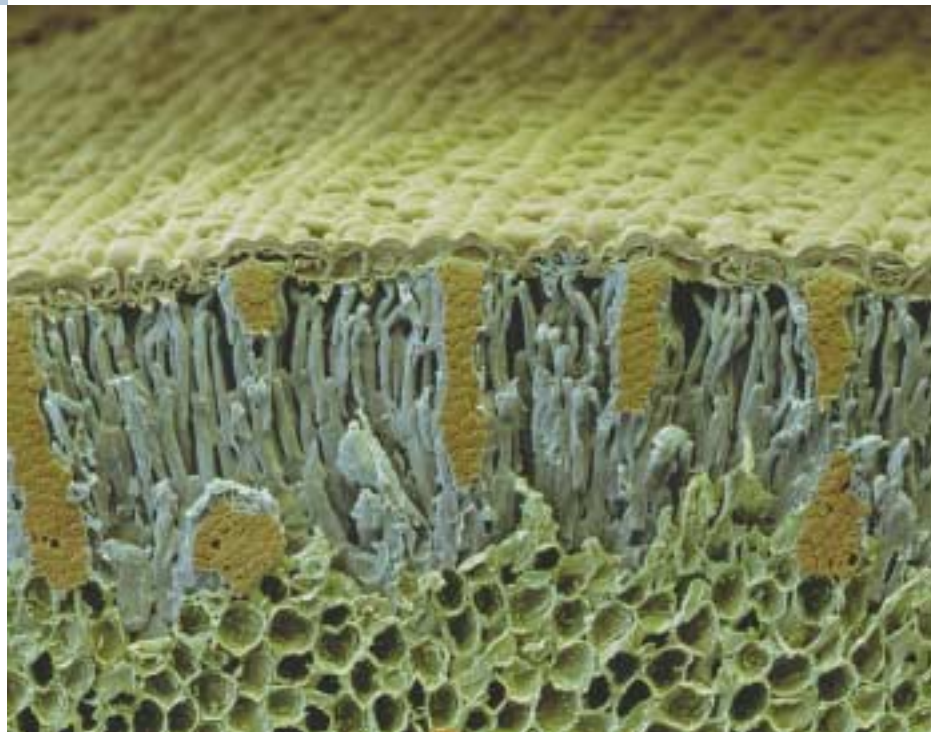UNIT

Transport and Translocation of Water and Solutes

Chapter

3

Water and Plant Cells

WATER PLAYS A CRUCIAL ROLE in the life of the plant. For every gram of organic matter made by the plant, approximately 500 g of water is absorbed by the roots, transported through the plant body and lost to the atmosphere. Even slight imbalances in this flow of water can cause water deficits and severe malfunctioning of many cellular processes. Thus, every plant must delicately balance its uptake and loss of water. This balancing is a serious challenge for land plants. To carry on photosynthesis, they need to draw carbon dioxide from the atmosphere, but doing so exposes them to water loss and the threat of dehydration.

A major difference between plant and animal cells that affects virtually all aspects of their relation with water is the existence in plants of the cell wall. Cell walls allow plant cells to build up large internal hydrostatic pressures, called **turgor pressure**, which are a result of their normal water balance. Turgor pressure is essential for many physiological processes, including cell enlargement, gas exchange in the leaves, transport in the phloem, and various transport processes across membranes. Turgor pressure also contributes to the rigidity and mechanical stability of nonlignified plant tissues. In this chapter we will consider how water moves into and out of plant cells, emphasizing the molecular properties of water and the physical forces that influence water movement at the cell level. But first we will describe the major functions of water in plant life.

WATER IN PLANT LIFE

Water makes up most of the mass of plant cells, as we can readily appreciate if we look at microscopic sections of mature plant cells: Each cell contains a large water-filled vacuole. In such cells the cytoplasm makes up only 5 to 10% of the cell volume; the remainder is vacuole. Water typically constitutes 80 to 95% of the mass of growing plant tissues. Common vegetables such as carrots and lettuce may contain 85 to 95% water. Wood, which is composed mostly of dead cells, has a lower water content; sapwood, which functions in transport in the xylem, contains 35 to
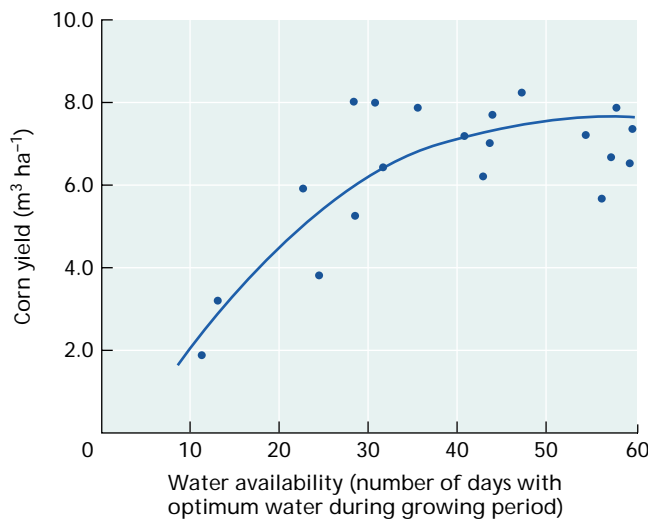
FIGURE 3.1   Corn yield as a function of water availability. The data plotted here were gathered at an Iowa farm over a 4-year period. Water availability was assessed as the number of days without water stress during a 9-week growing period. (Data from *Weather and Our Food Supply* 1964.)
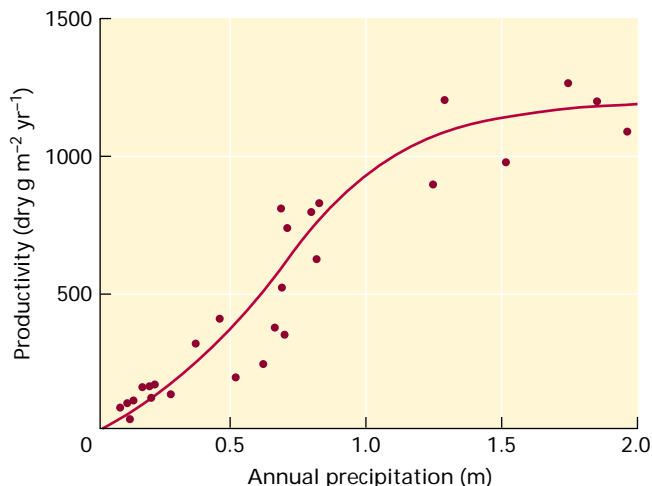

FIGURE 3.2   Productivity of various ecosystems as a function of annual precipitation. Productivity was estimated as net aboveground accumulation of organic matter through growth and reproduction. (After Whittaker 1970.)

75% water; and heartwood has a slightly lower water content. Seeds, with a water content of 5 to 15%, are among the driest of plant tissues, yet before germinating they must absorb a considerable amount of water.

Water is the most abundant and arguably the best solvent known. As a solvent, it makes up the medium for the movement of molecules within and between cells and greatly influences the structure of proteins, nucleic acids, polysaccharides, and other cell constituents. Water forms the environment in which most of the biochemical reactions of the cell occur, and it directly participates in many essential chemical reactions.

Plants continuously absorb and lose water. Most of the water lost by the plant evaporates from the leaf as the CO_2 needed for photosynthesis is absorbed from the atmosphere. On a warm, dry, sunny day a leaf will exchange up to 100% of its water in a single hour. During the plant's lifetime, water equivalent to 100 times the fresh weight of the plant may be lost through the leaf surfaces. Such water loss is called **transpiration**.

Transpiration is an important means of dissipating the heat input from sunlight. Heat dissipates because the water molecules that escape into the atmosphere have higher-than-average energy, which breaks the bonds holding them in the liquid. When these molecules escape, they leave behind a mass of molecules with lower-than-average energy and thus a cooler body of water. For a typical leaf, nearly half of the net heat input from sunlight is dissipated by transpiration. In addition, the stream of water taken up by the roots is an important means of bringing dissolved soil minerals to the root surface for absorption.

