Unit

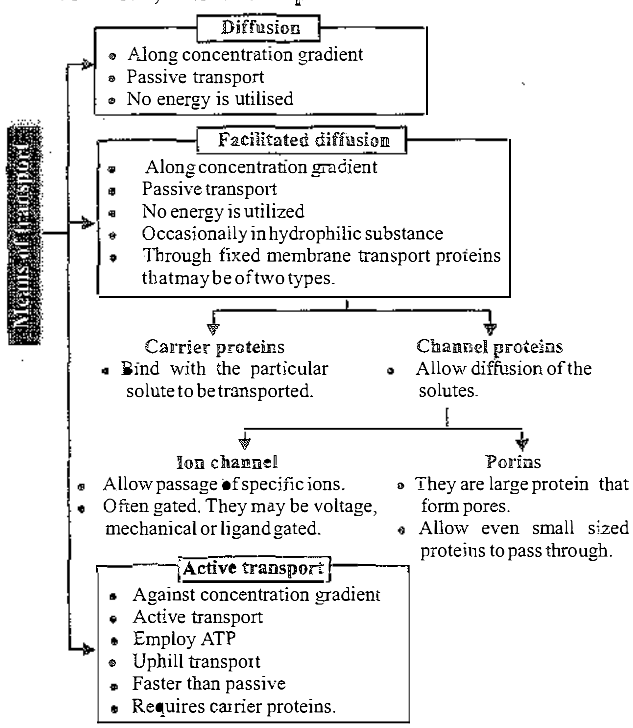
4 Plant Physiology

TRANSPORT IN PLANTS

- In Plants, substances like growth regulators, nutrients, water, prepared food etc. have to be transported from one plant part to another. Water taken up by the roots has to reach all parts of the plant, up to the very tip of the growing stem.
- Over small distances, substances move from cell to cell and no specialized tissues are required. Inside cell, it occurs by cytoplasmic streaming.
- The transport of substances over longer distances through the vascular tissue, *i.e.*, **xylem** and **phloem**, is called **translocation**. It occurs through mass flow. The direction of translocation is essentially **unidirectional in** case of water (from root to stem, leaves, flowers and fruits). It is **multidirectional** in case of minerals and organic solutes.

TRANSPORT METHODS

- Passage of materials into and out of the cells is carried out by a number of methods *viz.* **diffusion, facilitated diffusion, active transport**.



Diffusion

- Diffusion is the movement of molecules or ions of a solute or a solvent, whether a solid, liquid or gas from the region of its higher concentration to that of its lower concentration. Gases diffuse more rapidly than liquids. Solids are the slowest to diffuse. The pressure exerted by the tendency of the particles to diffuse from the area of its higher concentration to the region of its lower concentration is called **diffusion pressure (DP)**.
- Rise in temperature increases the rate of diffusion (due to increase in kinetic energy). The rate of diffusion is inversely proportional to the square root of the density of the diffusing substance (**Graham's law of diffusion**),

  i.e., $D \propto \frac{1}{\sqrt{d}}$

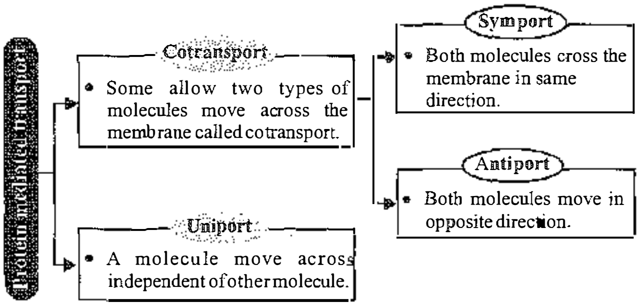
  where D = diffusion and d = density.

  Rate of diffusion is directly proportional to the diffusion pressure gradient (DPG).
- **Importance of diffusion** - Exchange of gases (CO_2 and O_2) between the plant's interior and outside air occurs through diffusion. Diffusion keeps the cell walls of the internal plant tissues moist. It is the process involved in transpiration.

Facilitated diffusion

- The passive absorption of solutes mediated by a carrier is called facilitated diffusion. Particles which are lipid soluble can easily pass directly through the cell membrane as it is mainly made of it. The hydrophilic solutes, find it difficult to pass through the membrane so their movement has to be facilitated. **Membrane proteins** provide sites at which such molecules cross the membrane. For this, the membranes possess **aquaporins** and **ion channels**.
- A concentration gradient must already be present for molecules to diffuse even if facilitated by the proteins. This process is called facilitated diffusion. In facilitated diffusion these proteins help move substance across membranes **without expenditure of ATP energy**. Facilitated diffusion cannot cause net transport of molecules from a low to a high concentration as this would require input of energy.
- Some carrier proteins allow transport only if two types of molecules move together *i.e.*, **cotransport**. Contransport is of two types: (i) **Symport** in which two types of molecules cross the membrane in the same direction. (ii) **Antiport** in which two types of molecules move in opposite direction.

