How might this possibility be tested? Could we obtain phloem for microscopic observation without causing the sap to surge to the cut surface?

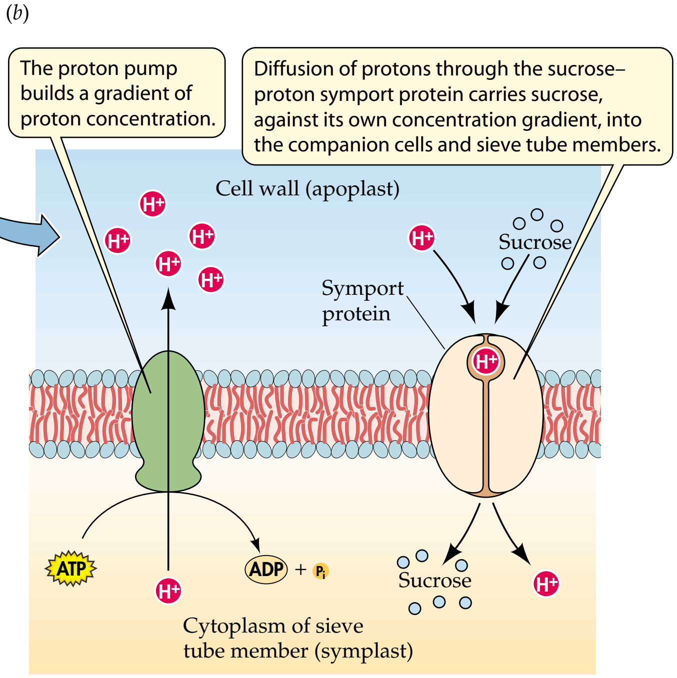
One way to prevent the surge of the sap is to freeze plant tissue before cutting it. Another way is to let the tissue wilt so that there is no pressure in the phloem before cutting. When these methods were used, the sieve plates were not clogged by the protein. Thus, the first condition of the pressure flow model is met.

NEIGHBORING CELLS LOAD AND UNLOAD THE SIEVE TUBE MEMBERS. If the pressure flow model is correct, there must be mechanisms for loading sugars and other solutes into the phloem in source regions and for unloading them in sink regions. One pathway of phloem loading has been demonstrated in some plant species.

Sugars and other solutes pass from cell to cell through the symplast in the mesophyll. When these substances reach cells adjacent to the ends of leaf veins, they leave the mesophyll cells and enter the apoplast, sometimes with the help of transfer cells. Then specific sugars and amino acids are actively transported into cells of the phloem, thus reentering the symplast (Figure 35.15).

Passage through the apoplast and back into the symplast selects substances to be accumulated for translocation because substances can enter the phloem only after passing through a differentially permeable membrane. In many plants, solutes reenter the symplast at the companion cells (see Chapter 34), which then transfer the solutes to the adjacent sieve tube members. As Figure 35.15 shows, in other plant species, sucrose or other sugars move from the mesophyll to the sieve tube members entirely within the symplast; that is, transfer of solutes from symplast to apoplast and back again is not a universal feature of phloem loading.





35.15 Pressure Flow in a Plant
(*a*) Sugars pass from cell to cell through the symplast in the mesophyll. After these substances reach cells adjacent to the ends of leaf veins, they may enter the apoplast, sometimes with the help of transfer cells. Specific compounds are actively transported into cells of the phloem, thus reentering the symplast. (*b*) Active transport of sugars into the phloem is carried out by sucrose–proton symport, which relies on a proton concentration gradient established by proton pumps.

A form of secondary active transport (see Chapter 5, pages 88–90) loads sucrose into the companion cells and sieve tube members. Sucrose is carried through the plasma membrane from apoplast to symplast by sucrose–proton symport; thus the entry of sucrose and of protons is strictly coupled. For this symport to work, the apoplast must have a high concentration of protons; the protons are supplied by a primary active transport system, the proton pump. The protons then diffuse back into the cell through the symport protein, bringing sucrose with them.

In sink regions, the solutes are actively transported out of the sieve tube members and into the surrounding tissues. This unloading serves two purposes: It helps maintain the gradient of solute potential and hence of pressure potential in the sieve tubes, and it promotes the buildup of sugars and starch to high concentrations in storage regions, such as developing fruits and seeds.

Plasmodesmata and material transfer between cells

Many substances move from cell to cell within the symplast by way of plasmodesmata (see Figure 34.7). Among their other roles, plasmodesmata participate in the loading and unloading of sieve tube members. Mechanisms vary among plant species, but the story in tobacco plants is a common one. In tobacco, sugars and other compounds in source tissues enter companion cells by active transport from the apoplast and move on to the sieve tube members through plasmodesmata. In sink tissues, plasmodesmata connect sieve tube members, companion cells, and the cells that will receive and use the transported compounds.

