Plant Water Relations

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Water is one of the most important constituents of life. Chemically, water is the hydride of oxygen. Oxygen, being more electronegative, exerts a strong attractive pull on its electrons. This unequal attraction results in small positive charge on two hydrogen molecules and a small negative charge on the oxygen molecule. The two lone pairs of electrons of the oxygen molecule result in bending of water molecule. The partial charges on oxygen and hydrogen molecules result in high electric dipole moment and polarity of water molecule. The distinct physical and chemical properties of water, namely, cohesion, surface tension, high specific heat, high heat of vaporization, lower density of ice, and solubility, are due to hydrogen bonding between water molecules (Fig. 1.1). Water forms solution with large number of compounds. It is thus usually referred as a universal solvent. The solvent action of water is of tremendous importance for the cells. All cells require water, dissolved ions, and sugars to survive. Cells undergo oxidation-reduction reactions, and water serves as the medium in which all these reactions are carried out. Plants, being immobile and autotrophic, have to depend on the supply of water and minerals from the soil and carbon dioxide and light from the atmosphere. Transport of water and minerals in the vascular strands is based on the differences in pressure and concentration gradients of both solutes and the solvent (water). The transport of minerals and water from the soil to xylem and from xylem to substomatal cavity is referred as **short-distance transport**. Once water enters the xylem elements, it is transported up to 100 m or more by the transpirational pull created in the leaves. Therefore, there is need to have an essential **long-distance transport** by two different transport systems involving transport in opposite directions. This chapter shall focus on various mechanisms of short- and long-distance transport in plants.

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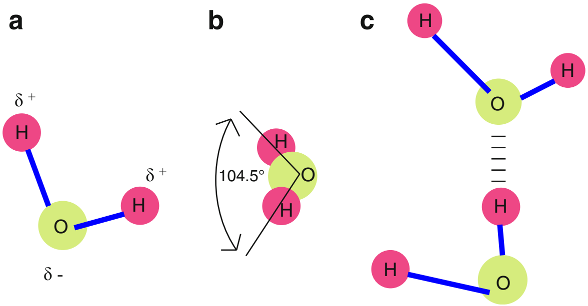


Fig. 1.1 Structure and unique features of water. (**a**) The two hydrogen atoms in water molecule carry partial positive charges, whereas oxygen atom carries a partial negative charge. (**b**) Water molecule has a bent geometry, thereby causing asymmetric distribution of charge. So, water is polar. (**c**) Neighboring water molecules are linked through hydrogen bonding between oxygen atom of one with hydrogen of the other

1.1 Water Potential and Its Components

The **free energy** of any molecule determines its capacity to perform work. The chemical potential is the free energy per mole of any substance in a chemical system. Chemical potential is a relative term. It is expressed as the difference between the potential of a substance in a given state and the potential of the same substance in a standard state. The chemical potential of water (plant physiologists use the term **water potential**) is the free energy of water. It is the chemical potential of water divided by partial molar volume. In other words, water potential is a measure of free energy of water per unit volume (Jm^{-3}). In terms of pressure units, water potential is expressed as MPa (megapascal). The lower the water potential of the plant, the greater is its ability to absorb water and vice versa. It also helps to measure the water deficit and stress in plants. Water potential is not an absolute value and is symbolized by the Greek letter Ψ_w (psi). Water potential of pure water is maximum and its value is zero at the atmospheric pressure**.** In a living cell, water potential refers to the sum of the following components:

$$\Psi_{w=}\Psi_s + \Psi_p + \Psi_m + \Psi_g$$

where Ψ_w is the water potential, Ψ_s solute/osmotic potential, Ψ_p pressure potential, Ψ_g gravitational potential, and Ψ_m matric potential.

1.1.1 Solute Potential

Osmotic potential (Ψ_s) or **solute potential** refers to the effect of solutes on water potential. Solutes reduce the free energy of water**.** The addition of solutes also changes the colligative properties of solutions. Macromolecules, like proteins, nucleic acids, and polysaccharides, have far less effects on the solute potential as compared to their respective monomers. The cell stores fuel as macromolecules (starch in plant cells or glycogen in animal cells), rather than glucose or other simple sugars to avoid drastic changes in osmotic potential.

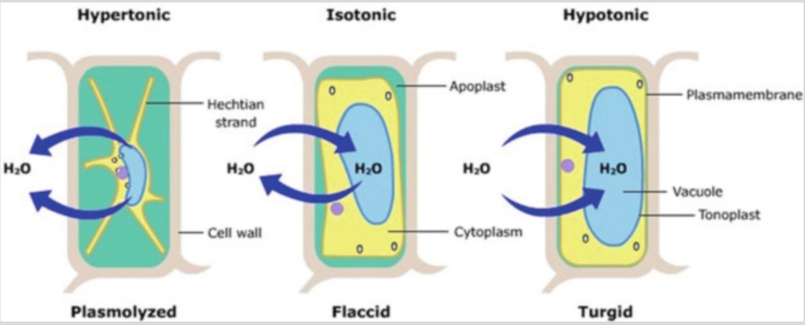
For dilute solutions, the osmotic potential can be calculated by using Van't Hoff equation

$$\Psi_s = -iCRT$$

where i is the ionization constant (for sucrose the value is 1, but for ionic solutes, it is multiplied by the number of dissociated particles), C solute concentration in moles, R gas constant (8.314 J.mol^{-1}), and T temperature in Kelvin (273 + $^{\circ}$C of solution). The –ve sign indicates that dissolved solutes reduce the water potential of the solution. This equation is valid for dilute solutions only. Using this equation, water potential and solute potential of a cell or tissue can be measured (Box 1.1).

Box 1.1: Methods to Measure Osmotic Potential

Plasmolytic method: A series of sucrose solutions with different osmotic potentials are prepared. Epidermal peels of Rhoeo, red onion containing anthocyanin, are placed in different solutions, and after about half an hour, the peels are observed under the microscope. Some of the peels from different solutions will show the cells to be fully turgid, or they become flaccid (plasmolyzed). The number of plasmolyzed and unplasmolyzed cells is counted and their percentage calculated. In some epidermal peels, 50% of the cells are just beginning to show the signs of plasmolysis (*incipient plasmolysis*). During incipient plasmolysis, the turgor pressure of the cell is zero, and the osmotic potential of the cell contents is equal to the water potential and osmotic potential of the external solution.



Cell placed in hypertonic solution (left) undergoes plasmolysis due to loss of water from vacuole. In an isotonic solution (center), cell remains flaccid, but in a hypotonic solution, the cell is fully turgid (right). Plasma membrane is

(continued)

Box 1.1 (continued)
connected to cell wall. These connections are retained in the form of thin strands at the time of plasmolysis. These are known as *Hechtian strands*.

Methods to Measure Water Potential

Gravimetric method: This method is the same as volumetric method. It involves the placement of pre-weighed plant tissue (potato tissue cylinders) into graded series of solutions of sucrose or other **osmoticum** (osmotically active solutes) at a defined osmotic potential. After 1 h of incubation, Tissue weight gain or loss is plotted against the water potential ($\Psi_w = \Psi_s$) of each solution. The water potential of the solution in which there is no net gain is equal to that of tissue.

Charadakov's or Falling drop method: Two series of sucrose solutions (ranging from 0.15 to 0.5 molal, in increments of 0.5 molality) are placed in two sets of test tubes. An equal amount of tissue is placed in the two sets of test tubes. In another set, equal and minute amount of methylene blue is added. After half an hour, incubated tissue is removed; a small drop of respective control solution is added in test solution. If the drop rises in the test solution, this indicates that the test solution is concentrated, i.e., water from the solution has entered into the tissue, making it more concentrated. If the drops fall, this indicates that water has come out from the tissue making the tissue lighter than the control solution. On the other hand, if drops float, it means there is no net movement of water. At this point, water potential of the tissue is equal to that of the sucrose solution of that particular concentration.

1.1.2 Pressure Potential

It is the hydrostatic pressure of the solution. It is denoted by ψ_p and is measured in MPa. It is always positive. Pure water has minimum pressure potential, i.e., zero. Increase in pressure increases the water potential of a solution. In other words, pressure potential of a cell is the amount of pressure required to stop further entry of water in the cell. In a cell, pressure potential is responsible for maintaining the turgidity, and hence it is known as **turgor pressure (TP)**. The turgor pressure (TP) of a cell is the difference between inside and outside hydrostatic pressures across the plasma membrane and cell wall. At equilibrium (i.e., when inside water potential is equal to outside water potential), TP will be equal to the difference in internal solute potential and that of external solute potential.

$$\mathrm{TP} = \Psi_{s(\mathrm{inside})} - \Psi_{s(\mathrm{outside})}$$

In plants a fully turgid cell experiences an equal and opposite pressure, known as **wall pressure**. The presence of cell wall in plant cells allows it to withstand a wide range of osmotic variations. In contrast, an animal cell can only survive in an **isotonic** solution. The plant cell placed in pure water swells but does not burst. The negative osmotic potential in vacuolated solution (cell sap) causes the movement of water only in the cell. Due to entry of water, plasma membrane is pressed against the cell wall.

1.1.3 Gravitational Potential

Gravitational pull has the same effect on water potential as the effect of pressure, and it is expressed as **gravitational potential** (Ψ_g). It is the sum of three forces: gravitational acceleration, height of water column, and density of water. When dealing with water transport at the cell level, the gravitational component is usually omitted because it is negligible as compared to solute potential and pressure potential. However, gravitational pull definitely affects water movement in tall trees.