- When a molecule moves across a membrane independent of other molecule, the process is called **uniport**.



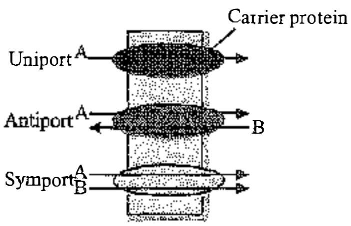


Fig.: Facilitated diffusion

Active transport

- In **active transport**, the movable carrier proteins are called pumps and employ ATP energy for transport across the membrane.

Comparison of different transport processes

- Proteins in the membrane are responsible for facilitated diffusion and active transport and hence show common characteristics of being highly selective; they are liable to saturate, respond to inhibitors and are under hormonal regulation. But diffusion whether facilitated or not- take place only along a gradient and do not use energy.
- The comparison of different transport processes is given in the table below.

PLANT WATER RELATION

Imbibition

- Imbibition is the phenomenon of **adsorption of water** or any other liquid by the solid particles of a substance without forming a solution. Solid substances or adsorbents which take part in imbibition are called **imbibants**, *e.g.*, seeds, dry wood etc.
- The liquid (usually water) which is imbibed is known as **imbibate.**
- Plant imbibants are hydrophilic (Gk. *hydro*-water, *philein* – to love) colloids. They have a highly negative water potential so, when they come in contact with water ($\psi_w = 0$), a steep water potential gradient is established. Water diffuses rapidly into the adsorbent till equilibrium is attained.

Table : Comparison of different transport processes

	Prokaryotic cell	Simple diffusion	Facilitated diffusion	Active transport
1.	Requires special membrane proteins	No	Yes	Yes
2.	Highly selective	No	Yes	Yes
3.	Transport saturates	No	Yes	Yes
4.	Uphill transport	No	No	Yes
5.	Requires ATP energy	No	No	Yes
6.	Response to protein inhibitors	No	Yes	Yes

- Imbibition increases the volume of the imbibant but the increase is less than the volume of water absorbed.
- During imbibition, the water molecules get tightly adsorbed and become **immobilised.** They lose most of their kinetic energy in the form of heat. It is called **heat of wetting** or **heat of hydration.** The heat of wetting can be experienced during the kneading of wheat flour where the starch and cellulose molecules imbibe water. The swelling imbibant also develops a pressure called **imbibition pressure** (matric potential).
- Amount of imbibition depends upon:
  - Water potential gradient between adsorbent and the liquid imbibed.
  - Affinity of adsorbent for water.
- **Importance of imbibition** - Water is absorbed by the germinating seeds through imbibition. **Breaking of the seed coat** in germinating seeds is due to greater imbibitional swelling of the seed kernel (starch and protein) as compared to seed coverings (cellulose).Seedling is able to come out of soil due to development of imbibition pressure. Besides, jamming of wooden frames during rains is caused by swelling of wood due to imbibition.

Water Potential (ψ_w)

- The difference between the free energy of water molecules in pure water and the energy of water in any other system (*e.g.*, water in a solution or in a plant cell or tissue) is termed as the **water potential.** It is represented by Greek letter ψ_w (psi) and is measured **in bars, pascals or atmospheres.** Water always moves from the area of high water potential or high energy to the area of low water potential or low energy.
- The water potential of a solution can be determined using pure water as the standard of reference. The pure water, at atmospheric pressure, has a water potential of zero (0). The presence of solute particles reduces the free energy of water and thus decreases the water potential (negative value). Therefore, the water potential of a solution is always less than zero.

- The water potential in a plant cell or tissue can be written as the sum of matric potential, solute potential and pressure potential.

