

36

Transport in Vascular Plants



A Figure 36.1 Coast redwoods (*Sequoia sempervirens*).

Key Concepts

- 36.1 Physical processes drive the transport of materials in plants over a range of distances
- 36.2 Roots absorb water and minerals from the soil
- 36.3 Water and minerals ascend from roots to shoots through the xylem
- 36.4 Stomata help regulate the rate of transpiration
- 36.5 Organic nutrients are translocated through the phloem

Overview

Pathways for Survival

The algal ancestors of plants absorbed water, minerals, and CO_2 directly from the water in which they were immersed; none of their cells were far from these ingredients. Bryophytes also lack an extensive transport system and are confined to living in very moist environments. For vascular plants, in contrast, the evolutionary journey onto land involved the differentiation of the plant body into roots and shoots. **Roots absorb water and minerals from the soil, and shoots absorb light and atmospheric CO_2 for photosynthesis.**

Xylem transports water and minerals from roots to shoots. Phloem transports sugars from where they are produced or stored to where they are needed for growth and metabolism. Such transport, which is necessary for a plant to function as a whole, may occur over long distances. For example, the highest leaves of some coast redwoods are more than 100 m (over 300 feet) from the roots (Figure 36.1). What enables a vascular plant to conduct water, minerals, and organic nutrients over such long distances? The mechanisms responsible for internal transport are the subject of this chapter.

Concept 36.1

Physical forces drive the transport of materials in plants over a range of distances

Transport in vascular plants occurs on three scales: (1) transport of water and solutes by individual cells, such as root hairs; (2) short-distance transport of substances from cell to cell at the levels of tissues and organs, such as the loading of sugar from photosynthetic leaf cells into the sieve tubes of the phloem; and (3) long-distance transport within xylem or phloem at the level of the whole plant. A variety of physical processes are involved in these different types of transport. **Figure 36.2 provides an overview of long-distance transport in a vascular plant.**

Selective Permeability of Membranes: A Review

We covered the transport of solutes and water across biological membranes in detail in Chapter 7. Here we reexamine a few of these transport processes in the specific context of plant cells. The selective permeability of a plant cell's plasma membrane controls the movement of solutes into and out of the cell. Recall from Chapter 7 that solutes tend to diffuse down their gradients and that diffusion across a membrane is called passive transport because it happens without the cell direct using metabolic energy. Active transport is the pumping of solutes across membranes against their electrochemical gradients, the combined effects of the concentration gradient of the solute and the voltage (charge difference) across the membrane. It is called "active" because the cell must expend e

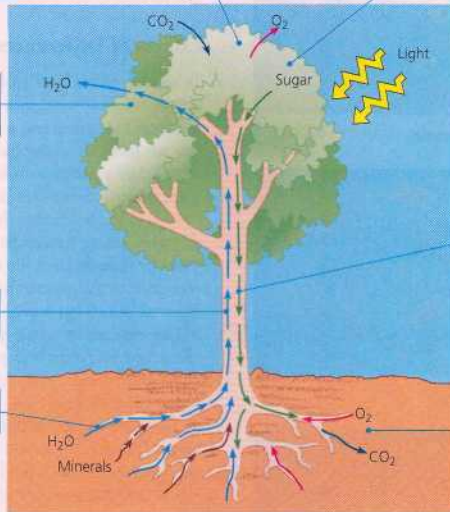
0 Through stomata, leaves take in CO_2 and expel O_2 . The CO_2 provides carbon for photosynthesis. Some O_2 produced by photosynthesis is used in cellular respiration.

0 Sugars are produced by photosynthesis in the leaves.

3 Transpiration, the loss of water from leaves (mostly through stomata), creates a force within leaves that pulls xylem sap upward.

0 Water and minerals are transported upward from roots to shoots as xylem sap.

0 Roots absorb water and dissolved minerals from the soil.



0 Sugars are transported as phloem sap to roots and other parts of the plant.

0 Roots exchange gases with the air spaces of soil, taking in O_2 and discharging CO_2 . In cellular respiration, O_2 supports the breakdown of sugars.

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

energy, usually in the form of ATP, to transport a solute "uphill"—counter to the net direction in which the solute diffuses.