1.1.4 Matric Potential

It is expressed as the adsorption affinity of water to colloidal substances and surfaces in plant cells. **Matric potential** is negligible in a hydrated cell but is of considerable importance in dehydrated cells and tissues such as seeds and desert plants. Under these conditions, water exists as a very thin layer bound to solid surfaces by electrostatic interactions. These interactions are not easily separated into their effects on solute and pressure potential and thus sometimes combined into matric potential. The adsorption of water by hydrophilic surfaces is known as hydration or **imbibition** (Box 1.2). Matric potential is measured in the same unit as water potential. A dry or hydrophilic substance has extremely negative potential (as low as −300 MPa). Figure 1.2 illustrates the changes in water potential, pressure potential, and osmotic potential as the cell volume changes. The relationship is expressed considering that there is no movement of solute into or out of the cell, and the cell volume changes because of movement of water only. It describes the status of a mature cell when placed in solutions of different osmotic potentials. There is gain or loss of water from the cells, but the total quantity of solute within the cell remains constant. Water potential and osmotic potential are always negative in a cell. In a fully turgid cell, the water potential becomes zero even in the presence of solute. As in plants, cell wall exerts pressure, and with the dilution of the cell sap, the water potential at that pressure becomes zero. The plant cell volume changes, but small change in it causes large changes in turgor pressure. A 10% increase in cell volume due to uptake of water gives rise to a fully turgid cell with a small change in solute potential. But

Box 1.2: Imbibition

It is a special type of diffusion involving adsorbents. During **imbibition**, the molecules of a liquid or gas diffuse into a solid substance, causing it to swell. In biological systems, it is the liquid water or water vapor diffusing into the colloidal matrix, causing it to swell. There is a need to have strong binding force between the molecules of the imbibant and the substance being imbibed. Such an intermolecular force exists between cellulose and water. If dry plant material is placed in water, it swells and results in considerable increase in volume. For imbibition to occur, a water potential gradient must exist between the surfaces of the adsorbent and liquid being imbibed, and an affinity is also essential between the components of the adsorbent and the imbibed substance. In some dry seeds, water potential of up to −900 bars has been observed. Therefore, dry seeds immediately imbibe water, and this is the first step in seed germination. This is followed by swelling of seeds and mobilization of reserve food materials and, finally, the emergence of root and shoot. The great reduction in the potential of the imbibed water is a result of the greatly decreased kinetic energy. The lost energy appears as heat. Imbibition invariably accompanies release of heat. Unlike osmosis imbibition does not require semipermeable membrane. Because of the high matric force of the cellulose, cell wall still retains water after complete desiccation of the cell. Only complete desiccation of a plant tissue, as by drying in an oven at relatively high temperature, will remove all the water imbibed in the cellulosic cell walls. Cell wall of dry seeds has minimum water, but it germinates only when it acquires water by imbibition. Imbibition also takes place in plants and animal products such as wood, cork, and sponge. In ancient times, this concept was used for stone-cutting technique. People used to place dry wooden logs into holes in rocks. The swelling of these logs would result in breaking the rocks. In nature, plants survive in the crevices of rocks because swollen seeds create space in the rocks and allow roots to grow.

growing cells do not show this relationship because, in these cells, cell wall expands and cell wall pressure decreases.

1.2 Intercellular Water Transport

All living cells contain approximately 60–95% of water, and water is required for their growth and reproduction. Even the dormant cells and tissues also have 10–20% of water. Water flow is a passive process, and it moves in response to physical forces toward regions of low water potential or low free energy. The intercellular or short-distance water transport takes place through diffusion, mass flow, or osmosis.

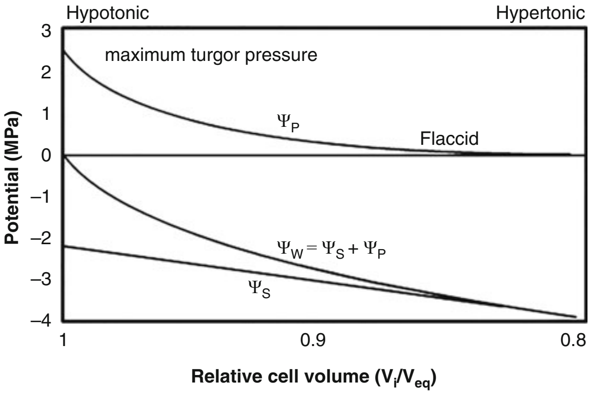


Fig. 1.2 The relationship between change in cell volume and change in water potential, solute potential, and pressure potential. In a fully turgid cell, the water potential, pressure potential, and solute potential are maximum. The pressure potential and solute potential are equal and opposite at zero water potential. V_i, initial volume; V_{eq}, volume at equilibrium

1.2.1 Diffusion

It is a physical process where movement of any substance or molecule takes place from the region of its higher concentration to the region of its lower concentration due to kinetic energy. **Diffusion** can take place in all three phases of matter. The rate of diffusion is affected by temperature, molecular density, diffusion medium, and chemical potential gradient. In plants, diffusion occurs in stomata to facilitate the exchange of carbon dioxide, oxygen, and water vapors between leaf cells and external atmosphere. Diffusion also plays an important role in gas exchange in lenticels present in the stem. The apoplastic and symplastic pathway of intercellular transport also involve diffusion. Imbibition during seed germination is also a special type of diffusion.

The rate of diffusion is directly proportional to the concentration gradient ($\Delta C_S/\Delta X$), which can be expressed as (Fick's equation)

$$Js \propto \left(\frac{\Delta C_s}{\Delta X}\right)$$

$$Js = -Ds\left(\frac{\Delta C_s}{\Delta X}\right)$$

where Js is the flux density, ΔC_S is the difference in the concentration of substance in two media, and ΔX is the distance travelled in cm by substance, i.e., substance (s) crossing a unit area per unit time. It is expressed in mol.m^{-2}.s^{-1}. Ds is the **diffusion coefficient** that measures the movement of a particular substance through a medium. The diffusion coefficient is characteristic of a substance and depends on the medium in which diffusion is taking place. The larger molecules have smaller diffusion coefficient, and diffusion in air is much faster than diffusion in a liquid medium. The negative sign in the equation is due to movement taking place down the gradient. In other words, **Fick's first law of diffusion** states that a substance diffuses faster if there is more difference in its concentration gradient or the diffusion coefficient is higher. Diffusion is rapid if the distance is small but it is extremely slow over long distances.

The time taken (t_c) for diffusion to reach one half of the concentration from the starting point is given by the formula

$$t_c = \frac{1}{2} = \frac{(\text{Distance})^2}{Ds} \times K$$

where K is constant which depends on the shape of the system. For example, in a cell of 50 μm diameter with diffusion coefficient of glucose being 10^{-9} $m^2.s^{-1}$, the diffusion of glucose molecule from one point to another to reach half the concentration will take 2.5 s.

$$t_c = \frac{1}{2} = \frac{\left(50 \times 10^{-6}\text{m}\right)^2}{10^{-9}\text{m}^2.\text{s}^{-1}} = 2.5 \text{ s}$$

But if we consider the diffusion of glucose molecule to 1 meter distance, it will take up to 32 years.

$$t_c = \frac{1}{2} = \frac{(1 \text{ m})^2}{10^{-9}\text{m}^2.\text{s}^{-1}} = 32 \text{ years}$$

At intercellular level, the movement of water can be due to diffusion, but it is not a viable option for long-distance travel.

1.2.2 Mass Flow

Mass flow or **bulk flow** is pressure-driven movement of molecules. In contrast to diffusion and osmosis, mass flow is independent of solute concentration. The protoplasm streaming in plant cells during active growing season is an example of mass flow. The rate of flow of protoplasm is approximately 25 $mm.h.^{-1}$ at room temperature. The upward longitudinal transport of water and dissolved substances in the xylem elements and in phloem transport takes place through mass flow. The xylem and phloem strands undergo many development changes to increase their conductance for bulk flow. The rate of flow in xylem vessels can be calculated by **Hagen-Poiseuille's equation**:

$$\text{Volume flow rate} = \frac{dV}{dt} = \frac{\pi.\Delta P.R^4}{8\eta L}$$

where ΔP is the pressure difference, R is the radius of xylem vessel, η is the viscosity of xylem sap, and L is the length of xylem vessel. The bulk flow rate is very sensitive to the radius of the vessel. If radius is doubled, then the rate of flow of water in xylem vessels will increase by 16-fold. Mass flow has a significant role in long-distance transport of water and minerals. During intercellular transport, mass flow faces many barriers, viz., cell wall, plasma membrane, tonoplast, and plasmodesmata. Vascular cells have adopted many changes for bulk movement of water, e.g., removal of end walls in xylem vessels, enlargement of plasmodesmata, and depletion of protoplasm.

1.2.3 Osmosis

It is a special type of diffusion which takes place in solvents through semipermeable membrane. **Osmosis** is a biological process where the solvent molecules move from their higher concentration (lower solute concentration) to lower concentration (higher solute concentration) through a semipermeable membrane (Box 1.3). It is controlled both by concentration and pressure gradient. The rate of osmosis can be increased by the addition of osmotically active substances and can be measured by **osmometer.** Osmosis is the process by which water is transported into and out of the cell. The growth, development, and turgidity of the cells are maintained by the process of osmoregulation (Box 1.4). The process of osmosis can be stopped or reversed by applying pressure. This is called **reverse osmosis**. This process is now commercially used for purifying water (Box 1.5).

Box 1.3: Demonstration of the Phenomenon of Osmosis
To understand the process of osmosis, pure water is taken in a beaker, and a thistle funnel containing sucrose solution is inserted in it, with the dipped end of the funnel being sealed with a semipermeable membrane. Keep this apparatus undisturbed for some time. Depending on the concentration of sucrose, water will move from beaker into the funnel by osmosis. Since pure water has maximum water potential, it will move from its higher potential to its lower potential, i.e., water will move in the funnel. In other words, water moves from **hypotonic** to **hypertonic** solution or from the direction of lower solute potential to higher solute potential.

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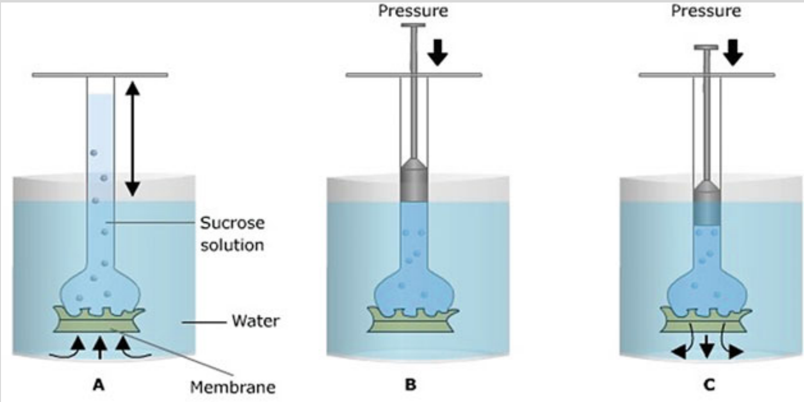
Box 1.3 (continued)



Water will keep on moving upward as long as the water potential difference exits between the two solutions. However, osmosis can be stopped by putting pressure. If pressure is continuously increased, water moves out from thistle funnel against the water potential difference.

