Chapter

4

Water Balance of Plants

LIFE IN EARTH'S ATMOSPHERE presents a formidable challenge to land plants. On the one hand, the atmosphere is the source of carbon dioxide, which is needed for photosynthesis. Plants therefore need ready access to the atmosphere. On the other hand, the atmosphere is relatively dry and can dehydrate the plant. To meet the contradictory demands of maximizing carbon dioxide uptake while limiting water loss, plants have evolved adaptations to control water loss from leaves, and to replace the water lost to the atmosphere.

In this chapter we will examine the mechanisms and driving forces operating on water transport within the plant and between the plant and its environment. Transpirational water loss from the leaf is driven by a gradient in water vapor concentration. Long-distance transport in the xylem is driven by pressure gradients, as is water movement in the soil. Water transport through cell layers such as the root cortex is complex, but it responds to water potential gradients across the tissue.

Throughout this journey water transport is passive in the sense that the free energy of water decreases as it moves. Despite its passive nature, water transport is finely regulated by the plant to minimize dehydration, largely by regulating transpiration to the atmosphere. We will begin our examination of water transport by focusing on water in the soil.

WATER IN THE SOIL

The water content and the rate of water movement in soils depend to a large extent on soil type and soil structure. Table 4.1 shows that the physical characteristics of different soils can vary greatly. At one extreme is sand, in which the soil particles may be 1 mm or more in diameter. Sandy soils have a relatively low surface area per gram of soil and have large spaces or channels between particles.

At the other extreme is clay, in which particles are smaller than 2 μm in diameter. Clay soils have much greater surface areas and smaller
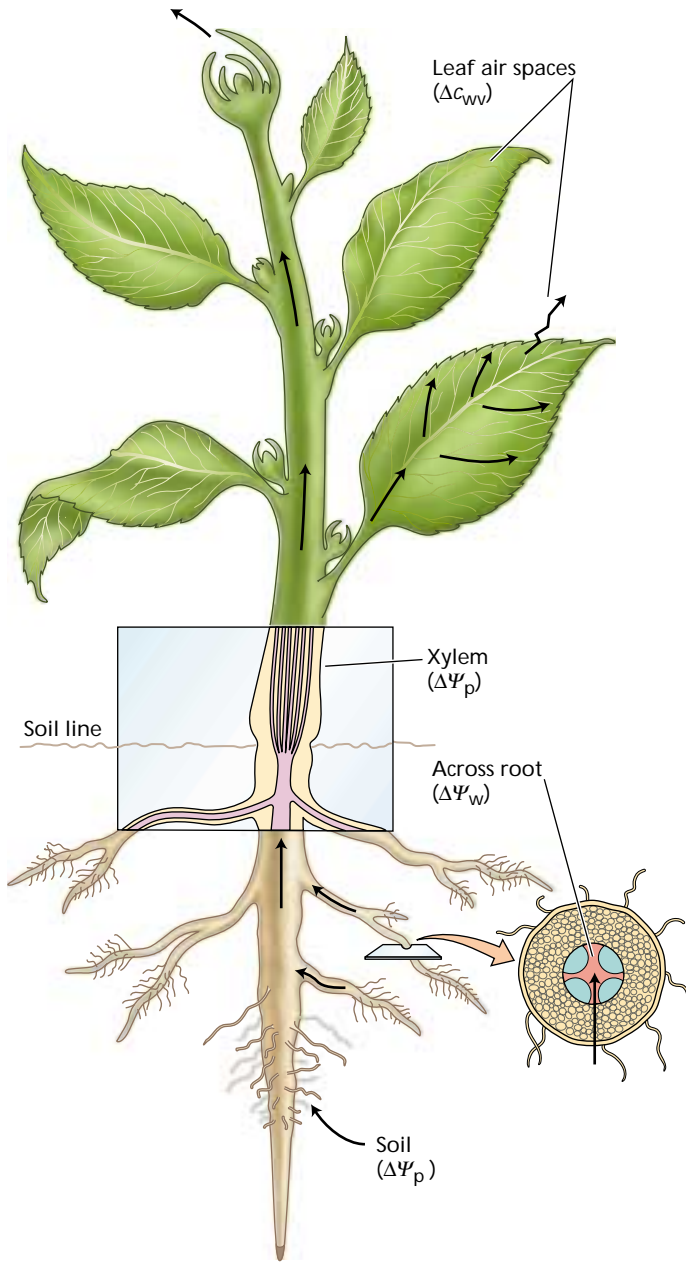
Leaf air spaces (Δc_{wv})

Xylem ($\Delta \Psi_p$)

Soil line

Across root ($\Delta \Psi_w$)

Soil ($\Delta \Psi_p$)

FIGURE 4.1   Main driving forces for water flow from the soil through the plant to the atmosphere: differences in water vapor concentration (Δc_{wv}), hydrostatic pressure ($\Delta \Psi_p$), and water potential ($\Delta \Psi_w$).

When a soil is heavily watered by rain or by irrigation, the water percolates downward by gravity through the spaces between soil particles, partly displacing, and in some cases trapping, air in these channels. Water in the soil may exist as a film adhering to the surface of soil particles, or it may fill the entire channel between particles.

In sandy soils, the spaces between particles are so large that water tends to drain from them and remain only on the particle surfaces and at interstices between particles. In clay soils, the channels are small enough that water does not freely drain from them; it is held more tightly (see Web Topic 4.1). The moisture-holding capacity of soils is called the **field capacity**. Field capacity is the water content of a soil after it has been saturated with water and excess water has been allowed to drain away. Clay soils or soils with a high humus content have a large field capacity. A few days after being saturated, they might retain 40% water by volume. In contrast, sandy soils typically retain 3% water by volume after saturation.

In the following sections we will examine how the negative pressure in soil water alters soil water potential, how water moves in the soil, and how roots absorb the water needed by the plant.

A Negative Hydrostatic Pressure in Soil Water Lowers Soil Water Potential

Like the water potential of plant cells, the water potential of soils may be dissected into two components, the osmotic potential and the hydrostatic pressure. The osmotic potential (Ψ_s; see Chapter 3) of soil water is generally negligible because solute concentrations are low; a typical value might be –0.02 MPa. For soils that contain a substantial concentration of salts, however, Ψ_s is significant, perhaps –0.2 MPa or lower.

The second component of soil water potential is hydrostatic pressure (Ψ_p) (Figure 4.1). For wet soils, Ψ_p is very close to zero. As a soil dries out, Ψ_p decreases and can become quite negative. Where does the negative pressure in soil water come from?

Recall from our discussion of capillarity in Chapter 3 that water has a high surface tension that tends to minimize air–water interfaces. As a soil dries out, water is first removed from the center of the largest spaces between particles. Because of adhesive forces, water tends to cling to the surfaces of soil particles, so a large surface area between soil water and soil air develops (Figure 4.2).

As the water content of the soil decreases, the water recedes into the interstices between soil particles, and the air–water surface develops curved air–water interfaces.

channels between particles. With the aid of organic substances such as humus (decomposing organic matter), clay particles may aggregate into "crumbs" that help improve soil aeration and infiltration of water.

TABLE 4.1
Physical characteristics of different soils

Soil	Particle diameter (µm)	Surface area per gram (m²)
Coarse sand	2000–200	
Fine sand	200–20	<1–10
Silt	20–2	10–100
Clay	<2	100–1000

Root   Root   Water   Sand   Clay   Air
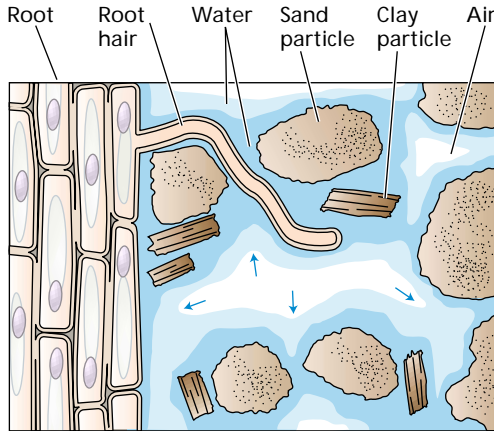   hair   particle   particle

FIGURE 4.2   Root hairs make intimate contact with soil particles and greatly amplify the surface area that can be used for water absorption by the plant. The soil is a mixture of particles (sand, clay, silt, and organic material), water, dissolved solutes, and air. Water is adsorbed to the surface of the soil particles. As water is absorbed by the plant, the soil solution recedes into smaller pockets, channels, and crevices between the soil particles. At the air–water interfaces, this recession causes the surface of the soil solution to develop concave menisci (curved interfaces between air and water marked in the figure by arrows), and brings the solution into tension (negative pressure) by surface tension. As more water is removed from the soil, more acute menisci are formed, resulting in greater tensions (more negative pressures).

Water under these curved surfaces develops a negative pressure that may be estimated by the following formula:

$$\Psi_\pi = \frac{-2T}{r} \qquad (4.1)$$

where T is the surface tension of water (7.28×10^{-8} MPa m) and r is the radius of curvature of the air–water interface.

The value of Ψ_p in soil water can become quite negative because the radius of curvature of air–water surfaces may become very small in drying soils. For instance, a curvature $r = 1$ μm (about the size of the largest clay particles) corresponds to a Ψ_p value of –0.15 MPa. The value of Ψ_p may easily reach –1 to –2 MPa as the air–water interface recedes into the smaller cracks between clay particles.

Soil scientists often describe soil water potential in terms of a matric potential (Jensen et al. 1998). For a discussion of the relation between matric potential and water potential see Web Topic 3.3.

Water Moves through the Soil by Bulk Flow

Water moves through soils predominantly by bulk flow driven by a pressure gradient. In addition, diffusion of water vapor accounts for some water movement. As plants absorb water from the soil, they deplete the soil of water near the surface of the roots. This depletion reduces Ψ_p in the water near the root surface and establishes a pressure gradient with respect to neighboring regions of soil that have higher Ψ_p values. *Because the water-filled pore spaces in the soil are interconnected, water moves to the root surface by bulk flow through these channels down the pressure gradient.*

The rate of water flow in soils depends on two factors: the size of the pressure gradient through the soil, and the hydraulic conductivity of the soil. **Soil hydraulic conductivity** is a measure of the ease with which water moves through the soil, and it varies with the type of soil and water content. Sandy soils, with their large spaces between particles, have a large hydraulic conductivity, whereas clay soils, with the minute spaces between their particles, have an appreciably smaller hydraulic conductivity.

As the water content (and hence the water potential) of a soil decreases, the hydraulic conductivity decreases drastically (see Web Topic 4.2). This decrease in soil hydraulic conductivity is due primarily to the replacement of water in the soil spaces by air. When air moves into a soil channel previously filled with water, water movement through that channel is restricted to the periphery of the channel. As more of the soil spaces become filled with air, water can flow through fewer and narrower channels, and the hydraulic conductivity falls.

