2

Functions and Properties of Water

INTRODUCTION

Water is one of the most common and most important substances on the earth's surface. It is essential for the existence of life, and the kinds and amounts of vegetation occurring on various parts of the earth's surface depend more on the quantity of water available than on any other single environmental factor. The importance of water was recognized by early civilizations, and it occupied a prominent place in ancient cosmologies and mythologies. The early Greek philosopher Thales asserted that water was the origin of all things, and it was one of the four basic elements (earth, air, fire, water) recognized by later Greek philosophers such as Aristotle. It was also one of the five elemental principles (water, earth, fire, wood, metal) of early Chinese philosophers. Today it is realized that the availability of water not only limits the growth of plants but can also limit the growth of cities and industries. This chapter discusses the ecological and physiological importance of water, its unique properties, and the properties of aqueous solutions.

Ecological Importance of Water

The distribution of plants over the earth's surface is controlled chiefly by water and temperature (see Chapters 9 and 12), and where temperature permits plants to grow, chiefly by the quantity and distribution of precipitation. Where rainfall is abundant and well distributed we find the lush vegetation of tropical rain forests, the Olympic Peninsula, and the cove forests of the southern Appalachians. Strong seasonal variations as in Mediterranean climates with hot dry summers result in the shrubby vegetation of the Mediterranean and southern California coasts and parts of the west coast of southern South America. Severe summer droughts result in forests being replaced by grasslands as in the steppes of Eurasia, the prairies of the United States and the pampas of Argentina, and finally in the driest areas by deserts. In contrast, where poor drainage results in more or less permanently saturated soil the vegetation characteristic of swamps and bogs occurs.

Even in humid climates, most of the year-to-year variation in the diameter growth of trees can be related to the variation in rainfall (Zahner in Kozlowski, 1968). From this relationship arose the study of dendrochronology (Fritts, 1976), dealing with the use of variation in width of tree rings to determine rainfall conditions in the past and the age of ancient buildings (Giddings, 1962). For example, the reduction in ring width of timbers in the cliff dwellings of the southwestern United States indicates that a severe drought occurred in that region in the 13th century which was responsible for abandonment of many settlements. Variations in width of tree rings in 1600-year-old bald cypress trees growing in the Coastal Plain of North Carolina indicate that wet and dry periods with an average duration of about 30 years have occurred in that region during the past 1600 years (Stahle *et al.,* 1988). The narrower rings in trees growing on fault lines, caused by root disturbance during earthquakes, were used by Jacoby *et al.* (1988) to date the occurrence of minor earthquakes in California.

The effects of temperature on vegetation are partly exerted through water relations because an amount of rainfall sufficient to maintain forests in a cool climate where the rate of evapotranspiration is low can only maintain grasslands in a warmer climate where the rates of evaporation and transpiration are much higher. As a result, the distribution of forests in the eastern and central United States is much better correlated with the ratio of rainfall to evaporation than with rainfall alone (Transeau, 1905). Currie and Paquin (1987) reported that three-fourths of the variation in numbers of tree species in North America, Great Britain, and Ireland could be explained by differences in annual evapotranspiration, and Rosenzweig (1968) concluded that differences in net annual aboveground productivity are well correlated with variations in evapotranspiration as calculated by the method of Thornthwaite and Mather (1957). These relationships exist because evapotranspiration depends on the combined effects of temperature, irradiation, and precipitation.

Physiological Importance of Water

The ecological importance of water is the result of its physiological importance. The only way in which an environmental factor such as water can affect

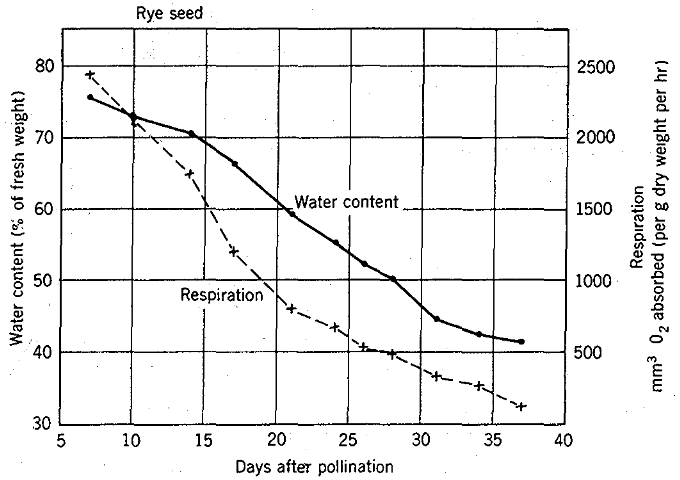

Figure 2.1 Decrease in water content and in rate of respiration during maturation of rye seed. From Kramer (1983), after Shirk (1942).

plant growth is by influencing physiological processes and conditions, as shown in Fig. 1.1.

Almost every plant process is affected directly or indirectly by the water supply. Many of these effects will be discussed later, but it can be emphasized here that within limits metabolic activity of cells and plants is closely related to their water content. For example, the respiration of young, maturing seeds is quite high, but it decreases steadily during maturation as water content decreases (see Fig. 2.1). The respiration rate of air-dry seeds is very low and increases slowly with increasing water content up to a critical point, at which there is a rapid increase in respiration with a further increase in water content (Fig. 2.2). The growth of plants is controlled by rates of cell division and enlargement and by the supply of organic and inorganic compounds required for the synthesis of new protoplasm and cell walls. Cell enlargement is particularly dependent on at least a minimum degree of cell turgor, and stem and leaf elongations are quickly checked or stopped by water deficits, as shown in Fig. 2.3. A decrease in water content inhibits photosynthesis (Fig. 2.3) and usually reduces the rate of respiration and other enzyme-mediated processes.

In summary, decreasing water content is accompanied by loss of turgor and wilting, cessation of cell enlargement, closure of stomata, reduction in photosynthesis, and interference with many other basic metabolic processes. Eventually, continued dehydration causes disorganization of the protoplasm and death of most organisms. The effects of water deficits on physiological processes are

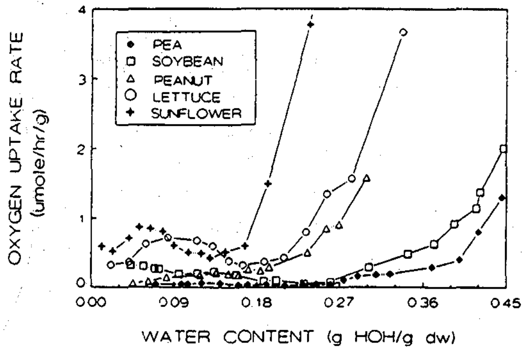

Figure 2.2 Relationship between water content and oxygen uptake for seeds of five species. At some critical water content the rate of oxygen uptake increases rapidly. Water probably is bound too firmly at lower contents to be available for physiological processes. From Vertucci and Roos (1990).

discussed in more detail in Chapters 9–11. So important are the effects of water on physiological processes that McIntyre (1987) suggested that water should be regarded as a major factor in the regulation of plant growth, with some effects of hormones being produced through the control of water status.

FUNCTIONS OF WATER IN PLANTS

The importance of water can be summarized by listing its most important functions under four general headings.