Of all the resources that plants need to grow and function, water is the most abundant and at the same time the most limiting for agricultural productivity (Figure 3.1). The fact that water is limiting is the reason for the practice of crop irrigation. Water availability likewise limits the productivity of natural ecosystems (Figure 3.2). Thus an understanding of the uptake and loss of water by plants is very important.

We will begin our study of water by considering how its structure gives rise to some of its unique physical properties. We will then examine the physical basis for water movement, the concept of water potential, and the application of this concept to cell–water relations.

THE STRUCTURE AND PROPERTIES OF WATER

Water has special properties that enable it to act as a solvent and to be readily transported through the body of the plant. These properties derive primarily from the polar structure of the water molecule. In this section we will examine how the formation of hydrogen bonds contributes to the properties of water that are necessary for life.

The Polarity of Water Molecules Gives Rise to Hydrogen Bonds

The water molecule consists of an oxygen atom covalently bonded to two hydrogen atoms. The two O—H bonds form an angle of 105° (Figure 3.3). Because the oxygen atom is more **electronegative** than hydrogen, it tends to attract the electrons of the covalent bond. This attraction results in a partial negative charge at the oxygen end of the molecule and a partial positive charge at each hydrogen.
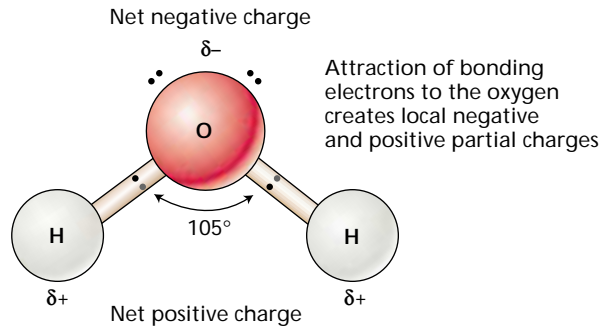
FIGURE 3.3   Diagram of the water molecule. The two intramolecular hydrogen–oxygen bonds form an angle of 105°. The opposite partial charges (δ– and δ+) on the water molecule lead to the formation of intermolecular hydrogen bonds with other water molecules. Oxygen has six electrons in the outer orbitals; each hydrogen has one.

These partial charges are equal, so the water molecule carries no *net* charge.

This separation of partial charges, together with the shape of the water molecule, makes water a *polar molecule*, and the opposite partial charges between neighboring water molecules tend to attract each other. The weak electrostatic attraction between water molecules, known as a **hydrogen bond**, is responsible for many of the unusual physical properties of water.

Hydrogen bonds can also form between water and other molecules that contain electronegative atoms (O or N). In aqueous solutions, hydrogen bonding between water molecules leads to local, ordered clusters of water that, because of the continuous thermal agitation of the water molecules, continually form, break up, and re-form (Figure 3.4).
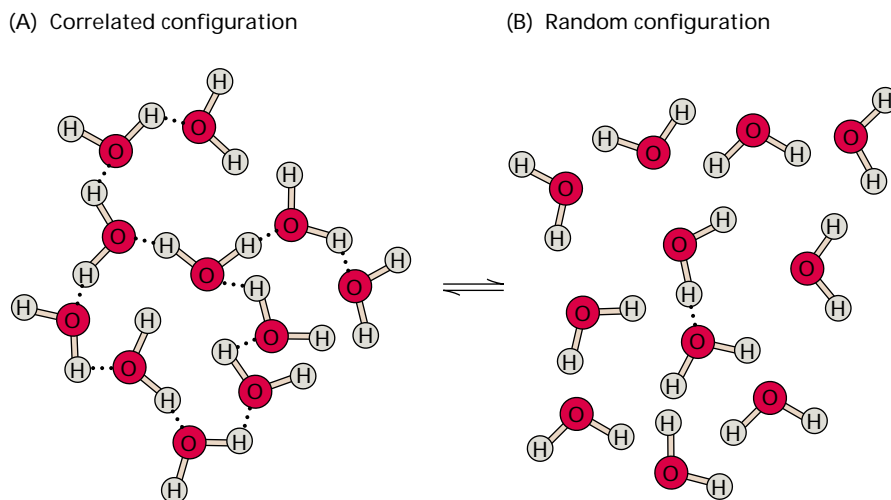
The Polarity of Water Makes It an Excellent Solvent

Water is an excellent solvent: It dissolves greater amounts of a wider variety of substances than do other related solvents. This versatility as a solvent is due in part to the small size of the water molecule and in part to its polar nature. The latter makes water a particularly good solvent for ionic substances and for molecules such as sugars and proteins that contain polar —OH or —NH$_2$ groups.

Hydrogen bonding between water molecules and ions, and between water and polar solutes, in solution effectively decreases the electrostatic interaction between the charged substances and thereby increases their solubility. Furthermore, the polar ends of water molecules can orient themselves next to charged or partially charged groups in macromolecules, forming **shells of hydration**. Hydrogen bonding between macromolecules and water reduces the interaction between the macromolecules and helps draw them into solution.

The Thermal Properties of Water Result from Hydrogen Bonding

The extensive hydrogen bonding between water molecules results in unusual thermal properties, such as high specific heat and high latent heat of vaporization. **Specific heat** is the heat energy required to raise the temperature of a substance by a specific amount.

When the temperature of water is raised, the molecules vibrate faster and with greater amplitude. To allow for this motion, energy must be added to the system to break the hydrogen bonds between water molecules. Thus, compared with other liquids, water requires a relatively large energy input to raise its temperature. This large energy input requirement is important for plants because it helps buffer temperature fluctuations.

Latent heat of vaporization is the energy needed to separate molecules from the liquid phase and move them into the gas phase at constant temperature—a process that occurs during transpiration. For water at 25°C, the heat of vaporization is 44 kJ mol^{-1}—the highest value known for any liquid. Most of this energy is used to break hydrogen bonds between water molecules.

The high latent heat of vaporization of water enables plants to cool themselves by evaporating water from leaf surfaces, which are prone to heat up because of the radiant input from the sun. Transpiration is an important component of temperature regulation in plants.

FIGURE 3.4   (A) Hydrogen bonding between water molecules results in local aggregations of water molecules. (B) Because of the continuous thermal agitation of the water molecules, these aggregations are very short-lived; they break up rapidly to form much more random configurations.

The Cohesive and Adhesive Properties of Water Are Due to Hydrogen Bonding

Water molecules at an air–water interface are more strongly attracted to neighboring water molecules than to the gas phase in contact with the water surface. As a consequence of this unequal attraction, an air–water interface minimizes its surface area. To increase the area of an air–water interface, hydrogen bonds must be broken, which requires an input of energy. The energy required to increase the surface area is known as **surface tension**. Surface tension not only influences the shape of the surface but also may create a pressure in the rest of the liquid. As we will see later, surface tension at the evaporative surfaces of leaves generates the physical forces that pull water through the plant's vascular system.

The extensive hydrogen bonding in water also gives rise to the property known as **cohesion**, the mutual attraction between molecules. A related property, called **adhesion**, is the attraction of water to a solid phase such as a cell wall or glass surface. Cohesion, adhesion, and surface tension give rise to a phenomenon known as **capillarity**, the movement of water along a capillary tube.

In a vertically oriented glass capillary tube, the upward movement of water is due to (1) the attraction of water to the polar surface of the glass tube (adhesion) and (2) the surface tension of water, which tends to minimize the area of the air–water interface. Together, adhesion and surface tension pull on the water molecules, causing them to move up the tube until the upward force is balanced by the weight of the water column. The smaller the tube, the higher the capillary rise. For calculations related to capillary rise, see Web Topic 3.1.

Water Has a High Tensile Strength

Cohesion gives water a high **tensile strength**, defined as the maximum force per unit area that a continuous column of water can withstand before breaking. We do not usually think of liquids as having tensile strength; however, such a property must exist for a water column to be pulled up a capillary tube.

We can demonstrate the tensile strength of water by placing it in a capped syringe (Figure 3.5). When we *push* on the plunger, the water is compressed and a positive **hydrostatic pressure** builds up. Pressure is measured in units called *pascals* (Pa) or, more conveniently, *megapascals* (MPa). One MPa equals approximately 9.9 atmospheres. Pressure is equivalent to a force per unit area (1 Pa = 1 N m^{-2}) and to an energy per unit volume (1 Pa = 1 J m^{-3}). A newton (N) = 1 kg m s^{-1}. Table 3.1 compares units of pressure.

