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SUBTOPIC NAME	**Water transport in plants**
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SEARCH KEYWORD	**Water transport in plants**

Absorption, transport of water and ions in plants

M.Sc. Biochemistry 2nd sem

CSJM University, Kanpur.

Objectives

- To understand the major functions of water in plant life
- To understand how water moves into and out of plant cells,
- To emphasize the molecular properties of water and the physical forces that influence water movement at the cell level.

WATER PLAYS A CRUCIAL ROLE in the life of the plant.

For every gram of organic matter made by the plant, approximately 500 g of water is absorbed by the roots, transported through the plant body and lost to the atmosphere.

Every plant must delicately balance its uptake and loss of water.

Cell walls allow plant cells to build up large internal hydrostatic pressures, called **turgor pressure**, which are a result of their normal water balance. Turgor pressure is essential for many physiological processes, including cell enlargement, gas exchange in the leaves, transport in the phloem, and various transport processes across membranes. Turgor pressure also contributes to the rigidity and mechanical stability of nonlignified plant tissues.

WATER IN PLANT LIFE

Water makes up most of the mass of plant cells, Each cell contains a large water-filled vacuole. In such cells the cytoplasm makes up only 5 to 10% of the cell volume; the remainder is vacuole. Water typically constitutes 80 to 95% of the mass of growing plant tissues.

Water is the most abundant and arguably the best solvent known. As a solvent, it makes up the medium for the movement of molecules within and between cells and greatly influences the structure of proteins, nucleic acids, polysaccharides, and other cell constituents. Water forms the environment in which most of the biochemical reactions of the cell occur, and it directly participates in many essential chemical reactions.

Of all the resources that plants need to grow and function, water is the most abundant and at the same time the most limiting for agricultural productivity.

THE STRUCTURE AND PROPERTIES OF WATER

Water has special properties that enable it to act as a solvent and to be readily transported through the body of the plant. These properties derive primarily from the polar structure of the water molecule.

The Polarity of Water Molecules Gives Rise to Hydrogen Bonds

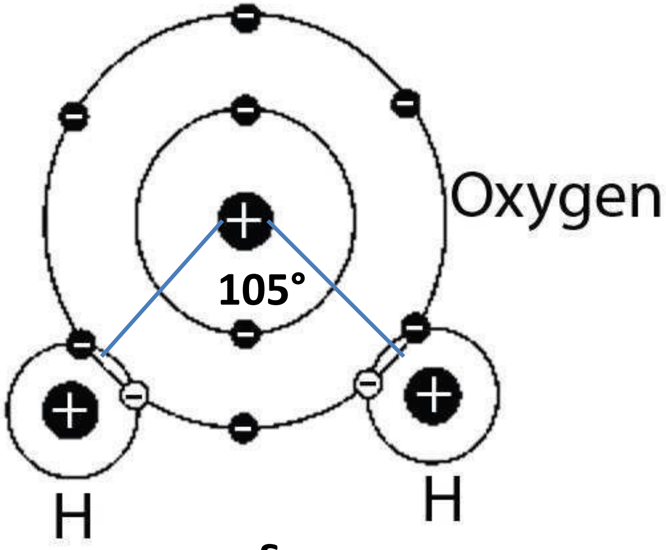
The water molecule consists of an oxygen atom covalently bonded to two hydrogen atoms. The two O—H bonds form an angle of 105°. Because the oxygen atom is more **electronegative than hydrogen**, it tends to attract the electrons of the covalent bond. This attraction results in a partial negative charge at the oxygen end of the molecule and a partial positive charge at each hydrogen.

The partial charges are equal, so the water molecule carries no *net charge.*

This separation of partial charges, together with the shape of the water molecule, makes water a *polar molecule* and the opposite partial charges between neighboring water molecules tend to attract each other.

The weak electrostatic attraction between water molecules **hydrogen bond**, is responsible for many of the unusual physical properties of water.

δ- Net negative charge



δ+ **δ+**

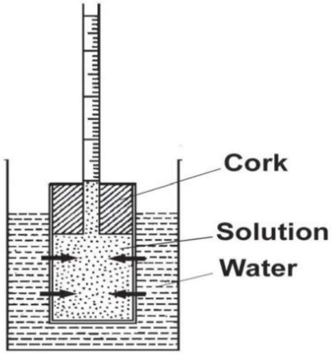
Net positive charge

Attraction of bonding electrons to the oxygen creates local negative and positive partial charges

- These hydrogen bonds of 1.3 to 4.5 kcal per mole water bond energy are stronger than Van der Waal’s forces (1 kcal per mole).
- Hydrogen bonds can also form between water and other molecules that contain electronegative atoms (O or N). In aqueous solutions, hydrogen bonding between water molecules leads to local, ordered clusters of water that, because of the continuous thermal agitation of the water molecules, continually form, break up, and re-form.

