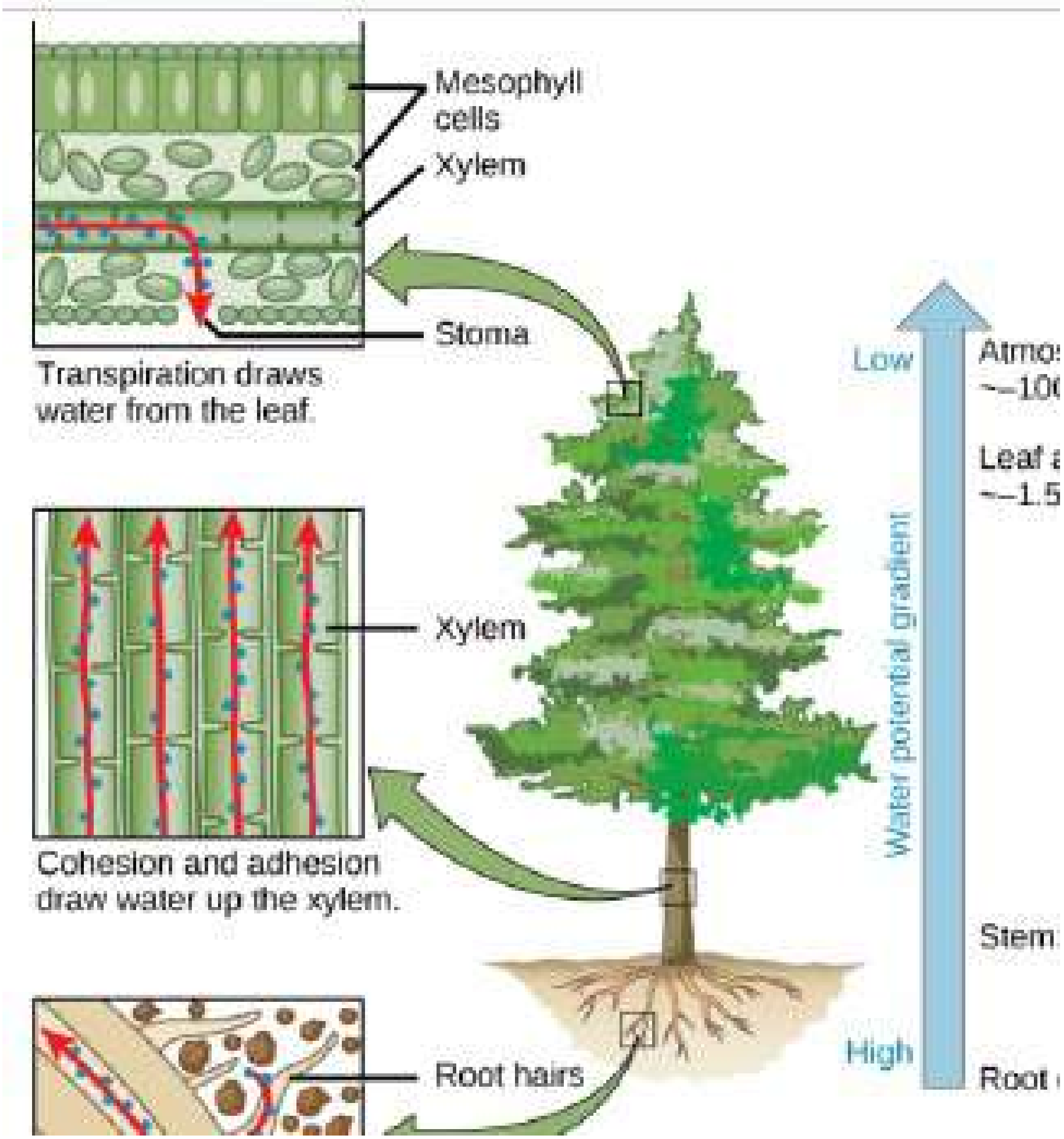
Water uptake and transport mechanism



PLANT AND WATER RELATIONSHIP

- Water being considered as universal solvent, occupies 75% of our planet in the form of oceans.

- Nearly 3.8 billion years ago, life took its origin as a speck of protoplasm in the churning oceanic water which was not salty as it is today.

- In the course of Chemical Evolution, the birth of life has chosen H_2O as the medium of biochemical activities. Thus water has become mother of life or “Solvent of Life”.

- Cells of all organisms are made up 90% or more of water. And all other components are either dissolved or suspended in water to form protoplasm, which is often referred to as physical basis of life.

Importance of water

• Water is the major component of living cells and constitutes more than 90% of protoplasm by volume and weight.

•In acts as medium for all biochemical reaction that takes place in the cell, and also acts a medium of transportation from one region to another region.

•Water is a remarkable compounded made up of Hydrogen and oxygen (2:1) and it has high specific heat, high heat of vaporization, high heat of fusion and expansion (colligative properties).

•Water because of its bipolar nature acts as universal solvent for it dissolves more substances than any other solvent.

• Electrolytes and non-electrolytes like sugars, and proteins dissolve very well. Even some hydrophobic lipid molecules show some solubility in water.

•Water acts as a good buffer against changes in the Hydrogen ion concentration (pH). This is because of its ionization property. Certain xerophytes use water as buffer system against high temperature.

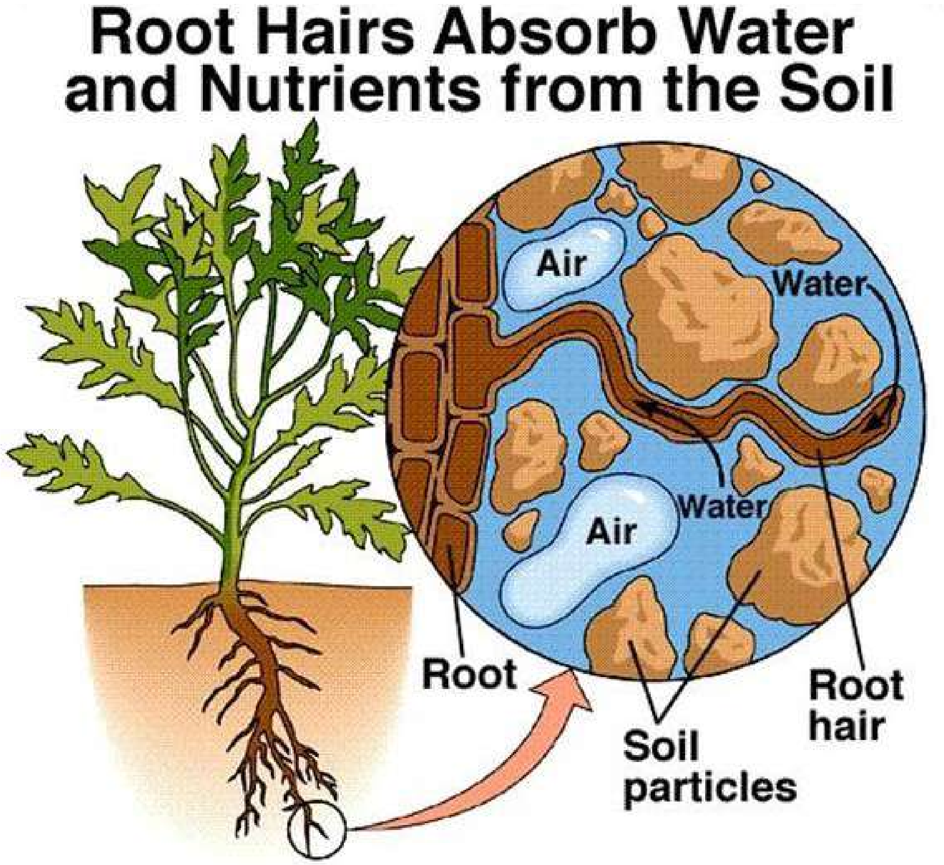
•Water also exhibits viscosity and adhesive properties. Because of hydrogen bonds, water molecules are attracted towards each other, they are held to each other with considerable force.

•This force of attraction is called cohesive force. Thus water possesses a high tensile strength. If this water is confined in very narrow columns of dimensions of xylem vessels, its tensile and cohesive forces reach very high values. And this force is very helpful in ascent of sap.

•Water is of great importance in osmoregulation, particularly in the maintenance of turgidity of cells, opening and closing of stomata and growth of the plant body.

