TRANSPORT IN PLANTS

INTRODUCTION

- Plant physiology is the branch of botany which deals with the study of life activities of plants. It includes the functional aspects of life processes both at cellular as well as subcellular level.
- Plants need to move molecules over very long distances, much more than animals do; they also do not have a circulatory system in place.
- Water is mainly absorbed by the roots of the plants from the soil, then it moves upward to different parts and is lost from the aerial parts, especially through the leaves.
- The food synthesised by the leaves also have to be moved to all parts including the root tips embedded deep inside the soil.
- In a flowering plant, the substances that are transported includes water, mineral nutrients, organic nutrients and plant growth regulators.
- An important aspect that needs to be considered is the direction of transport. In rooted plants, transport in xylem (of water and minerals) is essentially unidirectional, from roots to the stems. Organic and mineral nutrients transport through phloem and undergo multidirectional transport as well.

MEANS OF TRANSPORT ACROSS CELLS

There are three methods of transport of materials across the cells **- diffusion**, **facilitated diffusion** and **active transport**. Both the types of diffusion constitute passive transport.

DIFFUSION

- The movement of molecules or atoms or ions of materials from an area of higher concentration to an area of their lower concentration is called diffusion.
- The diffusion is continue till the dynamic equilibrium is not established. At this stage, the net movement of molecules is equal in both directions.
- The kinetic energy, which is present in the molecules of material is distributed equally in their available space by their nature.
- The diffused molecules or ions exert a pressure on the substance or medium in which diffusion takes place, known as **diffusion pressure**. This is developed due to differences in the concentration of molecules of the material.
- A pure solvent thus, possess maximum diffusion pressure and it decreases with the addition of solute in the solvent.
- Water molecules moves from their higher concentration to their lower concentration in plants.
- The rate of diffusion decreases with increasing size of molecules.
- Gases have highest rate of diffusion, followed by liquid and solid.
- **Diffusion rates** are affected by the gradient of concentration, the permeability of the membrane separating them, temperature and pressure.

SIGNIFICANCE OF DIFFUSION

- Exchange of gases like CO_2, O_2 take place through diffusion.
- The distribution of hormones in the plants take place through diffusion.
- The process of transpiration is a diffusion process. The evaporation of water from the intercellular spaces is linked with diffusion during the transpiration.
- The ions of the minerals may diffuse into the plant body.

FACILITATED DIFFUSION

- It is diffusion along the concentration gradient through specific sites present in cell membranes without the cell spending any energy on the movement.
- Rate of diffusion depends on the size of substances; smaller substances diffuse faster. Lipid soluble substances diffuse faster.
- The substance that have a hydrophobic moiety, find it difficult to pass through membrane. The movement of such molecules is facilitated by transporter proteins present in cell membranes which allow the passage of substances.
- In facilitated diffusion, the concentration gradient must be present.
- It is very specific and allows selected substances through the cell. It is also sensitive to inhibitors which react with protein side chains.
- Some protein channels present on membrane are always open; others can be controlled. The **porins** are proteins that form huge pores in the outer membranes of the plastids, mitochondria and some bacteria.

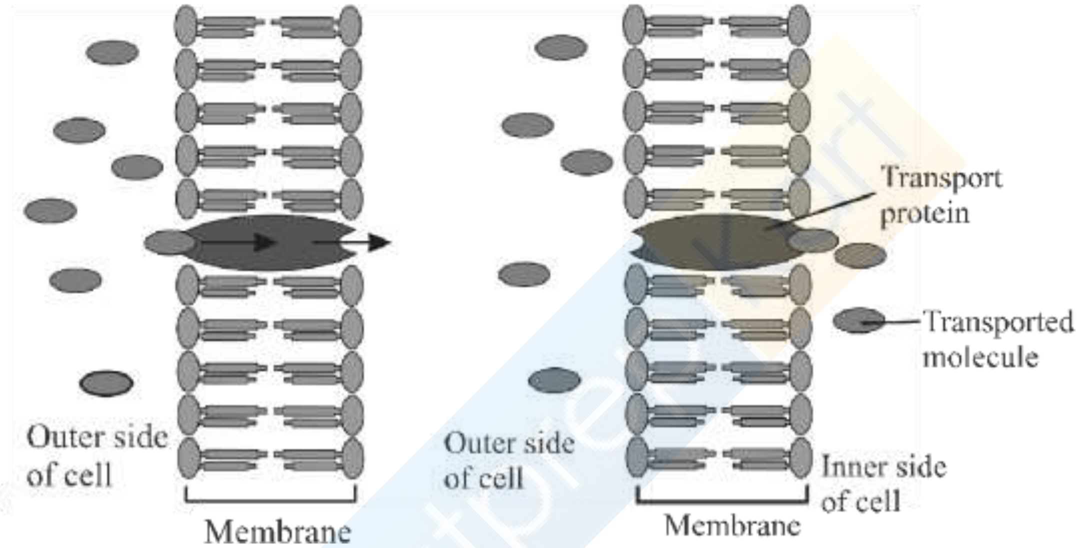


Fig. : Facilitated diffusion

PASSIVE SYMPORTS AND ANTIPORTS

- Few transport proteins or carrier proteins permit diffusion only if two types of molecules move together.
- In **symport**, both molecules cross the membrane in the same direction.
- In **antiport**, both molecules cross the membrane in opposite directions.
- In **uniport**, molecule moves across a membrane independent of other molecule.

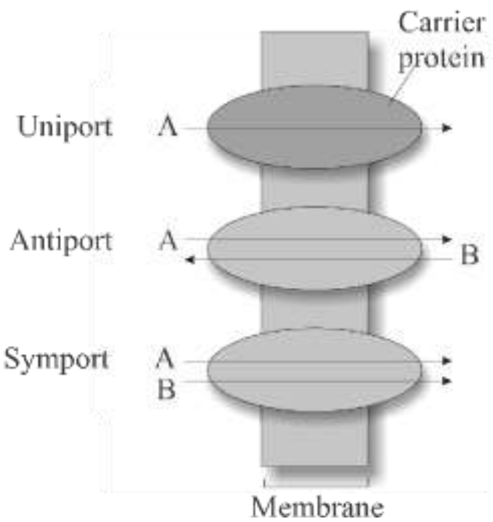


Fig. : Types of facilitated diffusion

ACTIVE TRANSPORT

- Active transport uses **energy** to pump molecules against a concentration gradient.
- It is carried out by membrane bound proteins.
- **Pumps** are proteins which can transport the substances by using energy. These pumps can transport the proteins from lower concentration to a higher concentration.

