1 Water absorption and transport

Intimate **contact** between the surface of **root** and the **soil** is essential for **effective water absorption**. **Root hairs** are filamentous outgrowths of root epidermal cells that greatly increase the surface area of the root, thus **providing greater capacity for absorption** of ions and water from the soil. Water enters the root most readily near the root tip.

The water absorption by the roots is related to its surface directly in contact with soil. Thus, **longer** and **younger** (**less suberized**) roots with **more root hairs** are essential for increasing the contact surface and improve the water absorption capacity of the soil.

The water flow of a plant is primarily **controlled** by the **transpiration rate**. In this flow system it is essential indeed that there are no limitations on water absorption by the root system. As the **roots absorb** water, there is a **reduction** in the **water potential** in the **soil** that is in contact with the roots (rhizosphere). This process establishes a **water potential gradient** between the rhizosphere and a neighboring region of the soil which presents a higher water potential and which coordinates the water movement towards the roots of a transpiring plant. This water movement in the soil occurs mainly through mass flow due to the fact that the water filled micro pores of the soil are interconnected. Therefore, water flows from soil to root at a rate **depending on the water potential gradient** between soil and plant which is affected by:

1. Plant water need
2. Hydraulic conductivity of the soil
3. Soil type and soil water content.

Sandy soils have higher conductivity due to greater porosity, but they also retain less water in relation to clay soils or soils rich in organic matter.

In humid regions, as **tropical rain forest**, plants usually **do not require very extensive** root systems (i.e. root: **shoot ratio < 0.15**), because a small volume of soil can meet the demands of transpiration. This condition in turn induces a reduction of the root: shoot ratio. On the other hand, in **dry regions**, the plants invest more in their roots, increasing the root: shoot ratio such that the roots can represent upper to **90% of a plant biomass** in some species of a desert climate.

1.1 Water flow pathways from epidermis to endodermis:

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

1.1.1 Apoplast pathway

The apoplast is the system of **adjacent cell walls** that is continuous throughout the plant, **except at the casparian strips** of the endodermis in the roots. The apoplastic movement of water occurs exclusively through the **intercellular spaces** and the **walls** of the cells. Movement through the apoplast **does not** involve **crossing the cell membrane**.

This movement is dependent on the **gradient**. The apoplast **does not provide any barrier** to water movement and water movement is through **mass flow**.

As **water evaporates** into the **intercellular spaces** or the **atmosphere**, **tension** develop in the continuous stream of water in the apoplast, hence **mass flow** of water occurs due to the **adhesive** and **cohesive** properties of water.

Cohesion = water attracted to other water molecules because of polar properties.

Hydrogen bonds hold the substance together, a phenomenon called cohesion. Cohesion is responsible for the transport of the water column in plants Cohesion among water molecules plays a key role in the transport of water **against gravity** in plants.

Adhesion = water attracted to other materials.

Because water has both adhesive and cohesive properties, capillary action is present.

Capillary Action is the water's adhesive property is the cause of capillary action. Water is attracted to some other material and then through cohesion, other water molecules move too as a result of the original adhesion.

