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Plant Physiology
Ördög Vince, Molnár Zoltán (2011)
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Chapter 2. Water and nutrients in plant

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Water balance of plant

Water in plant life

Water plays a crucial role in the life of plant. It is the most abundant constituents of most organisms. Water typically accounts for more than 70 percent by weight of non-woody plant parts. The water content of plants is in a continual state of flux. The constant flow of water through plants is a matter of considerable significance to their growth and survival. The uptake of water by cells generates a pressure known as **turgor**. Photosynthesis requires that plants draw carbon dioxide from the atmosphere, and at the same time exposes them to water loss. To prevent leaf desiccation, water must be absorbed by the roots, and transported through the plant body. Balancing the uptake, transport, and loss of water represents an important challenge for land plants. The thermal properties of water contribute to temperature regulation, helping to ensure that plants do not cool down or heat up too rapidly. Water has excellent solvent properties. Many of the biochemical reactions occur in water and water is itself either a reactant or a product in a large number of those reactions.

The practice of crop irrigation reflects the fact that water is a key resource limiting agricultural productivity. Water availability likewise limits the productivity of natural ecosystems (**Figure 1.1**). Plants use water in huge amounts, but only small part of that remains in the plant to supply growth. About 97% of water taken up by plants is lost to the atmosphere, 2% is used for volume increase or cell expansion, and 1% for metabolic processes, predominantly photosynthesis. Water loss to the atmosphere appears to be an inevitable consequence of carrying out photosynthesis. The uptake of CO2 is coupled to the loss of water (**Figure 1.2**). Because the driving gradient for water loss from leaves is much larger than that for CO2 uptake, as many as 400 water molecules are lost for every CO2 molecule gained.

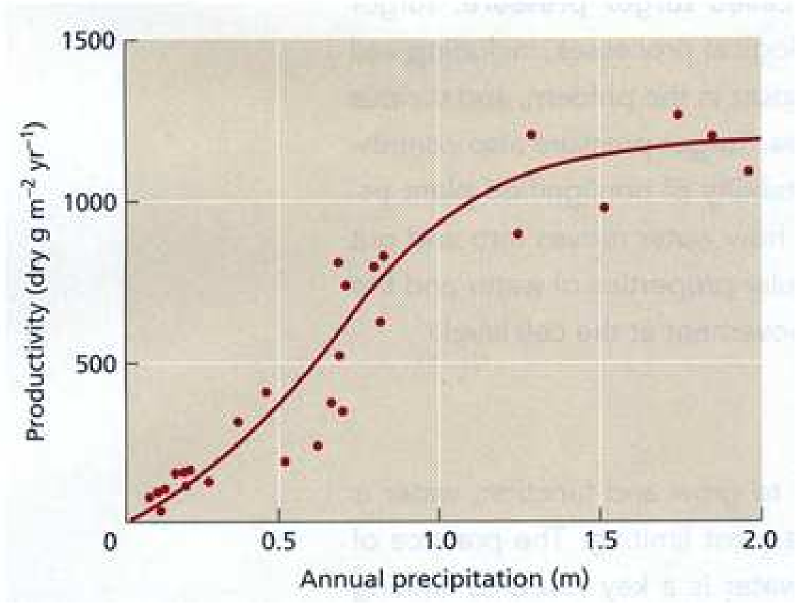

Figure 1.1 Productivity of various ecosystems as a function of annual precipitation (*source: Taiz L., Zeiger E., 2010*)

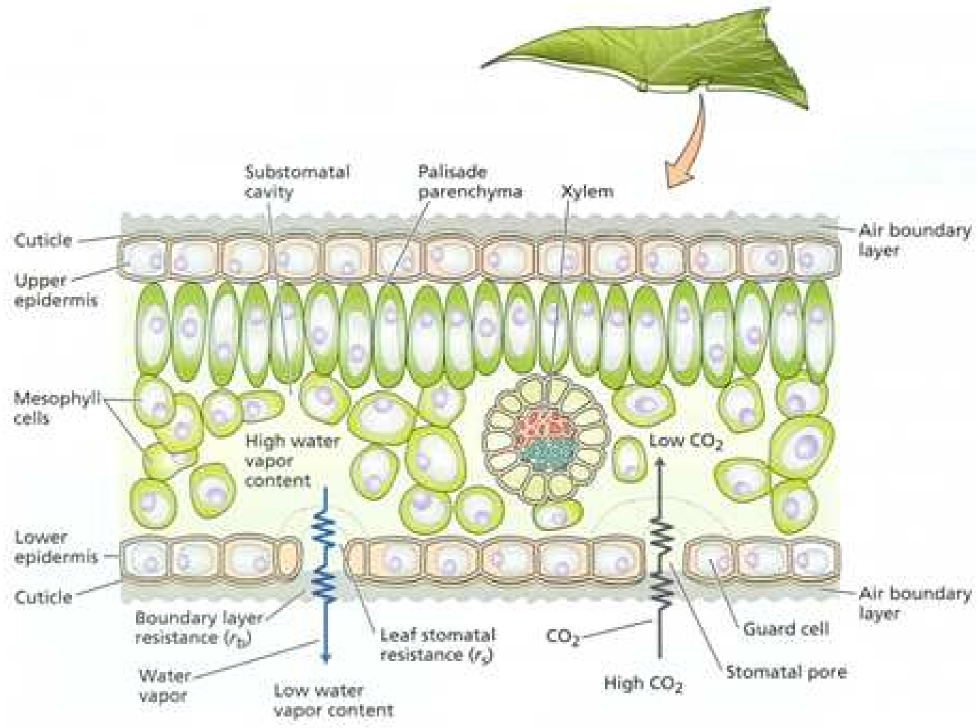

Figure 1.2 Water pathway through the leaf (*source: Taiz L., Zeiger E., 2010*)

