

Ascent of Sap

Majority of land plants obtain their necessary amount of water from the soil. Some quantities are lost during transpiration and some are utilized in other physiological processes. Hence, water must move from the region of absorption, through the intervening tissue to the tissues in which they are utilized or to other organs from which water passes out. This phenomenon of the *movement of water against the force of gravity* is called **conduction** or **translocation of water**.

The water which moves through the plant organ is not in a pure form, but it contains considerable amount of dissolved inorganic matters. The whole liquid content of water and minerals is known as *xylem sap*. So, whenever water moves through the plant it carries with it certain amount of solute matters. It is, therefore, better to define conduction of water, as **ascent of sap**.

Entry of water mainly takes place through the epidermal cells and root hairs which after passing the cortex, endodermis etc finally reaches the xylem vessels or tracheids of the root.

► **6.1 Path of Water Conduction** : It has been known for a long time that the xylem or wood is the water conducting path in the land plants and the xylem consists mainly of dead lignified tracheae or vessels and tracheids, which act as water pipes. Tracheids are elongated single cells which became thick walled in course of their development and then died. Vessels are more efficient conducting channels run from the roots through the stem and upto the veins of the leaves.

In small herbs, this conducting path is not considerable, whereas in large trees the path of water translocation may involve several hundreds of centimetres. From physiological and structural point of view, the course of water conduction in land plants consists of two parts. The xylem vessels comprise the important main part which is concerned in the dead cells of the xylem, the second part of water movement system consists of living cells hairs to cortical parenchyma are concerned ; the movement being due to suction tension by cell to cell osmosis.

That the wood vessels are the main path through which water moves can be shown by clogging the vessels of an *Impatiens* (Balsam) twig by dipping it in molten gelatin jelly and then putting it in water, the plant is found wilting. Secondly, by ringing the cortex of the woody plant, it is proved that plants do not wilt so long as the vessels are kept intact. This proves definitely that the xylem vessels are the path of ascent of water and dissolved mineral substances.

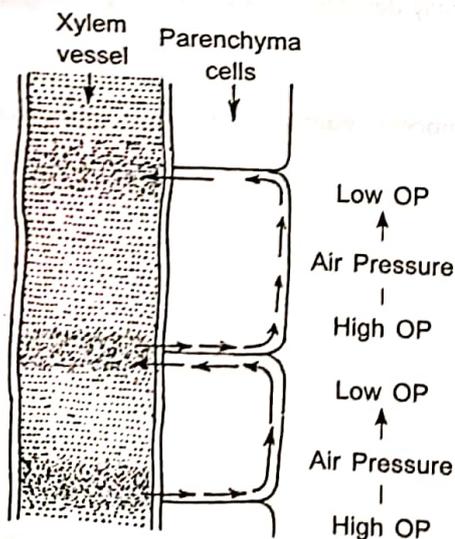


Fig 6.1 : Godlewski's concept of ascent of sap.

► **6.2 Theories of Ascent of Sap** : The mechanism by which sap moves to the top of a lofty tree is a puzzle to the physiologists and which is still not satisfactorily solved. Stephen Hales (1769) was the first person to realize that there was a relationship between the transpiration of a plant and the upward movement of sap in the wood. Later workers observed that when the intact stem of a transpiring plant was cut beneath the surface of a dye solution, the dye rushed in, going both up and down the stem in the xylem. The upward movement of indicator substances such as spectroscopically detectable salts, dyes and radioactive isotopes can usually be related to the rate of transpiration. Several theories have been put forwarded by different scientists to explain the phenomenon of ascent of sap. All these theories fall within three main categories : (i) vital theories, (ii) root pressure theory and (iii) physical force theories.

(i) **VITAL FORCE THEORIES** : Adherents of these theories believe that vessels through which translocation takes place are non-living and are in contact with living cells. For this reason,

proponents of these theories suggested that upward translocation of water and other substances takes place by the vital activities of the living cells.

The main advocates of these theories are Godlewski (1884) and Bose (1923). Godlewski proposed the **relay-pump theory**. According to his theory the movements of sap through the xylem are due to rhythmic changes in the osmotic pressure of the cells of the wood parenchyma and medullary ray cells. Due to increase and decrease in the osmotic pressure in these cells, water is driven out and is pumped into the vessels against gravity.