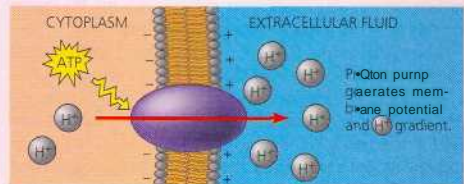
Most solutes cannot cross the lipid bilayer of the membrane; they must pass through **transport proteins** embedded in the membrane. Some transport proteins bind selectively to a solute on one side of the membrane and release the solute on the opposite side. Other transport proteins provide selective channels across the membrane. For example, membranes of most plant cells have potassium channels that allow potassium ions (K^+) to pass, but not other ions, such as sodium (Na^+). Later in this chapter, we will discuss how K^+ channels in guard cells function in the opening and closing of stomata. Some channels are gated, opening or closing in response to certain stimuli.

The Central Role of Proton Pumps

The most important active transport protein in the plasma membranes of plant cells is the **proton pump**, which uses energy from ATP to pump hydrogen ions (H^+) out of the cell. This results in a proton gradient with a higher H^+ concentration outside the cell than inside (**Figure 36.3**). The gradient is a form of potential (stored) energy because the hydrogen ions tend to diffuse "downhill" back into the cell, and this "flow" of H^+ can be harnessed to do work. And because the proton

pump moves positive charge, in the form of H^+ , out of the cell, the pump also contributes to a voltage known as a membrane potential, a separation of opposite charges across a membrane. Proton pumping makes the inside of a plant cell negative in charge relative to the outside. This voltage is called a membrane potential because the charge separation is a form of potential energy that can be harnessed to perform cellular work.

Plant cells use energy stored in the proton gradient and membrane potential to drive the transport of many different solutes. For example, the membrane potential generated by proton pumps contributes to the uptake of K^+ by root cells



▲ **Figure 36.3** Proton pumps provide energy for solute transport. By pumping H^+ out of the cell, proton pumps produce an H^+ gradient and a charge separation called a membrane potential. These two forms of potential energy can be used to drive the transport of solutes.

long-distance transport. Transpiration, the evaporation of water from a leaf, reduces pressure in the leaf xylem. This creates a tension that pulls xylem sap upward from the roots.

If you have ever dealt with a partially clogged drain, you know that the volume of flow through a pipe depends on the pipe's internal diameter. Clogs reduce flow because they reduce the effective diameter of the drainpipe. Such household experiences help us understand how the unusual structures of plant cells specialized for bulk flow—the sieve-tube members of the phloem and the tracheids and vessel elements of the xylem—fit their function. Recall from Chapter 35 that the cytoplasm of sieve-tube members is almost devoid of internal organelles and that mature tracheids and vessel elements, being dead cells, have no cytoplasm. Like unplugging a kitchen drain, loss of cytoplasm in a plant's "plumbing" allows for efficient bulk flow through the xylem and phloem. Bulk flow is also enhanced by the perforated end walls of vessel elements and the porous plates connecting sieve-tube members (see Figure 35.9).

Now that we have an overview of the basic mechanisms of transport at the cellular, tissue, and whole-plant levels, we will look more closely at how these mechanisms work together. For example, bulk flow due to a pressure difference is the mechanism of long-distance transport of phloem sap, but it is active transport of sugar at the cellular level that maintains this pressure difference. The four transport functions we will examine in more detail are the absorption of water and minerals by roots, the ascent of xylem sap, the control of transpiration, and the transport of organic nutrients within phloem.

Concept Check 36.1

1. Some farmers throughout the world irrigate crops using groundwater, which has a relatively high content of dissolved salts. How might this practice affect water potential in crops?
2. If a plant cell immersed in distilled water has a ψ of -0.7 MPa and a ψ_p of 0 MPa, what is the cell's ψ_s ? If you put the same cell in an open beaker of solution that has a ψ_r of -0.4 MPa, what would be the cell's ψ_p at equilibrium?

For suggested answers, see Appendix A.

Concept 36.2

Roots absorb water and minerals from the soil

Water and mineral salts from the soil enter the plant through the epidermis of roots, cross the root cortex, pass into the vascular cylinder, and then flow up tracheids and vessels to the

shoot system. This section focuses on short-distance transport between cells in the soil-to-xylem pathway. As you read, use Figure 36.9 to reinforce your understanding.

