

# The Ascent of Water in Plants

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The problem of the rise of water in tall plants is as old as the science of plant physiology. In this chapter, we consider the cohesion theory, which is the best formulation to explain how water can get to the top of tall trees and vines.

## 20.1 THE PROBLEM

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Let us consider why it is hard for water to get to the top of trees. A suction pump can lift water only to the barometric height, which is the height that is supported by atmospheric pressure (1.0 atm) or 1033 cm (10.33 m; 33.89 ft) (Salisbury and Ross, 1978; p. 49). If a hose or pipe is sealed at one end and filled with water, and then placed in an upright position with the open end down and in water, atmospheric pressure will support the water column to 10.33 m, theoretically. At this height, the pressure equals the vapor pressure of water at its temperature. Above this height of 1033 cm, water turns to vapor. When the pressure is reduced in a column of water so that vapor forms or air bubbles appear (the air coming out of solution), the column is said to cavitate (Salisbury and Ross, 1978; p. 49). My father, Don Kirkham, and his students tried to see how far they could climb the outside back stairs of the Agronomy Building at the Iowa State University with a hose, closed end in hand and with the hose's bottom in a water bucket on the ground. The column of water in the hose collapsed before they climbed 10.33 m. This was probably because of impurities on the hose wall. Engineers cannot pull water up out of water-logged mines more than about 9 m (Surridge, 2008).

## 20.2 HOW WATER GETS TO THE TOP OF TALL BUILDINGS AND ANIMALS

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How does water get to the top of tall trees? The tallest tree in the world was thought to be a *Sequoia* (an evergreen tree) in California, and its height

was estimated to be 111.6 m (366.1 ft) (Salisbury and Ross, 1978; p. 49). In 2000, a tree 367.5 ft tall was discovered (National Geographic, 2000). Then, in the summer of 2006, the world's tallest tree to date, a coastal redwood, was discovered (Preston, 2006, 2008; Economist, 2007). It is 379.1 ft tall (115.5 m). Redwoods can reach 150 ft in <100 years (Bourne, 2009; unpaginated fold-out between p. 38 and p. 39).

Let us first consider how water gets to the top of skyscrapers. Modern buildings in cities use electrical pumping systems to get water to high floors. But before electrical pumps were available, wooden tanks that hold water were used, and still are used, to raise water. People who live in a tall building and are not getting a good strong shower are probably too close to the holding tank (Weber, 1989). In those buildings in which the plumbing requires the help of gravity to create sufficient water pressure, a tank needs to be elevated at least 25 ft (762 cm) above a building's highest standpipe. One gets 1 lb/in<sup>2</sup> (0.06896 bars) of pressure for every 2.3 (70 cm) ft in height. In New York City, the skyline is dotted with >10,000 of these tanks, and they vary in size from 5000 to 50,000 gallons (19,000 to 190,000 L) and run from 12 to 20 ft (3.658–6.096 m) high. They have been in use since 1890. Tanks last for 60 years (Weber, 1989). To make a wooden tank, lumber is cut from yellow cedar from British Columbia or from California redwood. The people who replace the wooden tanks are highly trained and have a difficult and dangerous job getting the planks to great heights (National Public Radio, 2002).

Physicists who question how water can get to the top of trees point out that animals have pumps (hearts) that plants do not have. So let us consider how fluids get to the top of a giraffe, probably the tallest animal. An upright giraffe ought to suffer massive edema in its feet; moreover, when it lowers its head to drink, the blood should rush down into it and be unable to flow up again (Pedley, 1987). But pressure measurements in the giraffe reveal why neither of these things happens.

A countergravitational gradient of venous pressure ( $P_v$ ) exists in the giraffe's neck. Measurements of the gravitational (or hydrostatic) gradient of pressure with height, in an upright animal 3.5 m tall, show that blood pressure in an artery in the head is as much as 110 mm Hg ( $\sim 1.5$  m H<sub>2</sub>O or about 15 kPa) lower than the level of the heart, which is about 200 mm Hg above atmospheric pressure, double the human value. This high arterial pressure near the giraffe's heart provides normal blood pressure and perfusion to the brain (Hargens et al., 1987).

Two features of the peripheral circulation that inhibit edema in a standing giraffe are (1) a high resistance to flow in the thick-walled arterioles, which keeps venous pressure, and hence capillary pressure, well below arterial pressure [an arteriole is a small branch of an artery leading into capillaries (Hickman, 1961; p. 511)]; and (2) very tight skin in the

lower legs (an “antigravity suit”), which allows tissue pressure to be much higher than in humans (in humans, tissue pressure is about 0).

Even so, there is a net filtration pressure of  $>80$  mm Hg, and quietly standing giraffes will be susceptible to some edema. In the ambulant giraffe, however, the “muscle pump” comes into play, as in humans, squeezing blood up out of the lower veins as the skeletal muscles contract, and sucking it in again through the capillaries as they relax, backflow in the veins being prevented by valves. These pressures move fluid upward against gravity. The giraffe’s jaw muscles (chewing actions) do the same to pump blood up the neck. (A vein is about twice the cross-section of its corresponding artery. Veins, especially in the lower parts of the body, are provided with valves to prevent the backflow of blood (Hickman, 1961; p. 629).) Dinosaurs were even taller than giraffes, and they may have had several hearts to raise fluids to their heads (Dr Octave Levenspiel, Sigma Xi Lecture, “A Chemical Engineer Visits Dinosaurland”, Kansas State University, April 8, 2002).

## 20.3 COHESION THEORY

In plants, no standing tanks, pumps (hearts), or valves have been observed. If one looks through books on plant anatomy, one sees no such structures (Esau, 1965, 1977). So, again we ask, “How does water get to the top of tall trees?”

At present, the *cohesion theory*, or sap-tension theory, is the theory generally accepted as the one that explains most satisfactorily the way that water ascends in plants. (The dictionary defines *sap* as “the juices of a plant, especially the watery solution which circulates through the vascular tissue” (Webster’s Collegiate Dictionary, 1939).) Here we will use interchangeably the terms “sap” and “water in the tracheary cells of the xylem tissue”. We recognize that the fluid in the tracheary cells is not pure water, but a dilute aqueous solution (Nobel, 1974; p. 393). Even in mangroves, which grow in salt water, the sap in the xylem tissue is very nearly salt free and changes the melting point of water  $<0.1$  °C (Hammel and Scholander, 1976; p. 32). A  $0.1$  °C depression of the freezing point of water would be brought about by a  $0.027$  molal solution of NaCl at  $25$  °C, which is about  $-1$  bar (Lang, 1967). The  $<0.1$  °C depression in the freezing point, as observed by Hammel and Scholander (1976), would mean that the sap has an osmotic potential of  $>-1.0$  bar. Scholander et al. (1965) show that the osmotic potential ( $\Psi_{\pi}$ ) in the sap in mangrove is  $-0.3$  atm (Figure 20.1).