According to Godlewski, water moves up in the stem in a stair-case path under the influence of two forces i.e., air pressure and the osmotic pressure of medullary ray cells. The parenchyma cells absorb water from the xylem vessels by osmosis and the water moves up through the parenchyma cells by air pressure (Fig. 6.1). During the translocation of water osmotic pressure falls, so that the xylem pumped in the same water at a higher level and the process is repeated again and again.

Later, in 1923, Sir JC Bose proposed the **pulsatory movement theory** to explain the movement of water in plants. Bose's idea is really an elaboration of Godlewski's proposal of water movement. According to this theory, ascent of sap is due to pulsatory movements of these cells. When the cells contract, the sap is pumped up to the next higher cell which consequently expands. This expanded cell in turn contracts again, thus pushing or pumping up the sap in the next higher cell. Thus the sap moves from one cell to another and so on.

Sir JC Bose invented an electrical probe by which the activity of cell inside the plant body can be detected. He inserted a fine electric probe into the stem of *Desmodium* and connected it to a galvanometer and an electric circuit (Fig. 6.2). He inserted the needle of electric probe upto certain distance in the stem and found a maximum pulsating movement in the innermost cells of cortex. So, he came to the conclusion that cells associated with xylem show pumping action and pump its sap into the xylem cells.

By administering some heart-stimulating drugs Molisch (1928; '29) observed the increased movement of pulsation and thus supporting the view of Sir JC Bose.

The work of Strasburger (1893), however, shows that the upward movement of water is quite independent of the living cells of the stem, as the sap continues to flow even when all the living tissues have been killed by picric acid. Later on, it has been observed by other workers that the leaves of the treated plant whose living tissues have been killed previously, gradually wilt and wither. The main cause of this gradual wilt is that the killing of the stem causes the formation of substances which gradually plug the mouth of the xylem vessels. Further, the death of the cells causes the secretion of certain poisonous substances, which, when translocated to the leaves, cause their wilt. Although this theory apparently does not support the basic principle of the vital theories but the explanation of Strasburger's experiment indirectly supports that living cells of the stem have got an effect on the ascent of sap.

(ii) **ROOT PRESSURE THEORY** : It has been found that exudation of sap takes place from the freshly cut trunk of stem. This exudation is due to the pressure in the xylem sap as a result of root pressure. Stocking (1956) considered root pressure as an active process and defined as a pressure *developing in the tracheary elements of the xylem as a result of metabolic activities of the root*. The idea of the movement of water in woody plants is based on this phenomenon. Although root pressure helps in some plants for the conduction of water to a little distance, still this phenomenon is not considered to be the principal mechanism for the movement of water, because this phenomenon of root pressure is not observed in most conifers and other gymnosperms which are among the

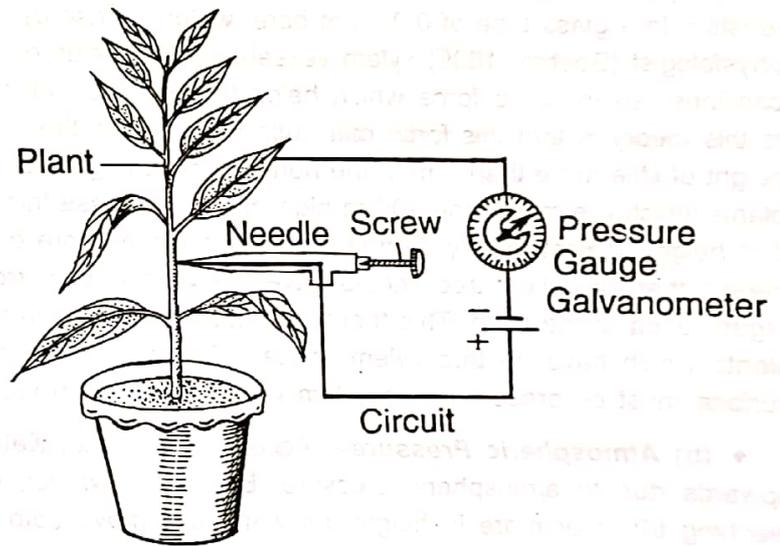


Fig 6.2 : Electric probe apparatus of Sir JC Bose.