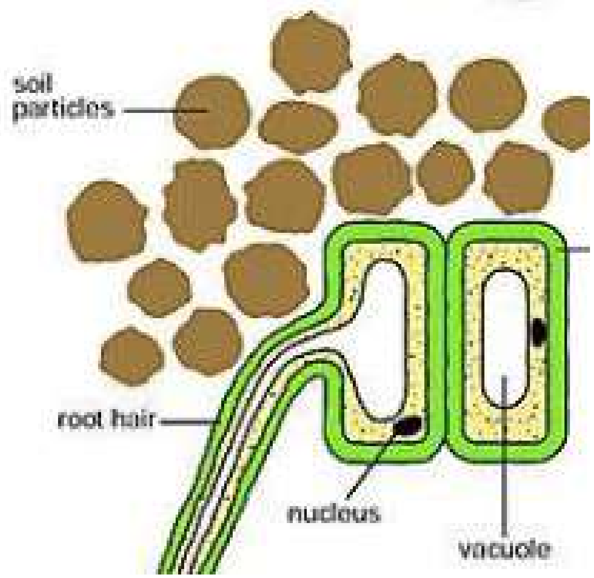
•Water is an important substrate in photosynthesis, for it provides reducing power in CO_2 fixation; water is also used in breaking or making chemical bonds of polypeptides, poly-nucleotides, carbohydrates etc.

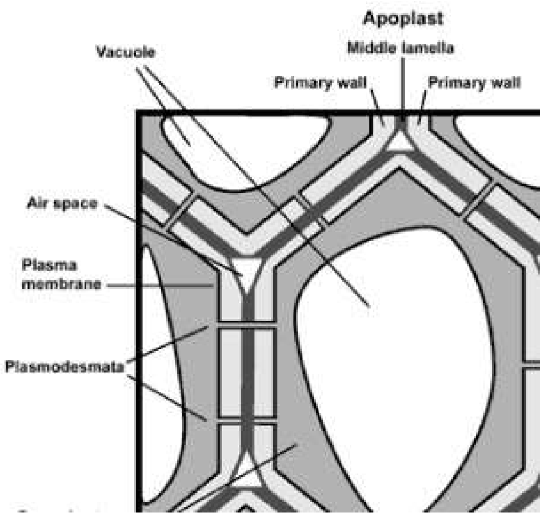
Water movement through root

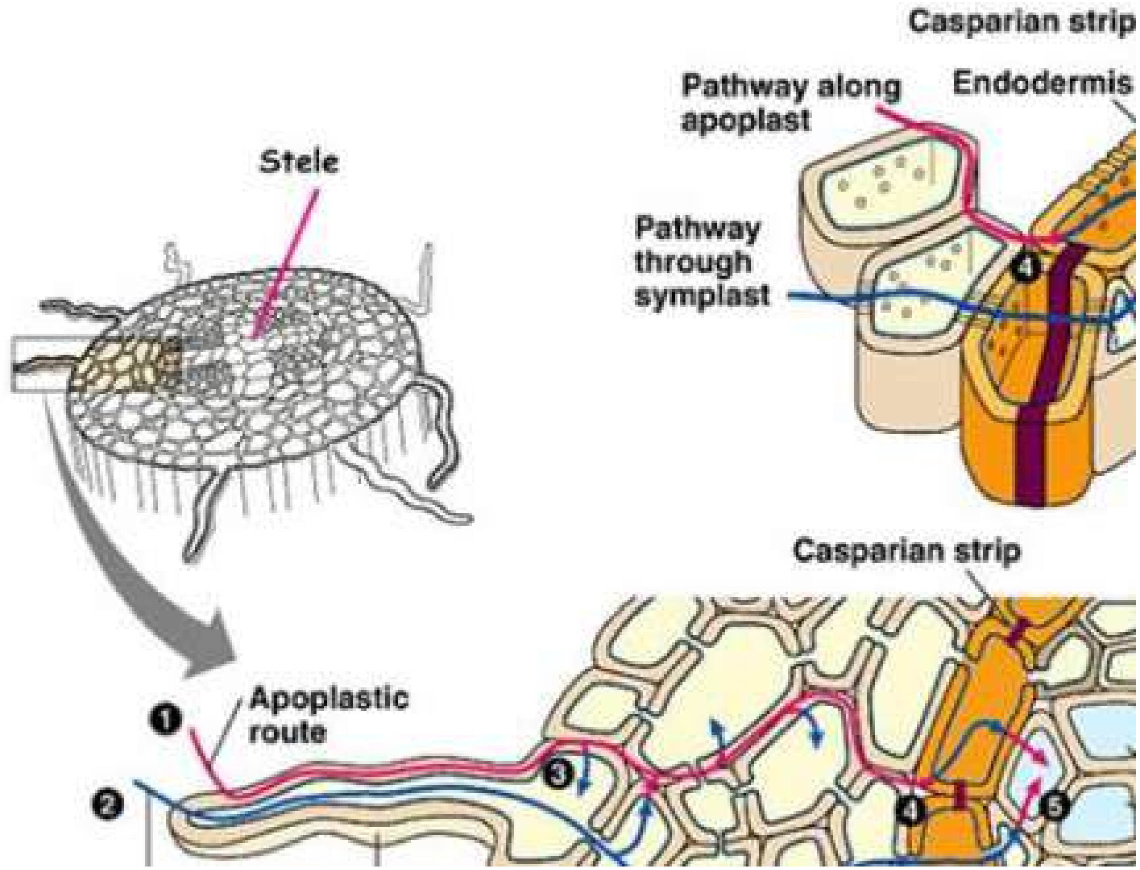


The root terminal region is made up various structures such as; from the tip towards base, apical meristem, zone of elongation, root hair zone and zone of maturation. The root hair zone is studded with root hairs; they are the extensions of epidermal cells in the form of tubular structures.

Most of the water is absorbed by the plants is through root hair zone. The figure shows the pathway of soil water into root system.







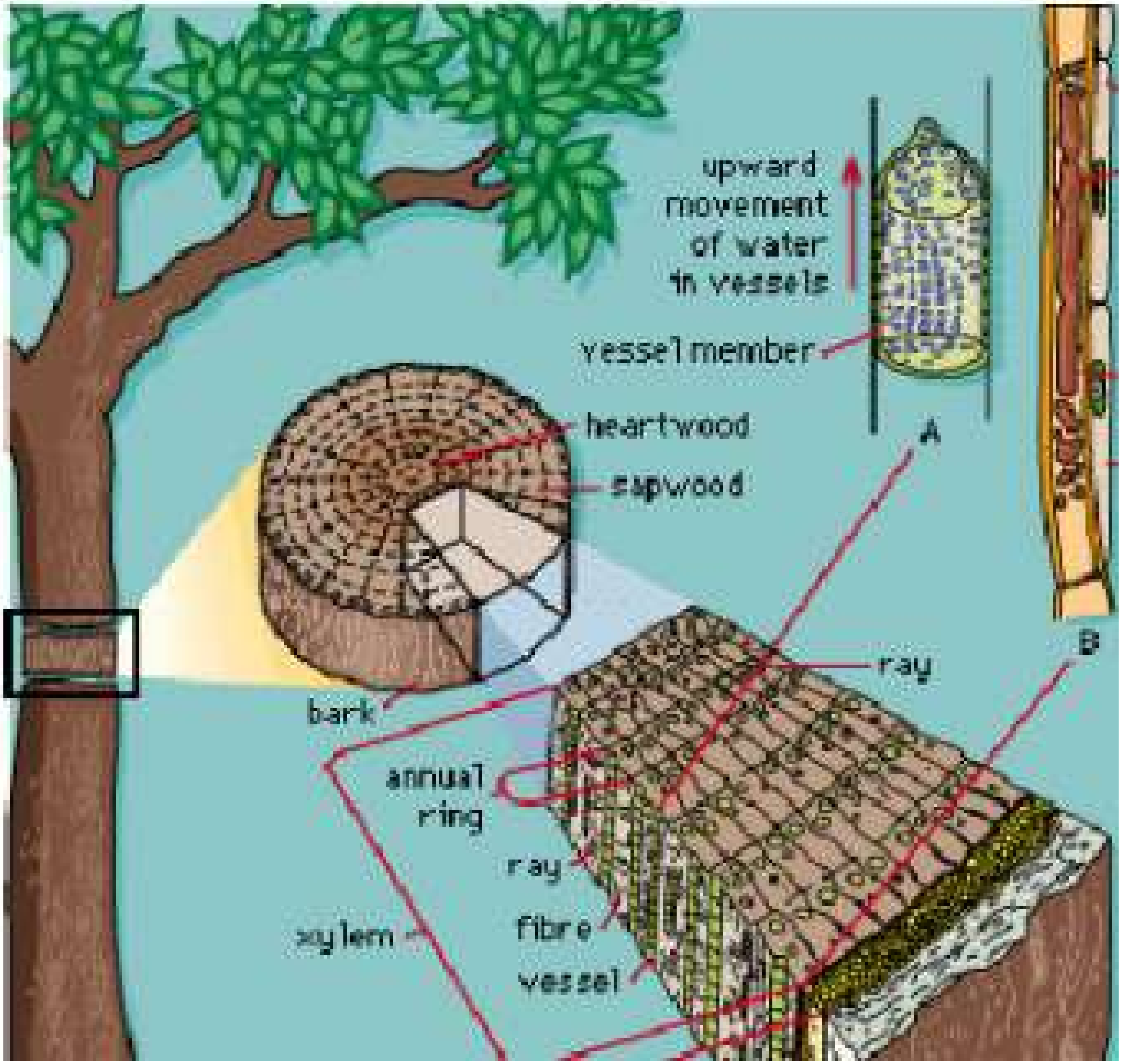
Apo plastic movement of water, that is the water moves through the space found in the cell wall.