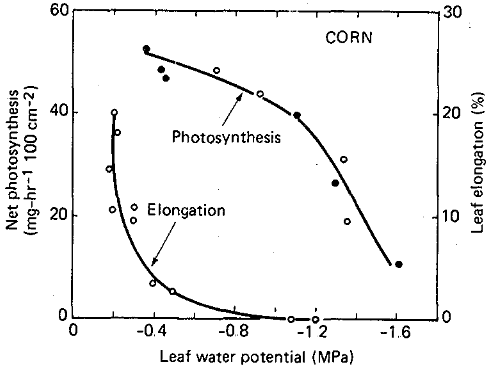

Figure 2.3 Relationship among leaf water potential, leaf elongation, and photosynthesis of corn. Note that leaf elongation almost ceases before there is much reduction in photosynthesis. From Kramer (1983), after Boyer (1970).

Constituent

Water is as important quantitatively as it is qualitatively, constituting 80–90% of the fresh weight of most herbaceous plant parts and over 50% of the fresh weight of woody plants. Some data on water content of various plant structures are shown in Table 2.1. Water is as important a part of the protoplasm as the protein and lipid molecules which constitute the protoplasmic framework, and the reduction of water content below some critical level is accompanied by changes in structure and ultimately in death. A few plants and plant organs can be dehydrated to the air-dry condition, or even to the oven-dry condition in the case of some kinds of seeds and spores, without loss of viability, but a marked decrease in physiological activity always accompanies a decrease in tissue water content (see Chapters 9 and 10). The relationship be-

Table 2.1 Water Content of Various Plant Tissues Expressed as Percentages of Fresh Weight[a]

	Plant parts	Water content (%)	Reference
Roots	Barley, apical portion	93.0	Kramer and Wiebe (1952)
	Pinus taeda, apical portion	90.2	Hodgson (1953)
	P. taeda, mycorrhizal roots	74.8	Hodgson (1953)
	Carrot, edible portion	88.2	Chatfield and Adams (1940)
	Sunflower, average of entire root system	71.0	Wilson *et al.* (1953)
Stems	Asparagus stem tips	88.3	Daughters and Glenn (1946)
	Sunflower, average of entire stems on 7-week-old plant	87.5	Wilson *et al.* (1953)
	Pinus banksiana	48.0–61.0	Raber (1937)
	Pinus echinata, phloem	66.0	Huckenpahler (1936)
	P. echinata, wood	50.0–60.0	Huckenpahler (1936)
	P. taeda, twigs	55.0–57.0	McDermott (1941)
Leaves	Lettuce, inner leaves	94.8	Chatfield and Adams (1940)
	Sunflower, average of all leaves on 7-week-old plant	81.0	Wilson *et al.* (1953)
	Cabbage, mature	86.0	Miller (1938)
	Corn, mature	77.0	Miller (1938)
Fruits	Tomato	94.1	Chatfield and Adams (1940)
	Watermelon	92.1	Chatfield and Adams (1940)
	Strawberry	89.1	Daughters and Glenn (1946)
	Apple	84.0	Daughters and Glenn (1946)
Seeds	Sweet corn, edible	84.8	Daughters and Glenn (1946)
	Field corn, dry	11.0	Chatfield and Adams (1940)
	Barley, hull-less	10.2	Chatfield and Adams (1940)
	Peanut, raw	5.1	Chatfield and Adams (1940)

[a] From Kramer (1983).

tween water content and protein structure has been discussed by Tanford (1963, 1980), Kuntz and Kauzmann (1974), Edsall and McKenzie (1978), and others. There is further discussion of the role of water in growth in Chapters 11 and 12.

Solvent

A second essential function of water in plants is as the solvent in which gases, minerals, and other solutes enter plant cells and move from cell to cell and organ to organ. The relatively high permeability of most cell walls and protoplasmic membranes to water results in a continuous liquid phase, extending throughout the plant, in which translocation of solutes occurs.

Reactant

Water is a reactant or substrate in many important processes, including photosynthesis and hydrolytic processes such as the amylase-mediated hydrolysis of starch to sugar in germinating seeds. It is just as essential in this role as carbon dioxide in photosynthesis or nitrate in nitrogen metabolism. There also is increasing interest in water as a ligand in chemical reactions (Rand, 1992).

Maintenance of Turgidity

Another role of water is in the maintenance of the turgor which is essential for cell enlargement and growth and for maintaining the form of herbaceous plants. Turgor is also important in the opening of stomata and the movements of leaves, flower petals, and various specialized plant structures. Inadequate water to maintain turgor results in an immediate reduction of vegetative growth, as shown in Fig. 2.3.

PROPERTIES OF WATER

The importance of water in living organisms results from its unique physical and chemical properties. These unusual properties were recognized in the 19th century (see Edsall and McKenzie, 1978, for references), and their importance was discussed early in the 20th century by Henderson (1913), Bayliss (1924), and Gortner (1938). Even today there is some uncertainty about the structure of water and some of its properties, as will be seen later. However, there is no doubt that water has the largest collection of anomalous properties of any common substance.

Unique Physical Properties

A substance with the molecular weight of water should exist as a gas at room temperature and have a melting point of below −100°C. Instead, water is a liquid at room temperature and its melting point is 0°C. It has the highest specific heat of any known substance except liquid ammonia, which is about 13% higher. The high specific heat of water tends to stabilize temperatures and is reflected in the relatively uniform temperature of islands and land near large bodies of water. This is important with respect to agriculture and natural vegetation. The standard unit for measuring heat, the calorie (cal), is 4.18 joules (J) and is based on the specific heat of water or the amount of energy required to warm 1 gram (g) of water 1°, from 14.5° to 15.5°C. The heat of vaporization is the highest known, 540 cal/g at 100°C, and the heat of fusion, 80 cal/g, is also unusually high. Because of the high heat of vaporization, evaporation of water has a pronounced cooling effect and condensation has a warming effect. Water is also an extremely good conductor of heat compared with other liquids and nonmetallic solids, although it is poor compared with metals. Water is transparent to visible radiation (390–760 nm). It allows light to penetrate bodies of water and makes it possible for algae to carry on photosynthesis and grow to considerable depths. It is nearly opaque to longer wavelengths in the infrared range so that water filters are fairly good heat absorbers (see Fig. 2.4).

Water has a much higher surface tension than most other liquids because of the high internal cohesive forces between molecules. This provides the tensile strength required by the cohesion theory of the ascent of sap. Water also has a high density and is remarkable in having its maximum density at 4°C instead of at the freezing point. Even more remarkable is the fact that water expands on freezing, so that ice has a volume about 9% greater than the liquid water from which it was formed (Fig. 2.5). This explains why ice floats and pipes and radiators burst when the water in them freezes. Incidentally, if ice sank, bodies of

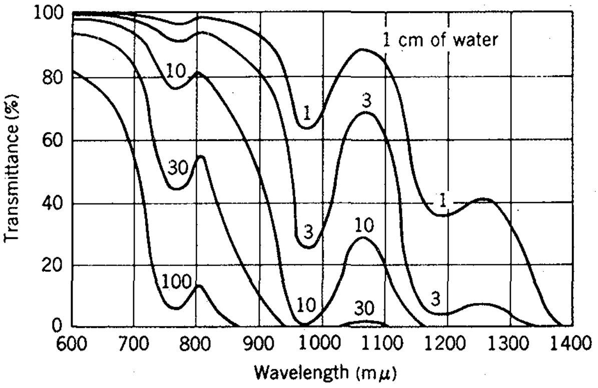

Figure 2.4 Transmission of radiation of various wavelengths through layers of water of different thicknesses. Radiation between 390 and 760 mμ is visible to the human eye. The numbers on the curves refer to the thickness of the layers in centimeters. Transmission is much greater at short than at long wavelengths. From Kramer (1983), after Hollaender (1956, p. 195).