tallest of trees. Secondly, the pressure which is set up is not sufficient to conduct water to the top of large trees. Values higher than 6 atmosphere have been found to be necessary for upward conduction of water, whereas root pressure more than 2 atmosphere is seldom obtained (Kramer, 1969). Therefore, root pressure could account for the ascent of sap only upto the height of about 20 m (one atmosphere is capable of causing a flow upto a height of about 10 m). This is far short of the height to which water is delivered to tall trees. Again in summer, while rapid transpiration is going on, exudation of sap even stops. Root pressure is commonly observed during favourable periods of growth when the transpiration rate is low, whereas when the transpiration rate is high root pressure is absent. Further, the amount of water exuded by the root pressure is very low. It is only about 5% of the total water lost during excessive transpiration. Finally, the xylem sap, under normal condition, is in a state of tension instead of pressure, suggesting that root pressure is not an important factor in water translocation. A good example of this, is guttation, a phenomenon caused by root pressure but noticeable only under low transpiration condition. For these reasons, root pressure can not be held responsible for the rise of sap in large trees.

[Regarding the modern concept on root pressure in the translocation process refer article 6.3].

(iii) **PHYSICAL FORCE THEORIES** : These theories clearly suggest that physical phenomena and not the living nature of the cell are wholly responsible for the ascent of sap in plants. The following are the physical theories which are responsible for the ascent of sap :

★ (a) **Capillary Force**—Water can rise to an appreciable height in fine capillary tubes because of high surface tension. In a glass tube of 0.01 mm bore, water will rise by capillarity to a height of about 3 m. According to some physiologist (Boehm, 1809) xylem vessels and tracheids occur in the plant in the form of small capillaries. These capillaries exert some force which helps to raise the water upto certain height of the stem. The main objection to this theory is that this force can raise the water in the stem only upto certain height. Water can only rise to a height of little more than 1 m in the normally occurring vessels having diameter of about 0.03 mm. There are many plants which are more than 100 m high. So, in that case this theory can not explain the translocation of water upto that height against gravity. Further, the narrower the bore of the tube, greater will be rise in the water column. It means that the tallest tree should have the vessels of narrowest bore, which does not tally with the anatomical organization of the stem. This theory cannot further explain the phenomenon occurring in the tall gymnospermous plants which have no true xylem vessels. The soil water is not directly connected with the vessels and a free surface must be present in the xylem vessel to maintain capillarity.

★ (b) **Atmospheric Pressure**— According to some, water together with mineral salts is found to be moving upwards due to atmospheric pressure. But this, however, can not explain the movement of sap in tall trees, reaching 60 m or more in height, as water can move upto a maximum height of only 9 m due to atmospheric pressure. Further, the operation of atmospheric pressure requires a free exposed surface which does not exist in the xylem vessels.

★ (c) **The Cohesion-Tension Theory**—A close relationship between transpiration and the rate of movement of water in stems suggests that evaporation is involved somehow in the mechanism of water transport. During transpiration, water is lost from the leaves by evaporation through the micro-capillaries of the walls of the leaf parenchyma cells. This loss of moisture leads to the movement of water from the protoplasm and vacuole to the cell wall. This movement results in an increase in the osmotic concentration of the leaf parenchyma cells, which will in turn osmotically attract water from adjoining cells of lower osmotic pressure. In this manner an osmotic gradient is built up across the leaf to the contents of the xylem elements of the leaf. The deficit of water in the terminal cell in this gradient will be satisfied by the withdrawal of water from the xylem elements.

Molecules of water, although in motion, are also strongly attracted to each other. This cohesive force, together with the attraction which exists between the water molecules and the molecules of the wall of the tube (adhesive force), prevent the water columns from breaking when they are subjected to a pull. Thus, as a consequence of the pull resulting from the loss of water from the leaves during transpiration, the water in the xylem ducts is drawn up the stem under a tension or negative pressure.

To sum up, the essential features of this theory are as follows :

(i) *Continuous water column* : Water column is continuous from the transpiring leaf cells to the walls of absorbing root cells via the xylem conducting system. MacDougal (1936) has named it as *hydrostatic system*.