$$\psi_w = \psi_m + \psi_s + \psi_p$$

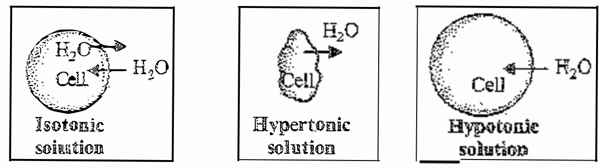
- **Matric potential** (ψ_m) is the component of water potential influenced by the presence of matrix. It is not significant in osmosis, so often disregarded. Thus equation may be simplified as

$$\psi_w = \psi_s + \psi_p$$

- **Solute potential (osmotic potential)** is defined as the amount by which the water potential is reduced as a result of the presence of solute. Solute potentials (ψ_s) are always in negative values. The more the solute molecules, the lower is the solute potential (ψ_s).
- **Hydrostatic pressure or pressure potential** is the pressure which develops in an osmotic system due to osmotic entry or exit of water from it. A positive pressure called **turgor pressure** (TP) develops in a plant cell or system due to entry of water into it.
- Loss of water produces a negative hydrostatic pressure or **tension**. It develops in xylem **due to loss of water in transpiration**. This is very important in transport of sap over long distance in plants.
- Due to turgor pressure the protoplast of a plant cell will press the cell wall to the outside. The cell wall, being elastic, presses the protoplast with an equal and opposite force.
- The force exerted by the cell wall over the protoplast is called **wall pressure (WP)**. Normally **wall pressure is equal and opposite to turgor pressure** except when the cell becomes flaccid.
- The values of these two opposing forces continue to rise till the cell becomes fully swollen or turgid. At this time the value of wall or turgor pressure becomes equal to osmotic potential, $\psi_p = \psi_s$.
- **Importance of turgor pressure** : It keeps the cells and their organelles **stretched**, essential for proper functioning of a cell, provides support to non woody tissues (*e.g.*, parenchyma), essential for **cell enlargement** during growth and keeps the leaves fully expanded and properly oriented to light. The opening and closing of stomata are caused by turgidity of guard cells.

Osmosis

- Osmosis is a special type of diffusion of solvent or water molecules from the region of their higher diffusion pressure or free energy to the region of their lower diffusion pressure or free energy across a semipermeable membrane.
- The direction and rate of osmosis depend upon the sum of two forces, pressure gradient (gradient of ψ_p) and concentration gradient (gradient of ψ_s).
- Osmosis is of two types : endosmosis and exosmosis. **Endosmosis** is the osmotic entry of water into a cell and **exosmosis** is the osmotic withdrawl of water from a cell.
- A solution having low osmotic concentration as compared to another solution is known as **hypotonic solution**. A solution having high osmotic concentration as compared to another solution is termed as **hypertonic solution**. The two solutions with the same concentration or potential are named as **isotonic solutions**. External hypotonic solution will cause endosmosis while hypertonic solution results in exosmosis.



Net effect : No loss or gain of water by the cell | Net effect : Water passes out of the cell | Net effect : Water enters the cell

Fig.: The effect of isotonic solution, hypertonic solution and hypotonic solution on cell

- Osmotic pressure of a solution is equivalent to the pressure which must be exerted upon it to prevent the flow of solvent across a semipermeable membrane. It is usually measured in **pascals**, Pa (1 Pa = 1 Newton/m^2) or **bars** or **atmospheres**. The osmotic pressure of a solution largely depends upon the ratio between the number of solute and solvent particles present in a given solution.
- Osmotic pressure is numerically equal to osmotic potential (= solute potential, ψ_s) but while osmotic potential has a negative value, **osmotic pressure (π, pi) has a positive value**, ($\psi_s = -\pi$). The instrument used for measuring osmotic pressure is called osmometer, *e.g.*, Berkeley and Hartley's osmometer, Pfeffer's osmometer, etc.
- In osmosis, the water (or solvent) molecules move as follows:

From the region of		To the region of
Pure solvent (water)	→	Solution
Dilute solution	→	Concentrated solution
Higher free energy of water molecules	→	Lower free energy of water molecules
Higher chemical potential (or water potential)	→	Lower chemical potential (or water potential)
Higher diffusion pressure of water	→	Lower diffusion pressure of water

- **Importance of osmosis** - Entry of soil water into root is carried out by osmosis. The soft organs like leaves, flowers, fruits and young stems are able to keep themselves stretched and erect due to turgidity of their cell which is dependent upon osmosis.

Plasmolysis

- Shrinkage of the protoplast of a cell from its cell wall under the influence of a hypertonic solution is called **plasmolysis**. Due to withdrawl of water from cytoplasm and central vacuole of cell, the size of protoplast reduces. This is the first stage of plasmolysis called **limiting plasmolysis**. An extra hypertonic external solution continues to withdraw water from the central vacuole by exosmosis and causes **incipient plasmolysis**. At this stage, hypertonic solution enters the cell in between the protoplast and the cell wall. If exosmosis is continued, protoplast shrinks further which is known as **evident plasmolysis**.