The Roles of Root Hairs, Mycorrhizae, and Cortical Cells

Much of the absorption of water and minerals occurs near root tips, where the epidermis is permeable to water and where root hairs are located. Root hairs, which are extensions of epidermal cells, account for much of the surface area of roots (see Figure 35.12). Soil particles, usually coated with water and dissolved minerals, adhere tightly to the root hairs. The soil solution flows into the hydrophilic walls of epidermal cells and passes freely along the apoplast into the root cortex. This exposes the symplast of all the cells of the cortex to the soil solution, providing a much greater surface area of membrane than the surface area of the epidermis alone.

As the soil solution moves along the apoplast into the roots, cells of the epidermis and cortex take up water and certain solutes into the symplast. Although the soil solution is usually very dilute, active transport enables roots to accumulate essential minerals, such as K^+ , to concentrations hundreds of times higher than in the soil.

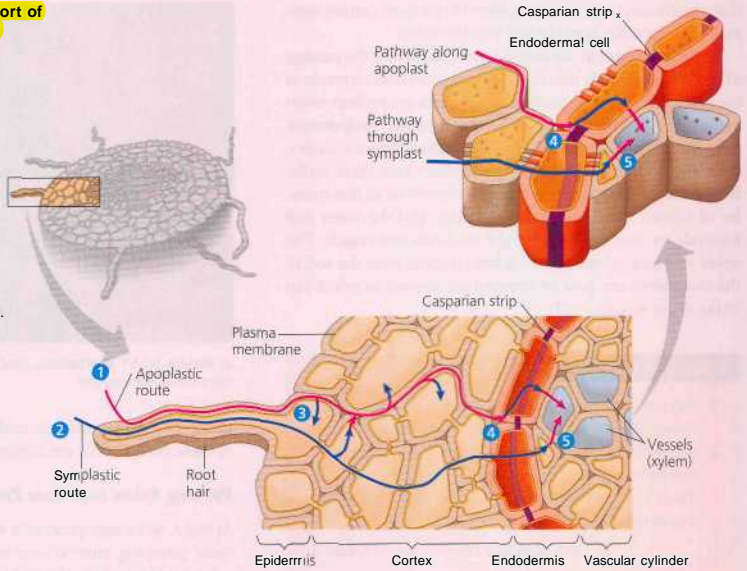
Most plants form mutually beneficial relationships with fungi, which facilitate the absorption of water and minerals from the soil. Roots and fungi form mycorrhizae, symbiotic structures consisting of plant roots united with fungal hyphae (filaments) (Figure 36.10). The hyphae absorb water and selected minerals, transferring much of these resources to the host plant. Chapter 37 highlights the role of mycorrhizae in plant nutrition, and Chapter 31 features the fungal partners in these mutualistic relationships. What is important to understand here is that the mycelium (network of hyphae) of the fungus endows mycorrhizae, and thus the plant roots, with an enormous surface area for absorption. As much as 3 m of hyphae can extend from each centimeter along a root's length, reaching a far greater volume of soil than the root alone could penetrate. Mycorrhizae enable even older regions of roots, kilometers from the root tips, to supply water and minerals to the plant.

The Endodermis: A Selective Sentry

Water and minerals that pass from the soil into the root cortex cannot be transported to the rest of the plant until they enter the xylem of the vascular cylinder. The endodermis, the innermost layer of cells in the root cortex, surrounds the vascular cylinder and functions as a last checkpoint for the selective passage of minerals from the cortex into the vascular tissue (see Figure 36.9). Minerals already in the symplast when they reach the endodermis continue through the plasmodesmata of endodermal cells and pass into the vascular cylinder. These minerals were already screened by the selective membranes they had to cross to enter the symplast in the epidermis c

Figure 36.9 Lateral transport of minerals and water in roots.

- Uptake of soil solution by the hydrophilic walls of root hairs provides access to the apoplast. Water and minerals can then soak into the cortex along this matrix of walls.
- Minerals and water that cross the plasma membranes of root hairs enter the symplast.
- As soil solution moves along the apoplast, some water and minerals are transported into the protoplasts of cells of the epidermis and cortex and then move inward via the symplast.
- Within the transverse and radial walls of each endodermal cell is the Casparian strip, a belt of waxy material (purple band) that blocks the passage of water and dissolved minerals. Only minerals already in the symplast or entering that pathway by crossing the plasma membrane of an endodermal cell can detour around the Casparian strip and pass into the vascular cylinder.