(ii) *Withdrawal of Water* : The evaporation of water from the mesophyll cells increases the diffusion-pressure deficit (DPD) or decreases the water potential of mesophyll cells causing withdrawal of water from the deeper or water free spaces (Weatherley, 1963).

(iii) *Development of Tension or Transpiration Pull* : Due to continuous withdrawal of water from the xylem, the whole water column of the plants comes under a tension or strain. As this tension is developed due to transpiration, it is known as **transpiration pull**.

(iv) *Cohesion or Tensile Strength of Water* : The transpiration pull this developed is unable to break the continuity of hydrostatic system as water molecules are attached with a strong **Cohesive force**. Due to this force water molecules cling together through their hydrogen bonding. This force is also called **tensile strength**.

(v) *Ascent of Sap* : On account of the tension created by transpiration the water column through the xylem is pulled up passively from below to the top of the plant. It is able to overcome both gravitational and frictional forces.

Although this theory was first postulated by Dixon and Joly (1894) but it was later on supported by Renner (1911; '15), Curties and Clark (1951), Kramer and Kozlowski (1960), Milburn and Johnson (1966) and Levitt (1969). This theory has variously been termed as **Cohesion hypothesis, Transpiration pull theory, Cohesion-tension theory**.

● **Evidences in Support of the theory** : The following facts support the cohesion tension and transpiration pull theory :

✦ (a) The osmotic pressure of mesophyll cells has been recorded upto 20 atm which is quite sufficient for ascent of sap.

✦ (b) It is a physical process which does not require any metabolic energy, even it requires, it is very negligible.

✦ (c) The rate of water absorption and hence ascent of sap increase or decrease with rise and fall in the rate of transpiration.

✦ (d) Huber and Schmidt (1936) used thermo-electric method to demonstrate that the sap is pulled upwards in the tree. According to this method, the contents of a xylem sap stream were moderately heated in one localised place and the upward movement of the heated sap was determined by means of a thermocouple placed at some distance upward from the point of application of the heat. This clearly proves that the driving force must be located in the leaves at the top of the tree. This accord with the cohesion-tension theory.

✦ (e) If a porous pot is placed at the top of a continuous water column and its water is subjected to evaporation, the water column is put under tension. The column is not broken due to cohesive property of water so long evaporation continues. Similar kind of mechanism may operate in plant to raise the water to the top of a tree (Fig. 6.3).

✦ (f) Further Zimmermann (1965) explained that a pressure of 0.15 atm per meter is required for the transport of water in plants. It means that a water potential difference of 45 atm is sufficient to raise water in any tall plant. The cohesive property or tensile strength of water is very high (according to some it is about 1000 atm ; according

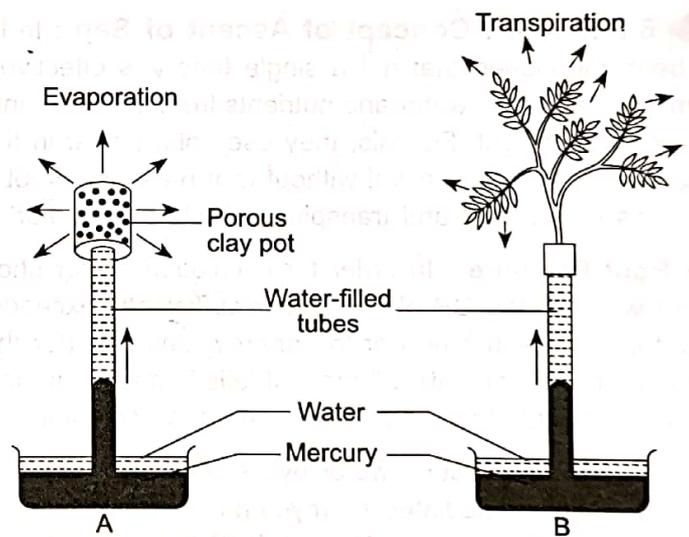


Fig 6.3 : A. Physical system for the demonstration of the cohesion-tension theory. B. Demonstration of the cohesion tension theory of ascent of sap. In A, evaporation and in B, transpiration of the leafy twig provides the tension necessary to pull up the column of mercury.

to others it is about 25-300 atm) and about 1300 atm is required to break this column. So, the force which exists in plant is sufficient to maintain the continuity of water column.