Plasmodesmata undergo developmental changes as an immature sink leaf matures into a mature source leaf. Plasmodesmata in sink tissues favor rapid unloading: They are more abundant, and they allow the passage of larger molecules. Plasmodesmata in source tissues are few in number.

It was long thought that only substances with molecular weights less than 1,000 could fit through a plasmodesma. Then biologists discovered that cells infected with tobacco mosaic virus (TMV) could allow molecules with molecular weights of as much as 20,000 to exit. We now know that TMV encodes a "movement protein" that produces this change in the permeability of the plasmodesmata—and that plants themselves normally produce at least one such movement protein. Even large molecules such as proteins and RNAs, with molecular weights up to at least 50,000, can thus move between living plant cells. We will see some consequences of this movement of macromolecules through plasmodesmata in later chapters. Biologists are exploring possible ways to regulate the permeability, number, and form of plasmodesmata as a means of modifying traffic in the plant. Such modifications might, for example, allow the diversion of more of a grain crop's photosynthetic products into the grain, increasing the crop yield.

Chapter Summary

Uptake and Transport of Water and Minerals

- Plant roots take up water and minerals from the soil.
- Water moves through biological membranes by osmosis, always moving toward cells with a more negative water potential. The water potential of a cell or solution is the sum of the solute potential and the pressure potential. All three parameters are expressed in megapascals (MPa). **Review Figure 35.1**
- Mineral uptake requires transport proteins. Some minerals enter the plant by facilitated diffusion; others enter by active transport. A proton pump facilitates the active transport of many solutes across membranes in plants. **Review Figure 35.2**
- Water and minerals pass from the soil to the xylem by way of the apoplast and symplast. In the root, water and minerals may pass from the cortex into the stele only by way of the symplast because Casparian strips in the endodermis block water and solute movement in the apoplast. **Review Figures 35.3, 35.4**

Transport of Water and Minerals in the Xylem

- Early experiments established that sap does not move via the pumping action of living cells.
- Root pressure is responsible for guttation and for the oozing of sap from cut stumps, but it cannot account for the ascent of sap in trees.
- Xylem transport is the result of the combined effects of transpiration, cohesion, and tension. Evaporation in the leaf produces tension in the surface film of water on the moist-walled mesophyll cells, and thus pulls water—held together by its cohesiveness—up through the xylem from the root. Dissolved minerals go along for the ride. **Review Figure 35.7**
- Support for the transpiration–cohesion–tension model of xylem transport came from studies using a pressure bomb. **Review Figure 35.8**

Transpiration and the Stomata

- Evaporation of water cools the leaves, but a plant cannot afford to lose too much water. Transpirational water loss is minimized by the waxy cuticle of the leaves.
- Stomata allow a compromise between water retention and carbon dioxide uptake. A pair of guard cells controls the size of the stomatal opening. A proton pump, activated by blue light, pumps protons from the guard cells to surrounding epidermal cells. As a result, the guard cells take up potassium ions, causing water to follow osmotically, swelling the cells and opening the stomata. Carbon dioxide level and water availability also affect stomatal opening. **Review Figures 35.9, 35.10**
- In most plants the stomata are open during the day and closed at night. CAM plants have an inverted stomatal cycle, enabling them to conserve water. **Review Figure 35.11**

Translocation of Substances in the Phloem

- Products of photosynthesis, and some minerals, are translocated through sieve tubes in the phloem by way of living sieve tube members. Translocation proceeds in both directions in the stem, although in a single sieve tube it goes only one way. Translocation requires a supply of ATP.

▶ Translocation in the phloem proceeds in accordance with the pressure flow model: The difference in solute concentration between sources and sinks allows a difference in pressure potential along the sieve tubes, resulting in bulk flow. **Review Figure 35.14, Table 35.1**

▶ The pressure flow model succeeds because the sieve plates are normally open, allowing bulk flow, and because neighboring cells load organic solutes into the sieve tube members in source regions and unload them in sink regions. **Review Figure 35.15**

▶ The distribution and properties of plasmodesmata differ between source and sink tissues. It may become possible to regulate plasmodesmata in crop plants.

For Discussion

1. Epidermal cells protect against excess water loss. How do they perform this function?
2. Phloem transports material from sources to sinks. What is meant by "source" and "sink"? Give examples of each.
3. What is the minimum number of plasma membranes a water molecule would have to cross in order to get from the soil solution to the atmosphere by way of the stele? To get from the soil solution to a mesophyll cell in a leaf.
4. Transpiration exerts a powerful pulling force on the water column in the xylem. When would you expect transpiration to proceed most rapidly? Why? Describe the source of the pulling force.
5. Plants that perform crassulacean acid metabolism (CAM plants) are adapted to environments in which water supply is limited; these plants open their stomata only at night. Could a non-CAM plant, such as a pea plant, enjoy an advantage if it opened its stomata only at night? Explain.