Table : Differences between Diffusion, Facilitated diffusion and Active Transport :

S. No.	Diffusion	Facilitated diffusion	Active transport
1.	Materials directly move through the cell membrane.	Materials directly move through the cell membrane.	Materials directly move through the cell membrane.
2.	No utilisation of energy.	No utilisation of energy.	Energy is utilized in the form of ATP.
3.	This process occurs in the direction of diffusion gradient *i.e.,* from lower concentration to higher concentration.	This also occurs in the direction of diffusion gradient.	This process occurs against the direction of diffusion gradient.
4.	In this process, proteins channels and transfer proteins do not participate.	In this process, proteins channels and carrier proteins, both participate.	Only carrier proteins participate.

PLANT-WATER RELATIONS

- Water is essential for all physiological activities of plants.
- Water acts as an excellent solvent and helps in the uptake and distribution of mineral nutrients and other solutes.
- Water is useful for maintaining the turgidity of cells which is essential for cell enlargement, growth & development.

OSMOSIS

- In plant cells, the cell membrane and the membrane of the vacuole (i.e., tonoplast) together are important determinants of movement of molecules in or out of the cell.

- The ability of a membrane to permit or restrict passage of substances through it is called **membrane permeability**.
- Osmosis is a **type of diffusion** in which water molecules diffuse from the region of **higher chemical potential** (or concentration) to its region of **lower chemical potential** (concentration) across a permeable membrane.
- The net direction and rate of osmosis depends on pressure gradient and concentration gradient.
- **Common experiment for demonstrating osmosis** is thistle funnel experiment and potato osmoscope.
  - **Thistle funnel experiment -** In the experiment, sucrose solution is taken in funnel which is separated from water through a semipermeable membrane. Water will move into the funnel until the equilibrium is reached.

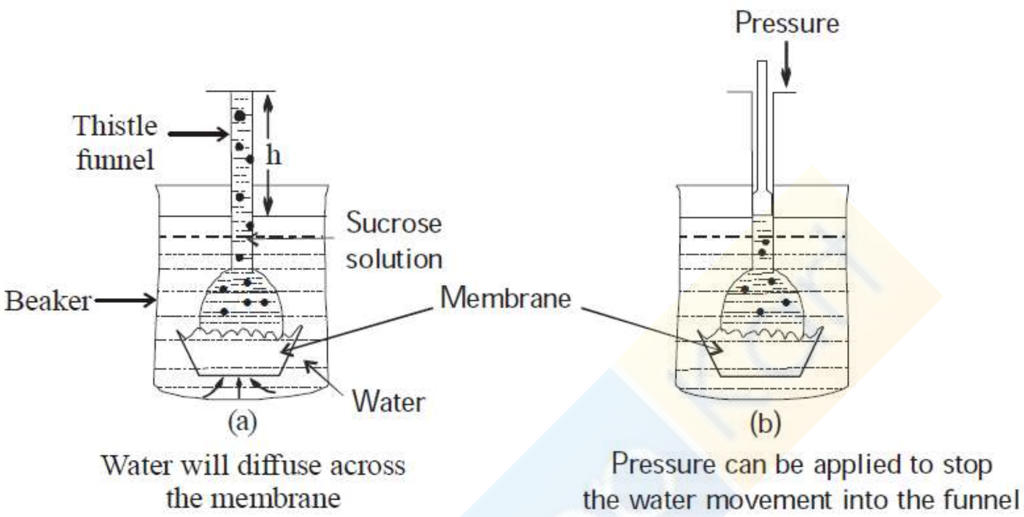


Fig. : A demonstration of osmosis theory 'Thistle funnel experiment'.

The experiment proves that the sugar solution is an osmotically active solution and can absorb water when it is separated from the water by a semipermeable membrane.

  - **Potato osmoscope -** Experiment useful for demonstrating osmosis by using living tissue is potato osmoscope. When the potato tuber is placed in water, the cavity in the potato tuber containing a concentrated sugar solution collects water due to osmosis. The entry of water into the sugar solution proves that sugar solution is osmotically active. The cytoplasm of the cells of the tuber that lie between the sugar solution and the water acts as a single semi-permeable membrane.

TYPES OF OSMOSIS

Depending upon the movement of water into or outside of the cell, osmosis is of two types **- endosmosis** & **exosmosis**.

- The osmotic flow of water into a cell, when it is placed in a solution whose solute concentration is less than that of the cell sap, is called **endosmosis**. e.g., swelling of raisins when they are placed in water.
- The osmotic outflow of water from a cell, when it is placed in a solution whose solute concentration is more than that of the cell sap is called **exosmosis**.
e.g., shrinkage of grapes when they are placed in a concentrated sugar solution.

OSMOTIC PRESSURE (o. P. π)

- **Osmotic pressure** (term proposed by Pfeffer) is the pressure required to prevent the entry of water into a solution.
- The osmotic pressure of pure water is zero.
- The osmotic pressure of a solution is directly proportional to the concentration of solute in it.

- The osmotic pressure in the following plants are as follows :

Hydrophytes < Mesophytes < Xerophytes < Halophytes

- Generally, osmotic pressure is less during the night and higher at noon.
- Osmotic pressure of a solution is measured by **Osmometer**.

O.P. of cell is measured by incipient plasmolysis.

- The formula of Vont Hoff for measuring O.P. :

$$O.P. = mRT$$

Here, m = molar concentration
R = Gas constant [0.082 mole/molecules]
T = Absolute temperature
The osmotic pressure of 1 mole. glucose solution at 0°C, O.P. = $1 \times 0.082 \times 273 = 22.4$ atm., for non electrolytes.

- The O.P. of electrolytes is calculated by the following formula,

$$O.P. = mRT\,I$$

Where I is the constant of ionization of electrolytes.

- The osmotic pressure of electrolytes is higher than that of non-electrolytes.
- For example - solution of 1 M NaCl and 1 M glucose. The molar concentration of both solutions are equal but O.P. of
1 M NaCl is higher than solution of 1 M glucose.
- Water moves from lower O.P. towards the higher O.P.

SIGNIFICANCE OF OSMOSIS

- Root hairs of the roots absorb water from the soil through the process of osmosis.
- The conduction of water from one cell to another cell in plant and distribution of water in plant is through osmosis.
- Turgidity is developed by the process of endosmosis which helps to maintain a definite shape of leaves, stems and flowers. Turgidity also provides mechanical strength to the plants.
- The opening and closing of stomata are also dependent on the process of osmosis.
- The leaves of Mimosa pudica (“Touch me not”) are drooping down only by contact and dehiscence of fruits depends upon turgor changes after osmosis.
- The resistance power increases due to high osmotic concentration against the dry climate and cold temperature.

Table : Differences between Diffusion and Osmosis.

S. No.	Diffusion	Osmosis
1.	Movement of molecules of solid, liquid and gas occurs in this process.	Movement of only solvent molecules occurs in this process.
2.	This process can occur in any medium solid, liquid or gas.	It can occur only in liquid medium.
3.	No membrane is required.	Semi-permeable or diffused permeable membrane is needed for this process.
4	Diffusion process takes place through high diffusion pressure to low diffusion pressure.	Osmosis takes place through solution of low osmotic pressure to solution of high osmotic pressure.