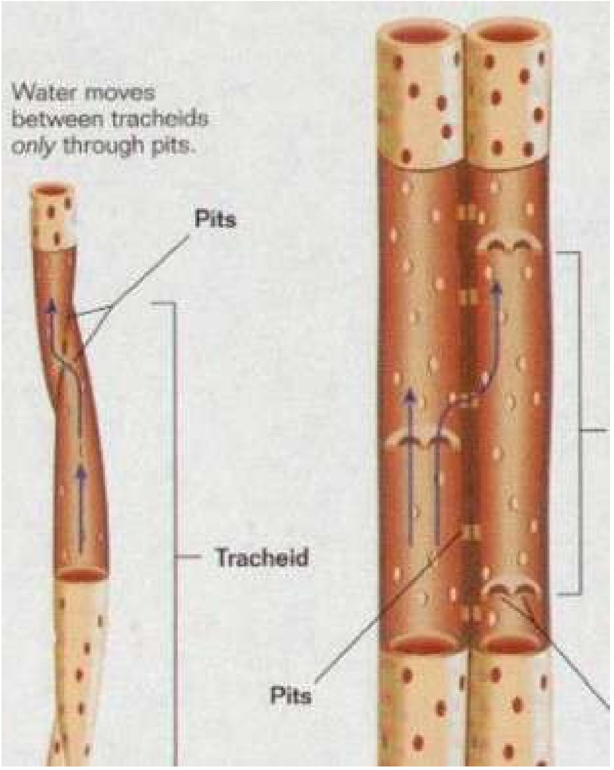
TRANSLOCATION OF WATER OR ASCENT OF SAP

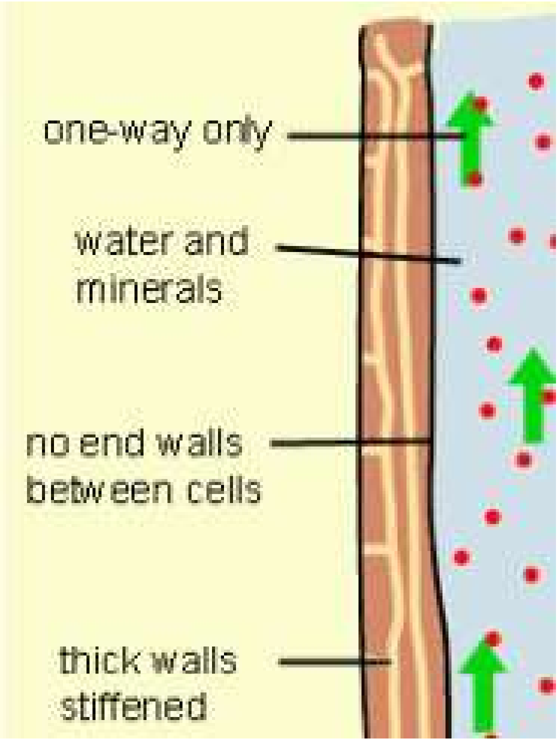
Water that is absorbed by roots has to be transported to the terminal regions of plants. This movement of water is called Ascent of Sap or Translocation of Water.

Structures involved in Ascent of Sap: Various experiments like girdling, staining and plugging, indicate that the xylem tissue is mainly responsible for the movement of water. As xylem consists of tracheae otherwise called vessels, they form a system of fine channels running from roots to all other regions of the plant body and form a beautifully branched supply system, which is almost similar to that of arteries in animals.

Note: In eudicots, vascular bundles are arranged in a ring within the stem. Each vascular bundle is orientated with the xylem on the interior and the phloem on the Outside of the xylem. In monocots, the vascular bundles are scattered throughout the stem rather than being arranged in a circle. Because of this girdling is not performed in monocots


upward movement of water in vessels
vessel member
heartwood
sapwood
A
B
ray
bark
annual ring
ray
fibre
xylem
vessel





Rate of direction of transportation: The rate with which the water is transported along the length of the stem varies from plant of plant. External conditions also play a significant role in controlling the rate of ascent of sap. But, under normal conditions the rate is 75-100 cm/hr. This is quite a rapid process. Generally most of the water is translocated upwards i.e. in longitudinal direction, but some of the water is also translocated horizontally to reach the peripheral tissues.

Theories of Ascent of Sap

- Water or sap is lifted from near the root tip to the shoot tip against the force of gravity, sometimes to height of 100 metres.

- The rate of translocation is 25-75 cm/minute (15- 45 m/hr). Several theories have been put forward to explain the mechanism of ascent of sap.

- The three main theories are **Vital Force**, **Root Pressure** and **Physical Force Theories**:.

1. Vital Force Theory:

A common vital force theory about the ascent of sap was put forward by J.C. Bose (1923). It is called pulsation theory. The theory believes that the innermost cortical cells of the root absorb water from the outer side and pump the same into xylem channels.

However, living cells do not seem to be involved in the ascent of sap as water continues to rise upward in the plant in which roots have been cut or the living cells of the stem are killed by poison and heat (Boucherie, 1840; Strasburger, 1891).

2. Root pressure theory: Absorption of water by roots has been mainly a passive process. However, the involvement of an active process is not ruled out totally. On a rainy day, when the atmospheric humidity is at its maximum, and transpiration is at its minimum, root system absorbs excess of water than it can normally absorb. As a result of it hydrostatic pressure is built up within the roots, and this is called root pressure. This is believed to act as the motive force to force the water into the xylem columns upwards. Under the above said environmental conditions, water is forced out of the water-stomata as guttated water. Hence root pressure has been considered as an important phenomenon in ascent of sap. However, it has been noted that, some of the tallest trees found on this planet do not show any root pressure. Thus this theory fails to explain the transportation of water especially in tall trees.

3. Passive or Physical Force Theories:

Physical forces like capillary force, collision force, atmospheric pressure, imbibitions, diffusion pressure, are found to operate in plants in one way or the other. Along with the development of science of plant physiology, people from time to time have come out with various theories involving one or to time have come out with various theories involving one or the other physical force as an explanation for ascent of sap.

These theories consider dead cells of xylem responsible for as-cent of sap. Capillary theory of Boehm 1863, Imbibition Theory of Unger 1868 and Cohesion-Tension Theory of Dixon and Joly 1894 are few physical theories. But cohesion-tension theory (also called cohesion-tension transpiration pull theory) of Dixon and Joly is most widely accepted one.

Atmospheric pressure theory: the protagonists of this theory have assumed that plants are closed systems. When water escapes by transpiration from the surface of the leaves, it is believed that vacuum will be created within the plant body. As the root system is submerged in soil water, with the atmospheric action on the soil water, in order to fill up the vacuum created in the xylem vessels, water just enters passively; thus the water is translocated upwards. Unfortunately plants are not closed systems but they exhibit openness, for, the gases can diffuse into and out of the plant system with ease and facility. Added to this, atmospheric pressure can support the water to be lifted only to a height of 34 feet; but there are plants which are taller than this and still there is transport of water. Hence it can be concluded that atmospheric pressure could not be the force for ascent of sap.

Capillary Force Theory: When one end of the blotting paper or a chalk piece is dipped into ink, the ink slowly moves up. This movement through the paper is called capillary movement. Blotting paper is made up of innumerable cellulose fibres interwoven into a close network. Between such fibres, extremely narrow spaces are found, which are connected with each other and form a fine net work of capillary canals. If water is provided to such capillary system at one end, water is sucked in and it moves along the channels of capillary network by a force called capillary force. According to capillary network by a force theory, such capillary system exists within the plant body. Tracheids and tracheae which are found longitudinally oriented in the vasculature have lumen as empty space, roots to terminal regions of the stem as continuous capillary system. When water is absorbed by the root system, the capillary system of xylem elements take up the water by capillary force and the water is supported to move upwards slowly but steadily.

Though the network xylem elements can be compared to capillary system, the rate of movement of water in a capillary system is extremely slow in comparison to the actual rate of ascent of sap observed. Furthermore the lumen of larger number of tracheids and tracheae has diameters greater than the large capillary spaces. Though capillary system may be contributing some force for the movement of water upwards, it cannot be considered as the sole force for the movement of water.