In very dry soils, the water potential (Ψ_w) may fall below what is called the **permanent wilting point**. At this point the water potential of the soil is so low that plants cannot regain turgor pressure even if all water loss through transpiration ceases. This means that the water potential of the soil (Ψ_w) is less than or equal to the osmotic potential (Ψ_s) of the plant. Because cell Ψ_s varies with plant species, the permanent wilting point is clearly not a unique property of the soil; it depends on the plant species as well.

WATER ABSORPTION BY ROOTS

Intimate contact between the surface of the root and the soil is essential for effective water absorption by the root. This contact provides the surface area needed for water uptake and is maximized by the growth of the root and of root hairs into the soil. **Root hairs** are microscopic extensions of root epidermal cells that greatly increase the surface area of the root, thus providing greater capacity for absorption of ions and water from the soil. When 4-month-old rye (*Secale*) plants were examined, their root hairs were found to constitute more than 60% of the surface area of the roots (see Figure 5.6).

Water enters the root most readily in the apical part of the root that includes the root hair zone. More mature regions of the root often have an outer layer of protective tissue, called an *exodermis* or *hypodermis*, that contains hydrophobic materials in its walls and is relatively impermeable to water.

The intimate contact between the soil and the root surface is easily ruptured when the soil is disturbed. It is for this reason that newly transplanted seedlings and plants
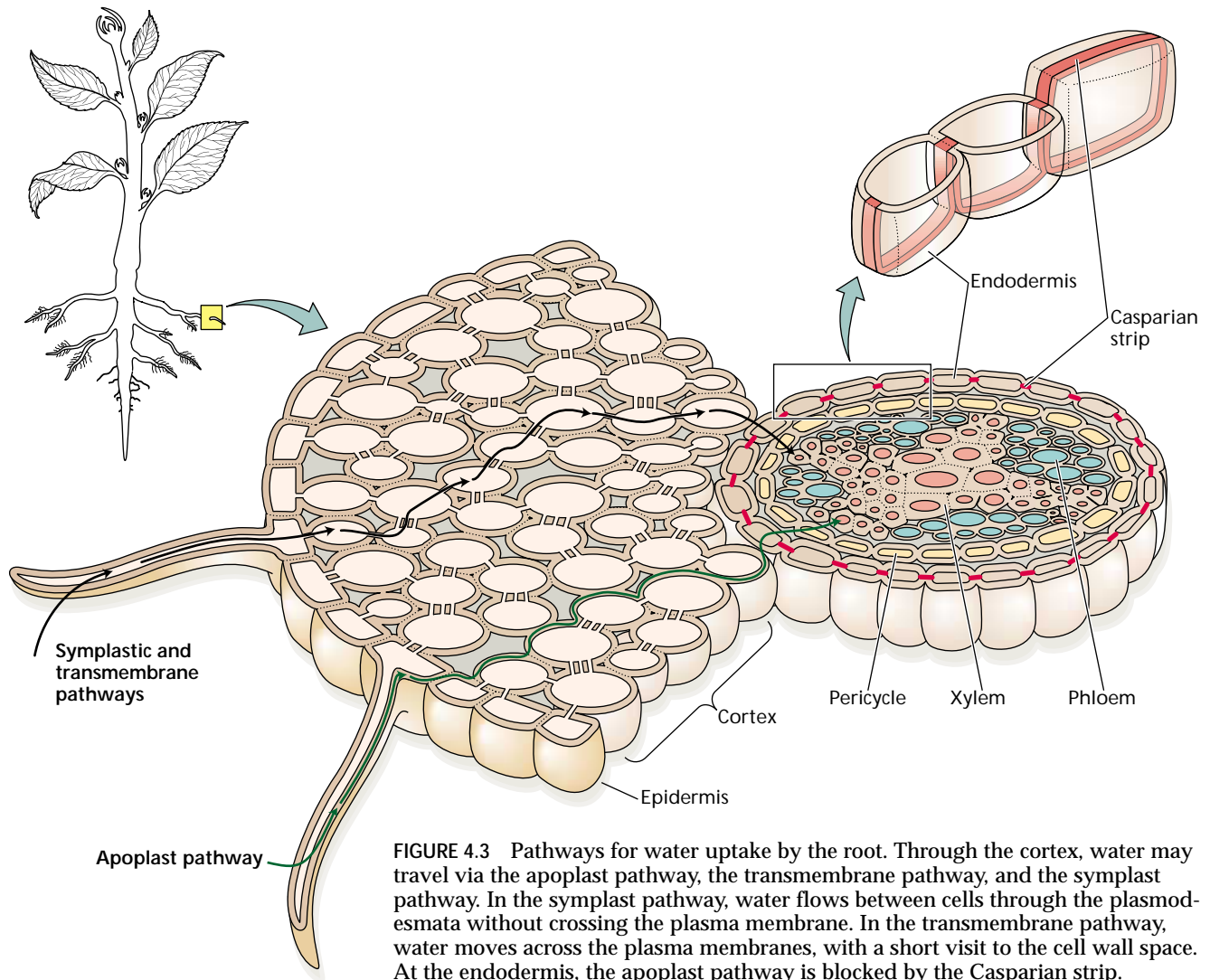
FIGURE 4.3   Pathways for water uptake by the root. Through the cortex, water may travel via the apoplast pathway, the transmembrane pathway, and the symplast pathway. In the symplast pathway, water flows between cells through the plasmodesmata without crossing the plasma membrane. In the transmembrane pathway, water moves across the plasma membranes, with a short visit to the cell wall space. At the endodermis, the apoplast pathway is blocked by the Casparian strip.

need to be protected from water loss for the first few days after transplantation. Thereafter, new root growth into the soil reestablishes soil–root contact, and the plant can better withstand water stress.

Let's consider how water moves within the root, and the factors that determine the rate of water uptake into the root.

Water Moves in the Root via the Apoplast, Transmembrane, and Symplast Pathways

In the soil, water is transported predominantly by bulk flow. However, when water comes in contact with the root surface, the nature of water transport becomes more complex. From the epidermis to the endodermis of the root, there are three pathways through which water can flow (Figure 4.3): the apoplast, transmembrane, and symplast pathways.

1. In the apoplast pathway, water moves exclusively through the cell wall without crossing any membranes. The apoplast is the continuous system of cell walls and intercellular air spaces in plant tissues.

2. The transmembrane pathway is the route followed by water that sequentially enters a cell on one side, exits the cell on the other side, enters the next in the series, and so on. In this pathway, water crosses at least two membranes for each cell in its path (the plasma membrane on entering and on exiting). Transport across the tonoplast may also be involved.

3. In the symplast pathway, water travels from one cell to the next via the plasmodesmata (see Chapter 1). The symplast consists of the entire network of cell cytoplasm interconnected by plasmodesmata.

Although the relative importance of the apoplast, transmembrane, and symplast pathways has not yet been clearly established, experiments with the pressure probe technique (see Web Topic 3.6) indicate that the apoplast pathway is particularly important for water uptake by young corn roots (Frensch et al. 1996; Steudle and Frensch 1996).

At the endodermis, water movement through the apoplast pathway is obstructed by the Casparian strip (see Figure 4.3). The **Casparian strip** is a band of radial cell

walls in the endodermis that is impregnated with the wax-like, hydrophobic substance **suberin**. Suberin acts as a barrier to water and solute movement. The endodermis becomes suberized in the nongrowing part of the root, several millimeters behind the root tip, at about the same time that the first protoxylem elements mature (Esau 1953). The Casparian strip breaks the continuity of the apoplast pathway, and forces water and solutes to cross the endodermis by passing through the plasma membrane. Thus, despite the importance of the apoplast pathway in the root cortex and the stele, water movement across the endodermis occurs through the symplast.

Another way to understand water movement through the root is to consider the root as a single pathway having a single hydraulic conductance. Such an approach has led to the development of the concept of **root hydraulic conductance** (see Web Topic 4.3 for details).

The apical region of the root is most permeable to water. Beyond this point, the exodermis becomes suberized, limiting water uptake (Figure 4.4). However, some water absorption may take place through older roots, perhaps through breaks in the cortex associated with the outgrowth of secondary roots.

Water uptake decreases when roots are subjected to low temperature or anaerobic conditions, or treated with respiratory inhibitors (such as cyanide). These treatments inhibit root respiration, and the roots transport less water. The exact explanation for this effect is not yet clear. On the other hand, the decrease in water transport in the roots provides an explanation for the wilting of plants in waterlogged soils: Submerged roots soon run out of oxygen, which is normally provided by diffusion through the air spaces in the soil (diffusion through gas is 10^4 times faster than diffusion through water). The anaerobic roots transport less water to the shoots, which consequently suffer net water loss and begin to wilt.
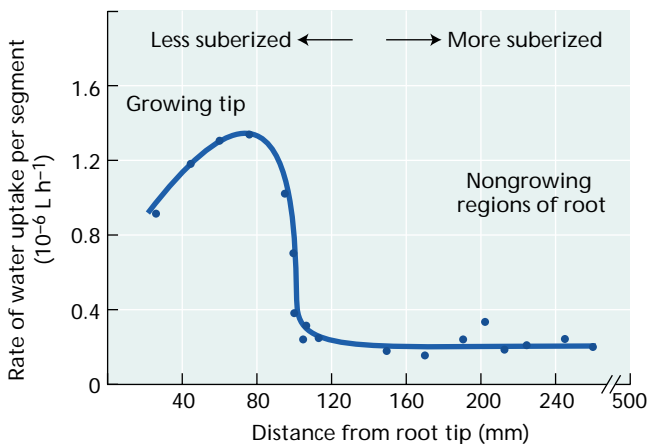
Solute Accumulation in the Xylem Can Generate "Root Pressure"

Plants sometimes exhibit a phenomenon referred to as **root pressure**. For example, if the stem of a young seedling is cut off just above the soil, the stump will often exude sap from the cut xylem for many hours. If a manometer is sealed over the stump, positive pressures can be measured. These pressures can be as high as 0.05 to 0.5 MPa.

Roots generate positive hydrostatic pressure by absorbing ions from the dilute soil solution and transporting them into the xylem. The buildup of solutes in the xylem sap leads to a decrease in the xylem osmotic potential (Ψ_s) and thus a decrease in the xylem water potential (Ψ_w). This lowering of the xylem Ψ_w provides a driving force for water absorption, which in turn leads to a positive hydrostatic pressure in the xylem. In effect, the whole root acts like an osmotic cell; the multicellular root tissue behaves as an osmotic membrane does, building up a positive hydrostatic pressure in the xylem in response to the accumulation of solutes.

Root pressure is most likely to occur when soil water potentials are high and transpiration rates are low. When transpiration rates are high, water is taken up so rapidly into the leaves and lost to the atmosphere that a positive pressure never develops in the xylem.