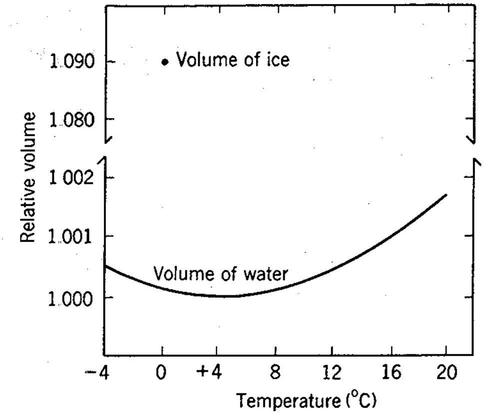

Figure 2.5 Change in volume of water with change in temperature. The minimum volume is at 4°C, and below that temperature there is a slight increase in volume as more molecules are incorporated into the lattice structure. The volume increases suddenly when water freezes because all molecules are incorporated into a widely spaced lattice. Above 4°C there is an increase in volume caused by increasing thermal agitation of the molecules. From Kramer (1983).

water in the cooler parts of the world would all be filled permanently with ice, with disastrous effects on the climate and on aquatic organisms.

Water is very slightly ionized; only one molecule in 55.5 × 10^7 is dissociated. It also has a high dielectric constant (ability to neutralize attraction between electrical charges) which contributes to its behavior as an almost universal solvent. It is a good solvent for electrolytes because the attraction of ions to the partially positive and negative charges on water molecules results in each ion being surrounded by a shell of water molecules which keeps ions of opposite charge separated (Fig. 2.6). It is a good solvent for many nonelectrolytes be-

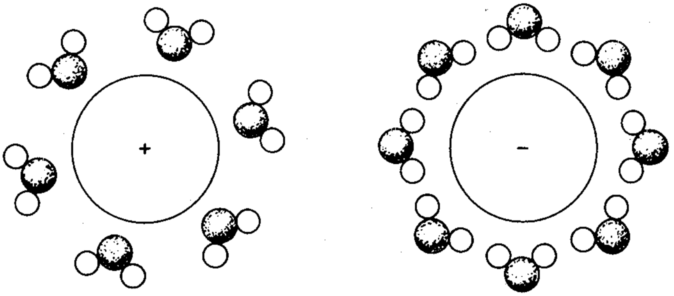

Figure 2.6 Diagram showing approximate arrangement of water molecules in shells oriented around ions. These shells tend to separate ions of opposite charge and enable them to exist in solution. They also disrupt the normal structure of water and slightly increase the volume. From Kramer (1983), after Buswell and Rodebush (1956).

cause it can form hydrogen bonds with N in amino groups and O in carbonyl groups. It tends to be adsorbed, or bound strongly, to the surfaces of clay micelles, cellulose, protein molecules, and many other substances. This characteristic is of great importance in soil and plant water relations.

Explanation of Unique Properties

It was realized early in this century that the unusual combination of properties found in water could not exist in a system consisting of individual H_2O molecules. At one time, it was proposed that water vapor is monomeric H_2O, that ice is a trimer $(H_2O)_3$ consisting of three associated molecules, and that liquid water is a mixture of a dimer $(H_2O)_2$ and a trimer. Now the unusual properties are explained by assuming that water molecules are associated in a more or less ordered structure by hydrogen bonding. Ice is characterized by an open crystalline lattice (Fig. 2.7). Liquid water has increasing disorder, and in the vapor phase the individual molecules are not associated at all. The properties and structure of water have been treated in many articles and books, including Kavanau (1964), Eisenberg and Kauzmann (1969), and a multivolume com-

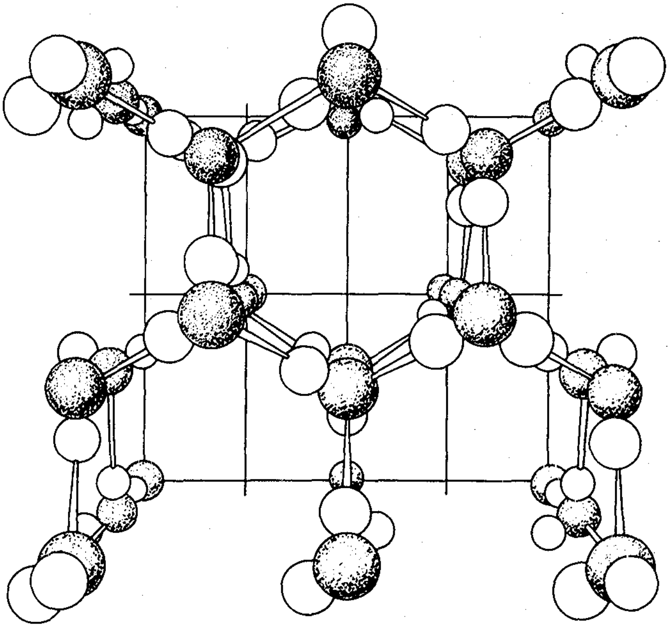

Figure 2.7 Diagram showing approximately how water molecules are bound together in a lattice structure in ice by hydrogen bonds. The dark spheres are oxygen atoms, and the light spheres are hydrogen atoms. From Kramer (1983), after Buswell and Rodebush (1956).

pendium edited by Franks (1975). More recent views are presented by Edsall and McKenzie (1978), Stillinger (1980), and Benson and Siebert (1992).

To explain the unusual properties of water requires a brief review of the kinds of electrostatic forces that operate among atoms and molecules. These include the strong ionic or electrovalent bonds and covalent bonds, weaker attractive forces known as van der Waals or London forces, and hydrogen bonds. Ionic bonds result from electrostatic attraction between oppositely charged partners, as between sodium and chlorine atoms in sodium chloride (NaCl). Such compounds usually ionize readily. Covalent bonds are formed by sharing electrons, as between oxygen and hydrogen atoms in water and carbon and hydrogen atoms in organic compounds. Such compounds do not ionize readily. Covalent bonds are strong, about 110 kcal/mol for the O-H bond in water, but they may be broken during chemical reactions.

If ionic or covalent bonds were the only types of bonding, there would be no liquids or solids because these do not allow individual molecules to interact with each other. However, there are intermolecular binding forces called van der Waals or London forces and hydrogen bonds that operate between adjacent molecules and affect the behavior of gases and liquids. Some molecules are polar or electrically asymmetric because they have partially positive and negative areas caused by an unequal sharing of electrons between atoms. These charged areas attract one molecule to another. Water shows this dipole effect rather strongly because the two hydrogen atoms form a bond angle of 104.5° with oxygen to give a V-shaped molecule resulting in the hydrogen bonding discussed later. Substances such as carbon tetrachloride and methane do not show permanent dipole effects because their molecules have no asymmetric distribution of electrons and consequently no charged areas.

Even electrically neutral molecules show anomalous properties, and in 1873 van der Waals suggested that the nonideal behavior of gases is caused by weak attractive forces operating between such molecules. In about 1930, London developed an explanation for these attractions based on the assumption that even those molecules that on the average are electrically symmetrical or neutral develop momentary or instantaneous dipoles from the motion of their electrons. These dipoles induce temporary dipoles in neighboring molecules, causing the instantaneous or momentary attraction between them known as van der Waals or London forces. This attraction is weak, about 1 kcal/mol, and effective only if molecules are very close together. In general, the physical properties of liquids such as the boiling point, heat of vaporization, and surface tension depend on the strength of intermolecular bonding. For example, gases condense into liquids when cooled enough so that the van der Waals and other attractions between molecules exceed the dispersive effect of their kinetic energy. For small molecules the size of water, temperatures usually must be very low to form liquids.