Water potential

The structure and properties of water

Water consists of an oxygen atom covalently bonded to two hydrogen atoms (**Figure 1.3**). The oxygen atom carries a partial negative charge, and a corresponding partial positive charge is shared between the two hydrogen atoms. This asymmetric electron distribution makes water a **polar molecule**. However, the partial charges are equal, and the water remains a neutral molecule. There is a strong electrical attraction between adjacent water molecules or between water and other polar molecules, which is called hydrogen bonding. The **hydrogen bonding** ability of water and its polar structure make it a particularly good solvent for ionic substances and for molecules such as sugars and proteins. The hydration shells that form around biologically important macromolecules are often referred to as **bound water**. Bound water prevents protein molecules from approaching close enough to form aggregates large enough to precipitate.

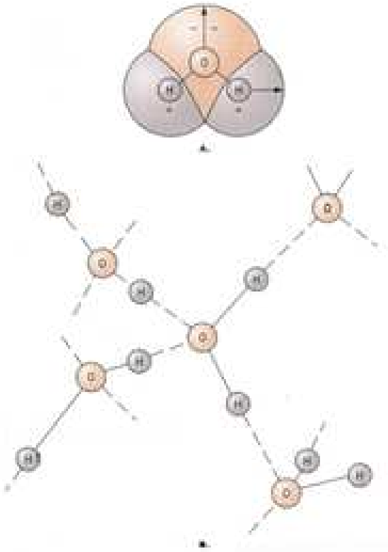

Figure 1.3 A) Structure of a water molecule B) Hydrogen bonds among water molecules (*source: Hopkins W.G., Hüner N.P.A., 2009*)

The extensive hydrogen bonding between water molecules results in water having both a high **specific heat capacity** and a high **latent heat of vaporization**. Because of its highly ordered structure, liquid water also has a high **thermal conductivity**. This means that it rapidly conducts heat away from the point of application. The combination of high specific heat and thermal conductivity enables water to absorb and redistribute large amounts of heat energy without correspondingly large increases in temperature. The heat of biochemical reactions may be quickly dissipated throughout the cell. Compared with other liquids, water requires a relatively large heat input to raise its temperature. This is important for plants, because it helps buffer temperature fluctuations. The latent heat of vaporization decreases as temperature increases, reaching a minimum at the boiling point (100°C). For water at 25°C, the heat of vaporization is 44kJ mol-1 – the highest value known for any liquid.

The excellent solvent properties of water are due to the highly polar character of the water molecule. The polarity of molecules can be measured by a quantity known as the **dielectric constant**. Water has one of the highest dielectric constant, which is as high as 78.4. The dielectric constant of benzene and hexane is 2.3 and 1.9, respectively. Water is thus an excellent solvent for charged ions or molecules, which dissolve very poorly in non-polar organic liquids.

The extensive hydrogen bonding in water gives a new property known as **cohesion**, the mutual attraction between molecules. A related property, called **adhesion**, is the attraction of water to a solid phase, such as cell wall. The water molecules are highly cohesive. One consequence of cohesion is that water has exceptionally high **surface tension**, which is the energy required to increase the surface area of a gas-liquid interface. Surface tension and adhesion at the evaporative surfaces in leaves generate the physical forces that pull water through the plant's vascular system. Cohesion, adhesion and surface tension give rise to a phenomenon known as **capillarity**. These combined properties of water help to explain why water rises in capillary tubes and are exceptionally important in maintaining the continuity of water columns in plants.

Hydrogen bonding gives water a high tensile strength, defined as the maximum force per unit area that a continuous column of water can withstand before breaking. Water can resist pressures more negative than -20 MPa, where the negative sign indicates tension, as opposed to compression. Pressure is measured in units called pascals (Pa), or more conveniently, megapascals (MPa). One MPa equals approximately 9.9 atmospheres.

Water movement by diffusion, osmosis and bulk flow

Movement of substances from one region to another is commonly referred to as translocation. Mechanisms for translocation may be classified as either active or passive. It is sometimes difficult to distinguish between active and passive transport, but the translocation of water is clearly a passive process. Passive movement of most substances can be accounted for by **bulk flow** or **diffusion**. The diffusion of water across a selectively permeable barrier is known as **osmosis**, which must also be taken into account.

Bulk flow accounts for some water movement in plants through the xylem tissues of plants. Movement of materials by bulk flow (or mass flow) is pressure driven. Bulk flow occurs when an external force, such as gravity or pressure, is applied. As a result, all of the molecules of the substance move in mass. Bulk flow is pressure-driven, diffusion is driven principally by concentration differences.

The molecules in a solution are not static, they are in continuous motion. Diffusion results in the net movement of molecules from regions of high concentration to regions of low concentration. This tendency for a system to evolve toward and even distribution of molecules can be understood as a consequence of the second law of thermodynamics, which tells us that spontaneous processes evolve in the direction of increasing entropy or disorder. Diffusion represents the natural tendency of systems to move toward the lowest possible energy state. Fick's first law describes the process of diffusion, which is most effective over short distances. Diffusion in solutions can be effective within cellular dimensions but is far too slow to be effective over long distances. The average time required for a glucose molecule to diffuse across a cell with a diameter of 50 µm is 2.5 s. However, the average time needed for the same glucose molecule to diffuse a distance of 1 m in water is approximately 32 years.

