

4

ABSORPTION OF WATER

Q. Explain the mechanism of water absorption in higher plants. What are the various external factors that affect absorption of water?

MECHANISM OF ABSORPTION OF WATER

In higher plants water is absorbed through root hairs which are in contact with soil water and form a root hair zone a little behind the root tips (Fig. 4.1). Root hairs are tubular hair like prolongations of the cells of the epidermal layer (when epidermis bears root hairs it is also known as piliferous layer) of the roots. The walls of root hairs are permeable and consist of pectic substances and cellulose which are strongly hydrophilic (water loving) in nature. Root hairs contain vacuoles filled with cell sap.

When roots elongate, the older hairs die and new root hairs are developed so that they are in contact with fresh supplies of water in the soil.

Mechanism of water absorption is of two types:

(1) Active Absorption of Water. In this process the root cells play active role in the absorption of water and metabolic energy released through respiration is consumed. Active absorption may be of two kinds:

(a) Osmotic absorption i.e., when water is absorbed from the soil into the xylem of the roots according to the osmotic gradient.

(b) Non-osmotic absorption i.e., when water is absorbed against the osmotic gradient.

(2) Passive Absorption of Water. It is mainly due to transpiration, the root cells do not play active role and remain passive.

(1a) ACTIVE OSMOTIC ABSORPTION OF WATER

First step in the osmotic absorption of water is the imbibition of soil water by the hydrophilic cell walls of root hairs.

Osmotic Pressure (O.P.) of the cell-sap of root hairs is usually higher than the O.P. of the soil water. Therefore, the Diffusion Pressure Deficit (D.P.D.) and the suction pressure

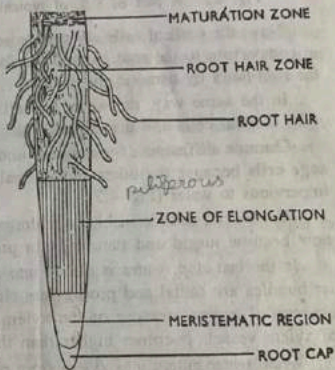


Fig. 4.1. Diagrammatic representation of root tip showing root hair zone.

the root hairs become higher and water from the cell walls enters into them through plasma-membrane (semi-permeable) by osmotic diffusion. As a result, the O.P., suction pressure and D.P.D. of root hairs now become lower, while their turgor pressure is increased.

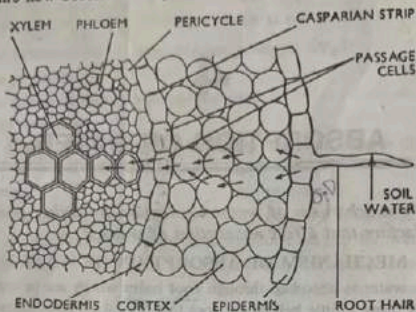


Fig. 4.2. A part of T.S. of typical dicot root. The arrows indicate the path of water.

Now, the cortical cells adjacent to root hairs have higher O.P., suction pressure and D.P.D. in comparison to the root hairs. Therefore, water is drawn into the adjacent cortical cells from the root-hairs by osmotic diffusion.

In the same way, the water by cell to cell osmotic diffusion gradually reaches the innermost cortical cells and the endodermis.

Osmotic diffusion of water into endodermis takes place through special thin walled passage cells because the other endodermal cells have casparian strips on their walls which are impervious to water (Fig. 4.2).

Water from endodermal cells is drawn into the cells of pericycle by osmotic diffusion which now become turgid and their suction pressure is decreased.

In the last step, water is drawn into xylem from turgid pericycle cells. (In roots the vascular bundles are radial and protoxylem elements are in contact with pericycle). It is because in absence of turgor pressure of the xylem vessels (which are non-elastic), the suction pressure of xylem vessels becomes higher than the suction pressure of the cells of the pericycle.

When water enters into xylem from pericycle, a pressure is developed in the xylem of roots which can raise the water to a certain height in the xylem. This pressure is called as root pressure.

(1b) ACTIVE NON-OSMOTIC ABSORPTION OF WATER

Sometimes, it has been observed that absorption of water takes place even when the O.P. of the soil water is higher than the O.P. of cell-sap. This type of absorption which is non-osmotic and against the osmotic gradient requires the expenditure of metabolic energy probably through respiration. Following evidences support this view :

- (i) the factors which inhibit respiration also decrease water absorption.
- (ii) poisons which retard metabolic activities of the root cells also retard water absorption.
- (iii) auxins (growth hormones) which increases metabolic activities of the cells stimulate absorption of water.

(2) PASSIVE ABSORPTION OF WATER

Passive absorption of water takes place when rate of transpiration is usually high. Rapid evaporation of water from the leaves during transpiration creates a tension in water in the xylem of the leaves. (For details see Chapter 6). This tension is transmitted to water in xylem of roots through the xylem of stem and the water rises upward to reach the transpiring surfaces. As a result, soil water enters into the cortical cells through root hairs to reach the xylem of roots to maintain the supply of water. The force for this entry of water is created in leaves due to rapid transpiration and hence, the root cells remain passive during this process.

During absorption of water by roots, the flow of water from epidermis to endodermis may take place through three different pathways, (i) apoplastic pathway (cell walls and intercellular spaces), (ii) transmembrane pathway (by crossing the plasma membranes) and (iii) symplast pathway (through plasmodesmata).

The mechanism of water absorption described earlier, infact belongs to the second category.

The relative importance of these three pathways in water absorption by roots is not clearly established. However, a combination of these three pathways is responsible for transport of water across the root.

EXTERNAL FACTORS AFFECTING ABSORPTION OF WATER

1. Available Soil Water

Sufficient amount of water should be present in the soil in such form which can easily be absorbed by the plants. Usually the plants absorb capillary water i.e., water present in films between soil particles. Other forms of water in the soil e.g., hygroscopic water, combined-water, gravitational water etc. are not easily available to plants.

Increased amount of water in the soil beyond a certain limit results in poor aeration of the soil which retards metabolic activities of root cells like respiration and hence, the rate of water absorption is also retarded.

2. Concentration of the Soil Solution

Increased conc. of soil solution (due to the presence of more salts in the soil) results in higher osmotic pressure. If the O.P. of soil solution will become higher than the O.P. of cell sap in root cells, the water absorption particularly the osmotic absorption of water will be greatly suppressed. Therefore, absorption of water is poor in alkaline soils and marshes.

3. Soil Air

Absorption of water is retarded in poorly aerated soils because in such soils deficiency of O_2 and consequently the accumulation of CO_2 will retard the metabolic activities of the roots like respiration. This also inhibits rapid growth and elongation of the roots so that they are deprived of the fresh supply of water in the soil.

Water logged soils are poorly aerated and hence, are physiologically dry. They are not good for absorption of water.

4. Soil Temperature

Increase in soil temperature up to about $30^\circ C$ favours water absorption. At higher temperatures water absorption is decreased. At low temp. also water absorption decreases so much that at about $0^\circ C$ it is almost checked. This is probably because at low temp :

- (i) the viscosity of water and protoplasm is increased,
- (ii) permeability of cell membranes is decreased,
- (iii) metabolic activities of root cells are decreased, and
- (iv) growth and elongation of roots are checked.

ASCENT OF SAP

Q. Write an essay on ascent of sap.

upward movement of water → Ascent of Sap

ASCENT OF SAP

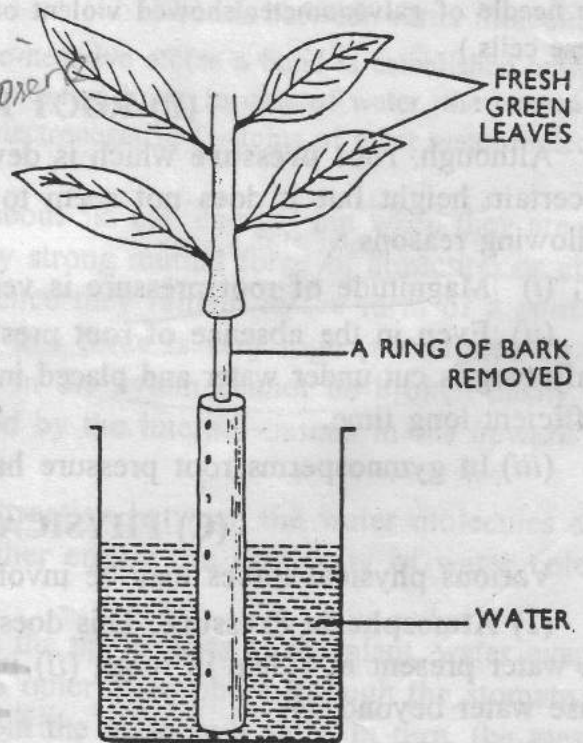
The water after being absorbed by the roots is distributed to all parts of the plant (excess of which is lost through transpiration). In order to reach the topmost parts of the plant, the water has to move upward through the stem. This **upward movement** of water is called as **Ascent of Sap**.

Ascent of sap can be studied under the following two heads : (A) Path of Ascent of Sap, and (B) Mechanism of Ascent of Sap.

(A) PATH OF ASCENT OF SAP

It is well established that the ascent of sap takes place through **xylem**. It can be shown by the following experiments :—

(i) A leafy twig of **balsam** plant (it has semi-transparent stem) is cut under water (to avoid entry of air-bubbles through the cut end) and placed in a beaker containing water with some **eosine** (a dye) dissolved in it. After sometime coloured lines will be seen moving upward in the stem. If sections of stem are cut at this time, only the xylem elements will appear to be filled with coloured water.



(ii) Ringing Experiment.

A leafy twig from a tree is cut under water and placed in a beaker filled with water. A **ring of bark** (all the tissues outer to vascular cambium) is removed from the stem. After sometime it is observed that the leaves above the ringed part of the stem remain fresh and green (Fig. 6.1). It is because water is being continuously supplied to the upper part of the twig through xylem.

Fig. 6.1. Ringing Experiment.

(B) MECHANISM OF ASCENT OF SAP

In small trees and herbaceous plants the ascent of sap can be explained easily, but in tall trees like Australian *Eucalyptus*, some conifers such as mighty **Sequoias** (*Sequoia*, *Sequoiadendron*, *Metasequoia* are the tallest and thickest trees of the present day flora, sometimes reaching a height of 300-400') where the water has to rise up to the height of several hundred feet, the ascent of sap, in fact, becomes a problem.

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Although the mechanism of ascent of sap is not well understood, a number of theories have been put forward to explain it.

(A) VITAL THEORIES

Supporters of vital theories think that the ascent of sap is under the control of vital activities in the stem. Two such theories are common but they are not very convincing :—

(1) According to Godlewski (1884) ascent of sap takes place due to the **pumping activity of the cells of xylem parenchyma** which are living. The cells of the **medullary rays** which are also living, in some way change their **O.P.** When their **O.P.** becomes high they draw water from the **lower vessel** and their **O.P.** becomes low. Now due to the low **O.P.**, water from the cells of xylem parenchyma is **pumped** into the **above vessel**. This process is repeated again and again and water rises upward in the xylem.

This theory seemed only hypothetical, and was further discarded by the experiments of **Strasburger**. (1891, 1893) who demonstrated that ascent of sap continues even in the stems in which living cells have been killed by the uptake of poisons.

(2) According to **Bose** (1923) upward translocation of water takes place due to the **pulsatory activity of living cells of inner most cortical layer** just outside the endodermis.

This theory was also rejected because many workers could not repeat his experiment and many others found no correlation between pulsatory activity and the ascent of sap.

(Bose, in his experiment used an electric probe which was connected to a galvanometer. When the needle of the electric probe was inserted into the stem slowly and slowly, the needle of the galvanometer showed some oscillations but when the electric probe needle reached the innermost layer of cortex, the needle of galvanometer showed violent oscillations. He attributed this to the pulsating activity of these cells.)

(B) ROOT PRESSURE THEORY

Although, **root pressure** which is developed in the xylem of the roots can raise water to a certain height but it does not seem to be an effective force in ascent of sap due to the following reasons :

(i) Magnitude of root pressure is very low (about 2 atms).

(ii) Even in the absence of root pressure, ~~absent~~^{ascent} of sap continues. For example, when a leafy twig is cut under water and placed in a beaker full of water it remains fresh and green for sufficient long time.

(iii) In gymnosperms root pressure has rarely been observed.

(C) PHYSICAL FORCE THEORIES

Various physical forces may be involved in the ascent of sap :—

(1) **Atmospheric Pressure.** This does not seem to be convincing because (i) it cannot act on water present in xylem in roots, (ii) in case it is working, then also it will not be able to raise water beyond 34'.

(2) **Imbibition.** Sachs (1878) supported the view that ascent of sap could take place by imbibition through the walls of xylem. Now it is well known that **imbibitional force** is insignificant in the ascent of sap because it takes place through the **lumen** of xylem elements and not through walls.

(A leafy twig is cut under water and the cut end is dipped in melted paraffin wax for sometime. A thin section of stem near cut end is removed to expose the cell walls. The twig is transferred to a beaker containing water. The twig soon wilts because the lumens of xylem elements have been plugged by wax).

(3) **Capillary Force.** In plants the xylem vessels are placed one above the other forming a sort of continuous channel which can be compared with long capillary tubes and it was thought

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that as water rises in capillary tube due to capillary force, in the same manner ascent of sap takes place in xylem. There are many objections to this theory :

- (i) For capillarity a free surface is required.
- (ii) The magnitude of capillary force is low.
- (iii) In spring when there is more requirement of water due to the development of new leaves, the wood consists of broader elements. While in autumn, when water supply decreases, the wood consists of narrow elements. This is against capillarity.
- (iv) In Gymnosperms usually the vessels are absent. Other xylem elements do not form continuous channels.