Let us review xylem tissue (Chapter 15, Section 15.1, Part G). The xylem tissue is made up of four types of cells (Table 15.1): vessel members (also called xylem elements), the conducting cells that occur only in

## The ascent of sap

Air

$$T = 20\text{ C}$$

$$RH = 50\%$$

$$\Psi = -943$$

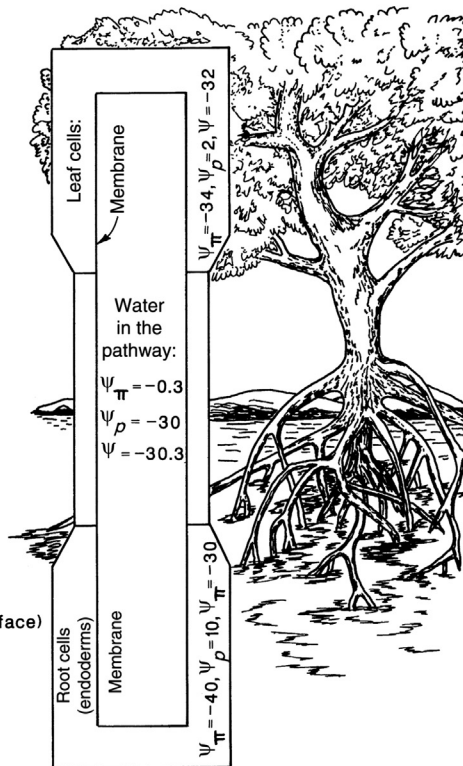
(Potentials in atmospheres)

Seawater

$$\Psi_{\pi} = -30$$

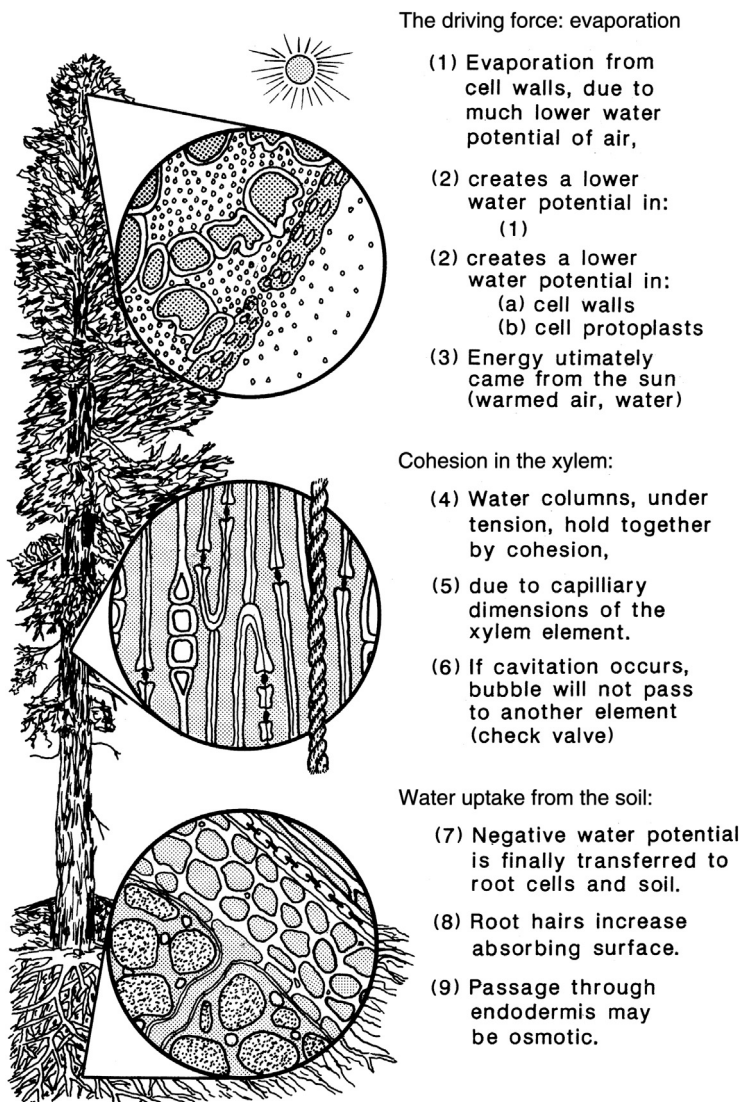
$$\Psi_p = -0(\text{at surface})$$

$$\Psi = -30$$



**FIGURE 20.1** Water relations of a mangrove growing with its roots immersed in seawater. The diagram indicates the essential parts of the mangrove tree from the standpoint of water relations, particularly the membranes of the endodermis and of the leaf cells. It is important to note that if leaf membranes should suddenly cease to be differentially permeable, salt and subsequently water would move from leaf cells into the pathway due to the high tension of water there, and thus, the leaf cells would collapse. Data from [Scholander et al. \(1965\)](#). From [Salisbury and Ross \(1978\)](#), p. 61. Reprinted with permission of Brooks/Cole, a division of Thomson Learning; [www.thomsonrights.com](http://www.thomsonrights.com). Fax 800 730-2215.

angiosperms (the flowering plants), the most highly evolved plants; tracheids, the conducting cells that occur in angiosperms and gymnosperms (e.g., the conifers); fibers, which give structural support; and parenchyma cells, which store carbohydrates and assist in lateral movement of water and solutes into and out of the conducting cells. At maturity, vessel members, tracheids, and fibers are dead. Only the parenchyma cells are living. Also, at maturity, the end walls of vessel members disintegrate, and, consequently, a long tube, called a xylem vessel, is formed ([Esau, 1977](#); pp. 101–124).



**FIGURE 20.2** The cohesion theory of the ascent of sap summarized. From *Salisbury and Ross (1978)*, p. 58. Reprinted with permission of Brooks/Cole, a division of Thomson Learning: [www.thomsonrights.com](http://www.thomsonrights.com). Fax 800 730-2215.

The cohesion theory of the ascent of sap was foreshadowed by Stephen Hales (1677–1761; English clergyman, physiologist, chemist, and inventor, famous for his pioneering studies in animal and plant physiology), Julius von Sachs (1832–1897; German botanist and outstanding plant

physiologist), and Eduard Strasburger (1844–1912; German botanist and one of first to realize the importance of the nucleus and chromosomes in heredity). They all concluded that transpiration produces the pull causing the ascent of sap (Kramer, 1983; p. 282). The first successful attempt to measure cohesion in water experimentally seems to have been made by Berthelot in 1850 (Greenidge, 1957). He obtained values to 50 atm by a method similar to that used later by Dixon and Joly (1895). Boehm (1893) demonstrated that transpiring branches could raise mercury above barometric pressure, but the demonstration by Askenasy (1895) and Dixon and Joly (1895), showing that water has considerable tensile strength, was necessary to make the cohesion theory acceptable (Kramer, 1983; p. 282).

The cohesion theory, as first set forth by Dixon and Joly (1895) and Dixon (1895, 1897, 1914), assumes that diffusion of water from the non-collapsible xylem elements in contact with the leaf cells creates a state of tension within the water columns in the xylem vessels. This tension is possible because of the cohesion of water molecules and their adhesion to the hydrophilic walls of the xylem elements. Briggs (1917, p. 108) points out the importance of adhesion. He said, “We may consider the outer surfaces of these cells to be saturated with water, which retreats into the wall tissue in such a way as to form a great number of capillary surfaces of high curvature, this curvature in fact being such as would be necessary to support a capillary column of the observed height”. Tension in the water columns is assumed to lift water from the roots to the leaves, in addition to reducing the potential energy of the water in the root xylem tissue until water diffuses from the soil into the root during absorption of the water. The cohesion theory assumes continuity of water columns, laterally and vertically, in the conducting elements of the xylem tissue. These water columns are ultimately placed under tensile strain. But widespread rupture is believed not to occur in the water columns under tensile strain owing to the purported cohesive properties of water when entrapped in small capillaries. Figure 20.2 from Salisbury and Ross (1978, p. 58) outlines the cohesion theory. (For a biography of Dixon, see the Appendix, Section 20.9, and for that of Joly, see the Appendix, Section 20.10.)

