# Ascent of Sap: 3 Theories

The following points highlight the three main theories regarding ascent of sap.

The theories are:

1. Vital-Force Theory

2. Root-Pressure Theory

3. Physical-Force Theory.

**Vital-Force Theory:** These theories state that the vital capacity of the living cells is responsible for the ascent of sap. Living cells like xylem parenchyma and ray cells remain intimately associated with the vessels and tracheid's. Due to this association many workers thought that ascent of sap was brought about in some manner by the living cells of the stem, although direct evidence in favor of this view was lacking.

**A brief account of various vital theories is given as follows:**

## (a) Godlewski's Relay-Pump Theory:

Godlewski (1884) proposed his clambering or relay-pump theory to explain the vertical movement of water through the plant. He thought that a rhythmic change in the water potential of the living cells like xylem parenchyma and medullary rays caused a pumping action to raise water vertically against gravity. With a decrease in water potential of these living cells water diffuses into them from the adjacent bordering vessels which acted as reservoirs of water.

This is followed by an increase in water potential of the living cells and hence the absorbed water is pumped into the vessel element situated above and the process is repeated again and again, thus resembling a kind of staircase movement of water in the xylem. The theory was well accepted at one time.

The theory was soon discredited by Strasburger, when he showed that water translocation continued in plants even after the living cells had been killed by high temperature or poison treatments. Overton (1911) and MacDougal (1929) further confirmed the observation of Strasburger. Metabolic inhibitors like mercuric chloride and picric acid failed to stop the longitudinal flow of water.

Furthermore, the structure of wood does not support this view. The living cells should be in between two vessels or tracheid's for efficient translocation. But actually they remain at the sides of the vessels.

## (b) Bose's Pulsatory Movement Theory:

Sir J.C. Bose (1923) proposed a vital theory for the ascent of sap. He experimentally showed that the living cells of the innermost layer of the cortex were in a state of pulsatory motion, i.e., alternate expansion and contraction. This pulsation, according to him, caused the pumping of water from cell to cell in an upward direction.

Of course, this idea is an elaboration of Godlewski's proposal of water translocation. He experimented with a self-made apparatus consisting of an electric probe, a galvanometer, an electric dry cell, and a thin copper wire. He took a potted plant to which one point, of the galvanometer was connected, the other point of which was connected with a probe as shown in the figure (Fig. 6.1).

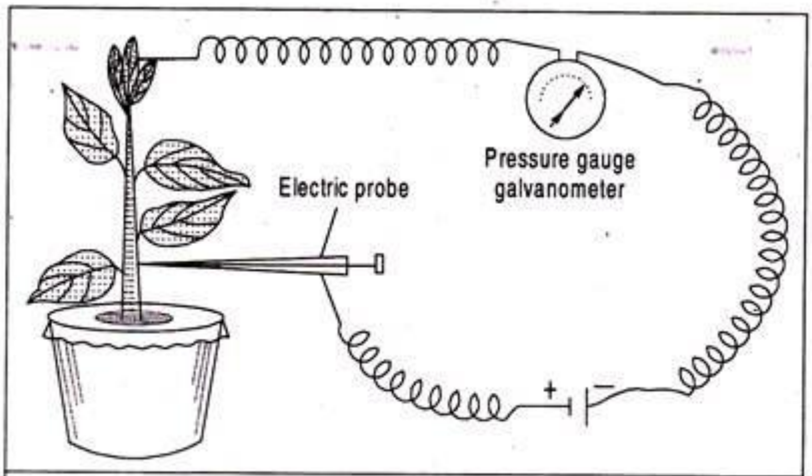


**Fig. 6.1 :** Electric probe apparatus of J.C. Bose

The probe was inserted into the stem slowly. When it reached the innermost layer of the cortex the galvanometer showed momentary deflection for a longer period. No such deflection was observed on either side of this particular layer. From this observation Bose concluded that the cells of this layer were in a state of pulsation.

On expansion the cells absorbed water from the lower cells and on contraction water was pumped into the next higher cells. Bose also observed that for one pulsation (i.e., contraction and expansion) it took 14 seconds to several minutes. This pulsation was called by J.C. Bose as the **'heart-beating of plants'**.

Molisch showed that the movement of pulsation could be greatly increased by administration of heart-stimulating drugs and this supported the view of J.C. Bose. Many workers like Dixon, Shull, MacDougal, etc., have pointed out that there is no relationship between such pulsatory movement and the rate of water translocation.