- Endodermal cells and also parenchyma cells within the vascular cylinder discharge water and minerals into their walls (apoplast). The xylem vessels transport the water and minerals upward into the shoot system.

cortex- Those minerals that reach the endodermis via the apoplast encounter a dead end that, blocks their passage into the vascular cylinder: In the transverse and radial walls of each endodermal cell is the Casparian strip, a belt made of suberin, a waxy material impervious to water and dissolved minerals. Thus, water and minerals cannot cross the endodermis and enter vascular tissue via the apoplast. The only way past this barrier is for the water and minerals to cross the plasma membrane of an endodermal cell and enter the vascular cylinder via the symplast.

The endodermis, with its Casparian strip, ensures that no minerals can reach the vascular tissue of the root without crossing a selectively permeable plasma membrane. If minerals do not enter the symplast of cells in the epidermis or cortex, they must enter endodermal cells or be excluded from the vascular tissue. The endodermis also prevents solutes that have been accumulated in the xylem sap from leaking back into the soil solution. The structure of the endodermis and its strategic location in the root fit its function as sentry of the border between the cortex and the vascular cylinder, a function



A Figure 36.10 Mycorrhizae, symbiotic associations of fungi and roots. The white mycelium of the fungus ensheathes these roots of a pine tree. The fungal hyphae provide an extensive surface area for the absorption of water and minerals.

that contributes to the ability of roots to transport certain minerals preferentially from the soil into the xylem.

The last segment in the soil-to-xylem pathway is the passage of water and minerals into the tracheids and vessel elements of the xylem. These water-conducting cells lack protoplasts when mature and are therefore part of the apoplast. Endodermal cells, as well as parenchyma cells within the vascular cylinder, discharge minerals from their protoplasts into their walls. Both diffusion and active transport are involved in this transfer of solutes from symplast to apoplast, and the water and minerals are now free to enter the tracheids and vessels. The water and mineral nutrients we have tracked from the soil to the root xylem can now be transported upward as xylem sap to the shoot system.

Concept Check 36.2

1. Why might a crop develop a severe phosphate deficiency after being sprayed with a fungicide?
2. A scientist adds a water-soluble inhibitor of photosynthesis to the roots of a plant. However, photosynthesis is not affected by addition of the inhibitor in this manner. Why?

For suggested answers, see Appendix A.

Concept 36.3

Water and minerals ascend from roots to shoots through the xylem

Here we will focus on the long-distance transport of xylem sap. The sap flows upward from roots throughout the shoot system to veins that branch throughout each leaf. Leaves depend on this efficient delivery system for their supply of water. Plants lose an astonishing amount of water by transpiration, the loss of water vapor from leaves and other aerial parts of the plant. Consider the example of maize (commonly called corn in the U.S.). A single plant transpires 125 L of water during a growing season. A maize crop growing at a typical density of 75,000 plants per hectare transpires almost 10 million L (10 million kg) of water per hectare every growing season (equivalent to about 1.25 million gallons of water per acre per growing season). Unless the transpired water is replaced by water transported up from the roots, the leaves will wilt and the plants will eventually die. The upward flow of xylem sap also brings mineral nutrients to the shoot system.

Factors Affecting the Ascent of Xylem Sap

Xylem sap rises to heights of more than 100 m in the tallest trees. Is the sap *pushed* upward from the roots, or is it *pulled*



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

upward by the leaves? Let's evaluate the relative contributions of these two possible mechanisms.

Pushing Xylem Sap: Root Pressure

At night, when transpiration is very low or zero, root cells continue pumping mineral ions into the xylem of the vascular cylinder. Meanwhile, the endodermis helps prevent the ions from leaking out. The resulting accumulation of minerals lowers the water potential within the vascular cylinder. Water flows in from the root cortex, generating root pressure, an upward push of xylem sap. The root pressure sometimes causes more water to enter the leaves than is transpired, resulting in guttation, the exudation of water droplets that can be seen in the morning on tips of grass blades or the leaf margins of some small, herbaceous eudicots (Figure 36.11). Guttation fluid differs from dew, which is condensed moisture produced during transpiration.

In most plants, root pressure is a minor mechanism driving the ascent of xylem sap, at most forcing water upward only a few meters. Many plants do not generate any root pressure. Even in plants that display guttation, root pressure cannot keep pace with transpiration after sunrise. For the most part, xylem sap is not pushed from below by root pressure but pulled upward by the leaves themselves.