## 20.4 LIMITATIONS OF THE COHESION THEORY

Even though most plant physiologists feel that the cohesion theory is probably the correct explanation for the rise of water in plants, the theory has limitations. The main difficulty is that it postulates a system of potentially great instability and vulnerability, although it is clear that the water-conducting system in plants must be both stable and



invulnerable. Objections to the theory include three major points (Kramer, 1983, p. 283; Salisbury and Ross, 1978, pp. 58–60):

1. The tensile strength of water is inadequate under the great tensions necessary to pull water to the top of plants, especially tall plants.
2. There is insufficient evidence for the existence of continuous water columns (i.e., water columns under tension are not stable and they cavitate, or form cavities, hollows, or bubbles).
3. It seems impossible to have tensile channels in the presence of free air bubbles, which can occur when trees in cold climates freeze and then thaw.

Let us consider each point. First, is the tensile strength of water adequate to pull water to the top of plants? Tensile strength is defined as the “resistance to lengthwise stress, measured by the greatest load in weight per unit area pulling in the direction of length that a given substance can bear without tearing apart” (Webster’s New World Dictionary of the American Language, 1959).

Nobel (1970, pp. 35–36, p. 40; 1974, pp. 46–47, pp. 52–53) calculates the tensile strength of water. Let us do the calculations that Nobel does. We must consider the structure of ice (Nobel, 1974; p. 46). Ice is a coordinated crystalline structure in which essentially all the water molecules are joined by hydrogen bonds (Figure 3.2). When heat is added so that the ice melts, some of these intermolecular hydrogen bonds are broken. The heat of fusion of ice at 0 °C is 80 cal/g or 1.44 kcal/mol (Remember: 18 g/mol for water;  $80 \text{ cal/g} \times 18 \text{ g/mol} = 1440 \text{ cal/mol} = 1.44 \text{ kcal/mol}$ ) The total rupture of the intermolecular hydrogen bonds involving each of its hydrogens would require 9.6 kcal/mol of water. The 9.6 kcal/mol is a given value. Nobel (1974, p. 46) gives references for the value. He cites work by Eisenberg and Kauzmann (1969; e.g., see p. 145, p. 269) and Pauling (1964; e.g., see p. 456) for references on the hydrogen bond energy. Nobel (1974, p. 46) points out that the actual magnitude of the hydrogen bond energy assigned to ice depends somewhat on the particular operational definition used in the measurement of the various bonding energies. Therefore, the quoted values vary somewhat.

The heat of fusion thus indicates that  $(100)/(9.6)$ , or at most 15%, of the hydrogen bonds are broken when ice melts. Some energy is needed to overcome van der Waal’s attractions, so that <15% of the hydrogen bonds are actually broken upon melting (Nobel, 1974; p. 46).

Conversely, >85% of the hydrogen bonds remain intact for liquid water at 0 °C. Because 1.00 cal is needed to heat 1 g of water 1 °C ( $1.00 \text{ cal/g}(25)(18 \text{ g/mol})(0.001 \text{ kcal/cal})$ ), or 0.45 kcal/mol is required to heat water from 0 to 25 °C. If all this energy were used to break hydrogen bonds, >80% of the bonds would still remain intact at 25 °C. (Note:  $0.45/9.6 = 0.047$ , which is <5%; so  $85 - <5\% = >80\%$ .) The extensive amount of

intermolecular hydrogen bonds present in the liquid state contributes to the unique and biologically important properties of water, including its high tensile strength, which is of interest to us now.

If 80% of the hydrogen bonds are intact in water at 25 °C (Nobel, 1974; p. 52), then the energy will be (0.80)(9.6) or 7.7 kcal/mol, which is (7.7 kcal/mol)/(18 g/mol) or 0.43 kcal/g of water. For a density of 1.00 g/cm<sup>3</sup>, and replacing kilocalories by  $4.184 \times 10^{10}$  erg, we calculate that the energy of the hydrogen bonds is  $1.8 \times 10^{10}$  erg/cm<sup>3</sup>. (Remember: 1 J =  $10^7$  erg; 1 cal = 4.184 J; therefore, 1 cal =  $4.184 \times 10^7$  erg; 1 kcal =  $4.184 \times 10^{10}$  erg.) The tension that is applied to a water column acts against this attractive energy of the hydrogen bonds.

When the fracture is just about to occur at each hydrogen bond, the maximum possible tensile strength is developed. Thus, the maximum tensile strength would represent an input of  $1.8 \times 10^{10}$  erg/cm<sup>3</sup>. Since an erg = dyne-cm and a bar =  $10^6$  dyn/cm<sup>2</sup>, the maximum tensile strength of water corresponds to 18,000 bars.

Nobel's (1974) theoretical considerations, therefore, show that the calculated value for the tensile strength of water is large (18,000 bars) and would permit the rise of water in plants even under great tensions. Tensions in higher (more evolved) plants probably never exceed 100 atm. Lower plants such as fungi apparently can grow in soil with a tension (or absolute value of matric potential) of |400| bars (Harris, 1981; p. 26). What values of the tension of water have been measured experimentally? Dixon and Joly (1895) estimated that water entrapped in glass tubes of a small diameter could withstand tensions >200 atm without fracture. Ursprung (1929) calculated that tensions on the order of 300 atm were reached in annulus cells of discharging fern sporangia. Briggs (1950) employed a centrifugal method to obtain values of about 220 atm for the tensile strength of water. (See Figure 20.3 for Briggs's method of measuring the cohesive properties of water using a bent centrifuge tube, called a Z-tube. His biography is given in Chapter 10, Section 20.5.) Centrifugal methods are now being used with xylem tissue segments (e.g., 28 cm long) to determine xylem vulnerability to embolism (Cochard et al., 2005, 2010).

In contrast to the foregoing rather large values, a number of other investigators have demonstrated that water may have a relatively low tensile strength. Loomis et al. (1960) suggested that Ursprung's values of the tensile strength of water were open to question because of a confusion of adsorption forces with cohesion. Scholander et al. (1955), through centrifugation in glass tubes, observed tensile values from 10 to 20 atm without producing cavitation of water. When the experiments were repeated using plant material, they observed much lower values (1–3 atm). Also, they were unable to fit hydrostatic pressures in transpiring grape vines into a pattern that followed the cohesion theory. Measured pressure did not indicate cohesion tension at any time, and they concluded that tensile sap



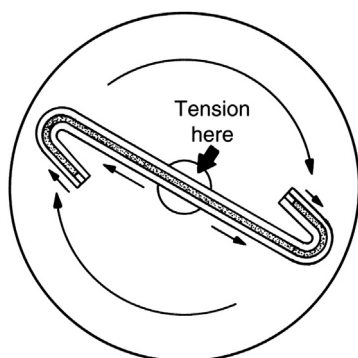


FIGURE 20.3 Method of measuring the cohesive properties of water using a centrifuged Z-tube. Small arrows indicate the direction of centrifugal force and principle of balancing due to the Z-tube. These tubes are centrifuged causing tension on the water at the center of the tube. The tension present when the water column breaks can be calculated. From [Salisbury and Ross \(1978\)](#), p. 59. Reprinted with permission of Brooks/Cole, a division of Thomson Learning: [www.thomsonrights.com](http://www.thomsonrights.com). Fax 800 730-2215.

columns, if any exist in the vessels of grapevine, are few. Measurements taken on Douglas fir (*Pseudotsuga menziesii*) trees, however, did follow the pattern that one would expect if water were rising in the plants according to the cohesion theory ([Scholander et al., 1965](#)) (Figure 20.4). That is, the hydrostatic pressure at the top of the trees was more negative than at the