Colligative properties of water: Plant water relations are governed largely by the colligative properties, the properties imparted to water when it comes in contact with surfaces and solutes and are applicable to dilute solutions.

Osmotic pressure: When pure water is separated from aqueous solution by a membrane permeable to water but impermeable to solute particles (semi-permeable membrane, the concept is though theoretical since no known membrane is absolutely impermeable to solutes, most membranes thus fall in the category of selectively permeable), then water moves across the membrane from pure water into the solution. The phenomenon is referred to as *osmosis and the pressure equivalent of the* force responsible for such a movement is referred to as *osmotic pressure. Osmotic* pressure has been defined as the property of the solution as expressed in pressure terms equivalent to the real pressure that could be developed in a perfect osmometer when it is placed in pure water at 1 atmospheric pressure.



A simple osmometer. The jar containing solution has porous walls with potassium ferrocyanide precipitate filling the pores, which functions as selectively permeable membrane

Thus, in an osmometer, the pressure which must be applied on the solution to prevent such a movement of water is the osmotic pressure of the solution. As the solvent (pure water) has zero osmotic pressure, the osmotic pressure is thus created due to the presence of solutes in the solution, and the osmotic pressure increases as the concentration of solute increases. This relationship between osmotic pressure and the concentration of solute can be given by the van't Hoff's equation (PV = RT) as:

$V = \mathbf{n_s RT}$

where = osmotic pressure in MPa, V = volume in L, n_s= moles of solute, R = gas constant (0.0083 L MPa/ degree mol at 273 °K), T = temperature in °K,

$\boldsymbol{\pi} = \mathbf{n_s RT/}V$

Or = m RT (for non-electrolytes) since $\mathbf{n_s/}V = m$ (molality)

or = mi RT (i = ionization constant for electrolytes)

According to this equation, the osmotic pressure of 1 molal (m) solution of a nonelectrolyte, eg, sucrose, works out to be 2.27 MPa, or 22.7 bars, or 22.4 atmospheres, at 273 °K. However, the osmotic pressure of 1 m solution of sucrose is actually measured to be higher than the theoretical value at 2.51 MPa due to binding of 6 water molecules by each molecule of sucrose by the phenomenon of hydration.

Osmotic pressure of 1 m solution of an electrolyte, e.g., NaCl is found to be 4.32 MPa. The value is higher than that of sucrose due to dissociation of a large number of NaCl molecules into Na+ and Cl- ions (particles) in solution and hydration of some undissociated molecules, but the osmotic pressure is less than double of sucrose as not all the NaCl molecules are dissociated into the two ions.

Osmosis Is Driven by a Water Potential Gradient

Membranes of plant cells are **selectively permeable**; that is, they allow the movement of water and other small uncharged substances across them more readily than the movement of larger solutes and charged substances.

Like molecular diffusion and pressure-driven bulk flow, **osmosis occurs spontaneously in response to a driving** force. In simple diffusion, substances move down a concentration gradient; in pressure-driven bulk flow, substances move down a pressure gradient; in osmosis, both types of gradients influence transport. *The direction and rate of water flow across a membrane are determined not solely by the concentration gradient of water or by the pressure gradient, but by the sum of these two driving forces.*

The Chemical Potential of Water Represents the Free-Energy Status of Water

- The chemical potential of water is a **quantitative expression** of the free energy associated with water. In thermodynamics, free energy represents the potential for performing work.
- Chemical potential is a relative quantity: expressed as the difference between the potential of a substance in a given state and the potential of the same substance in a standard state. The unit of chemical potential is energy per mole of substance (J mol–1).
- For historical reasons, plant physiologists have most often used a related parameter called **water potential,** defined as the chemical potential of water divided by the partial molal volume of water (the volume of 1 mol of water).

Water potential: In 1960 Slatyer and Taylor introduced the term *water potential,* a concept based on the thermodynamic property of matter, *Gibbs free energy (G) that* is defined as: G = E + PV – TS where E = internal energy (the sum of translational, rotational, vibrational, electronic and nuclear energies of the substance), PV = pressure-volume product, T = absolute temperature, S = entropy.