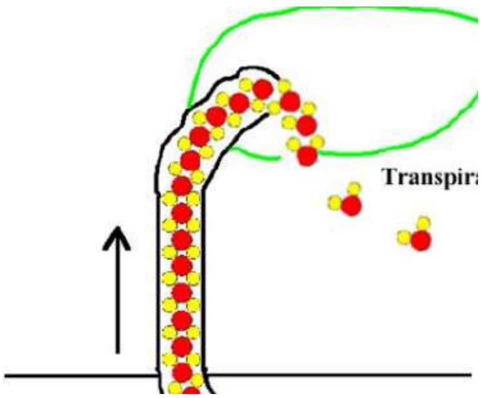
Imbibition theory: Dry wood when soaked in water swells; wooden shutters in rainy season are difficult to close; seeds soaked in water overnight get swollen. In all the above said instances the volume of the wood or seeds increases. This is due to the intake of water into the dry plant material. Wood is made up of cellulose, hemicelluloses and lignin. All these substances are hydrophilic or water loving in nature. When such materials come in contact with water, the hydrophilic substances imbibe water, which gets absorbed onto them. Because of the adsorption of water, the volume of the wood increases, simultaneously lot of energy is liberated. This phenomenon is called imbibition. If such materials are kept in a closed container and water is added, wood imbibes water and swells. This swelling creates enormous pressure ranging from 1000 to 10,000 amphospheres. People (stone breakers) using this natural phenomenon break open big stone boulders by inserting dry wooden pegs into holes, then adding water in the holes. As wooden pegs imbibe water, enormous amount of imbibition pressure develops, which is really responsible for breaking the rocks.

- Plants, being made up of cellulose cell walls, do exhibit imbibition. This is particularly conspicuous with xylem elements because their thick walls are made up of hydrophilic substances.

- When roots absorb water, xylem cells do imbibe water and there is no doubt about it; but the movement of water along the cell wall of these dead xylem water along the cell wall of these dead xylem elements seems to be incredible, but slow comparatively. Instead of water moving along the cell wall it has been found that water moves through the lumen of the xylem elements and this is a fact.

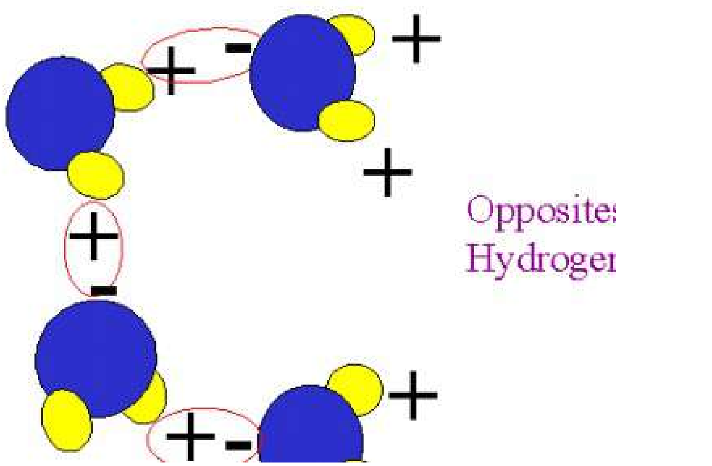
- The contribution of imbibition force in the movement of water upwards is very little and negligible and it cannot be considered as the mechanism of ascent of sap.

Cohesion/Transpiration pull theory: Molecules of similar kind are attracted towards each other and they are held together by a force of attraction called cohesion force. Water, oil, alcohol etc., depending upon the kind of the solvent molecules the force of attraction varies. In the case of water, hydrogen and ionic bonds are the forces of attraction, while in oils the hydrophobic bonds are the forces of attraction. When such solvents are put into very fine tube similar to the size of tracheae, the column of the solvent, here it is water, does not break, because of two forces acting up on such column of water, one is the cohesive force and the other is surface tension.



Plants contain a series of such xylem vessels connected to one another forming a continuous column of cells, form basal part of the roots to the terminal leaves at the extreme apex on the stem. The water found in such long columns is tenaciously held to the walls of the vessels, at the same time the column withstands the opposite pulls by its cohesive forces. When water is transpired from the surface cells of the leaf, water is drawn from the neighboring cells due to the development of DPD (diffusion pressure deficit) gradient between the transpiring surface cells and the inner cells. This sets up a chain reaction, and xylem elements filled with water. This leads to the diffusion of water from xylem elements found in 'lumen' into mesophyll cells towards the anterior surface. When millions of such cells are engaged in losing water by transpiration, enormous amount of DPD gradient develops which may amount for 100-200 atmospheres.

Note: Movement of water takes place from lower DPD to higher DPD



The totality of the force is so great on the water column found in xylem elements; the water is physically pulled upwards to meet the demand of the transpiring cells. This pull or force that drains the water is called transpiration pull or suction pressure. This kind of transpiration pull on the column upwards creates a kind of tension on the water column for the water column is also pulled downwards by gravitational force. Under these conditions, forces which have greater strength prevail and the water column is pulled towards that end. In this case, the transpiration pull is much more than the gravitation pull, hence the water is pulled upwards, provided that water column has to have strength or force of attraction to withstand tension. Fortunately the cohesive forces between the water molecules are so great, they can withstand this tension.

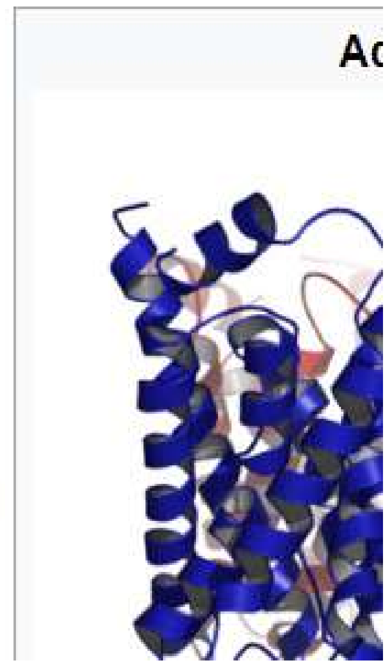
Thus water moves upwards in column as if there is a pump sucking the water upwards. Because of such tension the cells shrink, rather reduce their lumen, when the entire stem is taken into consideration. The stem exhibits a slight narrowing during maximum transpiration. These daily rhythmic movements of expansion (night) or contraction (day) has been demonstrated by Mc Dougal. One atmospheric pressure of transpiration pull is enough to pull the water unto the height of 20 feet or so; but normally, the transpiration pull that develops runs to about 20-100 atm, which is enough to pull the water to the height of 400 to 1000 ft and the tallest plant known to mankind is just about 400 ft. Certain objections like air bubble in water column are taken care of by this 'Cohesion' theory by Dixon and Jolly (1894).

Aquaporin

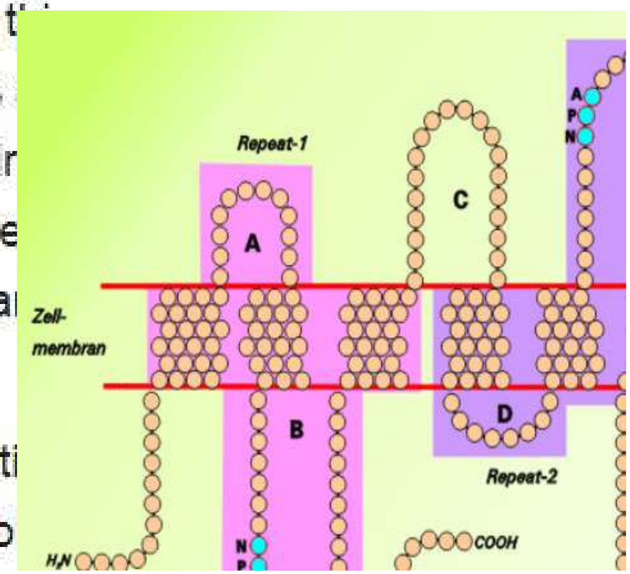
Aquaporins, also called **water channels**, are integral membrane proteins from a larger family of major intrinsic proteins that form pores in the membrane of biological cells, mainly facilitating transport of water between cells.[1] The cell membranes of a variety of different bacteria, fungi, animal and plant cells contain aquaporins through which water can flow more rapidly into and out of the cell than by diffusing through the phospholipid bilayer.[2]

The 2003 Nobel Prize in Chemistry was awarded jointly to Peter Agre for the discovery of aquaporins[3] and Roderick MacKinnon for his work on the structure and mechanism of potassium channels.[4]