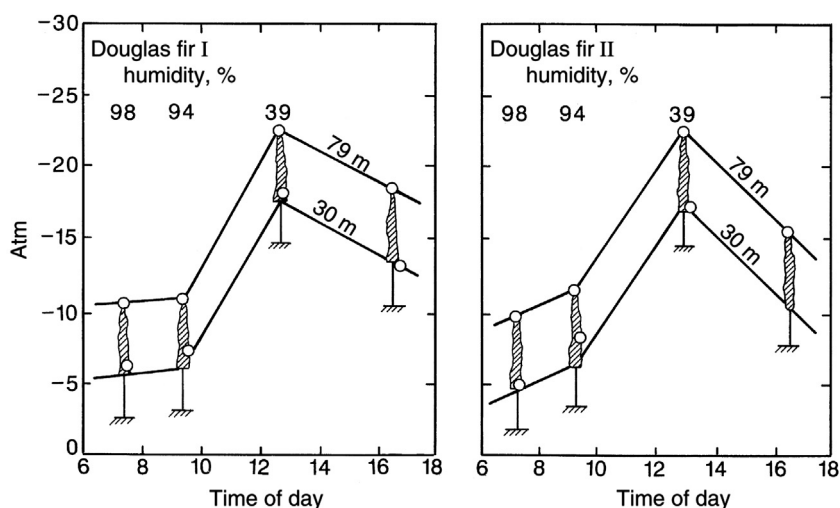


FIGURE 20.4 Differences in hydrostatic pressure in the upper and lower parts of crowns of Douglas fir trees at various times of the day as measured on excised twigs in a pressure chamber. Reprinted with permission from [Scholander et al. \(1965\)](#), American Association for the Advancement of Science.

bottom of the trees. [Greenidge \(1957\)](#) discusses different techniques used to measure the tensile strength of water that yield values ranging from 0.05 to 10 atm. [Smith \(1994\)](#) reviewed experimental measurements, which showed that the likely range of negative pressures that can be sustained in the xylem tissue is between  $-0.1$  and  $-0.6$  MPa.

It appears that, experimentally, water can withstand negative pressures (tensions) only up to about 300 bars without breaking ([Nobel, 1974](#); p. 52). The observed tensile strength depends on the wall material, the diameter of the xylem vessel, and any solutes present in the water. Local imperfections in the semicrystalline structure of water, such as those caused by  $H^+$  and  $OH^-$ , which are always present, even in pure water, reduce the observed tensile strength from the maximum value predicted based on hydrogen bond strengths. Nevertheless, the measured tensile strength for water provided by the intermolecular hydrogen bonds (up to 300 bars) is nearly 10% of that for copper or aluminum, and is sufficiently high to meet the demands encountered for water movement in plants ([Nobel, 1974](#); p. 53). The tensile strength of copper is 4140–4830 bars; for aluminum, it is 2070–2760 bars ([Weast, 1964](#); p. F-15).

Let us now consider the second problem with the cohesion theory. Are water columns in the xylem tissue stable under tension? Much has been written about the instability of water columns under tension and the ease with which they break by cavitation in glass capillary tubing ([Kramer, 1969](#); p. 275). It has been suggested that if they break as easily in the xylem of trees, they would soon become inoperative because of shocks such as those caused by swaying in the wind.

Considerations of nucleation prompted [Silver \(1942\)](#) to infer that the tensile strength of water is negligible. There is evidence of widespread fracture of stretched water columns and a high percentage of gas-filled, nonfunctional elements under field conditions ([Preston, 1938](#); [Greenidge, 1957](#); [Scholander, 1958](#)). However, it seems probable that the nature of the walls of the dead xylem tissue, which is filled with imbibed water, makes the water columns in the stems of plants more stable than those in glass tubes. If cavitation caused by air entry should occur in the conducting tubes of the xylem tissue, the matric potential component attributed to the hydrophilic nature of the surfaces involved could be expected to maintain surface films of water capable of transporting water up the stem ([Gardner, 1965](#)). The cell walls in the conducting cells of the xylem tissue are probably charged and exhibit double-layer characteristics. Thus, even if a column breaks, there is a thin layer of adsorbed water, with a concave curvature, which ensures that entrapped air eventually will be dissolved ([W.R. Gardner, personal communication, February 29, 2000](#)).

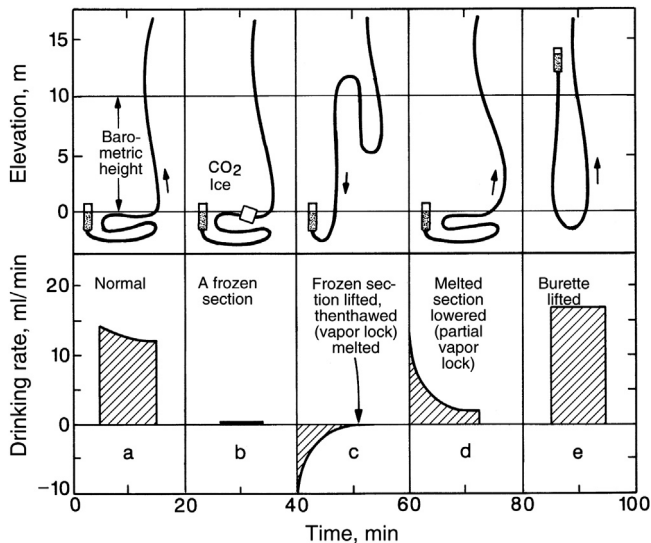
[Greenidge \(1955, 1957\)](#) did experiments in which a dye was injected into the xylem of trees after severing all vessels of the stem by two or more opposing saw cuts. The dye not only moved readily to the top of such

trees but it also completely stained the wood immediately below and above the saw cuts, indicating capillary movement under low tension and showing no evidence of rupture of stressed water columns. In other experiments, the dye moved to the top of tree trunks from which all leafy branches had been removed and all vessels severed at one or more points.

It is true that the water columns in large xylem vessels often break and that smaller vessels remain water filled. If vessels become filled with air (gas bubbles), the bubbles usually cannot spread beyond the vessel members or tracheids in which they developed (Kramer, 1983; p. 284). We will come back to this point in the next section when we see how bubbles cannot spread. Thus, the entire conducting system is not suddenly blocked by expanding bubbles. Utsumi et al. (2003) found that even though some tracheids in the sapwood of conifers had no water, some tracheids retained water. Water transport occurred mainly in earlywood tracheids, whereas latewood tracheids played no role or only a minor role in water transport. In a study of moisture relations in tall lianas, Scholander et al. (1957) found that allowing vessels of a cut vine to become plugged with air caused a lowered hydrostatic pressure in the plant, but did not reduce the rate of water uptake, indicating that water movement was shifted to the numerous tracheids of the stem. Again they found no direct evidence of cohesion tension. The work by Scholander (1958) and Scholander et al. (1957) indicated that there is a large "safety factor" (Kramer, 1983; p. 284) in the xylem. Although partial blockage increases the resistance to flow of water, the volume of flow is not necessarily reduced. The ability to hear the water columns break is supporting evidence that the columns are under tension, and, when they cavitate, the sound can be picked up acoustically. Milburn and Johnson (1966) developed an acoustic detector, and subsequent experimenters have monitored cavitation using the technique (e.g., see Tyree et al., 1986; Jackson and Grace, 1996). The method has been used to monitor water stress in crop plants and to tell when to irrigate (Senft, 1986).

Let us now consider the third problem. Microscopic observations have shown that an air blockage occurs when some trees in cold climates are frozen (Johnson, 1977). Inability to restore the water columns in the spring may well be the factor that excludes certain trees and especially vines with large vessels from these regions (Salisbury and Ross, 1978; p. 60) (Figure 20.5). But how do trees grow in such regions?