Box 1.4: Significance of Osmosis

All living cells are like bags carrying solutions in semipermeable membranes. The survival of a cell depends on the ability to maintain intracellular solute concentration. Living organisms develop many strategies to maintain a steady influx of water by osmosis. Some single-celled organisms, such as *Paramecium*, extrude water through special organelles called *contractile vacuoles.* Marine organisms adjust their internal concentration of solutes to match that of sea water. Many terrestrial animals have a circulating fluid which is isotonic and cells are bathed in it. The blood flowing in our body contains a high concentration of the protein albumin which elevates solute concentration of the blood to match with that of cell cytoplasm. The lack of cell wall in animal cells makes it more susceptible to osmotic lysis. Storing of blood, injecting of blood and drugs intravenously, and maintaining the pH of blood are very challenging and require maintaining osmotic concentration. The RBCs immediately burst if there is a slight change in their osmotic concentration. Most of the plant cells are hypertonic to their immediate environment. They contain a

(continued)

Box 1.4 (continued)
central vacuole which has high solute concentration, resulting in high hydrostatic pressure inside the cell. This hydrostatic pressure, known as turgor pressure, keeps the cell turgid and maintains its shape. During osmotic adjustment, vacuole losses solutes and thus protects the cells from turgor loss. The presence of rigid cell wall in the plant cell makes it sturdier, and it can withstand adverse environmental conditions. The plasmolyzed cells remain connected to the cell wall with the help of strands called **Hechtian strands.**

The transport of water and minerals from roots to leaves and carbohydrates from leaves to roots is dependent on osmosis. The opening and closing of stomata, touch response in plants, movement to catch insect by insectivorous plants are all regulated by osmosis. **Dialysis**, one of the major vital processes, where blood is purified by artificial kidney, is also based on the osmosis. Osmosis is used for preserving fruits, jams, and pickles. Preservation requires dehydration, which is achieved by the use of salt or sugar solution. The use of hypertonic solution causes the movement of water from the food tissue and protects it from microbes. During food preservation, more than 50% of the tissue water is removed by osmotic dehydration.

Box 1.5: Reverse Osmosis
Water contains significant amount of salts even after purification with high-grade filters, which poses health hazards. **Reverse osmosis** (RO) technology is used to demineralize or deionize water for making it potable. This process is reverse of osmosis. In reverse osmosis, water moves from its lower potential to higher potential under pressure through semipermeable membrane. Since it involves semipermeable membrane and the direction of flow is reverse, it is known as reverse osmosis. The RO system consists of membrane filters (usually 5) which do cross filtration. The solution passes through filters with two outlets. The clean or deionized water having few salts goes one way, and the rest of it comes out from the waste pipe. Cross filtration helps in cleaning the filters so that there are no depositions on the filter. The cleaned water is free from dissolved salts, organic matter, colloids, bacteria, and viruses. In addition to solvent, solute of smaller size also moves through semipermeable membrane.

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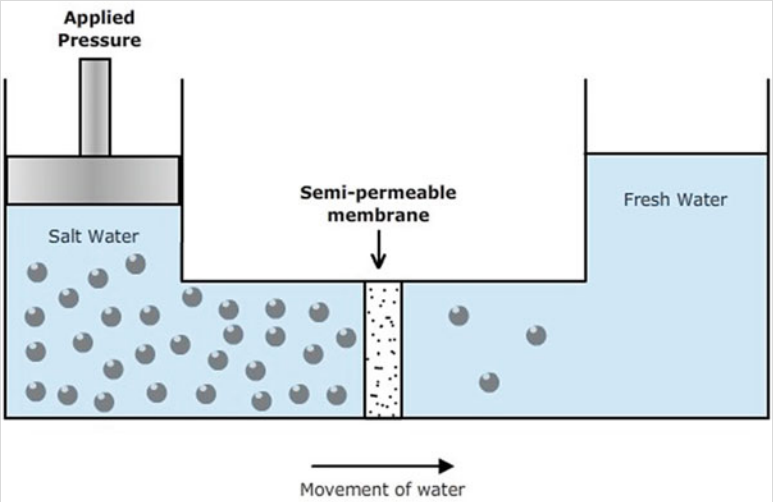
Box 1.5 (continued)



1.3 Short-Distance Transport

The movement of water from root to upper foliar parts of the plant requires integration of many levels of transport. The long-distance transport of water in xylem is supplemented by short-distance transport of water from the root to cortex and ultimately to the xylem. Basically, there are three levels of water transport in plants. The first level of water transport refers to the entry of water from the soil into the root cells, through the plasma membrane. At this level, the selective permeability of the plasma membrane regulates the movement of solutes and the solvent between the cell and extracellular solutions. The molecules tend to move down their concentration gradient. This has been already discussed in the above sections. In addition to active and passive transport, proteins present in the membrane speed up the movement across the membrane. The second level of transport is from root epidermal cells to the innermost layer of the cortex. This is referred as short-distance transport, and it includes **apoplast**, **symplast**, and **transcellular pathways** including transporters, channels, and plasmodesmata**.** The short-distance transport also includes water transport from xylem in the leaf veins to substomatal cavity**.** The third level of transport is the long-distance transport in xylary elements.

1.3.1 Water Absorption by Roots

The area covered by the plant roots is generally very high. It is, therefore, appropriate to call root as *the hidden half* of the plant body. Growth and development of roots can be analyzed by special subterranean camera, known as **rhizotrons.** The region of maximum water uptake is the region of active root hair development. The root hair density is an important factor in water uptake, and its extent of proliferation depends on the ecological conditions in which plants grow. The influx of water into roots is only through the apical zone just behind the zone of elongation of primary root where the root hair density is maximum (Fig. 1.3). Increased suberization in the older parts does not allow entry of the water**.** Water passes through the lipid layer (despite nonpolar in nature of lipids) due to water potential gradient between root cells and soil. As long as the water potential of root cells is more negative than that of soil, water is continuously being taken into the plant. Depending on the requirement by the plant, rate of water absorption keeps changing. The water absorption can be active (ATP is involved) or passive (through osmosis), or it can be facilitated by special membrane channels for water transport, mainly through aquaporins.

Once water and minerals are absorbed by the roots, they follow three pathways to reach vascular tissue of the root. These are apoplastic, symplastic, and transcellular pathways. Water may follow one or more possible pathways across the root depending on the requirement of water by the plant.

The diffusion of solute or solvent across the lipid membrane or any porous structure depends on the **permeability coefficient** (P_s). It is constant and depends on the type of membrane and the size of molecule to be diffused ($m.s^{-1}$). Thus, diffusion flux (J_s; $mol.m^{-2}.s^{-1}$), driven by a concentration gradient (ΔC_s) of uncharged molecules across a membrane, is given by the equation

$$J_s = P_s \times \Delta C_s$$

Thus, if molecules of equal size have to cross a membrane, the one with greater solubility in lipids will pass more quickly into the cell. On the other hand, if

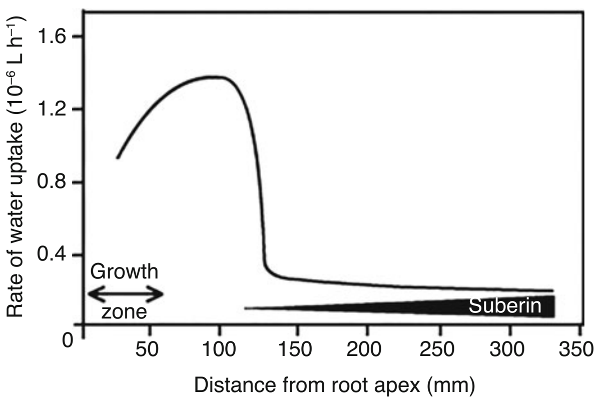


Fig. 1.3 The graph showing that maximum uptake of water in plants is from the small portion of root which is in between the zone of root growth and the zone of maturation (suberin gets deposited in the walls of root cells), i.e., zone of elongation

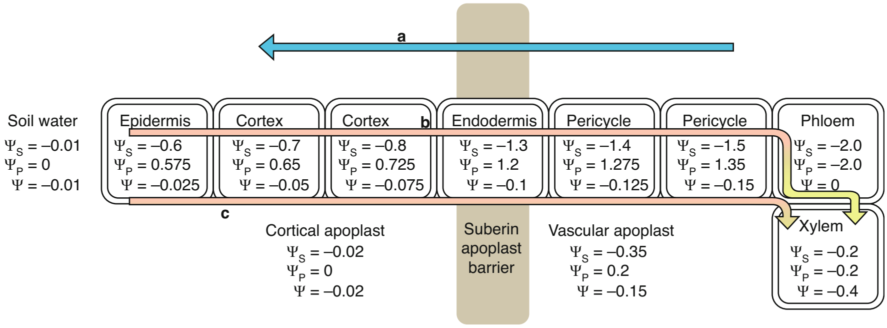


Fig. 1.4 The entry and pathway of water movement from and across the root. None of the root cells and apoplast fluid are in equilibrium. Water and solute potential gradient shown are responsible for the flow of water. Arrow “a” shows sucrose movement which maintains the solute potential across the root. The symplastic pathway is shown by arrow “b” and apoplastic by arrow “c”

molecules of equal solubility have to cross the membrane, the smaller ones penetrate faster. If diffusion flux is high, then permeability of the membrane will be more. The permeability of plasmodesmata is 10,000 times more than that of plasma membrane when the size of the molecule is less than 700 Dalton. The plasmodesmatal connections present in different regions shows different *limits of size exclusion* (ranging from molecule of 1 to 65 kDa). In roots, the size of molecules passing the plasmodesmatal connection is maximum, i.e., 65 kDa. It increases the flow of water and solutes between the adjacent cells. None of the root cells and apoplast fluids are in equilibrium (Fig. 1.4). Macromolecules, like RNA, proteins, and viruses, can also move through plasmodesmata.