- Chemical potential of water in a system, as compared to that of pure water, expressed in pressure units has been termed as **water potential and is denoted by the** letter **ψ_w** and can be defined as *chemical potential of water per unit partial molal volume. It is a relative quantity (as compared to the standard reference state of pure* water) like any other potential, eg, electrical potential.
- Thus Water potential is a ***measure of the free energy of water per unit volume*** (J m–3). The common measurement unit for **ψ_w** are equivalent to pressure units **pascal**.
- It is a physical quantity that **indicates the rate and direction of movement of water** just as electrical potential indicates the flow of electricity.
- Water potential (ψ_w) is the inbuilt free energy of water molecules that causes them to be in continuous random motion. But water will move from region where water molecules are higher to region where water molecules are lower.
- ψ_w depends on ***kinetic energy of water molecule*** and ***no. of water molecules***.
- Also ***temperature*** increase increases random motion and thus affects ψ_w.
- Direction : **Water moves from a point of higher water potential to** a point of **lower water potential**, i.e., from higher energy level towards lower energy level.
- Any substance that decreases random motion of water molecules, will lower the tendency for movement of water and thus contribute –ve value and decrease water potential.
- Thus addition of solute will decrease random motion of water mols, & so will decrease ψ_w

Components of water potential: The important factors that establish or alter water potential gradient are –temperature, pressure, presence of solutes, adsorption on charged surfaces and gravity. Accordingly, the main components of water potential under isothermal conditions are given as: **ψw = ψs + ψp + ψm + ψg**

ψw = *Water potential*. *It has a negative value and becomes lower (more negative) as* the concentration of solutes increases, pressure decreases or water adsorbing surfaces increase. It indicates net capacity of cells to take up water.

ψs = *Solute potential* or **osmotic potential**, represents **effect of dissolved solutes** on water potential. Solutes reduce the free energy of water. This is primarily an entropy effect, i.e. mixing of solutes and water increases the disorder of the system and thereby lowers free energy.*It has a negative value and becomes lower (more negative) as* the concentration of solutes increases. (More solute–lower **ψw)** It expresses the effect of solutes in the cell sap.

- For dilute solutions of nondissociating substances, like sucrose, the osmotic potential may be estimated by the **van't Hoff equation: ψ*s = –RTcs*** where *R is the gas constant (8.32 J mol–1 K–1), T is the* absolute temperature (in degrees Kelvin, or K), and *cs is the* solute concentration of the solution, expressed as **osmolality** (moles of total dissolved solutes per liter of water [mol L–1]). The minus sign indicates that dissolved solutes reduce the water potential of a solution relative to the reference state of pure water.
- For ionic solutes that dissociate into two or more particles, *cs must be multiplied by the number of dissociated* particles to account for the increased number of dissolved particles.

ψp = *Pressure potential*. *Usually positive, represents hydrostatic pressure in* cell. Main component of pressure potential is turgor pressure, may also include hydrostatic pressure of columns of water in conductive elements. Positive pressures raise water potential; negative pressures reduce it. However in xylem (conducting elements) of heavily transpiring plants and in plasmolysing cells, where a *tension, or negative hydrostatic pressure develops.*

- Water in the reference state is at ambient pressure, so by this definition ψ*p = 0 MPa for water in the standard* state. Thus the value of ψ*p for pure water in an open* beaker is 0 MPa, even though its absolute pressure is approximately 0.1 MPa (1 atmosphere).

ψm = *Matric potential*. *It has a negative value and represents the effects of water* binding colloids, surfaces and according to some workers it may also include capillary effects. Usually the main contribution towards matric potential is from primary cell wall material that adsorbs water. (for hydrophilic surface : -ve & for hydrophobic - +ve, will repel water).

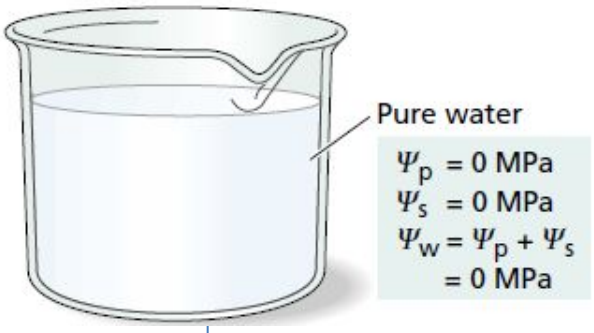
ψg = *Gravitational potential*. Gravity causes water to move downward unless the force of gravity is opposed by an equal and opposite force. ψ*g depends on height (h) of* the water above the reference-state water, density of water (*rw), and acceleration due to gravity (g).*
ψg = rwgh where *rwg has value of 0.01 MPa m–1. Thus a vertical distance* of 10 m translates into a 0.1 MPa change in ψw. *May be -ve, zero or +ve depending on* height.
It is generally believed that under most mesic conditions ψm is negligible compared to the osmotic potential and the hydrostatic pressurand if the height is not a variable, ψg is also negligible and these terms, therefore, can be dropped from the equation, thus:

$$\psi w = \psi s + \psi p$$

Water potential in the plant. *Cell growth, photosynthesis,* and crop productivity are all strongly influenced by water potential and its components. Like the body temperature of humans, water potential is a good overall indicator of plant health.