It has been estimated that the sap must flow through 230 to 400 pulsatory cells per second to account for the normal rate of ascent of sap. But it was already estimated by Bose that for one pulsation it took a minimum of 14 seconds. So, the theory could not explain satisfactorily the mechanism of ascent of sap and thus discarded.

**Root-Pressure Theory:** Due to accumulation of water absorbed by the roots a hydrostatic pressure is developed in the root system, called the root pressure. If the stem of a plant is cut near its base, xylem sap is seen to flow out through the cut end. This phenomenon is known as bleeding or exudation.

If a tube with a mercury manometer is attached to the bleeding stem, it can be seen that water is forced from the roots under considerable pressure. Pressures of 0.5 or 0.6 MPa have been recorded, although in most plants values do not exceed 0.1 MPa. This root pressure is an osmotic phenomenon.

So, the living cells of roots are involved in the phenomenon of ascent of sap. Some workers believe that upward movement of water in woody plants takes place due to this root pressure.

**Although root pressure may help in some plants for the conduction of water to a short distance, still this phenomenon is not considered to be universal mechanism to drive water to a distance of 114 meters in the trunks of tall trees as evidenced by the following findings:**

1. The root pressure magnitude in most plants does not exceed 0.1 MPa while a top to bottom pressure difference of about 2.2 MPa or 22 atm is needed to raise water to the top of tall trees.

2. The phenomenon of root pressure is not observed in most conifers and other gymnosperms, where water has to travel for a long vertical distance.

3. Transpiration rate is much greater than that of exudation.

4. During summer root pressure magnitude has been found to be lower when transpiration rate is very high, whereas during spring it becomes higher when transpiration rate is quite slow.

5. Finally, it has been found that the xylem sap usually remains under a state of tension instead of pressure. So, root pressure is not an important factor for the longitudinal transport of water against gravity.

**Physical-Force Theory:** Physical-force theories suggest that as ascent of sap takes place through the dead xylem vessels, the mechanism is entirely physical and living cells are not involved.

## (a) Boehm's Theory:

Boehm (1809) suggested that the xylem vessels behave like the capillary tubes. He believed that this capillarity of the vessels and the normal atmospheric pressure are responsible for the ascent of sap. The vessel capillaries exert some force which help to raise the water up to certain height of the stem.

The theory was discredited due to the fact that the capillary force can raise water in the stem only up to a certain height. Again, it is evident that narrower the bore of the tube greater will be the rise of water column. So, the tallest trees should have vessels of narrowest bore, but there is no such observation.

Furthermore, the conducting elements in gymnosperms are tracheid's with several porous septa. Capillarity also implies free surface, but the vessel elements are not in direct contact with the soil water.

The water column supported by the atmospheric pressure (1.0 atm) is only about 10.3 m or 34 ft which is called the barometric height. So, the theory could not explain the translocation of water up to a height of 114 metres against gravity.

## (b) Imbibition Theory of Sachs:

Sachs (1878) believed that water is imbibed through the cell wall materials and trans-located upwards. So, the theory states that ascent of sap takes place through the wall, but it is evident that water is trans-located through the lumen of the vessels.

## (c) Cohesion-Tension Theory:

Henry H. Dixon, an Irish botanist, and John Joly, a physicist, in 1894 developed the idea of cohesion-tension mechanism of ascent of sap. The work was published by Dixon in book-form with a great wealth of experimental details in 1914.

The theory states that transpiration pull or tension, cohesion property of water, and hydration of the cell walls (i.e., adhesion) are collectively responsible for the ascent of sap. Water movement through the xylem is a bulk flow caused by $\Delta\Psi_p$ (pressure difference) between one end of the system and the other.

A negative pressure or tension due to transpiration is transmitted through the continuous water column within the xylem to the root. The breaking of the water column (cavitation) is prevented by cohesion between adjacent molecules of water and adhesion between water molecules and cell walls.

The theory has been a controversy for more than a century surrounding a question whether the water column inside the xylem vessel can stand the large tensions (negative pressures) required to raise water to the top of the tall trees. Husken et al. (1978) failed to observe the expected large tensions in the xylem vessels puncturing them with a fine glass capillary connected to a pressure probe.

Many workers, however, after re-examination have shown that the water column inside the xylem vessels can indeed bear large tensions (Holbrook et al., 1995; Pockman et al., 1995).