Plants that develop root pressure frequently produce liquid droplets on the edges of their leaves, a phenomenon known as **guttation** (Figure 4.5). Positive xylem pressure

FIGURE 4.5   Guttation in leaves from strawberry (*Fragaria grandiflora*). In the early morning, leaves secrete water droplets through the hydathodes, located at the margins of the leaves. Young flowers may also show guttation. (Photograph courtesy of R. Aloni.)

FIGURE 4.4   Rate of water uptake at various positions along a pumpkin root. (After Kramer and Boyer 1995.)

causes exudation of xylem sap through specialized pores called *hydathodes* that are associated with vein endings at the leaf margin. The "dewdrops" that can be seen on the tips of grass leaves in the morning are actually guttation droplets exuded from such specialized pores. Guttation is most noticeable when transpiration is suppressed and the relative humidity is high, such as during the night.
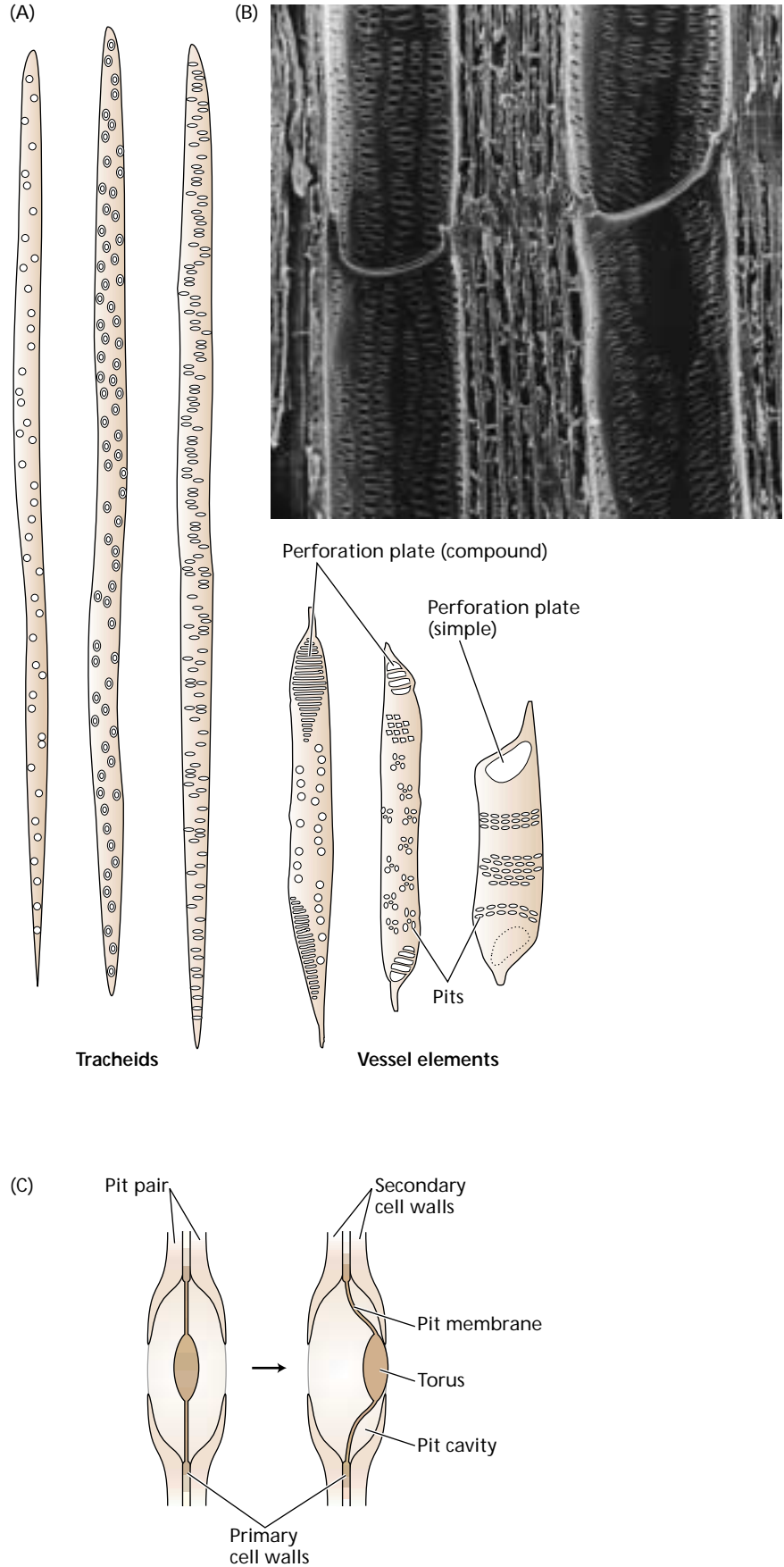
WATER TRANSPORT THROUGH THE XYLEM

In most plants, the xylem constitutes the longest part of the pathway of water transport. In a plant 1 m tall, more than 99.5% of the water transport pathway through the plant is within the xylem, and in tall trees the xylem represents an even greater fraction of the pathway. Compared with the complex pathway across the root tissue, the xylem is a simple pathway of low resistance. In the following sections we will examine how water movement through the xylem is optimally suited to carry water from the roots to the leaves, and how negative hydrostatic pressure generated by leaf transpiration pulls water through the xylem.

The Xylem Consists of Two Types of Tracheary Elements

The conducting cells in the xylem have a specialized anatomy that enables them to transport large quantities of water with great efficiency. There are two important types of **tracheary elements** in the xylem: tracheids and vessel elements (Figure 4.6). Vessel elements are found only in angiosperms, a small group of gymnosperms called the Gnetales, and perhaps some ferns. Tracheids are present in both angiosperms and gymnosperms, as well as in ferns and other groups of vascular plants.

The maturation of both tracheids and vessel elements involves the "death" of the cell. Thus, functional water-conducting cells have no membranes and no organelles. What re-

Tracheids

Vessel elements

Perforation plate (compound)

Perforation plate (simple)

Pits

Pit pair

Secondary cell walls

Pit membrane

Torus

Pit cavity

Primary cell walls

FIGURE 4.6   Tracheary elements and their interconnections. (A) Structural comparison of tracheids and vessel elements, two classes of tracheary elements involved in xylem water transport. Tracheids are elongate, hollow, dead cells with highly lignified walls. The walls contain numerous pits—regions where secondary wall is absent but primary wall remains. The shape and pattern of wall pitting vary with species and organ type. Tracheids are present in all vascular plants. Vessels consist of a stack of two or more vessel elements. Like tracheids, vessel elements are dead cells and are connected to one another through perforation plates—regions of the wall where pores or holes have developed. Vessels are connected to other vessels and to tracheids through pits. Vessels are found in most angiosperms and are lacking in most gymnosperms. (B) Scanning electron micrograph of oak wood showing two vessel elements that make up a portion of a vessel. Large pits are visible on the side walls, and the end walls are open at the perforation plate. (420×) (C) Diagram of a bordered pit with a torus either centered in the pit cavity or lodged to one side of the cavity, thereby blocking flow. (B © G. Shih-R. Kessel/Visuals Unlimited; C after Zimmermann 1983.)

mains are the thick, lignified cell walls, which form hollow tubes through which water can flow with relatively little resistance.

Tracheids are elongated, spindle-shaped cells (Figure 4.6A) that are arranged in overlapping vertical files. Water flows between tracheids by means of the numerous **pits** in their lateral walls (Figure 4.6B). Pits are microscopic regions where the secondary wall is absent and the primary wall is thin and porous (Figure 4.6C). Pits of one tracheid are typically located opposite pits of an adjoining tracheid, forming **pit pairs**. Pit pairs constitute a low-resistance path for water movement between tracheids. The porous layer between pit pairs, consisting of two primary walls and a middle lamella, is called the **pit membrane**.

Pit membranes in tracheids of some species of conifers have a central thickening, called a **torus** (pl. *tori*) (see Figure 4.6C). The torus acts like a valve to close the pit by lodging itself in the circular or oval wall thickenings bordering these pits. Such lodging of the torus is an effective way of preventing dangerous gas bubbles from invading neighboring tracheids (we will discuss this formation of bubbles, a process called cavitation, shortly).

Vessel elements tend to be shorter and wider than tracheids and have perforated end walls that form a **perforation plate** at each end of the cell. Like tracheids, vessel elements have pits on their lateral walls (see Figure 4.6B). Unlike tracheids, the perforated end walls allow vessel members to be stacked end to end to form a larger conduit called a **vessel** (again, see Figure 4.6B). Vessels vary in length both within and between species. Maximum vessel lengths range from 10 cm to many meters. Because of their open end walls, vessels provide a very efficient low-resistance pathway for water movement. The vessel members found at the extreme ends of a vessel lack perforations at the end walls and communicate with neighboring vessels via pit pairs.

Water Movement through the Xylem Requires Less Pressure Than Movement through Living Cells

The xylem provides a low-resistance pathway for water movement, thus reducing the pressure gradients needed to transport water from the soil to the leaves. Some numerical values will help us appreciate the extraordinary efficiency of the xylem. We will calculate the driving force required to move water through the xylem at a typical velocity and compare it with the driving force that would be needed to move water through a cell-to-cell pathway. For the purposes of this comparison, we will use a figure of 4 mm s^{-1} for the xylem transport velocity and 40 μm as the vessel radius. This is a high velocity for such a narrow vessel, so it will tend to exaggerate the pressure gradient required to support water flow in the xylem. Using a version of Poiseuille's equation (see Equation 3.2), we can calculate the pressure gradient needed to move water at a velocity of 4 mm s^{-1} through an *ideal* tube with a uniform inner radius of 40 μm. The calculation gives a value of 0.02 MPa m^{-1}. Elaboration of the assumptions, equations, and calculations can be found in Web Topic 4.4.

Of course, *real* xylem conduits have irregular inner wall surfaces, and water flow through perforation plates and pits adds additional resistance. Such deviations from an ideal tube will increase the frictional drag above that calculated from Poiseuille's equation. However, measurements show that the actual resistance is greater by approximately a factor of 2 (Nobel 1999). Thus our estimate of 0.02 MPa m^{-1} is in the correct range for pressure gradients found in real trees.

Let's now compare this value (0.02 MPa m^{-1}) with the driving force that would be necessary to move water at the same velocity from cell to cell, crossing the plasma membrane each time. Using Poiseuille's equation, as described in Web Topic 4.4, the driving force needed to move water through a layer of cells at 4 mm s^{-1} is calculated to be 2×10^8 MPa m^{-1}. This is ten orders of magnitude greater than the driving force needed to move water through our 40-μm-radius xylem vessel. Our calculation clearly shows that water flow through the xylem is vastly more efficient than water flow across the membranes of living cells.

What Pressure Difference Is Needed to Lift Water 100 Meters to a Treetop?