If instead of pushing on the plunger we *pull* on it, a tension, or *negative hydrostatic pressure*, develops in the water to resist the pull. How hard must we pull on the plunger before the water molecules are torn away from each other and the water column breaks? Breaking the water column requires sufficient energy to break the hydrogen bonds that attract water molecules to one another.
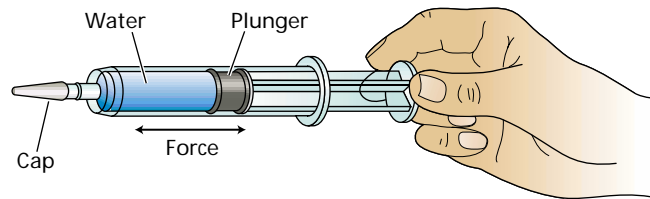
FIGURE 3.5   A sealed syringe can be used to create positive and negative pressures in a fluid like water. Pushing on the plunger compresses the fluid, and a positive pressure builds up. If a small air bubble is trapped within the syringe, it shrinks as the pressure increases. Pulling on the plunger causes the fluid to develop a tension, or negative pressure. Any air bubbles in the syringe will expand as the pressure is reduced.

Careful studies have demonstrated that water in small capillaries can resist tensions more negative than –30 MPa (the negative sign indicates tension, as opposed to compression). This value is only a fraction of the theoretical tensile strength of water computed on the basis of the strength of hydrogen bonds. Nevertheless, it is quite substantial.

The presence of gas bubbles reduces the tensile strength of a water column. For example, in the syringe shown in Figure 3.5, expansion of microscopic bubbles often interferes with the ability of the water to resist the pull exerted by the plunger. If a tiny gas bubble forms in a column of water under tension, the gas bubble may expand indefinitely, with the result that the tension in the liquid phase collapses, a phenomenon known as **cavitation**. As we will see in Chapter 4, cavitation can have a devastating effect on water transport through the xylem.

WATER TRANSPORT PROCESSES

When water moves from the soil through the plant to the atmosphere, it travels through a widely variable medium (cell wall, cytoplasm, membrane, air spaces), and the mechanisms of water transport also vary with the type of medium. For many years there has been much uncertainty

TABLE 3.1
Comparison of units of pressure

1 atmosphere = 14.7 pounds per square inch
= 760 mm Hg (at sea level, 45° latitude)
= 1.013 bar
= 0.1013 Mpa
= 1.013 × 10^5 Pa

A car tire is typically inflated to about 0.2 MPa.
The water pressure in home plumbing is typically 0.2–0.3 MPa.
The water pressure under 15 feet (5 m) of water is about 0.05 MPa.

about how water moves across plant membranes. Specifically it was unclear whether water movement into plant cells was limited to the diffusion of water molecules across the plasma membrane's lipid bilayer or also involved diffusion through protein-lined pores (Figure 3.6).

Some studies indicated that diffusion directly across the lipid bilayer was not sufficient to account for observed rates of water movement across membranes, but the evidence in support of microscopic pores was not compelling. This uncertainty was put to rest with the recent discovery of **aquaporins** (see Figure 3.6). Aquaporins are integral membrane proteins that form water-selective channels across the membrane. Because water diffuses faster through such channels than through a lipid bilayer, aquaporins facilitate water movement into plant cells (Weig et al. 1997; Schäffner 1998; Tyerman et al. 1999). Note that although the presence of aquaporins may alter the *rate* of water movement across the membrane, they do not change the direction of transport or the driving force for water movement. The mode of action of aquaporins is being acitvely investigated (Tajkhorshid et al. 2002).

We will now consider the two major processes in water transport: molecular diffusion and bulk flow.

Diffusion Is the Movement of Molecules by Random Thermal Agitation

Water molecules in a solution are not static; they are in continuous motion, colliding with one another and exchanging kinetic energy. The molecules intermingle as a result of
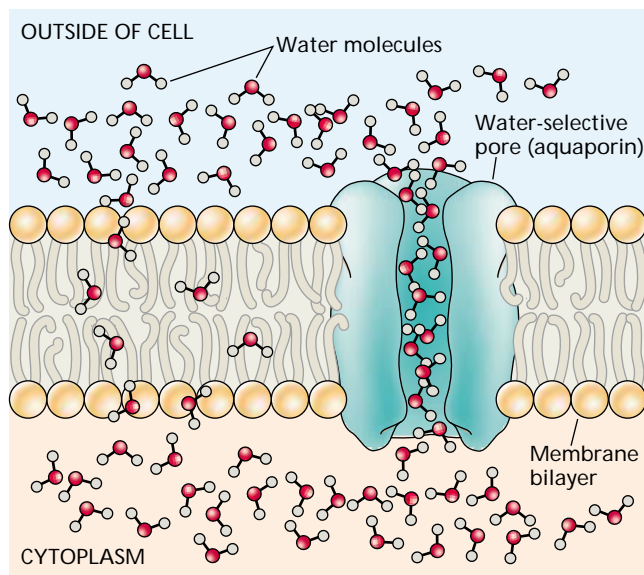
FIGURE 3.6 Water can cross plant membranes by diffusion of individual water molecules through the membrane bilayer, as shown on the left, and by microscopic bulk flow of water molecules through a water-selective pore formed by integral membrane proteins such as aquaporins.

their random thermal agitation. This random motion is called **diffusion**. As long as other forces are not acting on the molecules, diffusion causes the net movement of molecules from regions of high concentration to regions of low concentration—that is, down a concentration gradient (Figure 3.7).

In the 1880s the German scientist Adolf Fick discovered that the rate of diffusion is directly proportional to the concentration gradient ($\Delta c_s / \Delta x$)—that is, to the difference in concentration of substance s (Δc_s) between two points separated by the distance Δx. In symbols, we write this relation as Fick's first law:
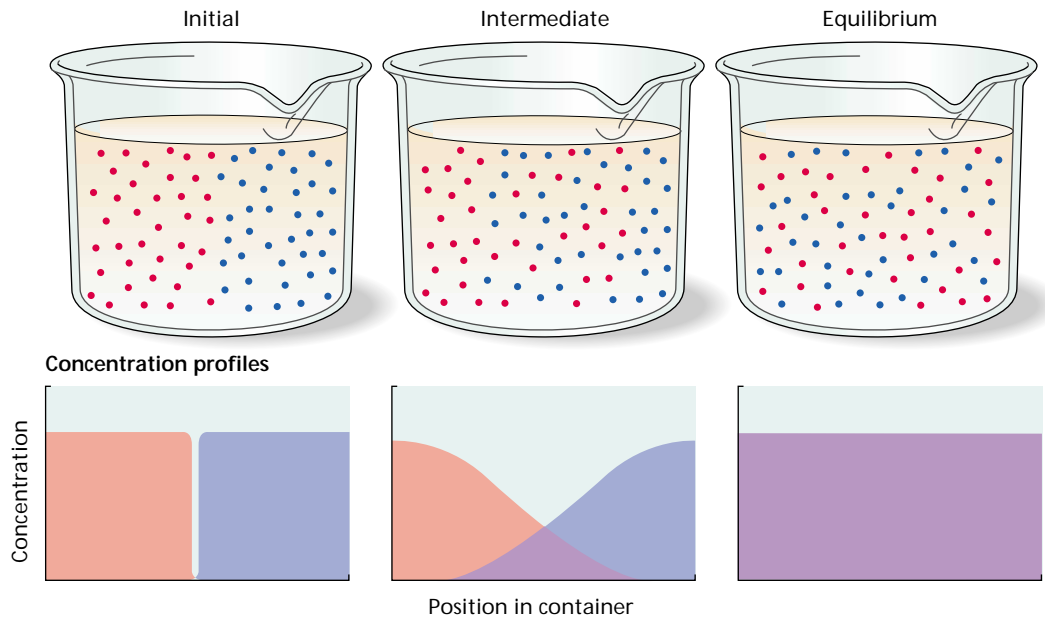
$$J_s = -D_s \frac{\Delta c_s}{\Delta x} \qquad (3.1)$$

The rate of transport, or the **flux density** (J_s), is the amount of substance s crossing a unit area per unit time (e.g., J_s may have units of moles per square meter per second [mol m^{-2} s^{-1}]). The **diffusion coefficient** (D_s) is a proportionality constant that measures how easily substance s moves through a particular medium. The diffusion coefficient is a characteristic of the substance (larger molecules have smaller diffusion coefficients) and depends on the medium (diffusion in air is much faster than diffusion in a liquid, for example). The negative sign in the equation indicates that the flux moves down a concentration gradient.