Pulling Xylem Sap: The Transpiration-Cohesion-Tension Mechanism

To move material upward, we can apply positive pressure from below or negative pressure from above (as when sucking liquid through a straw). Here we will focus on the process by which water is pulled upward by negative pressure in the xylem. As we investigate this mechanism of transport, we will see that transpiration provides the pull, and the cohesion of water due to hydrogen bonding transmits the upward pull along the entire length of the xylem to the roots.

Stomata: Major Pathways for Water Loss

About 90% of the water a plant loses escapes through stomata, though these pores account for only 1-2% of the external leaf surface. The waxy cuticle limits water loss through the remaining surface of the leaf. Each stoma is flanked by a pair of guard cells, which are kidney-shaped in eudicots and dumb-bell-shaped in many monocots. Guard cells control the diameter of the stoma by changing shape, thereby widening or narrowing the gap between the two cells (Figure 36.15a). The amount of water lost by a leaf depends on the number of stomata and the average size of their apertures.

The stomatal density of a leaf, which may be as high as 20,000 per square centimeter, is under both genetic and environmental control. For example, as a result of evolution by natural selection, desert plants have lower stomatal densities than do marsh plants. Stomatal density, however, is also a developmentally plastic feature of many plants. High light intensities and low carbon dioxide levels during leaf development tend to increase stomatal density in many plant species. By measuring the stomatal density of leaf fossils, scientists have been able to gain insight into the levels of atmospheric CO_2 in past climates. A recent British survey found that the stomatal density of many woodland species has decreased since 1927, when a similar survey was made. This survey is consistent with the finding that atmospheric CO_2 levels increased dramatically during the 20th century as a result of the increased burning of fossil fuels.

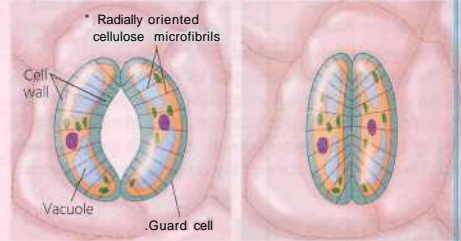
When guard cells take in water from neighboring cells by osmosis, they become more turgid and bowed. In most angiosperm species, the cell walls of guard cells are uneven in thickness, and the cellulose microfibrils are oriented in a direction that causes the guard cells to buckle outward when they are turgid, as you can see in Figure 36.15a. This buckling increases the size of the pore between the guard cells. When the cells lose water and become flaccid, they become less bowed and close the pore.

The changes in turgor pressure that open and close stomata result primarily from the reversible uptake and loss of potassium ions (K^+) by the guard cells. Stomata open when guard cells actively accumulate K^+ from neighboring epidermal cells (Figure 36.15b). This uptake of solute causes the water potential to become more negative within the guard cells, and the cells become more turgid as water enters by osmosis. Most of the K^+ and water are stored in the vacuole, and thus the vacuolar membrane also plays a role in regulating the water potential of guard cells. Stomatal closing results from an exit of K^+ from guard cells to neighboring cells, which leads to an osmotic loss of water. Regulation of aquaporins may also be involved in the swelling and shrinking of guard cells by varying the permeability of the membranes to water.

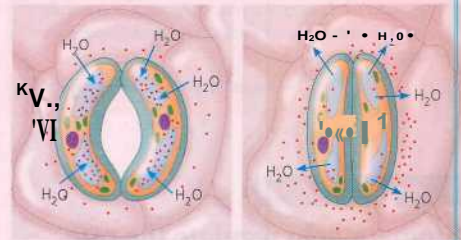
The K^+ fluxes across the guard cell membrane are coupled to the generation of membrane potentials by proton pumps.

Cells turgid/Stoma open

Cells flaccid/Stoma closed



(a) Changes in guard cell shape and stomatal opening and closing (surface view). Guard cells of a typical angiosperm are illustrated in their turgid (stoma open) and flaccid (stoma closed) states. The pair of guard cells buckle outward when turgid. Cellulose microfibrils in the walls resist stretching and compression in the direction parallel to the microfibrils. Thus, the radial orientation of the microfibrils causes the cells to increase in length more than width when turgor increases. The two guard cells are attached at their tips, so the increase in length causes buckling.



(b) Role of potassium in stomatal opening and closing. The transport of K^+ (potassium ions, symbolized here as red dots) across the plasma membrane and vacuolar membrane causes the turgor changes of guard cells.

A Figure 36.15 The mechanism of stomatal opening and closing.

Stomatal opening correlates with active transport of H^+ out of the guard cell. The resulting voltage (membrane potential) drives K^+ into the cell through specific membrane channels (see Figure 36.4a).