With the foregoing example in mind, let's see how large of a pressure gradient is needed to move water up to the top of a very tall tree. The tallest trees in the world are the coast redwoods (*Sequoia sempervirens*) of North America and *Eucalyptus regnans* of Australia. Individuals of both species can exceed 100 m. If we think of the stem of a tree as a long pipe, we can estimate the pressure difference that is needed

to overcome the frictional drag of moving water from the soil to the top of the tree by multiplying our pressure gradient of 0.02 MPa m^{-1} by the height of the tree (0.02 MPa m^{-1} × 100 m = 2 MPa).

In addition to frictional resistance, we must consider gravity. The weight of a standing column of water 100 m tall creates a pressure of 1 MPa at the bottom of the water column (100 m × 0.01 MPa m^{-1}). This pressure gradient due to gravity must be added to that required to cause water movement through the xylem. Thus we calculate that a pressure difference of roughly 3 MPa, from the base to the top branches, is needed to carry water up the tallest trees.

The Cohesion–Tension Theory Explains Water Transport in the Xylem

In theory, the pressure gradients needed to move water through the xylem could result from the generation of positive pressures at the base of the plant or negative pressures at the top of the plant. We mentioned previously that some roots can develop positive hydrostatic pressure in their xylem—the so-called root pressure. However, root pressure is typically less than 0.1 MPa and disappears when the transpiration rate is high, so it is clearly inadequate to move water up a tall tree.

Instead, the water at the top of a tree develops a large tension (a negative hydrostatic pressure), and this tension *pulls* water through the xylem. This mechanism, first proposed toward the end of the nineteenth century, is called the **cohesion–tension theory of sap ascent** because it requires the cohesive properties of water to sustain large tensions in the xylem water columns (for details on the history of the research on water movement, see Web Essay 4.1).

Despite its attractiveness, the cohesion–tension theory has been a controversial subject for more than a century and continues to generate lively debate. The main controversy surrounds the question of whether water columns in the xylem can sustain the large tensions (negative pressures) necessary to pull water up tall trees.

The most recent debate began when researchers modified the cell pressure probe technique to be able to measure directly the tension in xylem vessels (Balling and Zimmermann 1990). Prior to this development, estimates of xylem pressures were based primarily on pressure chamber measurements of leaves (for a description of the pressure chamber method, see Web Topic 3.6).

Initially, measurements with the xylem pressure probe failed to find the expected large negative pressures, probably because of cavitation produced by tiny gas bubbles introduced when the xylem walls are punctured with the glass capillary of the pressure probe (Tyree 1997). However, careful refinements of the technique eventually demonstrated good agreement between pressure probe measurements and the tensions estimated by the pressure chamber (Melcher et al. 1998; Wei et al. 1999). In addition, independent studies demonstrated that water in the xylem can sustain large negative tensions (Pockman et al. 1995) and that pressure chamber measurements of nontranspiring leaves do reflect tensions in the xylem (Holbrook et al. 1995).

Most researchers have thus concluded that the basic cohesion–tension theory is sound (Steudle 2001) (for alternative hypotheses, see Canny (1998), and Web Essays 4.1 and 4.2). One can readily demonstrate xylem tensions by puncturing intact xylem through a drop of ink on the surface of a stem from a transpiring plant. When the tension in the xylem is relieved, the ink is drawn instantly into the xylem, resulting in visible streaks along the stem.

Xylem Transport of Water in Trees Faces Physical Challenges

The large tensions that develop in the xylem of trees (see Web Essay 4.3) and other plants can create some problems. First, the water under tension transmits an inward force to the walls of the xylem. If the cell walls were weak or pliant, they would collapse under the influence of this tension. The secondary wall thickenings and lignification of tracheids and vessels are adaptations that offset this tendency to collapse.

A second problem is that water under such tensions is in a *physically metastable state*. We mentioned in Chapter 3 that the experimentally determined breaking strength of degassed water (water that has been boiled to remove gases) is greater than 30 MPa. This value is much larger than the estimated tension of 3 MPa needed to pull water up the tallest trees, so water within the xylem would not normally reach tensions that would destabilize it.

However, as the tension in water increases, there is an increased tendency for air to be pulled through microscopic pores in the xylem cell walls. This phenomenon is called *air seeding*. A second mode by which bubbles can form in xylem conduits is due to the reduced solubility of gases in ice (Davis et al. 1999): The freezing of xylem conduits can lead to bubble formation. Once a gas bubble has formed within the water column under tension, it will expand because gases cannot resist tensile forces. This phenomenon of bubble formation is known as **cavitation** or **embolism**. It is similar to vapor lock in the fuel line of an automobile or embolism in a blood vessel. Cavitation breaks the continuity of the water column and prevents water transport in the xylem (Tyree and Sperry 1989; Hacke et al. 2001).

Such breaks in the water columns in plants are not unusual. With the proper equipment, one can "hear" the water columns break (Jackson et al. 1999). When plants are deprived of water, sound pulses can be detected. The pulses or clicks are presumed to correspond to the formation and rapid expansion of air bubbles in the xylem, resulting in high-frequency acoustic shock waves through the rest of the plant. These breaks in xylem water continuity, if not repaired, would be disastrous to the plant. By blocking the main transport pathway of water, such embolisms would cause the dehydration and death of the leaves.

Plants Minimize the Consequences of Xylem Cavitation

The impact of xylem cavitation on the plant is minimized by several means. Because the tracheary elements in the xylem are interconnected, one gas bubble might, in principle, expand to fill the whole network. In practice, gas bubbles do not spread far because the expanding gas bubb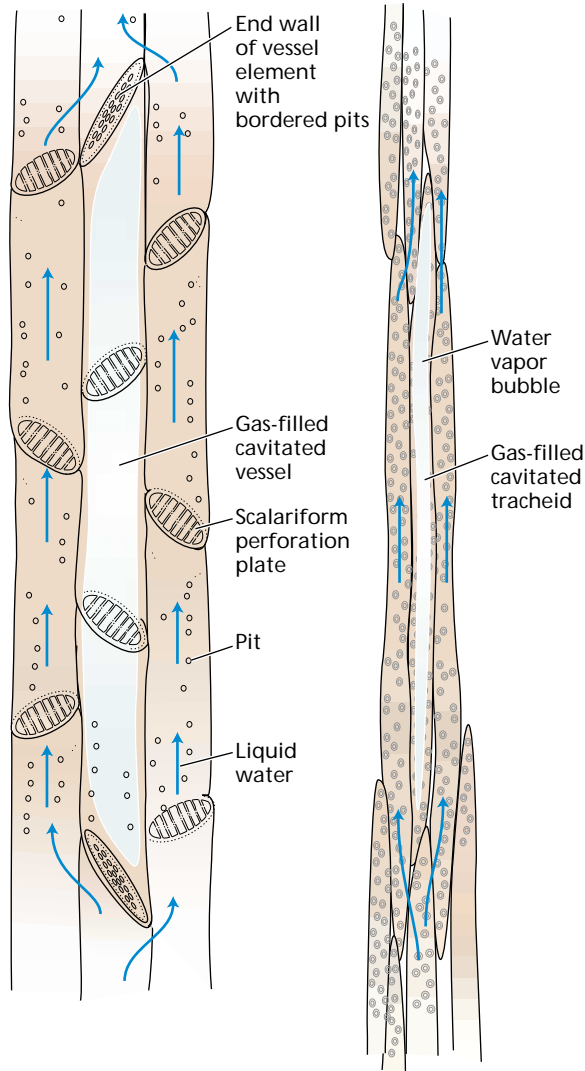le cannot easily pass through the small pores of the pit membranes. Since the capillaries in the xylem are interconnected, one gas bubble does not completely stop water flow. Instead, water can detour around the blocked point by traveling through neighboring, connected conduits (Figure 4.7). Thus the finite length of the tracheid and vessel conduits of the xylem, while resulting in an increased resistance to water flow, also provides a way to restrict cavitation.

Gas bubbles can also be eliminated from the xylem. At night, when transpiration is low, xylem Ψ_p increases and the water vapor and gases may simply dissolve back into the solution of the xylem. Moreover, as we have seen, some plants develop positive pressures (root pressures) in the xylem. Such pressures shrink the gas bubble and cause the gases to dissolve. Recent studies indicate that cavitation may be repaired even when the water in the xylem is under tension (Holbrook et al. 2001). A mechanism for such repair is not yet known and remains the subject of active research (see Web Essay 4.4). Finally, many plants have secondary growth in which new xylem forms each year. The new xylem becomes functional before the old xylem ceases to function, because of occlusion by gas bubbles or by substances secreted by the plant.

Water Evaporation in the Leaf Generates a Negative Pressure in the Xylem

The tensions needed to pull water through the xylem are the result of evaporation of water from leaves. In the intact plant, water is brought to the leaves via the xylem of the leaf vascular bundle(see Figure 4.1), which branches into a very fine and sometimes intricate network of **veins** throughout the leaf (Figure 4.8). This **venation pattern** becomes so finely
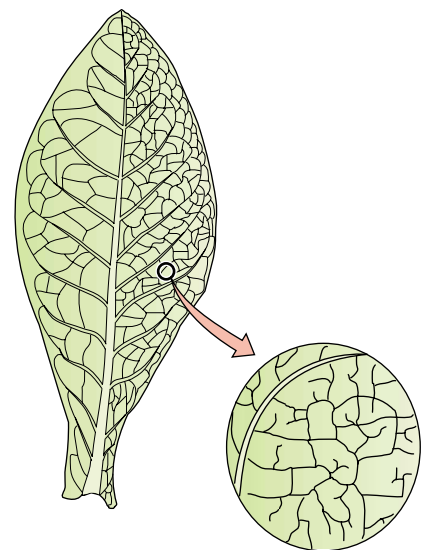

End wall of vessel element with bordered pits

Gas-filled cavitated vessel

Scalariform perforation plate

Pit

Liquid water

Water vapor bubble

Gas-filled cavitated tracheid

FIGURE 4.7 Tracheids (right) and vessels (left) form a series of parallel, interconnected pathways for water movement. Cavitation blocks water movement because of the formation of gas-filled (embolized) conduits. Because xylem conduits are interconnected through openings ("bordered pits") in their thick secondary walls, water can detour around the blocked vessel by moving through adjacent tracheary elements. The very small pores in the pit membranes help prevent embolisms from spreading between xylem conduits. Thus, in the diagram on the right the gas is contained within a single cavitated tracheid. In the diagram on the left, gas has filled the entire cavitated vessel, shown here as being made up of three vessel elements, each separated by scalariform perforation plates. In nature vessels can be very long (up to several meters in length) and thus made up of many vessel elements.

FIGURE 4.8 Venation of a tobacco leaf, showing ramification of the midrib into finer lateral veins. This venation pattern brings xylem water close to every cell in the leaf. (After Kramer and Boyer 1995.)

branched that most cells in a typical leaf are within 0.5 mm of a minor vein. From the xylem, water is drawn into the cells of the leaf and along the cell walls.