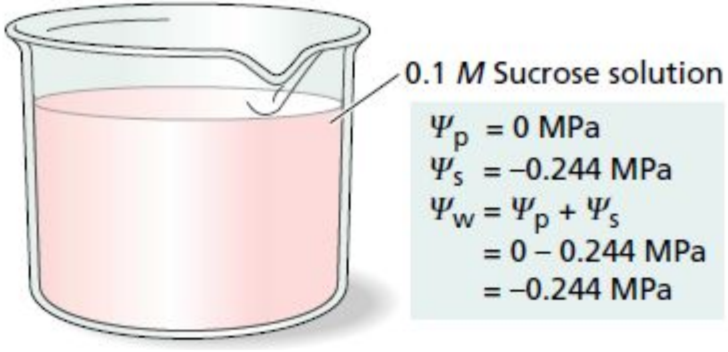
Water Enters the Cell along a Water Potential Gradient:

(A) Pure water



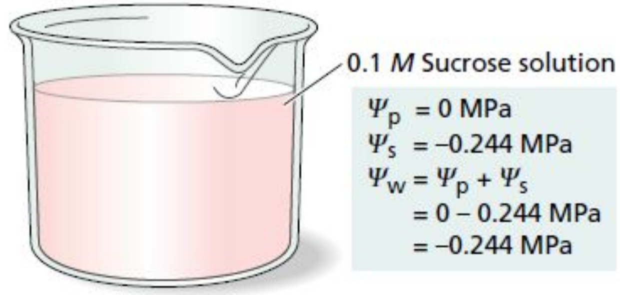
- **<u>An open beaker full of pure water at 20°C</u>**
  Because the water is open to the atmosphere, the hydrostatic pressure of the water is the same as atmospheric pressure, so $\psi p = 0$ *MPa*
- There are no solutes in the water, so $\psi s = 0$ *MPa;*
- $\psi w = \psi s + \psi p = 0$ *MPa*

(B) Solution containing 0.1 *M* sucrose



<u>If we dissolve sucrose in water to a concentration of 0.1 *M*</u> This addition lowers O.P. (ψs) *to –0.244 Mpa and* decreases the water potential (ψ) *to –0.244 MPa.*

(B) Solution containing 0.1 *M* sucrose



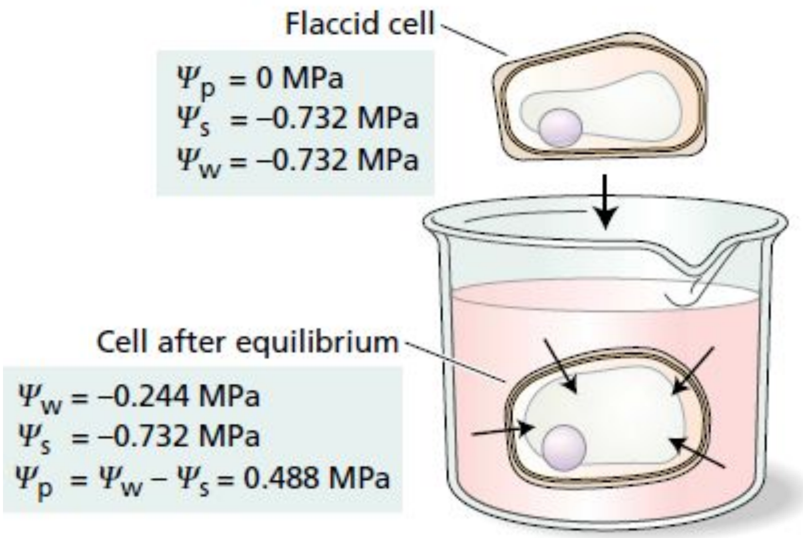
<u>**If we dissolve sucrose in water to a concentration of 0.1 *M***</u> This addition lowers O.P. (ψ*s) to –0.244 Mpa and* decreases the water potential (ψw *) to **–0.244 MPa**.*

Next if a flaccid, or limp, plant cell (i.e., a cell with no turgor pressure) that has a total internal solute concentration of 0.3 *M. This solute concentration* gives an O.P. ***ψs = –0.732 MPa****.*

As cell is flaccid, the internal pressure is same as ambient pressure, hydrostatic press. ψ*p = 0 MPa and* water potential of cell ***ψw = –0.732 MPa***.