(D) TRANSPIRATION PULL AND COHESION OF WATER THEORY

This theory was originally proposed by **Dixon and Joly** (1894) and greatly supported and elaborated by **Dixon** (1914, 1924). This theory is very convincing and has now been widely supported by many workers. It is based on the following features :—

(i) Cohesive and Adhesive properties of water molecules to form a continuous water column in the xylem.

(ii) Transpiration pull exerted on this water column.

Water molecules remain joined to each other due to the presence of H-bonds between them.

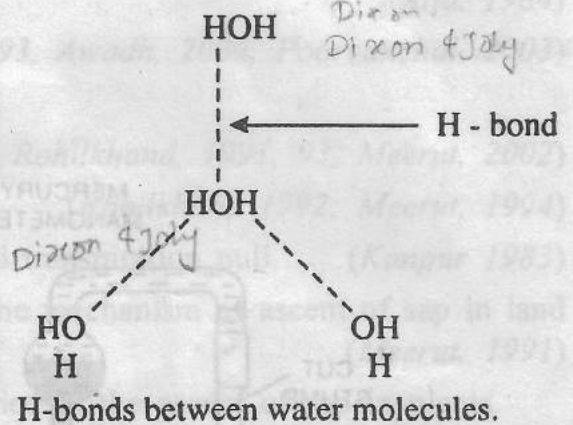
(Whenever a H-atom comes between two electro-negative atoms a bond is established between the two which is called as H bond and is represented by dotted lines. In case of water, the electropositive H-atoms of one water molecule are connected with electronegative O-atoms of other water molecules by H-bonds).

Although H-bond is very weak (containing about 5k. cal. energy) but when they are present in enormous numbers as in case of water, a very strong mutual force of attraction or cohesive force develops between water molecules and hence they remain in the form of a continuous water column in the xylem. The magnitude of this force is very high (sometimes up to 350 atmos.), therefore the continuous water column in the xylem cannot be broken easily due to the force of gravity or other obstructions offered by the internal tissues in the upward movement of water.

The adhesive properties of water i.e. the attraction between the water molecules and the container's walls (here the walls of xylem) further ensure the continuity of water column in xylem.

When transpiration takes place in leaves at the upper parts of the plant, water evaporates from the intercellular spaces of the leaves to the outer atmosphere through the stomata. More water is released into the intercellular spaces from the mesophyll cells. In turn, the mesophyll cells draw water from the xylem of the leaf. Due to all this, a tension is created in water in the xylem elements of the leaves. This tension is transmitted downward to water in xylem elements of the roots through the xylem of petiole and stem and the water is pulled upward in the form of continuous unbroken water column to reach the transpiring surfaces—upto the top of the plants.

According to some workers, the main objection against this theory is that certain air bubbles present in the conducting channels will break the continuity of the water column. This has been counteracted by others who say that there are no air bubbles and if at all they are present, they will not break the water column which will remain continuous through other elements of the xylem.



The **soil-plant-atmosphere continuum** (**SPAC**) is the pathway for water moving from soil through plants to the atmosphere.

Continuum in the description highlights the continuous nature of water connection through the pathway. The low water potential of the atmosphere, and relatively higher (i.e. less negative) water potential inside leaves, leads to a diffusion gradient across the stomatal pores of leaves, drawing water out of the leaves as vapour.^[1] As water vapour transpires out of the leaf, further water molecules evaporate off the surface of mesophyll cells to replace the lost molecules since water in the air inside leaves is maintained at saturation vapour pressure.

Water lost at the surface of cells is replaced by water from the xylem, which due to the cohesion-tension properties of water in the xylem of plants pulls additional water molecules through the xylem from the roots toward the leaf.

5

TRANSPIRATION AND GUTTATION

Q. What is transpiration? What are its kinds? Explain the mechanism of stomatal transpiration. What is the significance of transpiration?

TRANSPIRATION

Although large quantities of water are absorbed by plants from the soil but only a small amount of it is utilized. The excess of water is lost from the aerial parts of plants in the form of water vapours. This is called as transpiration. It can be demonstrated by the following experiment :

A potted plant is kept under bell-jar. Before this, the pot is covered in a polythene bag to check the evaporation of water from the soil and pot surfaces. The apparatus is made air-tight by applying some vaseline. After sometime water-drops will be seen on the inner walls of the bell-jar (Fig. 5.1).

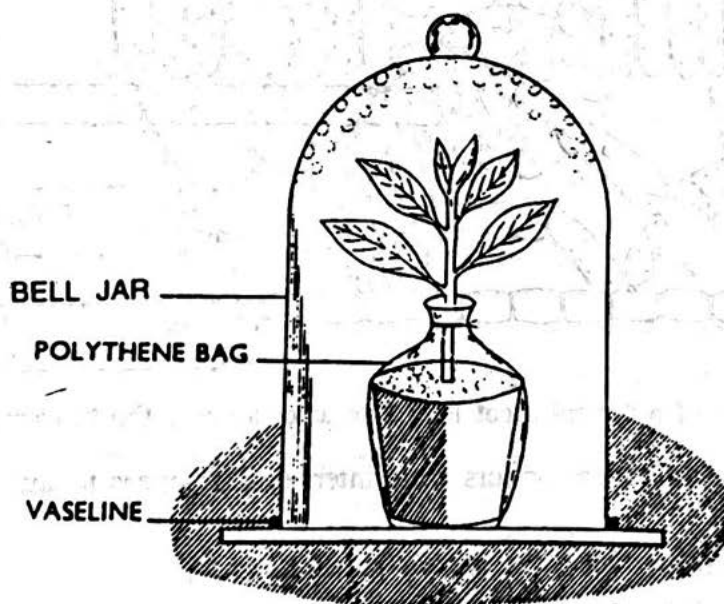


Fig. 5.1 Demonstration of transpiration.

(Transpiration differs from evaporation. Transpiration is a vital physiological process in plants in which water is lost from their aerial parts in the form of water vapours and for which living tissues are essential. Evaporation on the other hand, is a purely physical process in which there is conversion of any liquid into vapours without necessarily reaching the boiling point. Living tissues are not essential for evaporation)

KINDS OF TRANSPIRATION

It is of 3 types :

90-95%

(1) **Stomatal Transpiration.** Most of the transpiration takes place through stomata. Stomata are usually confined in more numbers on the lower sides of the leaves. In monocots e.g. grasses they are equally distributed on all sides. While in aquatic plants with floating leaves they are present on the upper surface.

(2) **Cuticular Transpiration. (Peristomatal transpiration)** Although cuticle is impervious to water, still some water may be lost through it. It may contribute a maximum of about 10% of the total transpiration.

(3) **Lenticular Transpiration.** Some water may be lost by woody stems through lenticels which is called as lenticular transpiration.

(Transpiration from leaves is called as foliar transpiration)

MECHANISM OF STOMATAL TRANSPIRATION

The mechanism of stomatal transpiration which takes place during the day time can be studied in 3 steps :

(i) **Osmotic diffusion** of water in the leaf from xylem to intercellular spaces above the stomata through the mesophyll cells.

(ii) **Opening and closing of stomata (stomatal movement), and**

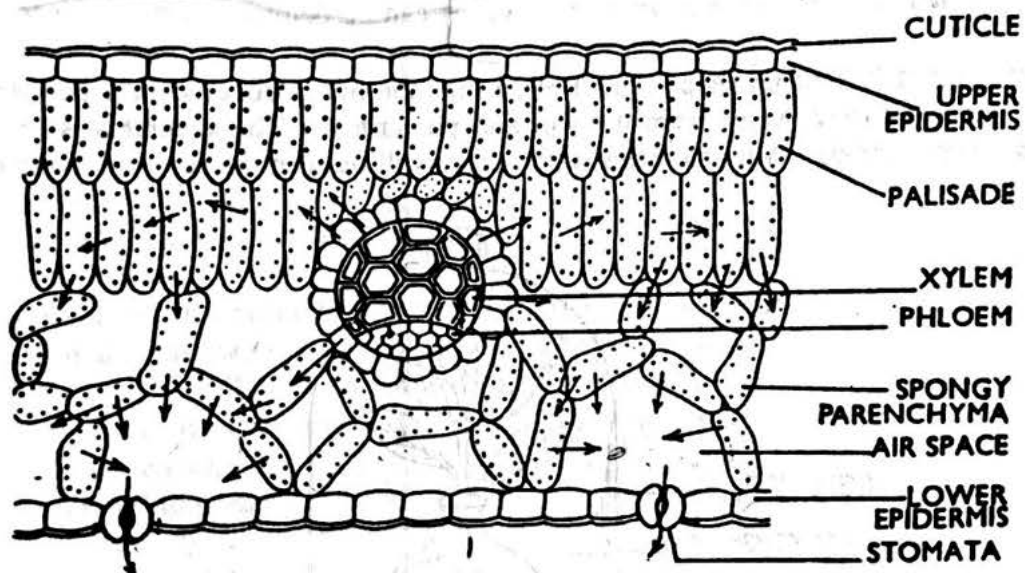


Fig. 5.2. V.T.S. of a typical dicot leaf. The arrows show the movement of water.

(iii) **Simple diffusion** of water vapours from intercellular spaces to outer atmosphere through open stomata.

Details of the above mentioned steps are given below :

(i) Inside the leaf, the mesophyll cells are in contact with xylem, and on the other hand with intercellular spaces above the stomata as shown in the Fig. 5.2. When mesophyll cells draw water from the xylem they become turgid and their diffusion pressure deficit (D.P.D.) and osmotic pressure (O.P.) decrease with the result that they release water in the form of vapours in intercellular spaces close to stomata by osmotic diffusion. Now in turn, the O.P. and D.P.D. of mesophyll cells become higher and hence, they draw water from xylem by osmotic diffusion.

(ii) **Opening and Closing of Stomata (Stomatal Movement).**

The stomata are easily recognised from the surrounding epidermal cells by their peculiar shape. The epidermal cells that immediately surround the stomata may be similar to other epi-

dermal cells or may be different and specialised. In the latter case, they are called as **subsidiary cells**.

The guard cells differ from other epidermal cells also in containing chloroplasts and peculiar thickenings on their adjacent surfaces (in closed stomata) or on surfaces adjacent to stomatal pore (in open stomata). There is radial micellation of cellulose microfibrils in the walls of the guard cells, the cellulose microfibrils radiating from the pore outward around their circumference. This allows guard cells to elongate lengthwise and prevents their elongation crosswise when they become turgid.

Consequent to an increase in the osmotic pressure (O.P.) and diffusion pressure deficit (D.P.D.) of the guard cells (which is due to accumulation of osmotically active substances), osmotic diffusion of water from surrounding epidermal cells and mesophyll cells into the guard cells follows. This increases the turgor pressure (T.P.) of the guard cells and they become turgid. The guard cells swell, increase in length and their adjacent thickened surfaces stretch forming a pore and thus the stomata open (Fig. 5.3).

On the other hand, when O.P. and D.P.D. of guard cells decrease (due to depletion of osmotically active substances) relative to the surrounding epidermal and mesophyll cells, water is released back into the latter by osmotic diffusion and the guard cells become flaccid. The thickened surfaces of the guard cells come close to each other, thereby closing the stomatal pore and the stomata (Fig. 5.3)

Using thermodynamic terminology, osmotic diffusion of water into guard cells occur when their osmotic potential (ψ_s) and water potential (ψ_w) decrease (i.e., become more negative) relative to those of surrounding epidermal and mesophyll cells. The guard cells become flaccid when their osmotic potential and water potential increase (i.e., become less negative) relative to the surrounding cells. (Movement of water takes place from a region of higher water potential i.e. less negative to a region of lower water potential i.e. more negative).

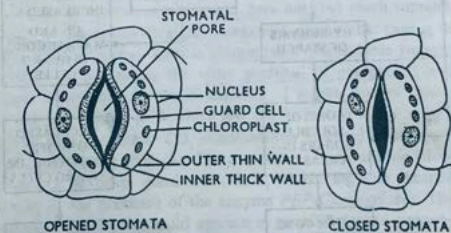


Fig. 5.3. Opened and closed stomata.

There may be several different agents or mechanisms which create osmotic potential in the guard cells and control stomatal movements such as hydrolysis of starch into sugars in guard cells, synthesis of sugars or organic acids in them and the active pumping of K^+ ions in the guard cells which is accompanied by Cl^- or organic acids counter ions. An integrated scheme of the probable mechanisms of stomatal opening is given in Fig. 5.4 while details of these are as follows :

(a) **Starch-Sugar Interconversion Theory.** This classical theory is based on the effect of pH on Starch phosphorylase enzyme which reversibly catalyses the conversion of starch + inorganic phosphate into glucose-1-phosphate. During the day, pH in guard cells is high. This

favours hydrolysis of starch (which is insoluble) into glucose-1-phosphate (which is soluble) so that osmotic potential becomes lower in the guard cells. Consequently water enters into the guard cells by osmotic diffusion from the surrounding epidermal and mesophyll cells. Guard cells become turgid and the stomata open. During dark reverse process occurs. Glucose-1-phosphate is converted back into starch in the guard cells thereby increasing the osmotic potential. The guard cells release water, become flaccid and the stomata become closed.