The net movement of water across a selectively permeable barrier is referred to as osmosis. Membranes of plant cells are selectively permeable. The diffusion of water directly across the lipid bilayer is facilitated by **aquaporins**, which are integral membrane proteins that form water-selective channels across membrane. In osmosis the maximization of entropy is realized by the volume of solvent diffusing through the membrane to dilute the solute. Osmosis can be easily demonstrated using a device known as an osmometer, constructed by closing off the open end of a thistle tube with a selectively permeable membrane (**Figure 1.4**). If the tube is filled with a sugar solution and inverted in a volume of pure water, the volume of solution in the tube will increase over time. The increase in the volume of the solution will continue until the hydrostatic pressure developed in the tube is sufficient to balance the force driving the water into the solution.

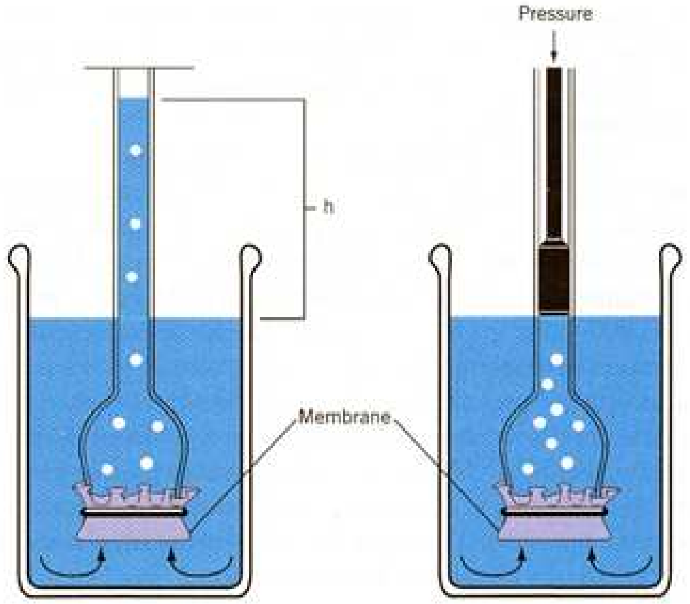

Figure 1.4 A demonstration of hydrostatic pressure (*source: Hopkins W.G., Hüner N.P.A., 2009*)

The concept of water potential

All living things, including plants, require a continuous input of free energy to maintain and repair their highly organised structures, as well as to grow and reproduce. Chemical potential is a quantitative expression of the free energy associated with a substance. The chemical potential of the water represents the free energy associated with water. Water flows without energy input from regions of higher chemical potential to ones of lower chemical potential. The concept of water potential was introduced in 1960 by R.O. Slatyer and S.A. Taylor, as a measure of the free energy of water per unit volume (J m-3). These units are equivalent to pressure units such as the pascal, which is the common measurement unit for water potential.

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

$\Psi w = \Psi s + \Psi p + \Psi g$

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

The term Ψs, called the **solute potential** or the **osmotic potential**, represents the effect of dissolved solutes on water potential. Solutes reduce the free energy of water by diluting the water. It’s value is negative or maximum zero. The minus sign indicates that dissolved solutes reduce the water potential of a solution relative to the reference state of pure water. Osmosis can be easily demonstrated using a device known as osmometer. The increase in the volume of the solution will continue until the hydrostatic pressure developed in the tube of the osmometer is sufficient to balance the force driving the water into the solution. This force, measured in units of pressure, is known as osmotic pressure. It is convention to define osmotic potential as the negative of the osmotic pressure, since they are equal but opposite forces.

The term Ψp is the **hydrostatic pressure** of the solution. Positive pressures raise the water potential; negative pressures reduce it. The positive hydrostatic pressure within cells is the turgor pressure. Negative hydrostatic pressure (**tension**) develops in the xylem and in the walls between cells. Gravity causes water to move downward unless the force of gravity is opposed by an equal and opposite force. The term Ψg depends on the height (h) of the water above the reference state water. The gravitational component (Ψg) of the water potential is generally omitted in considerations of water transport in the cell level. Thus in these cases the equation can be simplified as follows:

$$\Psi w = \Psi s + \Psi p$$

Water potentials can be measured by different methods, among others by the Sholander's pressure chamber (**Figure 1.5**). In this technique, the organ to be measured is excised from the plant and is partly sealed in a pressure chamber. Before excision, the water column in the xylem is under tension. When the water column is broken by excision of the organ (i.e., its tension is relieved allowing its ΨP to rise to zero), water is pulled rapidly from the xylem into the surrounding living cells by osmosis. The cut surface consequently appears dull and dry. To make a measurement, the investigator pressurizes the chamber with compressed gas until the distribution of water between the living cells and the xylem conduits is returned to its initial, pre-excision, state. This can be detected visually by observing when the water returns to the open ends of the xylem conduits that can be seen in the cut surface. The pressure needed to bring the water back to its initial distribution is called the balance pressure and is readily detected by the change in the appearance of the cut surface, which becomes wet and shiny when this pressure is attained. Pressure chamber measurements provide a quick and accurate way of measuring leaf water potential. Because the pressure chamber method does not require delicate instrumentation or temperature control, it has been used extensively under field conditions.