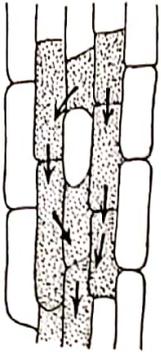


Fig 6.4 : Milburn and Johnson's explanation to show the continuity of water as maintained by the side tracks.

✦ (g) MacDougal (1936) by using dendrographic measurement observed a decrease of trunk diameter during excessive transpiration due to strain on water column by tension. This further supports the theory.

● **Objection to Cohesion-Tension Theory** : Due to variation of temperature during day and night, there is a fair chances of gas bubbles being entered in water column, which may break the continuity of water column. But this objection has been clearly explained by Milburn and Johnson (1966). They observed that since there are several rows of continuous water channels run together, the water continuity is maintained by the side tracks (Fig. 6.4). When, however, tension is relieved (by rain or simply at night) the gases are dissolved in solution and the column become continuous.

Further, it has been demonstrated in the root pressure theory that water can exude from the cut stem without any leafy shoot and it completely devaluates this theory, as there is no transpiration occurring here. In spite of several weaknesses this theory still remains the most reasonable single explanation for the rise of liquid in plant body.

Considering all the foregoing theories regarding the ascent of sap in plants, it is evident, that not a single theory can explain fully the mechanism of water translocation. But an amalgamated effect of all these theories will be helpful in elucidating the process of water translocation in plants. The root pressure gives a pressure from below and the active transpiration pulls the water column through the xylem vessels which are in a cohesion tension, thus favouring the easy flow of liquids through the stem to the top of a lofty tree.

▶ **6.3 Modern Concept of Ascent of Sap** : In the concluding part of the mechanism of ascent of sap, it has been mentioned that not a single theory is effective in explaining the massive upward flow of water through xylem. Plants absorb water and nutrients from environment under various conditions and circulate it through the body, often to large height. For this, they use solar power-in the form of transpiration. But transpiration alone would not guarantee for plant's survival without root pressure. Root pressure achieves a reverse osmosis in the root tips and serves as the "starter and transpiration acts as a motor" mechanism which help in circulating it through the plant.

● **Root Pressure** : In order for circulation, water should evaporate from leaves, so that it can replenished by ground water, if the OP of the leaves sufficiently exceeds that of the ground. But it cannot be realised by a plant without enough sunshine (for the energy) and rain (for the water) as well as low enough osmolarity of the ground (for the osmotic gradient). Whereas it fails in darkness, desert ocean and during droughts. For these reasons, plants have invented additional back ups in their transpiration system, among them most important is the "root pressure".

Plants avail the ground water by establishing osmotic gradient in the cortex layer of their root tips. Sometimes, supply of water is mediated by mycorrhizae which functions as the merchants of the soil (Read, 1997). According to Kramer and Kozlowski (1979) all land living plants are capable of building up root pressure. Root tips acquire their ground water and supply it in the stem at low osmolarity in order to give their leaves a chance to pull it up osmotically again, a reverse osmosis must take place in the root which is physically impossible without an actively powered engine. Root pressure relies on the presence of pumps.

Since work is done, a 'molecular motors' system may be accounted (Block, 1997 ; Howard, 1997) which may be effective only with the help of a piston. In the internal morphology of a root (Fig. 6.5) we could not find anything like piston other than the wall across which the water potential jumps uphill.

Strasburger et al (1971) consider it as "endodermal jump"—a jump of osmotic concentration across the outer endodermal wall, which serve as an osmotic barrier i.e., to be the site of the reverse osmosis. Once water has crossed the outer periclinal endodermis wall, it has only to cross the single-cell layer pericycle in order to reach the 'dead' xylem vessels whose sap is known to be of low osmolarity, at least by the time when it reaches the stem.

The recent explanation of exudation phenomenon (Kundt. and Robnik, 1998) where a *mechanical pump* system exists in the innermost cortex layer across the osmotic barrier in the outer endodermal wall. A simple such device is a movable (outer endodermal) wall, like a piston of a bicycle pump which is equipped with sluices or "filter valves". The piston would transfer the high pressure on the cortex side to the central cylinder when its valves are closed, but would snap back and allow the sap to pass, at reduced osmolarity, during the second half of a pumping cycle when its valves are open. Now, there is a lot of independent evidences for the proposed working scheme.