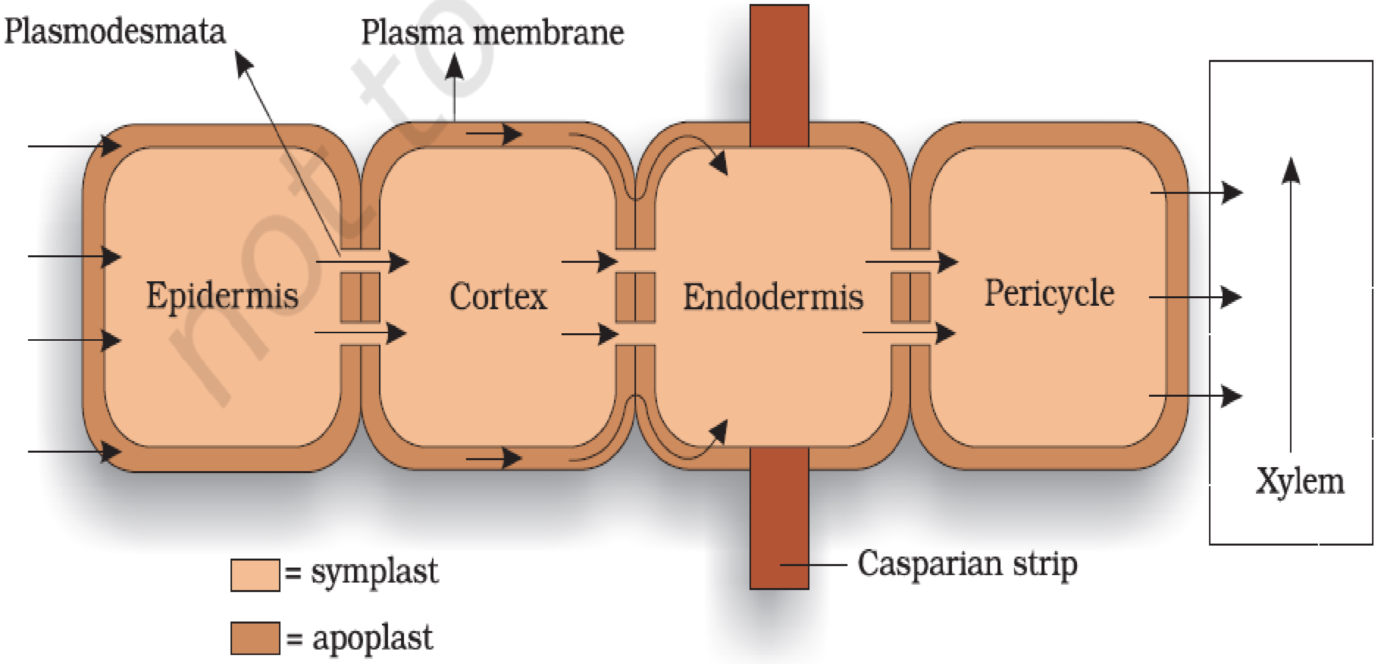
1.1.2 Symplast pathway

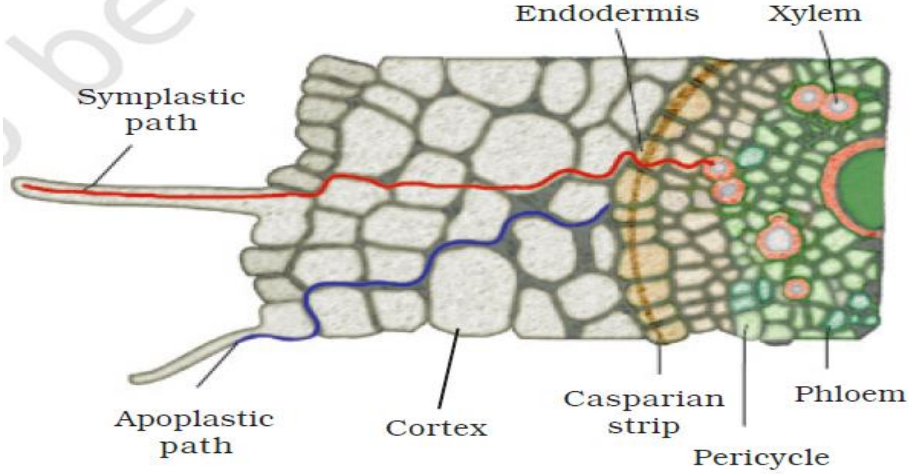
The symplastic system is the system of **interconnected protoplasts**. Neighboring cells are connected through **cytoplasmic strands** that extend through **plasmodesmata**. During symplastic movement, the water travels through the cells – their cytoplasm; intercellular movement is through the plasmodesmata. Water has to enter the cells through the **cell membrane**; hence the movement is relatively slower. Movement is again **down a potential gradient**. Symplastic movement may be aided by cytoplasmic streaming.