TURGOR PRESSURE (T.P.) AND WALL (PRESSURE W.P.)

- When a cell is immersed in water, then water enters into the cell because osmotic pressure of the cell sap is higher. The cell contents develop a pressure against the cell wall which is called **turgor pressure**.
- Turgor pressure is also known as **hydrostatic pressure**.
- Turgor pressure is not applicable for free solution. This is only applicable for osmotic system.
- The turgor pressure balanced by an equal but opposite pressure of the thick cell wall on the enclosed solution or protoplasm is known as **wall pressure**. It means the amount of pressure exerted by cytoplasm on the cell wall is the same and in the opposite direction as the pressure exerted by the cell wall towards the inner side on the cytoplasm.
- Therefore, wall pressure and turgor pressure are equal to each other but W.P. is inward in direction.

T.P. = W.P.

- Plant cell does not burst when placed in pure water due to wall pressure but an animal cell bursts when placed in pure water because wall pressure is absent due to absence of cell wall.
- For example, the consequence of endosmosis on animals can be demonstrated by placing RBCs of human blood in distilled water contained in a dish. When examined after some time, the RBCs are found to burst upon leaving their cell membranes as empty cases.
- A flaccid cell has zero turgor pressure.
- The highest value of turgor pressure is found in fully turgid cell and it is equal to the osmotic pressure.

SIGNIFICANCE OF T.P.

- The protoplasm of the cell is attached with the cell wall due to turgidity of the cell in stretched condition. It maintains the normal shape of the cell in which physiological processes are going on.

- The spatial 3-D structure of mitochondria, chloroplast and microbodies is maintained due to turgor pressure which is essential for their physiological activities.
- Turgor pressure is essential for maintaining definite shape of delicate organs.
- Turgor pressure helps in cell elongation or growth of cell.
- Plant movement like, movement of guard cells of stomata, and seismonastic movements etc. are dependent upon turgor pressure change.
- Turgor pressure provides essential power to the plumule to come out from the soil and help in penetration of radicle into the soil.

DIFFUSION PRESSURE DEFICIT (DPD) OR SUCTION PRESSURE (SP)

- The difference between the diffusion pressure of the solution and it's pure solvent at a particular temperature is called DPD or suction pressure.
- DPD determines the direction of osmosis and it is the power of absorption of water for the cell.
- This is also known as the demand of water in the cell.

DPD is directly proportional to the concentration of the solute.

- Diffusion of water takes place from the region of lower DPD to the region of higher DPD in the process of osmosis.
- Normally, osmotic pressure is greater than the turgor pressure in a cell. The difference between osmotic pressure and turgor pressure is called suction pressure or DPD.

$DPD = OP - TP$ or WP

- The DPD of any free solution is equal to the osmotic pressure of that solution.

$DPD = OP$, because TP is zero in the solution.

DPD in partially turgid or in normal cell

$DPD = OP - TP$

DPD for fully turgid cell

When a cell placed in pure water or hypotonic solution, then water enters into the cell, as a result, turgor pressure develops in the cell. The cell starts swelling due to the turgor pressure. Simultaneously, concentration of cell sap decreases due to continuous inflow of water. Therefore, OP decreases and T.P. increases when value of TP is equal to the OP then DPD will be zero.

At this stage, cell becomes fully turgid.

Therefore, in a fully turgid cell

When, $OP = TP$ or, $OP - TP = 0$

$DPD = OP - TP$

So that, $DPD = 0$

DPD in flaccid cell

If the cell is in flaccid state then its T.P. or W.P. would be zero and the value of DPD would be equal to OP.

TP or $WP = 0$

Therefore, DPD or $SP = OP$

If a flaccid cell is placed in water then water enters into cell because DPD of the cell sap is higher than water.

DPD for plasmolysed cell

Sometimes the value of turgor pressure is negative as in plasmolysed cell. In this state,

$DPD = OP - TP$

$\therefore$ $TP = -ve$

DPD = OP – [–TP] = OP + TP
DPD = OP + TP
So that the DPD of the plasmolysed cell is greater than osmotic pressure.
The DPD in the following cells are as follows:
Plasmolysed cell > Flaccid cell > Partially turgid cell > Fully turgid cell

WATER POTENTIAL (Ψ_W)

- The difference between the free energy of molecules of pure water and free energy of the solution is called water potential of the system.
- The water potential of pure water is maximum. Pure water has greater free energy. The free energy is lowered down by the addition of solute.
- Water always flows from higher water potential to lower water potential.
- Water potential is represented by Greek word ψ (Psi)/ψ_W and it is measured in bars or Pascal (Pa).
- Water potential is equal to DPD but opposite in sign. Its value is negative.

So $\boxed{\psi_W = -\text{DPD}}$

Water potential has following components –

OSMOTIC POTENTIAL (Ψ_S)

Osmotic pressure is also called **solute potential** or **osmotic potential**.
Osmotic pressure and osmotic potential are numerically equal, but osmotic potential has a negative sign.
$\Psi_s = -\pi$ [when Ψ_s = Osmotic potential of solution;
π = osmotic pressure].
Osmotic potential or solute potential is measured in bars. [1 bar = 0.987 atmospheric pressure].
Osmotic pressure = 22.4 atm
$\Rightarrow$ Osmotic potential = – 22.4 atm
(For 1M glucose solution)

PRESSURE POTENTIAL (Ψ_P)

• It is shown by positive sign (+ve).
• If a pressure greater than atmospheric pressure is applied to pure water or a solution, its water potential increases. It is also known as **Turgor pressure**.

MATRIC POTENTIAL (Ψ_M)

Matric is the term used for the surface (such as soil particles, cell walls, protoplasms etc.) to which water molecules are adsorbed. The matric potential (ψ_m) is the component of water potential influenced by the presence of a matrix. It has a negative value.
According to this concept, their relation is as follows.
Water potential = Osmotic potential + Pressure potential + Matric potential
$\Delta\psi$ or $\psi_W = \psi_S + \psi_P + \psi_m$
$\psi_W = \psi_S + \psi_P$
As ψ_m and ψ_g (Matric potential and gravitational potential are negligible).
ψ_W = –ve, ψ_S = – ve, ψ_P = +ve
According to the above concept, the relation of the three phases of the cell by the water potential will be as follows:

(a) In case of fully turgid cell :

There is no flow of water in a turgid cell , because the cell is in equilibrium with water which is present outside the cell, so that water potential will be zero at this state and because osmotic potential and pressure potential are equal in the cell.
For example, if the value of osmotic potential of a cell is –10 and pressure potential (ψ_P) is +10 then water potential will be zero as :
$\psi_W = \psi_S + \psi_P$, $\psi_W = -10 + 10$, $\psi_W = 0$

(b) In case of flaccid cell :
Turgor pressure is zero at this stage. It means pressure potential is zero.
$\psi_W = \psi_S$
If osmotic potential of the cell is –10 bars then,
$\psi_W = \psi_S + \psi_P$
$\therefore\ \psi_P = 0 = TP$
$\psi_W = -10 + 0$ bar
$\psi_W = -10$ bar

(c) In plasmolysed cell :
The pressure potential (ψ_P) means turgor pressure is negative in this stage. Therefore, water potential (ψ_W) of this cell will be more negative. If the value of osmotic potential is –10 bars of a plasmolysed cell and value of pressure potential is 2 bars then its water potential (ψ_W) will be – 12 bars.
$\psi_W = \psi_S + \psi_P$, $\psi_W = -10 + (-2)$ bars, $\psi_W = -12$ bars
So, it is concluded that water always moves from higher water potential towards the lower water potential.