First, the endodermal cells are unique in the presence of Casparian strips which guarantee rigidity of the cells during the reduced pressure phase of a pumping cycle. *Second*, Schreiber et al (1994) showed the presence of folded structure with sub- μm grooves in the outer (periclinal) endodermal layer, which gives it a certain flexibility so that it can periodically bulge out (slightly), as it required for a piston. *Third*, the periclinal wall carries a large number of pits traversed by large number of plasmodesmata, the required filter-valves. These plasmodesmata have outlets ("orificers") which are very thin, as is required for valves and are surrounded by "neck constrictions" which can serve as "sphincters". The outlets are traversed by the endoplasmic reticulum (ER) which latter appear to play an active role in enforcing the right flow direction through the outlet up locally against the water potential gradient.

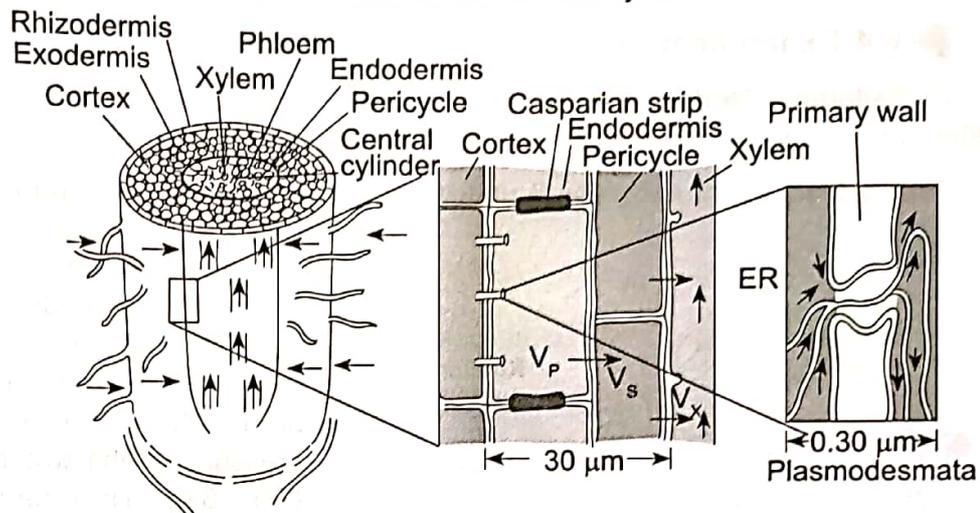


Fig 6.5 : Sketch of the proposed mechanical pump in the ring of endodermis cells of a primary root in the root-hair zone. Water is osmotically attracted through the cortex and is forced through plasmodesmata pit fields in the outer endodermis wall which serves as filter valves. Casparian strips rigidity the endodermis cells except for their outer periclinal wall which is flexible and serves as a piston which compresses the diluted sap on the side of the central cylinder (xylem). Essential for the functioning of the pumps is the ER which control the local water potential and the sphincter which closes the valves periodically.

So, the endodermal ring serves as mechanical pumps, transferring the high cortex pressure across to the central cylinder without much degradation. The presence of plasmodesmata found in a single (periclinal) cell wall narrow the ring-shaped outlets to the width of individual water molecules i.e. to achieve a selectively higher transmissivity for pure water than all the solutes in the sap. In this way, valves allow dilution to take place at the expense of thermal energy. It is, therefore, consider to be a heat engine which achieves the reverse osmosis by cooling the sap which, however, could violet the second law of thermodynamics, if it converted thermal energy to osmotic energy. Therefore, an active device is necessary which guarantees the flow of the sap up the water potential gradient, through the outlets of the plasmodesmata. Such an active device is definitely encountered by ATP of the sphincters surrounding the neck of a plasmodesma and its traversing ER.

Thus from the above discussion it is evident how root pressure is likely to be built up in a plant. Now to determine the *frequency* at which the endodermal pumps operate, let us calculate it from

$$P = 2A\Delta H/v$$

$$(\text{Pumping period}) = 1s (\Delta H/1.5 \mu\text{m})$$

Which is found to be similar to that of the *human heart* for a piston amplitude ΔH of $1.5 \mu\text{m}$ and a symplastic flow velocity (v) through the cortex of $3 \mu\text{m/s}$.