Imagine a northern tree thawing in the spring. As the ice melts, the tracheids become filled with liquid containing the many bubbles of air that had been forced out by freezing. As melting continues and transpiration begins, tension begins to develop in the xylem tissue. Because of the small dimensions of the tracheids involved, the pressure difference across the curved air–water interface bounding the bubbles would be considerable, resulting in a much higher pressure in an air bubble than would



**FIGURE 20.5** Scholander's experiments with tropical rattan vines (*Calamus* sp.). (a) The vine is cut off under water and a burette is attached, allowing measurement of the rate of water uptake. If the burette is stoppered, water continues to be taken up until a vacuum is created in the burette, and the water boils. (b) To freeze the water in the vine, the burette first had to be taken off so that air entered all the xylem elements, vapor-locking the system. Then, after freezing, the vapor-locked portion (~2 m) was cut off under water and the burette was attached again. There was still no water uptake, indicating that freezing had indeed blocked the system. (c) If the vapor-locked portion was hoisted above the barometric height and allowed to thaw, some water ran out, but there was no uptake, indicating that the system was now vapor locked. (d) If the vapor-locked portion was lowered to the ground, there was a rapid initial uptake as vapor condensed to water, breaking the vapor lock, but then the uptake was slower than it was originally because some air had been excluded from freezing. (e) When the burette was elevated 11 m, the rate of water uptake returned to the original level, indicating that the vapor lock had now been completely eliminated. *Data from Scholander et al. (1961). Reprinted with permission from Scholander et al. (1961), American Association for the Advancement of Science.*

exist in the water. Any bubbles that form should dissolve fairly readily, restoring the integrity of the water column (Gardner, 1965). Studies of wood in the spring indicate that about 10% of the tracheids are filled with vapor, but the remaining 90% appear ample to handle sap movement (Salisbury and Ross, 1978, p. 60; Kramer, 1983) (Figure 20.6). Gymnosperms with their tracheids are especially well adapted to cold climates. Trees, and especially vines with large, long vessels, are practically absent from cold climates, but are abundant in the tropics.

Dividing cambial cells in the spring also produce new water-filled conducting cells in the xylem tissue. In some ring-porous trees (trees with large vessel members) virtually all the water moves in these newly

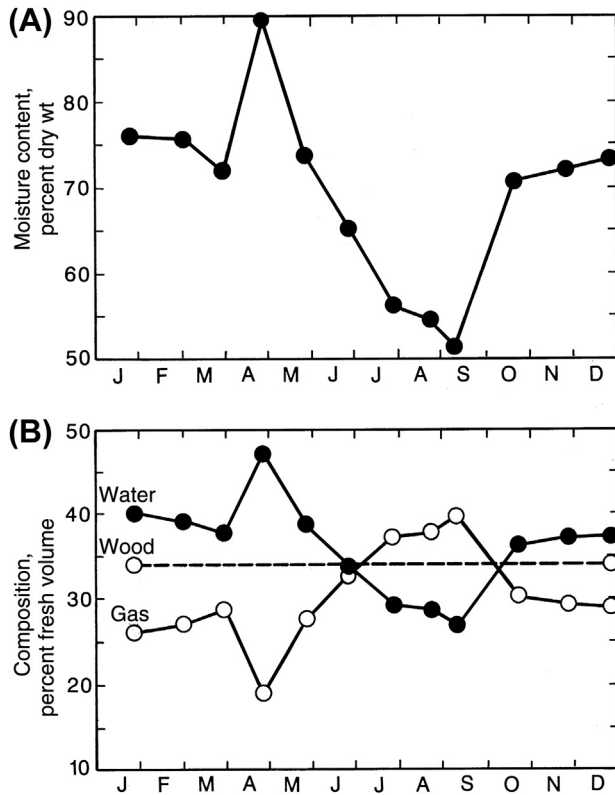


FIGURE 20.6 (A) Seasonal changes in the water content of yellow birch trunks calculated from disks cut from the base, middle, and top of the trunks. (B) Seasonal changes in the gas and water content of yellow birch tree trunks calculated as the percentage of the total volume. From [Kramer \(1983\)](#), p. 285. Reprinted by permission of Academic Press.

formed tubes ([Salisbury and Ross, 1978](#); p. 60). Root pressure may also help in filling vessel members and tracheids in the spring after freezing. *Root pressure* is a positive pressure that develops in the xylem resulting in guttation or exudation from stumps of detopped plants ([Kramer, 1983](#); p. 198). Root pressure appears to be an osmotic process in which root systems function as osmometers because of the accumulation of solutes in the xylem sap. Two factors are necessary for root pressures to exist: a differentially permeable membrane, which in most cases occurs in the endodermis in roots, and a source of solutes, which are in the xylem sap ([Kramer, 1983](#); p. 223). Root pressures of 5 or 6 bars have been recorded ([Salisbury and Ross, 1978](#); p. 50). These pressures are not sufficient to get water to the top of tall trees. Root pressures are not seen in conifer trees, including the *Sequoia* and the Douglas fir trees, under any conditions

(Salisbury and Ross, 1978; p. 50). Douglas fir trees reach over 200 ft (61 m) (Bailey, 1974; p. 117). Therefore, root pressure cannot be invoked for the force that moves water to the top of tall trees, even though it may be important for water transport in short plants such as rice (*Oryza sativa*), as pointed out by Singh et al. (2009).

## 20.5 ALTERNATIVE THEORIES TO THE COHESION THEORY

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For many decades, the cohesion theory was accepted and essentially no experiments related to it were performed between about 1960 and mid-1990s. With the advent of the pressure probe (Chapter 17, Section 17.6), measurements made with it contradicted the cohesion theory (Zimmermann et al., 1994, 1995). They showed that the necessary high tensions in the xylem were not present and that the gradient of tension with height was not present. Canny (1995), therefore, put forward a theory, called the *compensating-pressure theory*, to account for the rise of water in plants. He noted that the xylem has ray cells throughout it. These are living parenchyma cells. He said that compensating pressure is provided by the tissue pressure of xylem ray cells pressing onto the closed fluid spaces of the tracheary elements and squeezing them. The driving force is provided, as in the cohesion theory, by evaporation and the tensions generated in curved menisci in the wet cell walls of the leaf. The force is transmitted, as in the cohesion theory, by tension in the water in the tracheary elements. But this tension is maintained by compression from tissue pressure around the tracheary elements. The gravitational gradient of tension up a tall tree is compensated by increasing tissue pressure of the xylem parenchyma with height, and the need for a tension gradient to sustain the standing columns disappears. Canny's theory apparently considers that solutes in the parenchyma cells of the tissue around the tracheids and vessel members cause an imbibing of water and create a pressure on the tracheary elements. This pressure on the tracheary elements keeps the water in them from cavitation. Canny's theory was challenged by Comstock (1999), who pointed out that extreme reinforcement would be needed to sustain tissue pressures postulated by Canny's model and they are unlikely to exist. If the water potential gradient were such that the parenchyma cells have a lower water potential than the tracheary cells, water would move from the tracheary cells to the parenchyma, which does not happen. Canny's model postulates a pump-and-valve system. Flow characteristics are set by an active water pump in the roots and a one-way, regulating valve in the leaves, but a viable mechanism has not been identified (Comstock, 1999).



The pressure probe has been reevaluated (Steudle, 2001). The earlier measurements with the probe, which did not support the cohesion theory, were likely due to experimental artifacts and limitations of the probe. Tensions as high as 10 MPa are claimed to exist in the xylem, and pressure probes cannot measure such high values (Steudle, 2001). Old and more recent evidence provides strong support for the cohesion theory (Wei et al., 1999; Steudle, 2001).

Nevertheless, the cohesion theory is still challenged. Zimmermann et al. (2004) said that the rise of water in tall trees cannot depend on negative pressure gradients of several megapascals through continuous water columns from the roots to the foliage because water under such negative pressure is unstable. They postulated other forces that are involved in water ascent and suggested that water can be lifted by a series of “watergates” such as those that exist on ships in staircase locks. However, Esau (1965, 1977) does not show watergates in her books on plant anatomy. The article by Zimmermann et al. (2004) was challenged by many scientists involved in the study of long-distance water transport in plants (Angeles et al., 2004). Angeles et al. (2004) list 23 articles that support the cohesion theory.