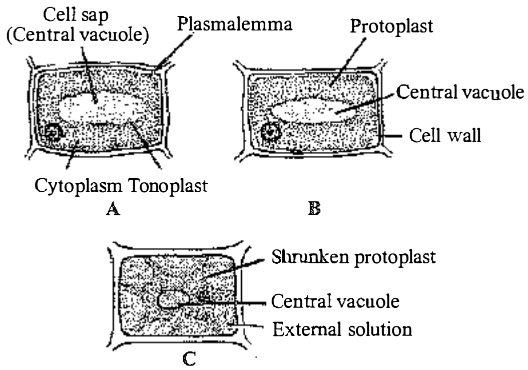


Fig.: Plasmolysis in a cell. **A.** turgid cell; **B.** incipient plasmolysis; **C.** evident plasmolysis.

- The swelling up of a plasmolysed protoplast under the influence of hypotonic solution is called **deplasmolysis**. It is possible only immediately after the plasmolysis.

Diffusion Pressure Deficit (DPD)

- The reduction in the diffusion pressure of water in a solution over its pure state is called diffusion pressure deficit or DPD. This term was given by **Meyer**. Diffusion pressure deficit is also called **suction pressure**. Its value is equal to the osmotic pressure or potential (positive value taken in bars or atm) of the solution in a cell or system minus the wall pressure (= turgor pressure) which opposes the entry of water into it provided the external water is pure.

$$DPD = OP - WP\ (TP)$$

ABSORPTION OF WATER

- Land plants absorb water mainly from the soil. For long distance transport, plants have developed a **mass** or **bulk flow system**. Mass flow is the movement of substances in bulk or *en masse* from one point to another as a result of pressure differences between the two points. In mass or bulk flow all the substances dissolved or suspended in solution travel at the same pace.
- Translocation operates either due to positive hydrostatic pressure gradient (like a garden hose) as in phloem or a negative hydrostatic pressure gradient (like suction through a straw) as in xylem. There are two vascular tissues, xylem and phloem. Xylem translocation is mainly from roots to aerial parts. It transports water with mineral salts, some organic nitrogen and hormones. Phloem translocates organic substances and inorganic solutes from leaves to all other parts of the plant and storage organs.

Pathways of water movement in roots

- There are two pathways of water passage from root hairs to xylem inside the root: **apoplast** and **symplast**. The concept of apoplast and symplast was introduced by **Munch** in 1930.
- In **apoplast pathway** water passes from root hairs to xylem through the walls of intervening cells without crossing any membrane or cytoplasm. It provides the least resistance to movement of water. It occurs only upto endodermis as it is interrupted by the presence of impermeable lignosuberin casparian strips in the walls of endodermal cells.

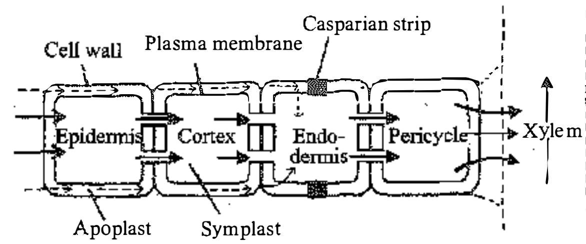


Fig.: Pathways of water movement inside the root

- In **symplast pathway** water passes from cell to cell through their protoplasm facing plasmalemma (cell membrane) at least at one place. It is also called **transmembrane pathway**. It does not enter cell vacuoles. The cytoplasm of the adjacent cells are connected through bridges called plasmodesmata. Symplastic movement is aided by cytoplasmic streaming of individual cells. It is , however, slower than apoplastic movements.
- In **mycorrhizal association** large number of fungal hyphae (associated with the young roots) extend to sufficient distance into the soil and have a large surface area. These hyphae are specialised to absorb both water and minerals and provide them to the root.

Mechanism of water absorption

- Water absorption is of two types, **passive** (water is absorbed **through the root**) and **active** (water is absorbed **by the root**). Passive absorption of the movement of water from the soil into the plant is due to the more negative water potential in the xylem than that in the soil water. It can occur independently of any activity of roots.
- When the water is absorbed due to the activity of root itself, particularly root hairs, it is termed **active absorption**. The first step in the absorption of water is its imbibition on the cell wall surface.

Mineral ions absorption

- Unlike water, all minerals cannot be passively absorbed by the roots. Two factors account for this:
  - Minerals are present in the soil as charged particles (ions) which cannot move across cell membranes.
  - The concentration of minerals in the soil is usually lower than the concentration of minerals in the root.
- Therefore, most minerals must enter the root by **active absorption** into the cytoplasm of epidermal cells. This needs energy in the form of ATP.
- The active uptake of ions is partly responsible for the water potential gradient in roots, and therefore for the uptake of water by osmosis. Some ions also move into the epidermal cells passively. **Ions are absorbed from the soil by both passive and active transport.**
- Specific proteins in the membranes of root hair cells actively pump ions from soil into the cytoplasm of the epidermal cells.
- The absorbed sap enters endodermal cells *via* cortex and other cells. Like all cells, the endodermal cells have many transport proteins embedded in their plasma membrane; they let some solutes cross the membrane, but not others.