Most researchers have concluded that the basic theory is sound and the probe measurements were erroneous.

**Therefore, the cohesion theory for the ascent of sap has three basic elements:** The driving force, the cohesion of water, and the hydration of the cell wall.

## i. The Driving Force:

The driving force is the gradient in decreasing water potentials from the soil through the plant to the liquid gas interface at the evaporating surfaces within the leaf. As water evaporates from the leaf mesophyll cells, it causes a decrease (more negative) in water potentials ($\Psi_w$) of those cells in direct contact with the air spaces of the leaf. Due to the negative water potentials of the surface cells, water moves into them from the deeper cells of the leaf.

In an attempt to equate water potential value, the leaf cells ultimately have to draw water from the veins of the leaf, thus subjecting the water in the xylem tissue to a state of tension or negative pressure which is ultimately transmitted to the root system through the unbroken column of water inside the stem. So, a top to bottom pressure difference ($\Delta\Psi_p$) is developed, called the driving force.

The pressure gradient within the actively transpiring trees ranges from 0.01 to 0.05 MPa $m^{-1}$ (0.0987 – 0.493 atm). A normal driving force in trees well supplied with water is 0.015 MPa $m^{-1}$ (0.148 atm $m^{-1}$). Thus, a tree of 100 m height will not require tensions lower than – 1.5 MPa (14.8 atm) to move water up the xylem.

Under conditions of severe water deficit the water potential values of the leaf cells may reach up to – 10 MPa (Milburn, 1979). The volume flow of water through the xylem vessels is proportional to the square of the radius.

**This can be analysed by the Hagen-Poiseuille equation:**

$$J_v = \frac{r^2}{8\eta} \Delta\psi_P$$

where, $J_v$ = volume flow of water ($m^3\ m^{-2}\ s^{-1}$)
η(eta) = the viscosity (Pa s)

$\Delta\Psi_P$ = hydrostatic pressure gradient (Pa)
r = the radius

The equation can be used to estimate the pressure gradient needed to move water at a velocity. This pressure gradient overcomes the viscous drag arising due to the movement of water through an ideal vessel. Xylem vessels have irregular inner wall surfaces and constrictions at the junctions. Tracheid's, with their smaller diameters and perphorated cross walls, create greater resistance to water flow.

Such deviations from an ideal pipe increases the frictional drag. However, in agreement with the equation it has been found that the vines have large open xylem vessels. Ring porous species such as Oak are close to theoretical values.

## ii. The Cohesion of Water:

Water has the property of both cohesion and adhesion. Cohesion means holding together of the like substances, i.e., strong intermolecular attraction due to specific distribution of electrons in the molecules. Water molecules behave as an electrical dipole, although it has no net charge.

For this reason water molecules form a kind of complex electrostatic union through hydrogen bonds. So, water has a high enough tensile strength, defined as the ability to resist a pulling force. By now, enough data has been accumulated to support the cohesion hypothesis.

Several experimental measurements suggest that water has a high enough tensile strength. Two separate steel plates were held together by a thin film of water. The force required to separate the plates was measured. It has been found that the required force is high enough (Fig. 6.2).

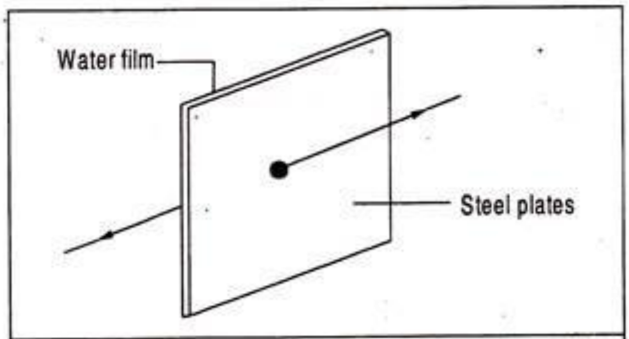


**Fig. 6.2 :** Two steel plates held together by thin water film

In 1914, Dixon measured the cohesive force of water with the help of a J-shaped glass tube of 1 mm diameter filled with xylem sap of Ilex aquifolium. The sap was heated until it almost filled the tube, which was then sealed.

The tube was gently, inclined and the long limb was filled up with the sap. Cavitation did not occur when the tube was cooled and again inverted, due to cohesive and adhesive forces of water molecules (Fig. 6.3).