Fick's first law says that a substance will diffuse faster when the concentration gradient becomes steeper (Δc_s is large) or when the diffusion coefficient is increased. This equation accounts only for movement in response to a concentration gradient, and not for movement in response to other forces (e.g., pressure, electric fields, and so on).

Diffusion Is Rapid over Short Distances but Extremely Slow over Long Distances

From Fick's first law, one can derive an expression for the time it takes for a substance to diffuse a particular distance. If the initial conditions are such that all the solute molecules are concentrated at the starting position (Figure 3.8A), then the concentration front moves away from the starting position, as shown for a later time point in Figure 3.8B. As the substance diffuses away from the starting point, the concentration gradient becomes less steep (Δc_s decreases), and thus net movement becomes slower.

The average time needed for a particle to diffuse a distance L is equal to L^2/D_s, where D_s is the diffusion coefficient, which depends on both the identity of the particle and the medium in which it is diffusing. Thus the average time required for a substance to diffuse a given distance increases in proportion to the *square* of that distance. The diffusion coefficient for glucose in water is about 10^{-9} m^2 s^{-1}. Thus the average time required for a glucose molecule to diffuse across a cell with a diameter of 50 μm is 2.5 s. However, the average time needed for the same glucose molecule to diffuse a distance of 1 m in water is approxi-

Initial   Intermediate   Equilibrium

Concentration profiles

Concentration

Position in container

FIGURE 3.7 Thermal motion of molecules leads to diffusion—the gradual mixing of molecules and eventual dissipation of concentration differences. Initially, two materials containing different molecules are brought into contact. The materials may be gas, liquid, or solid. Diffusion is fastest in gases, slower in liquids, and slowest in solids. The initial separation of the molecules is depicted graphically in the upper panels, and the corresponding concentration profiles are shown in the lower panels as a function of position. With time, the mixing and randomization of the molecules diminishes net movement. At equilibrium the two types of molecules are randomly (evenly) distributed.

(A)   (B)

0   0

Concentration   Concentration

Δc_s Δc_s

Time

← Distance Δx →   ← Distance Δx →
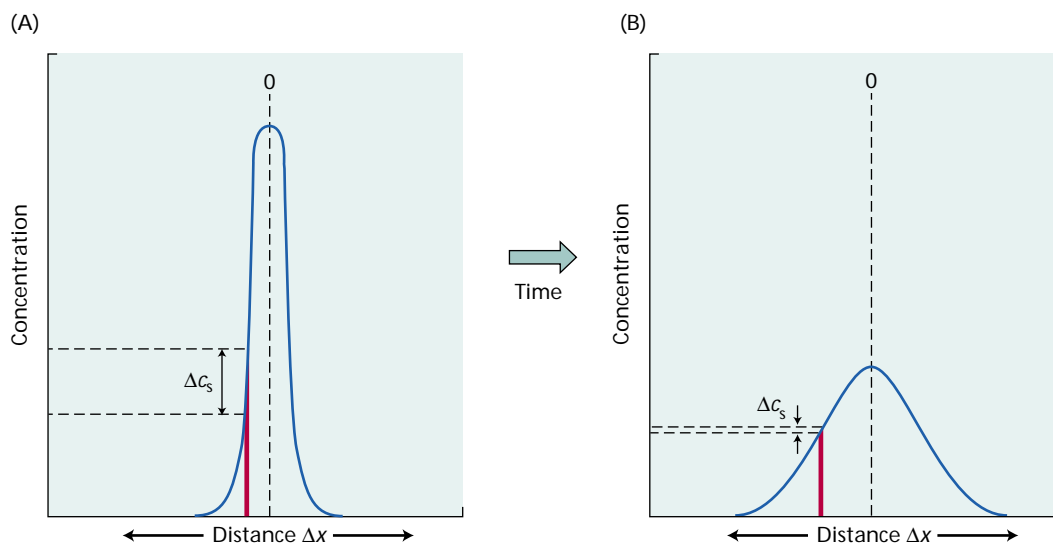
FIGURE 3.8 Graphical representation of the concentration gradient of a solute that is diffusing according to Fick's law. The solute molecules were initially located in the plane indicated on the x-axis. (A) The distribution of solute molecules shortly after placement at the plane of origin. Note how sharply the concentration drops off as the distance, x, from the origin increases. (B) The solute distribution at a later time point. The average distance of the diffusing molecules from the origin has increased, and the slope of the gradient has flattened out. (After Nobel 1999.)

mately 32 years. These values show that diffusion in solutions can be effective within cellular dimensions but is far too slow for mass transport over long distances. For additional calculations on diffusion times, see Web Topic 3.2.

Pressure-Driven Bulk Flow Drives Long-Distance Water Transport

A second process by which water moves is known as **bulk flow** or **mass flow**. Bulk flow is the concerted movement of groups of molecules en masse, most often in response to a pressure gradient. Among many common examples of bulk flow are water moving through a garden hose, a river flowing, and rain falling.

If we consider bulk flow through a tube, the rate of volume flow depends on the radius (r) of the tube, the viscosity (η) of the liquid, and the pressure gradient ($\Delta\Psi_p/\Delta x$) that drives the flow. Jean-Léonard-Marie Poiseuille (1797–1869) was a French physician and physiologist, and the relation just described is given by one form of Poiseuille's equation:

$$\text{Volume flow rate} = \left(\frac{\pi r^4}{8\eta}\right)\left(\frac{\Delta\Psi_p}{\Delta x}\right) \qquad (3.2)$$

expressed in cubic meters per second ($m^3 s^{-1}$). This equation tells us that pressure-driven bulk flow is very sensitive to the radius of the tube. If the radius is doubled, the volume flow rate increases by a factor of 16 (2^4).

Pressure-driven bulk flow of water is the predominant mechanism responsible for long-distance transport of water in the xylem. It also accounts for much of the water flow through the soil and through the cell walls of plant tissues. In contrast to diffusion, pressure-driven bulk flow is independent of solute concentration gradients, as long as viscosity changes are negligible.

Osmosis Is Driven by a Water Potential Gradient

Membranes of plant cells are **selectively permeable**; that is, they allow the movement of water and other small uncharged substances across them more readily than the movement of larger solutes and charged substances (Stein 1986).

Like molecular diffusion and pressure-driven bulk flow, **osmosis** occurs spontaneously in response to a driving force. In simple diffusion, substances move down a concentration gradient; in pressure-driven bulk flow, substances move down a pressure gradient; in osmosis, both types of gradients influence transport (Finkelstein 1987). *The direction and rate of water flow across a membrane are determined not solely by the concentration gradient of water or by the pressure gradient, but by the sum of these two driving forces.*

We will soon see how osmosis drives the movement of water across membranes. First, however, let's discuss the concept of a composite or total driving force, representing the free-energy gradient of water.

The Chemical Potential of Water Represents the Free-Energy Status of Water

All living things, including plants, require a continuous input of free energy to maintain and repair their highly organized structures, as well as to grow and reproduce. Processes such as biochemical reactions, solute accumulation, and long-distance transport are all driven by an input of free energy into the plant. (For a detailed discussion of the thermodynamic concept of free energy, see Chapter 2 on the web site.)

The **chemical potential** of water is a quantitative expression of the free energy associated with water. In thermodynamics, free energy represents the potential for performing work. Note that chemical potential is a relative quantity: It is expressed as the difference between the potential of a substance in a given state and the potential of the same substance in a standard state. The unit of chemical potential is energy per mole of substance ($J mol^{-1}$).

For historical reasons, plant physiologists have most often used a related parameter called **water potential**, defined as the chemical potential of water divided by the partial molal volume of water (the volume of 1 mol of water): $18 \times 10^{-6} m^3 mol^{-1}$. Water potential is a measure of the free energy of water per unit volume ($J m^{-3}$). These units are equivalent to pressure units such as the pascal, which is the common measurement unit for water potential. Let's look more closely at the important concept of water potential.