Genetic defects involving aquaporin genes have been associated with several

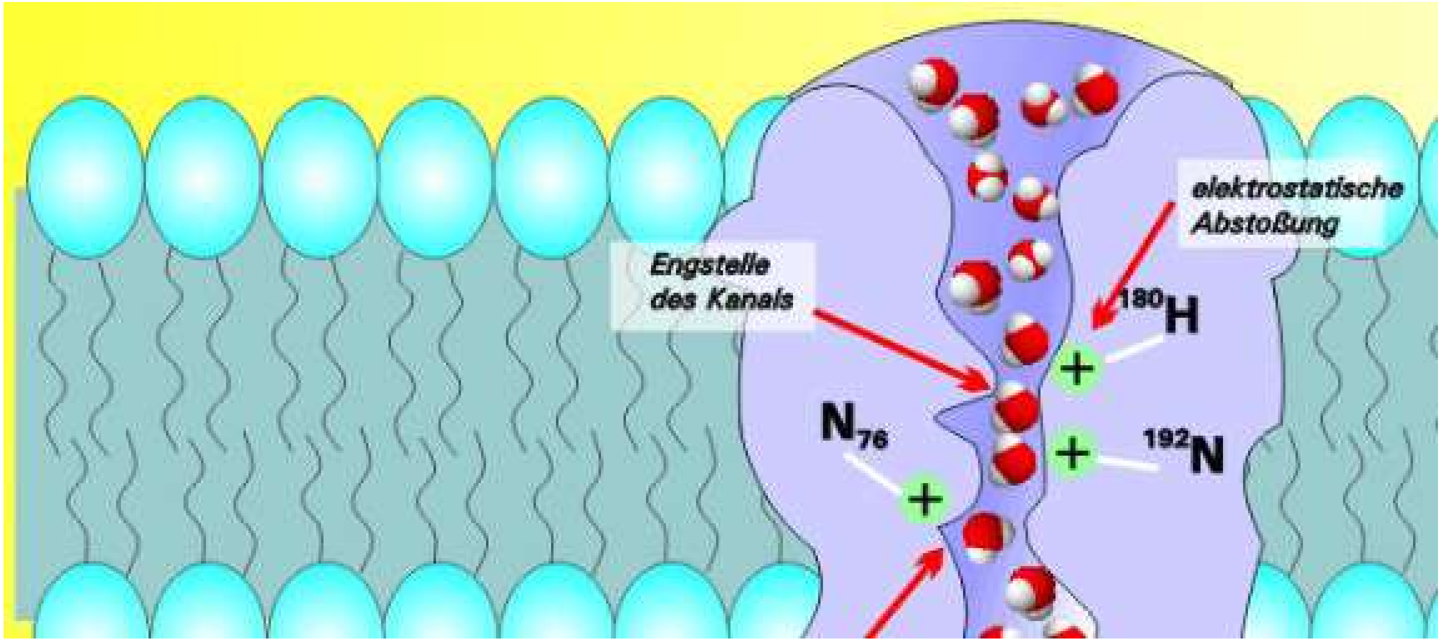


Aquaporin proteins are composed of a bundle of six transmembrane are embedded in the cell membrane. The amino and carboxyl ends f of the cell.[26][29] The amino and carboxyl halves resemble each othe repeating a pattern of nucleotides. Some researchers believe that t by the doubling of a formerly half-sized gene. Between the helices (A – E) that loop into or out of the cell membrane, two of them hydr with an asparagine–proline–alanine ("NPA motif") pattern. They cre hourglass shape, making the water channel narrow in the middle a end.

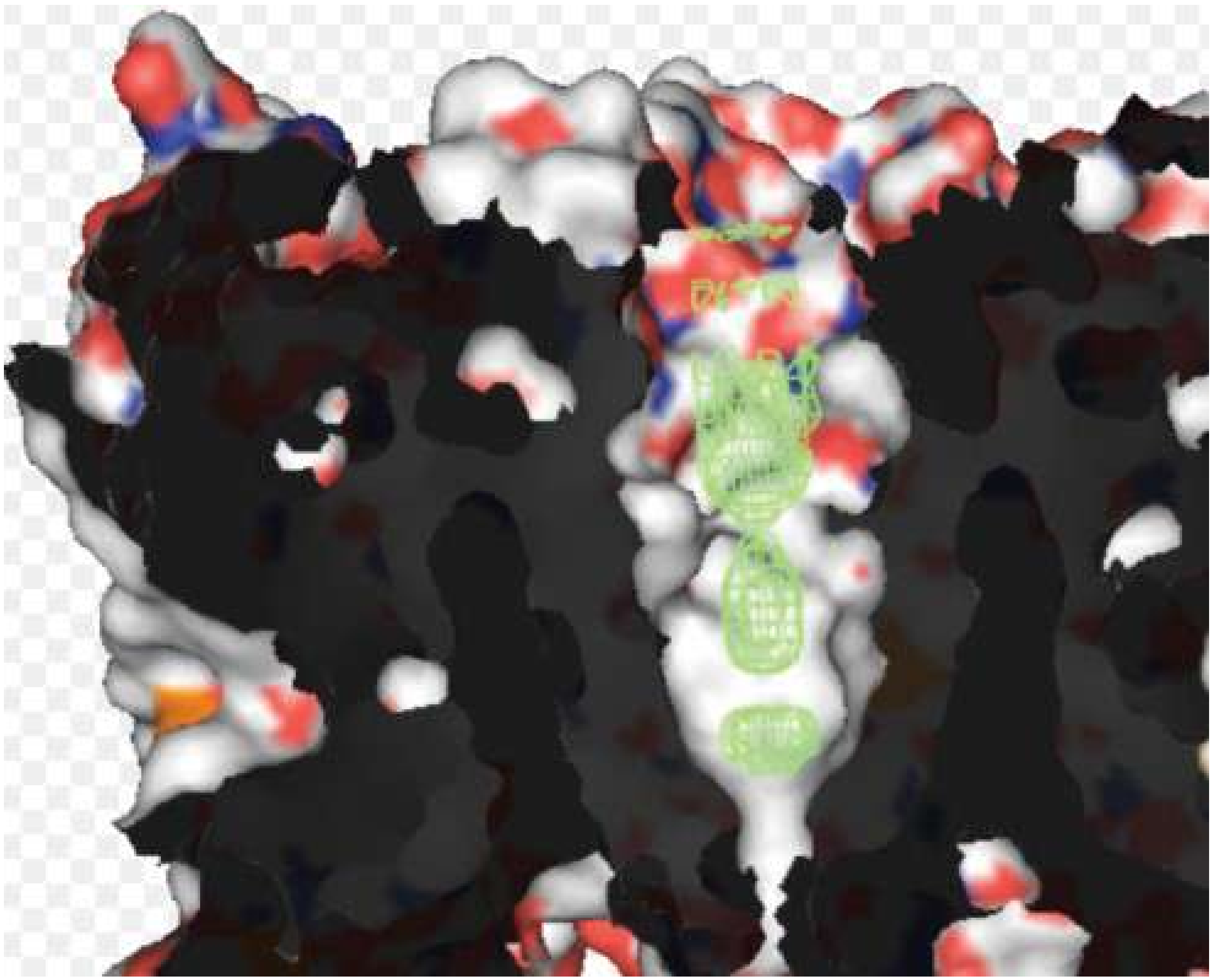


Another and even narrower place in the channel is the "ar/R selecti cluster of amino acids enabling the aquaporin to selectively let thro passage of different molecules.

Aquaporins form four part clusters in the cell membrane, with each o monomers acting as a water channel.[26] Different aquaporins have c water channels, the smallest types allowing nothing but water throug