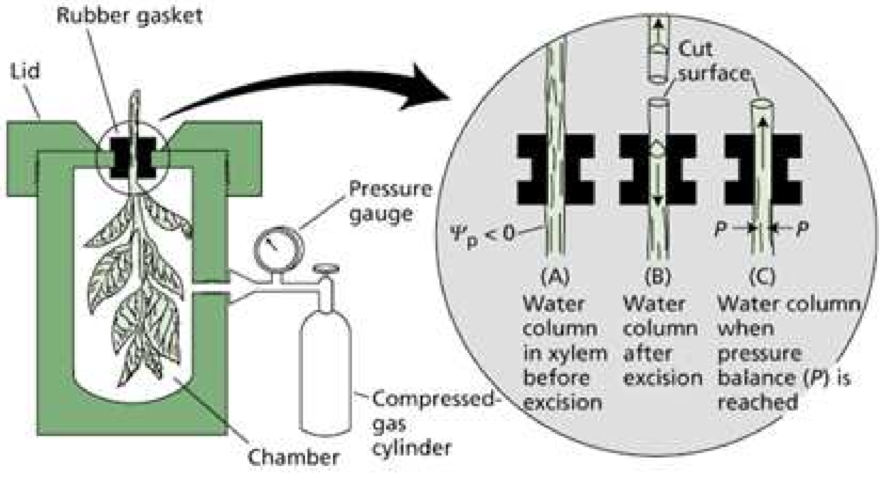

Figure 1.5 The pressure chamber method for measuring plant water potential (*source: Taiz L., Zeiger E., 2010*)

Cell growth, photosynthesis, and crop productivity are all strongly influenced by water potential and its components. Plant scientists have thus expended considerable efforts in devising accurate and reliable methods for evaluating the water status of plants. Plant cells typically have water potentials ≤0 MPa. A negative value indicates that the free energy of water within the cell is less than that of pure water. In leaves of well-watered plants, Ψw ranges from -0.2 to about -1.0 MPa in herbaceous plants and to 2.5 MPa in trees and shrubs. Within cells of well-watered garden plants (examples include lettuce, cucumber seedlings, and bean leaves) Ψs may be as high as 0.5 MPa (low cell solute concentration), although values of -0.8 to -1.2 MPa are more typical. The Ψs of the apoplast is typically -0.1 to 0 MPa. In general, water potentials in the xylem and cell walls are dominated by Ψp, which is typically less than zero. Values for Ψp within cells of well-watered plants may range from 0.1 to as much as 3 MPa. The plant **wilts** when the turgor pressure inside the cells of such tissues falls toward zero.

Absorption by roots

Water in the soil

The water content and the rate of water movement in soils depend to a large extent on soil type and soil structure. Like the water potential of the plant cells, the water potential of soils may be dissected into three components: the osmotic potential, the hydrostatic pressure and the gravitational potential. The osmotic potential (Ψs) of soil water is generally negligible. The second component of soil water potential is hydrostatic pressure (Ψp). For wet soils, Ψp is very close to zero. As soil dries out Ψp decreases and can become quite negative. As the water content of the soil decreases, the water recedes into the interstices between soil particles, forming air-water surfaces whose curvature represents the balance between the tendency to minimize the surface area of the air-water interface and the attraction of the water for the soil particles. Water under a curved surface develops a negative pressure (like in leaf mesophyll). As soil dries out, water is first removed from the largest spaces between soil particles. The value of Ψp may easily reach -1 to -2 MPa as the air-water interface recedes into the smaller spaces between clay particles. The third component is gravitational potential (Ψg). Gravity plays an important role in drainage.

Water absorption by roots

Intimate contact between the surface of root and the soil is essential for effective water absorption. **Root hairs** are filamentous outgrowths of root epidermal cells that greatly increase the surface area of the root, thus providing greater capacity for absorption of ions and water from the soil (**Figure 1.6**). Water enters the root most readily near the root tip. The intimate contact between the soil and the root surface is easily ruptured when the soil is disturbed. It is for this reason that newly transplanted seedlings and plants need to be protected from water loss for the first few days after transplantation.

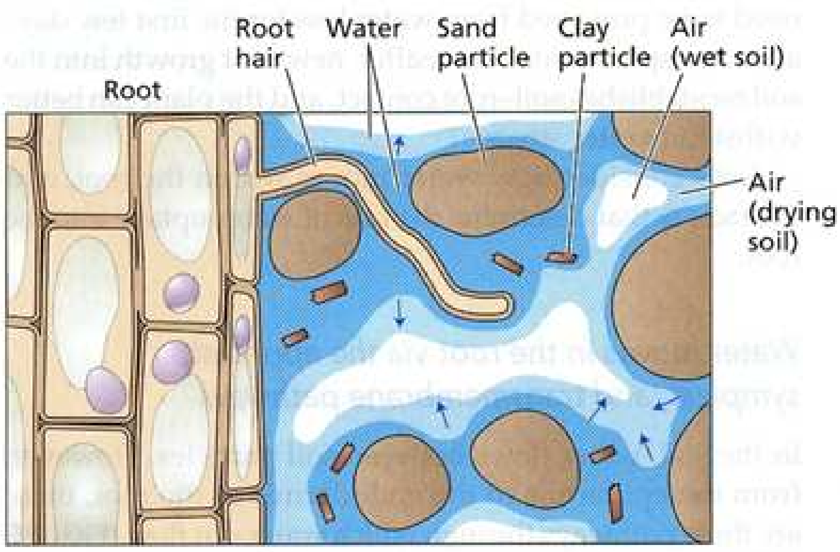

Figure 1.6 Root hairs intimate contact with soil particles and greatly amplify the surface area used for water absorption by the plant (*source: Taiz L., Zeiger E., 2010*)

From the epidermis to the endodermis of the root, there are three pathways through which water can flow: the apoplast, the symplast and the transmembrane pathway (**Figure 1.7**).