The negative pressure that causes water to move up through the xylem develops at the surface of the cell walls in the leaf. The situation is analogous to that in the soil. The cell wall acts like a very fine capillary wick soaked with water. Water adheres to the cellulose microfibrils and other hydrophilic components of the wall. The mesophyll cells within the

leaf are in direct contact with the atmosphere through an extensive system of intercellular air spaces.

Initially water evaporates from a thin film lining these air spaces. As water is lost to the air, the surface of the remaining water is drawn into the interstices of the cell wall (Figure 4.9), where it forms curved air–water interfaces. Because of the high surface tension of water, the curvature of these interfaces induces a tension, or negative pressure, in the water. As more water is removed from the wall, the radius of curvature

FIGURE 4.9   Tensions or negative pressures originate in leaves. As water evaporates from the surface film that covers the cell walls of the mesophyll, water withdraws farther into the interstices of the cell wall, and surface tension causes a negative pressure in the liquid phase. As the radius of curvature decreases, the pressure decreases (becomes more negative), as calculated from Equation 4.1.

	Radius of curvature (μm)	Hydrostatic pressure (MPa)
(A)	0.5	−0.3
(B)	0.05	−3
(C)	0.01	−15
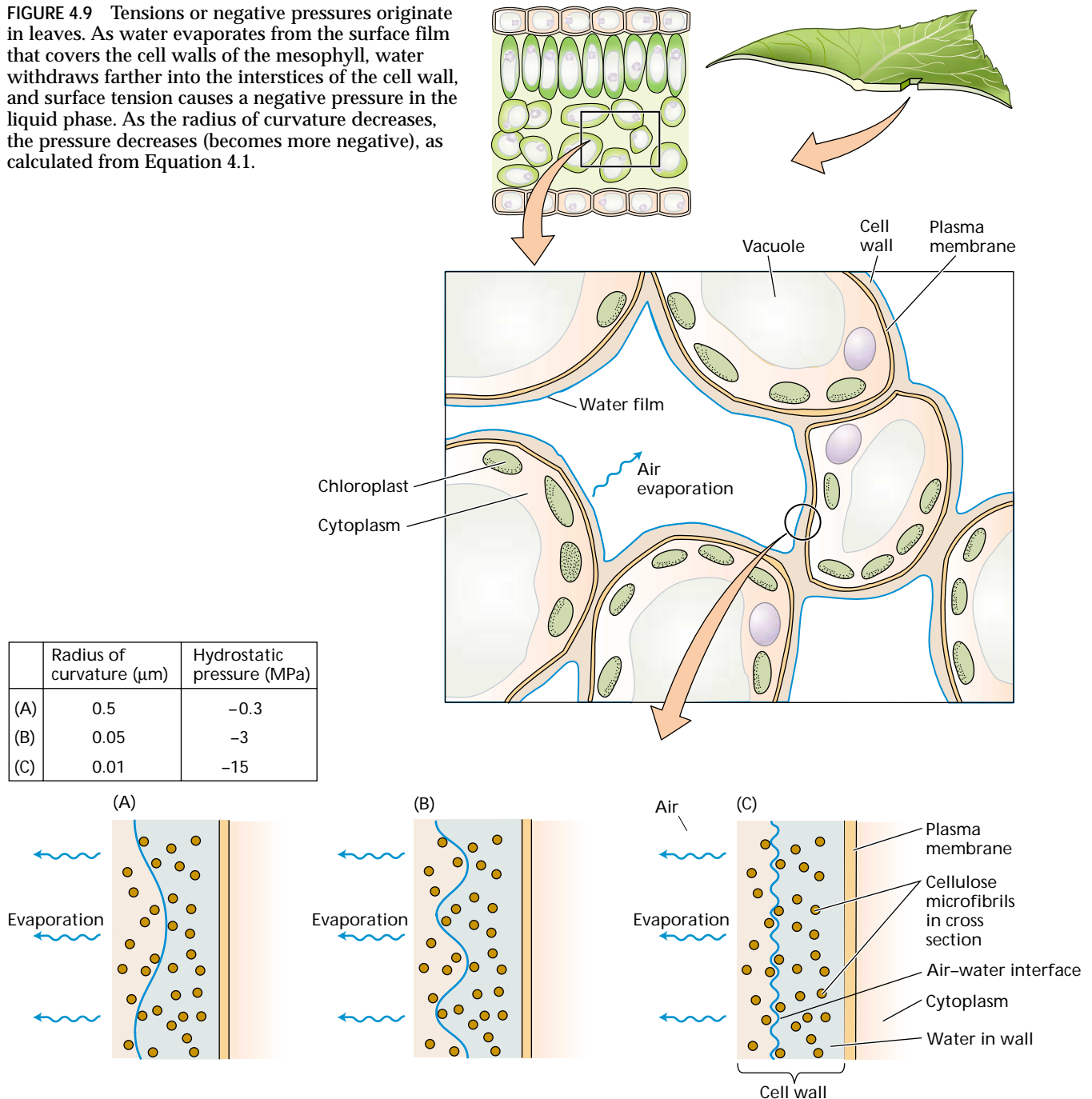
of the air–water interfaces decreases and the pressure of the water becomes more negative (see Equation 4.1). Thus the motive force for xylem transport is generated at the air–water interfaces within the leaf.

WATER MOVEMENT FROM THE LEAF TO THE ATMOSPHERE

After water has evaporated from the cell surface into the intercellular air space, diffusion is the primary means of any further movement of the water out of the leaf. The waxy cuticle that covers the leaf surface is a very effective barrier to water movement. It has been estimated that only about 5% of the water lost from leaves escapes through the cuticle. Almost all of the water lost from typical leaves is lost by diffusion of water vapor through the tiny pores of the stomatal apparatus, which are usually most abundant on the lower surface of the leaf.

On its way from the leaf to the atmosphere, water is pulled from the xylem into the cell walls of the mesophyll, where it evaporates into the air spaces of the leaf (Figure 4.10). The water vapor then exits the leaf through the stomatal pore. Water moves along this pathway predominantly by diffusion, so this water movement is controlled by the *concentration gradient* of water vapor.

We will now examine the driving force for leaf transpiration, the main resistances in the diffusion pathway from the leaf to the atmosphere, and the anatomical features of the leaf that regulate transpiration.

Water Vapor Diffuses Quickly in Air

We saw in Chapter 3 that diffusion in liquids is slow and, thus, effective only within cellular dimensions. How long would it take for a water molecule to diffuse from the cell wall surfaces inside the leaf to the outside atmosphere? In Chapter 3 we saw that the average time needed for a molecule to diffuse a distance L is equal to L^2/D_s, where D_s is the diffusion coefficient. The distance through which a water molecule must diffuse from the site of evaporation inside the leaf to the outside air is approximately 1 mm $(10^{-3}$ m), and the diffusion coefficient of water in air is 2.4×10^{-5} m^2 s^{-1}. Thus the average time needed for a water
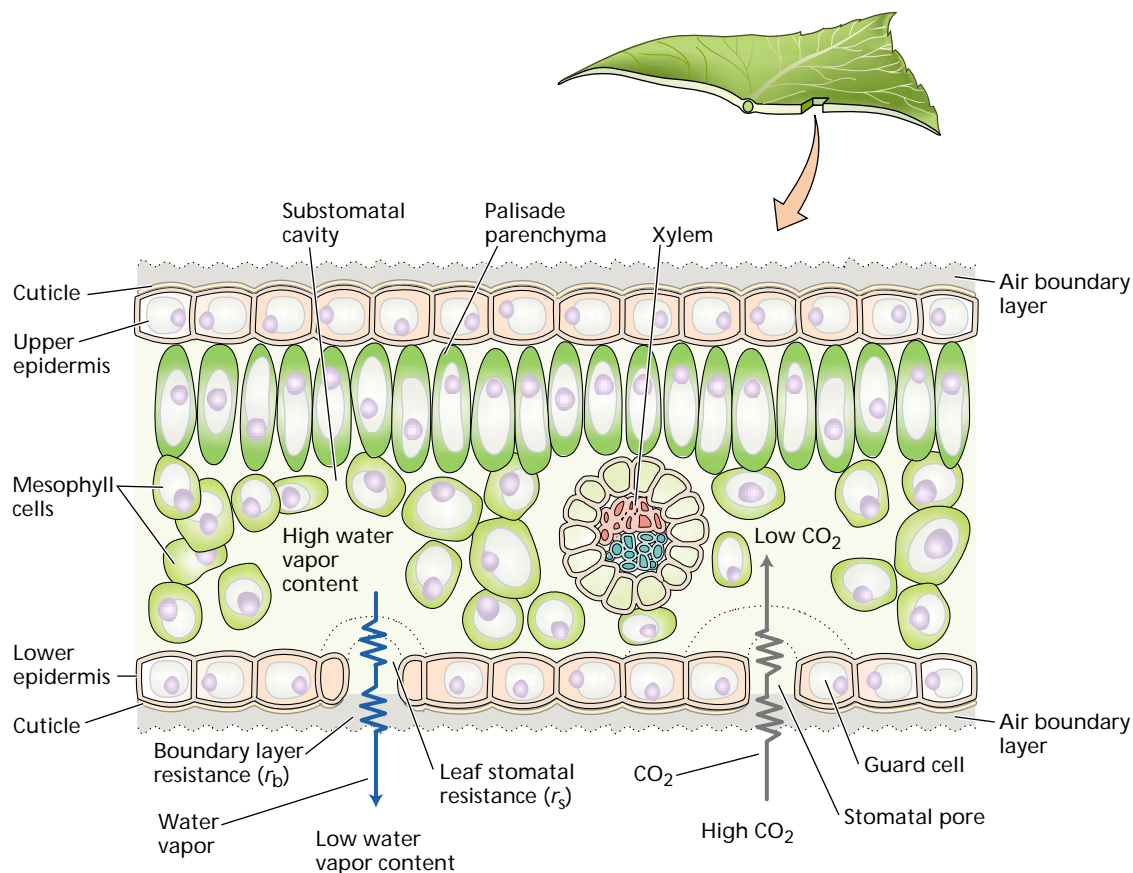

FIGURE 4.10 Water pathway through the leaf. Water is pulled from the xylem into the cell walls of the mesophyll, where it evaporates into the air spaces within the leaf. Water vapor then diffuses through the leaf air space, through the stomatal pore, and across the boundary layer of still air found next to the leaf surface. CO$_2$ diffuses in the opposite direction along its concentration gradient (low inside, higher outside).

molecule to escape the leaf is approximately 0.042 s. Thus we see that diffusion is adequate to move water vapor through the gas phase of the leaf. The reason that this time is so much shorter than the 2.5 s calculated in Chapter 3 for a glucose molecule to diffuse across a 50 μm cell, is that diffusion is much more rapid in a gas than in a liquid.