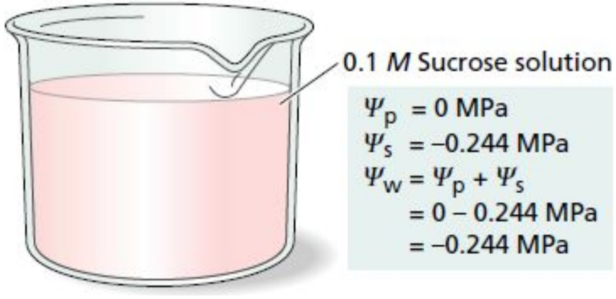
If this cell is placed in beaker containing 0.1 *M sucrose? Because the water* potential of the sucrose solution (ψ*w = –0.244 MPa; Fig* 3.9B) is greater than the water potential of the cell (ψ*w* = –0.732 MPa), water will move from the sucrose solution to cell (from high to low water potential).

(C) Flaccid cell dropped into sucrose solution

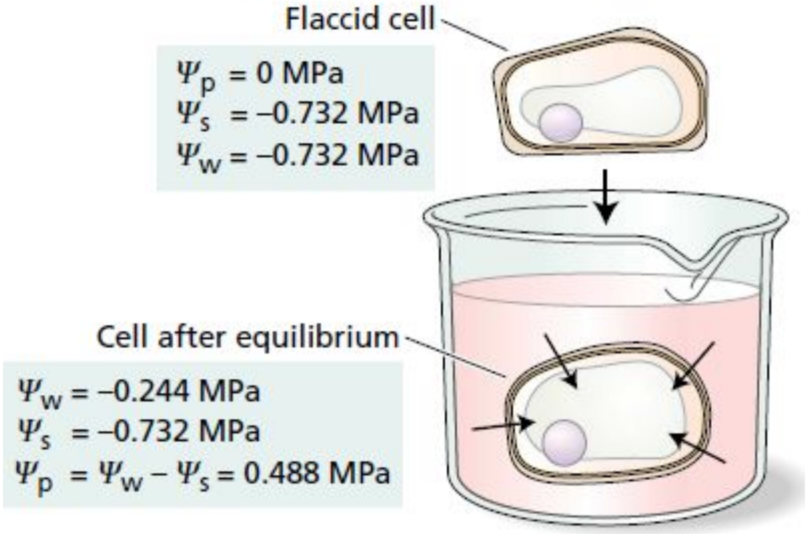


As plant cells are surrounded by relatively rigid cell walls, even a slight increase in cell volume causes a large increase in hydrostatic pressure within cell. As water enters the cell, CW is stretched by contents of the enlarging protoplast. The wall resists such stretching by pushing back on the cell. As water moves into cell, the hydrostatic pressure, or turgor pressure (ψ*p), of cell increases. Consequently,* cell water potential (ψ*w) increases, and difference* between inside and outside water potentials (Δψ*w) is* reduced. Eventually, cell ψ*p increases enough to raise the* cell ψ*w to the same value as the* ψ*w of the sucrose solution.*

(B) Solution containing 0.1 *M* sucrose



(C) Flaccid cell dropped into sucrose solution



At this point, equilibrium is reached ($\Delta\ \psi w = 0$ *MPa), and* net water transport ceases.

Because the volume of the beaker is much larger than that of the cell, *the tiny amount of water taken up by the cell does not significantly affect the solute concentration of the sucrose solution*. Hence ψs*,* ψp*, and* ψw *of the sucrose* solution are not altered. Therefore, at equilibrium, ψw*(cell)* = ψw*(solution) = –0.244 MPa.*

The exact calculation of cell ψp *and* ψs *requires knowledge* of the change in cell volume. However, if we assume that the cell has a very rigid cell wall, then the increase in cell volume will be small. Thus we can assume to a first approximation that ψs*(cell) is unchanged during the equilibration* process and that ψs*(solution) remains at –0.732 MPa.*

We can obtain cell hydrostatic pressure as follows:

$$\psi p = \psi w - \psi s = (-0.244) - (-0.732) = 0.488 \text{ MPa.}$$

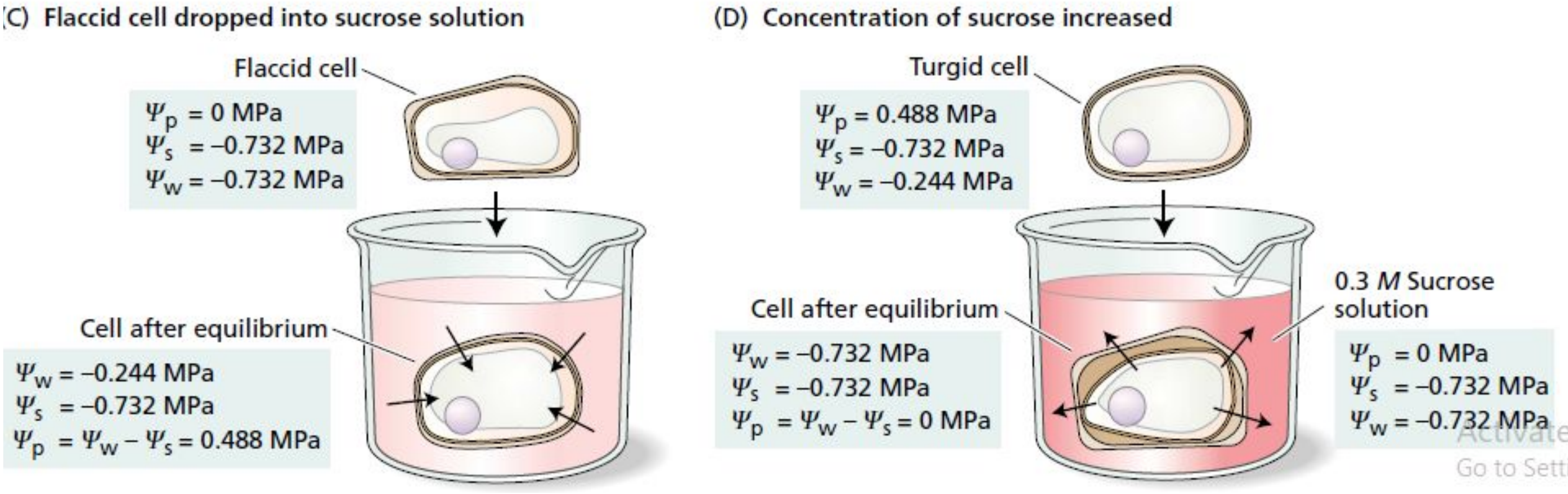
Water Can Also Leave the Cell in Response to a Water Potential Gradient

Water can also leave the cell by osmosis. If, in the previous example, we remove our plant cell from the 0.1 *M sucrose* solution (C) and place it in a 0.3 *M sucrose solution (D).*

ψw(solution) (–0.732 MPa) is more negative than ψw(cell) (–0.244 MPa), and water will move from the turgid cell to the solution.

As water leaves the cell, the cell volume decreases. As the cell volume decreases, cell ψ*p and* ψ*w decrease also until* ψ*w(cell) =* ψ*w(solution) = –0.732 MPa.*

Thus at equilibrium, ψ*p = 0 MPa. As before, we assume that the change in cell* volume is small, so we can ignore the change in ψ*s.*