Most of the water flow in the roots occurs via the **apoplast** since the cortical cells are loosely packed, and hence offer no resistance to water movement. However, the inner boundary of the cortex, the endodermis, is impervious to water because of a band of suberized matrix called the **casparian strip**. Water molecules are unable to penetrate the layer, so they are directed to wall regions that are not suberized, into the cells proper through the membranes. The water then moves through the symplast and again crosses a membrane to reach the cells of the xylem.

The movement of water through the root layers is ultimately **symplastic** in the endodermis. This is the only way water and other solutes can enter the **vascular cylinder**.

Once **inside the xylem**, **water** is again **free** to move between cells as well as through them. In young roots, water enters directly into the xylem vessels and/or tracheids. These are non-living conduits and so are parts of the apoplast.



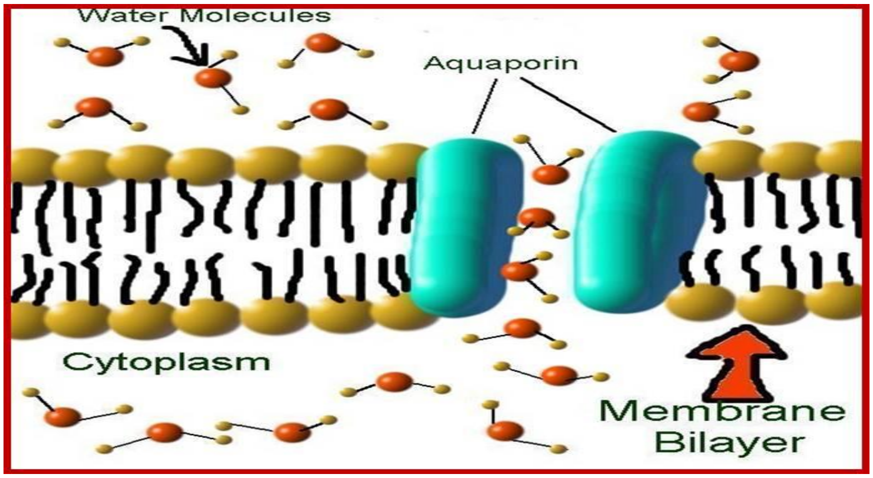


Some plants have additional structures associated with them that help in water (and mineral) absorption. A **mycorrhiza** is a **symbiotic association** of a **fungus** with a root system. The fungal filaments form a network **around** the young root or they **penetrate** the root cells. The hyphae have a **very large surface area** that **absorb** mineral ions and water from the soil from a much larger volume of soil that perhaps a root cannot do.

The **fungus** provides **minerals and water** to the roots, in turn the **roots** provide **sugars** and **N**-containing compounds to the mycorrhizae. Some plants have an **obligate** association with the mycorrhizae. For example, *Pinus* seeds **cannot germinate** and establish **without** the presence of **mycorrhizae**.

With regard to water absorption control in the roots, plants also have membrane water transporter proteins (water-channel proteins), called **aquaporins**.

The **number** of these proteins available for the root surface is variable throughout the day, being **higher during the photoperiod** due to the **higher demands** of **photo-transpiration**. The maintenance of this process - as a result - depends on the output (in the atmosphere) of water vapor present in the intercellular spaces. The water vapor moves from leaf intercellular spaces to the atmosphere predominantly through stomatal diffusion. This process of the loss of water vapor by the leaves is called transpiration and corresponds to the majority (90%) of the volume of water absorbed by plants.