Transpiration from the leaf depends on two major factors: (1) the **difference in water vapor concentration** between the leaf air spaces and the external air and (2) the **diffusional resistance (*r*)** of this pathway. We will first discuss how the difference in water vapor concentration controls transpiration rates.

The Driving Force for Water Loss Is the Difference in Water Vapor Concentration

The difference in water vapor concentration is expressed as $c_{wv(leaf)} - c_{wv(air)}$. The water vapor concentration of bulk air ($c_{wv(air)}$) can be readily measured, but that of the leaf ($c_{wv(leaf)}$) is more difficult to assess.

Whereas the volume of air space inside the leaf is small, the wet surface from which water evaporates is comparatively large. (Air space volume is about 5% of the total leaf volume for pine needles, 10% for corn leaves, 30% for barley, and 40% for tobacco leaves.) In contrast to the volume of the air space, the internal surface area from which water evaporates may be from 7 to 30 times the external leaf area. This high ratio of surface area to volume makes for rapid vapor equilibration inside the leaf. Thus we can assume that the air space in the leaf is close to water potential equilibrium with the cell wall surfaces from which liquid water is evaporating.

An important point from this relationship is that within the range of water potentials experienced by transpiring leaves (generally <2.0 MPa) the equilibrium water vapor concentration is within a few percentage points of the saturation water vapor concentration. This allows one to estimate the water vapor concentration within a leaf from its temperature, which is easy to measure. (Web Topic 4.5 shows how we can calculate the water vapor concentration in the leaf air spaces and discusses other aspects of the water relations within a leaf.)

The concentration of water vapor, c_{wv}, changes at various points along the transpiration pathway. We see from Table 4.2 that c_{wv} decreases at each step of the pathway from the cell wall surface to the bulk air outside the leaf. The important points to remember are (1) that the driving force for water loss from the leaf is the *absolute* concentration difference (difference in c_{wv}, in mol
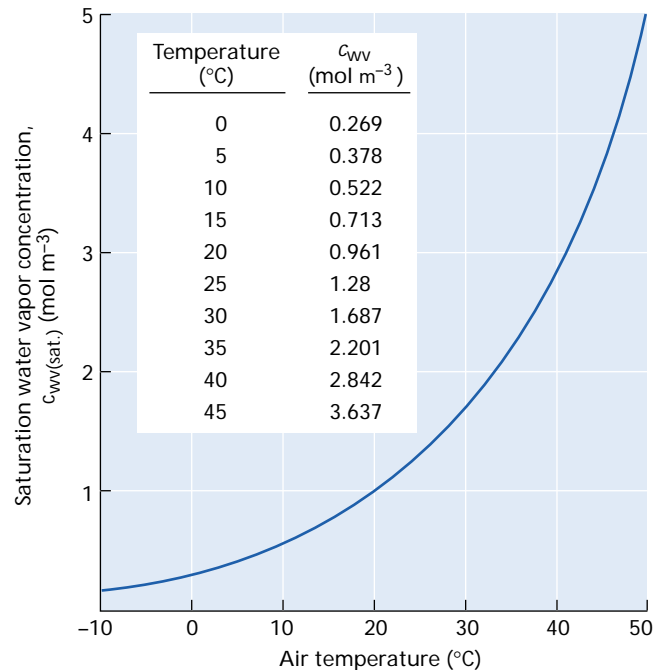

Temperature (°C)	c_{wv} (mol m⁻³)
0	0.269
5	0.378
10	0.522
15	0.713
20	0.961
25	1.28
30	1.687
35	2.201
40	2.842
45	3.637

FIGURE 4.11   Concentration of water vapor in saturated air as a function of air temperature.

m⁻³), and (2) that this difference depends on leaf temperature, as shown in Figure 4.11.

Water Loss Is Also Regulated by the Pathway Resistances

The second important factor governing water loss from the leaf is the diffusional resistance of the transpiration pathway, which consists of two varying components:

1. The resistance associated with diffusion through the stomatal pore, the **leaf stomatal resistance** (r_s).

2. The resistance due to the layer of unstirred air next to the leaf surface through which water vapor must

TABLE 4.2
Representative values for relative humidity, absolute water vapor concentration, and water potential for four points in the pathway of water loss from a leaf

Location	Relative humidity	Water vapor Concentration (mol m⁻³)	Water vapor Potential (MPa)[a]
Inner air spaces (25°C)	0.99	1.27	−1.38
Just inside stomatal pore (25°C)	0.95	1.21	−7.04
Just outside stomatal pore (25°C)	0.47	0.60	−103.7
Bulk air (20°C)	0.50	0.50	−93.6

Source: Adapted from Nobel 1999.
Note: See Figure 4.10.
[a]Calculated using Equation 4.5.2 in Web Topic 4.5; with values for $RT/\overline{V}_w$ of 135 MPa at 20°C and 137.3 MPa at 25°C.

diffuse to reach the turbulent air of the atmosphere (see Figure 4.10). This second resistance, r_b, is called the leaf **boundary layer resistance.** We will discuss this type of resistance before considering stomatal resistance.

The thickness of the boundary layer is determined primarily by wind speed. When the air surrounding the leaf is very still, the layer of unstirred air on the surface of the leaf may be so thick that it is the primary deterrent to water vapor loss from the leaf. Increases in stomatal apertures under such conditions have little effect on transpiration rate (Figure 4.12) (although closing the stomata completely will still reduce transpiration).

When wind velocity is high, the moving air reduces the thickness of the boundary layer at the leaf surface, reducing the resistance of this layer. Under such conditions, the stomatal resistance will largely control water loss from the leaf.

Various anatomical and morphological aspects of the leaf can influence the thickness of the boundary layer. Hairs on the surface of leaves can serve as microscopic windbreaks. Some plants have sunken stomata that pro-
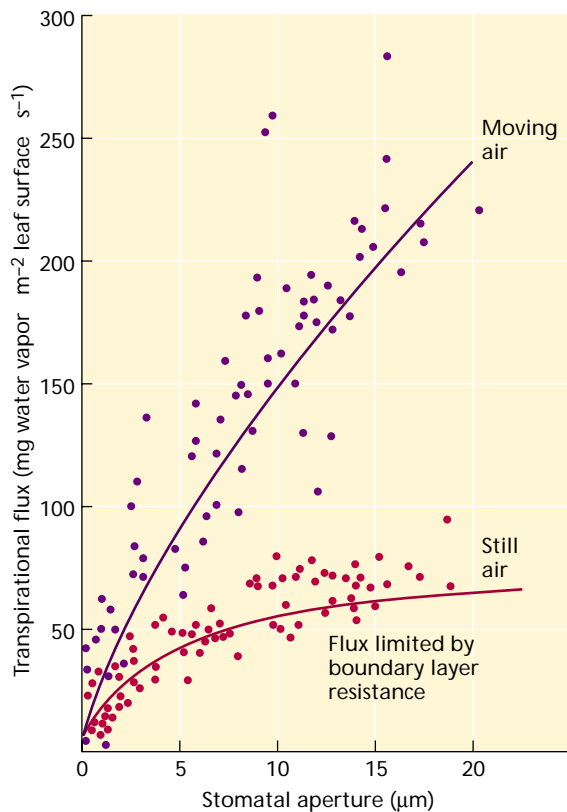

FIGURE 4.12   Dependence of transpiration flux on the stomatal aperture of zebra plant (*Zebrina pendula*) in still air and in moving air. The boundary layer is larger and more rate limiting in still air than in moving air. As a result, the stomatal aperture has less control over transpiration in still air. (From Bange 1953.)

vide a sheltered region outside the stomatal pore. The size and shape of leaves also influence the way the wind sweeps across the leaf surface. Although these and other factors may influence the boundary layer, they are not characteristics that can be altered on an hour-to-hour or even day-to-day basis. For short-term regulation, control of stomatal apertures by the guard cells plays a crucial role in the regulation of leaf transpiration.

Stomatal Control Couples Leaf Transpiration to Leaf Photosynthesis

Because the cuticle covering the leaf is nearly impermeable to water, most leaf transpiration results from the diffusion of water vapor through the stomatal pore (see Figure 4.10). The microscopic stomatal pores provide a *low-resistance pathway* for diffusional movement of gases across the epidermis and cuticle. That is, the stomatal pores lower the diffusional resistance for water loss from leaves. Changes in stomatal resistance are important for the regulation of water loss by the plant and for controlling the rate of carbon dioxide uptake necessary for sustained CO_2 fixation during photosynthesis.

All land plants are faced with competing demands of taking up CO_2 from the atmosphere while limiting water loss. The cuticle that covers exposed plant surfaces serves as an effective barrier to water loss and thus protects the plant from desiccation. However, plants cannot prevent outward diffusion of water without simultaneously excluding CO_2 from the leaf. This problem is compounded because the concentration gradient for CO_2 uptake is much, much smaller than the concentration gradient that drives water loss.

When water is abundant, the functional solution to this dilemma is the *temporal* regulation of stomatal apertures— open during the day, closed at night. At night, when there is no photosynthesis and thus no demand for CO_2 inside the leaf, stomatal apertures are kept small, preventing unnecessary loss of water. On a sunny morning when the supply of water is abundant and the solar radiation incident on the leaf favors high photosynthetic activity, the demand for CO_2 inside the leaf is large, and the stomatal pores are wide open, decreasing the stomatal resistance to CO_2 diffusion. Water loss by transpiration is also substantial under these conditions, but since the water supply is plentiful, it is advantageous for the plant to trade water for the products of photosynthesis, which are essential for growth and reproduction.

On the other hand, when soil water is less abundant, the stomata will open less or even remain closed on a sunny morning. By keeping its stomata closed in dry conditions, the plant avoids dehydration. The values for ($c_{wv(leaf)}$ − $c_{wv(air)}$) and for r_b are not readily amenable to biological control. However, stomatal resistance (r_s) can be regulated by opening and closing of the stomatal pore. This biological control is exerted by a pair of specialized epidermal cells, the **guard cells**, which surround the stomatal pore (Figure 4.13).

The Cell Walls of Guard Cells Have Specialized Features

Guard cells can be found in leaves of all vascular plants, and they are also present in organs from more primitive plants, such as the liverworts and the mosses (Ziegler 1987). Guard cells show considerable morphological diversity, but we can distinguish two main types: One is typical of grasses and a few other monocots, such as palms; the other is found in all dicots, in many monocots, and in mosses, ferns, and gymnosperms.