Table : Differences between active and passive absorption

	Active absorption	Passive absorption
1.	The driving force is root pressure and thus it is against DPD gradient.	The driving force is transpiration and thus proceeds through DPD gradient.
2.	It is at the expense of ATP.	No ATP is needed.
3.	ATP is derived from cellular respiration and thus rate of respiration increases during absorption.	Since ATP is not required, rate of respiration remains unaffected during absorption.
4.	Oxygen is needed for respiration.	Not affected by increase or decrease in the level of oxygen.
5.	The movement of water is against concentration gradient.	Movement of water is in accordance to osmotic or concentration gradient.
6.	It usually occurs in night when transpiration stops due to closure of stomata.	It occurs in day when transpiration is going on and stops in night when transpiration is stopped.
7.	Bleeding and guttation are closely associated with active absorption.	Transpiration is associated with passive absorption.

- Transport proteins of endodermal cells are control points, where a plant adjusts the quantity and types of solutes that reach the xylem. Note that the root endodermis because of the layer of suberin has the ability to actively transport ions in one direction only.

Ascent of sap

- The upward movement of water with dissolved mineral (sap) from roots towards the tips of stem branches and their leaves is called **ascent of sap**. Many theories have been put forward to explain the upward movement of water. Some of them are discussed here.

Vital force theory

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

Relay pump theory

- Relay pump theory was put forward by Godlewski (1884).
- According to this, **upward conduction of water is due to the pumping activity of xylem parenchyma cells** and the **cells of medullary rays.**

Root pressure theory

- It was put forward by **Priestley** (1916). **Root pressure is a positive pressure that develops in the xylem sap** of the root of some plants. It is a manifestation of active water absorption. Root pressure is maximum during rainy season (in tropical region) and spring season (in temperate zone).
- It is retarded or absent under conditions of starvation, low temperature, drought and reduced availability of oxygen. This theory can account for the ascent of sap **only in the herbaceous plants**. In the tall trees the magnitude of pressure developed is too small to push the water to the apical regions.

Capillary force theory

- Theory of capillarity was given by Bohm (1863). It deals that the upward **movement of water** will **continue** till the **forces of adhesion** and **cohesion are balanced by the downward pull of gravity.**
- It is operational to only small sized plants and cannot operate in plants having tracheids due to the presence of end walls.

Cohesion-Tension theory

- It is also known as **transpiration pull theory**. It was put forward by **Dixon and Jolly in 1894.** According to this theory, there is a continuous column of water from root through the stem and into the leaves. Water molecules remain attached to one another by a strong mutual force of attraction called **cohesion force**. This is due to the **hydrogen bonds** formed amongst adjacent water molecules.
- There is another force called **adhesion force** between the walls of tracheary elements and water molecules. It produces **surface tension** that accounts for high capillarity through tracheids and vessels.

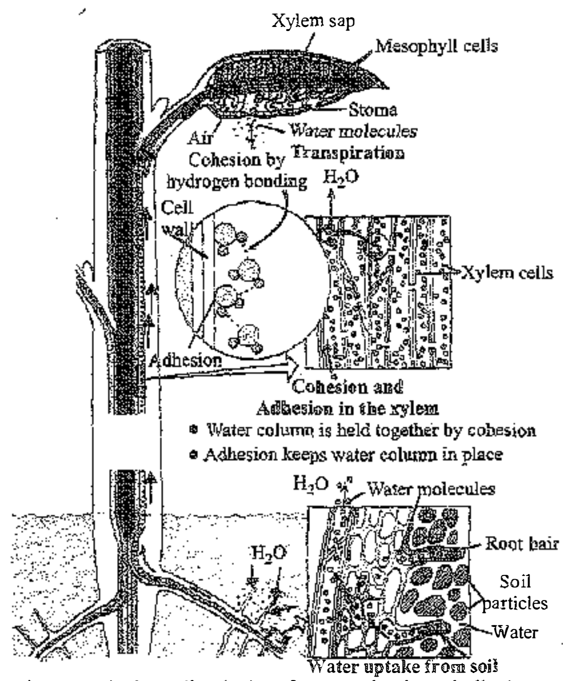


Fig.: Transpiration pull, cohesion of water molecules and adhesion between water molecules and wall of xylem elements.