Three Major Factors Contribute to Cell Water Potential

The major factors influencing the water potential in plants are *concentration, pressure*, and *gravity*. Water potential is symbolized by Ψ_w (the Greek letter psi), and the water potential of solutions may be dissected into individual components, usually written as the following sum:

$$\Psi_w = \Psi_s + \Psi_p + \Psi_g \qquad (3.3)$$

The terms Ψ_s, Ψ_p, and Ψ_g denote the effects of solutes, pressure, and gravity, respectively, on the free energy of water. (Alternative conventions for components of water potential are discussed in Web Topic 3.3.) The reference state used to define water potential is pure water at ambient pressure and temperature. Let's consider each of the terms on the right-hand side of Equation 3.3.

Solutes.   The term Ψ_s, called the **solute potential** or the **osmotic potential**, represents the effect of dissolved solutes on water potential. Solutes reduce the free energy of water by diluting the water. This is primarily an entropy effect; that is, the mixing of solutes and water increases the disorder of the system and thereby lowers free energy. This means that the osmotic potential is independent of the specific nature of the solute. For dilute solutions of nondisso-

ciating substances, like sucrose, the osmotic potential may be estimated by the **van't Hoff equation**:

$$\Psi_\sigma = -RTc_\sigma \qquad (3.4)$$

where R is the gas constant (8.32 J mol^{-1} K^{-1}), T is the absolute temperature (in degrees Kelvin, or K), and c_s is the solute concentration of the solution, expressed as **osmolality** (moles of total dissolved solutes per liter of water [mol L^{-1}]). The minus sign indicates that dissolved solutes reduce the water potential of a solution relative to the reference state of pure water.

Table 3.2 shows the values of RT at various temperatures and the Ψ_s values of solutions of different solute concentrations. For ionic solutes that dissociate into two or more particles, c_s must be multiplied by the number of dissociated particles to account for the increased number of dissolved particles.

Equation 3.4 is valid for "ideal" solutions at dilute concentration. Real solutions frequently deviate from the ideal, especially at high concentrations—for example, greater than 0.1 mol L^{-1}. In our treatment of water potential, we will assume that we are dealing with ideal solutions (Friedman 1986; Nobel 1999).

Pressure. The term Ψ_p is the **hydrostatic pressure** of the solution. Positive pressures raise the water potential; negative pressures reduce it. Sometimes Ψ_p is called *pressure potential*. The positive hydrostatic pressure within cells is the pressure referred to as *turgor pressure*. The value of Ψ_p can also be negative, as is the case in the xylem and in the walls between cells, where a *tension*, or *negative hydrostatic pressure*, can develop. As we will see, negative pressures outside cells are very important in moving water long distances through the plant.

Hydrostatic pressure is measured as the deviation from ambient pressure (for details, see Web Topic 3.5). Remember that water in the reference state is at ambient pressure, so by this definition $\Psi_p = 0$ MPa for water in the standard state. Thus the value of Ψ_p for pure water in an open beaker is 0 MPa, even though its absolute pressure is approximately 0.1 MPa (1 atmosphere).

Gravity. Gravity causes water to move downward unless the force of gravity is opposed by an equal and opposite force. The term Ψ_g depends on the height (h) of the water above the reference-state water, the density of water (ρ_w), and the acceleration due to gravity (g). In symbols, we write the following:

$$\Psi_g = \rho_w g h \qquad (3.5)$$

where $\rho_w g$ has a value of 0.01 MPa m^{-1}. Thus a vertical distance of 10 m translates into a 0.1 MPa change in water potential.

When dealing with water transport at the cell level, the gravitational component (Ψ_g) is generally omitted because it is negligible compared to the osmotic potential and the hydrostatic pressure. Thus, in these cases Equation 3.3 can be simplified as follows:

$$\Psi_w = \Psi_s + \Psi_p \qquad (3.6)$$

In discussions of dry soils, seeds, and cell walls, one often finds reference to another component of Ψ_w, the matric potential, which is discussed in Web Topic 3.4.

Water potential in the plant. Cell growth, photosynthesis, and crop productivity are all strongly influenced by water potential and its components. Like the body temperature of humans, water potential is a good overall indicator of plant health. Plant scientists have thus expended considerable effort in devising accurate and reliable methods for evaluating the water status of plants. Some of the instruments that have been used to measure Ψ_w, Ψ_s, and Ψ_p are described in Web Topic 3.5.

Water Enters the Cell along a Water Potential Gradient

In this section we will illustrate the osmotic behavior of plant cells with some numerical examples. First imagine an open beaker full of pure water at 20°C (Figure 3.9A). Because the water is open to the atmosphere, the hydrostatic pressure of the water is the same as atmospheric pressure ($\Psi_p = 0$ MPa). There are no solutes in the water, so $\Psi_s = 0$ MPa; therefore the water potential is 0 MPa ($\Psi_w = \Psi_s + \Psi_p$).

TABLE 3.2
Values of RT and osmotic potential of solutions at various temperatures

Temperature (°C)	RT^a (L MPa mol^{-1})	Osmotic potential (MPa) of solution with solute concentration in mol L^{-1} water			Osmotic potential of seawater (MPa)
		0.01	0.10	1.00	
0	2.271	−0.0227	−0.227	−2.27	−2.6
20	2.436	−0.0244	−0.244	−2.44	−2.8
25	2.478	−0.0248	−0.248	−2.48	−2.8
30	2.519	−0.0252	−0.252	−2.52	−2.9

$^aR = 0.0083143$ L MPa mol^{-1} K^{-1}.

(A) Pure water

Pure water
$\Psi_p = 0$ MPa
$\Psi_s = 0$ MPa
$\Psi_w = \Psi_p + \Psi_s$
$= 0$ MPa

(B) Solution containing 0.1 *M* sucrose

0.1 *M* Sucrose solution
$\Psi_p = 0$ MPa
$\Psi_s = -0.244$ MPa
$\Psi_w = \Psi_p + \Psi_s$
$= 0 - 0.244$ MPa
$= -0.244$ MPa

(C) Flaccid cell dropped into sucrose solution

Flaccid cell
$\Psi_p = 0$ MPa
$\Psi_s = -0.732$ MPa
$\Psi_w = -0.732$ MPa

Cell after equilibrium
$\Psi_w = -0.244$ MPa
$\Psi_s = -0.732$ MPa
$\Psi_p = \Psi_w - \Psi_s = 0.488$ MPa

(D) Concentration of sucrose increased

Turgid cell
$\Psi_p = 0.488$ MPa
$\Psi_s = -0.732$ MPa
$\Psi_w = -0.244$ MPa

Cell after equilibrium
$\Psi_w = -0.732$ MPa
$\Psi_s = -0.732$ MPa
$\Psi_p = \Psi_w - \Psi_s = 0$ MPa

0.3 *M* Sucrose solution
$\Psi_p = 0$ MPa
$\Psi_s = -0.732$ MPa
$\Psi_w = -0.732$ MPa

(E) Pressure applied to cell

Applied pressure squeezes out half the water, thus doubling Ψ_s from -0.732 to -1.464 MPa

0.1 *M* Sucrose solution

Cell in initial state
$\Psi_w = -0.244$ MPa
$\Psi_s = -0.732$ MPa
$\Psi_p = \Psi_w - \Psi_s = 0.488$ MPa

Cell in final state
$\Psi_w = -0.244$ MPa
$\Psi_s = -1.464$ MPa
$\Psi_p = \Psi_w - \Psi_s = 1.22$ MPa

FIGURE 3.9   Five examples illustrating the concept of water potential and its components. (A) Pure water. (B) A solution containing 0.1 *M* sucrose. (C) A flaccid cell (in air) is dropped in the 0.1 *M* sucrose solution. Because the starting water potential of the cell is less than the water potential of the solution, the cell takes up water. After equilibration, the water potential of the cell rises to equal the water potential of the solution, and the result is a cell with a positive turgor pressure. (D) Increasing the concentration of sucrose in the solution makes the cell lose water. The increased sucrose concentration lowers the solution water potential, draws water out from the cell, and thereby reduces the cell's turgor pressure. In this case the protoplast is able to pull away from the cell wall (i.e, the cell plasmolyzes) because sucrose molecules are able to pass through the relatively large pores of the cell walls. In contrast, when a cell desiccates in air (e.g., the flaccid cell in panel C) plasmolysis does not occur because the water held by capillary forces in the cell walls prevents air from infiltrating into any void between the plasma membrane and the cell wall. (E) Another way to make the cell lose water is to press it slowly between two plates. In this case, half of the cell water is removed, so cell osmotic potential increases by a factor of 2.