Regarding the number of such pumps (N) for a large tree having an area $A^{3.5}\mu\text{m}^2$ and a mass flow rate M (of the sap) in units of a ton/day

$$N = M/\rho Av = 10^9 (M/\text{td}^{-1})$$

So, in a large tree, a billion mono-cellular pumps have to act jointly to set up its root pressure. For a small plant, place their mass-flow rate in units of ton/day and get a correspondingly smaller N. In case of halophytes (with a problem of getting water) two rings (endodermis and exodermis) both possess Casparian strips, therefore have two similar sets of pumps working in series.

► 6.4 Experiments on Conduction of Water :

(i) **Palladin's Method to show Conduction of Water**—Both the ascent of liquids through the stem and the effect of transpiration on the rise of liquids can be studied in this experiment.

Take a leafy shoot and keep it under water. Remove all leaves from one of the side branches and cut it partly

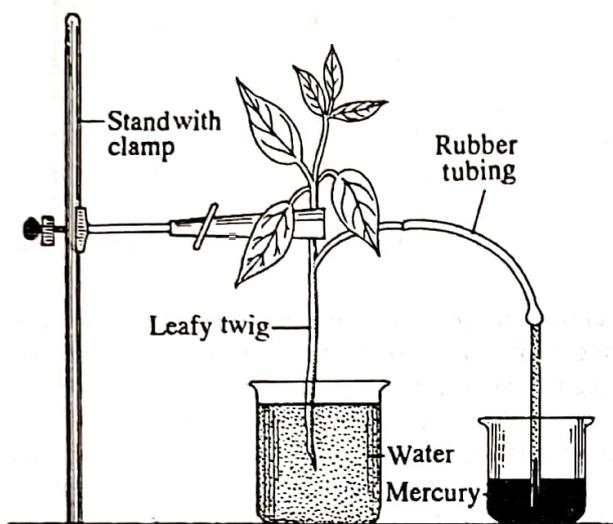


Fig 6.6 : Demonstrating the movement of water in a woody twig.

with a knife and attach a short piece of rubber tubing. Connect the other side of this tubing with a narrow glass tube (about 0.4 mm internal diameter). Then fill the glass tube with water and immerse it in a beaker containing mercury or boiling water containing a dye so that it can be easily seen (boiling removes all dissolved air that could form bubbles and exert a negative pressure on the water content). Make all connections air tight (Fig. 6.6). Now the water is continuous throughout the whole system extending from the mesophyll cells in the leaf, down through the xylem vessels of the stem into the rubber tubing and glass tube ending in the beaker at the base. After a few hours, mercury or water will be found to rise the narrow glass tube (exhibited by their colour if the water is coloured).

Under these conditions as water molecules are lost by transpiration from the upper surface of a leaf, the attraction of water molecules (cohesion) exerted as a pull causing mercury or coloured water to move up into the stem.

(ii) Experiment to Show the Path of Water Conduction :

✦ (a) Immerse a *Peperomia* plant in a beaker containing 2% solution of eosin. Keep it for some time and it should be observed that the red colour appears to be coming up through the stem which indicates that the red colour after being absorbed by roots has ascended to the stem.

Now, cut transverse section of the stem and observe under a microscope. The red colour appears to be present only in the xylem vessels which shows distinctly that ascent of sap takes place through the xylem vessels.

✦ (b) Ringing Experiment—Take a potted plant and remove all the peripheral tissues (upto phloem and cambium) of the stem in the form of a ring, leaving only the xylem intact. Keep the plant as it is after removing the tissues for 2-3 days. It should be observed that no wilting of the plant body takes place during the period which proves that the movement of water and liquids takes place through the xylem vessels and not through the outer peripheral tissues of the stem.

✦ (c) Take a leafy twig of *Vinca* and immerse the cut end in a strong solution of CuSO_4 for a considerable period. As a result of this treatment, all the living cells of the treated region have been killed. If now, such a twig is placed in a beaker containing coloured water, no wilting of the leaves will take place normally and since all the living cells have been dead it proves definitely that the living cells have got nothing to do with the movement of water in plants.