1. The apoplast is the continuous system of cell walls and intercellular air spaces. In this pathway water moves without crossing any membranes as it travels across the root cortex.

2. The symplast consists of the entire network of cell cytoplasm interconnected by plasmodesmata. In this pathway, water travels across the root cortex via the plasmodesmata.

3. The transmembrane pathway is the route by which water enters a cell on one side, exits the cell on the other side, enters the next in the series, and so on. In this pathway, water crosses the plasma membrane of each cell in its path twice.

Though there are three pathways, water moves not according to a single chosen path, but wherever the gradients and resistances direct it. At the endodermis the Casparian strip breaks the continuity of the apoplast pathway, forcing water and solutes to pass through the plasma membrane in order to cross the endodermis. The requirement that water move symplastically across the endodermis helps explain why the permeability of roots to water depends strongly on the presence of aquaporins.

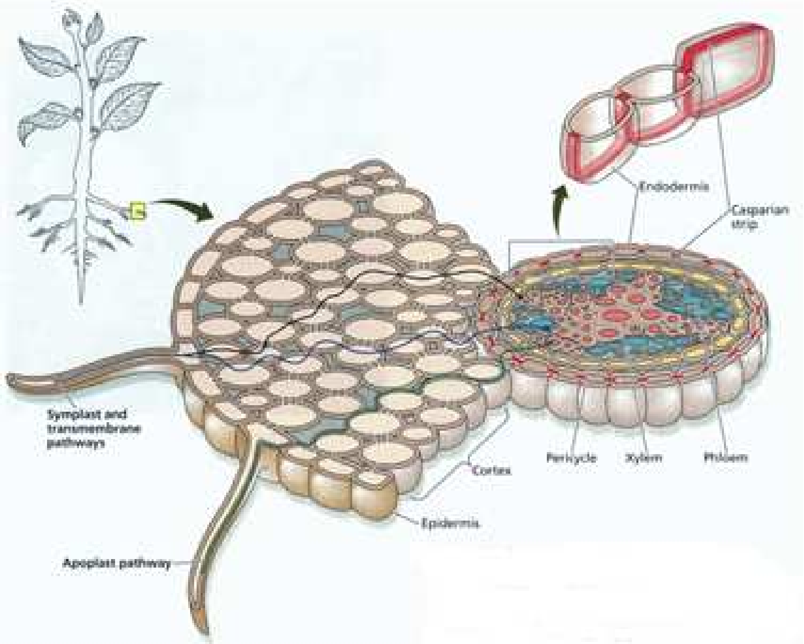

Figure 1.7 Pathways (symplast, transmembrane and apoplast) for water uptake by the root (*source: Taiz L., Zeiger E., 2010*)

Water uptake decreases when roots are subjected to low temperature or anaerobic conditions. Decreased rate of respiration, in response to low temperature or anaerobic conditions, can lead to increases in intracellular pH. This increase in cytoplasmic pH alters the conductance of aquaporins in root cells, resulting in roots that are markedly less permeable to water.

Plants sometimes exhibit a phenomenon referred to as **root pressure**. If the stem of a young seedling is cut off just above the soil, the stump will often exude sap from the cut xylem for many hours. If a manometer is sealed over the stump, positive pressures as high as 0.05 to 0.2 MPa can be measured. Plants that develop root pressure frequently produce liquid droplets on the edges of their leaves, a phenomenon known as **guttation**. Guttation is most noticeable when transpiration is suppressed and the relative humidity is high, such as at night.

Transport through the xylem

Vascular tissues include the xylem and phloem, which conduct water and nutrients between the various organs. In leaves, the larger veins subdivide into smaller veins such that no photosynthetic leaf cell is more than a few cells removed from a small vein ending. Xylem tissue is responsible for the transport of water and dissolved minerals from the root to the stem to aerial organs. Phloem, on the other hand, is responsible primarily for the translocation of organic materials from sites of synthesis to storage sites or sites of metabolic demand.

Transpiration speeds up the movement of xylem sap, but it seems unlikely that this is an essential requirement.

Transpiration involves the evaporation of water, it can assume a significant role in the cooling of leaves. However, the main evolutionary function of stomata is to ensure an adequate supply of carbon dioxide for photosynthesis

The xylem consists of two types of tracheary elements

There are two main types of **tracheary elements** in the xylem: tracheids and vessel elements. Vessel elements are found in angiosperms. Tracheids are present in both angiosperms and gymnosperms. Both tracheids and vessel elements dead cells with thick, lignified cell walls, which form hollow tubes through which water can flow with relatively little resistance. **Tracheids** are elongated, spindle-shaped cells that are arranged in overlapping vertical files. **Vessel elements** tend to be shorter and wider than tracheids and have perforated end walls that form a perforation plate at each end of the cell.

Water moves through the xylem by pressure-driven bulk flow

Pressure-driven bulk flow of water is responsible for long-distance transport of water in the xylem. It is independent of solute concentration gradient, as long as viscosity changes are negligible. It is extremely sensitive to the radius of the tube. If the radius is doubled, the volume of flow rate increases by a factor of 16 (24). Vessel elements up to 500 μm in diameter are, nearly an order of magnitude greater than the largest tracheids.