Even though a pump-and-valve system as postulated by Canny (1995) and watergates as postulated by Zimmermann et al. (2004) have not been identified anatomically, the pit membrane in cell walls of tracheids and vessel members does have a structure that operates like a valve to shut off water moving from one part of the xylem to another (Figure 20.7, Esau, 1965; p. 40). A *pit* is a recess or cavity in the cell wall where the primary wall is not covered by a secondary wall. A pit is usually a member of a pit pair. A *pit pair* is two complementary pits of two adjacent cells. Essential components of a pit pair are two pit cavities and the pit membrane. A *pit cavity* is the entire space within a pit from pit membrane to the cell lumen. The *pit membrane* is the part of the intercellular layer and primary cell wall that limits a pit cavity externally (Esau, 1977; p. 520). A *bordered pit* is a pit in which the secondary wall overarches the pit membrane (Esau, 1977; p. 504). The *torus* is the central thickened part of the pit membrane in a bordered pit consisting mainly of middle lamella and two primary walls (Esau, 1977; p. 529).

The closest structure in a plant that looks like a valve is the pit membrane, which, as noted in the previous paragraph, is part of the intercellular layer and primary cell wall that limits a pit cavity in a cell wall. But pit membranes do not act in the same ways as valves do in veins. The pit membrane, as shown in Figure 20.7, is a middle lamella (not a living membrane), which is a layer of intercellular material, chiefly pectic substances, cementing together the primary walls of contiguous cells (Esau, 1977; p. 516). The torus in the center of the pit can move to one side to plug the pit, behaving like an inanimate valve.

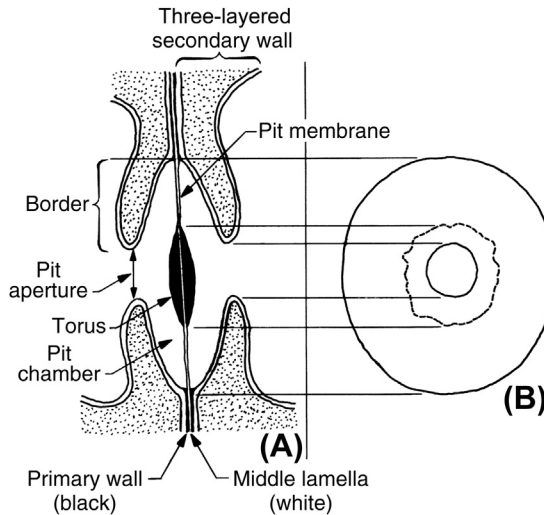


FIGURE 20.7 Bordered pit pair of *Pinus* in sectional (A) and face (B) views. The pit membrane consists of two primary walls and the intercellular lamella, but is thinner than the same triple structure in the unpitted part of the wall. The torus is formed by the thickening of the primary wall. In (B), the outline of the torus is uneven. From [Esau \(1965\)](#), p. 40. This material is used by permission of John Wiley & Sons, Inc.

Water under tension, when it is transported to substantial heights against the force of gravity, is susceptible to spontaneous phase changes from liquid to vapor (cavitation), which results in embolism that can severely limit water transport. To counteract this potentially lethal problem ([Holbrook and Zwieniecki, 2008](#)), plants employ a highly compartmentalized transport system of xylem conduits (a *conduit* is a pipe or channel) that allows failure in the integrity of a water column to be isolated from functioning conduits. The conduits are separated by the pit membranes that permit the movement of water from one conduit to the next but limit the movement of gas ([Choat et al., 2006](#)). The pit membranes have very small holes (typically 5–20 nm in diameter) that allow the passage of water ([van Doorn et al., 2011](#)). These pits prevent air in already damaged conduits from entering functional ones and “air seeding” ([Wheeler et al., 2005](#); [Cochard et al., 2009](#)). Air seeding through the pit membranes is the principal mechanism of spread of drought-induced embolisms ([Brodersen et al., 2013](#)). Cavitation apparently occurs when the torus slips from its sealing position against the aperture, allowing air to enter the functional conduit ([Pittermann et al., 2006](#)). The adhesion of the torus to the pit border may be a main determinant of cavitation resistance ([Delzon et al., 2010](#)). Older vessels are more vulnerable to cavitation than are younger vessels. [Melcher et al. \(2003\)](#) found that in

sugar maple (*Acer saccharum*) bordered pit membranes of vessels located in current year xylem withstood greater applied gas pressure (3.8 MPa) compared to bordered pit membranes in vessels located in older annual rings (2.0 MPa). Pit membranes also limit the movement of pathogens. Bacteria are able to passively move long distances from stem to leaf, when pit membranes are broken (Thorne et al., 2006). Plants can refill cavitated vessels by hydraulically isolating the damaged tissue, pumping ions from the surrounding cells, and fostering water entry through bordered pits (Bloom and Holbrook, 2001). The twining habit (Silk and Holbrook, 2005) also might allow water to move to heights. When the vine is wrapped horizontally around its support, water is under less tension than when the vine is oriented vertically. Water could puddle in the horizontal locations forming a new “ground level”, which might help push the water up the vine by capillarity.

## 20.6 NEW TECHNIQUES TO CONFIRM THE COHESION THEORY

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Experiments to study tensile values of water in plants have been done with plants that have been punched with manometers (Scholander et al., 1955), cut (Scholander et al., 1957), sawed (Greenidge, 1955), punctured with a pressure probe (Tomos and Leigh, 1999), frozen (Cochard et al., 2000), or otherwise disturbed. If it were possible to study plants under natural conditions, when they were intact, one might come to a better understanding as to what tension water is under in plants, and if tensions are built up, if they are sufficient to account for the rise of water.

Equipment has been developed that can be used to nondestructively measure the characteristics of water transport in the soil–plant–atmosphere continuum, such as nuclear magnetic resonance imaging (Scheenen et al., 2000) or sap flow gauges (Green and Clothier, 1988). The difficulty is in getting the equipment to the top of giant trees. Tall platforms have been constructed to access the top of forest canopies (12 m high) (Ellsworth, 1999). (See the cover of *Plant, Cell Environment*, March, 2006, issue for a photograph of a platform and an accompanying article (Ryan et al., 2006) that discusses hydraulic limitation to growth of tall trees.) For example, sap flow gauges could be put at the top of a tall tree to see if the flux was upward, as predicted by the cohesion theory, or downwards. Reverse flow occurs in plants if the water potential gradients allow it (Kirkham, 1983; Emmerman, 1996; Song et al., 2000; Huang, 1999). Maybe Scholander’s measurements were correct (1955, 1957) and the tension does not increase with height. (It has been said that Scholander got his measurements of tension in the top of tall vines and trees by shooting branches down with a gun and then putting them in

his pressure chamber.) It may be that tall trees and vines absorb water from the air during rainfall and that water does not need to rise from the roots. Researchers have found that giant redwood trees can absorb water through their branches hundreds of meters above the ground (Royal Society of New Zealand, 2002). Measurements of the direction of sap flow in the tops of intact tall plants are needed.

Even though the water in the xylem is frozen, the cryoscanning electron microscope (SEM) technique has been used to validate the Scholander assumption, that is, that the vessels cut open should fill with air as the water is drained away by continued transpiration (Tyree et al., 2003). In the method, petioles are frozen in liquid nitrogen soon after the petiole is cut. The petioles are then cut at different distances from the original cut surface while frozen and examined in a cryo-SEM facility, where one can distinguish vessels filled with air from those filled with ice.