1.3.1.1 Movement of Water Across Endodermis

Once water reaches the endodermis, further passage through the cell wall (apoplastic) is blocked by Casparian strips. The cells of endodermis have connecting walls embedded with the waterproof material—suberin. This layer blocks the apoplastic pathway and controls water and nutrient flow to the xylem. The Casparian band does not allow passage of water and nutrients across it into the deeper cells (Fig. 1.5). Some of the endodermal cells show absence of thickenings. These are referred as **passage cells**. Water crosses the endodermis layer through these passage cells or through symplasm. Radial water movement through cortical cells is fast, and transport rate increases as water moves toward the central stele. The rate of water movement from xylem parenchyma to tracheary elements (tracheids and vessels) increases because of aquaporins, which plays a very pivotal role in radial transport.

1.3.1.2 Intercellular Transport Between Xylem and Nonvascular Cells

In roots, loading of water and nutrients into the xylem strands involves multiple cellular pathways and transporters. Through plasmodesmata and membrane transporters, water and minerals are transported to xylem parenchyma. Xylem parenchyma cells also have highly active transporters. Parenchyma surrounding

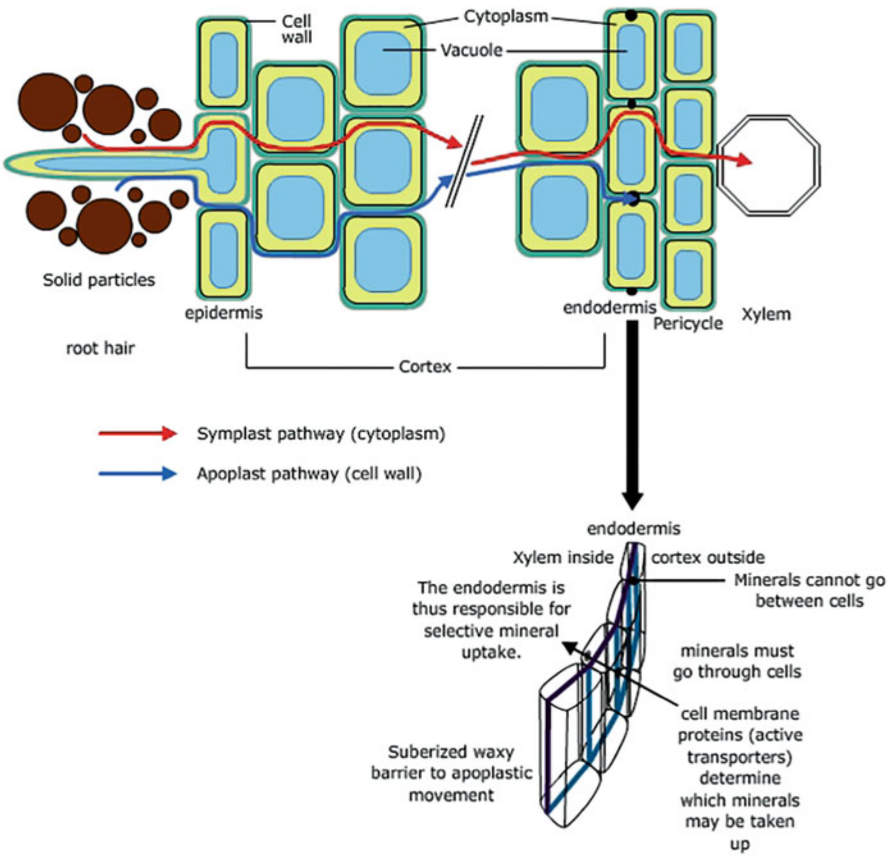


Fig. 1.5 The pattern of radial transport or short-distance transport across root. The entry of water from the soil to root takes place due to water potential difference by osmosis or through water channels. The intercellular transport through the cortex follows apoplast or symplast pathway. Once it reaches the endodermis, the apoplastic entry of water is stopped by the Casparian bands in the endodermis. Water crosses this layer through symplast pathway or passage cells and reaches the xylary elements

the xylary elements invaginate the cell wall under the pit membrane to increase the surface area for transport. In addition to water, some of the nutrients are also transported through xylem. At the root surface, some nutrients and salts enter into the xylem. One such example is K^+ which is delivered to xylem at the root surface and transported to the shoot through xylem. Anions, such as NO^-_3 and Cl^-, are also released in xylem sap by anion channels. The concentration of nutrients in xylem varies with water flow rate, soil composition, and nutritional status of the plant. Similarly, unloading of water and nutrients in the leaves also involves multiple cellular pathways and specific transporters. These transporters are responsible for silicon uptake and its loading and unloading in xylem. Loading and unloading of element in xylem are under the control of abscisic acid (ABA) and signals from the shoot. During stress conditions, ABA accumulates and decreases xylem loading of ions. Roots accumulate more ions keeping solute concentration higher and thus help to maintain turgor pressure and growth.

1.4 Long-Distance Transport

For the survival of land plants, long-distance transport of water and nutrients is an important process. Angiosperms and gymnosperms are the most advanced land plants with well-developed vascular systems. Water and nutrient entry into the xylary elements in roots and their transport against gravity to the top of the aerial parts of the plants is referred as long-distance transport.

1.4.1 Water Transport Through Xylem

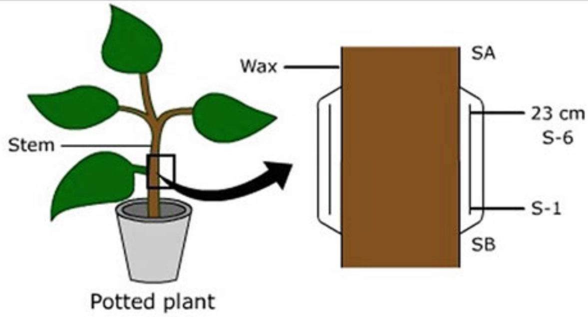
The upward movement of water through the xylem tissues is referred as **ascent of sap**. Water travels long distances in plants through xylem strands (Box 1.6). The upward movement of water is facilitated by transpirational pull and cohesive-adhesive properties of water molecules. Mature xylem consists of tracheids and vessels. It is responsible for upward movement of water. Xylem carries the water stream from the site of absorption (roots) to the site of evaporation (leaves). Water potential regulates the entry of water into the xylem. The upward transport of xylem sap is rapid during the daytime when transpiration rates are high. The ascent of xylem sap is slowest in evergreen conifers, intermediates in deciduous trees and herbaceous plants, and is highest in vines and lianas.

Box 1.6: Experimental Evidence for Xylem Transport

In a potted plant, phloem is separated from xylem (approximately at 25 cm height above soil) with the help of wax paper**.** The separation of xylem and phloem stops lateral transport of water in this region. The segment above the stripped zone is labeled SA and segment below it as SB. There are six segments in the stripped area numbered as S_1–S_6. The roots are exposed to a soluble dye containing ^{42}K, and the different sections are analyzed for radioactive potassium in both xylem and phloem. The section where xylem is separated from phloem, the content of potassium is highly reduced in phloem while it is high in xylem. The sections below and above the stripped region have the equal content of potassium in both phloem and xylem. This indicates that water moves through xylem and is laterally transported in phloem.

(continued)

Box 1.6 (continued)



	Stem segment	^{42}K in xylem (ppm)	^{42}K in phloem (ppm)
Above strip	SA	47	53
Stripped Section	S6	119	11.6
	S5	122	0.9
	S4	112	0.7
	S3	98	0.3
	S2	108	0.3
	S1	113	20.0
Below stripped	SB	58	84.0

1.4.2 Mechanism of Transport Across Xylem

1.4.2.1 Root Pressure

It is a positive hydrostatic pressure (1–2 bars) developed due to the difference in solute potential between the soil solution and xylem sap. It often develops at night when the rate of transpiration is low or absent and humidity is high. In roots, the development of pressure takes place due to high salt concentration and presence of Casparian bands in endodermis**.** Ion accumulation decreases the solute potential of roots, and despite the absence of transpiration, water enters into the root and into the xylem. Root pressure is insignificant in tall trees but has a significant role in the young plants (Sect. 1.6; Guttation). During seed germination and bud growth, prior to the development of leaf and transpiration stream, water uptake is due to root pressure.

1.4.2.2 Capillary Rise

Liquids in small tubes show a rise in the meniscus level due to **adhesion** of liquid with the wall of tube. This rise of meniscus of liquid in the tube is known as **capillarity** or **capillary rise**. Water has high **tensile strength** due to cohesion of its molecules. In addition, water also has adhesion between water molecules and xylem elements, and there exists **surface tension** among water molecules**.** These factors are responsible for capillary rise of water in plants. The rate of capillary rise is indirectly proportional to the radii of xylem elements. In order to reach a height of 100 m in tall trees by capillary rise, there have to be cells with diameter of 0.15 μm (which is much smaller than the diameter of smallest tracheids). Moreover, the capillary rise in small capillary tubes is due to open space in the tube, whereas water in xylem does not have open menisci (xylem is filled with water).