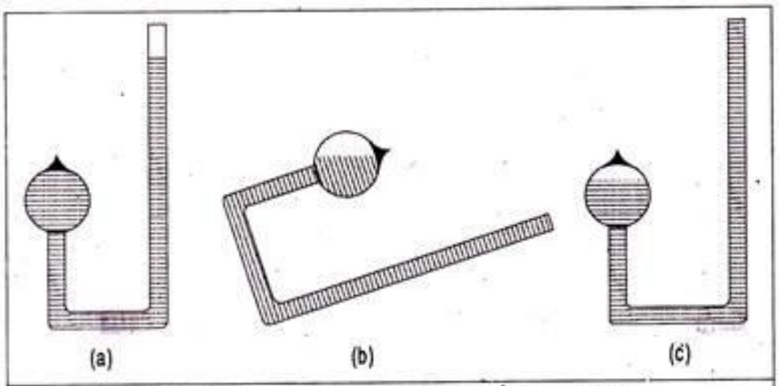


Fig. 6.3 : Demonstration of tensile strength of xylem sap

These and other methods have produced values for the tensile strength of water to the order -10 to -30 MPa. The most clear-cut experimental approach was made by Lyman Briggs in 1950, using capillary Z-tube made of glass with two open ends.

The water filled Z-tube was centrifuged to exert a tension on the water at the center. The tension at the time of water-column breakage can easily be calculated (Fig. 6.4). Of course, it depends on the diameter of the capillary tube. With rather fine capillaries, values as negative as – 26.4 MPa were measured.

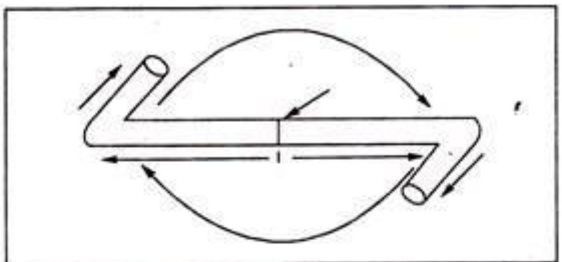

Fig. 6.4 : Method of measuring the cohesive force of water utilizing a Z-centrifuge tube

So. the cohesive force of water seems to be sufficient for the cohesion mechanism of the ascent of sap, provided that the water is held in tubes of small enough diameter. Thus, it is the special anatomy of the xylem tissue that makes the cohesion mechanism to work.

## iii. Hydration of the Cell Wall:

Cell wall polysaccharides have a great affinity for water molecules. Wall surfaces usually have a net negative charge that attracts the slightly positive sides of the polar water molecules and this is called hydration. This wall surface which can bind with water is called a matrix.

The matric potential ($\Psi_m$) is a measure at atmospheric pressure of the tendency for a matrix to adsorb additional water molecules. Water can be held by hydrophilic wall surfaces with tension of the order of -100 MPa to -300 MPa. Gravity, i.e., the weight of water column in the xylem vessel, cannot remove water against such powerful forces.

The large tensions transmit an inward force to the vessel walls. The secondary wall thickenings and lignification of tracheid's and vessels prevent them from collapsing under the influence of such large tension.

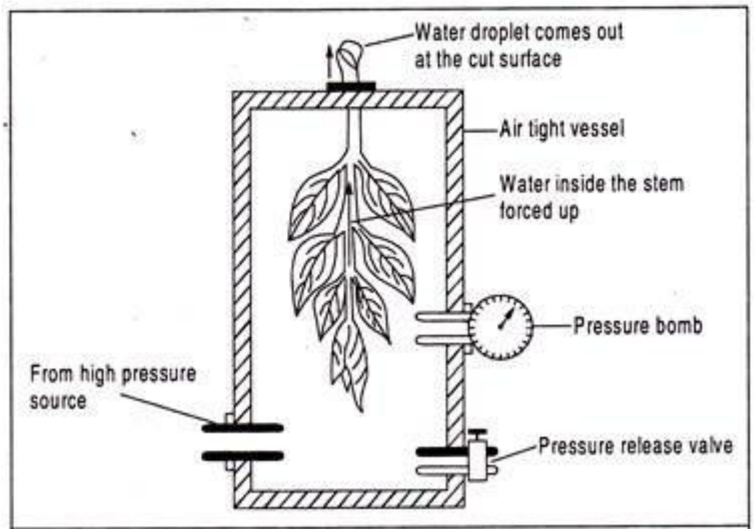


**Fig. 6.5 : Pressure bomb device to measure the tension due to transpiration**

The theory is not applicable to the broken water column. For this reason the cohesion theory has been criticized on the grounds that flow continues when large number of vessels are air-filled and also that deep overlapping incisions do not completely stop water flow. Water under tensions remains in a physically metastable state.