A synthetic tree that duplicates the tensions observed in tall trees has been developed (Surridge, 2008; Wheeler and Stroock, 2008). Water flows in the tree at pressures of around  $-10$  atm ( $-10.1$  bars). To create their tree, Wheeler and Stroock (2008) used a hydrogel, which mimics the mesophyll of leaves by holding water in molecular-scale pores. Even though the tree is only 5 cm long and the flow is a little over  $2\text{ }\mu\text{g}$  of water per second, the synthetic tree can provide a test device for theories of how water rises in tall trees.

## 20.7 CONTROVERSY ABOUT THE COHESION THEORY

In spite of difficulties in demonstrating, in some experiments, appreciable values of tension in water columns of plants, most plant physiologists continue to assume that high tension values are readily obtainable and that the cohesion theory is correct (Kramer, 1983; Baker, 1984). Feelings get vehement when scientists are either defending or refuting the cohesion theory, and this has been the case for decades. When a physicist published a book questioning the validity of the cohesion theory (Bose, 1923), plant physiologists who reviewed the book used strong language to show that he was wrong. For example, MacDougal and Overton (1927) said, "Every page of Bose's book on the ascent of sap ... is utterly lacking in scientific significance. Such books appearing on the lists of scientific publications constitute a menace and danger to sound science". Other reviewers were critical of Bose's work (Anonymous, 1929; Shull, 1923). The Bose questioning the cohesion theory was Sir Jagadis Chunder Bose, who was the teacher of Satyendra Nath Bose (Ghosh, 1992). S.N. Bose was the Bose of the Bose–Einstein condensation, a purely quantum phenomenon whereby a macroscopic number of identical atoms occupy the same single-particle state (Wyatt, 1998). (In physics, bosons compromise

one of two classes of elementary particles and they are named after Satyendra Nath Bose. Examples of bosons include fundamental particles such as the Higgs boson. The Nobel Prize in Physics in 2013 was awarded to Peter Higgs and François Englert, who developed theory that predicted the Higgs boson.) The heated debates about the cohesion theory continue today. In their book on the ascent of sap in trees, Tyree and Zimmermann (2002, p. 49) say, “At the time of writing, there has been more controversy over the cohesion theory than at any other time, excluding the initial controversy when it was originally proposed”. Charged words were used in the review of Zimmermann et al. (2004) (note the first author is Ulrich Zimmermann, not Martin Zimmermann, the coauthor with Tyree of the 2002 book on the ascent of sap), who said that “many plant physiologists still view the Cohesion Theory as the absolute and universal truth because [of] clever wording from the proponents”. Zimmermann et al. (2004) continued by saying that “the arguments of the proponents of the Cohesion Theory are completely misleading”. Angeles et al. (2004), who believe that the fundamentals of the cohesion theory remain valid, responded to the review by Zimmermann et al. (2004), and the exchange between them was moderated by Woodward (2004), who said that debate is encouraged. Brown (2013) reviews the argument between Zimmermann et al. (2004) and Angeles et al. (2004) as well as other literature dealing with the theory of the rise of sap in trees. He points out (Brown, 2013; p. 351), the “complexity” of the problem. The ongoing controversy about the cohesion theory shows that more experiments are needed to accept its assumptions fully.

## 20.8 POTENTIALS IN THE SOIL–PLANT–ATMOSPHERE CONTINUUM

No matter how water gets to the top of tall trees, the gradient in water potential from the soil to the top of the tree is calculated to be large. Nobel (1974, p. 402; 1983, p. 507; 1991, p. 521; 1999, p. 384; 2005, p. 460; 2009, p. 484) shows representative values for the water potential,  $\Psi$ , and its components ( $\Psi_m$ , matric potential;  $\Psi_s$ , solute potential;  $\Psi_g$ , gravitational potential;  $\Psi_p$ , turgor potential) in the soil–plant–atmosphere continuum. Let us choose three values of the water potential and its components that he gives: one for the soil, one for the plant, and one for the atmosphere just over the plant (the reference level is at the soil surface):

Soil: 0.1 m below the ground and 10 mm from the root:

$\Psi$ ,  $-0.3$  Mpa.

$\Psi_m$ ,  $-0.2$  Mpa.

$\Psi_s$ ,  $-0.1$  Mpa.

$\Psi_g$ ,  $0.0$  MPa.

Vacuole of leaf mesophyll cell at 10 m:

$\Psi$ ,  $-0.8$  Mpa.

$\Psi_p$ ,  $0.2$  Mpa.

$\Psi_{sr}$ ,  $-1.1$  Mpa.

$\Psi_g$ ,  $0.1$  Mpa.

Air just across the boundary layer of the leaf at 50% relative humidity:

$\Psi$ ,  $-95.1$  Mpa.

$\Psi_p$ ,  $0.0$  Mpa.

$\Psi_{sr}$ ,  $0.0$  Mpa.

$\Psi_g$ ,  $0.1$  Mpa.

Potential of the air at 50% RH (relative humidity):  $-95.2$  MPa.

Therefore, we see that the water potential changes from  $-0.3$  MPa in the soil to  $-95.1$  MPa in the air just outside the leaf—a change of  $94.8$  MPa.

The representative values will, in actuality, be affected by three factors. First, the water potential goes through a diurnal cycle (Nobel, 1974; pp. 406–408; 1983, pp. 516–518; 1991, pp. 532–533; 1999, pp. 393–394; 2005, pp. 471–473; 2009, pp. 495–497) (Figure 20.8). The water potential is typically at its highest value just before dawn, when the plant has had a chance to rehydrate during the night, and it is usually the lowest right after midday. Because the water potential is always changing throughout a day, it is important to measure it at the same time each day during an experiment, unless one wishes to document the diurnal changes. Figure 20.8 is for a general situation. The format of Figure 20.8 was

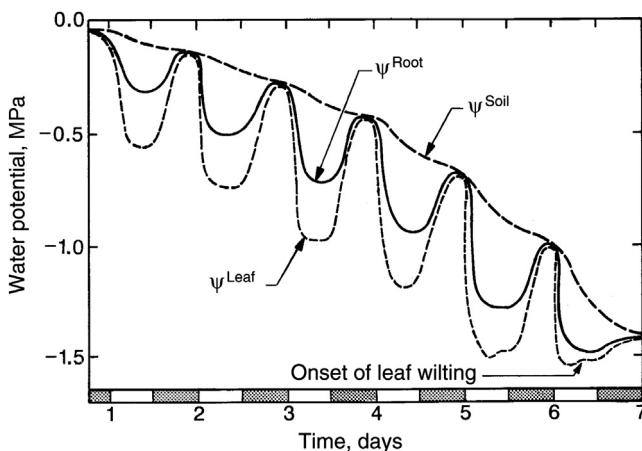


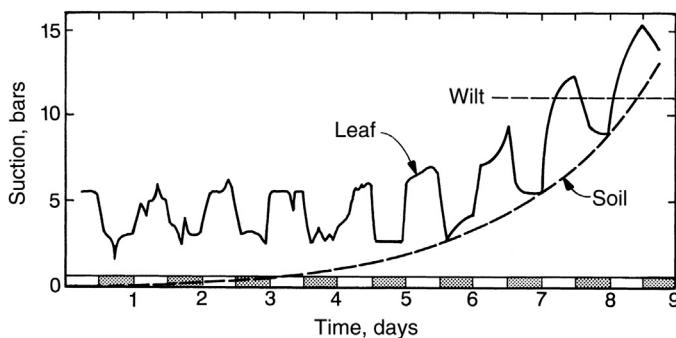
FIGURE 20.8 Schematic representation of daily changes in the water potentials in the soil, root, and leaf of a plant in an initially wet soil that dries out over a one-week period.  $\Psi^{\text{soil}}$  is the water potential in the bulk soil,  $\Psi^{\text{root}}$  is that in the root xylem, and  $\Psi^{\text{leaf}}$  is the value in a leaf mesophyll cell. From Nobel (1983), p. 517. Used with permission.



originally drawn by [Gardner and Nieman \(1964\)](#), who presented actual data for a pepper ([Figure 20.9](#)).