2 Guttation and root pressure

Plants sometimes exhibit a phenomenon referred to as **root pressure**. For example, if the stem of a young seedling is cut off just above the soil, the stump will often exude sap from the cut xylem for many hours. If a manometer is sealed over the stump, positive pressures can be measured. These pressures can be as high as 0.05 to 0.5 MPa. Roots generate positive hydrostatic pressure by absorbing ions from the dilute soil solution and transporting them into the xylem. The buildup of solutes in the xylem sap leads to a increase in the xylem osmotic potential (Ψs) and thus a decrease in the xylem water potential (Ψw). This lowering of the xylem Ψw provides a driving force for water absorption, which in turn leads to a positive hydrostatic pressure in the xylem. In effect, the whole root acts like an osmotic cell; the multicellular root tissue behaves as an osmotic membrane does, building up a positive hydrostatic pressure in the xylem in response to the accumulation of solutes. Root pressure is most likely to occur when soil water potentials are high and transpiration rates are low. When transpiration rates are high, water is taken up so rapidly into the leaves and lost to the atmosphere that a positive pressure never develops in the xylem. Plants that develop root pressure frequently produce liquid droplets on the edges of their leaves, a phenomenon known as **guttation**. Positive xylem pressure auses exudation of xylem sap through specialized pores called hydathodes that are associated with vein endings at the leaf margin. The “dewdrops” that can be seen on the tips of grass leaves in the morning are actually guttation droplets exuded from such specialized pores. Guttation is most noticeable when transpiration is suppressed and the relative humidity is high, such as during the night.