The cohesion-tension theory explains water transport in the xylem

In theory, the pressure gradients needed to move water through the xylem could result from the generation of positive pressures at the base of the plant or negative pressures at the top of the plant. However, root pressure is typically less than 0.1 MPa and disappears when the transpiration rate is high or when soils are dry, so it is clearly inadequate to move water up a tall tree. Instead, the water at the top of a tree develops a large tension (negative hydrostatic pressure), and this tension pulls water through the xylem (**Figure 1.8**). This mechanism, first proposed toward the end of the nineteenth century, is called the cohesion-tension theory of sap ascent because it requires the cohesive properties of water to sustain large tensions in the xylem water column. The theory is generally credited to H.H. Dixon, who gave the first detailed account of it in 1914.

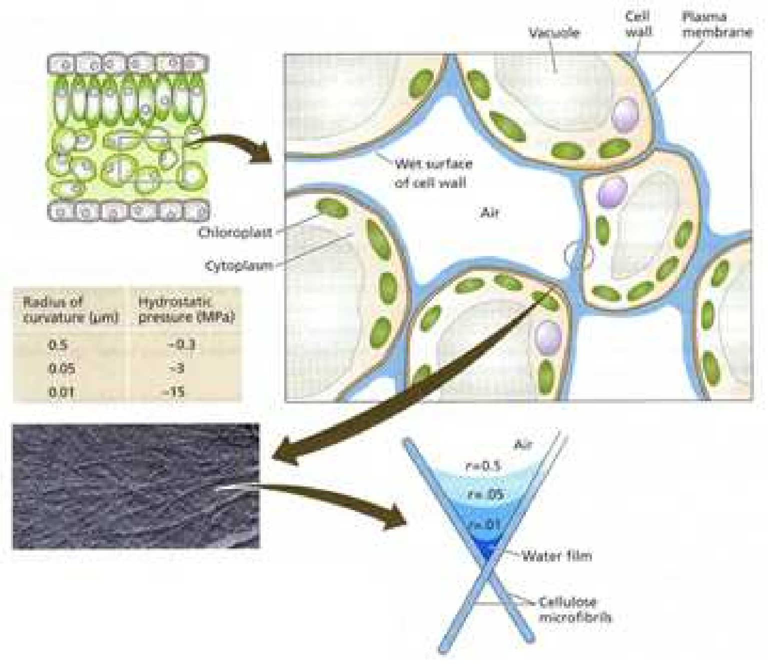

Figure 1.8 The driving force for water movement through plants originates in leaves (*source: Taiz L., Zeiger E., 2010*)

The negative pressure that causes water to move up through the xylem develops at the surface of the cell walls in the leaf. As water evaporates from mesophyll cells within the leaf, the surface of the remaining water is drawn into the interstices of the cell wall, where it forms curved air interfaces. Because of the high surface tension of water, the curvature of these interfaces induces a tension, or negative pressure, in water. The cohesion-tension theory explains how the substantial movement of water through plants occur without the direct expenditure of metabolic energy.

Transpiration

Water movement is determined by differences in water potential. It can be assumed that the driving force for transpiration is the difference in water potential between the substomatal air space and the external atmosphere. However, because the problem is now concerned with the diffusion of water vapour rather than liquid water, it will be more convenient to think in terms of vapour systems. We can say that when a gas phase has reached equilibrium and is saturated with water vapour, the system will have achieved its **saturation vapour pressure**. The vapour pressure over a solution at atmospheric pressure is influenced by solute concentration and mainly by temperature. In principle we can assume that the substomatal air space of leaf is normally saturated or very nearly saturated with water vapour. On the other hand, the atmosphere that surrounds the leaf is usually unsaturated and may often have a very low water content. This difference in water vapour pressure between the internal air spaces of the leaf and the surrounding air is the driving force of transpiration.

On its way from the leaf to the atmosphere, water is pulled from the xylem into the cell walls of the mesophyll, where it evaporates into the air spaces of the leaf. The water vapor than exits the leaf through the stomatal pore. The movement of liquid water through the living tissues of the leaf is controlled by gradients in water potential. However, transport in the vapor phase is by diffusion, so the final part of the transpiration stream is controlled by the concentration gradient of water vapor. Almost all of the water lost from leaves is lost by diffusion of water vapour through the tiny stomatal pores. The stomatal transpiration accounts for 90 to 95% of water loss from leaves. The remaining 5 to 10% is accounted for by cuticular transpiration. In most herbaceous species, stomata are present in both the upper and lower surfaces of the leaf, usually more abundant on the lower surface. In many tree species, stomata are located only on the lower surface of the leaf.

The driving force for transpiration is the difference in water vapour concentration

Transpiration from the leaf depends on two major factors: (1) the **difference in water vapor concentration** between the leaf air spaces and the external bulk air and (2) the **diffusional resistance** of this pathway. Air space volume is about 10% in corn leaves, 30% in barley, and 40% in tobacco leaves. In contrast to the volume of the air space, the internal surface area from which water evaporates may be from 7 to 30 times the external leaf area. The air space in the leaf is close to water potential equilibrium with the cell wall surfaces from which liquid water is evaporating. The concentration of water vapor changes at various points along the transpiration pathway from the cell wall surface to the bulk air outside the leaf.