In grasses (see Figure 4.13A), guard cells have a characteristic dumbbell shape, with bulbous ends. The pore proper is a long slit located between the two "handles" of the dumbbells. These guard cells are always flanked by a

(A)

Cytosol and vacuole

Pore

Heavily thickened guard cell wall

(C)

Stomatal pore   Guard cell

(B)

Guard cells
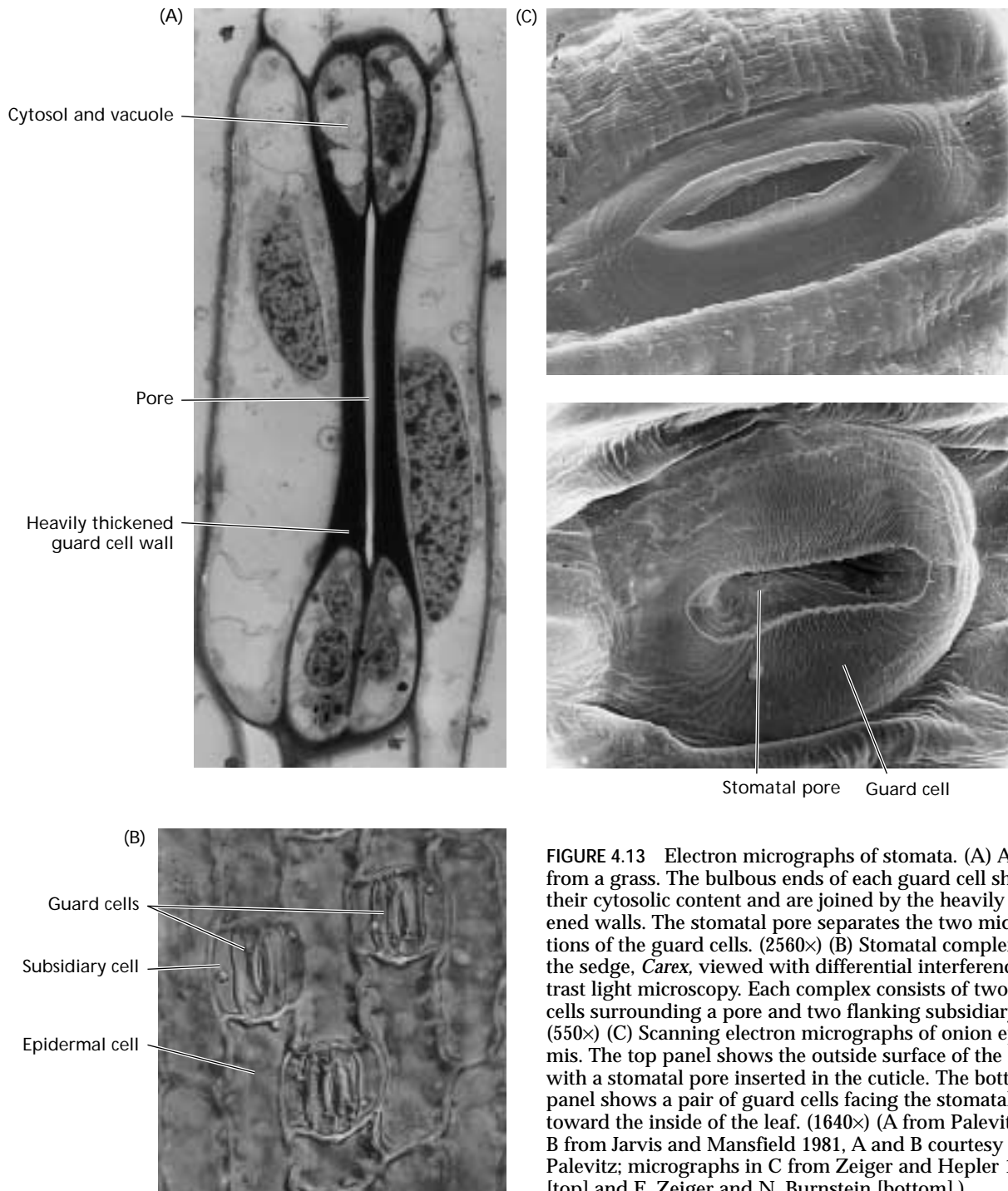
Subsidiary cell

Epidermal cell

FIGURE 4.13   Electron micrographs of stomata. (A) A stoma from a grass. The bulbous ends of each guard cell show their cytosolic content and are joined by the heavily thickened walls. The stomatal pore separates the two midportions of the guard cells. (2560×) (B) Stomatal complexes of the sedge, *Carex,* viewed with differential interference contrast light microscopy. Each complex consists of two guard cells surrounding a pore and two flanking subsidiary cells. (550×) (C) Scanning electron micrographs of onion epidermis. The top panel shows the outside surface of the leaf, with a stomatal pore inserted in the cuticle. The bottom panel shows a pair of guard cells facing the stomatal cavity, toward the inside of the leaf. (1640×) (A from Palevitz 1981, B from Jarvis and Mansfield 1981, A and B courtesy of B. Palevitz; micrographs in C from Zeiger and Hepler 1976 [top] and E. Zeiger and N. Burnstein [bottom].)

pair of differentiated epidermal cells called **subsidiary cells**, which help the guard cells control the stomatal pores (see Figure 4.13B). The guard cells, subsidiary cells, and pore are collectively called the **stomatal complex**.

In dicot plants and nongrass monocots, kidney-shaped guard cells have an elliptical contour with the pore at its center (see Figure 4.13C). Although subsidiary cells are not uncommon in species with kidney-shaped stomata, they are often absent, in which case the guard cells are surrounded by ordinary epidermal cells.

A distinctive feature of the guard cells is the specialized structure of their walls. Portions of these walls are substantially thickened (Figure 4.14) and may be up to 5 μm across, in contrast to the 1 to 2 μm typical of epidermal cells. In kidney-shaped guard cells, a differential thickening pattern results in very thick inner and outer (lateral) walls, a thin dorsal wall (the wall in contact with epidermal cells), and a somewhat thickened ventral (pore) wall (see Figure 4.14). The portions of the wall that face the atmosphere extend into well-developed ledges, which form the pore proper.

The alignment of **cellulose microfibrils**, which reinforce all plant cell walls and are an important determinant of cell shape (see Chapter 15), plays an essential role in the opening and closing of the stomatal pore. In ordinary cells having a cylindrical shape, cellulose microfibrils are oriented transversely to the long axis of the cell. As a result, the cell expands in the direction of its long axis because the cellulose reinforcement offers the least resistance at right angles to its orientation.

In guard cells the microfibril organization is different. Kidney-shaped guard cells have cellulose microfibrils fanning out radially from the pore (Figure 4.15A). Thus the cell girth is reinforced like a steel-belted radial tire, and the guard cells curve outward during stomatal opening (Sharpe et al. 1987). In grasses, the dumbbell-shaped guard cells function like beams with inflatable ends. As the bulbous ends of the cells increase in volume and swell, the beams are separated from each other and the slit between them widens (Figure 4.15B).

An Increase in Guard Cell Turgor Pressure Opens the Stomata

Guard cells function as multisensory hydraulic valves. Environmental factors such as light intensity and quality, temperature, relative humidity, and intracellular CO_2 concentra-
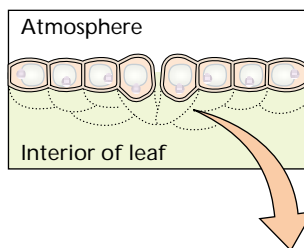

FIGURE 4.14   Electron micrograph showing a pair of guard cells from the dicot *Nicotiana tabacum* (tobacco). The section was made perpendicular to the main surface of the leaf. The pore faces the atmosphere; the bottom faces the substomatal cavity inside the leaf. Note the uneven thickening pattern of the walls, which determines the asymmetric deformation of the guard cells when their volume increases during stomatal opening. (From Sack 1987, courtesy of F. Sack.)

FIGURE 4.15   The radial alignment of the cellulose microfibrils in guard cells and epidermal cells of (A) a kidney-shaped stoma and (B) a grasslike stoma. (From Meidner and Mansfield 1968.)
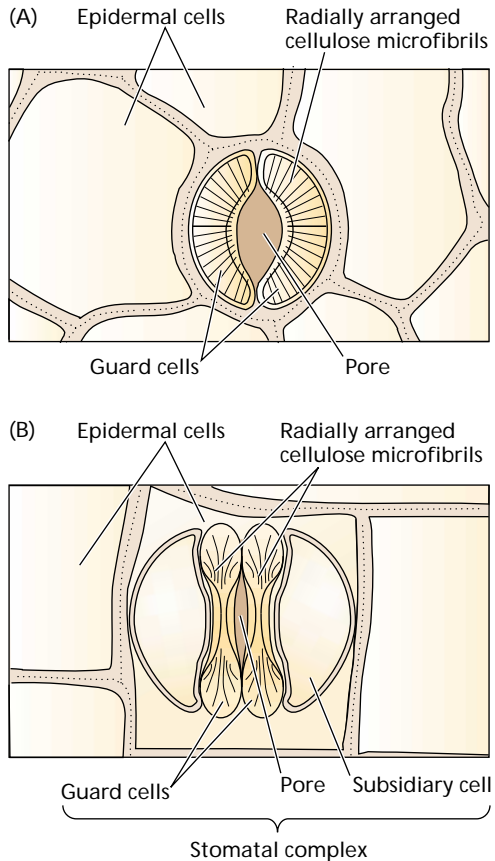
The Transpiration Ratio Measures the Relationship between Water Loss and Carbon Gain

The effectiveness of plants in moderating water loss while allowing sufficient CO_2 uptake for photosynthesis can be assessed by a parameter called the **transpiration ratio**. This value is defined as the amount of water transpired by the plant, divided by the amount of carbon dioxide assimilated by photosynthesis.

For typical plants in which the first stable product of carbon fixation is a three-carbon compound (such plants are called C_3 plants; see Chapter 8), about 500 molecules of water are lost for every molecule of CO_2 fixed by photosynthesis, giving a transpiration ratio of 500. (Sometimes the reciprocal of the transpiration ratio, called the *water use efficiency*, is cited. Plants with a transpiration ratio of 500 have a water use efficiency of $1/500$, or 0.002.)

The large ratio of H_2O efflux to CO_2 influx results from three factors:

1. The concentration gradient driving water loss is about 50 times larger than that driving the influx of CO_2. In large part, this difference is due to the low concentration of CO_2 in air (about 0.03%) and the relatively high concentration of water vapor within the leaf.

2. CO_2 diffuses about 1.6 times more slowly through air than water does (the CO_2 molecule is larger than H_2O and has a smaller diffusion coefficient).

3. CO_2 uptake must cross the plasma membrane, the cytoplasm, and the chloroplast envelope before it is assimilated in the chloroplast. These membranes add to the resistance of the CO_2 diffusion pathway.