1.4.2.3 Cohesion-Adhesion and Tension Theory

H.H. Dixon (1914) stated that water in xylem is under constant tension due to transpirational pull. Many experiments gave evidence that xylem is constantly under three types of pressures, viz., the driving force or the transpirational pull, cohesion force due to cohesion of water molecules, and adhesion force between water molecules and the wall of xylem elements. These three forces lead to the formation of a continuous column of water, which is pulled from roots to the leaves. One of the driving forces for ascent of sap is **transpirational pull** (Fig. 1.6). Transpiration is the evaporation of water in the form of water vapor from the

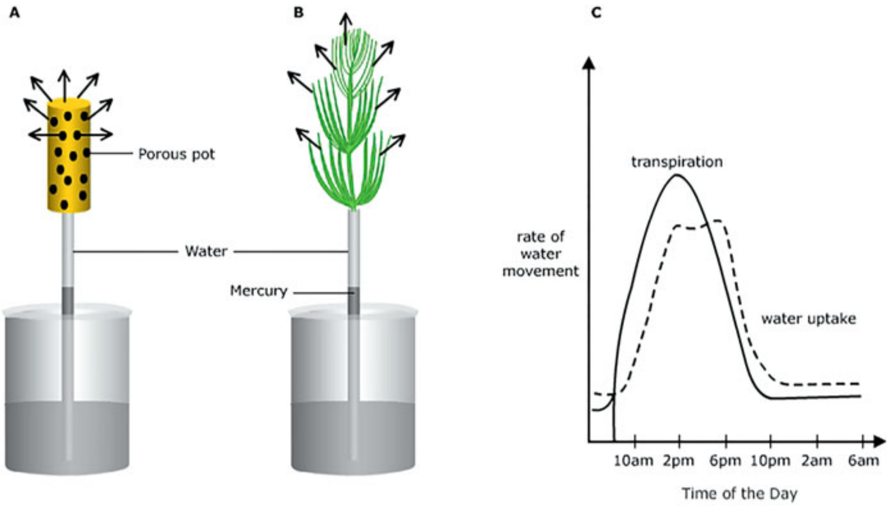


Fig. 1.6 Demonstration of transpiration pull. (**a**) Water molecules evaporated from porous pot create suction pressure leading to a rise in the mercury level. (**b**) The pot is replaced by a healthy twig. Due to transpiration pull, suction is created in xylem vessels and mercury level rises. The suction pressure due to transpiration is very high due to which it can pull heavy metal like mercury**.** (**c**) Pattern of uptake of water in plant begins after a rise in the rate of transpiration. The rate of transpiration is maximum at noon, and water uptake is also maximum during that period

aboveground parts of the plant. During rapid transpiration period, water moves in xylem at an average rate of 4 mm. s^{-1}, causing development of pressure of more than −5 MPa. Tension in xylem can be measured using different methods. Water can withstand tension of −21 MPa which is enough to overcome the gravitational force in large trees. These tensions and water potential difference in xylem are transferred to root and finally to the soil, leading to soil-plant-atmosphere continuum (Table. 1.1). This continuous column can only be maintained due to cohesion of water molecules by hydrogen bonding. Sometimes the gaps in certain tracheary elements cannot withstand large tensions, and continuation of column is not maintained, leading to disruption in transport.

1.4.2.4 Cavitation and Embolism

The continuity of water in the xylem strands is broken down despite filtration provided by the roots. The reason for breakage of water column in xylem is the high tension in xylem cells. This tension in xylem causes water to change into vapor state. The breakage of column can be due to air getting trapped in or water getting converted to vapors in the xylem. This sudden reversal of liquid water into water vapors, leading to breakage of water column, is known as **cavitation**. The presence of large number of pores in xylem strands breaks surface tension of water, and it draws minute bubbles in the xylem column. Cavitation due to trapping of air is called "air seeding." Air seeding is a very common phenomenon in plants. In this process, the air enters tracheids through pit membranes. Tension in tracheids causes damage to pit membrane and increases its pore size, and air gets filled into it. The process of filling of the vessel or tracheids with air is called **embolism** (Fig. 1.7). The main causes of cavitation are water stress during high transpiration, freezing of xylem sap in winter, and pathogen attack (Fig. 1.8). Whenever there is a breakage of water column in the tracheids, it creates click-like sound which can be recorded using acoustic methods. As the plant experiences water stress due to high rate of transpiration during the daytime, the frequency of cavitation increases. The loss of xylem

Table 1.1 Transpiration flow in the leaf is maintained by decreasing water potential from xylem sap to external atmosphere immediately around the leaf

		Solute potential	Pressure potential	Gravitational potential	Water potential
Leaf					
	Xylem sap	–0.2	–2.5	1.5	–1.2
	Bundle sheath	–3.3	0.1	1.5	–1.7
	Apoplast	–3.5	–0.7	1.5	–2.7
	Substomatal cavity				–8
External atmosphere					–100

The solute potential and pressure potential show variations, but gravitational pull is the same at different locations in the leaf cell. All the values are in MPa

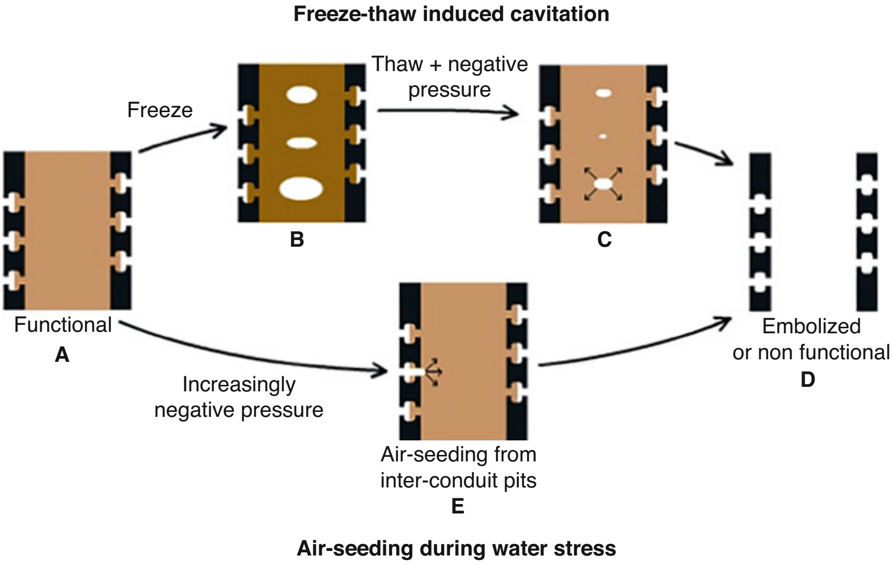


Fig. 1.7 The process of cavitation in xylem. (**a**) A functional xylary element. (**b**) and (**c**) During the process of thawing, after freezing temperature, water molecules experience very high negative pressure resulting in breaking of water column. Air gets trapped and spreads resulting in air seeding from inter-conduit pits (**d**) followed by complete embolization of the cell. (**e**) The air is pulled through pit membrane from adjacent embolized cell or under water stress conditions. The process of air getting trapped is called air seeding which results in embolized cell

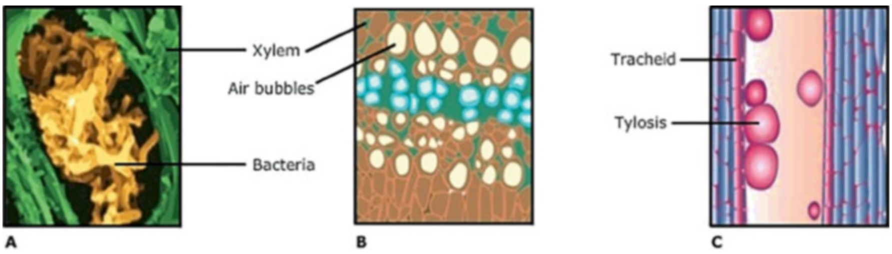


Fig. 1.8 Causes of cavitation in xylem. (**a**) Xylem-filled with bacterial pathogen. (**b**) Xylem tracheids showing inward bursting of air bubbles. (**c**) Blockage of tracheid due to tyloses in gymnosperms

function due to cavitation varies in different plants. Bordered pits present in gymnospermous tracheids act like valves. The torus present in it closes the pit and avoids spreading of cavitation to adjacent functional tracheids. Vessels are more susceptible to air seeding as compared to tracheids. The absence of xylem vessels in gymnosperms growing in the cold temperate zones is one of the adaptations to avoid air seeding during freezing temperatures. The embolized xylem cells are repaired at night when transpiration stops or slows down. Water moves from the adjacent tracheids and maintains water uptake**.** At the root level, the solutes are pumped into xylem, lowering its water potential as compared to the soil. Water moves from the soil and develops a positive root pressure. This pressure forces water to move up to 10 m and fills the embolized xylem cells. In herbaceous plants, the refilling of tracheary elements occurs during night due to root pressure. Aquaporins in xylem-associated cells are also involved in refilling of the embolized tracheids.

1.4.2.5 Unloading of Water and Nutrients from Xylem in Leaves

In the leaves, a network of major and minor veins helps in the distribution of water and nutrients throughout. The xylary elements in the leaves are present in minor leaf veins. The leaf veins are enclosed by a bundle sheath. Water and nutrients in the minor veins are unloaded in the spongy parenchyma. Water transport from the spongy parenchyma to the site of evaporation (stomata) may follow symplastic or transcellular pathways, as in roots. However, apoplastic pathway is blocked in the leaves. As in roots, unloading of water and nutrients again involves transporters and specific intercellular pathways. Some of these transporters block the entry of nutrients in the leaves, and such nutrients are again taken back by the phloem to the root. Na^+ is one such example. Plants protect leaves from salt stress by recirculating Na^+. Nutrients are targeted to different cells of the leaves according to the plant type, and water moves through spongy parenchyma to the substomatal cavity.

1.5 Water Movement from Leaves to the Atmosphere

The driving force for water movement from soil to leaves and from the leaves to atmosphere is transpiration. The upward translocation of water in the xylem from roots to the leaves is coupled with the pressure of transpiration and is referred as **transpirational stream** (Fig. 1.9). During the process of rapid evapotranspiration, the rate of water transport in xylem is about 4 $mm.s^{-1}$. Water lost by transpiration must be replenished by the absorption of an equivalent amount of water from the soil. One sunflower plant "imbibes" and "perspires" 17 times more water than a human every 24 h. A single maize plant transpires approximately 150 l of water in its average life span (Box 1.7).