Second, marked changes in the hydrostatic pressure in the xylem can cause plants to have measurable diurnal fluctuations in their diameters ([Nobel, 1974](#); p. 404). When the transpiration rate is high, the large tension within the xylem vessel members is transmitted to the water in the cell walls of the xylem vessels, then to water in adjacent cells, and eventually all the way across the stem. The decrease in the hydrostatic pressure in a trunk can, therefore, cause a whole tree to contract during the day. At night, the hydrostatic pressure in the xylem may become positive, and the tree diameter then increases, generally by about 1%. Such changes in tree diameter, and therefore volume, represent the net release of water during the day and storage at night.

Strain gauges are used to monitor the change in stem diameter. In an experiment done at the Iowa State University, strain gauges were cemented to poplar trees ([Iowa State University, 1984](#)). When light intensity increased at sunrise, the stem contracted in response to increased evaporation. The stem reached its smallest size around 3:00 pm. As evaporative demand dropped in the evening, the stem expanded. Two hours after sunset, the stem was back to the size of the previous night plus the growth of the day. As the tree dried out, the stem contracted, and eventually it did not recover at night and the stem did not expand. The measurements with strain gauges can be used to determine when to irrigate; however, they cannot be used on small stems, like those of soybean plants, because they do not stay attached.



**FIGURE 20.9** Diurnal fluctuation of the suction (diffusion pressure deficit) of a pepper leaf (solid line) and average soil suction in root zone (dashed line). Solid bars along the abscissa indicate 12 h dark periods. The horizontal dashed line indicates leaf suction at which wilting symptoms appear. The plant was grown in a 3-gallon (11.4-L) jar containing clay loam soil. Reprinted with permission from [Gardner and Nieman \(1964\)](#), *American Association for the Advancement of Science*.

Third, the water potential in the vacuole of the leaf will depend on osmotic adjustment. Osmotic adjustment is the lowering of the osmotic potential of a plant when the osmotic potential of the root medium decreases (Bernstein, 1961, 1963). At the cell level, osmotic adjustment is defined as the net accumulation of solutes in a cell in response to a fall in the water potential of the cell's environment. As a consequence of this net accumulation, the osmotic potential of the cell is lowered, which, in turn, attracts water into the cell and tends to maintain turgor potential (Blum et al., 1996). Osmotic adjustment is under genetic control (Zhang et al., 1999). Therefore, the representative value for osmotic potential given by Nobel (1974, 1983, 1991, 1999, 2005, 2009) ( $-1.1$  MPa) can be changed by osmotic adjustment. Under arid conditions or in halophytes, the osmotic potential could fall to as low as  $-5.0$  MPa.

## 20.9 APPENDIX: BIOGRAPHY OF HENRY DIXON

Henry Horatio Dixon (1869–1953), Irish botanist, was born in Dublin, Ireland, in 1869, the son of George and Rebecca (Yeates) Dixon. He got his Sc.D. at Trinity College, Dublin, and also was educated at the University of Bonn in Germany (Marquis Who's Who, 1968). He married Dorothea Mary Franks in 1907, and they had three sons. Between 1892 and 1904, he rose from assistant to professor of botany at Dublin University and was university professor of botany from 1904 to 1950. He was professor of plant biology at Trinity College, Dublin, from 1922; director of the botanical gardens at Trinity College from 1906 to 1951; and its keeper of the herbarium from 1910 to 1951. He was a trustee of the Imperial Library of Ireland. He became a commander of the Irish Lights from 1924. He was a visiting professor at the University of California in 1927. He was honorary chairman of the 6th International Botanical Congress held in Amsterdam, The Netherlands, in 1935; and he was honorary president of the International Botanical Congress held in Stockholm, Sweden, in 1950.

He was recipient of the Boyle Medal in 1917. In 1908, he became a fellow of the Royal Society and was its Croonian lecturer. He was a member of the International Institute of Agriculture and was its chairman for the Committee on Biochemistry in 1927. He was a member of the Royal Dublin Society and was its president from 1945 to 1949. He was a corresponding member of the American Society of Plant Physiologists. He was a member of the British Association for the Advancement of Science and was the president of its Botanical Section in 1922. He was author of several books, including *Transpiration and the Ascent of Sap in Plants* (1914), *Practical Plant Biology* (1922), and *The Transpiration Stream* (1924). He is best

known for his research on plant transpiration. He died December 20, 1953 ([Marquis Who's Who, 1968](#)).

## 20.10 APPENDIX: BIOGRAPHY OF JOHN JOLY

John Joly (1857–1933), a British physicist and geologist, was born in 1857 ([Calef, 1971](#)). He was the son of J.P. and Julia (de Lusi) Joly. He was educated at Trinity College, Dublin, Ireland, where he got a B.A., M.A., and D.Sc. ([Marquis Who's Who, 1968](#)). He got an LL.D. at the University of Michigan; an Sc.D. (honorary) at Cambridge University, England; and an Sc.D. at the National University of Ireland. At Trinity College, he was a demonstrator in civil engineering from 1882 to 1891, a demonstrator of experimental physics in 1893, and from 1897 a professor of geology and mineralogy. He was Warden, Alexandra College for Higher Education of Women.

He was senior commander of the Irish Lights and was science adviser to Dr Steevens' Hospital, Dublin. He was a member of the British educational mission to the United States in 1918. He became a fellow of the Royal Society in 1892 and he got its Royal Medal in 1910. He was a fellow of the Geological Society and got its Murchison Medal in 1923. He was a member and president of the Royal Dublin Society and got its Boyle Medal in 1911. He was a member of the British Association and was president of the Geological Section in 1908. He was an honorary member of the Academy of Science of Russia.

He was the author of several books, including *On the Specific Heats of Gases at Constant Volume*, *On a Method of Photography in Natural Colours* (1896), *Radio-activity and Geology*, *The Local Application of Radium in Therapeutics* (1914), *The Birth-Time of the World and Other Scientific Essays* (1915), *Synchronous Signalling in Navigation*, *Reminiscences and Anticipations* (1920), *Radioactivity and the Surface History of the Earth* (1924), and *The Surface History of the Earth* (1925; 2nd ed., 1930). He was editor (with others) of the *Philosophical Magazine* from 1901. He devised the diffusion phytometer, meldometer, and steam calorimeter. (The meldometer, described in an article by Joly in *Nature* in 1885, was an apparatus that was an adjunct to the mineralogical microscope, and it allowed the approximate determination of the melting point of minerals.) He developed a uniform radiation method for use in cancer treatment and was a color-photography pioneer ([Marquis Who's Who, 1968](#)).

Joly's work on crust formation of the earth is his best known, in which he presented a theory on continental origins based on the process of convection ([Calef, 1971](#)). He proposed that heat was generated in the interior of the earth by decay of radioactive elements. Because the heat

could not escape sufficiently rapidly by other means, it started convection currents that carried hot material toward the surface where it cooled and sank, thus setting up a convective cell circulation. He suggested that the earth's crust was dragged sidewise at the top of the cell, which caused buckling and folding and thus mountain making, and the crust collapsed above the sinking portion of the convection cell. The greatest difficulty with this theory was a lack of observational data indicating any convection currents or cells (Calef, 1971). Joly died December 8, 1933.

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