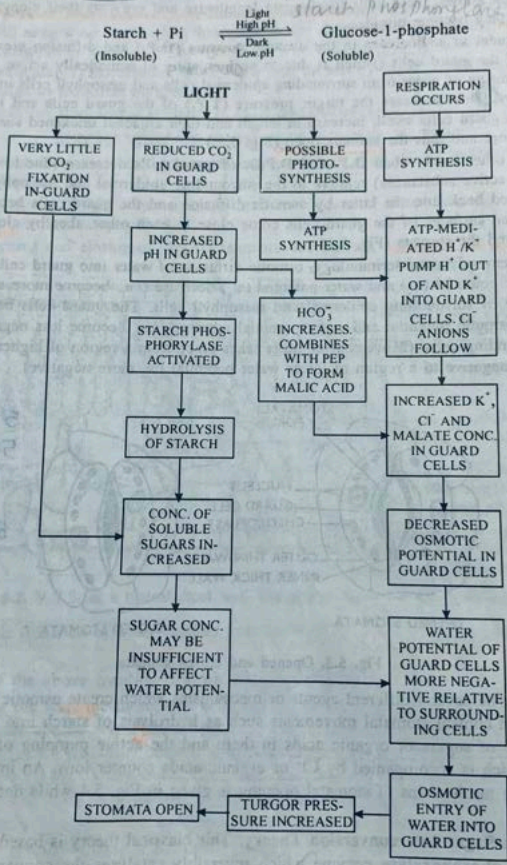


Fig. 5.4. An integrated scheme of the probable mechanisms of stomatal opening.

According to **Steward (1964)** the conversion of starch and inorganic phosphate into glucose-1-phosphate does not cause any appreciable change in the osmotic pressure because the inorganic phosphate and glucose-1-phosphate are equally active osmotically. In his scheme (Fig. 5.5) he has suggested that (i) glucose-1-phosphate should be further converted into glucose and inorganic phosphate for the opening of stomata, and (ii) metabolic energy in the form of ATP would be required for the closing of stomata which probably comes through respiration.

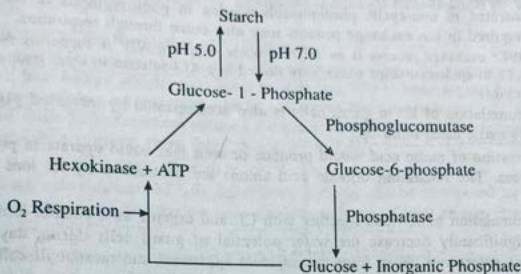


Fig. 5.5. Steward's scheme of metabolic reactions involved in the opening and closing of stomata.

(The chloroplasts of guard cells are usually non-functional. The starch in guard cells is therefore, derived from the mesophyll tissue.)

However, the Starch-Sugar interconversion theory is not universally applicable. It may operate under certain circumstances only and does not find much support by recent workers.

(b) Synthesis of Sugars or Organic Acids in Guard Cells. During daylight photosynthesis occurs in guard cells as they contain chloroplasts. The soluble sugars formed in this process may contribute in decreasing the water potential of guard cells and hence resulting in stomatal opening. However, very small amounts of soluble sugars (osmotically active) have been extracted from the guard cells which are insufficient to affect water potential.

As a result of photosynthesis, CO_2 concentration in guard cells decreases which leads to increased pH in them during daylight. There may be some build up of organic acids, chiefly malic acid during this period in guard cells (HCO_3^- combining with phosphoenol pyruvate (PEP) to form malic acid in the presence of the enzyme PEP-Carboxylase). The formation of malic acid would produce protons that could operate in an ATP-driven-proton- K^+ exchange pump moving protons into the adjacent epidermal cells and K^+ ions into the guard cells and this may contribute in decreasing water potential of the guard cells and leading to stomatal opening.

Reverse process would occur in darkness.

(c) ATP-Driven Proton (H^+) - K^+ Exchange Pump Mechanism in Guard Cells. There is growing evidence for the operation of such mechanism in plants which control movements of stomata and the possibility of such a mechanism is much more widely accepted than the classical starch hydrolysis theory.

According to this mechanism, there is accumulation of K^+ ions in the guard cells during daylight period.

The protons (H^+) are 'pumped out' from the guard cells into the adjacent epidermal (or subsidiary) cells and in exchange K^+ ions are 'pumped in' into them from the adjacent epidermal cells.

This exchange of H^+ and K^+ ions is followed by entry of Cl^- anions into the guard cells which results in response to the electrical differential in the guard cells due to accumulation of K^+ ions in them.

The exchange of H^+ and K^+ ions is mediated through ATP and thus is an active process. ATP is generated in non-cyclic photophosphorylation in photosynthesis in the guard cells. The ATP required in ion exchange process may also come through respiration.

(That H^+/K^+ exchange process is an active process requiring ATP is supported by the fact that addition of ATP to epidermal strips which were floated in a KCl solution in light, greatly increased the stomatal openings).

The accumulation of K^+ in guard cells is also accompanied by increased pH and organic acids (mostly malic acid) build up.

The formation of malic acid would produce protons that could operate in proton- K^+ exchange process. The remaining organic acid anions are neutralised by K^+ ions in the guard cells.

The accumulation of K^+ ions together with Cl^- and organic acid counter-ions is sufficient enough to significantly decrease the water potential of guard cells during daylight. Consequently, water enters into them from the adjacent epidermal and mesophyll cells thereby increasing their turgor pressure and opening the stomatal pore.

Reverse situation prevails during dark when stomata are closed. There is no accumulation of K^+ in guard cells in dark.

(Although accumulation of K^+ in guard cells in plants was first noticed by Macallum in 1905 and confirmed by others such as Lloyd (1925), Iijin (1915) etc. but main credit for implicating the role of K^+ in stomatal movement goes to some Japanese workers (such as Imamura 1943; Yamashita 1952; Fujino 1959) and R.A. Fisher, 1968, 72, 73. Fujino, 1959, proposed that movement of K^+ into the guard cells and its subsequent accumulation there is sufficient enough to increase their osmotic pressure and to induce stomatal opening. Since then, role of K^+ in stomatal opening in plants has been described by different workers.

(The existence of K^+ fluxes in the guard cells of plants has also been confirmed in recent years with a very sensitive apparatus known as electron beam microprobe).

(iii) The last step in the mechanism of transpiration is the simple diffusion of water vapours from the intercellular spaces to the outer atmosphere through open stomata. This is because the intercellular spaces are more saturated with moisture in comparison to the outer atmosphere in the vicinity of the stomata.

SIGNIFICANCE OF TRANSPIRATION

Plants waste much of their energy in absorbing large quantities of water, most of which is ultimately to be lost through transpiration. While some people think transpiration as advantageous to plant which in fact is not true, others regard it as an unavoidable process which is rather harmful.

(A) SUPPOSED ADVANTAGES OF TRANSPIRATION

(1) Supposed Role in the Movement of Water

Although transpiration plays an important role in the upward movement of water i.e., ascent of sap in plants, it does not mean that the translocation of water will be stopped without it. It has been observed that even in the absence of transpiration water continues to rise upward to maintain the turgidity of the cells for various metabolic processes.

(2) Supposed Role in the Absorption and Translocation of Mineral Salts

Previously, it was thought that more rapid rate of transpiration resulted in an increase in the rate of absorption of mineral salts through increased rate of water absorption. But now it is well established that the absorption of water and absorption of mineral salts are entirely independent processes. Therefore, transpiration has nothing to do with the absorption of mineral salts.

However, once the mineral salts have been absorbed by the plants, their further translocation or distribution may be facilitated by transpiration through translocation of water in the xylem elements.

(3) Supposed Role in the Regulation of Temperature

Some of the light energy absorbed by the leaves is utilised in photosynthesis, rest is converted into heat energy which raises their temperature. It has been argued by many workers that transpiration plays an important role in controlling the temperature of the plants. Rapid evaporation of water from the aerial parts of the plant through transpiration brings down their temperature and thus prevents them from excessive heating.

But this view is not correct because :

(i) although some amount of heat input from sunlight can be dissipated by transpiration, but transpiration cannot account for the total dissipation (loss) of heat energy from leaves and other parts of the plant.

(ii) plants kept under intense sunlight with their stomata plugged by vaseline do not show much increase in their temperature, and

(iii) some xerophytes having structural modifications and adaptations to check excessive transpiration can withstand higher temperatures without appreciable damage to protoplasm.

Dissipation of heat energy from the leaves and other parts of the plant into the outer atmosphere takes place by simple physical process which in case of leaves and other objects have also been termed as **thermal emission**.

(B) TRANSPIRATION AS A NECESSARY EVIL

It is quite obvious from the above discussion that transpiration is not of much importance to plants. Besides unnecessary wastage of energy in water absorption due to transpiration, it may be sometimes harmful to them in other respects also. For example :

(i) Very often, when the rate of transpiration is high and soil deficient in water an **internal water deficit** is created in the plants which may affect metabolic processes.

(ii) Many xerophytes have to develop structural modifications and adaptations to check transpiration.

(iii) Deciduous trees have to shed their leaves during autumn to check loss of water.

But, in spite of the various disadvantages the plants **cannot avoid transpiration** due to their peculiar internal structure particularly those of leaves. Their internal structure although basically meant for gaseous exchange for respiration, photosynthesis etc. is such that it cannot check the evaporation of water. Therefore, many workers like Curtis (1926) have called transpiration as **necessary evil**.

Q In the light of recent researches discuss the factors that affect stomatal movements.

FACTORS AFFECTING STOMATAL MOVEMENTS

The factors that greatly influence and control stomatal movements i.e., opening and closing of stomata are as follows :

Light

Light has strong controlling influence on the stomatal movements. Stomata generally open in light and close in darkness.

The amount of light required to achieve maximal stomatal openings varies with the species. For instance, some plants like tobacco require low light intensities (as low as 2.5% of full daylight) while others may require full sunlight.

The stomata of plants showing CAM (Crassulacean Acid Metabolism) are exceptional because they open at night and close during the day. These plants absorb CO_2 and fix it into organic acids at night. During the day time, CO_2 is released from the organic acids and is reduced photosynthetically. For details see Chapter 11.

According to Kramer (1959), the stomata in some plants may be induced to open by bright moonlight.

The duration during which stomata remain open in daylight and close at night varies among plant species.

The effect of different wavelengths of light on stomatal opening also varies. For instance, Zelitch (1963) did not observe stomatal opening in tobacco leaves which were exposed to far-red or ultra-violet irradiations. Green light was also ineffective in stomatal opening.

The action spectrum* of the effect of light on stomata bears a resemblance with that of photosynthesis with a blue light effect superimposed. Some plants lack the photosynthetic spectrum and are sensitive to blue light only. The photosynthetic component may be due to photosynthesis in guard cells which contain chloroplasts. Thus, light may have controlling influence on stomatal opening in the following ways :

(i) Photosynthesis reduces the CO_2 conc. in guard cells which has powerful stimulus for opening the stomata.

(ii) Osmotically active substances such as soluble sugars are synthesised during photosynthesis which may contribute in decreasing the water potential of guard cells.

(iii) Photophosphorylation may provide ATP which is required to operate H^+/K^+ ions exchange pumps in which H^+ ions are pumped out and K^+ ions, Cl^- ions and organic anions are pumped into the guard cells. These ions decrease water potential of guard cells.

(iv) In many plants illumination of the guard cells results in an increase of pH (which may be a consequence of reduced conc. of CO_2 in guard cells). High pH favours hydrolysis of starch into osmotically active sugars (glucose-1-phosphate) in the presence of enzyme *starch phosphorylase* thereby decreasing the water potential of guard cells. (Reverse reaction occurs in dark when pH is low). However, this starch \rightleftharpoons sugars interconversion hypothesis is not widely accepted because (a) it is not universally true and (b) very small amounts of osmotically active or soluble sugars have been extracted from the guard cells.

(v) Low conc. of CO_2 and high pH (pH 7) in guard cells in daylight may favour synthesis of malic acid from $\text{HCO}_3^- + \text{Phosphoenol pyruvic acid (PEP)}$ in the presence of the enzyme, *PEP-carboxylase*. Malic acid would produce protons (H^+) which can operate in ATP-driven H^+/K^+ ions exchange pumps.

• The blue light component of action spectrum on the effect of light on stomatal opening is related to a different photoactive control through cryptochrome (most probably through the carotenoid zeaxanthin).

According to one such scheme, blue light is perceived by zeaxanthin in the chloroplast of guard cells. The excitation of zeaxanthin by blue light then starts signal transduction process that includes, (i) isomerization of zeaxanthin, (ii) conformational changes of an apoprotein, (iii) transmission of blue light signal across the chloroplast membrane by a second messenger (most probably Ca^{++} , phosphatases, calcium binding protein, calmodulin and inositol triphosphate i.e., IP_3), (iv) activation of $\text{H}^+ - \text{ATPase}$ at the guard cell plasmamembrane resulting in pumping of protons across the membrane and intake of K^+ ions.

For explanation of action spectrum see Chapter 11.

Blue light also stimulates degradation of starch and synthesis of malate. Accumulation of solutes in guard cells ultimately leads to stomatal opening.

For details of cryptochrome, see Chapter 25.

2. Carbon dioxide concentration

Concentration of CO_2 has pronounced effect on stomatal movement. Reduced CO_2 conc. favours opening of stomata while an increase in CO_2 conc. promotes stomatal closing.

Under experimental conditions, the stomata can be induced to open even in dark if conc. of CO_2 is significantly lowered below that of normal air. On the other hand, a marked increase in CO_2 conc. above that of normal air causes the stomata to close in dark as well as in light.

