## 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 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. The fact that water is limiting is the reason for the practice of crop irrigation. Water availability likewise limits the productivity of natural ecosystems. Thus, an understanding of the uptake and loss of water by plants is very important.

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. 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°. 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
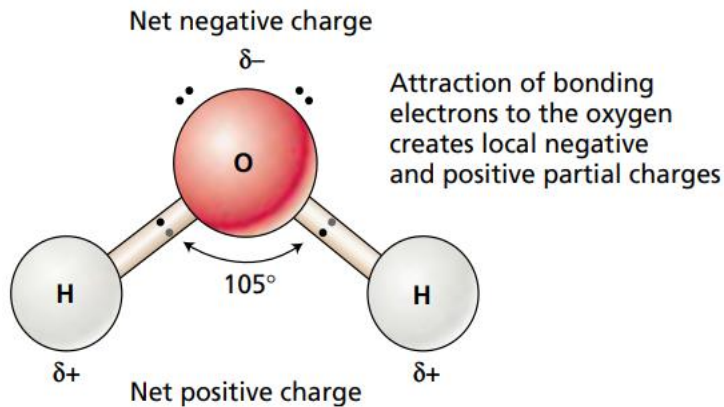
These partial charges are equal, so the water molecule carries no net charge. This separation of partial charges, together with the shape of the water molecule, makes water a polar molecule, and the opposite partial charges between neighboring water molecules tend to attract each other. The weak electrostatic 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
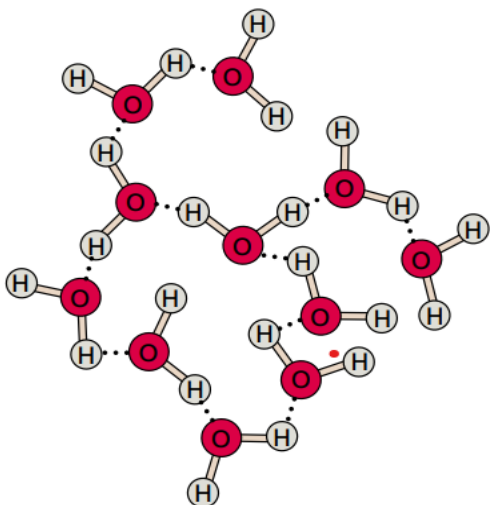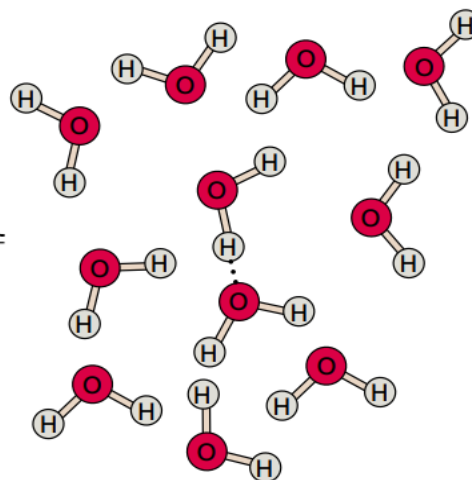
(A) Hydrogen bonding between water molecules results in local aggregations of water molecules. (B) Because of the continuous thermal agitation of the water molecules, these aggregations are very short-lived; they break up rapidly to form much more random configurations.

The 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 —NH2 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.

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

Water molecules at an air–water interface is 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 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)

(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.

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. 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. 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 about how water moves across plant membranes. 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. 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. We will now consider the two major processes in water transport: molecular diffusion and bulk flow.
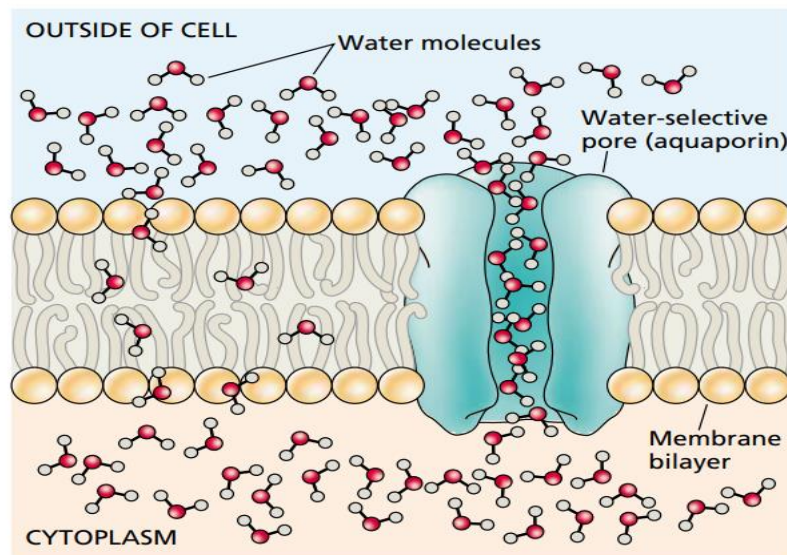
Diffusion Is the Movement of Molecules by Random Thermal Agitation
Water molecules in a solution are not static; they are in continuous motion, colliding with one another and exchanging kinetic energy. The molecules intermingle as a result of their random thermal agitation. This random motion is called 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.
In the 1880s the German scientist Adolf Fick discovered that the rate of diffusion is directly proportional to the concentration gradient that is, to the difference in concentration of substance between two points separated by the distance. In symbols, we write this relation as Fick's first law:

$$J_s = -D_s \frac{\Delta c_s}{\Delta x}$$

The rate of transport, or the flux density (Js), is the amount of substance s crossing a unit area per unit time (e.g., Js may have units of moles per square meter per second [mol m^{-2} s^{-1}]). The diffusion coefficient (Ds) 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 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). 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 then the concentration front moves away from the starting position. As the substance diffuses away from the starting point, the concentration gradient becomes less steep and thus net movement becomes slower.

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, most often in response to a pressure gradient. 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. 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.

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.

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, is a measure of the free energy of water per unit volume.

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

$$\Psi_w = \Psi_s + \Psi_p + \Psi_g$$

The terms Ψs, Ψp, and Ψg denote the effects of solutes, pressure, and gravity, respectively, on the free energy of water. The reference state used to define water potential is pure water at ambient
pressure and temperature.

Solutes. The term Ψs, 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.

Pressure. The term Ψp is the hydrostatic pressure of the solution. Positive pressures raise the water potential; negative pressures reduce it. Sometimes Ψp is called *pressure potential*. The positive hydrostatic pressure within cells is the pressure referred to as *turgor pressure*. The value of Ψp 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.

Gravity. Gravity causes water to move downward unless the force of gravity is opposed by an equal and
opposite force. The term Ψg depends on the height (*h*) of the water above the reference-state water, the density of water (*D*w), and the acceleration due to gravity (*g*).

$$\Psi_g = \rho_w g h$$

where *Dwg* 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 (Y_g) is generally omitted because it is negligible compared to the osmotic potential and the hydrostatic pressure. Thus, in these cases the equation can be simplified as follows:

$$\Psi_w = \Psi_s + \Psi_p$$

Imagine an open beaker full of pure water at 20°C. 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 ($\Psi_w = \Psi_s + \Psi_p$).

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, accumulation 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. In leaves of well-watered
plants, Y_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.