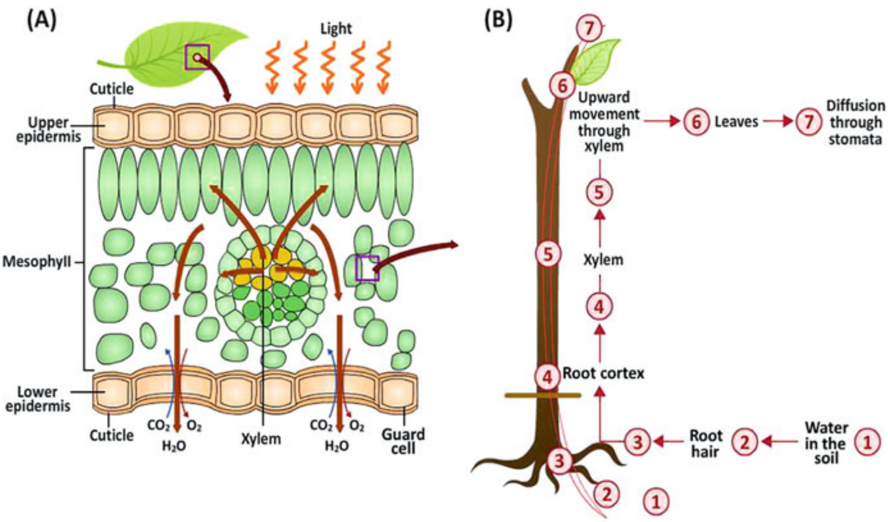


Fig. 1.9 (**a**) Evaporation of water from leaf surface. Water from xylem enters into air spaces of spongy parenchyma and diffuses out through stomata present on the lower epidermis. Gas exchange takes place when stomata open up. Carbon dioxide is taken in and oxygen is released. (**b**) Transpiration from leaf creates a continuous water stream up to the soil

Box 1.7: Transpiration Ratio

It is used to determine the efficiency of plants to fix CO_2, relative to the amount of water loss by transpiration. The opening of stomata during daytime is a compromise between photosynthesis and transpiration. Plants balance water loss with photosynthesis. Carbon dioxide concentration in the substomatal cavity plays a key role in balancing the two processes. This shows that plant regulates stomatal movement in response to the extent of photosynthesis. Plants adapt many strategies to reduce transpiration. The relative amounts of photosynthesis (CO_2 in) and transpiration (H_2O out) occurring at any time depend on the amount of CO_2 and H_2O in the atmosphere inside and outside the leaf, respectively. For every unit of CO_2 used in photosynthesis, plants lose about 600 units of H_2O. The amount of water loss is quite high. Thus, transpiration as a necessary evil is justified. This ratio of CO_2 taken in and water lost by the plant is known as **transpiration ratio** or **water use efficiency.** C_4 and CAM plants are more efficient because they are well adapted to reduce transpiration. Transpiration ratio usually varies from 100 to 1000 among different plants, depending on the environmental conditions. There is more than twofold difference in the transpiration ratio between C_3 and C_4 plants. This difference is due to leaf anatomy and pathway of CO_2 fixation.

1.5.1 Transpiration

The uptake of CO_2 for photosynthesis requires moist surface, but when water is exposed, it gets evaporated. Plants face this challenge of taking more carbon dioxide and at the same time loss of water. Plants lose 400–600 molecules of water while gaining 1 molecule of carbon dioxide. Thus, both photosynthesis and loss of water by transpiration are inseparable processes in the life of green plants. Water has high **latent heat of vaporization**. At 30 °C, 1000 gm (1 kg) of water absorbs 580 Kcal of heat from its environment**.** Large amount of water is being evaporated from plants, and the heat required for vaporization is being drawn from leaf. It helps plants to maintain the temperature and tolerate harsh environmental pressures. The main advantage of transpiration is creation of suction pressure for uptake of water and minerals from the soil. Once plants build up enough transpirational pull during early hours of the day, water uptake by the plants begins. Transpiration is definitely a necessary evil. There are three modes of transpiration in plants, viz., cuticular transpiration, stomatal transpiration, and lenticular transpiration. The cuticular transpiration is the loss of water from the surface of the plant. This type of transpiration takes place when cuticle is very thin and there is no water scarcity. It accounts for only 2% of water loss. The stomatal transpiration takes place through stomata, and more than 95% of water loss takes place through stomatal openings present on the leaf epidermis. The third mode of transpiration is through lenticels present on the bark and in the peel of some fruits (e.g., apple). Water loss through lenticels is minimal. The driving forces for transpiration are **vapor pressure** and **vapor density** in the substomatal area. The concentration of water molecules in vapor phase is expressed as vapor mass per unit volume ($g.m^{-3}$) and is referred as vapor density. Vapors cause pressure on the walls of the stomatal chamber.

The substomatal air space is saturated with water vapors, while the immediate air around leaves is unsaturated. This gradient around the substomatal area and air around the leaves lead to vapor loss through transpiration (Table 1.1). The rate of transpiration (T) is governed by vapor pressure gradient between the leaf (e_{leaf}) and the surrounding (e_{air}):

$$T \propto e_{leaf} - e_{air}$$

Transpiration also undergoes considerable resistance by stomata and vapors present in the atmosphere. There are two main boundaries that create high resistance to water movement. The first one is at the stomatal pore, called the **leaf stomatal resistance** (r_{leaf}), and the other is the air immediately around the leaf, called **boundary layer resistance** (r_{air}).

This can be expressed as

$$T = \frac{e_{\text{leaf}} - e_{\text{air}}}{r_{\text{leaf}} + r_{\text{air}}}$$

In other words, the rate of transpiration is directly proportional to the difference in vapor pressure between the leaves and atmosphere divided by the sum of resistance encountered by air and the leaves. The number and size of stomatal pores contribute to leaf stomatal resistance (r_{leaf}) and the degree of difference in vapor pressure between leaf and air to boundary layer resistance (r_{air}) (Box 1.8).

Box 1.8: Measurement of Transpiration Rate

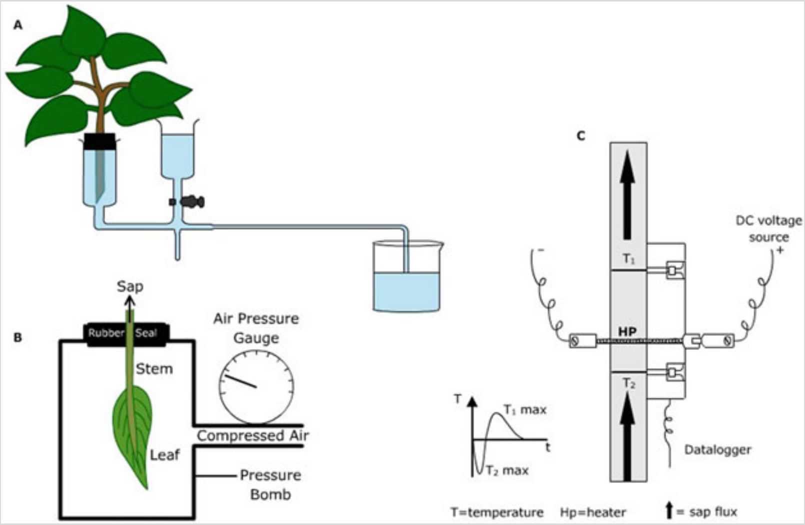
Lysimeter or gravimetric method: The amount of water used by plants for their growth is just 1% of the total water absorbed from the soil. In this method, it is presumed that loss of weight in plants is due to loss of water, i.e., transpiration. A potted plant with soil covered with plastic bag is taken. Plant is weighed at different intervals. The higher the rate of transpiration, the more will be the loss of weight. On the same principle, a simple method to find out the rate of transpiration in small twigs is using a device called Ganong's **potometer**. The rate of transpiration is measured by tracking the distance travelled by the air bubble in graduated tube per unit time.

Gas exchange or cuvette methods: In this method, the twig is kept in a sealed container with two openings, and relative humidity and temperature of air going inside and air coming out are measured at the beginning of the experiment. After an interval, again the relative humidity and temperature are measured. Absolute humidity (vapor density and vapor pressure) is measured by **hygrometer**. The rate of transpiration will be equal to the change of vapor density in the air going in and air coming out of the container. It can be used for large number of plants. The relative humidity, however, changes with time and that affects the rate of transpiration.

Stemflow or thermocouple method: The amount of water flowing through stem helps to get a reliable calculation of the rate of transpiration. Thermocouple method involves giving a heat pulse to the stem at a given point. The temperature is then measured above at some point. The time required to reach the same temperature at the second position indicates the velocity of xylem sap flow.

(continued)

Box 1.8 (continued)



A. Ganong's potometer. **B**. A pressure bomb used for measuring the rate of transpiration. **C**. Thermocouple

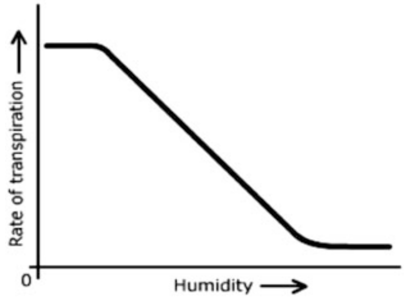
1.5.1.1 Factors Affecting Rate of Transpiration

The rate of transpiration is affected by the plant water status, its anatomy, as well the environmental factors. The most important environmental factors are humidity, light, temperature, wind velocity, and availability of soil water. These factors are discussed here individually, but in natural habitat, they are influencing each other and affect the rate of transpiration.

Humidity Atmospheric humidity changes with change in temperature or vapor pressure. A rise or fall in temperature with no change in vapor pressure will drop or raise relative humidity, respectively. Similarly, with no change in temperature, rise or fall of vapor pressure will cause rise and fall of relative humidity, respectively. Whenever there is a rise in relative humidity, the rate of transpiration decreases (Table 1.2). A vapor pressure gradient in the vicinity of the leaves and in substomatal chamber determines the rate of transpiration. Whenever this gradient is steep, the rate of transpiration rises.

Temperature The rise in temperature, with all other factors nearly constant, increases the rate of transpiration. The increase in temperature also increases the difference in vapor pressure of the leaf and outside the atmosphere. Hence, the rate of transpiration increases. However, stomata close at temperature higher than 35 °C.

Table 1.2 (**A**) The relative humidity and the water potential of air. At 100% relative humidity, the water potential is zero leading to highly reduced transpiration. (**B**) The rate of transpiration reduces with increase in relative humidity

(A)		(B)
Relative humidity (%)	**Water potential of air (MPa)**	
100	0	
95	–2.50	
90	–14.2	
50	–93.6	
Less than 10	–300	

Therefore, the rate of transpiration falls beyond that temperature. With the temperature and stomata showing diurnal variations, transpiration rate also exhibits a clear diurnal rhythm, i.e., the rate of transpiration is high during daytime, reaches maximum at midday, and drops during night when stomata are closed and temperature is low. Temperature and relative humidity modify the magnitude of the vapor pressure gradient which, in turn, influences the rate of transpiration (Fig. 1.10a).