The stomata which are forced to close by high CO_2 conc., do not reopen rapidly simply by flushing the leaf with CO_2 free air and in dark. However, during subsequent light exposure such stomata open soon. It is because CO_2 trapped inside the leaf is consumed in photosynthesis during light exposure. Therefore, it is infact that CO_2 which is present inside the leaf (intercellular) rather than that of the outer atmosphere which has controlling influence on stomatal movement. The cuticle present over the guard cells and epidermal cells is quite impermeable to CO_2 and ensures response of stomata to CO_2 present in the leaf rather than that of the outer atmosphere.

3. Temperature

Usually an increase in temperature results in increased stomatal opening provided water does not become a limiting factor. Stomata of some plants, e.g., *Camellia* do not open at very low temperatures (below 0°C) even in strong light. On the other hand in some plants the stomata tend to close even at high temperatures (more than 30°C). This may be due to increased CO_2 conc. inside the leaves caused by increased respiration rate at high temp. and heat-impaired photosynthesis in the latter category of plants.

4. Water deficits and abscisic acid (ABA)

When rate of transpiration exceeds the rate of absorption of water, a water deficit is created in plants. Such plants begin to show signs of wilting and are known as **water-stressed plants**. Most of the mesophytes under such conditions close their stomata quite tightly and completely in order to protect them from the damage which may result due to extreme water shortage. The stomata reopen only when water potential of these plants is restored. This type of control of stomatal movement by water is called as **hydropassive control**.

Accumulation of **phytohormone abscisic acid (ABA)** in the guard cells of many different water-stressed plants is now well established. The **ABA** causes stomata of such plants to close. When water potential of the water-stressed plant is restored, the stomata reopen and ABA gradually disappears from the guard cells. This type of control of stomata by water (mediated through ABA) has been called as **hydroactive control**. Externally applied ABA to leaves of normal plants is also known to induce closure of stomata and the idea is growing that ABA is a primary regulator of stomatal action in water-stressed plants.

Q Describe various methods for the measurement of transpiration in plants.

MEASUREMENT OF TRANSPIRATION

The following four methods are usually employed for the measurement of transpiration in plants :

A. WEIGHING METHODS

These methods consist in weighing the potted plants after intervals. The loss of weight over a prescribed period of time represents the weight of transpired water. In such cases the pot and the soil surfaces are covered by a water-proof covering to check evaporation of water from surfaces other than the aerial parts of the plant.

These methods are also employed in case of isolated parts of the plant such as leaves, branches etc. However, they are not applicable in case of large plants and trees.

B. COBALT CHLORIDE METHOD

This method is based on the fact that the dry cobalt chloride is blue in colour while the moist cobalt chloride is pink in colour. Actually in this method the weight of transpired water is not measured, it measures only the rate of transpiration.

Small pieces of filter papers are soaked in 3% cobalt chloride solution and thoroughly dried. A single cobalt chloride paper is now clipped under a glass cover slip along with an ordinary standard pink and an ordinary standard blue coloured paper on the surface of the transpiring leaf (Fig. 5.6). The colour of the cobalt chloride will gradually change from blue to pink. The time taken for this change is noted by means of a stop-watch. The stop-watch is started when the cobalt chloride paper begins to change its blue colour, and is stopped when it has acquired the pink colour. The ordinary standard blue and pink papers act as indicators. The rate of the colour change is an indication of the rate of transpiration.

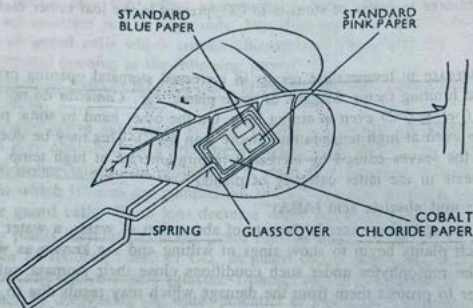


Fig. 5.6. Measurement of the rate of transpiration by cobalt chloride method.

C. COLLECTING AND WEIGHING TRANSPIRED WATER

This method consists in passing the air of known moisture content over a potted plant kept under a closed glass chamber through an opening. The air after being mixed with tran-

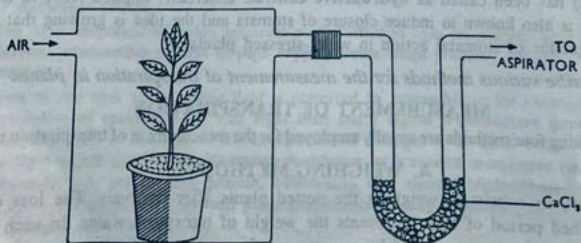


Fig. 5.7. An apparatus for the measurement of transpiration. See text.

spired water is passed out over anhydrous calcium chloride whose weight is already known (Fig. 5.7). The increase in the weight of anhydrous calcium chloride will be equal to the weight of transpired water plus the original moisture content of the air. The weight of the original moisture content of the air being known, the weight of the transpired water is easily calculated.

D. POTOMETER METHODS

These methods are based on the assumption that the rate of absorption of water is approximately equal to the rate of transpiration. Actually, in these methods only the amount of water which is absorbed by the plant is measured which may not be approximately equal under certain conditions to the amount of transpired water. The apparatuses used for such purposes are called as **potometers**. The following three types of potometers are very common :

(1) Darwin's Potometer

It consists of a straight glass tube with a side limb the mouths of which are fitted with corks. A long narrow capillary tube is inserted into the lower mouth of the straight tube through a hole in the cork. A scale is attached on one side of the capillary tube. Whole of the apparatus is filled with water and after inserting a fresh leafy twig into the mouth of the side limb through of hole in the cork all the joints are made air-tight. As the transpiration proceeds the level of water begins to rise in the capillary tube. As soon as an air bubble enters, the capillary tube is dipped in water contained in a beaker (Fig. 5.8). As the transpiration proceeds further, the air bubble will move upward. The distance (l) travelled by the air bubble is noted on the scale. The radius (r) of the capillary tube being known, the volume of the water absorbed and transpired by the plant can be calculated by the formula $\pi r^2 l$. Actual amount of this water can also be determined by multiplying the volume with density of water. Moreover, the rapidity with which the air bubble ascends in the capillary tube is indicative of the rate of transpiration.

(2) Farmer's Potometer

It consists of a wide mouthed glass bottle fitted with a cork containing three holes. In one hole is inserted a narrow capillary tube bent at three places and attached to a scale. Through the middle hole is inserted a fresh leafy twig, while through the third hole the narrow end of a water reservoir is inserted which is provided with a stop cock (Fig. 5.9). Whole of the apparatus is filled with water, the reservoir is closed by stopcock and the apparatus is made airtight. As soon as transpiration proceeds and an air bubble enters into the capillary tube, its free end is dipped in water contained in a beaker. The distance travelled by the air bubble inside the capillary tube measures the rate of transpiration which can be noted on the scale.

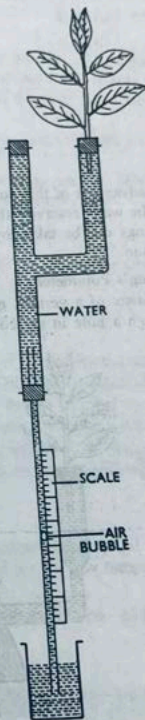


Fig. 5.8. Darwin's Potometer

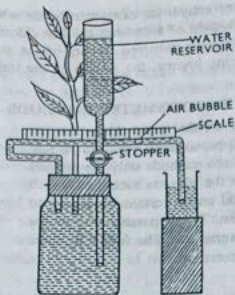


Fig. 5.9. Farmer's Potometer

The advantage of this potometer over the Darwin's potometer is that by opening the stopcock of the water reservoir the air bubble can be pushed back in the capillary tube. Thus several readings can be taken by once setting the apparatus for the measurement of the rate of transpiration.

(3) Ganong's Potometer

It consists of a vertical glass tube fitted with a cork. A fresh leafy twig is inserted into tube through a hole in the cork. The lower end of this tube after bending continues into a

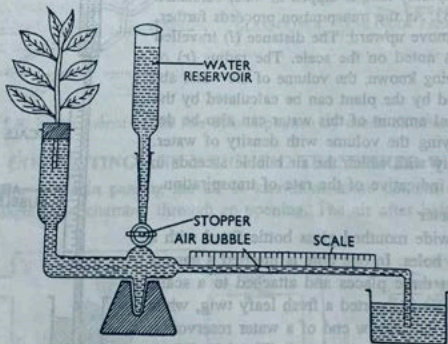


Fig. 5.10. Ganong's Potometer.

horizontally placed capillary tube which is attached to a scale and bent near its free end. A water reservoir provided with the stopcock is also attached near the other end of the capillary tube (Fig. 5.10). Whole of this apparatus is filled with water and the joints are made airtight. As soon as the air bubble enters into the capillary tube, its free end is dipped in water contained in a beaker. The movement of the air bubble in the capillary tube is noted on the scale which measures the rate of transpiration.

As in case of Farmer's potometer, in Ganong's potometer also the air-bubble can be pushed back by opening the water reservoir and many readings can be taken without disturbing the apparatus.

Q Give an account of the various factors which affect rate of transpiration. What are plant antitranspirants? How would you account for the diurnal fluctuations in the rate of stomatal transpiration? What is guttation?

5 mark FACTORS AFFECTING RATE OF TRANSPIRATION

A. EXTERNAL FACTORS

humid - ↓
atmos

1. Atmospheric Humidity ↓

In humid atmosphere (when the Relative Humidity is high) the rate of transpiration decreases. It is because the atmosphere is more saturated with moisture and retards the diffusion of water vapours from the intercellular spaces of the leaves to the outer atmosphere through stomata.

In dry atmosphere the relative humidity is low and the air not saturated with moisture and hence, the rate of transpiration increases.

(Actual amount of moisture content present in the air is the absolute humidity. When it is expressed as a percentage of the total amount of moisture necessary to saturate the air at a particular temperature it is called as Relative Humidity).

2. Temperature

An increase in temperature brings about an increase in the rate of transpiration by

- lowering the relative humidity, and
- opening the stomata widely.

3. Wind

- When the wind is stagnant (*i.e.*, not blowing) the rate of transpiration remains normal.
- When the wind is blowing gently the rate of transpiration increases because it removes moisture from the vicinity of the transpiring parts of the plant, thus facilitating the diffusion of water vapours from the intercellular spaces of the leaves to the outer atmosphere through stomata.
- When the wind is blowing violently the rate of transpiration is decreased because it creates hindrance in the outward diffusion of water vapours from the transpiring parts and may also close the stomata.

4. Atmospheric Pressure

Ultimate effect of atmospheric pressure on the rate of transpiration is nil. The positive effect of low atmospheric pressure (*e.g.*, at hills) is neutralised by the low temperature associated with it.

Similarly, the negative effect of high atm. pressure in plains on the rate of transpiration is neutralised by comparatively higher temperature of the plains.

5. Light ↑

Light increases the rate of transpiration because : (i) in light stomata open, and (ii) it increases the temperature. ↑

In dark due to the closure of the stomata, the stomatal transpiration is almost stopped.

6. Available Soil Water

Rate of transpiration will decrease if there is not enough water in the soil in such a way which can be easily absorbed by the roots.

7. CO_2

An increase in CO_2 concentration in the atmosphere (over the usual conc.) more so inside the leaf, leads towards stomatal closure and hence, it retards transpiration.

B. INTERNAL FACTORS

1. Internal Water Condition

It is very essential for transpiration. Deficiency of water in the plants will result in decrease of transpiration rate. Increased rates of transpiration continuing for longer periods often create **internal water deficit** in plants because absorption of water does not keep pace with it.

2. Structural Features

The number, size, position and the movement of stomata affect rate of transpiration. In dark stomata are closed and stomatal transpiration is checked.

Sunken Stomata help in reducing the rate of stomatal transpiration. When they are situated in grooves and sometimes protected by hairs, the rate of transpiration is further decreased.

In xerophytes the leaves are reduced in size or may even fall to check foliar transpiration.

Thick cuticle or presence of wax coating on exposed parts reduces cuticular transpiration.

PLANT ANTITRANSPIRANTS

A number of substances are known which when applied to the plants retard their transpiration. Such substances are called as **antitranspirants**.

Knowledge of plant antitranspirants may find its use in crop production e.g., cultivation of high-priced crops, in seedling transplantation in nurseries or in other circumstances. A brief account of antitranspirants is given below :

Some antitranspirants such as **colourless plastics, silicone oils and low viscosity waxes** when sprayed on leaves, form a thin film which is impermeable to water but not to CO_2 or O_2 .

Some antitranspirants consist of substances which when sprayed on leaves cause partial closure of their stomata. When used in proper concentrations these antitranspirants have very little adverse effect on leaf tissues. The fungicide, **phenyl mercuric acetate** is one such substance. **Foliar spray with 10^{-4} M conc.** of this fungicide has been found to partially close the stomata for a period of 2 weeks or more. **Abscisic acid (ABA)**, a plant growth hormone also induces closure of stomata.

CO_2 is also known to act as antitranspirant. An increase in CO_2 conc. in atmosphere from usual 0.03% to about 0.05% causes partial closure of stomata. In very high conc. however, it may cause complete stomatal closure and thus retard photosynthesis too. Use of CO_2 as antitranspirant is economical and practically feasible only in glasshouses.

DIURNAL FLUCTUATIONS IN THE RATE OF STOMATAL TRANSPIRATION

(DAILY PERIODICITY OF TRANSPIRATION)

Stomatal transpiration does not take place at the same rate throughout the daily period of 24 hours. There are fluctuations (changes) in its rate.

(i) In the **morning**, when light falls on plants the stomata begin to open and transpiration starts at a certain rate.