In general, stomata are open during the day and closed at night. This prevents the plant from losing water when it is too dark for photosynthesis. At least three cues contribute to stomatal opening at dawn. First, light itself stimulates guard cells to accumulate K^+ and become turgid. This response is triggered by the illumination of a blue-light receptor in the plasma membrane of guard cells. Activation of these blue-light receptors stimulates the activity of ATP-powered proton pumps in the plasma membrane of the guard cells, in turn promoting the uptake of K^+ .

A second stimulus causing stomata to open is depletion of CO_2 within air spaces of the leaf, which occurs when photosynthesis begins in the mesophyll. A plant will actually open its stomata at night if it is placed in a chamber devoid of CO_2 .

A third cue causing stomatal opening is an internal "clock" in the guard cells. Even if you keep a plant in a dark closet, stomata will continue their daily rhythm of opening and closing. All eukaryotic organisms have internal clocks that regulate cyclic processes. Cycles that have intervals of approximately 24 hours are called circadian rhythms. You will learn more about circadian rhythms and the biological clocks that control them in Chapter 39.

Environmental stresses can cause stomata to close during the daytime. When the plant suffers a water deficiency, guard cells may lose turgor and close stomata. In addition, a hormone called abscisic acid, which is produced in the roots in response to water deficiency, signals guard cells to close stomata. This response reduces further wilting but also restricts intake of CO_2 and thereby slows photosynthesis. This is one reason why droughts reduce crop yields.

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

Merophyte Adaptations That Reduce Transpiration

Plants adapted to arid climates, called xerophytes, have various leaf modifications that reduce the rate of transpiration. Many xerophytes have small, thick leaves, an adaptation that limits water loss by reducing surface area relative to leaf volume. A thick cuticle gives some of these leaves a leathery consistency. Some other xerophyte adaptations are highly reflective leaves and hairy leaves that trap a boundary layer of water. The stomata of xerophytes are concentrated on the lower (shady) leaf surface, and they are often located in depressions that shelter the pores from the dry wind (Figure 36.16). During the driest months, some desert plants shed their leaves. Others, such as cacti, subsist on water the plant stores in fleshy stems during the rainy season.

An elegant adaptation to arid habitats is found in succulents of the family Crassulaceae, in ice plants, and in many other plant families. These plants assimilate CO_2 by an alternative photosynthetic pathway known as CAM, for crassulacean acid metabolism (see Figure 10.20). Mesophyll cells in a CAM plant have enzymes that can incorporate CO_2 into organic acids during the night. During the daytime, the organic acids are broken down to release CO_2 in the same cells, and sugars are synthesized by the conventional (C_3) photosynthetic pathway. Because the leaf takes in CO_2 at night, the stomata can close during the day, when transpiration would be greatest.

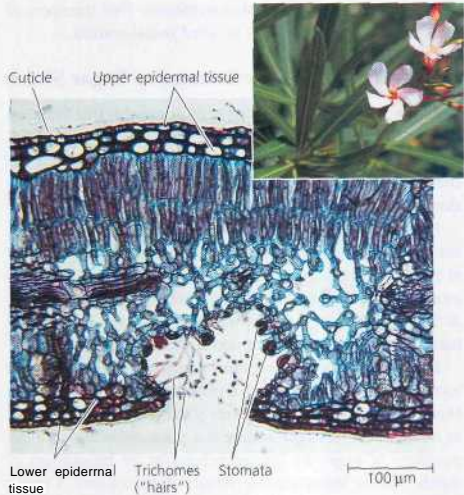


Figure 36.16 Structural adaptations of a xerophyte leaf. Oleander (*Nerium oleander*), shown in the inset, is commonly found in arid climates. The leaves have a thick cuticle and multiple-layered epidermal tissue that reduce water loss. Stomata are recessed in "crypts," an adaptation that reduces the rate of transpiration by protecting the stomata from hot, dry wind. The trichomes ("hairs") also help minimize transpiration by breaking up the flow of air, allowing the chamber of the crypt to have a higher humidity than the surrounding atmosphere (LM).

Concept Check 36.4

1. Some leaf molds, which are fungi that parasitize plants, secrete a chemical that causes guard cells to accumulate potassium ions. How does this adaptation enable the leaf mold to infect the plant?
2. Describe the environmental conditions that would minimize the transpiration-to-photosynthesis ratio for a C_3 plant, such as an oak tree.