Now imagine dissolving sucrose in the water to a concentration of 0.1 *M* (Figure 3.9B). This addition lowers the osmotic potential (Ψ_s) to –0.244 MPa (see Table 3.2) and decreases the water potential (Ψ_w) to –0.244 MPa.

Next consider a flaccid, or limp, plant cell (i.e., a cell with no turgor pressure) that has a total internal solute concentration of 0.3 *M* (Figure 3.9C). This solute concentration gives an osmotic potential (Ψ_s) of –0.732 MPa. Because the cell is flaccid, the internal pressure is the same as ambient pressure, so the hydrostatic pressure (Ψ_p) is 0 MPa and the water potential of the cell is –0.732 MPa.

What happens if this cell is placed in the beaker containing 0.1 *M* sucrose (see Figure 3.9C)? Because the water potential of the sucrose solution (Ψ_w = –0.244 MPa; see Figure 3.9B) is greater than the water potential of the cell (Ψ_w = –0.732 MPa), water will move from the sucrose solution to the cell (from high to low water potential).

Because plant cells are surrounded by relatively rigid cell walls, even a slight increase in cell volume causes a large increase in the hydrostatic pressure within the cell. As water enters the cell, the cell wall is stretched by the contents of the enlarging protoplast. The wall resists such stretching by pushing back on the cell. This phenomenon is analogous to inflating a basketball with air, except that air is compressible, whereas water is nearly incompressible.

As water moves into the cell, the hydrostatic pressure, or turgor pressure (Ψ_p), of the cell increases. Consequently, the cell water potential (Ψ_w) increases, and the difference between inside and outside water potentials ($\Delta\Psi_w$) is reduced. Eventually, cell Ψ_p increases enough to raise the cell Ψ_w to the same value as the Ψ_w of the sucrose solution. At this point, equilibrium is reached ($\Delta\Psi_w$ = 0 MPa), and net water transport ceases.

Because the volume of the beaker is much larger than that of the cell, the tiny amount of water taken up by the cell does not significantly affect the solute concentration of the sucrose solution. Hence Ψ_s, Ψ_p, and Ψ_w of the sucrose solution are not altered. Therefore, at equilibrium, $\Psi_{w(cell)}$ = $\Psi_{w(solution)}$ = –0.244 MPa.

The exact calculation of cell Ψ_p and Ψ_s requires knowledge of the change in cell volume. However, if we assume that the cell has a very rigid cell wall, then the increase in cell volume will be small. Thus we can assume to a first approximation that $\Psi_{s(cell)}$ is unchanged during the equilibration process and that $\Psi_{s(solution)}$ remains at –0.732 MPa. We can obtain cell hydrostatic pressure by rearranging Equation 3.6 as follows: $\Psi_p = \Psi_w - \Psi_s$ = (–0.244) – (–0.732) = 0.488 MPa.

Water Can Also Leave the Cell in Response to a Water Potential Gradient

Water can also leave the cell by osmosis. If, in the previous example, we remove our plant cell from the 0.1 *M* sucrose solution and place it in a 0.3 *M* sucrose solution (Figure 3.9D), $\Psi_{w(solution)}$ (–0.732 MPa) is more negative than

$\Psi_{w(cell)}$ (–0.244 MPa), and water will move from the turgid cell to the solution.

As water leaves the cell, the cell volume decreases. As the cell volume decreases, cell Ψ_p and Ψ_w decrease also until $\Psi_{w(cell)}$ = $\Psi_{w(solution)}$ = –0.732 MPa. From the water potential equation (Equation 3.6) we can calculate that at equilibrium, Ψ_p = 0 MPa. As before, we assume that the change in cell volume is small, so we can ignore the change in Ψ_s.

If we then slowly squeeze the turgid cell by pressing it between two plates (Figure 3.9E), we effectively raise the cell Ψ_p, consequently raising the cell Ψ_w and creating a $\Delta\Psi_w$ such that water now flows *out* of the cell. If we continue squeezing until half the cell water is removed and then hold the cell in this condition, the cell will reach a new equilibrium. As in the previous example, at equilibrium, $\Delta\Psi_w$ = 0 MPa, and the amount of water added to the external solution is so small that it can be ignored. The cell will thus return to the Ψ_w value that it had before the squeezing procedure. However, the components of the cell Ψ_w will be quite different.

Because half of the water was squeezed out of the cell while the solutes remained inside the cell (the plasma membrane is selectively permeable), the cell solution is concentrated twofold, and thus Ψ_s is lower (–0.732 × 2 = –1.464 MPa). Knowing the final values for Ψ_w and Ψ_s, we can calculate the turgor pressure, using Equation 3.6, as $\Psi_p = \Psi_w - \Psi_s$ = (–0.244) – (–1.464) = 1.22 MPa. In our example we used an external force to change cell volume without a change in water potential. In nature, it is typically the water potential of the cell's environment that changes, and the cell gains or loses water until its Ψ_w matches that of its surroundings.

One point common to all these examples deserves emphasis: *Water flow is a passive process. That is, water moves in response to physical forces, toward regions of low water potential or low free energy.* There are no metabolic "pumps" (reactions driven by ATP hydrolysis) that push water from one place to another. This rule is valid as long as water is the only substance being transported. When solutes are transported, however, as occurs for short distances across membranes (see Chapter 6) and for long distances in the phloem (see Chapter 10), then water transport may be coupled to solute transport and this coupling may move water against a water potential gradient.

For example, the transport of sugars, amino acids, or other small molecules by various membrane proteins can "drag" up to 260 water molecules across the membrane per molecule of solute transported (Loo et al. 1996). Such transport of water can occur even when the movement is against the usual water potential gradient (i.e., toward a larger water potential) because the loss of free energy by the solute more than compensates for the gain of free energy by the water. The net change in free energy remains negative. In the phloem, the bulk flow of solutes and water within sieve tubes occurs along gradients in hydrostatic

(turgor) pressure rather than by osmosis. Thus, within the phloem, water can be transported from regions with lower water potentials (e.g., leaves) to regions with higher water potentials (e.g., roots). *These situations notwithstanding, in the vast majority of cases water in plants moves from higher to lower water potentials.*

Small Changes in Plant Cell Volume Cause Large Changes in Turgor Pressure

Cell walls provide plant cells with a substantial degree of volume homeostasis relative to the large changes in water potential that they experience as the everyday consequence of the transpirational water losses associated with photosynthesis (see Chapter 4). Because plant cells have fairly rigid walls, a change in cell Ψ_w is generally accompanied by a large change in Ψ_p, with relatively little change in cell (protoplast) volume.

This phenomenon is illustrated in plots of Ψ_w, Ψ_p, and Ψ_s as a function of relative cell volume. In the example of a hypothetical cell shown in Figure 3.10, as Ψ_w decreases from 0 to about –2 MPa, the cell volume is reduced by only 5%. Most of this decrease is due to a reduction in Ψ_p (by about 1.2 MPa); Ψ_s decreases by about 0.3 MPa as a result of water loss by the cell and consequent increased concentration of cell solutes. Contrast this with the volume changes of a cell lacking a wall.

Measurements of cell water potential and cell volume (see Figure 3.10) can be used to quantify how cell walls influence the water status of plant cells.

1. Turgor pressure ($\Psi_p > 0$) exists only when cells are relatively well hydrated. Turgor pressure in most cells approaches zero as the relative cell volume decreases by 10 to 15%. However, for cells with very rigid cell walls (e.g., mesophyll cells in the leaves of many palm trees), the volume change associated with turgor loss can be much smaller, whereas in cells with extremely elastic walls, such as the water-storing cells in the stems of many cacti, this volume change may be substantially larger.