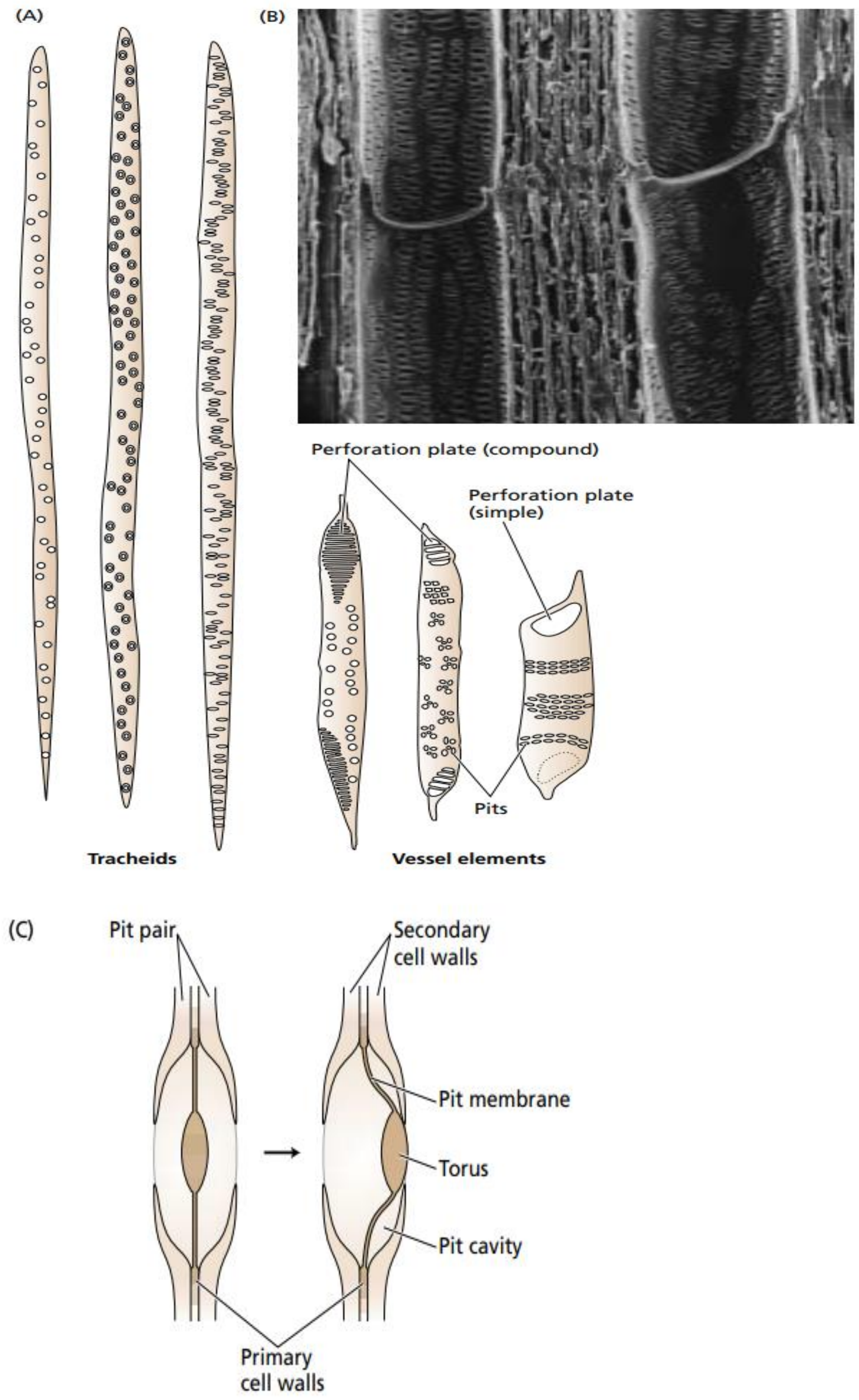
1.1.1 Transport through the xylem

In most plants, the xylem constitutes the longest part of the pathway of water transport. In a plant 1 m tall, more than 99.5% of the water transport pathway through the plant is within the xylem, and in tall trees the xylem represents an even greater fraction of the pathway.

The conducting cells in the xylem have a specialized anatomy that enables them to transport large quantities of water with great efficiency. There are two important types of **tracheary elements** in the xylem: tracheids and vessel elements. Vessel elements are found only in angiosperms, a small group of gymnosperms called the Gnetales (Gnetophytes), and perhaps some ferns. Tracheids are present in both angiosperms and gymnosperms, as well as in ferns and other groups of vascular plants. The maturation of both tracheids and vessel elements involves the “death” of the cell. Thus, functional water-conducting cells have no membranes and no organelles. What remains are the thick, lignified cell walls, which form hollow tubes through which water can flow with relatively little resistance.

Tracheids are elongated, spindle-shaped cells that are arranged in overlapping vertical files. Water flows between tracheids by means of the numerous pits in their lateral walls. Pits are microscopic regions where the secondary wall is absent and the primary wall is thin and porous. Pits of one tracheid are typically located opposite pits of an adjoining tracheid, forming pit pairs. Pit pairs constitute a low-resistance path for water movement between tracheids. The porous layer between pit pairs, consisting of two primary walls and a middle lamella, is called the pit membrane. Pit membranes in tracheids of some species of conifers have a central thickening, called a torus (pl. tori). The torus acts like a valve to close the pit by lodging itself in the circular or oval wall thickenings bordering these pits. Such lodging of the torus is an effective way of preventing dangerous gas bubbles from invading neighboring tracheids.

Vessel elements tend to be shorter and wider than tracheids and have perforated end walls that form a perforation plate at each end of the cell. Like tracheids, vessel elements have pits on their lateral walls. Unlike tracheids, the perforated end walls allow vessel members to be stacked end to end to form a larger conduit called a vessel. Vessels vary in length both within and between species. Maximum vessel lengths range from 10 cm to many meters. Because of their open-end walls, vessels provide a very efficient low resistance pathway for water movement.



In theory, the pressure gradients needed to move water through the xylem could result from the generation of positive pressures at the base of the plant or negative pressures at the top of the plant. We mentioned previously that some roots can develop positive hydrostatic pressure in their xylem—the so-called root pressure. However, root pressure is typically less than 0.1 MPa and disappears when the transpiration rate is high, so it is clearly inadequate to move water up a tall tree.

Instead, the water at the top of a tree develops a large tension (a negative hydrostatic pressure), and this tension pulls water through the xylem. This mechanism, first proposed toward the end of the nineteenth century, is called the **cohesion–tension theory of sap** ascent because it requires the cohesive properties of water to sustain large tensions in the xylem water columns.