- Intercellular spaces present amongst mesophyll cells of the leaves are always saturated with water vapours and connected to the outside air through stomata. Outside air has a lower water potential than the moist air present inside the leaf, thus water vapours diffuse out of the leaves. As a result, the **turgor pressure of mesophyll cells decreases** and **the diffusion pressure deficit (DPD) increases**. Now these cells take water from adjoining cells and the turgor of those adjoining cells decreases. This process is repeated and ultimately water is absorbed from nearest xylem vessels of leaf.
- As there is a continuous water column inside the xylem elements, a **tension** or **transpiration pull is transmitted down** and finally transmitted to root, **resulting in the upward movement of water**. As a tension of one atmosphere is sufficient to pull water to a height of about 10 metres, a tension of 10–20 atm is sufficient to raise water to the height of the tallest tree over 130 m.

TRANSPIRATION

- The loss of water in the form of vapours from the living tissues of aerial parts of the plant is termed as transpiration. Approximately 98-99% of the water absorbed by a plant is lost in transpiration, 0.2% is used in photosynthesis while the remaining is retained in the plant during growth.
- Transpiration occurs through various plant parts and accordingly it may be **cuticular** (from cuticle or epidermal cells of leaves), **stomatal** (from stomata), **bark** (from corky covering *i.e.*, bark of stem), and **lenticular** (from lenticles).

Stomatal apparatus

- 50 – 70% of total transpiration occurs through stomatal apparatus. The stomata are **tiny pores** present in the **epidermal surface** of leaves, young stems and in certain fruits (*e.g.*, banana, citrus, cucumber, etc.).
- This pore is surrounded by two **kidney shaped** or **bean shaped epidermal cells** called **guard cells**. These cells are living having nucleus, chloroplasts and cytoplasm. The outer wall of these cells is thin and inner wall is thick and elastic. These guard cells are surrounded by some specialized epidermal cells called **subsidiary cells** or **accessory cells**. These all together constitute stomatal apparatus which can be opened or closed with by help of guard cells.

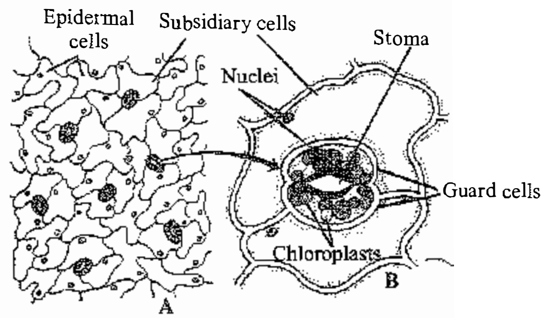


Fig. : A. Lower epidermis of a leaf to show stomata
B. Structure of one stoma.

- Usually the lower surface of a dorsiventral (often dicotyledonous) leaf has a greater number of stomata while in an isobilateral (often monocotyledonous) leaf they are about equal on both surfaces. Transpiration is affected by **several external factors**: temperature, light, humidity, wind speed. Plant factors that effect transpiration include number and distribution of stomata, number of stomata open, their percentage on leaf surface, water status of the plant, canopy structure, etc.

Opening and closing of stomata

- Opening and closing of stomata are governed by change in O.P. or turgidity of guard cells. When guard cells are turgid, stomata open and when guard cells are flaccid, stomata close. Different theories about stomatal movements have been given :

Stomatal apparatus

Structure
- A stoma (pore) surrounded by two kidney shaped guard cells.
- A few subsidiary cells present.

Distribution on leaf
- **Apple or mulberry type (Hypostomatic):** On lower surface only.
- **Potato type :** On both surfaces but more on lower surface.
- **Oat type (Amphistomatic):** Equal on both surfaces.
- **Water lily type:** Only on upper surface.
- **Potamogeton type (*Astomatic*):** Either absent or vestigeal.

Period of opening
- **Alfalfa type:** Open throughout the day.
- **Barley type:** Open only for a few hours in day.
- **Potato type :** Open throughout the day and night, closing only under stress.
- **Equisetum type:** Stomata seldom close, usually remain open throughout as in potato type.
- **Succulent xerophytes type :** Close during day and open at night.