The peculiar physical properties of water result from additional intermolecular forces much stronger than van der Waals forces. These strong attractive forces are hydrogen bonds that result from the weak electrostatic attraction of the partially positively charged hydrogen atoms of one water molecule to the partially negatively charged oxygen atoms of adjacent molecules. They operate over considerable distances and have a binding force of about 1.3–4.5 kcal/mol in water. The forces produced by the asymmetric distribution of charges on water molecules bind them in the symmetrical crystalline lattice structure of ice, shown diagrammatically in Fig. 2.7. The water molecules in ice are arranged in a lattice with unusually wide spacing, resulting in a density lower than that of liquid water.

As ice melts, 13–15% of the bonds break, and about 8% of the molecules escape from the lattice. This results in a partial collapse of the lattice into a more disorderly but also more compact structure and an increase to maximum density at 4°C. As the temperature rises above 4°C, further increases in breakage and deformation of hydrogen bonds result in an increase in volume (see Fig. 2.5). There has been, and still is, some uncertainty about the structure of liquid water, i.e., the manner in which the molecules are oriented in relation to one another (Amato, 1992; Benson and Siebert, 1992). Incidentally, the concept of structure refers only to average positions of molecules because they are continually in motion and exchanging bonds. At one time it was believed that liquid water consisted of "flickering clusters" or "icebergs" of structured water molecules surrounded by unstructured molecules (Némethy and Scheraga, 1962). However, Stillinger (1980) stated that recent studies tend to rule out the iceberg concept. He regards liquid water as a three-dimensional network of hydrogen-bonded molecules showing a tendency toward tetrahedral geometry but containing many strained or broken bonds. Benson and Siebert (1992) propose that liquid water consists of hydrogen-bonded cyclic tetramers and octamers. Because hydrogen bonds have a half-life of only about 2×10^{-10} sec, these structures are difficult to detect.

Only part of the structure is destroyed by heating, and about 70% of the hydrogen bonds found in ice remain intact in liquid water near 100°C. The high boiling point of water results from the large amount of energy required to break the remaining hydrogen bonds and vaporize liquid water. The structure is somewhat modified by the pH, because it affects the distance between the hydrogen and the oxygen atoms, and by ions, because of their attraction for water molecules.

Ions also form dipole bonds with water molecules. The result is that the ions become surrounded by firmly bound shells of water molecules (Fig. 2.6). In fact, Bernal (1965) described ions, protein molecules, and cell surfaces as being coated with "ice," i.e., with layers of structured water molecules. It is now considered unlikely that water can form a uniform layer over the surface of protein

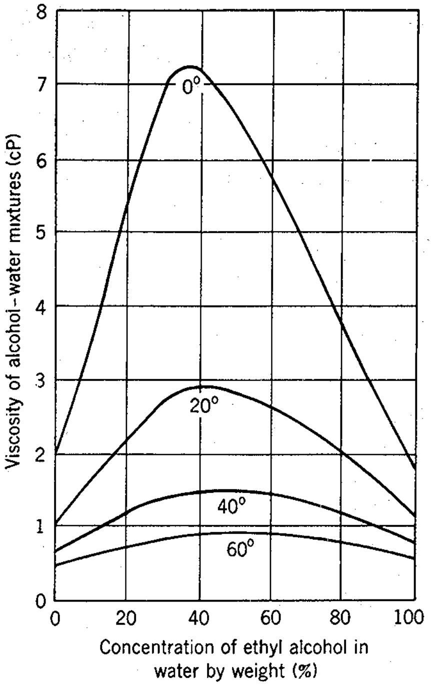

Figure 2.8 The effect of various concentrations of ethanol on the viscosity of water at four temperatures. Mixtures of water with polar organic liquids often show large increases in viscosity at low temperatures because they have a more tightly packed structure than the component liquids alone. From Kramer (1983), after Bingham and Jackson (1918).

molecules, but it probably can form such layers on the surfaces of cellulose and other substances having a more uniform distribution of bonding sites. Solutions of alcohols, amides, or other polar liquids in water result in a more strongly structured system than occurs in the separate substances. This is seen in the high viscosity of such solutions. For example, the viscosity of an ethyl alcohol–water mixture at 0°C is four times that of water or alcohol alone. However, this structure is easily broken by high temperatures (see Fig. 2.8). The addition of nonpolar substances such as benzene or other hydrocarbons to water breaks bonds and produces "holes" or disorganized areas in the structure which are surrounded by areas with a tighter structure. The water bound to large molecules such as proteins has an important effect on their structure; Tanford (1963, 1980) cites evidence suggesting that the relative stability of the structure of viruses, DNA, and globular proteins is affected by the water associated with them.

It was mentioned earlier that the changes in volume of water during freezing and thawing are caused by changes in the proportion of water molecules bound in an organized lattice by hydrogen bonds. The high boiling point results principally from the large amount of energy required to break hydrogen bonds, nearly two of which must be broken for each molecule evaporated. Methane (CH_4) has almost the same molecular weight as water, but it boils at −161°C because no hydrogen bonding occurs and only a small amount of energy is required to break the weak van der Waals forces holding the molecules together in the liquid.

The unusually high viscosity and surface tension of water also result from the fact that hydrogen bonds between water molecules resist rearrangement. Water wets and adheres to glass, clay micelles, cellulose, and other substances having exposed oxygen atoms at the surface with which hydrogen bonds can be formed. It does not wet paraffin and other hydrocarbons because it cannot form hydrogen bonds with the C atoms in them, but it wets cotton because it forms numerous hydrogen bonds with the O atoms of the cellulose molecules.

According to Jenniskens and Blake (1994), the ice formed on the interstellar dust of molecular clouds and comets is formed from less structured or amorphous water. They observed three forms of amorphous water ice during warming from 15 to 188 K and stated that these changes in structure explain some anomalous properties of astrophysical ice.

Bound Water

In the period from 1920 to 1950 considerable attention was given to what was termed "bound water" as a factor in cold and drought tolerance. Gortner (1938) discussed the origin of the term and methods of measuring it and Kramer (1955) reviewed the literature. The concept of bound water originated from observations that a variable fraction of water in both living and nonliving systems has a lower vapor pressure, remains unfrozen at −20° or −25°C, does not function as a solvent, and seems to be less available physiologically than bulk water. For example, the rate of respiration of seeds is low at a low water content, but suddenly increases rapidly above a certain water content, when the amount of free water increases, as shown in Fig. 2.2.

Attempts to explain cold or drought tolerance in terms of differences in bound water content proved disappointing (Levitt, 1980, pp. 179–182; Burke *et al.*, 1976) and bound water was neglected for several decades. However, improvements in the technology used to measure it has resulted in renewed interest in its possible importance. Burke *et al.* (1974) used nuclear magnetic resonance spectroscopy to observe increase in water binding in cold acclimating dogwood stems and NMR imaging is now being used. G. A. Johnson *et al.* (1987) were able to follow simultaneous changes in total and bound water in stems of transpiring geranium plants and Veres *et al.* (1991) followed dehydration and rehydration in fern stems. Leopold and his colleagues (Vertucci and Leopold, 1987a,b) studied bound water in seeds and other tissues using sorption isotherms. They found that tissues easily injured by dehydration had a lower water-binding capacity than more tolerant tissues and conclude that binding of water has a protective effect. Rascio *et al.* (1992) found that the more drought tolerant of two varieties of wheat also bound more water. Parsegian and his coworkers (Colombo *et al.,* 1992) found that some proteins such as hemoglobin show a change in the amount of water bound when they bind substrate, and propose that this change is an important part of catalysis. It seems probable that there will be more research by use of the new technology on the possible effects of bound water.