(ii) Stomata gradually open widely increasing the rate of transpiration till it reaches its maximum a little before noon.

(iii) At about noon, **internal water deficit** is created because absorption of water fails to keep pace with the rate of transpiration. This lowers the **turgor pressure** of the guard-cells which now become flaccid to close the stomata. Both these factors result in sharp decline in the rate of transpiration, (leaves at this stage may even fade out).

(iv) Internal water deficit in plants is made good in the **afternoon** gradually due to the absorption of more water by the roots. Stomata again open and the rate of transpiration increases (but is not maximum).

(v) In the **evening** the stomata begin to close due to diffused light and the rate of transpiration falls.

(vi) At **night** the stomata are closed and the stomatal transpiration is almost completely stopped.

GUTTATION

In some plants such as garden nasturtium, tomato, strawberry, *Colocasia* etc., watery drops ooze out from the uninjured margins of the leaves where a main vein ends. This is called as **guttation** and takes place usually early in the morning when the rate of water absorption and the root pressure are higher while the transpiration is very low. The watery drops consist of water in which many inorganic and organic substances are dissolved. After the drops have dried the salts and organic substances etc., remain in the form of a residue on the margins of the leaves.

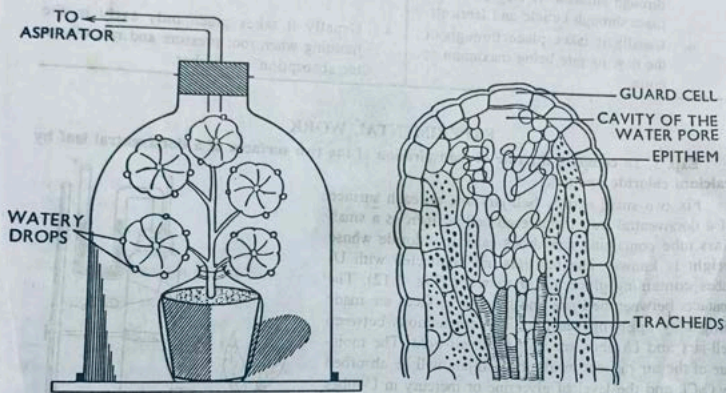


Fig. 5.11. A. Demonstration of guttation. B. Vertical section of a leaf through a hydathode.

The phenomenon of guttation can be demonstrated by a simple experiment (Fig. 5.11 A). A well watered potted plant of garden nasturtium is kept under a bell-jar on a glass sheet. Before this, the pot is covered in a polythene bag to check the evaporation of water from the soil. The apparatus is made air-tight by applying vaseline. The bell-jar is connected to an aspirator. Air is sucked from the bell-jar by means of the aspirator. After a very short time watery drops will appear on the margins of the leaves.

The phenomenon of guttation is associated with the presence of special types of stomata at the margins of the leaves which are called as **water stomata** or **hydathodes**. Each hydathode consists of a **water pore** which remains permanently open. Below this there is a small **cavity** followed by a loose tissue called as **epithem**. The epithem is in close association with the ends of the vascular elements of veins (Fig 5.11 B). Under higher root pressure the water is given to the epithem by the xylem of the veins. From epithem the water is released into the cavity. When this cavity is completely filled with the watery solution, the latter begins to ooze out in the form of watery drops through the water pore.

Q Differentiate between transpiration and guttation.

Differences Between Transpiration & Guttation

Transpiration	Guttation
1. In transpiration, water is lost from aerial parts of plants in the form of invisible water vapours.	1. In guttation, watery solution oozes from uninjured margins of aerial leaf only.
2. It occurs in all vascular plants.	2. It occurs only in some Angiosperms such as strawberry, garden nasturtium (<i>Tropaeolum</i>), <i>Colocasia</i> , tomato etc.
3. Transpiration occurs mostly through stomata. It may also take place through cuticle and lenticels.	3. It occurs only through hydathodes (W Stomata).
4. Usually it takes place throughout the day, its rate being maximum at noon.	4. Usually it takes place only early in morning when root pressure and rate of water absorption are higher.

EXPERIMENTAL WORK

Exp. 1. To compare the rate of transpiration of the two surfaces of a dorsiventral leaf by calcium chloride method.

Fix two small narrow bell-jars one on each surface of a dorsiventral leaf. Inside each bell-jar there is a small glass tube containing anhydrous calcium chloride whose weight is known. The bell-jars are connected with U-tubes containing glycerine or mercury (Fig. 5.12). The contacts between bell-jars and the leaf surfaces are made tight by applying vaseline. The connections between bell-jars and U-tubes are also made air-tight. The moisture of the air present inside the bell-jars will be absorbed by CaCl_2 and the level of glycerine or mercury in U-tubes will fall, thus confirming that the apparatus is perfectly airtight. After a few hours the glass tubes are taken out from the bell-jars and reweighed. Their weight is increased. The difference between the initial and final weights of the glass tubes will be higher in the lower bell-jar than in the upper bell-jar. (The increase in weight of the glass tubes is because anhydrous calcium chloride absorbs the water vapours transpired from the leaf surfaces). Thus, this experiment confirms that the rate of stomatal transpiration is higher than that of cuticular transpiration.

Exp. 2. To compare the rate of absorption of water by transpiration. Take a large glass bottle



ABSORPTION OF MINERAL SALTS

Q. Explain the mechanism of absorption of mineral salts from the soil by plants.
What is Donnan's Equilibrium ?

MECHANISM OF MINERAL SALT ABSORPTION

Previously, it was thought that the absorption of mineral salts from the soil took place along with the absorption of water but it is now well established that the mineral salt absorption and water absorption are two different processes.

Mineral salts are absorbed from the soil solution in the form of ions. They are chiefly absorbed through the meristematic regions of the roots near the tips.

However, some mineral salts may also be absorbed at other locations on the root surface or over the entire root surface including zone of elongation and root hairs that depends upon the high availability of such minerals around them and/or strong tissue demand at such locations.

- (Some mineral salts can also be absorbed by leaves of the plants during foliar application of chemical fertilizers on them).

Plasma membrane of the root cells is not permeable to all the ions. It is selectively permeable. All the ions of the same salt are not absorbed at equal rate but there is unequal absorption of ions.

First step in the absorption of mineral salts is the process of Ion-Exchange which does not require metabolic energy but greatly facilitates mineral salt absorption.

ION-EXCHANGE

The ions adsorbed on the surface of the walls or membranes of root cells may be exchanged with the ions of same sign from external solution. For example, the cation K^+ of the external soil solution may be exchanged with H^+ ion adsorbed on the surface of the root cells. Similarly, an anion may be exchanged with OH^- ion. There are two theories regarding the mechanism of ion exchange :

i) Contact Exchange Theory

According to this theory, the ions adsorbed on the surface of root cells and clay particles (or clay micelles) are not held tightly but oscillate within small volume of space. If the root and clay particles are in close contact with each other, the oscillation volume of ions adsorbed on root-surface may overlap the oscillation volume of ions adsorbed on clay particles, and the ions adsorbed on clay particle may be exchanged with the ions adsorbed on root-surface directly without first being dissolved in soil solution (Fig. 7.1 A).

ii) Carbonic Acid Exchange Theory

According to this theory, the CO_2 released during respiration of root cells combines with

water to form **carbonic acid** (H_2CO_3). Carbonic acid dissociates into H^+ and an anion HCO_3^- in soil solution. These H^+ ions may be exchanged for cations adsorbed on clay particles. The cations thus released into the soil solution from the clay particles, may be adsorbed on root cells in exchange for H^+ ions or as ion pairs with bicarbonate (Fig. 7.1 B). Thus, soil solution plays an important role in carbonic acid exchange theory.

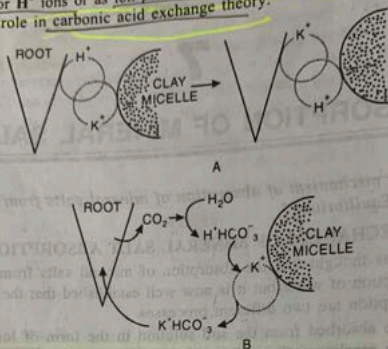


Fig. 7.1. Diagrammatic representation of (A) the contact-exchange theory and (B) the carbonic acid exchange theory.

The further process of the absorption of mineral salts may be of two types :

- (1) Passive and (2) Active

(1) PASSIVE ABSORPTION OF MINERAL SALTS

When the concentration of mineral salts is higher in the outer solution than in the cell sap of the root cells, the mineral salts are absorbed according to the concentration gradient by simple process of **diffusion**. This is called as **passive absorption** because it does not require expenditure of metabolic energy. It is now known that during passive absorption, the mineral salts may diffuse through cell membranes directly through lipid bilayer but mainly through transmembrane **ion-selective protein channels** or **transmembrane carrier proteins**. Carrier or channel mediated passive transport of mineral salts across the membrane is also called as **facilitated diffusion** (Fig. 7.6).

(2) ACTIVE ABSORPTION OF MINERAL SALTS

It has often been observed that the cell sap in plants accumulates large quantities of mineral salts ions **against the concentration gradient**. For example in alga *Nitella* the cell sap contains hundreds times greater than in the pond water in which the plant was growing.

This cannot be explained by simple diffusion or Donnan's Equilibrium and has led people to believe that absorption and accumulation of mineral salts **against the concentration gradient** is an **active process** which involves the **expenditure of metabolic energy** through respiration. Following evidences favour this view :

- (i) the factors like low temp., deficiency of O_2 , metabolic inhibitors etc. which inhibit metabolic activities like respiration in plants also **inhibit accumulation of ions**.

(ii) rate of respiration is increased when a plant is transferred from water to salt solution (Salt Respiration).

It has now been accepted that active absorption of mineral salts involves the operation of a carrier compound present in the plasma membrane of the cells.

THE CARRIER CONCEPT

According to this theory the plasma membrane is impermeable to free ions. But some compound present in it acts as carrier and combines with ions to form carrier-ion-complex which can move across the membrane. On the inner surface of the membrane this complex breaks releasing ions into the cell while the carrier goes back to the outer surface to pick up fresh ions (Fig. 7.2).

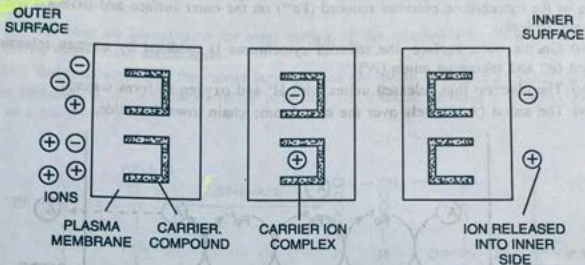


Fig. 7.2. Diagrammatic representation of a model illustrating the carrier concept.

Following observations strongly support the carrier concept of active absorption of mineral salts :

(i) Isotopic Exchange

Several times, it has been found that actively absorbed radio active ions (such as $^{35}\text{SO}_4$) cannot diffuse back or be exchanged with other ions in the outer solution indicating thereby that the plasma membrane is not permeable to free ions.

(ii) Saturation Effects

Beyond a certain limit, increased concentration of salts in outer solution does not bring about an increase in the rate of mineral salt absorption. It is because the active sites on the carrier compound become saturated with ions.

(iii) Specificity

Active sites on carrier compound may be specific which can bind only some specific ions. This also explains the selective and unequal absorption of ions by the plants.

There are two common hypotheses based on the carrier concept to explain the mechanism of active salt absorption, although they are not universally accepted.

(1) Lundegardh's Cytochrome Pump Theory

Lundegardh and Burstrom (1933) believed that there was a definite correlation between respiration and anion absorption. Thus when a plant is transferred from water to a salt solution the rate of respiration increases. This increase in rate of respiration over the normal respiration has been called as anion respiration or salt respiration.

The inhibition of salt respiration and the accompanying absorption of anions by CO and cyanides (which are known inhibitors of *cytochrome oxidase* of electron transport chain in mitochondria), later on led **Lundegardh** (1950, 54) to propose cytochrome pump theory which is based on the following assumptions :

- (i) the mechanism of anion and cation absorption is different.
- (ii) anions are absorbed through cytochrome* chain by an active process.
- (iii) cations are absorbed passively.

According to this theory (Fig. 7.3), (i) **dehydrogenase reactions** on inner side of the membrane give rise to protons (H^+) and electrons (e^-).

(ii) The electron travels over the cytochrome chain towards outside the membrane, so that the Fe of the cytochrome becomes reduced (Fe^{2+}) on the outer surface and oxidised (Fe^{3+}) on the inner surface.

(iii) On the outer surface, the reduced cytochrome is oxidised by oxygen releasing the electron (e^-) and taking an anion (A^-).

(iv) The electron thus released unites with H^+ and oxygen to form water.

(v) The anion (A^-) travels over the cytochrome chain towards inside.

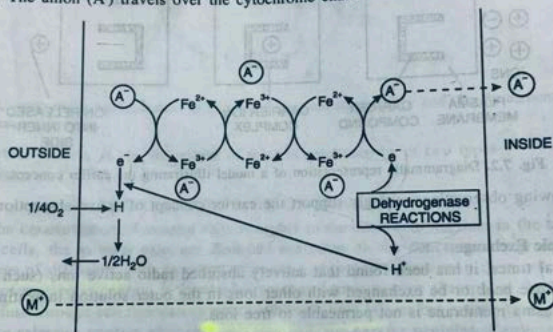


Fig. 7.3 Diagrammatic representation of the Lundegardh's cytochrome pump theory.

(vi) On the inner surface the oxidised cytochrome becomes reduced by taking an electron produced through the dehydrogenase reactions, and the **anion (A^-) is released**.