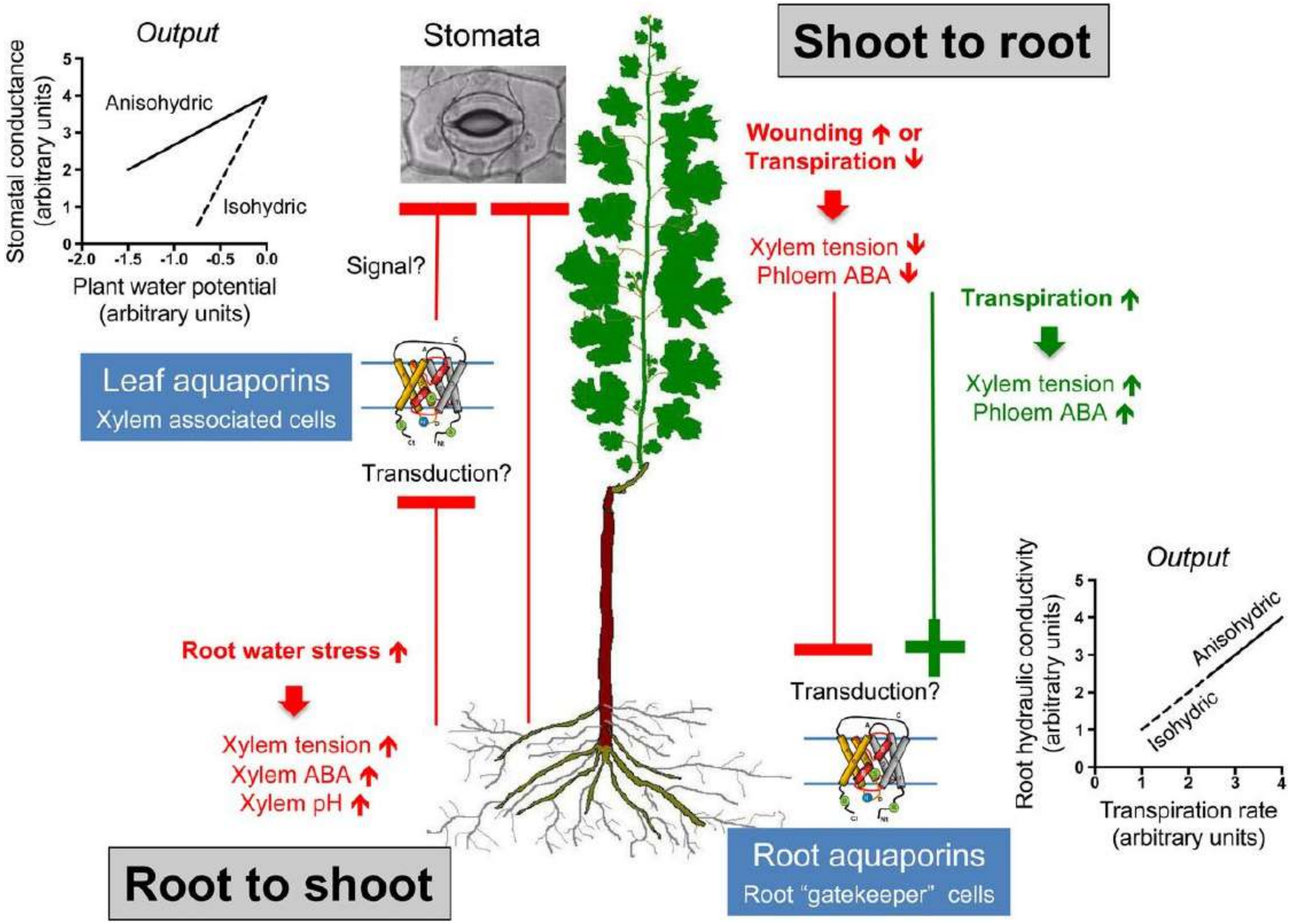


Schematic depiction of water movement through the narrow selectivity filter of the aquaporin channel



The 3D structure of aquaporin Z highlighting the 'hourglass'-shaped water channel that cuts through the center of the protein

Long-distance signaling within plants involving aquaporins to coordinate water demand by the shoot with supply by the roots.



François Chaumont, and Stephen D. Tyerman Plant Physiol. 2014;164:1600-1618

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Mycorrhizal association helpful in absorption of water in plants

Mycorrhiza is a symbiotic association of fungi with the root systems of some plants. The fungal hyphae either form a dense network around the young roots or they penetrate the cells of the roots. The large surface area of the fungal hyphae is helpful in increasing the absorption of water and minerals from the soil. In return, they get sugar and nitrogenous compounds from the host plants. The mycorrhizal association is obligate in some plants. For example, Pinus seeds do not germinate and establish in the absence of mycorrhizal.

In mycorrhiza a large number of fungal hyphae are associated with the young roots. The fungal hyphae extend to sufficient distance into the soil. They have a large surface area. The hyphae are specialised to absorb both water and minerals.

The two are handed over to the root which provides the fungus with both sugars and N-containing compounds. Mycorrhizal association between fungus and root is often obligate. Pinus and orchid seeds do not germinate and establish themselves into plants without mycorrhizal association.

Water and Solute Potential

Solute potential: (osmotic potential) pressure which needs to be applied to a solution to prevent the inward flow of water across a semipermeable membrane.

Transpiration: the loss of water by evaporation in terrestrial plants, especially through the stomata; accompanied by a corresponding uptake from the roots

Water potential: Water potential is the measure of potential energy in water and drives the movement of water through plants. the potential energy of water per unit volume; designated by ψ

Water Potential

- Water potential is denoted by the Greek letter ψ (psi) and is expressed in units of pressure (pressure is a form of energy) called megapascals (MPa).

- Plants are phenomenal hydraulic engineers. Using basic laws of physics and manipulation of potential energy, plants can move water to the top of a 116-meter-tall tree. Plants use hydraulics to generate enough force to split rocks and buckle sidewalks.

- Plants use ψ to transport water to the leaves so that photosynthesis can take place.

- Water always moves from the system with a higher ψ to the system with a lower ψ.

- Internal ψ of a plant cell is more negative than pure water; this causes water to move from the soil into plant roots via osmosis.

(a) (b)

Water potential in plants:
heights nearing 116 meters
coastal redwoods (Se
sempervirens) are the tallest tre

- **Water potential is a measure of the potential energy in water, or the difference in potential energy between a given water sample and pure water (at atmospheric pressure and ambient temperature).**

- **The potential of pure water (Ψw pure H2O) is designated a value of zero (even though pure water contains plenty of potential energy, that energy is ignored). Water potential values for the water in a plant root, stem, or leaf are, therefore, expressed in relation to Ψw pure H2O.**

The water potential in plant solutions is influenced by solute concentration, pressure, gravity, and factors called matrix effects.

Water potential can be broken down into its individual components using the following equation:

$\Psi system = \Psi total = \Psi s + \Psi p + \Psi g + \Psi m$

where
Ψs = solute potential
Ψp, = pressure potential
Ψg, = gravity potential
Ψm = matric potential

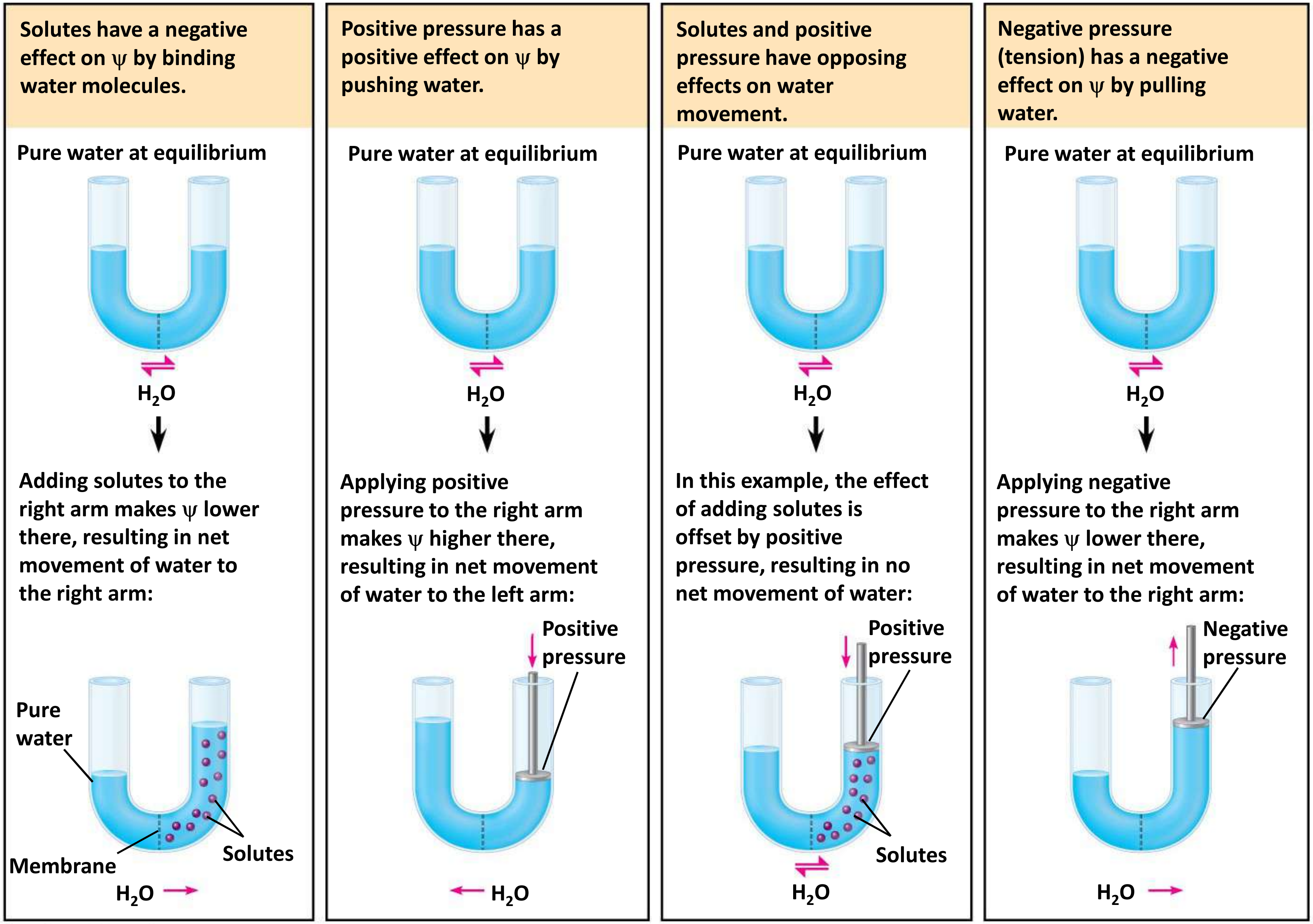
"System" can refer to the water potential of the soil water (Ψsoil), root water (Ψroot), stem water (Ψstem), leaf water (Ψleaf), or the water in the atmosphere (Ψatmosphere), whichever aqueous system is under consideration.