For example, if the water potential of cell A is –10 bars and water potential of cell B is – 12 bars in two cells, then water will flow from cell A to cell B.

PLASMOLYSIS

The behaviour of the plant cells (or tissues) with regard to water movement depends on the surrounding solution.
There are mainly 3-types of solutions which are as follows :

- **Isotonic solution** : If the solution in which a cell is placed, has equal osmotic concentration to that of cell sap, the outer solution is called isotonic solution.
- **Hypotonic solution** : If the osmotic concentration of outer solution is less than that of the cell sap, the outer solution is called hypotonic solution. If a cell is placed in such a solution endosmosis takes place resulting in swelling of the cell e.g., swelling of dried grapes (raising).
- **Hypertonic solution** : If the osmotic concentration of a solution is higher than that of the other (cell sap) solution, the solution is known as hypertonic.

If a cell is placed in this type of solution, exosmosis takes place. It means water of the cell sap diffuses out into the outer solution causing the cell to become flaccid, e.g., grapes placed in higher concentration of sugar solution becomes flaccid (contracts).
The shrinkage of the protoplast of a living cell from its cell wall due to exosmosis under the influence of a hypertonic solution is called plasmolysis.

The various sequences of plasmolysis are as follows:

- **First stage of plasmolysis or limiting plasmolysis** : In this stage, protoplasm just begins to contract away from the cell wall. There is a gradual loss of water from the cytoplasm and central vacuole decreases, TP or ψ_P to zero.
- **Incipient Plasmolysis** : Continued exosmosis beyond limiting plasmolysis decreases the size of protoplasm further. However, cell wall cannot contract more. Therefore, contracting protoplasm withdraws from cell wall. Contraction is initially from the corners.

- **Evident Plasmolysis** : The stage when the cell wall has reached its limit of contraction and the protoplasm has detached from cell wall attaining spherical shape is called evident plasmolysis.

SIGNIFICANCE OF PLASMOLYSIS

- A living cell is distinguished from the non-living (dead) cell through plasmolysis because plasmolysis does not occur in dead cells.
- The osmotic pressure of any cell can be measured by incipient plasmolysis.
- If plasmolysis continues for long duration in a cell then it dies. By salting, the weeds can be killed and the growth of plants can be prevented in the cracks of walls. Fishes and meats are prevented from spoilage by salting, which inhibits the growth of bacteria and fungus.
- Higher concentration of sugar in jams and jellies stops the growth of bacteria and fungus.
- High amount of chemical fertilizers near the root causes death or browning of the plant due to plasmolysis.
- The fresh water growing plants are either wilted or die when they are kept in marine water.

DEPLASMOLYSIS

The swelling up of a plasmolysed protoplast due to endosmosis under the influence of a hypotonic solution or water is called deplasmolysis. Deplasmolysis is possible only immediately after plasmolysis otherwise the cell protoplast becomes permanently damaged. The value of T.P. becomes zero at the time of limiting plasmolysis and below zero during incipient and evident plasmolysis. Leaf of Tradescantia is used for demonstration of plasmolysis in laboratory.

Table : Differences between Osmosis and Plasmolysis.

S. No.	Osmosis	Plasmolysis
1.	This process occurs between solutions of different concentrations or between protoplasm and surrounding solution or the cells of different osmotic pressure.	This process occurs between the living plant cell and hypertonic solution.
2.	Semi-permeable membrane or diffused permeable membrane is essential in this process.	Protoplasm cell and tonoplast act as a semi-permeable membrane.
3.	Osmosis can be of two types-endosmosis and exosmosis.	Plasmolysis is an exosmosis process in which water moves from cell-sap to the surrounding hypertonic solution.
4.	In endosmosis, water is absorbed through root hair, cells become turgid, while in exosmosis, cells become flaccid.	Due to plasmolysis, cells are always in flaccid condition. Sometimes bacteria and fungi etc. die due to the plasmolysis of protoplasm.

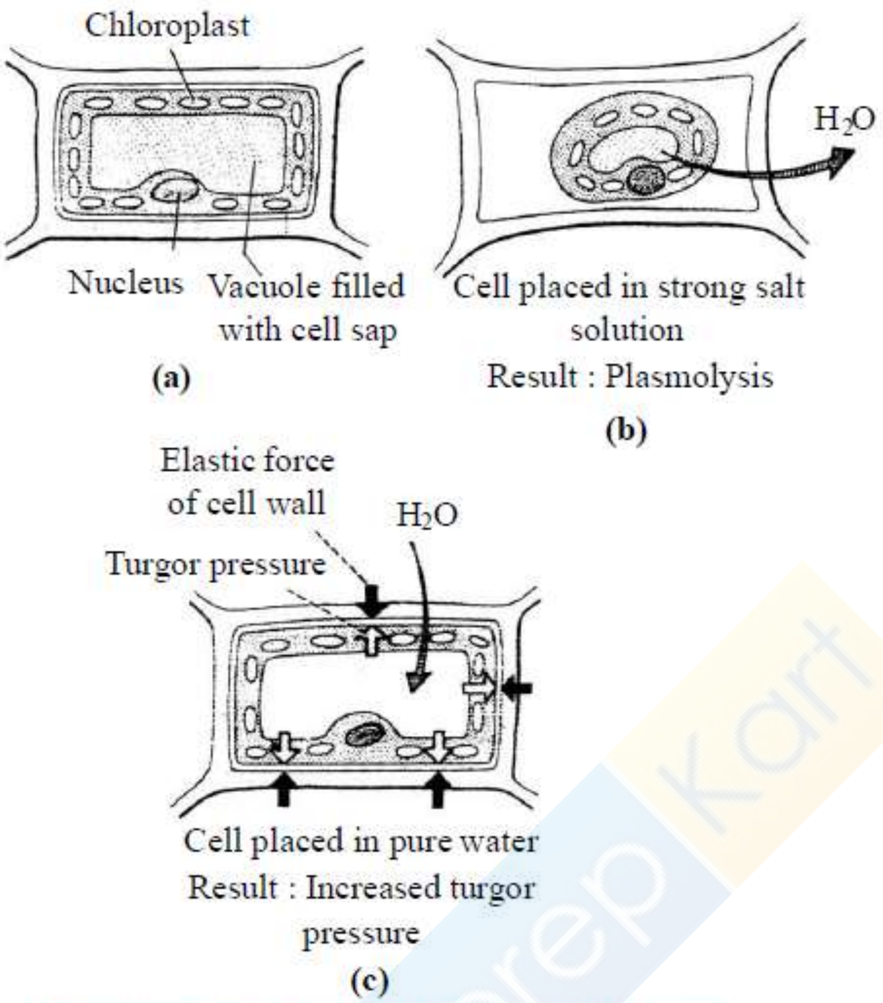


Fig.: Plasmolysis and deplasmolysis (a) Normal cell (b) Plasmolysed cell
(c) Deplasmolysed cell and increased turgor pressure