(vii) As a result of anion absorption, a **cation (M^+) moves passively** from outside to inside to balance the anion.

Main defects of the above theory are :

- (i) It envisages active absorption of only anions.

* (Cytochromes are iron-porphyrin proteins that act as enzymes and help in some oxidation-reduction reactions in the cells. These are very important intermediate 'one electron redox-systems' of electron transport chains in chloroplasts and mitochondria transferring electrons from one end of the chain to other along an electrochemical gradient. Cytochromes are usually divided into 3 classes; cytochromes *a*, *b* and *c*.)

oxidation is a chemical process in which a substance gains oxygen or loses electrons and hydrogen

(ii) It does not explain selective uptake of ions.

(iii) It has been found that cations also stimulate respiration.

(2) Bennet-Clark's Protein-Lecithin Theory

In 1956, **Bennet-Clark** suggested that because the cell membranes chiefly consist of phospholipids and proteins and certain enzymes seem to be located on them, the carrier could be a **protein associated with the phosphatide called as lecithin**. He also assumed the presence of different phosphatides to correspond with the number of known competitive groups of cations and anions (which will be taken inside the cell).

According to this theory (Fig. 7.4), (i) the phosphate group in the **phosphatide** is regarded as the active centre binding the cations, and the basic **choline** group as the anion binding centre.

(ii) The ions are liberated on the inner surface of the membrane by decomposition of the lecithin by the enzyme **lecithinase**.

(iii) The regeneration of the carrier lecithin from phosphatidic acid and choline takes place in the presence of the enzymes **choline acetylase** and **choline esterase** and ATP. The latter acts as a source of energy.

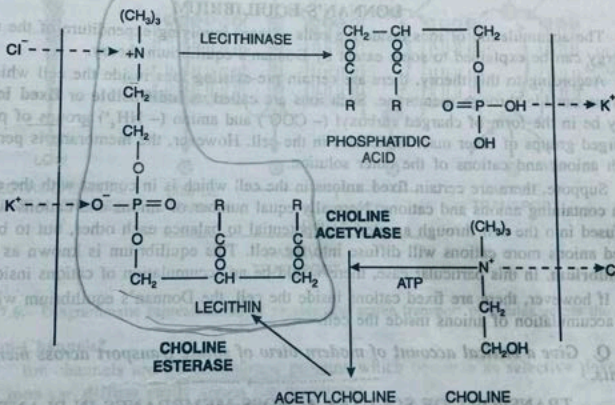


Fig. 7.4. Diagrammatic representation of the Bennet-Clark's Protein-Lecithin theory.

Once inside the epidermal cells of the root, the mineral salts in their ionic form move from one cell to another by (i) **apoplastic pathway** (i.e., through cell walls and intercellular spaces), (ii) **trans membrane pathway** (i.e., by crossing the membranes) and (iii) **symplastic pathway** (i.e., through plasmodesmata), and ultimately reach to xylem vessels and tracheids (Fig. 7.5) from where they are carried to different parts of the shoot along with ascent of sap.

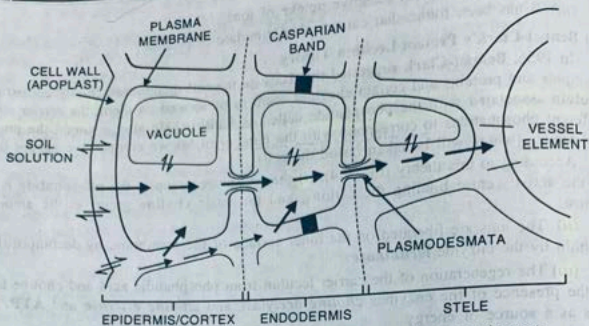


Fig. 7.5. Radial paths of movement of mineral nutrient ions in root

DONNAN'S EQUILIBRIUM

The accumulation of ions inside the cells without involving expenditure of the metabolic energy can be explained to some extent by Donnan's equilibrium theory.

According to this theory, there are certain pre-existing ions inside the cell which cannot diffuse outside through membrane. Such ions are called as **indiffusible** or **fixed ions** which may be in the form of charged carboxyl ($-COO^-$) and amino ($-NH_4^+$) groups of proteins or charged groups of other macromolecules in the cell. However, the membrane is permeable to both anions and cations of the outer solution.

Suppose, there are certain **fixed anions** in the cell which is in contact with the outer solution containing anions and cations. Normally equal number of anions and cations would have diffused into the cell through an electrical potential to balance each other, but to balance the fixed anions more cations will diffuse into the cell. This equilibrium is known as **Donnan's equilibrium**. In this particular case, there would be an accumulation of cations inside the cell.

If however, there are fixed cations inside the cell, the Donnan's equilibrium will result in the accumulation of anions inside the cell.

Q. Give a critical account of modern view of solute transport across membranes in plants.

TRANSPORT OF SOLUTES ACROSS MEMBRANES IN PLANTS

As has been discussed earlier, the **mineral salts** are absorbed by plants in their **ionic form** and so is their transport within plants. Certain solutes such as **sugars** are however transported across the membranes in **uncharged state**.

For **uncharged solutes (non-electrolytes)**, their movement across the membrane depends upon their **concentration gradient i.e., gradient of chemical potential only** on two sides of the membrane. But, in case of charged solutes or ions (**electrolytes**) the situation becomes different. Since, charged solutes or ions carry an **electric charge**, their movement across the membrane depends not only on their chemical potential but also on their **electrical potential**. In other words, transport of ions across the membrane depends upon their **electro-chemical potential gradient**. Therefore, **electrical properties of the cell or its trans membrane potential** is a very important component of ions transport through membranes.

In either case, the transport of solutes across the membrane is called as **passive transport** if it is along the **chemical potential gradient** or **electrochemical potential gradient** (for non-electrolytes and electrolytes respectively). When solute transport across the membrane occurs **against the chemical potential gradient** or **electrochemical potential gradient**, it is called as **active transport** and requires **additional input of energy** (Fig. 7.6).

The movement of solutes into the cytosol through membrane (such as plasmamembrane or tonoplast) is called as **influx** while their exit from the cytosol is termed as **efflux**.

In recent years much work has been done on permeability of cell membranes especially **plasmamembrane** and **tonoplast (vacuolar membrane)** and various **trans membrane transporters (proteins)** have been identified in them which enhance movement of solutes across such membranes. These transporter proteins are **highly specific** with complex structure and different models have been given by scientists to explain their functioning. These **membrane transporter proteins** can be grouped in three categories, (i) **ion-channels**, (ii) **carriers** and (iii) **pumps** (Fig. 7.6).

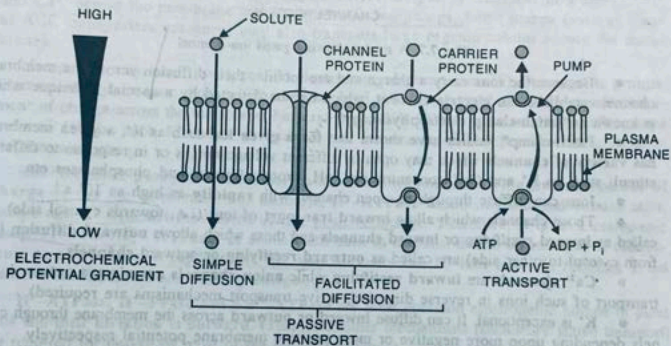


Fig. 7.6. Diagrammatic representation of passive and active transport of solutes across the membrane.

1. Ion-Channels*

- Ion-channels are **transmembrane proteins** which function as **selective pores** through which **ions** can **diffuse** easily across the membrane.
- Ion-channels are usually **highly specific** for one or limited number of ion species. The **specificity** depends upon the **size of the pore** and density of **surface electric charges** on its interior lining more than on selective binding of ions.
- **Transport of ions through channels is always passive.**
- The channels are not open all the time but are '**gated**' (Fig. 7.7). The gates open or close in response to external stimuli that include, (i) **voltage changes**, (ii) **light**, (iii) **hormone binding** and (iv) **ions themselves**. When gates are open, the ions can diffuse through the channels but not when they are closed.

The channel proteins are believed to contain a **sensing region** or **sensor** which responds to the appropriate stimulus by changing conformation of channel protein opening the **gate**.

* **Roderick Mackinnon**, An American Biophysicist got Nobel Prize of 2003 in Chemistry in recognition for his structural and mechanistic studies of ion-channels.

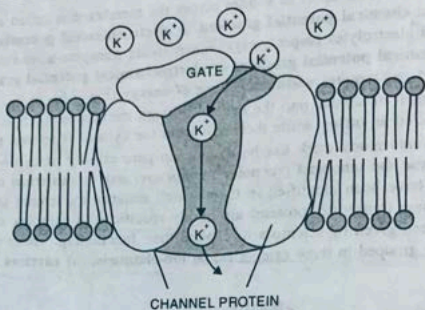


Fig. 7.7. A model showing gated ion-channel

• Because the ions carry a charge and are mobile, their diffusion across the membrane channel establishes an **electric current**, which can be detected by a special technique which is known as '**patch-clamp electrophysiology**'.

• Patch-clamp* studies have shown that for a given ion such as K^+ , a given membrane has **variety of channels** which may open in different voltage ranges or in response to different stimuli such as K^+ and Ca^{2+} concentrations, pH, protein kinases and phosphatases etc.

• Ions can diffuse through an open channel with **rapidity** as high as 10^8 s^{-1} .

• Those channels which allow **inward transport** of ions (*i.e.*, towards cytosol side), are called as **inward rectifying** or **inward channels** and those which allows **outward diffusion** (*i.e.*, from cytosol to other side) are called as **outward rectifying** or **outward channels**.

• **Ca^{2+} channels are inward rectifying while anion channels are always outward**, (for transport of such ions in reverse direction, active transport mechanisms are required)

• K^+ is exceptional. It can diffuse **inward or outward** across the membrane through channels depending upon more negative or more positive membrane potential respectively.

• Many **channel proteins are inducible** *i.e.*, they are **synthesized by the cell** when a particular solute is available for absorption.

(Some **slow vacuolar (SV) channels** may be present on tonoplast which allow diffusion of some cations and also anions from vacuole to cytosol).

2. Carriers

• These transmembrane transporter proteins **do not form pores** in membrane, instead they **selectively bind the solute** to be transported to a **specific site** on them. This causes **conformational change** in carrier protein which exposes the solute to other side of the membrane. After the **solute is released** from the binding site, the **carrier protein reverts back to its original conformation** to pick up a fresh solute molecule or ion (Fig. 7.2). Thus, binding and release of solute through carrier is **similar to an enzyme catalysed reaction**.

• Carrier mediated transport of solutes enables transport of much wider range of solutes, but is **slower** (about $10^4 - 10^5 \text{ s}^{-1}$) as compared to **channel mediated solute transport**.

• Carrier mediated solute transport may be of two types, (i) **passive transport** and (ii) **active transport**.

• Patch-clamp technique was invented by two German Scientists, Erwin Neher and Bert Sakmann Nobel Laureates of 1991 in Physiology or Medicine category.

Passive Transport

• Carrier mediated passive transport of solutes occurs along the electrochemical potential gradient and does not require expenditure of energy. This has also been called as **facilitated diffusion**. According to some scientists, both carrier mediated passive transport and channel mediated transport should come under the purview of facilitated diffusion.

Active Transport.

• Carrier mediated active transport of solutes takes place against the electrochemical potential gradient and requires additional input of energy that chiefly comes from hydrolysis of ATP. In such cases, the carrier proteins are called as 'pumps' and the transport of solutes is called as **primary active transport** because it directly utilizes energy from hydrolysis of ATP.

3. Pumps

As mentioned earlier, the membrane transporter proteins involved in primary active transport of solute are called as **pumps**. Most of the pumps transport ions such as H^+ and Ca^{2+} across the membrane and are known as **ion-pumps**. Some pumps (such as those of ABC transporters category) may also transport large organic solutes across the membranes.

Ion-pumps may be of two types, (i) **electroneutral pumps** and (ii) **electrogenic pumps**. Electroneutral pumps are those which are associated with transport of ions with no net movement of charge across the membrane. For example $H^+/K^+-ATPase$ of some animal cells, pumps out one H^+ for each K^+ taken in with no net movement of charge. Therefore, it is an electroneutral pump.

Electrogenic pumps on the other hand, transport ions involving net movement of charge across the membrane. For example, $H^+-ATPase$ found in plant and animal cells, pumps out H^+ with net movement of one positive charge. Therefore, it is an electrogenic pump. (The $Na^+/K^+ - ATPase^*$ of animal cells such as neurons, is also an example of electrogenic pumps because it expels three Na^+ ions for every two K^+ ions taken in resulting in net outward movement of one positive charge.)

$H^+-ATPase$, $H^+-PPase$ and $Ca^{2+}-ATPase$ are most common electrogenic pumps in plant cells and their direction is outward. (Therefore, other mechanisms (secondary active transport) are required for uptake of most of the mineral nutrients).

A brief account of some of the most common pumps in plant cells is as follows:

(i) Proton-ATPase Pumps ($H^+-ATPases$)

These pumps are also known as **P-type ATPases** and are found in plasmamembrane, tonoplast and possibly other cell membranes. These are structurally distinct and operate in reverse of F-type ATPases i.e., they hydrolyse ATP instead of synthesizing it (ATPases of mitochondria and chloroplast are also known as F-type ATPases)

Fig 7.8 shows a model of plasma membrane $H^+-ATPase$ (also known as P-type ATPase). This enzyme protein is a **single chain polypeptide with 10 hydrophobic trans membrane segments or domains** (only three of these are shown as helical coils while others are shown as cylinders in the figure). These segments are joined by **hydrophilic loops** which project in cytosol and cell wall (apoplast). The **ATP binding site** is believed to be an **aspartic acid residue (D)** situated on loop connecting 4th and 5th segments towards cytosolic side. **Hydrolysis of ATP causes conformational change** in the protein and one H^+ ion is transported from cytosol to outside across the plasmamembrane.