Isotopes of Water

The three isotopes of hydrogen having atomic weights of 1, 2, and 3 make it possible to differentiate tracer water from ordinary water. In the 1930s, heavy water [water containing deuterium (hydrogen of atomic weight 2)] became available and was used widely in biochemical studies. It was also used extensively in studies of permeability of animal and plant membranes (e.g., Ordin and Kramer, 1956; Ussing, 1953). However, deuterium was largely supplanted as a tracer by water containing tritium (hydrogen of atomic weight 3), e.g., in the experiments of Raney and Vaadia (1965a,b) and Couchat and Lasceve (1980). Tritium is radioactive and therefore more convenient as a label, being easier to detect than deuterium, which requires use of a mass spectrometer.

A stable isotope of oxygen with an atomic weight of 18 makes it possible to study the role of oxygen in water. An example is the series of experiments with $H_2{}^{18}O$ which demonstrates that the oxygen released during photosynthesis comes from water instead of from carbon dioxide (Ruben *et al.,* 1941).

The ratio of deuterium to hydrogen in water has been used in various ways ranging from reconstruction of past climates to study of the fractionation of water in leaves and cells. As $H_2{}^{16}O$ evaporates more rapidly than $H_2{}^{18}O$, leaf water has higher ratios of ^{18}O than root or stem water, although the enrichment is not strictly proportional to the rate of transpiration (Farris and Strain, 1978; Flanagan *et al.,* 1991). Yakir *et al.* (1990) and Yakir (1992) concluded from studying the effects of high and low rates of transpiration on the isotopic ratio of water in leaves that water must exist in three compartments: a fraction in the veins, a symplastic pool, and a pool from which evaporation occurs. Pedersen (1993) used tritiated water to demonstrate root pressure and guttation in submerged flowering plants. The use of stable isotopes of water for research on plants was reviewed by White (1989) and in a book edited by Ehleringer *et al.* (1993).

Unorthodox Views Concerning Water

It is generally believed that although most of the water in cells possesses the structure and properties of bulk water, a small amount is adsorbed on the surfaces of membranes and macromolecules. This is the ice of Bernal (1965) and the bound water of Gortner (1938) and others. However, according to Ling (1969), Cope (1967), and a few other physiologists, a significant amount of the water in living cells has a structure different from bulk water. This vicinal or associated water is said by them to affect the accumulation of ions and eliminate the classical role of cell membranes and their associated ion pumps (see Hazelwood and others in Drost-Hansen and Clegg, 1979). This concept has not been widely accepted (Kolata, 1979), and it seems especially doubtful that it could apply to plant cells with their large volume of vacuolar water.

It also was suggested by Drost-Hansen (1965) and others that there are anomalies in the physical properties of water at about 15°, 30°, and 45°C. For example, it is claimed that there are peaks in the disjoining pressure and viscosity of water adsorbed on surfaces, caused by phase transitions in vicinal water, i.e., water adsorbed on surfaces of macromolecules in cells (Etzler and Drost-Hansen in Drost-Hansen and Clegg, 1979). It was also claimed by these writers and by Nishiyama (1975) and Peschel (in Lange *et al.*, 1976) that there are peaks in seed germination, growth of microorganisms, and other biological processes which are related to these anomalies. These claims have been received skeptically (Eisenberg and Kauzmann, 1969), and Falk and Kell (1966) concluded that the reported discontinuities in physical properties are no greater than the errors of measurement. It seems likely that discontinuities in biological processes are related more to phase transitions in membranes than to phase transitions or discontinuities in the properties of water.

Another anomaly is the polywater reported by Russian investigators in the 1960s. This was believed to be a polymeric form of water with anomalous properties, but it later turned out to be water containing a high concentration of solute (Davis *et al.*, 1971). The story of polywater was told in detail by Franks (1981). It has also been claimed by Russian investigators that water from freshly melted snow stimulates certain biological processes. Other Russian investigators claimed that water boiled to remove all dissolved gas and then quickly cooled not only has greater density, viscosity, and surface tension but also stimulates plant and animal growth; concrete prepared with it is stronger than that prepared with ordinary water (Maugh, 1978). These claims have not been verified elsewhere and should be treated with caution.

PROPERTIES OF AQUEOUS SOLUTIONS

In plant physiology we seldom deal with pure water because the water in plants and in their root environment contains a wide range of solutes. Therefore, it is necessary to understand how the properties of water in solution differ from those of pure water. Only a brief discussion is possible here, and readers are referred to physical chemistry texts for full development of these ideas.

The characteristics of water in solution can be shown concisely by tabulation

Table 2.2 Colligative Properties of a Molal Solution of a Nonelectrolyte Compared with Water

	Pure water	Molal solution
Vapor pressure	0.61 kPa at 0°C 101.3 kPa at 100°C	Decreased according to Raoult's law
Boiling point	100°C	100.518°C
Freezing point	0°C	−1.86°C
Osmotic pressure	0	2.27 MPa at 0°C
Chemical potential	Reference	2.27 MPa below reference at 0°C

of its colligative properties, i.e., the properties associated with the concentration of solutes dissolved in it. These are shown in Table 2.2 and include the effects on vapor pressure, boiling and freezing points, osmotic pressure, and water potential. They occur because the addition of solute dilutes or lowers the concentration of the water.

Pressure Units

Many of the colligative properties of water are described in terms of pressure, which is the force applied to a unit area of the enclosing surface, and the primary units are dynes per square centimeter or newtons per square meter. Pressure units also are equivalent to energy per unit volume such as ergs per cubic centimeter or joules per cubic meter because a unit of work or energy is a dyne-cm (erg) or newton-meter (joule). Vapor pressure often is expressed in millimeters (mm) of mercury or millibars (mbar) and atmospheric pressure in bars (1 bar = 0.987 atm). However, there is a strong tendency toward the use of SI (Système International) units (Incoll *et al.*, 1977), and for the most part these units are used in this book. The primary pressure unit is then the pascal (Pa = 1 newton per square meter), and 1 bar = 10^5 Pa, 100 kPa, or 0.1 MPa (megapascal). In general, megapascals will be used in place of bars and kPa in place of millibars. One millibar is equal to 0.1 kPa, and standard atmospheric pressure is 101.3 kPa (760 mmHg, or 1013 mbar).

Vapor Pressure

The vapor pressure of water in solution is decreased essentially because the water is diluted by the addition of solutes. This is shown by Raoult's law, which states that the vapor pressure of solvent vapor in equilibrium with a dilute solution is proportional to the mole fraction N_w of solvent in the solution of nondissociating solute

$$e = e_o N_w = e_o \frac{n_w}{n_w + n_s}, \tag{2.1}$$

where e is the vapor pressure of the solution, e_o is the vapor pressure of pure solvent, n_w is the number of moles of solvent, n_s is the number of moles of solute, and $N_w = n_w/(n_w + n_s)$. This is strictly applicable only to dilute molal solutions, i.e., those prepared with a mole or less of solute per 1000 g of water, and the relation holds because the surface of the solution is occupied by fewer water molecules due to the presence of solute at the surface.