IMBIBITION

- **Imbibition** is a special type of diffusion when water is absorbed by solids - colloids - causing them to enormously increase in volume.
- The classical examples are seeds and dry wood.
- The various factors which influence the rate of imbibitions are **nature of imbibant**, **surface area of imbibant**, **temperature**, **degree of dryness of imbibant**, **concentration of solutes**, **pH of imbibant** etc.
- Imbibition capacity in the following compounds are as follows :
Agar-Agar > Pectin > Protein > Starch > Cellulose.
- The pressure that is produced by the swelling of wood had been used by prehistoric man to split rocks and boulders.
- Imbibition is less in compactly arranged material like wood, and more in lighter or soft material like gelatin.

SIGNIFICANCE OF IMBIBITION

- Absorption of water during the seed germination is only initiated through imbibition.

- Breaking of seed coat during seed germination is due to imbibition.
- Initial process of water absorption in roots by root hairs is imbibition.
- Resurrection in many plants like Selaginella, lichen, takes place due to the process of imbibition.
- Water enters into the aerial roots and dry fruits due to imbibition.

Movement of water molecules :
Higher D.P.→ Lower D.P.
Lower O.P.→ Higher O.P.
Lower DPD→ Higher DPD
Higher ψ_W → Lower ψ_W
Higher T.P.→ Lower T.P.
Hypotonic solution → Hypertonic solution
Lower conc. of solution → Higher conc. of solution.

ABSORPTION OF WATER BY PLANTS

- **Soil water** : The chief source of soil water is rain. The total amount of water present in the soil is called **holard**, of this the water available to the plant is called **chresard** and the water which cannot be absorbed by the plants is called **echard**.

Water that occurs freely deep in the soil and above the parent rock is called **groundwater**.

- **Gravitational water** : When water enters the soil and passes to spaces between the soil particles and reaches the water table, the type of soil water is called gravitational water.
- **Capillary water** : It is the water which is held around soil particles in the capillary space present around them due to capillary force of surface tension.
- **Hygroscopic water** : This is the form of water which is held by soil particles due to imbibition. As imbibition force is several times higher than osmotic potential found in plant roots, hygroscopic water is largely unavailable to plants.
- **Run-away water** : After the rain, water that does not enter the soil but drained of along the slopes is called run-away water. Plants fail to avail this water.
- **Chemically combined water** : Some of the water molecules are chemically combined with soil minerals (e.g., silicon, iron, aluminium, etc.). This water is not available to the plants.
- **Water vapour** : This occur in soil pore space along with air. It cannot be absorbed by plant roots.
- **Water holding capacity** : The amount of water actually retained by the soil is called field capacity or water holding capacity of the soil. It is about 25-35% in common loam soil. The excess amount of water beyond the field capacity produces water logging.

PATH OF WATER ABSORPTION

- Soil solution → Root hair → Epiblema/Epidermis → Cortex (Epiblema) → Cortex → Endodermis (Passage cell) → Pericycle cell → Protoxylem → Metaxylem
- Water situated in the soil has to reach up to the xylem of root. Root hairs remains in contact of water. First of all, water is adsorbed on pectin wall of root hairs, then water enters into the epidermis of root hairs. From here, water reaches up to the endodermis through the cortex.

The walls of endodermis are suberised. But cells that lie in front of the protoxylem are thin walled known as **passage cells**. These cells transfer water to the xylem. From here, water reaches to the xylem from endodermal cells through the thin walled **pericycle cells**.

- Water is absorbed along with mineral solutes, by the root hairs, purely by diffusion. Once water is absorbed by the root hairs, it can move deeper into root layers by two distinct pathways
  - **apoplast pathway**
  - **symplast pathway**

(A) Apoplastic movement of water occurs exclusively through the cell wall and intercellular spaces; without crossing any membrane.
This movement is dependent on the gradient. The apoplast does not provide any barrier to water movement and water movement is through mass flow. As water evaporates into the intercellular spaces or the atmosphere, tension develops in the continuous stream of water in the apoplast, hence mass flow of water occurs due to the adhesive and cohesive properties of water.

(B) Symplastic movement occurs from cell to cell through plasmodesmata.

- During symplastic movement, water travels through the cells – their cytoplasm; intercellular movement is through the plasmodesmata.
- Major proportion of water flow in the root cortex occurs via the apoplast.

MYCORRHIZAL WATER ABSORPTION

- In mycorrhiza, a large number of fungal hyphae are associated with young root and also extend into soil. The hyphae have large surface area for absorption. The hyphae absorbs water and minerals and hand over them to root. Root provides the fungus with sugar and nitrogenous compounds.
- **Transmembrane pathway** : Water after passing through cortex is blocked by **casparian strips** present on **endodermis**. The casparian strips are formed due to deposition of wax like substance, suberin. In this pathway, water crosses at least two membranes from each cell in its path. These two plasma membranes are found on entry and exit of water. Here, water may also enter through tonoplast surrounding the vacuole i.e., also called as **vacuolar pathway**.

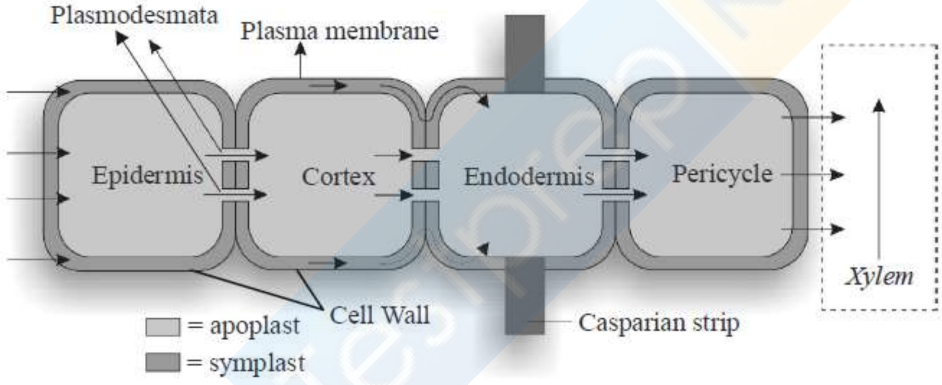


Fig. : Absorption of water (pathway of water movement in root)

MECHANISM OF WATER ABSORPTION

Water is absorbed by two different ways :

- Active water absorption
- Passive water absorption

ACTIVE ABSORPTION OF WATER

According to this method, water is absorbed due to the activity of roots or by expenditure of ATPs.