As the tension increases air tends to be pulled through microscopic pores in the vessel walls, a phenomenon called **"air seeding"**. Since gases cannot resist tensile strength the bubble expands, a fact known as cavitation or embolism. It is similar to vapor lock in the fuel line of an automobile or embolism in a blood vessel.
It breaks the water column continuity and stops water transport. However, as only a relatively limited number of vessels is required to meet transpirational demand and as cohesion is effective laterally as well as vertically, liquid continuity can be

maintained around cuts and air-filled vessels (Fig. 6.6). Of course, the resistance is greater for this alternative pathway.

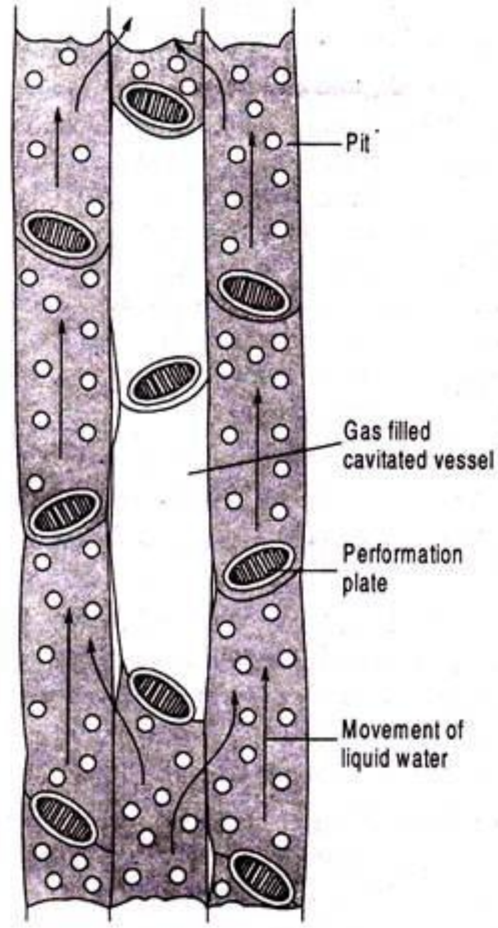


**Fig. 6.6 : Vessels form a series of parallel, interconnecting pathways for water movement. As the vessels are interconnected through pits water can move around the blocked vessels, thus preventing embolisms**

As tension due to transpiration is the driving force for the ascent of sap, the question naturally arises whether the water columns inside the vessels are really under tension. Direct evidence is lacking. In 1965, Scholander et al., were the first to measure the tension indirectly by the pressure-bomb method.

In this technique a freshly cut twig was enclosed in a pressure bomb projecting out the cut end through a pore and the pore was made airtight (Fig. 6.5). The gas pressure on the branch was increased until the water in the xylem could be observed with a hand lens to return to the cut surface.

The pressure in the bomb, equivalent to the value of the tension in the stem was measured. The values differed in different types of plants. Mesophytes have the least negative tensions, whereas xerophytes and halophytes have more negative tensions. Cohesive tensions may also be evidenced in plant stems.

The stem is immersed in a dye solution and then cut at a point. The dye instantly snaps apart up and down the stem inside the xylem vessels and then stops. The cut suddenly releases the tension on the water column for the reason that dye solution is pulled away from the cut ends.

However, all the methods to determine tension are indirect, since in all the cases continuity of the water column is disrupted, thus eliminating any tension that might be present.

**So, from the above discussion it is clear that the cohesion tension theory has got the following essential features:**

1. Water inside the xylem vessels forms a continuous column from top to bottom.

2. Water evaporates-from the mesophyll cell surface (transpiration) due to which driving force or pulling force develops putting the water column inside the plant under tension.

3. The tension may cause a break in the water column but due to the cohesive and adhesive property of water the continuous column does not break.

The theory is criticized due to the fact that the tracheid’s are more suitable than the vessels for the ascent of sap as also Dixon believed. The partition walls of tracheid’s actually give support to hold the Water column against gravity. If it were so, the question arises as to why the present-day dominant flora, the angiosperms, have adopted vessels in place of tracheid’s. There is no adequate explanation for the question.