Some plants are adapted for life in particularly dry environments or seasons of the year. These plants, designated the C_4 and CAM plants, utilize variations in the usual photosynthetic pathway for fixation of carbon dioxide. Plants with C_4 photosynthesis (in which a four-carbon compound is the first stable product of photosynthesis; see Chapter 8) generally transpire less water per molecule of CO_2 fixed; a typical transpiration ratio for C_4 plants is about 250. Desert-adapted plants with CAM (crassulacean acid metabolism) photosynthesis, in which CO_2 is initially fixed into four-carbon organic acids at night, have even lower transpiration ratios; values of about 50 are not unusual.

OVERVIEW: THE SOIL–PLANT–ATMOSPHERE CONTINUUM

We have seen that movement of water from the soil through the plant to the atmosphere involves different mechanisms of transport:

• In the soil and the xylem, water moves by bulk flow in response to a pressure gradient ($\Delta \Psi_p$).

tions are sensed by guard cells, and these signals are integrated into well-defined stomatal responses. If leaves kept in the dark are illuminated, the light stimulus is perceived by the guard cells as an opening signal, triggering a series of responses that result in opening of the stomatal pore.

The early aspects of this process are ion uptake and other metabolic changes in the guard cells, which will be discussed in detail in Chapter 18. Here we will note the effect of decreases in osmotic potential (Ψ_s) resulting from ion uptake and from biosynthesis of organic molecules in the guard cells. Water relations in guard cells follow the same rules as in other cells. As Ψ_s decreases, the water potential decreases and water consequently moves into the guard cells. As water enters the cell, turgor pressure increases. Because of the elastic properties of their walls, guard cells can reversibly increase their volume by 40 to 100%, depending on the species. Because of the differential thickening of guard cell walls, such changes in cell volume lead to opening or closing of the stomatal pore.

- In the vapor phase, water moves primarily by diffusion, at least until it reaches the outside air, where convection (a form of bulk flow) becomes dominant.

- When water is transported across membranes, the driving force is the water potential difference across the membrane. Such osmotic flow occurs when cells absorb water and when roots transport water from the soil to the xylem.

In all of these situations, *water moves toward regions of low water potential or free energy.* This phenomenon is illustrated in Figure 4.16, which shows representative values for water potential and its components at various points along the water transport pathway.

Water potential decreases continuously from the soil to the leaves. However, the components of water potential can be quite different at different parts of the pathway. For example, inside the leaf cells, such as in the mesophyll, the water potential is approximately the same as in the neigh-

boring xylem, yet the components of Ψ_w are quite different. The dominant component of Ψ_w in the xylem is the negative pressure (Ψ_p), whereas in the leaf cell Ψ_p is generally positive. This large difference in Ψ_p occurs across the plasma membrane of the leaf cells. Within the leaf cells, water potential is reduced by a high concentration of dissolved solutes (low Ψ_s).

SUMMARY

Water is the essential medium of life. Land plants are faced with potentially lethal desiccation by water loss to the atmosphere. This problem is aggravated by the large surface area of leaves, their high radiant-energy gain, and their need to have an open pathway for CO_2 uptake. Thus there is a conflict between the need for water conservation and the need for CO_2 assimilation.

The need to resolve this vital conflict determines much of the structure of land plants: (1) an extensive root system

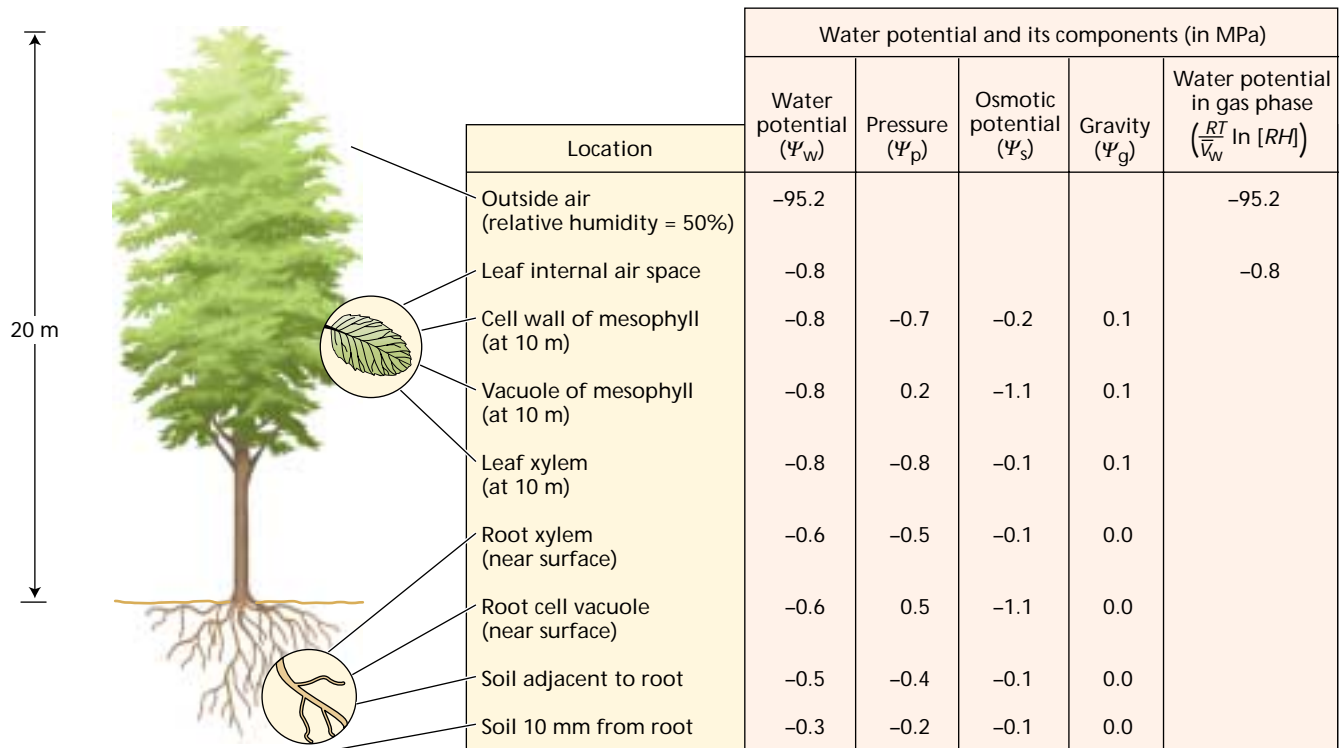| Location	Water potential and its components (in MPa)				
	Water potential (Ψ_w)	Pressure (Ψ_p)	Osmotic potential (Ψ_s)	Gravity (Ψ_g)	Water potential in gas phase ($\frac{RT}{\bar{V}_w}$ ln [RH])
Outside air (relative humidity = 50%)	−95.2				−95.2
Leaf internal air space	−0.8				−0.8
Cell wall of mesophyll (at 10 m)	−0.8	−0.7	−0.2	0.1	
Vacuole of mesophyll (at 10 m)	−0.8	0.2	−1.1	0.1	
Leaf xylem (at 10 m)	−0.8	−0.8	−0.1	0.1	
Root xylem (near surface)	−0.6	−0.5	−0.1	0.0	
Root cell vacuole (near surface)	−0.6	0.5	−1.1	0.0	
Soil adjacent to root	−0.5	−0.4	−0.1	0.0	
Soil 10 mm from root	−0.3	−0.2	−0.1	0.0	

20 m

FIGURE 4.16   Representative overview of water potential and its components at various points in the transport pathway from the soil through the plant to the atmosphere. Water potential (Ψ_w) can be measured through this continuum, but the components vary. In the liquid part of the pathway, pressure (Ψ_p), osmotic potential (Ψ_s), and gravity (Ψ_g), determine Ψ_w. In the air, only the relative humidity ($RT/\bar{V}_w \times$ ln[RH]) is important. Note that although the water potential is the same in the vacuole of the mesophyll cell and in the surrounding cell wall, the components of Ψ_w can differ greatly (e.g., in this case Ψ_p is 0.2 MPa inside the mesophyll cell and –0.7 MPa outside). (After Nobel 1999.)

to extract water from the soil; (2) a low-resistance pathway through the xylem vessel elements and tracheids to bring water to the leaves; (3) a hydrophobic cuticle covering the surfaces of the plant to reduce evaporation; (4) microscopic stomata on the leaf surface to allow gas exchange; and (5) guard cells to regulate the diameter (and diffusional resistance) of the stomatal aperture.

The result is an organism that transports water from the soil to the atmosphere purely in response to physical forces. No energy is expended directly by the plant to translocate water, although development and maintenance of the structures needed for efficient and controlled water transport require considerable energy input.

The mechanisms of water transport from the soil through the plant body to the atmosphere include diffusion, bulk flow, and osmosis. Each of these processes is coupled to different driving forces.

Water in the plant can be considered a continuous hydraulic system, connecting the water in the soil with the water vapor in the atmosphere. Transpiration is regulated principally by the guard cells, which regulate the stomatal pore size to meet the photosynthetic demand for CO_2 uptake while minimizing water loss to the atmosphere. Water evaporation from the cell walls of the leaf mesophyll cells generates large negative pressures (or tensions) in the apoplastic water. These negative pressures are transmitted to the xylem, and they pull water through the long xylem conduits.

Although aspects of the cohesion–tension theory of sap ascent are intermittently debated, an overwhelming body of evidence supports the idea that water transport in the xylem is driven by pressure gradients. When transpiration is high, negative pressures in the xylem water may cause cavitation (embolisms) in the xylem. Such embolisms can block water transport and lead to severe water deficits in the leaf. Water deficits are commonplace in plants, necessitating a host of adaptive responses that modify the physiology and development of plants.

Web Material

Web Topics

4.1 Irrigation
A discussion of some widely used irrigation methods and their impact on crop yield and soil salinity.

4.2 Soil Hydraulic Conductivity and Water Potential
Soil hydraulic conductivity determines the ease with which water moves through the soil, and it is closely related to soil water potential.

4.3 Root Hydraulic Conductance
A discussion of root hydraulic conductance and an example of its quantification.

4.4 Calculating Velocities of Water Movement in the Xylem and in Living Cells
Calculations of velocities of water movement through the xylem, up a tree trunk, and across cell membranes in a tissue, and their implications for water transport mechanism.

4.5 Leaf Transpiration and Water Vapor Gradients
An analysis of leaf transpiration and stomatal conductance, and their relationship with leaf and air water vapor concentrations.

Web Essays

4.1 A Brief History of the Study of Water Movement in the Xylem
The history of our understanding of sap ascent in plants, especially in trees, is a beautiful example of how knowledge about plant is acquired.

4.2 The Cohesion–Tension Theory at Work
A detailed discussion of the Cohesion–Tension theory on sap ascent in plants, and some alternative explanations.

4.3 How Water Climbs to the Top of a 112-Meter-Tall Tree
Measurements of photosynthesis and transpiration in 112-meter tall trees show that some of the conditions experienced by the top foliage compares to that of extreme deserts.

4.4 Cavitation and Refilling
A possible mechanism for cavitation repair is under active investigation.

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