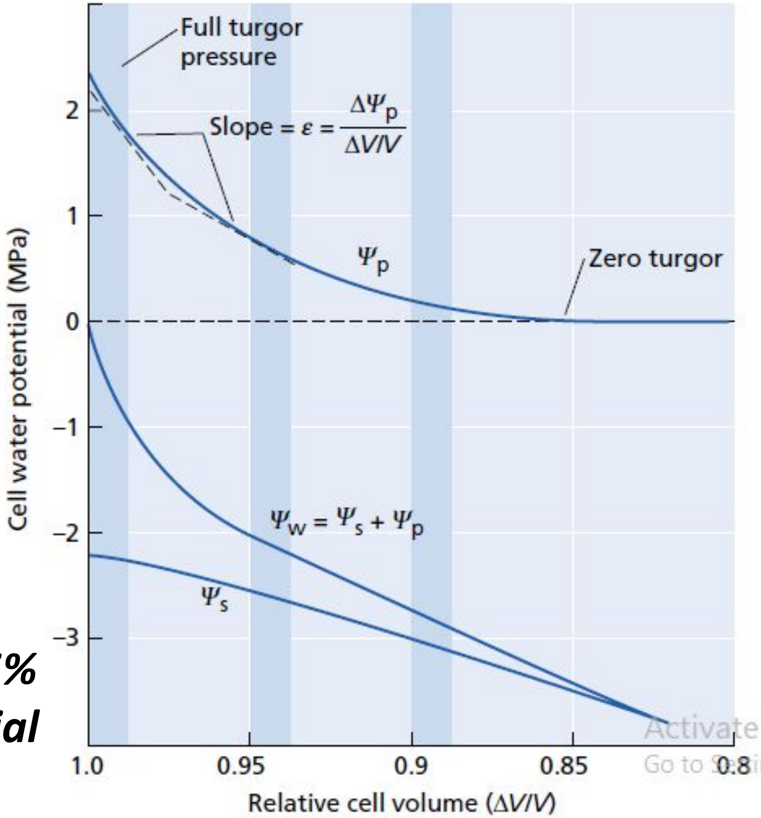


- One point common to all these examples is: *Water flow is a passive process. That is, water moves in response to physical forces, toward regions of low water potential or low free energy. There are no metabolic "pumps" (reactions* driven by ATP hydrolysis) that push water from one place to another.
- When solutes are transported, however, as occurs for short distances across membranes and for long distances in the phloem, then water transport may be coupled to solute transport and this coupling may move water against a water potential gradient. For example, the transport of sugars, amino acids, or other small molecules by various membrane proteins can "drag" up to 260 water molecules across the membrane per molecule of solute transported. Such transport of water can occur even when the movement is against the usual water potential gradient (i.e., toward a larger water potential) because the loss of free energy by the solute more than compensates for the gain of free energy by the water. The net change in free energy remains negative.
- In the phloem, the bulk flow of solutes and water within sieve tubes occurs along gradients in hydrostatic (turgor) pressure rather than by osmosis. Thus, within the phloem, water can be transported from regions with lower water potentials (e.g., leaves) to regions with higher water potentials (e.g., roots). *These situations notwithstanding, in the vast majority of cases water in plants moves from higher to lower water potentials.*

Small Changes in Plant Cell Volume Cause Large Changes in Turgor Pressure: Cell walls provide plant cells with a substantial degree of volume homeostasis relative to the large changes in water potential that they experience as the everyday consequence of the transpirational water losses. Because plant cells have fairly rigid walls, a change in cell ψ*w is generally accompanied* by a large change in ψ*p, with relatively little change in cell* volume.

This phenomenon is illustrated in plots of ψ*w, ψp, and ψs as a function of relative cell volume. In the example of* a hypothetical cell, as ψ*w decreases* from 0 to about –2 MPa, the cell volume is reduced by only 5%. Most of this decrease is due to a reduction in ψ*p (by* about 1.2 MPa); ψ*s decreases by about 0.3 MPa as a result* of water loss by the cell and consequent increased concentration of cell solutes. Contrast this with the volume changes of a cell lacking a wall.

1 Turgor pressure (ψ*p > 0) exists only when cells are* relatively well hydrated. Turgor pressure in most cells approaches zero as the relative cell volume decreases by 10 to 15%. However, for cells with very rigid cell walls (e.g., mesophyll cells in the leaves of many palm trees), the volume change associated with turgor loss can be much smaller, whereas in cells with extremely elastic walls, such as the water-storing cells in the stems of many cacti, this volume change may be substantially larger.



Turgor pressure (ψp) decreases steeply with the initial 5% decrease in cell volume. In comparison, osmotic potential (ψs) changes very little.

Osmotic vs non-osmotic uptake of water

- It is in general agreement now that **all water uptake**, from the ambient medium in which the roots are growing to the root cells, **is along gradients of decreasing ψ**. It has been, however, found that the **production of gradient is different in slowly and rapidly transpiring plants**. This results in **two different mechanisms of water uptake**. Classically, these have been referred to by Renner (1912) as:

1. *Active absorption:* ***Water taken up osmotically in slowly transpiring*** **plants.**
2. *Passive absorption:* ***Water uptake mainly by mass flow in rapidly*** **transpiring plants.**

- In slowly transpiring plants on moist soils, water in the xylem is often under positive pressure as is indicated by guttation and exudation of sap from the cut stumps. But, when transpiration is rapid, water in the xylem is usually under tension or pull and consequently no guttation or exudation is seen. Also, slow movement of transpiration stream keeps the pressure in these roots positive. These roots thus function as osmometer and there is influx of water driven mainly by the 'osmotic' phenomenon.
- Renner (1912) called water uptake in slowly transpiring plants as 'active' as it was responsible for root pressure and dependent on the presence of living cells in the roots.
- As the transpiration increases in rapidly transpiring plants, water uptake could take place with dead or anesthetized roots or even in the absence of roots; the roots functioned merely as passive absorbing surfaces, and thus called as 'passive' absorption. there is increase in water influx by the phenomenon of mass flow. This dilutes the root xylem sap and thus makes the osmotic mechanism of water uptake less effective. The **absorption of water in rapidly transpiring plants is controlled predominantly by pressure potential (pull) in the xylem sap**. Since the driving force is not osmotic, in contrast to that in the slowly transpiring plants, the mechanism is preferably called **'nonosmotic'**.

Roots hairs and water uptake

-**Root hair**, the protrusions or projections from the epiblema cells in the roots, are believed to be the main organs of absorption of water by the plants.

-localized in maturation region (differentiation zone) above zone of elongation in root apex.

-Devoid of a cuticular covering and thus little resistance to water movement across walls.

-The presence of root hair in *large numbers* greatly *increases the surface area* of the *absorptive surface of roots in contact with the soil solution*.

-~ 90 % of water is absorbed through this region of roots. However, it has been observed that some water can also be absorbed through the older unsuberised parts and some can be absorbed even through the old and suberised parts of stem.