Boiling and Freezing Points

The effects of solutes on the boiling and freezing points are exerted through their effects on the vapor pressure of water (see Fig. 2.9). The addition of solute lowers its freezing point because it dilutes the water and lowers its vapor pressure, thereby decreasing the temperature at which the vapor, liquid, and solid phases are in equilibrium. It can be calculated that the vapor pressure at freezing of a molal solution of a nonelectrolyte in water is decreased from 0.610 to 0.599 kPa and that a reduction in temperature of 1.86° below zero is required to bring about freezing.

Water boils when its vapor pressure is raised to that of the atmosphere. When the vapor pressure has been lowered by the addition of solute, the water in a

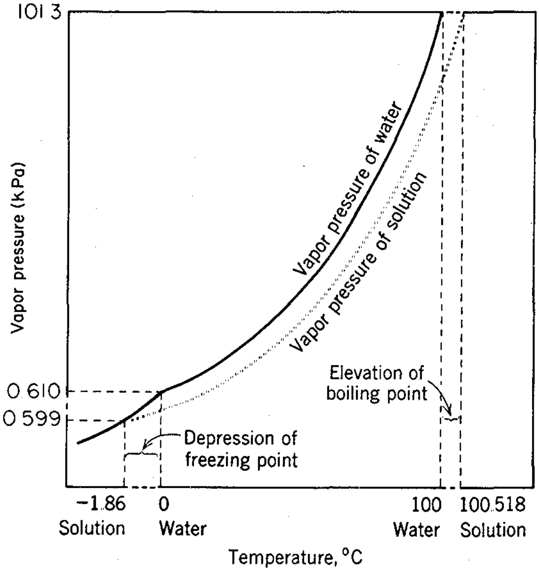

Figure 2.9 Effects of 1 mol of nonelectrolyte per 1000 g of water (a 1 molal solution) on the freezing and boiling points and vapor pressure of the solution. Note that this diagram is not drawn to scale. From Kramer (1983).

solution must be heated to a higher temperature than pure water to produce the required increase in vapor pressure. At high altitudes water boils below 100°C, sometimes causing practical problems in cooking food.

Osmotic Pressure or Osmotic Potential

Raoult's law shows that the vapor pressure of water in a solution is lowered in proportion to the extent to which the mole fraction of water in the solution is decreased by adding solute. Therefore, if water is separated from a solution by a membrane permeable to water but impermeable to the solute, water will move across the membrane along a gradient of decreasing water mole fraction into the solution. The pressure, which must be applied to the solution to prevent movement in a system such as that shown in Fig. 2.10, is termed the osmotic pressure. It is often denoted by the symbol π.

The osmotic pressure is present only when a balancing pressure is applied to the solution as in Fig. 2.10. The fundamental property causing the movement is the osmotic potential resulting from the dilution of water by the addition of solute (Gibbs, 1931) and it is always present for a solution. When in the apparatus in Fig. 2.10, the osmotic potential is opposed by the pressure, and the osmotic potential Ψ_s, is equal to the negative of the osmotic pressure at balance, that is, $\Psi_s = -\pi$. Outside of the apparatus, there is no osmotic pressure and the solution is affected only by Ψ_s. The basis for the use of the term potential is discussed in the following section (Chemical Potential of Water).

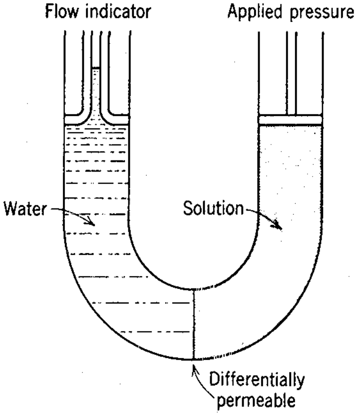

Figure 2.10 Diagram of osmometer in which a membrane permeable to water but impermeable to solute separates pure water from a solution. The osmotic pressure of the solution is equal to the pressure that must be applied to prevent movement of water into it. Water movement is observed by a change in the level of water in the capillary tube on the left. From Kramer (1983).

Van't Hoff developed an equation relating osmotic pressure to solute concentration in the solution (see Appendix 2.1). Mathematically expressed,

$$\pi V = n_s RT, \tag{2.2}$$

where π is the osmotic pressure in megapascals, V is the volume of solvent in cubic meters, n_s is the moles of solute, R is the gas constant (8.32×10^{-6} MPa $\cdot$ m$^3 \cdot$ mol$^{-1} \cdot$ K^{-1}), and T is the temperature in degrees Kelvin (K). For 1 mole of solute in 1 liter of solvent at 273 K (0°C), this equation gives a value for π of 22.7×10^5 Pa or 2.27 MPa (22.4 atm or 22.7 bars).

Direct measurements have shown that this relationship is approximately correct for dilute solutions of nondissociating substances. However, there are large deviations from the theoretical value for electrolytes that ionize in solution and release more particles than nondissociating substances. Thus, the osmotic pressure of a molal solution of NaCl is approximately 4.32 MPa (43.2 bars) instead of the theoretical 2.27 MPa (22.7 bars) of a nonelectrolyte. Assuming complete dissociation of the NaCl, the osmotic pressure should be 4.54 MPa and the discrepancy can probably be attributed chiefly to van der Waals forces operating between ions. Some nondissociating molecules become hydrated or bind water molecules. This binding of water reduces the effective concentration of water and increases the observed osmotic pressure. An example is sucrose solution in which each sucrose molecule apparently binds six molecules of water, and the osmotic pressure of a molal solution of sucrose is approximately 2.51 MPa (25.1 bars) instead of the expected 2.27 MPa (22.7 bars).

The relationships among concentration, vapor pressure, freezing point, and osmotic pressure make it possible to calculate the osmotic pressure of a solution from the freezing point depression. Since the theoretical depression of the freezing point of an ideal molal solution is 1.86°C and the osmotic pressure is 2.27 MPa at 0°C, the osmotic pressure of a solution can be calculated from the depression of the freezing point (T) by the following equation:

$$\pi = \frac{\Delta T}{1.86} \times 2.27 \text{ MPa}, \tag{2.3}$$

where ΔT is the observed depression. The derivation of this relationship can be found in Crafts *et al.* (1949) or in a physical chemistry text. The freezing point method is widely used, and if suitable corrections are made for supercooling, it gives accurate results. The problems encountered in using it on plant sap are discussed in Chapter 7 of Crafts *et al.* (1949) and by Barrs (in Kozlowski, 1968).

The osmotic pressure can also be calculated from the vapor pressure or, more readily, from the relative vapor pressure or relative humidity, $e/e_0 \times 100$, according to Raoult's law [see later and Eq. (2.1) and Appendix 2.1]. In recent years, thermocouple psychrometers have been used extensively to measure e/e_0.

Their operation is discussed in Chapter 3 in connection with the measurement of the water status of plants.