Wind Velocity An increase in the rate of transpiration is not directly proportional to wind velocity. During high wind velocity, stomata close. Therefore, the rate of transpiration also drops. But wind at low velocity increases the rate of transpiration. As wind disperses the air around the leaf and reduces the vapor pressure in the immediate vicinity of stomata, it increases the rate of transpiration (Fig. 1.10b).

Internal Factors One of the most important factors affecting transpiration rate is leaf-shoot ratio**.** The magnitude of transpiration will be more in leaves with greater leaf area. However, the rate of transpiration has no correlation with leaf size when per unit leaf area is considered. The leaf structure is very important in regulating the rate of transpiration. Leaf adapts many strategies to reduce transpiration (Sect. 1.5.1.3; Antitranspirants). Stomatal frequency (number of stomata present in per unit area of leaf), pore size, and distribution show tremendous variation in plants growing in different habitats (Table 1.3).

1.5.1.2 Ecological Adaptations to Reduce Transpiration

Plants develop many adaptations to avoid water loss due to transpiration. The presence of thick cuticle, sunken stomata, and stomata only on the lower side of the leaves are some of the adaptive mechanisms developed by plants. Plants growing in desert experience more water crisis. They need to restrict the rate of transpiration.

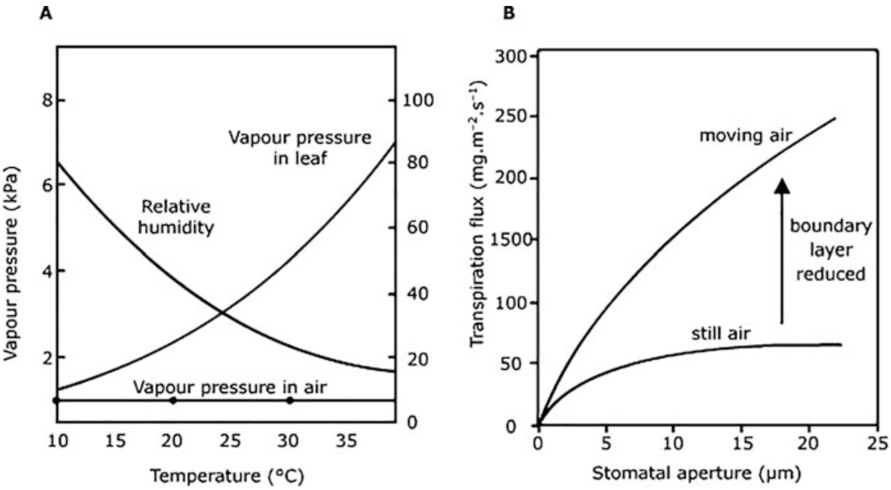


Fig. 1.10 (**a**) With the increase in temperature, the relative humidity decreases resulting in high vapor pressure gradient in leaf and outside air, leading to stomatal opening and increase in the rate of transpiration. (**b**) Effect of wind velocity on the rate of transpiration. As wind velocity increases, it reduces the boundary layer resistance around stomata leading to opening of stomata and hence more transpiration. In still air, the boundary layer resistance is high. Therefore, the rate of transpiration is same

The ecological adaptations of desert plants are reduction of leaf area, presence of thick cuticle, sunken stomata, and stomata opening during night, special water storage capacity, modified root structure, and C_4 photosynthesis.

1.5.1.3 Antitranspirants

These are the chemicals which decrease water loss from plants due to transpiration. They are also useful for avoiding transplantation shock to the nursery plants and plants raised in tissue culture. An antitranspirant should be nontoxic and affect only stomata. It should not cause permanent damage to stomatal mechanism, and the effect should persist only for short duration. There are mainly four types of antitranspirants: **stomatal-closing types** – some fungicides, like phenyl mercuric acetate (PMA), and herbicides, like atrazine, act as antitranspirants by closing the stomata. **Film-forming type**: These chemicals form coating on the surface of leaves. Hence, stomatal pores are blocked resulting in reduction in the rate of transpiration. The material used is either plastic or waxy in nature. **Reflectance type:** These are white materials which form a coating on the leaves and increase the leaf reflectance. Materials like kaolin, hydrated lime, calcium carbonate, magnesium carbonate, and zinc sulfate are used to reduce transpiration in this category. **Growth retardant**: ABA can bring stomatal closure. Chemicals like cycocel reduce shoot growth and increase root growth, thus enabling the plants to resist drought. It is useful for improving water status of the plant.

Table 1.3 (**A**) Distribution and frequency of the stomata in horizontally and vertically oriented leaves. (**B**) Stomatal frequency in monocot leaves is nearly equal in both upper and lower surfaces, while in dicot leaves, stomatal frequency is more on lower surface

(**A**)

Orientation of the leaf	Upper epidermis	Lower epidermis
Horizontal		
Malus	0	38,660
Bean	4051	24,906
Oak	0	58,040
Pumpkin	2791	26,932
Vertical		
Corn	9800	10,900
Pine	12,000	11,000
Onion	16,900	16,900

(**B**)

Type	Name of the plant	Upper epidermis	Lower epidermis
Monocot	Wheat	50	40
	Onion	160	160
	Barley	75	80
Dicot	Sunflower	115	165
	Alfalfa	169	182
	Geranium	29	175

1.5.2 Stomatal Movement

The stomata make up 15–40% of the total leaf volume. However, the stomatal pore accounts for only 1% of the total surface area, and it is responsible for more than 90% of water loss due to transpiration. The guard cells are bean-shaped in dicots and dumbbell-shaped in monocots (Fig. 1.11a). In addition to structural differences from epidermal cells, guard cells lack plasmodesmatal connections and have chloroplasts. The wall of the lining of pore is thicker than the outer wall of the guard cells, which are thin. A fully open stomatal pore measures 5–15 μm wide and is about 20 μm long. The ratio of CO_2 diffusion through a perforated membrane varies in proportion to the diameter of pore and not the area, i.e., as the pore size decreases, the efficiency of CO_2 diffusion per unit area increases severalfolds. This is due to spillover effect for diffusion of CO_2 through a stomatal aperture (Fig. 1.11b).

1.5.2.1 Mechanism of Guard Cell Movement

The stomatal opening and closing take place due to the movement of guard cells. Microfibrils are located around the circumference of the elongated guard cell. This arrangement of radiating microfibrils is called as **radial micellation** (Fig. 1.11). When water enters into the guard cells, it cannot increase much in its diameter due to the presence of radial microfibrils. However, it increases in length, especially along its outside thin wall. With the increase in size, guard cells exert pressure on the microfibrils, and, in turn, microfibrils pull the inner (thicker) wall of the stomata, leading to the opening of pore. In intact leaf, the guard cells obtain K^+ from adjacent cells. There is evidence to show that the level of K^+ controls stomatal movement. K^+

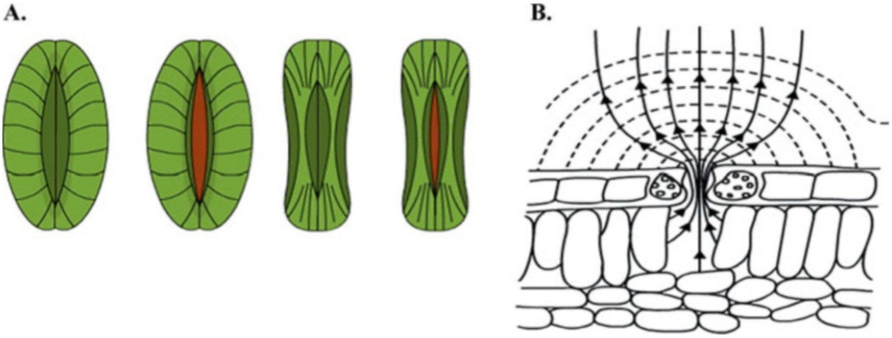


Fig. 1.11 (**a**) Bean-shaped stomata present in dicot leaves (left) and dumbbell-shaped as observed in monocot leaves. Note the presence of radial micelle in both types of stomata and the deposition of thickening in boundary around stomatal pore. (**b**) The spillover effect for diffusion of CO_2 through a stomatal pore. The dashed lines are isobar representing region of equivalent CO_2 partial pressure

Table 1.4 The amount of K^+(mM) in open and close stomata

Species	K^+(mM) in stomata	
	Open	Close
Vicia faba	552	112
Commelina communis	448	95

levels are high when stomata are open, and it is low when stomata are closed (Table 1.4). The amount of K^+ present in the vacuole of guard cells is enough to cause a decrease in the osmotic potential by 2.0 MPa. The fungal toxin fusicoccin is known to cause an active proton extrusion, and its treatment stimulates stomatal opening. Proton extrusion is balanced with K^+ movement in guard cells resulting in opening of stomata and wilting of plant. In *Vicia* leaves, it has been observed that when K^+ moves out of guard cells, an equal amount of H^+ are also released. These H^+ are, during the formation of organic acids, mainly malic acid. The rise in H^+ leads to a drop in the pH of guard cells. The excessive H^+, if not extruded out, will further drop the pH of the guard cells. Thus, H^+ is extruded out and is exchanged with K^+ influx into the guard cells. If the proton pumps are inhibited, stomata remain closed even in blue light. Application of inhibitors of photosynthesis prevents organic acid formation, and stomatal opening is blocked.

$$\begin{array}{l}\text{Starch} \rightarrow \text{Phosphoglyceric acid} \xrightarrow{\text{carboxylase}} \text{Phosphoenol pyruvic acid} + CO_2 \\ \qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad \downarrow \\ \qquad\qquad\qquad\qquad\qquad\qquad \text{Malic acid} \leftarrow \text{Oxaloacetic acid}\end{array}$$

The increase in malic acid content and entry of K^+ further drop the osmotic potential. K^+ uptake is balanced by uptake of chloride ion (Cl^-) into the guard cells and transport of H^+ released from organic acid (malic acid). Thus, all these factors are responsible for the opening of stomata. The stomata closure is due to efflux of K^+

and Cl^-, and conversion of malate into starch results in a decrease in solute potential. Water moves out from the guard cells leading to stomata closure**.** Vacuole of the guard cells has two different classes of K^+-permeable channels. The fast-vacuolar channels (FV) are inhibited by an increase in Ca^{2+} level and are activated when pH of the cytosol increases. On the other hand, vacuolar K^+ channels (VK), which are highly selective for K^+ over other monovalent cations, are activated by low Ca^{2+} concentrations and are inhibited by increasing cytosolic pH. Stomatal closure is usually followed by an increase in Ca^{2+} in the guard cells. So, VK channels actively release K^+ from the vacuoles. In the absence of a change in Ca^{2+}, pH plays an important role in the closing of stomata. FV channels will open leading to release of K^+ from the guard cells, and closing of stomata takes place. VK channels have been identified in *Arabidopsis* and these channels have Ca^{2+}-binding domain**.**

1.5.2.2 Factors Affecting Stomatal Movement

Environment immediately around the plants keeps changing and so is the stomatal aperture. Stomata keep adjusting to these changes. Environment signals are perceived by the guard cells. These signals are transduced into ion fluxes leading to change in the turgor pressure of the guard cells. Some of the important environmental factors affecting stomatal movement are as follows.