- **Osmotically active** : According to this method, water is absorbed due to the osmotic activity of roots in order of OP and DPD. No direct ATP are consumed in this method.
- **Non-osmotically active** : According to this method, absorption of water occurs against the osmotic concentration by direct investment/expenditure of metabolic energy in the form of ATPs. Generally, this process is found in halophytes.

PASSIVE ABSORPTION OF WATER

According to this method, forces for the absorption of water originates in the aerial parts by rapid transpiration and roots remain as passive organ. According to Kramer, water absorption in plants is followed by transpiration. About 96% of water is absorbed by passive method. Due to rapid transpiration, DPD of leaf cells increases, results in suction force which sucks the water from roots.

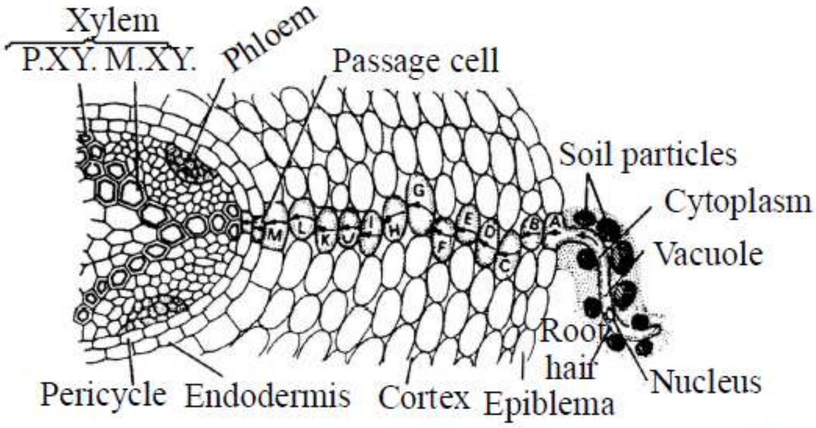


Fig : Passive absorption of water through root hair

FACTORS AFFECTING THE RATE OF WATER ABSORPTION

The different factors which influence the rate of water absorption by a plant can be divided into external or environmental and internal factors.

EXTERNAL OR ENVIRONMENTAL FACTORS

- **Amount of soil water** : Water absorption is optimum at field capacity. It decreases above it. It begins to decline and stops at permanent wilting point.
- **Concentration of the soil solution** : If the concentration of solutes increases in the soil water, its O.P. also increases which slows down or even inhibits the absorption of water.
- **Soil aeration** : Water absorption is more efficient in well aerated soil. Deficiency of oxygen stops the respiration of roots and causes accumulation of CO_2 thus, the protoplasm becomes viscous and the permeability of plasma membrane decreases. Due to all these factors, the rate of water absorption is reduced. This is the reason for death of plants in flooded areas.
- **Soil temperature** : The optimum temperature for maximum rate of water absorption ranges between 20°C and 30°C. Too high temperature kills the cells. At very low temperatures (4°C), water absorption is reduced or stopped and at about 0ºC, it is almost checked.
- **Rate of transpiration** : The rate of absorption of water is directly proportional to the rate of transpiration. A higher rate of transpiration increases the rate of water absorption.

INTERNAL FACTORS

- **Efficiency of the root system** : A plant with deep and elaborate root system can absorb more water. The number of root hairs will be more in a highly branched and elaborate root system, thus, more of its surface area will be in contact with water.
- In **gymnosperms**, root hairs are absent but, are able to absorb water due to the presence of mycorrhizal hyphae.
- In **epiphytes** (orchid), the roots develop a special type of hygroscopic tissue called velamen which can absorb atmospheric moisture.
- **Metabolic activity of roots** : Poor aeration or use of metabolic inhibitors (e.g., KCN) inhibits the rate of water absorption. The metabolic activities help in proper growth of root system and generation of energy for absorption of certain vital minerals.

ASCENT OF SAP

- The upward movement of absorbed water against the gravitational force upto the top parts of plants is called as ascent of sap. Xylem is the water conducting tissue in plants.
- Experiments which prove that water is conducted through xylem vessels and xylem tracheids in plants are as follows :
  - **Girdling or Ringing experiment** : Girdling (ringing) a stem is removing tissues external to xylem in a ring. It does not prevent movement of water to organs attached to stem above the ring. On the contrary, cutting through the xylem tissue of the stem results in almost immediate wilting of leaves attached to the stem above the ring.
  - **Experiment on Balsam plant** : The upward conduction of water takes place through the xylem which can be further proved by immersing the cut end of a branch in an aqueous solution of a dye, e.g., eosine or basic fuchsin. In such an experiment, only xylem vessels and tracheids get stained.
  - **Blockage experiments by Dixon** : To test this, the cut end of a branch is dipped in molten paraffin and a thin slice of the cut end is removed with a blade so that molten wax is present in the lumen of xylem ducts but the walls are free of wax. If such a twig is immersed in safranin solution, the leaves wilt and coloured solution does not rise to the leaves. This experiment makes it clear that water moves up the stem through the lumen of xylem vessels and tracheids rather than their walls.

MECHANISM OF ASCENT OF SAP

Various theories are given to explain the mechanism of ascent of sap.

(1) VITAL FORCE THEORIES
According to these theories, living cells are involved in ascent of sap.

- **Westermaier's Theory (1883)** : According to him, ascent of sap is due to the activity of xylem parenchyma cells.
- **Godlewski's theory (1884)** : According to him, the ascent of sap is due to rhythmic change of osmotic pressure of xylem parenchyma and medullary rays. This theory is also known as relay pump theory.
- **Pulsation theory of Bose** : According to this theory, ascent of sap is due to the pulsatory activity of the innermost layer of cortex. Bose explains his theory with help of galvanometer of electric probe.

Objection to Bose's theory : Before 1900, it was shown by Strasburger (1891,1893) that plants cut at the base would take up a poisonous liquid (picric acid) which killed the living cells of the stem. But picric acid was drawn up the stem which indicated that the living cells were not required for ascent of sap.

(2) ROOT PRESSURE THEORY
Root pressure theory was proposed by Priestley (1916).
According to this theory, the water which is absorbed by the root-hairs from the soil, collects in the cells of the cortex. The cortical cells become fully turgid. In such circumstances, the elastic walls of the cortical cells exert pressure on their fluid-contents and force them towards the xylem vessels. Due to this loss of water, cortical cells become flaccid, again absorb water, become turgid and thus again force out their fluid contents. This pressure forces water up the xylem vessels.