* $Na^+/K^+ - ATPase$, first discovered by Jens C. Skou, Nobel Laureate of 1997 in Chemistry.

Q. Give an account of mycorrhizae and their role in absorption of mineral salts by higher plants.

MYCORRHIZAE AND THEIR ROLE IN ABSORPTION OF MINERAL SALTS

The association of a fungus with root of a plant is called as mycorrhiza (plural, mycorrhizae).

Mycorrhizae play very important and significant role in facilitating absorption of mineral salts by plant roots through them. In nature, more than 80% angiosperms (both dicots and monocots) including virtually all plant species of economic importance and almost all gymnosperms are known to form mycorrhizal associations. However, mycorrhizae are rarely present in (i) aquatic plants, (ii) plants belonging to the families Brassicaceae, Chenopodiaceae and Proteaceae, (iii) hydroponically grown plants, (iv) young rapidly growing crop plants and (v) plants growing in flooded or very dry or saline soils or soils with very low or very high fertility.

- The relationship of mycorrhizae is symbiotic or of mutualism in which both partners are benefited. The fungus absorbs mineral salts from the soil and releases them into cells of host root. In return, the host root cells provide carbohydrates supply to the fungus.

- The mycorrhizal fungi extend the rhizosphere and also the nutrient depletion zone in the soil (Fig. 7.11). This greatly facilitates absorption of mineral elements especially those which are less soluble and relatively immobile in soil such as phosphorous.

(The limits of soil from where roots are able to readily extract mineral nutrients constitute the nutrient depletion zone).

Those parts of mycorrhizal fungi which are in direct contact with organic litter in the soil, may also hydrolyze complex organic compounds to release minerals which are subsequently absorbed by them.

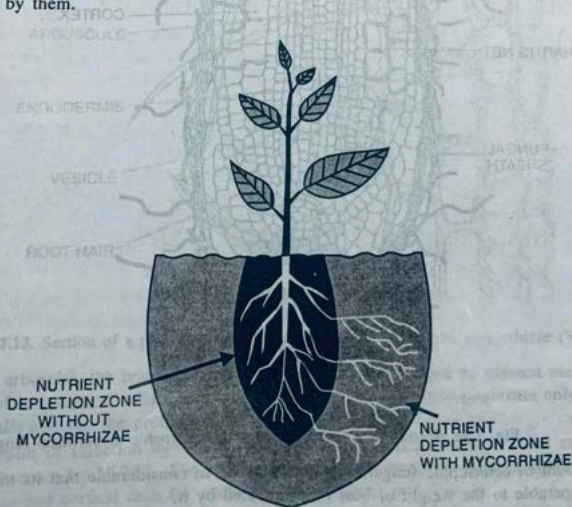


Fig. 7.11. Extension of nutrient depletion zone in the soil by mycorrhizae.

Numerous studies done with **pin**es and other **tree seedlings** by scientists in U.S.A., Australia and other countries have shown an increase of 30-150% in dry weight of seedlings infected with mycorrhizal fungi as a result of increased absorption of mineral salts through mycorrhizae as compared to non-infected controls. Similar results have also been obtained with **agricultural plants** like maize.

The mycorrhizal fungi many of which are specific to host species may be grouped in two categories (i) **ectotrophic mycorrhizae** and (ii) **vesicular arbuscular mycorrhizae (VAM)**.

I. Ectotrophic Mycorrhizae

These mycorrhizae form a **thick mantle** around the roots, part of which enters in between the cortical cells of the roots (without penetrating them) and forming an **intercellular network of hyphae** which is called as **Hartig net** (Fig. 7.12). Some of the hyphae from thick mantle around the roots extend into the soil reaching beyond **nutrient depleted areas** of the soil near the roots to tap fresh supply of mineral nutrients. *Eg: Basidiomycetes*

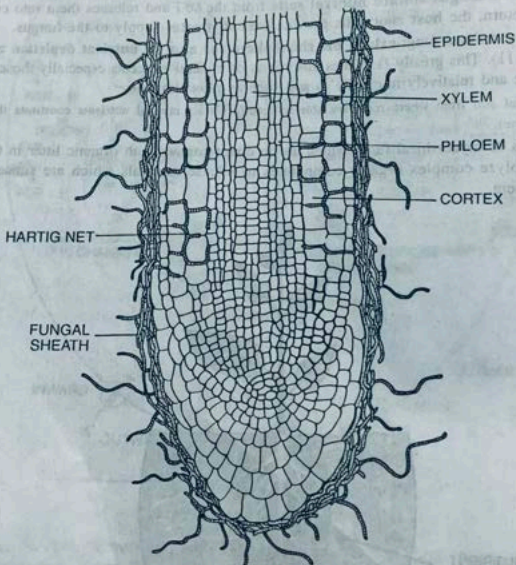


Fig. 7.12. Section of a root infected with ectotrophic mycorrhizal fungi.

The amount of ectotrophic fungal mycelium may be so considerable that its total weight may be comparable to the weight of host roots infected by it.

- Ectotrophic mycorrhizal fungi infect exclusively **gymnosperms** (such as pines) and **woody angiosperms**.

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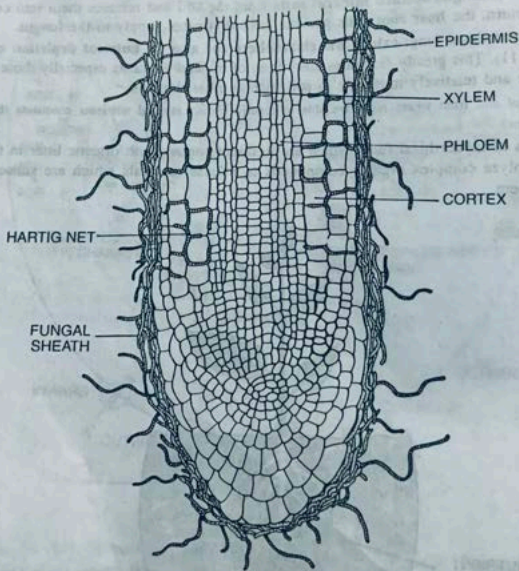


Fig. 7.12. Section of a root infected with ectotrophic mycorrhizal fungi.

The amount of ectotrophic fungal mycelium may be so considerable that its total weight may be comparable to the weight of host roots infected by it.

● Ectotrophic mycorrhizal fungi infect exclusively **gymnosperms** (such as pines) and **woody angiosperms**.

• The mineral salts absorbed by ectotrophic mycorrhizal fungi directly diffuse into cortical cells of host roots through Hartig net.

2. Vesicular Arbuscular Mycorrhizae (VAM)

Vesicular arbuscular mycorrhizal fungi infect roots of most of the species of herbaceous angiosperms, but unlike ectotrophic mycorrhizae do not form a thick mantle around the roots. Their total weight also is far lesser (about 10%) as compared to weight of roots which they infect.

The mycelium of VAM penetrates the host roots through root hairs and epidermal cells. The hyphae extend in between the cortical cells and also penetrate the latter where they form small ellipsoid oval structures called as vesicles and highly branched tree like structures called as arbuscles (Fig. 7.13).

Eg: Zygomycetes.

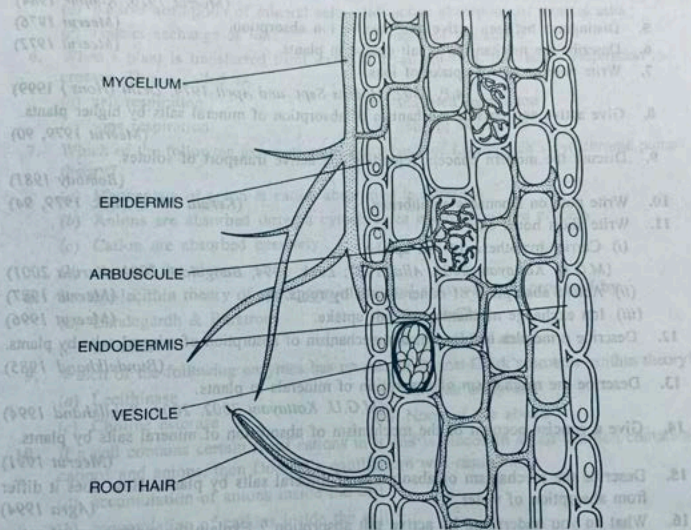


Fig. 7.13. Section of a plant root infected with vesicular-arbuscular mycorrhizae (VAM)

• In arbuscles, the branches of fungal hyphae are surrounded by plasma membrane or tonoplast of host cortical cells. Therefore, the fungal hyphae actually penetrate only the cortical cell walls and not the protoplast.

As a result of infection by VAM, the cytoplasmic volume of the cortical cells of host roots may increase by 20-25%. The arbuscles serve to increase the contact surface area between hyphae and cortical cells for exchange of nutrients by 2-3 times.

In VAM, the minerals may diffuse from arbuscles to cortical cells of host root either (i) directly or (ii) by releasing their contents into the latter when they disintegrate.

15

TRANSLOCATION OF ORGANIC SOLUTES

Q. Write an essay on translocation of organic solutes in higher plants.

The movement of organic food materials or the solutes in soluble form from one place to another in higher plants is called as **translocation of organic solutes**.

Translocation of organic solutes is essential in higher plants because :-

(i) In higher plants, only the green parts can manufacture food and it must be supplied to other non-green parts for consumption and also for storage.

(ii) During the germination of the seeds, the insoluble reserve food material of the seed is converted into soluble form and is supplied to the growing regions of young seedling till it has developed its own photosynthetic system i.e., leaves.

Translocation of organic solutes always takes place from the region of higher concentration of soluble form i.e., the supply end (source) to the region of lower concentration of its soluble form i.e., the consumption end (sink).

DIRECTIONS OF TRANSLOCATION

Translocation of organic solutes may take place in the following directions :—

1. Downward Translocation

Mostly, the organic food material is manufactured by leaves and is translocated downward to stem and the roots for consumption and storage.

2. Upward Translocation

It takes place mainly during the germination of seeds, tubers etc. when stored food after being converted into soluble form is supplied to the upper growing parts of the young seedling till it has developed green leaves.

Upward translocation of solutes also takes place through stem (i) to buds which resume growth in the spring (ii) to developing leaves situated closer to its apex (iii) to opening flowers and developing fruits which are situated near the ends of the branches.

3. Radial Translocation

Radial translocation of organic solutes also takes place in plants from the cells of the pith to cortex.

PATH OF THE TRANSLOCATION OF ORGANIC SOLUTES

Path of Downward Translocation

Downward translocation of the organic solutes takes place through **phloem**. This view is supported by the following evidences :—

(i) Tissues other than phloem cannot account for downward translocation. Ascent of sap takes place through xylem, so naturally organic solutes are not translocated through it. The

cells of the ground tissue are structurally neither suitable for translocation nor they contain soluble organic solutes which could be translocated. These cells usually have organic solutes in insoluble form.

Thus, only phloem is left which can account for translocation of the organic solutes. The end to end arrangement of the sieve tubes in phloem whose cross walls are perforated by sieve pores form continuous channels and is best suited for it (Fig. 15.1). Further, in Cucurbits where the leaves are usually larger, the stem contains **bicollateral** vascular bundles to cope with the rapid translocation of food materials through it.

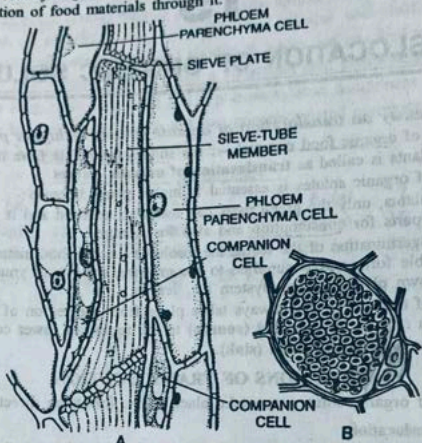


Fig. 15.1 (A) Sieve tubes along with companion cells and phloem parenchyma cells in longitudinal section. (B) Face views of a sieve plate showing sieve pores represented by black areas.

(ii) **Blocking of phloem.** Translocation of food materials stops when sieve pores are plugged due to the deposition of a chemical compound, the callose.

(iii) **Chemical analysis of phloem sap.** Cells of phloem contain large quantities of organic solutes mainly sugars such as sucrose in soluble form.

(iv) **Isotopic studies.** It has been observed that if a leaf of the plant is allowed to photosynthesize in presence of labelled ^{13}C , the translocation of carbohydrates labelled with ^{13}C isotope takes place through the stem. But, if some segments of the stem including phloem were killed by hot wax, no movement of carbohydrates could be detected.

(v) **Ringing experiment.** If a ring of bark including phloem is removed from the stem of a plant, the downward translocation of food material stops and food material accumulates just above the ring. As a result after some time, the tissue above the ring swells and may even develop adv. roots (Fig. 15.2) while the lower parts of the plant below the ringed portion gradually dry up.