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

1. The resistance associated with diffusion through the stomatal pore, the **leaf stomatal resistance**.
2. The resistance due to the layer of unstirred air next to the leaf surface through which water vapor must diffuse to reach the turbulent air of the atmosphere. This second resistance is called the leaf boundary layer resistance.

Some species are able to change the orientation of their leaves and thereby influence their transpiration rates. Many grass leaves roll up as they experience water deficits, in this way increasing their boundary layer resistance.

Stomatal control couples leaf transpiration to leaf photosynthesis

Because the cuticle covering the leaf is nearly impermeable to water, most leaf transpiration results from the diffusion of water vapor through the stomatal pore. The microscopic stomatal pores provide a low-resistance pathway for diffusional movement of gases across the epidermis and cuticle. Changes in stomatal resistance are important for the regulation of water loss by the plant and for controlling the rate of carbon dioxide uptake necessary for sustained CO2 fixation during photosynthesis. At night, when there is no photosynthesis and thus no demand for CO2 inside the leaf, stomatal apertures are kept small or closed, preventing unnecessary loss of water. Leaf can regulate its stomatal resistance by opening and closing of the stomatal pore. This biological control is exerted by a pair of specialized epidermal cells, the **guard cells**, which surround the stomatal pore.

The cell walls of guard cells have specialized features

Guard cells are found in leaves of all vascular plants. In grasses, guard cells have a characteristic dumpbell shape, with bulbous ends (**Figure 1.9**). These guard cells are always flanked by a pair of differentiated epidermal cells called **subsidiary cells**, which help the guard cells control the stomatal pores. In dicots and nongrass monocots, guard cells have an elliptical contour (often called “kidney-shaped”) with the pore at their center. Subsidiary cells are often absent, the guard cells are surrounded by ordinary epidermal cells. A distinctive feature of guard cells is the specialized structure of their walls. The alignment of cellulose microfibrils, which reinforce all plant cell walls and are an important determinant of cell shape, play an essential role in the opening and closing of the stomatal pore.

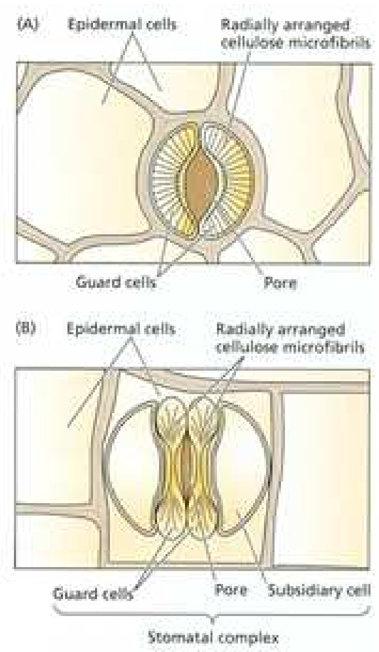

Figure 1.9 The radial alignment of the cellulose microfibrils in guard cells and epidermal cells of (A) a kidney-shaped stoma and (B) a grasslike stoma (*source: Taiz L., Zeiger E., 2010*)

An increase in guard cell turgor pressure opens the stomata

Guard cells function as multisensory hydraulic valves. Environmental factors such as light intensity and quality, temperature, leaf water status, and intracellular CO2 concentrations are sensed by guard cells, and these signals are integrated into well-defined stomatal responses. The early aspects of this process are ion uptake and other metabolic changes in the guard cells. The decrease of osmotic potential (Ψs) resulting from ion uptake and from biosynthesis of organic molecules in the guard cells. Water relations in guard cells follow the same rules as in other cells. As Ψs decreases, the water potential decreases, and water consequently moves into the guard cells. As water enters the cell, turgor pressure increases. Because of the elastic properties of their walls, guard cells can reversible increase their volume by 40 to 100%, depending on the species. Such changes in cell volume lead to opening or closing of the stomatal pore. Subsidiary cells appear to play an important role in allowing stomata to open quickly and to achieve large apertures.

The transpiration ratio measures the relationship between water loss and carbon gain

The effectiveness of plants in moderating water loss while allowing sufficient CO2 uptake for photosynthesis can be assessed by a parameter called the **transpiration ratio**. This value is defined as the amount of water transpired by the plant divided by the amount of carbon dioxide assimilated by photosynthesis. For plants in which the first stable product of carbon fixation is a 3-carbon compound (C3 plants), as many as 400 molecules of water are lost every molecule of CO2 fixed by photosynthesis, giving a transpiration ratio of 400. Plants in which a 4-carbon compound is the first stable product of photosynthesis (C4 plants), generally transpire less water per molecule of CO2 fixed than C3 plants do. A typical transpiration ratio for C4 plants is about 150. Plants with crassulacean acid metabolism (CAM) photosynthesis the transpiration ratio is low, values of about 50 are not unusual.

Plant water status

The water status of plant cells is constantly changing as the cells adjust to fluctuations in the water content of the environment or to changes in metabolic state. The plant water status is dependent on: the soil moisture content, the capacity for water absorption by roots, and the hydraulic conductivity of root and shoot tissues. Water potential is often used as a measure of the water status of a plant. Plants are seldom fully hydrated. During periods of drought, they suffer from water deficits that lead to inhibition of plant growth and photosynthesis. Several physiological changes occur as plants experience increasingly drier conditions (**Figure 1.10**). Cell expansion is most affected by water deficit. In many plants reductions in water supply inhibit shoot growth and leaf expansion but stimulate root elongation. Drought does impose some absolute limitations on physiological processes, although the actual water potentials at which such limitations occur vary with species.