Factors affecting water uptake by plant roots

The efficiency of water absorption by roots is believed to be governed by several factors:

I. ***Genotypic factors: Plant factors that include:***

1. The extent of root system and the exposed root surfaces.
2. Root permeability which is affected by age, stage of development and the environmental conditions.
3. Metabolic activity, e.g., root respiration, ABA metabolism, etc.

II. ***Environmental factors: Determinants outside the plants body, including:***

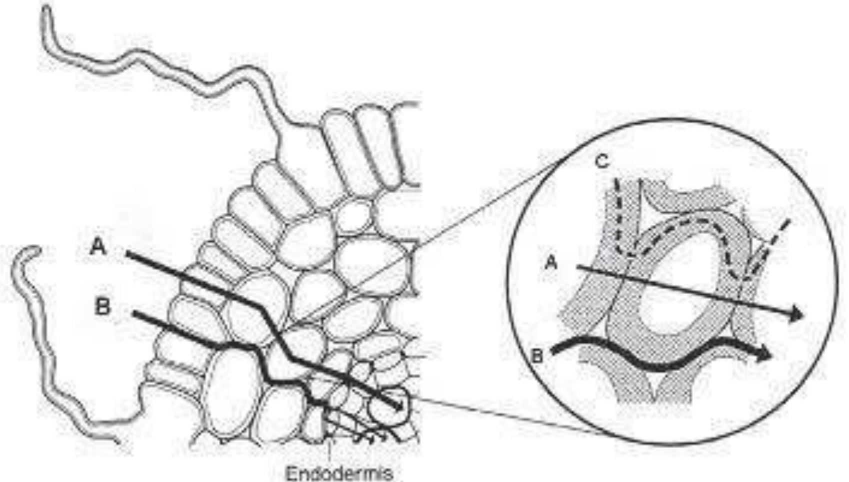
1. Availability of water.
2. Hydraulic conductivity of soils – movement of soil water to the root surface.
3. Concentration of salts in soil and soil composition – soil salinity, soil .
4. Nutrient disorders – deficiencies and toxicities of minerals.
5. Soil temperature – low temperature reduces water absorption.
6. Soil aeration – aeration deficiency increases root resistance to water absorption.

Route of water movement in roots

After absorption by the root hair, water passes through epidermis and the cortical cells to the xylem of the stele. In this path, the endodermis is regarded as the major barrier to the movement of water due to the presence of thickened casparian strips on the radial walls of the endodermal cells. This thickening restricts the passage of water through the apoplastic movement (through the cell walls). In some cases, though, there are gaps in the thickenings which appear to permit passage of water.

There are suggestions that the movement of water across the cortex may take one or more of the following courses:

1. *Vacuolar: From the vacuole of one cell to the vacuole of the next cell.* Water movement along this path is calculated to encounter high resistance due to involvement of four membranes in the pathway (Fig. 10, path A in the inset).
2. *Apoplastic: Water is suggested to move along the cell wall material (Fig.* 10, path B in the inset). Some workers believe that this pathway encounters high resistance and do not favour it.
3. *Symplastic: Water moves through the cytoplasmic continuity passing from* one cell to the next through the plasmodesmata (Fig. 10, path C in inset).



Diagrammatic representation of the cross sectional view of root tissues showing different cell components instrumental in conduction of water after absorption through the epidermis and the vacuolar (A), apoplastic (B) and symplastic (C) pathways of water transport across the cortex

Aquaporins

Aquaporins are channel proteins present in the plasma and intracellular membranes of cells, where they facilitate the transport of water and/or small neutral solutes. Although the term aquaporin was initially restricted to watertransporting MIPs (major intrinsic proteins), this term is now used in a broader sense, referring to all plant MIPs as aquaporins. These aqueous channels are 23–31 kDa proteins comprising six membrane spanning domains. Each aquaporin is composed of a single polypeptide chain of approximately 270 amino acids, and spans the membrane six times forming a constricted passage in the membrane with an average diameter of 3 – 4 A°. Since average diameter of water molecules is about 2.8 A°, the aquaporins provide a convenient passage. Though the water molecules are reported to move in a single file due to narrowness of the passage, the aquaporins enhance considerably the permeability of membranes. These transport proteins are reported to facilitate rapid, passive exchange of water between the medium, the cells, apoplast and protoplast in the tissues. One aquaporin protein is capable of transporting 109 water molecules per second making it one of the fastest membrane transport systems in cell. Apart from water, plant aquaporin protein can also transport various other low molecular weight compounds like carbon dioxide, silicon, boron, ammonia, formamide, acetamide, methylammonium, hydrogen peroxide, urea, arsenite, antimonite and some organic acids like lactate. At the tissue level, aquaporins point to the importance of transcellular water transport as an alternative to apoplastic and symplastic transport.