Cohesion-tension theory

The presence of plants outside the water environment has been related to the evolution of the **vascular system**, which allows for the ***speedy upward movement of water*** to meet the demand of transpiration from the leaves. The need for a vascular system is more evident when we observe a tree during a hot day, which demands a **large flow of water** (for example, **200 to 400 liters day-1**) to fit a transpiring surface that is situated along elevated positions, and in some species is higher than **100 meters.** The water flows from the roots to the shoot of the plant through the **xylem**. The general mechanism to explain this upward movement of water is the **cohesion-tension hypothesis.**

We know that in an ordinary pipe, like that attached to a well pump, you can only "**pull**" water to a height of **10 m** with a **vacuum**. After that, **gravity** pulls on the water column and it breaks under its own weight.

First off, trees don't have large diameter tubes inside. Instead, they have **tracheid** and **vessel** elements. The diameters of these cells range from **20 µ** to nearly **500 µ**, depending on species. Studies with water in capillary tubes show that ***water in small diameter tubes can withstand tensions of up to 300 bars (or 4500 psi*** (pound per square inch) tension!!).

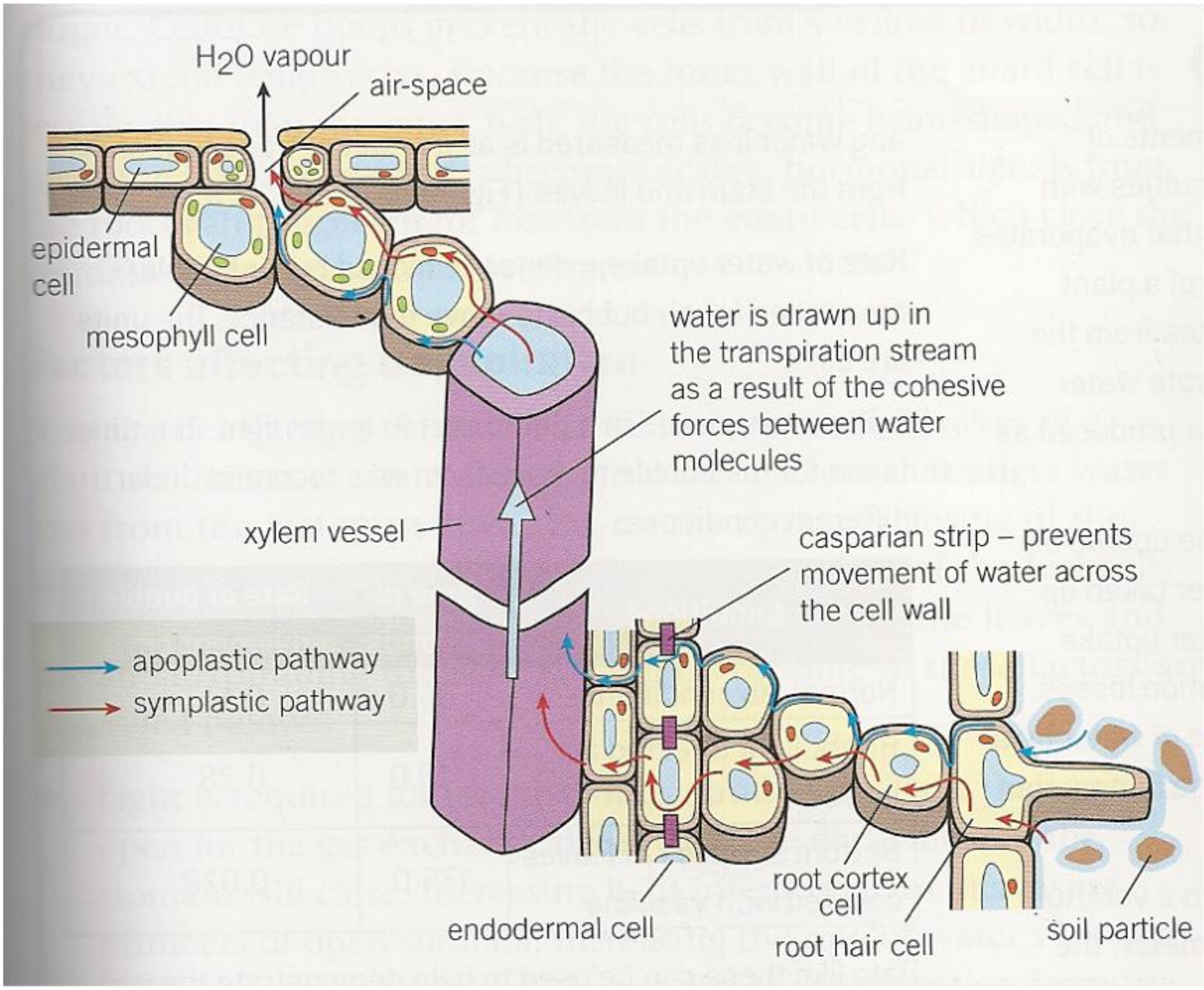
The **cohesion-tension hypothesis** is the most widely-accepted model for movement of water in vascular plants. Cohesion-tension essentially combines the process of **capillary action** with **transpiration**, water from the plant stomata and **cohesion** of water molecules.