Light Stomata of most plants open during daytime and close during nighttime. However, in succulent plants stomata open during nighttime and close in the presence of light. This adaption of CAM plants leads to carbon dioxide absorption during nighttime when transpiration stress is low. The effect of light on stomatal movement is independent of photosynthesis. Stomata respond to light even in leaves where photosynthesis has been reduced to zero by the application of photosynthesis inhibitor (e.g., cyanazine). Blue light has direct effect on the opening of stomata, independent of CO_2 concentration. Thus, in *Allium cepa*, guard cells swell in the presence of K^+ when blue light is given. Blue light enhances the H^+ transport leading to proton gradient which, in turn, causes the opening of K^+ channels. Red light also stimulates stomatal opening, but blue light is ten times more effective than red light.

Carbon dioxide It is mainly the internal level of CO_2 which controls the opening and closing of stomata. In most plants, low CO_2 concentration in intercellular spaces causes the stomatal opening during nighttime as well. High concentrations of CO_2 in intercellular spaces cause partial closure of stomata during daytime. Once stomata closes, external CO_2 concentration does not affect the stomatal movement. High level of intracellular CO_2 induces closure of stomata in the same way as ABA-induced closure.

Relative Humidity Stomata close when the vapor content of the air and that of intercellular space exceeds a critical level. The water potential of the leaf also affects stomatal movement. As water potential decreases (water stress), the stomata are closed.

pH Generally high pH favors closing while low pH favors opening of stomata. pH regulates K^+ movement in the guard cells. Mostly alkaline pH enhances the K^+ outflow and results in stomatal closure.

Temperature The stomatal pore closes as the temperature rises above 30–35 °C. To ensure gas exchange at high temperature, stomata opens during nighttime. Temperature has indirect effect on stomatal movement. It affects the balance of respiration and photosynthesis. Whenever there is increase in temperature, it leads to rise in respiration rate. Due to high rate of respiration, the level of CO_2 increases and it causes closure of stomata. In some plants, high temperature induces stomatal opening to increase the transpiration rate (cooling effect) so that temperature of leaf is maintained.

Water Stress Sometimes, due to water stress, guard cell loses more water as compared to its intake. It loses its turgidity and stomatal closure takes place. This is called **hydropassive closure** of stomata. On the other hand, stomata also experience ABA-mediated **hydroactive closure**. ABA is synthesized in leaves, but during water stress, it is synthesized in roots and quickly transported to leaves. ABA induces stomatal closure by opening Cl^- channels and allows the Cl^- efflux from the guard cells. ABA also inhibit H^+ pump. This loss of ions further opens up K^+ channels and K^+ also diffuses out of the guard cells. The solute concentration decreases followed by loss of water and closure of stomata. ABA is also referred as an antitranspirant. It regulates stomatal closure and thus reduces transpiration rate. When stomatal closure is induced by ABA, large numbers of ion channels are regulated by Ca^{2+} signals.

1.6 Guttation

Guttation is the process of extrusion of liquid droplets from the leaves through special structures called water stomata or **hydathodes**. During early morning in summer, when relative humidity is very high, small droplets appear on the vein endings of grasses or serrate margins of certain leaves (Fig. 1.12a). Guttation takes place only when relative humidity is high and the rate of transpiration is extremely low because only in these conditions significant root pressure develops. Thus, this phenomenon can only be seen in small plants where root pressure has significance. Although water coming out due to guttation looks like dew drops, it contains minerals, organic acid, sugars, and even enzymes. On evaporation, the solutes that remain on the leaves cause salt burning, which is called **guttation burn**. Hydathodes are restricted to the apex or the serrated edges of the margins of leaves. It consists of a simple pore in the epidermal layer found at the tip and is surrounded by a special parenchymatous tissue, called **epithem**. The cells of epithem are isodiametric in shape, are loosely arranged, and enclose lot of intercellular spaces. The xylem elements of leaf vein terminate in epithem (Fig. 1.12b). Cells of epithem contain a large number of finger-like projections (a characteristic of transfer cells) to increase

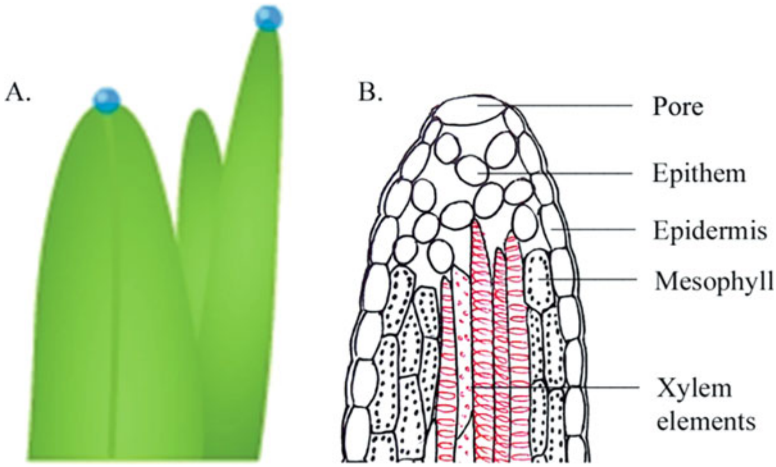


Fig. 1.12 (**a**) Grass leaves showing guttation through hydathodes. (**b**) Sectional view of a hydathode

the surface area for transport of water. Plants which loose water by guttation are restricted to few taxons in the plant kingdom. There are about 150–250 plants showing this phenomenon, e.g., tomato, grasses, *Colocasia*, cucurbita members, balsam, etc.

Summary

- The chemical potential of water is the free energy of water. Water moves from its higher potential to lower potential. The gradient of water potential from soil to leaf, which creates soil-root-air continuum, is the key to the transport of water. The additive effects of solute potential and pressure potential ultimately affect water potential.
- Mode of water transport changes at three different levels. The first level of water transport refers to entry of water from the soil into the root cells, through the plasma membrane. The absorption and release of water and solutes by individual cells occur through diffusion, osmosis, or mass flow. A key component of cellular transport is crossing the plasma membrane. The second level of transport is from root epidermal cells to the innermost layer of cortex. This is referred as short-distance transport, and it includes apoplast, symplast, and transcellular pathways, including transporters, channels, and plasmodesmata. The third level of transport is the long-distance transport in xylary elements, also known as ascent of sap. Water moves against gravity by three forces, viz., transpirational force, cohesion, and tension. Loading of water into xylem again involves transporters, pumps, and channels.
- The driving force for water movement from soil to leaves and from leaves to atmosphere is transpiration. Transpiration is the evaporation of water from the

aerial part of the plants. The most important environmental factors are humidity, light, temperature, wind velocity, and availability of soil water. Water vapor leaves the air spaces of the plant via the stomata. Stomata open up during the day for gaseous exchange. At night when transpirational pull is almost negligible, roots actively absorb solutes. Water passively enters into roots and creates pressure. Due to this pressure, water is forced out of the leaf tips through structures called as hydathodes by a process called guttation.

Multiple-Choice Questions

1. Which of the following phenomenon is involved in shrinkage of grapes when placed in hypertonic sugar solution?
   (a) Deplasmolysis
   (b) Imbibition
   (c) Exosmosis
   (d) Osmosis
2. Guard cells differ from epidermal cells in having:
   (a) Mitochondria
   (b) Chloroplast
   (c) Nucleus
   (d) Golgi body
3. When water enters a cell, it builds up positive:
   (a) Osmotic pressure
   (b) Turgor pressure
   (c) Vapor pressure
   (d) Atmospheric pressure
4. The surface of leaves remains cool due to:
   (a) Transpiration
   (b) Guttation
   (c) Transport of water
   (d) Evaporation
5. During daytime, if carbon dioxide concentration around the leaves increases:
   (a) Stomata will open gradually.
   (b) Stomata will open suddenly.
   (c) No change in transpiration.
   (d) Decrease in transpiration due to closure of stomata.
6. The movement of water in xylem is due to:
   (a) Cohesive force among water molecules
   (b) Adhesive force between water and wall of xylem element
   (c) Transpirational pull
   (d) Cohesion and transpirational pull

7. How would you treat an epidermal peel if stomatal pore is to be opened?
   (a) Float the peel in abscisic acid.
   (b) Take buffer of pH 7 and add KCl and immerse the peel in it.
   (c) Use sucrose solution.
   (d) Use fusicocin.
8. A potato tuber weighing 0.5 gm and water potential of 1 MPa is immersed in coconut for 1 h. The tuber is removed and again weighed. What do you conclude about the water potential of coconut water if potato tuber weight after the treatment is reduced to 0.35 gm?
   (a) Less than 1 MPa.
   (b) More than 1 MPa.
   (c) 0 MPa.
   (d) It is not possible to find water potential of coconut water.
9. Four solutions contain 1 g/L of the following molecules. Which one would have lowest water potential?
   (a) Sucrose
   (b) Glucose
   (c) DNA
   (d) Starch
10. Guttation is shown by the plants when:
   (a) Root pressure is equal to transpiration.
   (b) Temperature and relative humidity are low.
   (c) Temperature is high and relative humidity is low.
   (d) Root pressure is high due to high temperature and relative humidity.

Answers

1. c 2. b 3. b 4. a 5. d 6. d 7. b
8. a 9. d 10. d

Suggested Further Readings

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