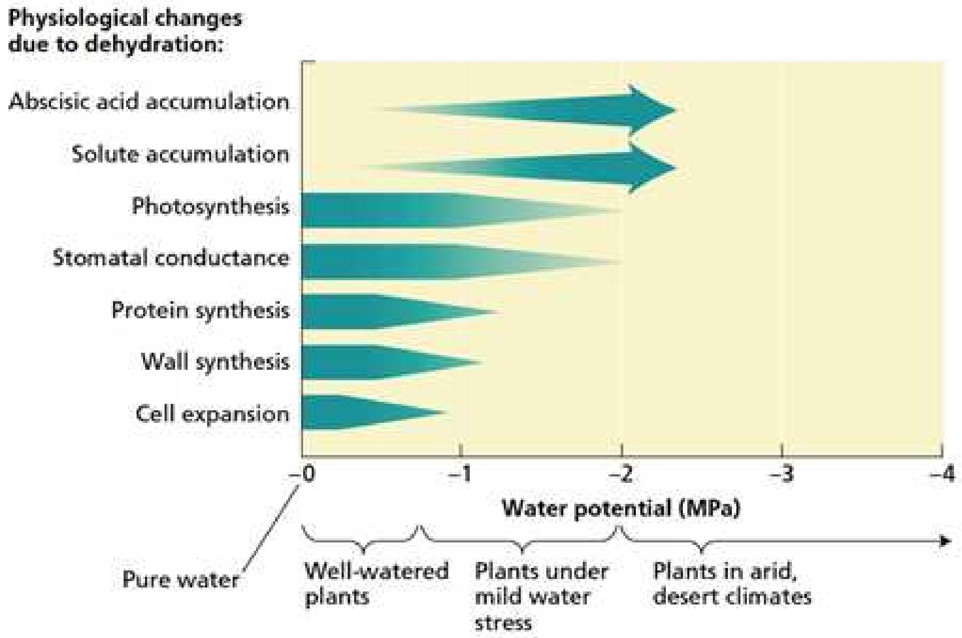

Figure 1.10 Sensitivity of various physiological processes to changes in water potential under various growing conditions (*source: Taiz L., Zeiger E., 2010*)

The plant may *spend energy* to accumulate solutes to maintain turgor pressure, invest in the growth of non-photosynthetic organs such as roots to increase water uptake capacity, or build xylem conduits capable of withstanding large negative pressures. Thus, physiological responses to water availability reflect a trade-off between the benefits accrued by being able to carry out physiological processes (e.g., growth) over a wider range of environmental conditions and the costs associated with such capability.

Water stress typically leads to an *accumulation of solutes* in the cytoplasm and vacuole of plant cells, thus allowing the cells to maintain turgor pressure despite low water potential. Some physiological processes appear to be influenced directly by turgor pressure. However, the existence of stretch-activated signalling molecules in the plasma membrane suggests that plant cells may sense changes in their water status via changes in volume, rather than by responding directly to turgor pressure.

Influence of extreme water supply

Plant growth can be limited both by water deficit and by excess water. *Drought* is the meteorological term for a period of insufficient precipitation that results in plant water deficit. *Excess water* occurs as the result of flooding or soil compaction. The deleterious effects of excess water are a consequence of the displacement of oxygen from the soil.

When soil is water-saturated, the water potential (Ψw) of the soil solution may approach zero, but drying can reduce the soil Ψw to below -1.5 MPa, the point at which *permanent wilting* can occur. The relative humidity of the air determines the vapour pressure gradient between the leaf stomatal cavity and the atmosphere, and this vapour pressure gradient is the driving force for transpirational water loss.

When a soil dries, its hydraulic conductivity decreases very sharply, particularly near the permanent wilting point (that is, the soil water content at which plant cannot regain turgor upon rehydration). Redistribution of water within the roots often occurs at night, when evaporative demand from leaves is low. Water-deficient plants tend to become rehydrated at night, allowing leaf growth during the day. But at the permanent wilting point, water delivery to the roots is too slow to allow the overnight rehydration of plants that have wilted during the day. Thus, decreasing soil water conductivity hinders rehydration after wilting.

Water deficit is stressful, but too much water can also have several potentially negative consequences for a plant. Flooding and soil compaction result in poor drainage, leading to reduced O2 availability to cells. Flooding fills soil pores with water, reducing O2 availability. Dissolved oxygen diffuses so slowly in stagnant water that only a few cm of soil near the surface remain oxygenated. At low temperatures the consequences are relatively harmless. However, when temperatures are higher (greater than 20°C), O2 consumption by plant roots, soil fauna, and microorganisms can totally deplete O2 from the soil in as little as 24 hours. Flooding sensitive plants are severely damaged by 24 hours of anoxia (lack of oxygen). The yield of flooding-sensitive garden-pea (*Pisum sativum*) may decrease by fifty percent. Corn is affected by flooding in a milder way, and is more resistant to flooding. It can withstand anoxia temporarily, but not for periods of more than a few days.

Soil anoxia damage plant roots directly by inhibiting cellular respiration. The *critical oxygen pressure* (COP) is the oxygen pressure below which respiration rates decrease as a result of O2 deficiency. The COP for the corn root tip growing in a well-stirred nutrient solution at 25°C is about 20 kilopascals (kPa), or 20% O2 by volume, close to the oxygen concentration in ambient air.

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