1. **Transpiration** (evaporation) occurs because stomata are open to allow gas exchange for photosynthesis. As transpiration occurs, creating negative pressure (**tension or suction**). **The tension** created by transpiration "pulls" water in the plant xylem, drawing the **water upward** in much the same way that you draw water upward when you **suck on a straw.** Tension is simply **negative pressure**. Transpiration is caused by the evaporation of water at the leaf, or atmosphere interface; it creates **negative pressure** (**tension**) equivalent to **–2 MPa** at the leaf surface.

   The tensions needed to pull water through the xylem are the result of evaporation of water from leaves. In the intact plant, water is brought to the leaves via the xylem of the leaf vascular bundle, which branches into a very fine branched that most cells in a typical leaf are within 0.5 mm of a minor vein. From the xylem, water is drawn into the cells of the leaf and along the cell walls. The negative pressure that causes water to move up through the xylem develops at the surface of the cell walls in the leaf. The situation is analogous to that in the soil. The cell wall acts like a very fine capillary wick soaked with water. Water adheres to the cellulose microfibrils and other hydrophilic components of the wall. The mesophyll cells within the leaf are in direct contact with the atmosphere through an extensive system of intercellular air spaces.

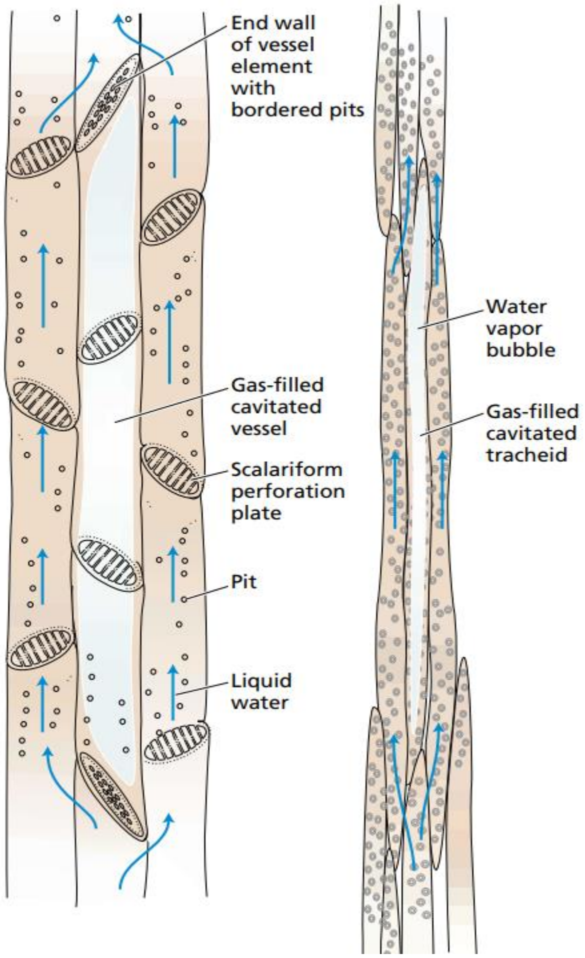
Initially water evaporates from a thin film lining these air spaces. As water is lost to the air, the surface of the remaining water is drawn into the interstices of the cell wall, where it forms curved air–water interfaces. Because of the high surface tension of water, the curvature of these interfaces induces a tension, or negative pressure, in the water. As more water is removed from the wall, the radius of curvature and sometimes intricate network of **veins** throughout the leaf. As more water is removed from the wall, the radius of curvature of the air–water interfaces decreases and the pressure of the water becomes more negative. Thus, the motive force for xylem transport is generated at the air– water interfaces within the leaf. After water has evaporated from the cell surface into the intercellular air space, diffusion is the primary means of any further movement of the water out of the leaf.