Chemical Potential of Water

The properties of solutions are described by the thermodynamic concept of the potential first put forth by J. Willard Gibbs (1875–1876). The chemical potential μ of a substance is a measure of the capacity of 1 mol of that substance to do work (see Appendix 2.2). It is equal to the partial molal Gibbs free energy (Nobel, 1991, pp. 76–77; Slatyer, 1967; Spanner, 1964). The mole basis of the potential indicates that the free energy is expressed for Avogadro's number of molecules or, in other words, on a per molecule basis. The concept of energy or work that can be done by a molecule has many applications, and the energy can be affected by many factors, including the concentration of water molecules, that is, the mole fraction of the water. The degree to which the presence of solute reduces the chemical potential of the water in the solution below that of pure free water is shown by

$$(\mu_w - \mu_o) = RT\ln N_w, \tag{2.4}$$

where μ_w is the chemical potential of water in the solution, μ_o is the chemical potential of pure water at the same temperature, R and T have the usual meaning, and N_w is the mole fraction of water. For use with ionic solutions, the mole fraction is replaced by the activity of water, a_w, and for general use, where water may not be in a simple solution, by the relative vapor pressure, e/e_o [see Eq. (2.1)]. Equation (2.4) is then written

$$(\mu_w - \mu_o) = RT\ln\frac{e}{e_o}. \tag{2.5}$$

When the vapor pressure of the water in the system under consideration is the same as that of pure free water, $\ln(e/e_o)$ is zero, and the potential difference $(\mu_w - \mu_o)$ is also zero. When the vapor pressure of the system is less than that of pure water, $\ln(e/e_o)$ is a negative number; hence, the potential of the system is less than that of pure free water and the potential difference is expressed as a negative number.

The expression of chemical potential in energy units such as joules per mole is inconvenient in discussions of cell water relations. It is more convenient to use units of pressure. Dividing both sides of Eq. (2.5) by the partial molal volume of water $\bar{V}_w$ (m^3/mol) gives energy in units of joules/m^3 which is equivalent to pressure in newtons per square meter or megapascals in SI units:

$$\Psi_w = \frac{\mu_w - \mu_o}{\bar{V}_w} = \frac{RT}{\bar{V}_w}\ln\frac{e}{e_o}. \tag{2.6}$$

The resulting term is called the water potential Ψ_w. For the conversion to pressure units, $\bar{V}_w$ is a constant in dilute solutions ($18 \times 10^{-6}\,m^3/mol$) and Ψ_w is proportional to the chemical potential (see Appendix 2.2).

The water potential in any system is decreased by those factors that reduce the relative vapor pressure, including:

1. Addition of solutes which dilute the water and decrease its activity by hydration of the solute molecules or ions.
2. Addition of porous solids which displace water and have surface forces and microcapillary forces. These forces together are called matric force and are found in soils, cell walls, protoplasm, and other substances that adsorb or bind water (for a fuller description, see Appendix 2.3).
3. Application of negative pressure or tensions such as those in the xylem of transpiring plants.

The water potential in any system is increased by those factors that increase the relative vapor pressure, including:

1. Dilution or removal of solutes.
2. Hydration of matrices.
3. Application of pressure above atmospheric, such as that exerted by the elastic cell wall on the cell contents (turgor).

Temperature affects the water potential according to the term T in Eq. (2.6), although there also is a slight effect of T on $\bar{V}_w$ because of changes in water density. Decreasing T makes Ψ_w less negative whereas increasing T causes the opposite effect. Because T has units of K, the effect is not large over the biological range of temperatures.

The water status of plants usually is described in terms of water potential because it is physically defined and allows experiments to be easily repeated. Also, water moves through the soil–plant system because of the water potential or forces included in the water potential. Sinclair and Ludlow (1985) argued that relative water content should be used instead because it is better correlated with physiological processes. As pointed out in later chapters, decreases in cell water content can concentrate cell constituents and probably cause changes in enzyme action. However, the water content often fails as an indicator of plant water status, as seen for example in Fig. 10.2 which shows the difference in photosynthesis between *Fucus*, a marine plant, and sunflower, a land plant, as relative water content or water potential varies. Because water content is based on a biological and thus variable reference, *Fucus* and sunflower appear to have maximum photosynthesis at a similar water status (Fig. 10.2A). In reality, the seawater that fully hydrates *Fucus* is markedly inhibitory to sunflower (Fig. 10.2B). The relative water content does not adequately detect this difference and, while water content is important, the water potential is preferred.

Throughout the discussion, we have explained the colligative properties of solutions using the example of the lowering of the concentration of the solvent, water, by the addition of solute. However, Hammel (1976) and Hammel and Scholander (1976) argued that the addition of a solute lowers the chemical potential of the solvent by creating a negative pressure or tension on the solvent molecules. Andrews (1976) discussed their arguments in detail and concluded that there is no mechanism by which solvent and solute molecules can sustain different pressures. The writers agree that the classical solvent dilution theory adequately explains the behavior of solutions.

SUMMARY

Water plays essential roles in plants as a constituent, a solvent, a reactant in various chemical processes, and in the maintenance of turgidity. The physiological importance of water is reflected in its ecological importance; plant distribution over the earth's surface is controlled by the availability of water wherever temperature permits growth. Its importance is a result of its numerous unique properties, most of which arise from the fact that water molecules are organized into a definite structure held together by hydrogen bonds. Furthermore, the water bound to proteins, cell walls, and other hydrophilic surfaces has important effects on their physiological activity.

Water in plants and soils contains solutes that modify its colligative properties by diluting it. As a result of this dilution, the chemical potential, vapor pressure, osmotic potential, and freezing point are lowered in proportion to the concentration of solute present. The best measure of the energy status of water in plants and soil is the water potential (Ψ_w), which is the amount by which its chemical potential is reduced below that of pure water. Some writers argue that relative water content is a better indication of plant water status than water potential with respect to physiological processes, but the water potential has the advantage of being physically defined and the force that causes water movement. Thus, the water potential seems preferable.

SUPPLEMENTARY READING

Alberty, R. A., and Daniels, F. (1979). "Physical Chemistry," 5th Ed. Wiley, New York.

Andrews, F. C. (1976). Colligative properties of simple solutions. *Science* **194,** 567–571.

Edsall, J. T., and McKenzie, H. A. (1978). Water and proteins. I. The significance and structure of water: Its interaction with electrolytes and non-electrolytes. *Adv. Biophys.* **10,** 137–207.

Eisenberg, D., and Kauzmann, W. (1969). "The Structure and Properties of Water." Oxford University Press, London/New York.

Franks, F., ed. (1982). "Water: A Comprehensive Treatise," Vol. 7. Plenum Press, New York.

Gibbs, J. W. (1931). "The Collected Works of J. Willard Gibbs," Vol. 1. Longmans, Green and Co., New York.

Hammel, H. T. (1976). Colligative properties of a solution. *Science* **192,** 748–756.

Somero, G. N.; Osmond, C. B., and Bolis, C. T., eds. (1992). "Water and Life." Springer-Verlag, Berlin.

Stillinger, F. H. (1980). Water revisited. *Science* 209, 451–457.

Tanford, C. (1980). "The Hydrophobic Effect." Wiley, New York.

Tinoco, I., Sauer, K., and Wang, J. C. (1978). "Physical Chemistry: Principles and Applications: Biological Sciences." Prentice-Hall, Englewood, NJ.

Appendix 2.1: The van't Hoff Relation

The van't Hoff equation is a simplified version of the equation relating the solute concentration to the chemical potential according to the mole fraction of the water

$$(\mu_w - \mu_o) = RT\ln\frac{n_w}{n_s + n_w}, \tag{2.7}$$

where R is the gas constant (8.32×10^{-6} MPa · m^3· mol^{-1} · K^{-1}), T is the Kelvin temperature (K), n_s is the number of moles of solute, n_w is the number of moles of water, and the mole fraction of water is $n_w/(n_s + n_w)$.