- **Photosynthetic production theory** (given by **Schwendener**, 1881).
- **Starch-sugar interconversion theory** (given by **Lloyd**, 1908 and by **Sayre** 1926). It was modified by **Steward** (1964).
- **Active K^+ ion transport theory** (given by **Levitt**, 1974)

- The photosynthetic production theory, can be summarised as below:

During day(light)	**During night (dark)**
Photosynthesis in guard cells (due to presence of chloroplast)	No photosynthesis in guard cells
↓	↓
Produces sugars (osmotically active substances)	Sugar converted into starch
↓	↓
Increased O.P. of guard cells	Decreased O.P. of guard cells
↓	↓
Endosmosis into guard cells	Exosmosis from guard cells
↓	↓
Guard cells become turgid	Guard cells become flaccid
↓	↓
Stomata open	Stomata close

- According to starch-sugar inter conversion theory:

During day (light)	**During night (dark)**
↓	↓
CO_2 evolved in respiration	CO_2 evolved in respiration
↓	↓
Absorbed in photosynthesis	No photosynthesis
↓	↓
No accumulation of CO_2 in guard cells	CO_2 accumulates in guard cells
↓	↓
pH of guard cells increases to 7	pH of cell sap decreases to 5
↓	↓
Enzyme starch phosphorylase favours formation of glucose-1-phosphate from starch and phosphate	Formation of starch from glucose-1-phosphate occurs
↓	↓
Stomata open	Stomata close

- **Active K^+ ion transport theory** was initially given by Fujino (1959) and later modified by Levitt (1974). This is the most accepted modern theory of stomatal movements now a days. This theory may be represented as –

During day (light)	**During night (dark)**
CO_2 concentration decreases	CO_2 concentration increases
↓	↓
Malic acid formed in guard cells	ABA released to stop the K^+ exchange
↓	↓
Dissociates into malate ions and H^+	K^+ ions transported back into subsidiary cells
↓	↓
K^+ ion exchange from subsidiary cells	Decreased pH of guard cells
↓	↓
O.P. of guard cells increased (due to entry of K^+ and malate ions)	Starch synthesized in guard cells
↓	↓
Endosmosis into guard cells	Decreased O.P. of guard cells
↓	↓
Guard cells turgid	Exosmosis from guard cells
↓	↓
Stomata open	Stomata close

Significance of transpiration

- It controls the **rate of absorption of water** from soil.
- It helps in **absorption of mineral salts**.
- It is responsible for ascent of sap.
- It regulates the plant temperature by contributing to **cooling of leaves** and also the surroundings. It **protects the leaves from heat injury**, particularly under conditions of high temperature and intense sunlight.
- On the other hand, transpiration causes loss of huge amount of water absorbed by plants and leads to wilting and injury in plants. It also checks photosynthesis, reduces growth and if too severe may cause death from desiccation. Inspite of various detrimental disadvantages the plants cannot avoid transpiration due to their peculiar structure of leaves which is basically meant for gaseous exchange during respiration and photosynthesis. Therefore, transpiration is also regarded as "necessary evil" by Curtis (1926) or "unavoidable evil" by Steward (1959).

Antitranspirants

- Transpiration can be artificially retarded by using plant antitranspirants which is essential to retard transpiration in plants during seedling transplant or for the cultivation of some high priced field crops. An ideal antitranspirant is one which decreases the transpiration rate without affecting CO_2 fixation in photosynthesis.
- There are two types of antitranspirants:
  - Those that form a **physical barrier** – forming a film impermeable to water but permeable to CO_2 *e.g.*, colourless plastics (S - 600).
  - Those substances that cause a **partial closure** of the **stomata** decreasing transpiration (photosynthesis not affected) like dodecenyl succinic acid (DSA), phenylmercuric acetate (PMA) and abscisic acid.

- **CO_2 is another effective antitranspirant** which induces partial closure of stomata when its concentration is raised from 300 ppm in atmosphere to 500 ppm.
- An actively photosynthesising plant has an insatiable need for water. Photosynthesis is limited by available water which can be swiftly depleted by transpiration. The humidity of rainforests is largely due to this vast cycling of water from root to leaf to atmosphere and back to the soil.
- The evolution of the C_4 photosynthetic system is probably one of the strategies for maximising the availability of CO_2 while minimising water loss. C_4 plants are twice as efficient as C_3 plants in terms of fixing carbon (making sugar). However, a C_4 plant loses only half as much water as a C_3 plant for the same amount of CO_2 fixed.

GUTTATION

- Loss or excretion of water in the form of liquid droplets from the tips and margins of leaves is called **guttation**. It was first studied by **Bergerstein** in 1887. All plants do not show guttation. It is restricted to about 345 genera of herbaceous and some woody plants. In general, **guttation occurs when transpiration rate is very low** as compared to rate of water absorption. Due to this, root pressure is developed and water is pushed out through specialized pores at vein endings called **hydathodes**. So guttation is not due to activity of hydathodes but **due to root pressure**.
- Water lost in guttation is **impure water**, *i.e.*, a dilute solution of different inorganic and organic salts.
- These salts sometimes are redissolved back into leaves and cause **'salt injury'**.