Effects of root pressure is also observable at night and early morning when evaporation is low, and excess water collects in the form of droplets around special openings of veins near the tips of grass blades, and leaves of many herbaceous parts. Such water loss in its liquid phase is known as guttation (term coined by Bergerstein) which takes place through hydathodes.

Objection :

- Root pressure is absent in woody plants.
- When root pressure is high, during the night, then ascent of sap is low.
- Root pressure does not account for the majority of water transport; most plants meet their needs by transpiration pull.

(3) PHYSICAL FORCE THEORIES

- **Capillary force theory** : According to this, vessels and tracheids acts as capillaries and ascent of sap takes place due to capillary force.
- **Transpiration pull and cohesion force theory** : This is the most widely accepted theory of ascent of sap put forward by Dixon and Jolly in 1894.

According to it, 3 components are involved in ascent of sap:

- **Cohesion** : Mutual attraction between the water molecule is known as cohesion which forms a continuous water column in the xylem elements.
- **Adhesion** : Attraction between xylem walls and water molecules is called adhesion force which helps in maintenance of water column of xylem.
- **Transpiration pull** : A tension or negative pressure develops in xylem, due to rapid transpiration in leaves (because of high DPD), this creates a transpiration pull, which is responsible for the pulling up of water column in xylem. So ascent of sap is the constitutive effect of cohesion, adhesion and transpiration pull.

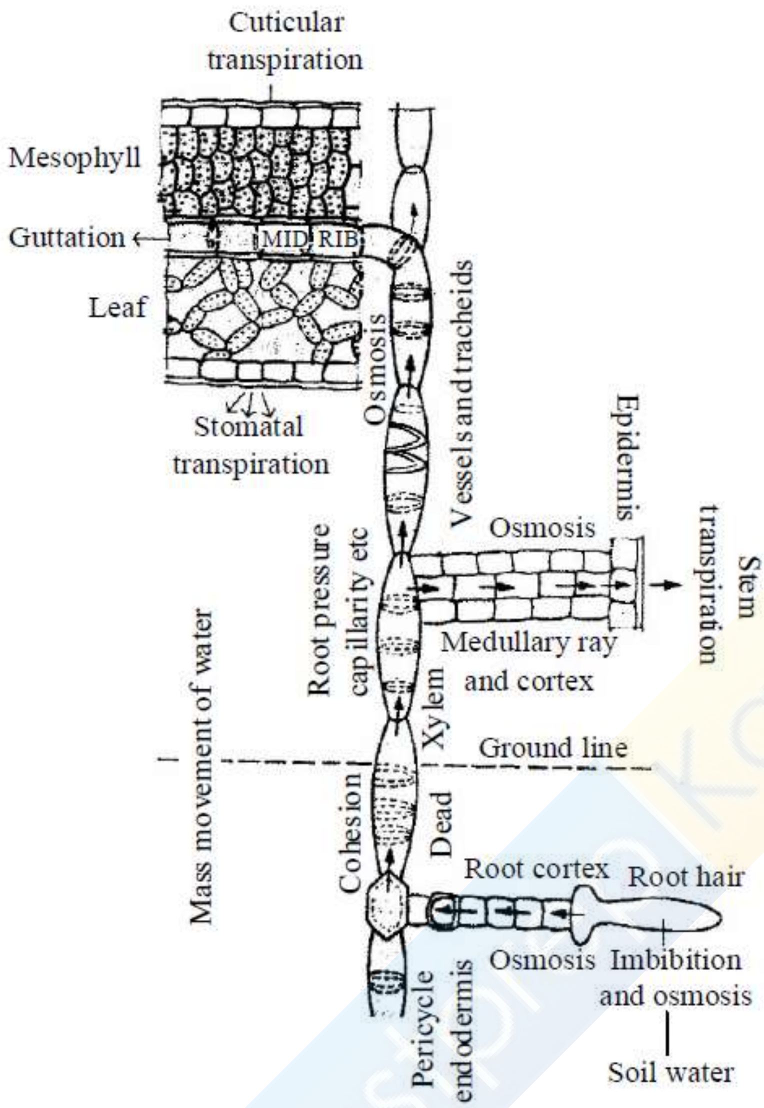


Fig. : Path of ascent of sap showing transpiration pull

FOOD TRANSLOCATION IN PLANTS

- Food/organic material conduction in plants mainly occurs by phloem. (Proved by Girdling experiment).
- In plants, food production occurs mainly in green plants but translocated to all parts of a plant.
- Food conduction occurs between source and sink. Source is net exporter while sink is a net importer.
- Generally, green photosynthetic plant parts act as source like leaves while non-photosynthetic parts like root, shoot, fruits act as a sink.
- The transfer of food depends on requirement and seasonal activities. For example in germinating potato tuber, tuber acts as source and developing buds acts as sink, similarly in early spring, roots acts as source and developing buds as sink.
- Food conduction may be in any required direction unlike the water conduction which is a unidirectional process.
- Translocation of food mainly occurs in the form of sucrose or non-reducing sugar and chemically inert in its pathway of conduction.

- **Pressure flow/Mass flow hypothesis of food/sucrose translocation** : This hypothesis is given by Munch.
- This is the most accepted theory of food conduction in plants.
- According to it, food translocation between source and sink follows the turgor pressure gradient i.e. high T.P. to low T.P.
- **Phloem loading/sucrose loading at source** : It is an active process helped by carrier molecules. At source, due to sucrose loading, concentration of cell sap of sieve cells increases. It results in the increase of osmotic pressure and water moves from nearby xylem into sieve cells resulting in increased turgor pressure (T.P.) and increase in water potential (ψ_W). It establishes a higher T.P. at source and in sieve tubes. Sucrose moves from source in sieve tubes towards sink from high T.P. (high ψ_W) towards the low T.P. (low ψ_W).
- **Phloem unloading/sucrose unloading at sink** : It is an active process helped by carrier molecules. At sink, sucrose is unloaded, which results in a decrease in osmotic pressure (O.P.). It results in exit of water into nearby xylem leading to decrease in turgor pressure (T.P.) and water potential (ψ_W) of phloem. In sink cells, the unloaded sucrose is either changed into starch (as starch does not change O.P.) or consumed, to maintain low O.P. and continuous unloading.
- So, the process of sucrose loading at source and unloading at sink continues. This turgor pressure difference will be maintained and water will continue to move in at source and out at sink.
- This mechanism was experimentally demonstrated by Bimodel experiment of Munch.
- According to evidence of modern research, phloem conduction is an active process and it requires metabolic energy in phloem cells.