For dilute solutions, the mole fraction of water can be approximated by

$$\frac{n_w}{n_s + n_w} = 1 - \frac{n_s}{n_s + n_w} \approx 1 - \frac{n_s}{n_w}, \tag{2.8}$$

and the natural logarithm can be further approximated with the Taylor expansion for a dilute solution

$$\ln\left[1 - \frac{n_s}{n_w}\right] \approx -\frac{n_s}{n_w} \tag{2.9}$$

so that

$$(\mu_w - \mu_o) \approx -RT\frac{n_s}{n_w}. \tag{2.10}$$

Dividing both sides of Eq. 2.10 by the partial molal volume of water, $\bar{V}_w = V/n_w$, gives the osmotic potential

$$\Psi_s = \frac{\mu_w - \mu_o}{\bar{V}_w} \approx -\mathrm{RTn_s}/V, \tag{2.11}$$

and since the concentration of solute $C = n_s/V$, Eq. 2.11 becomes

$$\Psi_s \approx -RTC, \tag{2.12}$$

and because $\Psi_s = -\pi$,

$$\pi \approx RTC, \tag{2.13}$$

which was first derived by van't Hoff. This equation only works for dilute solutions of nondissociating solutes but it shows the practical result that Ψ_s is proportional to the concentration of solute under these conditions. It also shows that at lower temperatures the osmotic potential becomes less negative and at absolute zero the osmotic potential becomes zero.

Appendix 2.2: The Chemical Potential

When we consider molecules of any kind, we know that all of them contain energy in their atoms and chemical bonds that can be exchanged with the surroundings by their motions, chemical reactions, and radiational exchanges (here we assume that the isotopic composition remains stable). The energy exchanges always result in a rearrangement of chemical or atomic structure that in itself requires energy. Thus, a fraction of the energy goes to the rearrangements and a fraction goes to the surroundings; the latter fraction can be made to do work. The rearrangement energy is termed the entropy and the energy available for work is the free energy.

It readily can be seen that the amount of work is determined by the number of molecules exchanging energy. Doubling the number of molecules doubles the work, all other factors remaining constant. Often, however, it is more desirable to know the work per molecule or per mole of molecules than the total work. Gibbs (1931) recognized this and defined the term "potential" and symbol μ as the way to describe the work that a mole of molecules can do.

The work is not known in absolute terms because the total amount of energy in molecules is not known. Therefore, the work is determined by comparing the chemical potential of the system with a reference potential. For liquid water, the reference has been chosen to be pure unrestrained water at atmospheric pressure, a defined gravitational position, and the same temperature as the system being compared. If we define the chemical potential of the system to be measured as μ_w and the chemical potential of the reference as μ_o, $(\mu_w - \mu_o)$ is the comparison we wish to make. When the system is not pure water, the μ_w is lower than μ_o, and $(\mu_w - \mu_o)$ is negative. When the system is pure water, $(\mu_w - \mu_o)$ is zero.

The $(\mu_w - \mu_o)$ is the energy state of the molecules. It does not matter how the molecules get to that state, the energy is the same whenever $(\mu_w - \mu_o)$ is at the same level. The energy represents the maximum work that can be done if the molecules are part of an ideal machine. Pure water moving through a selective membrane into a solution on the other side is a machine allowing work to be done. If the membrane allows water to pass but not solute (the membrane reflects solute), more water will move to the solution side than to the other side because the free energy of the pure water is higher than in the solution. The work is determined by the potential difference on the two sides of the membrane and the net volume of water moved. The work can be measured by opposing this movement with a potential that counters the movement, such as with pressure.

If the membrane is not reflective for solute, the volume of water moving into the solution is essentially the same as the volume of water and solute moving in the opposite direction. No work is done because there is no net volume change. Nevertheless, at the beginning, the $(\mu_w - \mu_o)$ is the same as when the reflective membrane was present. Thus, the ability to do work is identical but the work actually done depends on the characteristics of the machine.

This example illustrates that the $(\mu_w - \mu_o)$ is an intrinsic property of the molecules. The membrane simply determines the work extracted from the molecules. The reflectiveness of the membrane is the determining factor and is usually described by the reflection coefficient, which is 1 for a perfectly reflective membrane but 0 for a nonreflective one. The osmotic effectiveness of a solution is determined by the membrane reflectiveness for the solute even though large concentration differences exist on the two sides of the membrane. In other words, the $(\mu_w - \mu_o)$ will bring about osmosis only if the membrane is reflective for the solute *even though* $(\mu_w - \mu_o)$ *can be measured in a vapor pressure osmometer or similar apparatus.*

Because the chemical potential is normally given in energy units per mole but can be converted to pressure units according to

$$\Psi_w = \frac{(\mu_w - \mu_o)}{\bar{V}_w}, \tag{2.14}$$

the units of the water potential Ψ_w are energy per volume = force per unit area = pressure. The pressure is usually expressed in megapascals where 1 megapascal = 10^6 pascals = 10^6 newtons $\cdot$ m^{-2} = 10^6 joule $\cdot$ m^{-3} = 10^7 ergs $\cdot$ cm^{-3} = 10^7 dynes $\cdot$ cm^{-2} = 10 bars = 9.87 atmospheres or 145 pounds per square inch.

This works well when $\bar{V}_w$ is a constant. The $\bar{V}_w$ is the volume of a mole of liquid water mixed with other molecules in the system and is nearly a constant 18 cm^3 $\cdot$ mol^{-1} over most of the temperatures and water contents of cells and soils. Therefore, the Ψ_w is simply $(\mu_w - \mu_o)$ divided by a constant. In concentrated solutions, dry soils, dry seeds, and other systems of low water content, this simplification may not hold because interactions between water and the other molecules can be so extensive that 1 mol of water no longer occupies 18 cm^3. In this case, the proportionality breaks down, and $(\mu_w - \mu_o)$ should be used without converting to pressure units. Pressure units become meaningless anyway when systems are dry enough not to have a continuous liquid phase, usually whenever Ψ_w is below about -10 MPa.

Appendix 2.3: Matric Potentials

Matric potentials occur because the surface of a liquid has properties that differ from those in the interior. At the surface, the molecules interact with other liquid molecules only on the liquid side of the surface. In bulk liquid, they interact in all directions. At the surface, the molecules tend to be pulled into the bulk by their attraction to other molecules, and this forms a surface tension. In the bulk liquid, there is no surface tension. A porous medium extends the surface as water enters the pores, and thus increases the amount of water having surface properties. Often the surface of the medium is wettable mostly because of hydrogen bonding between water and O and OH groups on the surfaces. Also, surface charges attract the water dipole and ions in the water. The total effect is to constrain water and solute next to the surfaces. The wettability and solute constraint attracts water from the air or any aqueous liquid and, because of bonding between water molecules, liquid water tends to be dragged into the pores, filling the matrix. The meniscus in the pore exhibits surface tension that keeps the pore filled. Electrically constrained ions next to the pore surfaces also move water into the matrix with osmotic-like force. As a consequence, the water content of the matrix can become very large, as seen in many gels. Pressures are generated next to the surfaces and the whole matrix can swell.

For most plant cells, the walls are the major site of the matric potential (Boyer, 1967b). The surfaces are highly wettable, and water fills the pores. Because of their small diameter, tensions (negative pressures) of as much as −75 MPa can be present without draining them. Note that the tension on the pore water can vary between zero and the tensions that just cause the pores to drain. Thus, as plants generate tensions, the wall pores remain water filled as long as the tensions do not exceed about −75 MPa.

When the matrix dehydrates enough to drain the pores, the remaining water lines the surfaces and is strongly constrained. It is capable of attracting liquid water with great force. As a consequence, dry seeds can absorb water against large external forces, even though the cell membranes are nonfunctional.