Table : Differences between transpiration and guttation

	Transpiration	Guttation
1.	Loss of water is in vapour form.	Loss is in liquid form.
2.	It occurs during day time.	It occurs during night or early morning.
3.	Loss of pure water.	Loss of impure water.
4.	Through stomata or epidermis or cuticle or lenticels.	Through hydathodes.
5.	Controlled phenomenon.	Uncontrolled phenomenon.
6.	Associated with regulation of temperature.	No such role has been given to guttation.

BLEEDING

- Plant bleeding is different from guttation.
- It is the exudation of sap or watery solution from the cut or injured parts of the plant, *e.g.*, *Agave*, *Acer*, *Vitis*, etc. It occurs due to root pressure, phloem pressure, local pressure in xylem (stem pressure) and latex or resin.

PHLOEM TRANSPORT (FOOD TRANSPORT)

- In plants, food is required to each part, for its nutrition and development. Food is mostly synthesized in the leaves and also in young stems. The leaves therefore serve as the **'source'**. The synthesised food is translocated to the growing regions and also to the storage organs of the plant. So, these regions serve as **'sink'**. But, the source and sink may be reversed depending on the season, or the plant's needs. Since the source-sink relationship is variable, the direction of movement in the phloem can be upwards or downwards, *i.e.*, bidirectional. This contrasts with that of the xylem where the movement is always **unidirectional**, *i.e.*, upwards.
- The most accepted mechanism used for the translocation of sugars from source to sink is called the **pressure flow** or **mass flow hypothesis** (Munch 1930). As glucose is prepared at the source *i.e.*, in leaves (by photosynthesis), it is converted to sucrose (a dissacharide). The sugar is then moved in the form of sucrose into adjacent companion cells and then into the living phloem *i.e.*, in sieve tube cells by **active transport**.
- This process of **loading** at the source produces a hypertonic condition in the phloem. Water in the adjacent xylem moves into the phloem by osmosis. As osmotic pressure builds up, the phloem sap will move to areas of lower pressure. At the sink, osmotic pressure must be reduced. Again **active transport** is necessary to move the sucrose out of the phloem sap and into the cells which will use the sugar converting it into energy, starch, or cellulose. As sugars are removed, the osmotic pressure of the phloem decreases and water moves out of the phloem.
- **Ringing** or **girdling** experiment strongly suggests that the food is translocated through phloem (at least in downward direction) but not through xylem. A ring of bark, completely encircling a branch is removed from the wood (including the phloem). Under this condition, the upper part of the plant remains attached to the lower part, by the central xylem cylinder and the pith. This condition (*i.e.*, a girdle made at the stem) results in the accumulation of food materials just above the ring which is evidenced by the swelling of tissues as well as rooting or appearance of buds just above the girdle. As the phloem is removed, this food cannot move further down. The lower part which is below the ring, shrinks and shows the signs of degeneration as it is not getting food from the leaves, due to the removal of phloem.

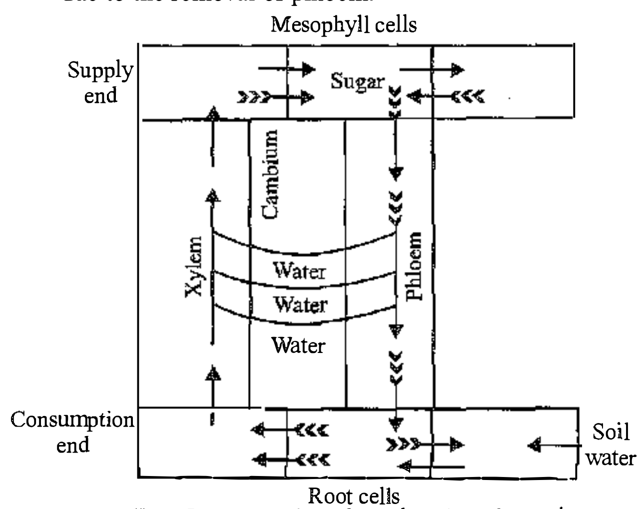


Fig.: Representation of translocation of organic solutes according to Munch

- Factors that affect translocation of solutes are – temperature (25°-35°C is optimum), light (reduced light reduces translocation), oxygen (aerobic process thus oxygen is essential, metabolism (because it requires energy) and humidity (moisture stress reduces translocation).
- In plants uptake and removal of gases occurs through diffusion from body surface and stomata only. No, other structure specialized for the function is observed.