2. The Ψ_p curve of Figure 3.10 provides a way to measure the relative rigidity of the cell wall, symbolized by ε (the Greek letter epsilon): $\varepsilon = \Delta\Psi_p/\Delta$(relative volume). ε is the slope of the Ψ_p curve. ε is not constant but decreases as turgor pressure is lowered because nonlignified plant cell walls usually are rigid only when turgor pressure puts them under tension. Such cells act like a basketball: The wall is stiff (has high ε) when the ball is inflated but becomes soft and collapsible ($\varepsilon = 0$) when the ball loses pressure.

3. When ε and Ψ_p are low, changes in water potential are dominated by changes in Ψ_s (note how Ψ_w and Ψ_s curves converge as the relative cell volume approaches 85%).
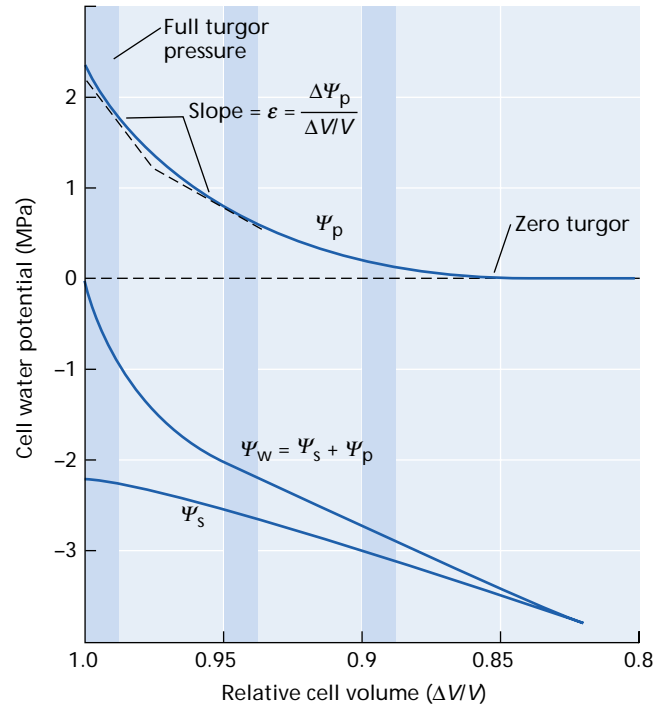

FIGURE 3.10 Relation between cell water potential (Ψ_w) and its components (Ψ_p and Ψ_s), and relative cell volume ($\Delta V/V$). The plots show that turgor pressure (Ψ_p) decreases steeply with the initial 5% decrease in cell volume. In comparison, osmotic potential (Ψ_s) changes very little. As cell volume decreases below 0.9 in this example, the situation reverses: Most of the change in water potential is due to a drop in cell Ψ_s accompanied by relatively little change in turgor pressure. The slope of the curve that illustrates Ψ_p versus volume relationship is a measure of the cell's elastic modulus (ε) (a measurement of wall rigidity). Note that ε is not constant but decreases as the cell loses turgor. (After Tyree and Jarvis 1982, based on a shoot of Sitka spruce.)

Water Transport Rates Depend on Driving Force and Hydraulic Conductivity

So far, we have seen that water moves across a membrane in response to a water potential gradient. The direction of flow is determined by the direction of the Ψ_w gradient, and the rate of water movement is proportional to the magnitude of the driving gradient. However, for a cell that experiences a change in the water potential of its surroundings (e.g., see Figure 3.9), the movement of water across the cell membrane will decrease with time as the internal and external water potentials converge (Figure 3.11). The rate approaches zero in an exponential manner (see Dainty 1976), with a half-time (half-times conveniently characterize processes that change exponentially with time) given by the following equation:

$$t_{1/2} = \left(\frac{0.693}{(A)(Lp)}\right)\left(\frac{V}{\varepsilon - \Psi_s}\right) \qquad (3.7)$$

where V and A are, respectively, the volume and surface of

(A)

Ψ_w = −0.2 MPa
Ψ_w = 0 MPa
$\overline{\Delta\Psi_w = 0.2\ \text{MPa}}$

Water flow

Initial $J_v = Lp\ (\Delta\Psi_w)$
   $= 10^{-6}\ \text{m s}^{-1}\ \text{MPa}^{-1}$
   $\times\ 0.2\ \text{MPa}$
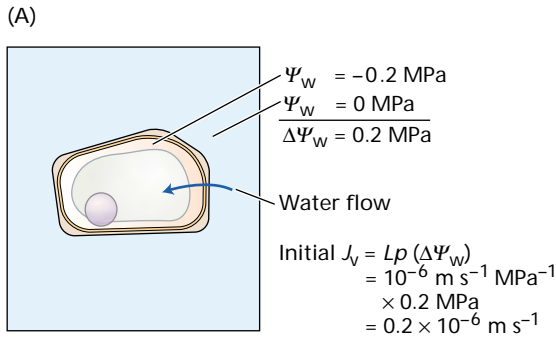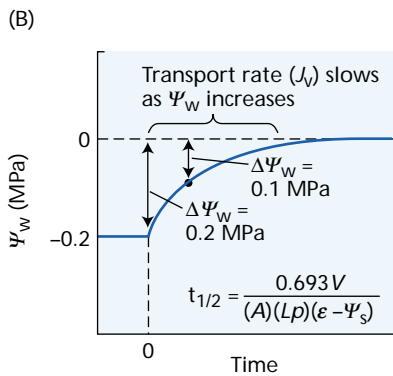 $= 0.2 \times 10^{-6}\ \text{m s}^{-1}$

FIGURE 3.11   The rate of water transport into a cell depends on the water potential difference ($\Delta\Psi_w$) and the hydraulic conductivity of the cell membranes (Lp). In this example, (A) the initial water potential difference is 0.2 MPa and Lp is 10^{-6} m s^{-1} MPa^{-1}. These values give an initial transport rate (J_v) of 0.2×10^{-6} m s^{-1}. (B) As water is taken up by the cell, the water potential difference decreases with time, leading to a slowing in the rate of water uptake. This effect follows an exponentially decaying time course with a half-time ($t_{1/2}$) that depends on the following cell parameters: volume (V), surface area (A), Lp, volumetric elastic modulus (ε), and cell osmotic potential (Ψ_s).

(B)

Transport rate (J_v) slows as Ψ_w increases

$\Delta\Psi_w = 0.1$ MPa

$\Delta\Psi_w = 0.2$ MPa

$t_{1/2} = \dfrac{0.693\,V}{(A)(Lp)(\varepsilon - \Psi_s)}$

Time

the cell, and Lp is the **hydraulic conductivity** of the cell membrane. Hydraulic conductivity describes how readily water can move across a membrane and has units of volume of water per unit area of membrane per unit time per unit driving force (i.e., m^3 m^{-2} s^{-1} MPa^{-1}). For additional discussion on hydraulic conductivity, see Web Topic 3.6.

A short half-time means fast equilibration. Thus, cells with large surface-to-volume ratios, high membrane

hydraulic conductivity, and stiff cell walls (large ε) will come rapidly into equilibrium with their surroundings. Cell half-times typically range from 1 to 10 s, although some are much shorter (Steudle 1989). These low half-times mean that single cells come to water potential equilibrium with their surroundings in less than 1 minute. For multicellular tissues, the half-times may be much larger.

The Water Potential Concept Helps Us Evaluate the Water Status of a Plant

The concept of water potential has two principal uses: First, water potential governs transport across cell membranes, as we have described. Second, water potential is often used as a measure of the *water status* of a plant. Because of transpirational water loss to the atmosphere, plants are seldom fully hydrated. They suffer from water deficits that lead to inhibition of plant growth and photosynthesis, as well as to other detrimental effects. Figure 3.12 lists some of the physiological changes that plants experience as they become dry.