As individual components change, they raise or lower the total ψ of a system. When this happens, water moves to equilibrate, moving from the system or compartment with a higher ψ to the system or compartment with a lower ψ.

This brings the difference in ψ between the two systems (Δ) back to zero (Δ = 0). Therefore, for water to move through the plant from the soil to the air (a process called transpiration), the conditions must exist as such: Ψsoil > Ψroot > Ψstem > Ψleaf > Ψatmosphere.

Note: Water only moves in response to Δ, not in response to the individual components. However, because the individual components influence the total Ψsystem, a plant can control water movement by manipulating the individual components (especially Ψs).

Figure 36.8



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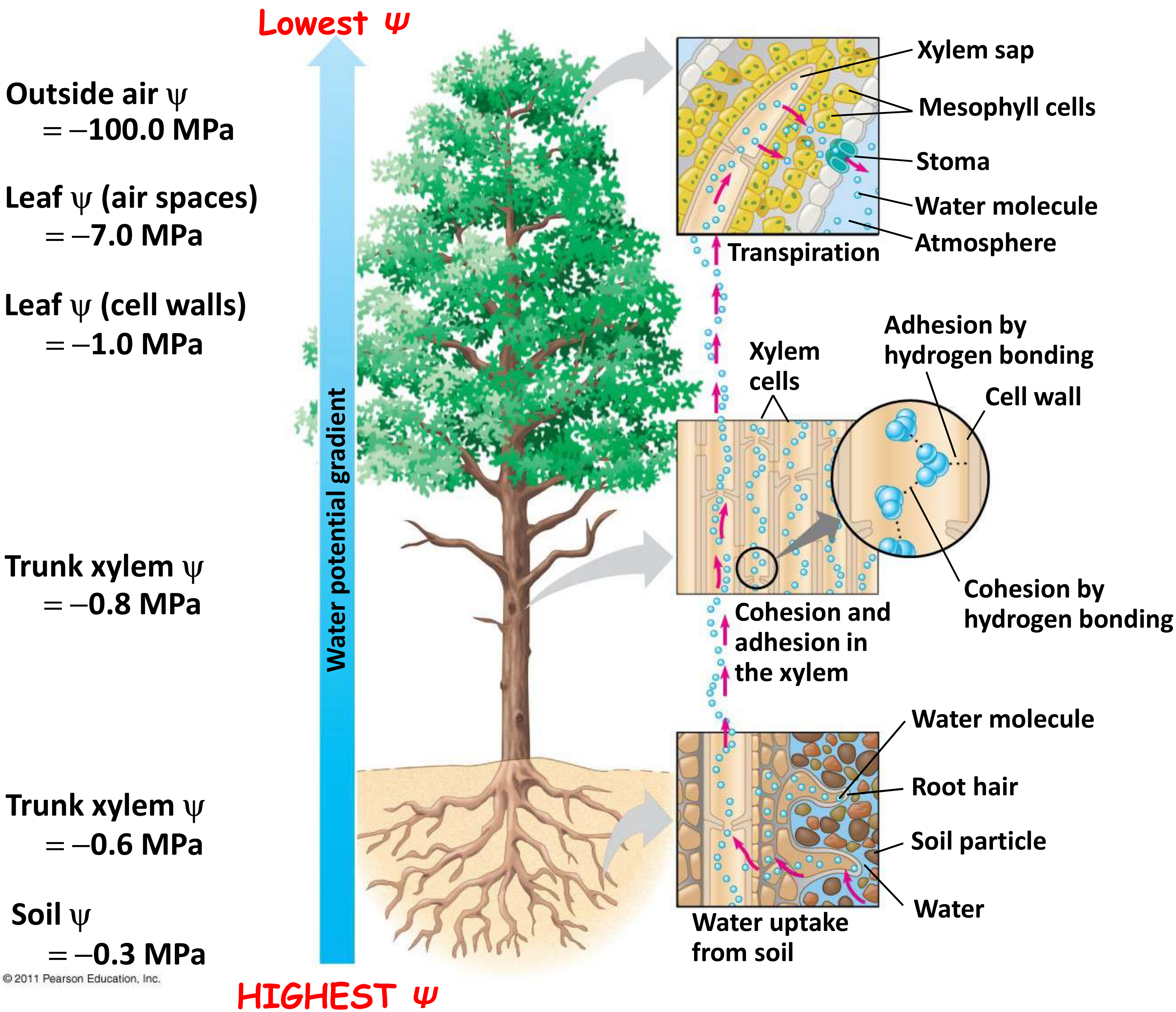

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Solute Potential

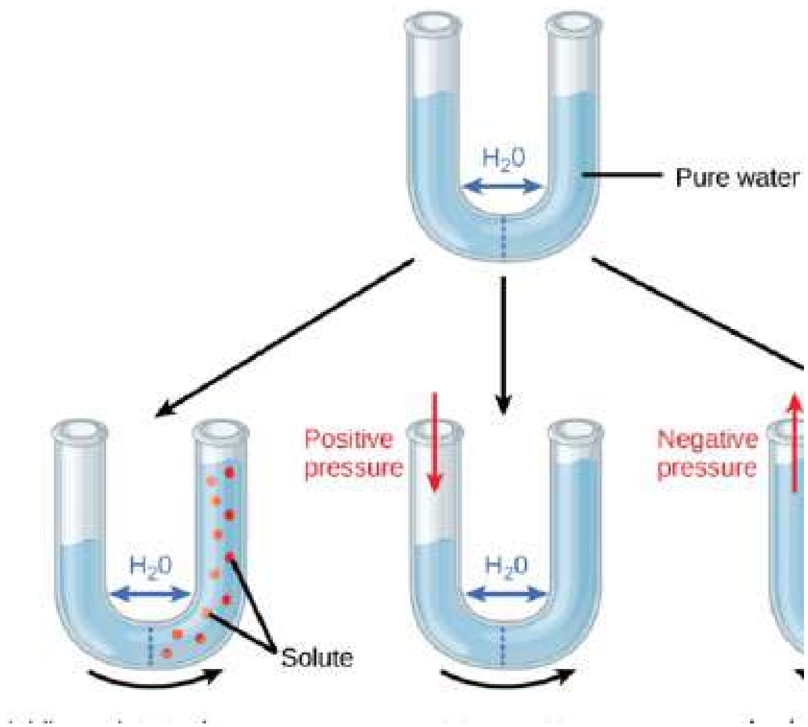
Solute potential (Ψs), also called osmotic potential, is negative in a plant cell and zero in distilled water. Typical values for cell cytoplasm are –0.5 to –1.0 MPa.

Solutes reduce water potential (resulting in a negative Ψw) by consuming some of the potential energy available in the water. Solute molecules can dissolve in water because water molecules can bind to them via hydrogen bonds; a hydrophobic molecule like oil, which cannot bind to water, cannot go into solution.

The energy in the hydrogen bonds between solute molecules and water is no longer available to do work in the system because it is tied up in the bond. In other words, the amount of available potential energy is reduced when solutes are added to an aqueous system.
Solute potential (Ψs) decreases with increasing solute concentration; a decrease in Ψs causes a decrease in the total water potential.

Thus, Ψs decreases with increasing solute concentration. Because Ψs is one of the four components of Ψsystem or Ψtotal, a decrease in Ψs will cause a decrease in Ψtotal.

The internal water potential of a plant cell is more negative than pure water because of the cytoplasm's high solute content. Because of this difference in water potential, water will move from the soil into a plant's root cells via the process of osmosis. This is why solute



Solute potential: In this example with a semipermeable membrane between two aqueous systems, water will move from a region of higher to lower water potential until equilibrium is reached. Solutes (Ψs), pressure (Ψp), and gravity (Ψg) influence total water potential for each side of the tube (Ψtotal right or left) and, therefore, the difference between Ψtotal on each side (Δ). (Ψm, the potential due to interaction of water with solid substrates, is ignored in this example because glass is not especially hydrophilic). Water moves in response to the difference in water potential between two systems (the left and right sides of the tube).

Plant cells can metabolically manipulate Ψs (and by extension, Ψtotal) by adding or removing solute molecules. Therefore, plants have control over Ψtotal via their ability to exert metabolic control over Ψs.