For suggested answers, see Appendix A.

Concept 36.5

Organic nutrients are translocated through the phloem

Xylem sap flows from roots to leaves, in a direction opposite to that necessary to transport sugars from leaves to other parts of the plant. It is a second vascular tissue, the phloem, that

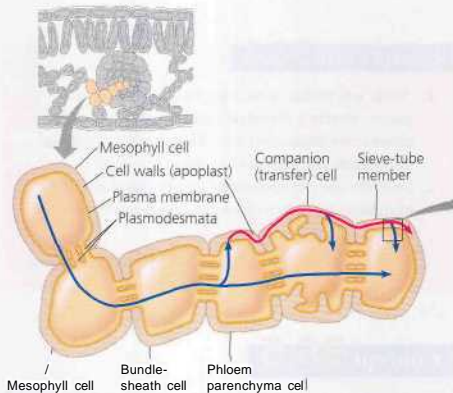
transports the products of photosynthesis. This transport of organic nutrients in the plant is called **translocation**.

Movement from Sugar Sources to Sugar Sinks

In angiosperms, the specialized cells of phloem that function as the conduits for translocation are the sieve-tube members, arranged end to end to form long sieve tubes. Between the cells are sieve plates, structures that allow the flow of sap along the sieve tube (see Figure 35.9).

Phloem sap is an aqueous solution that differs markedly in composition from xylem sap. By far the most prevalent solute in phloem sap is sugar, primarily the disaccharide sucrose in most species. The sucrose concentration may be as high as 30% by weight, giving the sap a syrupy thickness. Phloem sap may also contain minerals, amino acids, and hormones.

In contrast to the unidirectional transport of xylem sap from roots to leaves, the direction that phloem sap travels is variable. However, sieve tubes always carry sugars from a sugar source to a sugar sink. A **sugar source** is a plant organ that is a net producer of sugar, by photosynthesis or by breakdown of starch. Mature leaves are the primary sugar sources. A **sugar sink** is an organ that is a net consumer or storer of sugar. Growing roots, buds, stems, and fruits are sugar sinks. A storage organ, such as a tuber or a bulb, may be a source or a sink, depending on the season. When stockpiling carbohydrates in the summer, it is a sugar sink. After breaking dormancy in the spring, it is a source as its starch is broken down to sugar, which is carried to the growing tips of the plant.



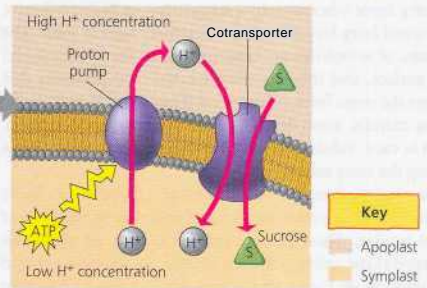
(a) Sucrose manufactured in mesophyll cells can travel via the symplast (blue arrows) to sieve-tube members. In some species, sucrose exits the symplast (red arrow) near sieve tubes and is actively accumulated from the apoplast by sieve-tube members and their companion cells.

A sugar sink usually receives sugar from the nearest source. Upper leaves on a branch may send sugar to the growing shoot tip, whereas lower leaves export sugar to roots. A growing fruit may monopolize sugar sources around it. For each sieve tube, the direction of transport depends on the locations of the source and sink connected by that tube. Therefore, neighboring tubes may carry sap in opposite directions. Direction of flow may also vary by season or developmental stage of the plant.

Sugar must be loaded into sieve-tube members before being exported to sinks. In some species, it moves from mesophyll cells to sieve-tube members via the symplast, passing through plasmodesmata. In other species, it moves by symplastic and apoplastic pathways (Figure 36.17a). In maize leaves, for example, sucrose diffuses through the symplast from chloroplast-containing mesophyll cells into small veins. Much of it then moves into the apoplast and is accumulated by nearby sieve-tube members, either directly or through companion cells, in some plants, companion cells have many ingrowths of their walls, enhancing transfer of solutes between apoplast and symplast. Such modified cells are called transfer cells (see Figure 29.5).

In maize and many other plants, phloem loading requires active transport because sucrose concentrations in sieve-tube members are two to three times higher than in mesophyll. Proton pumping and cotransport of sucrose and H^+ enable the cells to accumulate sucrose (Figure 36.17b).

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



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

A Figure 36.17 Loading of sucrose into phloem.