The process that is most affected by water deficit is cell growth. More severe water stress leads to inhibition of cell division, inhibition of wall and protein synthesis, accumu-

Physiological changes due to dehydration:

Abscisic acid accumulation
Solute accumulation
Photosynthesis
Stomatal conductance
Protein synthesis
Wall synthesis
Cell expansion

−0   −1   −2   −3   −4
Water potential (MPa)

Pure water

Well-watered plants

Plants under mild water stress
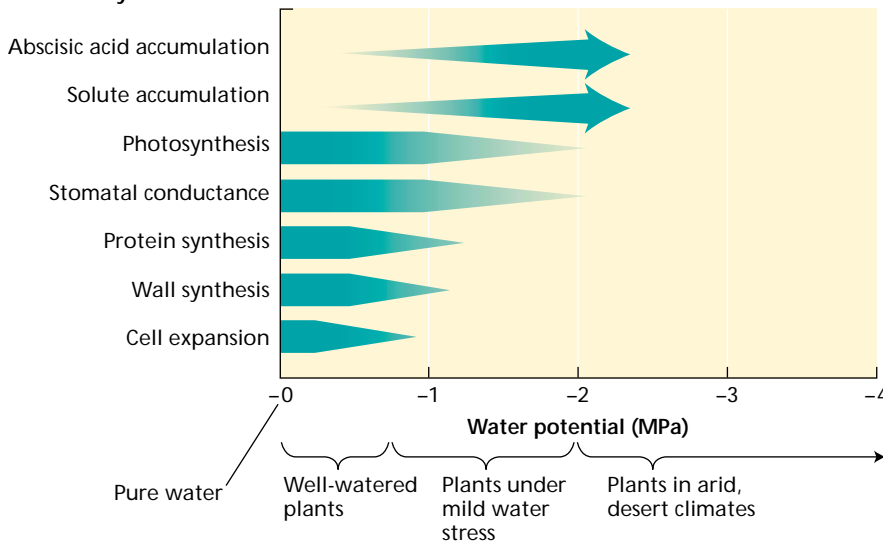
Plants in arid, desert climates

FIGURE 3.12   Water potential of plants under various growing conditions, and sensitivity of various physiological processes to water potential. The intensity of the bar color corresponds to the magnitude of the process. For example, cell expansion decreases as water potential falls (becomes more negative). Abscisic acid is a hormone that induces stomatal closure during water stress (see Chapter 23). (After Hsiao 1979.)

lation of solutes, closing of stomata, and inhibition of photosynthesis. Water potential is one measure of how hydrated a plant is and thus provides a relative index of the *water stress* the plant is experiencing (see Chapter 25).

Figure 3.12 also shows representative values for Ψ_w at various stages of water stress. In leaves of well-watered plants, Ψ_w ranges from –0.2 to about –1.0 MPa, but the leaves of plants in arid climates can have much lower values, perhaps –2 to –5 MPa under extreme conditions. Because water transport is a passive process, plants can take up water only when the plant Ψ_w is less than the soil Ψ_w. As the soil becomes drier, the plant similarly becomes less hydrated (attains a lower Ψ_w). If this were not the case, the soil would begin to extract water from the plant.

The Components of Water Potential Vary with Growth Conditions and Location within the Plant

Just as Ψ_w values depend on the growing conditions and the type of plant, so too, the values of Ψ_s can vary considerably. Within cells of well-watered garden plants (examples include lettuce, cucumber seedlings, and bean leaves), Ψ_s may be as high as –0.5 MPa, although values of –0.8 to –1.2 MPa are more typical. The upper limit for cell Ψ_s is set probably by the minimum concentration of dissolved ions, metabolites, and proteins in the cytoplasm of living cells.

At the other extreme, plants under drought conditions sometimes attain a much lower Ψ_s. For instance, water stress typically leads to an accumulation of solutes in the cytoplasm and vacuole, thus allowing the plant to maintain turgor pressure despite low water potentials.

Plant tissues that store high concentrations of sucrose or other sugars, such as sugar beet roots, sugarcane stems, or grape berries, also attain low values of Ψ_s. Values as low as –2.5 MPa are not unusual. Plants that grow in saline environments, called **halophytes**, typically have very low values of Ψ_s. A low Ψ_s lowers cell Ψ_w enough to extract water from salt water, without allowing excessive levels of salts to enter at the same time. Most crop plants cannot survive in seawater, which, because of the dissolved salts, has a lower water potential than the plant tissues can attain while maintaining their functional competence.

Although Ψ_s *within* cells may be quite negative, the apoplastic solution surrounding the cells—that is, in the cell walls and in the xylem—may contain only low concentrations of solutes. Thus, Ψ_s of this phase of the plant is typically much higher—for example, –0.1 to 0 MPa. Negative water potentials in the xylem and cell walls are usually due to negative Ψ_p. Values for Ψ_p within cells of well-watered garden plants may range from 0.1 to perhaps 1 MPa, depending on the value of Ψ_s inside the cell.

A positive turgor pressure (Ψ_p) is important for two principal reasons. First, growth of plant cells requires turgor pressure to stretch the cell walls. The loss of Ψ_p under water deficits can explain in part why cell growth is so sensitive to water stress (see Chapter 25). The second reason positive

turgor is important is that turgor pressure increases the mechanical rigidity of cells and tissues. This function of cell turgor pressure is particularly important for young, nonlignified tissues, which cannot support themselves mechanically without a high internal pressure. A plant **wilts** (becomes flaccid) when the turgor pressure inside the cells of such tissues falls toward zero. Web Topic 3.7 discusses plasmolysis, the shrinking of the protoplast away from the cell wall, which occurs when cells in solution lose water.

Whereas the solution inside cells may have a positive and large Ψ_p, the water outside the cell may have negative values for Ψ_p. In the xylem of rapidly transpiring plants, Ψ_p is negative and may attain values of –1 MPa or lower. The magnitude of Ψ_p in the cell walls and xylem varies considerably, depending on the rate of transpiration and the height of the plant. During the middle of the day, when transpiration is maximal, xylem Ψ_p reaches its lowest, most negative values. At night, when transpiration is low and the plant rehydrates, it tends to increase.

SUMMARY

Water is important in the life of plants because it makes up the matrix and medium in which most biochemical processes essential for life take place. The structure and properties of water strongly influence the structure and properties of proteins, membranes, nucleic acids, and other cell constituents.

In most land plants, water is continually lost to the atmosphere and taken up from the soil. The movement of water is driven by a reduction in free energy, and water may move by diffusion, by bulk flow, or by a combination of these fundamental transport mechanisms. Water diffuses because molecules are in constant thermal agitation, which tends to even out concentration differences. Water moves by bulk flow in response to a pressure difference, whenever there is a suitable pathway for bulk movement of water. Osmosis, the movement of water across membranes, depends on a gradient in free energy of water across the membrane—a gradient commonly measured as a difference in water potential.

Solute concentration and hydrostatic pressure are the two major factors that affect water potential, although when large vertical distances are involved, gravity is also important. These components of the water potential may be summed as follows: $\Psi_w = \Psi_s + \Psi_p + \Psi_g$. Plant cells come into water potential equilibrium with their local environment by absorbing or losing water. Usually this change in cell volume results in a change in cell Ψ_p, accompanied by minor changes in cell Ψ_s. The rate of water transport across a membrane depends on the water potential difference across the membrane and the hydraulic conductivity of the membrane.

In addition to its importance in transport, water potential is a useful measure of the water status of plants. As we will see in Chapter 4, diffusion, bulk flow, and osmosis all

help move water from the soil through the plant to the atmosphere.

Web Material

Web Topics

3.1 Calculating Capillary Rise

Quantification of capillary rise allows us to assess the functional role of capillary rise in water movement of plants.

3.2 Calculating Half-Times of Diffusion

The assessment of the time needed for a molecule like glucose to diffuse across cells, tissues, and organs shows that diffusion has physiological significance only over short distances.

3.3 Alternative Conventions for Components of Water Potential

Plant physiologists have developed several conventions to define water potential of plants. A comparison of key definitions in some of these convention systems provides us with a better understanding of the water relations literature.

3.4 The Matric Potential

A brief discussion of the concept of matric potential, used to quantify the chemical potential of water in soils, seeds, and cell walls.

3.5 Measuring Water Potential

A detailed description of available methods to measure water potential in plant cells and tissues.

3.6 Understanding Hydraulic Conductivity

Hydraulic conductivity, a measurement of the membrane permeability to water, is one of the factors determining the velocity of water movements in plants.

3.7 Wilting and Plasmolysis

Plasmolysis is a major structural change resulting from major water loss by osmosis.

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