Pressure, Gravity, and Matric Potential

Water potential is affected by factors such as pressure, gravity, and matric potentials.

Pressure Potential

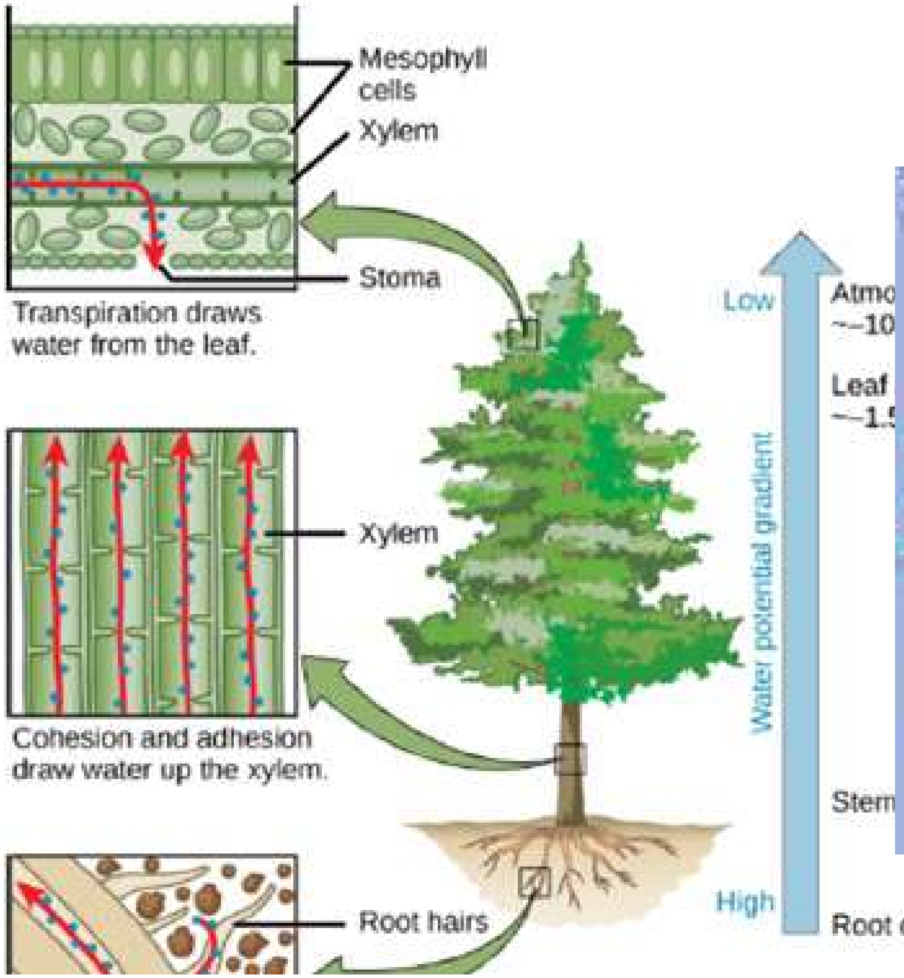
Pressure potential is also called turgor potential or turgor pressure and is represented by Ψp. Pressure potential may be positive or negative; the higher the pressure, the greater potential energy in a system, and vice versa. Therefore, a positive Ψp (compression) increases Ψtotal, while a negative Ψp (tension) decreases Ψtotal. Positive pressure inside cells is contained by the cell wall, producing turgor pressure in a plant. Turgor pressure ensures that a plant can maintain its shape. A plant's leaves wilt when the turgor pressure decreases and revive when the plant has been watered.

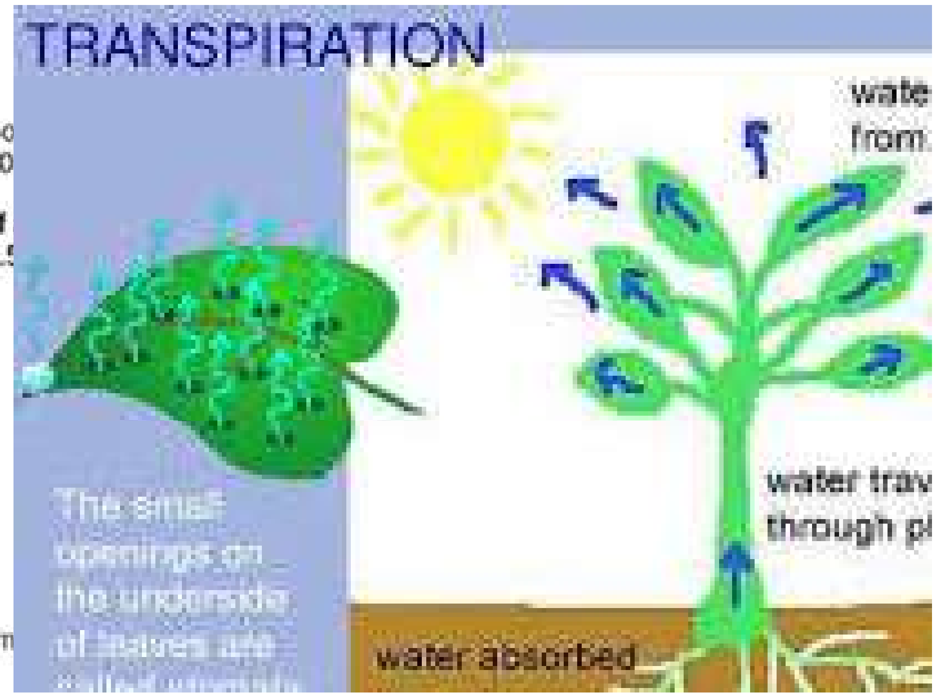
Gravity Potential

Gravity potential (Ψg) is always negative or zero in a plant with no height. Without height, there is no potential energy in the system. The force of gravity pulls water downwards to the soil, which reduces the total amount of potential energy in the water in the plant (Ψtotal). The taller the plant, the taller the water column, and the more influential Ψg becomes. On a cellular scale and in short plants, this effect is negligible and easily ignored. However, over the height of a tall tree like a giant coastal redwood, the plant must overcome an extra 1MPa of resistance because of the gravitational pull of –0.1 MPa m-1.

Matric Potential

Matric potential (Ψm) is the amount of water bound to the matrix of a plant via hydrogen bonds and is always negative to zero. In a dry system, it can be as low as –2 MPa in a dry seed or as high as zero in a water-saturated system. Every plant cell has a cellulosic cell wall, which is hydrophilic and provides a matrix for water adhesion, hence the name matric potential. The binding of water to a matrix always removes or consumes potential energy from the system. Ψm is similar to solute potential because the hydrogen bonds remove energy from the total system. However, in solute potential, the other components are soluble, hydrophilic solute molecules, whereas in Ψm, the other components are insoluble, hydrophilic molecules of the plant cell wall. m cannot be manipulated by the plant and is typically ignored in well-watered roots, stems, and leaves.





Cohesion–Tension Theory of Sap Ascent: The cohesion–ter
sap ascent is shown. Evaporation from the mesophyll cell
negative water potential gradient that causes water to move

Control of Transpiration

Transpiration is a passive process: metabolic energy in the f
not required for water movement. The energy driving transp
difference in energy between the water in the soil and the w
atmosphere. However, transpiration is tightly controlled. The
to which the leaf is exposed drives transpiration, but it also c
massive water loss from the plant. Up to 90 percent of the w
up by roots may be lost through transpiration.

the loss of water. Regulation of transpiration, therefore, is ach primarily through the opening and closing of stomata on the l Stomata are surrounded by two specialized cells called guarc which open and close in response to environmental cues suc intensity and quality, leaf water status, and carbon dioxide concentrations. Stomata must open to allow air containing ca dioxide and oxygen to diffuse into the leaf for photosynthesis respiration. When stomata are open, however, water vapor is external environment, increasing the rate of transpiration. The plants must maintain a balance between efficient photosynthe water loss.

Plants have evolved over time to adapt to their local environm reduce transpiration. Desert plant (xerophytes) and plants tha other plants (epiphytes) have limited access to water. Such p

Reducing Transpiration: Plants are suited to their local e
Xerophytes, like this prickly pear cactus (*Opuntia* sp.) and (b)
as this tropical *Aeschynanthus perrottetii* have adapted to ver
resources. The leaves of a prickly pear are modified into
lowers the surface-to-volume ratio and reduces water loss.
takes place in the stem, which also stores water. (b) *A. pe*
have a waxy cuticle that prevents water loss. (c) Goldenrod (
a mesophyte, well suited for moderate environments. (d) Hy

(a) (b)

Xerophytes and epiphytes often have a thick covering of t
stomata that are sunken below the leaf's surface. Trichome
specialized hair-like epidermal cells that secrete oils and o
and reduce transpiration. Multiple epidermal layers are al
found in these types of plants

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