2. **Capillarity action of water: due to:**
   a. **Cohesion** (water sticking to each other) causes more water molecules to fill the gap in the xylem as the top-most water is pulled toward the stomata.
   b. **Adhesion** the attraction of water molecules to the vessel and tracheid capillary tubes.



3 Cavitation and Embolisms

Cavitation occurs in xylem of vascular plants when the **tension of water within the xylem becomes so high** that dissolved air within water expands to fill either the vessels or the tracheid. The **blocking of a xylem** vessel or tracheid by an air bubble or cavity is called as **embolism**.



If cavitation or embolism occurs only in a **few xylem vessels or tracheid**, the upward movement of water **may continue** uninterrupted through adjacent un-embolized xylem vessels or tracheid bypassing the un-emboli zed ones. But, **widespread cavitation** or embolism in xylem (as under **severe water stress**) **reduces a plant's capacity to transport water** from soil to leaves. This reduction in xylem's hydraulic conductivity can **impair rate of carbon fixation** by **inducing stomatal closure to prevent further cavitation** and desiccation of leaf tissues.

3.1 Mechanisms of Embolism Formation:

1. **Water Stress-Induced Embolism:**

Under severe water stress, **tension of water in xylem becomes so high** that ***dissolved air within water expands to fill either the vessel or tracheid*** elements and cavitation occurs.

2. **Embolism Formation by Winter Freezing:**

Embolism formation by winter freezing has been observed in many plants such as sugar maple (***Acer saccharum***) and grapevine (***Vitis spp.*). Several studies have shown that when **xylem is frozen** while under tension, extensive **embolism develops after thaw** (melting of ice) as **air bubbles forced out of solution during freezing expand and nucleate cavitation**. Embolisms may also form in frozen vessels by sublimation; is a chemical process where a solid turn into a gas without going through a liquid stage. An example of sublimation is when ice cubes shrink in the freezer.

3. **Pathogen-Induced Embolism:**

It has been known for quite some time that **vascular diseases** caused by pathogens induce water-stress in host by **reducing the hydraulic conductivity** of the xylem and formation of embolism.

3.2 Embolism Repair:

Plants adopt various strategies to avoid long term damage caused by embolism:

1. An effective method of repairing embolism in **herbaceous plants** occurs at **night** when **transpiration is low** or absent and **root pressure is high**. Under such situation, root pressure generates **positive xylem pressure** which reduces tension in xylem water and allows **air to re-dissolve** in the xylem solution. But, how embolism might be reversed in tall trees is not so clear. However, positive xylem pressures have been observed in trees such as sugar maple and woody vines in spring and those plants are known to recover from freezing- induced embolisms in spring.

2. Another effective mechanism to restore hydraulic conductivity in xylem after cavitation is to produce **new xylem** conduits in those plants which possess capacity for **secondary growth**. New xylem vessels and tracheid produced each spring in such plants (shrubs or trees) replace the older activated and non-functional xylem conduits which may fulfill the hydraulic conductivity needs of these plants.