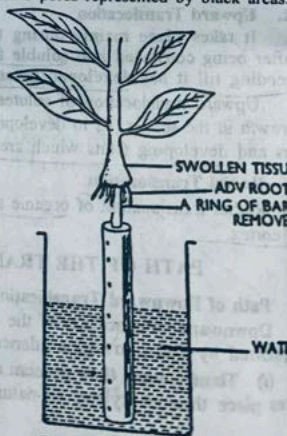


Fig. 15.2. Ringing experiment.

2. Path of upward translocation

There has been controversy regarding the path of upward translocation of organic solutes in plants. Although translocation of organic solutes takes place through phloem, but under certain conditions it may take place through xylem.

3. Path of Radial Translocation

Radial translocation of organic solutes from pith to cortex takes place through medullary rays.

MECHANISM OF TRANSLOCATION THROUGH PHLOEM

Various theories have been put forward to explain the mechanism of phloem conduction but they are not fully satisfactory. Among them Munch's (1930) hypothesis is most convincing.

MUNCH'S MASS FLOW OR PRESSURE FLOW HYPOTHESIS

According to this hypothesis put forward by Munch (1930) and elaborated by Craft (1938) and others, the translocation of organic solutes takes place *en mass* through phloem along a gradient of turgor pressure from the region of higher conc. of soluble solutes *i.e.*, supply end to the region of lower conc. *i.e.*, consumption end.

The principle involved in this hypothesis can be explained by a simple physical system as shown in the Fig. 15.3.

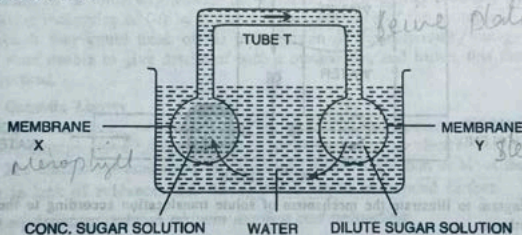


Fig. 15.3. Diagram illustrating the principle of Munch's Mass Flow hypothesis.

Two membranes X and Y permeable only to water and dipping in water are connected by a tube T to form a closed system. Membrane X contains more concentrated sugar solution than in membrane Y.

Due to higher osmotic pressure of the concentrated sugar solution in membrane X, water enters into it so that its **turgor pressure** is increased. The increase in the turgor pressure results in **mass flow** of sugar solution to membrane Y through the tube T till the concentration of sugar solution in both the membranes is equal.

If in the above system it could be possible to maintain continuous supply of sugars in membrane X and its utilization or conversion into insoluble form in membrane Y, the flow of sugar solution from X to Y will continue indefinitely.

According to Munch's hypothesis, a similar analogous system for the translocation of organic solutes exists in plants. As a result of photosynthesis, the **mesophyll cells** in the leaves contain higher concentration of organic food material in them in soluble form and correspond to membrane X or supply-end. The cells of **stem** and **roots** where the food material is utilized

or converted into insoluble form correspond to membrane Y or consumption end. While the sieve tubes in phloem which are placed end to end correspond to the tube T.

Mesophyll cells draw water from the xylem of the leaf due to higher osmotic pressure and suction pressure of their sap so that their turgor pressure is increased. The turgor pressure in the cells of stem and the roots is comparatively low and hence, the soluble organic solutes begin to flow en mass from mesophyll through phloem down to the cells of stem and the roots under the gradient of turgor pressure. In the cells of stem and the roots the organic solutes are either consumed or converted into insoluble form and the excess water is released into xylem through cambium (Fig. 15.4).

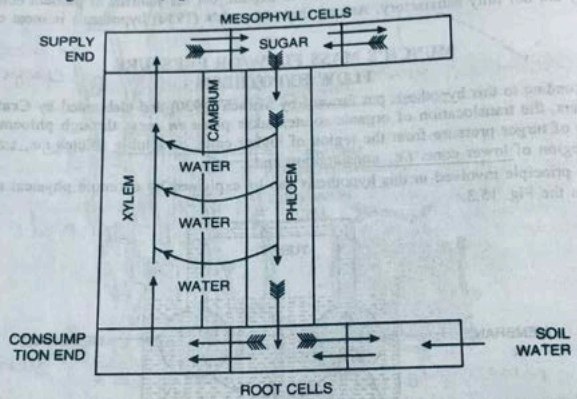


Fig. 15.4. Diagram to illustrate the mechanism of solute translocation according to the Munch's hypothesis.

Demerits of Munch's Hypothesis

- (1) This hypothesis accounts for the translocation in only one direction at a time, although there may be simultaneous upward and downward translocation of solutes.
- (2) There is considerable doubt regarding the magnitude of the turgor pressure at the supply end which may not be sufficient enough to overcome the resistance offered by the sieve plates in the translocation of solutes through sieve tubes.
- (3) Turgor pressure may not always be higher at the supply end.
- (4) This hypothesis is based on purely physical assumptions and does not take into account the fact that whole of the translocation process is dependent upon the plant's metabolism and the metabolic energy.

OTHER THEORIES OF MECHANISM OF TRANSLOCATION

(1) Protoplasmic Streaming Theory

According to this hypothesis first proposed by De Vries (1885) and later supported by Curtis (1935) protoplasmic streaming occurs in sieve tube elements of phloem and the molecules caught up in the circulating cytoplasm are carried from one end to the other end of the sieve tube from where they diffuse to the next sieve tube elements through the cytoplasmic strands in the sieve plates.

This theory was supported because (i) it accounted for simultaneous movement of solutes in both upward and downward directions in the same sieve tube and (ii) that the factors like low temperature and oxygen deficiency which retard protoplasmic streaming also checked the translocation of solutes.

But, the strongest objection against this theory is that the protoplasmic streaming has not been observed in mature sieve tube elements.

Protoplasmic theory has recently been re-emphasized by Cany (1952) and Thaine (1962, 64) who observed the 'transcellular strands' (cytoplasmic strands) traversing the sieve tube elements in petiolar tissue. They also observed (i) the movement of solute particles from one sieve tube element to another and (ii) particles moving in opposite directions in adjacent transcellular strands in the same sieve tube element.

(2) Interfacial Flow Hypothesis

According to this hypothesis proposed by Van den Honert (1932) the solute particles could move along the interfaces such as between the vacuole and the protoplast. But this theory did not find support, the main objection against this theory being (i) the lack of evidences in support of such a mechanism in plants and (ii) that the plant membranes are not static but constantly changing.

(3) Activated Diffusion Hypothesis

According to this hypothesis put forward by Mason and Phillis (1936) the protoplasm of sieve tube elements in some way hastens the diffusion of the solutes probably (i) by activating the diffusing molecules or (ii) by decreasing the resistance of the protoplasm to their diffusion. Although they could think of the participation of the respiratory energy during this process but were unable to give details of such a mechanism, and hence, this theory also has not been accepted.

(4) Electro-Osmotic Theory

According to this theory put forward by Fensom (1957) and Spanner (1958) the translocation of solutes through sieve tubes takes place probably due to an electric potential across the sieve plates. The electric-potential could be maintained by the circulation of K^+ at the sieve plates.

But due to lack of evidences this theory could not be elaborated further.

Q. Write an explanatory note on phloem loading and unloading.

PHLOEM LOADING AND UNLOADING

As mentioned earlier, translocation of organic solutes such as sucrose (i.e., photosynthates) takes place through sieve tube elements of phloem from **supply end** (or **source**) to **consumption end** (or **sink**). But, before this translocation of sugars could proceed, the soluble sugars must be transferred from mesophyll cells to sieve tube elements of the respective leaves. This transfer of sugars (photosynthates) from mesophyll cells to sieve tube elements in the leaf is called as **phloem loading**. On the other hand, the transfer of sugars (photosynthates) from sieve tube elements to the receiver cells of consumption end (i.e., sink organs) is called as **phloem unloading**. Both are energy requiring processes.

PHLOEM LOADING

As a result of photosynthesis, the sugars such as sucrose produced in mesophyll cells move to the sieve tubes of smallest veins of the leaf either directly or through only 2-3 cells depending upon the leaf anatomy. Consequently, the concentration of sugars increases in sieve tubes in comparison to the surrounding mesophyll cells.

The movement of sugars from mesophyll cells to sieve tubes of phloem may occur either through **symplast** (i.e., cell to cell through plasmodesmata, remaining in the cytoplasm) or the sugars may enter the **apoplast** (i.e., cell walls outside the protoplasts) at some point en route to phloem sieve tubes. In the latter case, the sugars are actively loaded from apoplast to

sieve tubes by an energy driven transport located in the plasmamembrane of these cells. The mechanism of phloem loading in such case has been called as **sucrose-H⁺ symport or cotransport mechanism**. According to this mechanism (Fig. 15.5) protons (H⁺) are pumped out through the plasmamembrane using the energy from ATP and an ATPase carrier enzyme, so that concentration of H⁺ becomes higher outside (in the apoplast) than inside the cell. Spontaneous tendency toward equilibrium causes protons to diffuse back into the cytoplasm through **sucrose-H⁺ symporter** located in the plasmamembrane.

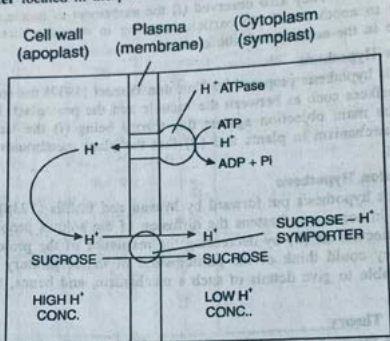


Fig. 15.5. Sucrose-H⁺ symport or cotransport mechanism.

The mechanism of the transfer of sugars (sucrose) from mesophyll cells to apoplast is however, not known.

Phloem loading is specific and selective for transport sugars.

Both symplastic and apoplastic pathways of phloem loading are used in plants but in different species. In some species however, phloem loading may occur through both the pathways in the same sieve tube element or in different sieve tube elements of the same vein or in sieve tubes in veins of different sizes.

Experimental findings have revealed certain patterns in apoplastic and symplastic loading of sugars in phloem (Table 15.1), which appears to be related with the type of sugar transported to phloem, type of companion cells (ordinary, transfer or intermediary) and number of plasmodesmata (few or abundant) connecting the sieve tubes (including the companion cells) to surrounding cells in smaller veins.

Table 15.1 Patterns in apoplastic and symplastic phloem loading.

	Apoplastic loading	Symplastic loading
Type of sugar transported	Sucrose	Sucrose + other oligosaccharides
Type of companion cells in the small veins	Ordinary or transfer cells	Intermediary cells
Number of plasmodesmata connecting the sieve tubes (including companion cells) to surrounding cells	Fewer	Abundant

To some extent, phloem loading is also correlated with the family of plant, its habit (trees, shrubs, vines or herbs) and climate such as temperate, tropical or arid climate.

(After phloem loading, the sugars are translocated to consumption end or sink organs by mass flow as has been described earlier in this chapter).

PHLOEM UNLOADING

It occurs in the consumption end or sink organs (such as developing roots, tubers, reproductive structures etc.) Sugars move from sieve tubes to receiver cells in the sink involving following steps :

(i) **Sieve element unloading.** In this process, sugars (imported from the source) leave sieve elements of sink tissues.

(ii) **Short distance transport.** The sugars are now transported to cells in sink by a short distance pathway which has also been called as post-sieve element transport.

(iii) **Storage and metabolism.** Finally, sugars are stored or metabolized in the cells of the sink.

As with the phloem loading process, sucrose unloading also occurs through symplast via plasmodesmata or through apoplast at some point en route to sink cells.

Phloem unloading is typically symplastic in growing and respiring sinks such as meristems roots, and young leaves etc. in which sucrose can be rapidly metabolized. (Young leaves act as sink until their photosynthetic machinery is fully developed, at which point they become sources).

Usually, in storage organs such as fruits (grape, orange etc.), roots (sugar beet) and stems (sugarcane), sucrose unloading is known to occur through apoplast. However, according to Oparka (1986), phloem unloading in potato tubers from sieve elements to cortical cells is a symplastic passive process.

Because, there are wide varieties of sinks in plants which differ in structure and function, no one scheme of phloem unloading is available.

Q. What is assimilates partitioning? Give a brief account of the factors that control translocation of assimilates and their partitioning in higher plants.

ASSIMILATES PARTITIONING

The products of carbon assimilation or photosynthesis such as **hexoses, sucrose, starch** etc. (i.e., fixed carbon) are called as **photosynthates** or **photoassimilates** or simply as **assimilates**. These assimilates are produced in green leaves of higher plants which constitute the **sources**. Within various compartments of photosynthesizing cells (sources), these assimilates are (i) **metabolically utilized**, (ii) **stored** or (iii) **converted into transport sugars** mainly **sucrose** for export to various sinks (through phloem) such as **young leaves, roots, tubers, stems, fruits and seeds**. At the sinks, assimilates are **metabolically utilized** and/or **stored** in **receiver cells** of sinks. Depending upon the nature and specific requirement of the sinks, the photoassimilates are differentially distributed in different sinks. This **differential distribution of photoassimilates** in different sinks of plant is called as **assimilates partitioning**.

Usually, the amount of assimilates transported to the **harvest organ** is much more in comparison to other organs of the plant. Therefore, transport of assimilates and their partitioning are of great research interest in agricultural plant physiology because of their roles in **crop productivity**.

Although attempts to increase photosynthetic activities of the leaves have met with only very little success, but the **harvest index** (i.e., the ratio of the harvest yield such as grains to the total shoot yield) or yields of many crop plants such as **oats, barley, wheat, cotton, soybean, peanuts** etc., has considerably been increased during recent years by sustained **plant breeding efforts** in selecting and developing varieties with improved transport of assimilates to edible or economically important portions of the plant.