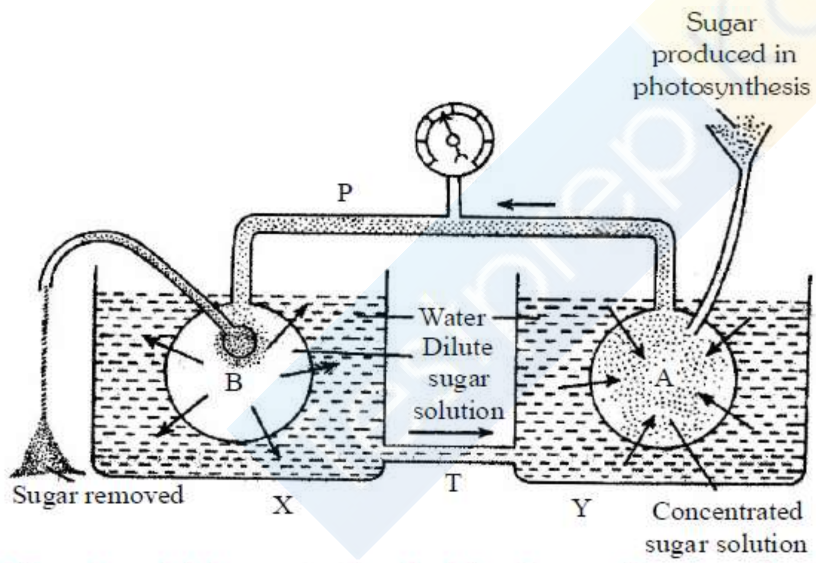


Fig. : A model demonstrating the Munch mass flow hypothesis

FACTORS AFFECTING TRANSLOCATION

- **Temperature** : Optimum temperature for translocation ranges between 20-30°C. The rate of translocation increases with the increase of temperature upto an upper limit and then starts declining. At low temperature, the rate of translocation decreases.
- **Light** : The movement of assimilates of a leaf depends upon radiant energy. Increase in light intensity increases the translocation of food to roots than shoots. At lower intensity, the growth of root and shoot is inhibited thereby, the rate of translocation also decreases.
- **Hormones** : Cytokinins have a pronounced effect on the translocation of water soluble nitrogen compounds.
- **Oxygen** : Oxygen is necessary during transfer of food from mesophyll cells to phloem which is called as phloem loading.

- **Minerals** : Boron is highly essential for translocation of sugar. Phosphorus also helps in translocation of solutes.
- **Water** : Translocation of photosynthates is highly sensitive to the amount of water in plant cells.
- **Metabolic inhibitors** : The metabolic inhibitors which inhibit the process of respiration (e.g., iodoacetate, HCN, carbon monoxide etc.) adversely affect the process of translocation because phloem loading and unloading requires ATP.

TRANSPIRATION

- Loss of water in vapour form, from the aerial parts(organs) of living plants is known as **transpiration**.
- Only few percentage (1-2%) of absorbed water is used by the plants while remaining (98-99%) of water is lost in the atmosphere.
- Minimum transpiration is found in succulent xerophytes and no transpiration is found in submerged hydrophytes.
- Maximum transpiration is found in mesophytes.

TYPES OF TRANSPIRATION

Transpiration is of the three types :

- **Stomatal Transpiration** : Transpiration which takes place through the stomata which are present on the leaves of the plants and aerial organs, is called stomatal transpiration. Maximum amount of water is lost by this type of transpiration. About 80% to 90% transpiration occurs through the stomata.
- **Cuticular Transpiration** : Loss of water through the cuticle which is present on the herbaceous stem and leaves is called cuticular transpiration. Cuticle is a wax like thin layer present on epidermis. About 9% transpiration is cuticular.
- **Lenticular Transpiration** : Minute pore like structures found on the stem of some woody plants and epidermis of some fruits is called lenticels. Some amount of water lost by lenticels is known as lenticular transpiration. However, it is approximately 0.1% to 1% of the total water lost.

Bark Transpiration : It occurs through the corky covering of stem. The amount is 0.5% of the total transpiration.

STOMATA

- Stomata are found on the aerial organs and outer surface of the leaves in the form of minute pores.
- Stomatal pore is surrounded by two specialised epidermal cells called **guard cells**. They are kidney shaped. The guard cells in **monocots** (gramineae) is dumb-bell shaped.
- Guard cells are epidermal cells. But due to the presence of chloroplast they are different from epidermal cells.
- The outer wall of the guard cells is thin and elastic while inner wall is thick and non-elastic.
- Guard cells are surrounded by some specialized epidermal cells called **subsidiary cells** or **accessory cells**.
- Stomata are found on both upper and lower surface of leaves. Stomata are attached with air chambers and forms a cavity called **substomatal-cavity**.
- In **xerophytic plants**, position of stomata is deep in the surface of the leaf. These type stomata are called **sunken stomata**.

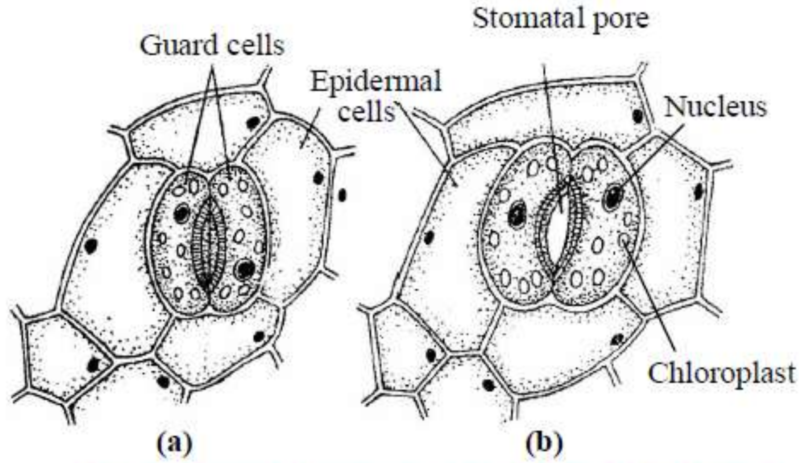


Fig. : Stomatal apparatus (a) Closed (b) Open

MECHANISM OF OPENING AND CLOSING OF STOMATA

(1) Photosynthesis in guard cell hypothesis

According to this theory, guard cell chloroplasts perform photosynthesis during the day and produce sugars in guard cells. It increases the O.P. of the guard cells, compared to adjacent epidermal cells (subsidiary cells). Water enters the guard cells from subsidiary cells by endosmosis. Due to this, guard cells become turgid and stomata opens.

Objection

- In CAM plants, stomata open during dark/night.
- Chloroplasts of guard cells in monocot plants are non-functional (inactive) photosynthetically.

(2) Starch ⇌ Sugar interconversion theory

First of all, Lloyd stated that amount of sugar in guard cells increases during the day time and starch increases at night.

Detailed study of this change was done by Sayre who gave **starch hydrolysis theory**. According to Sayre, starch converts into sugars during day time, when the pH of guard cells is high. Sugar changes into starch during night at low pH in guard cells (supported by Scarth). Sayre stated that CO_2 reacts with water during night, due to accumulation of H_2CO_3, pH in guard cell decreases.

Hanes stated that this change takes place by the enzyme phosphorylase.

$$\text{Starch} + \text{pi} \underset{\substack{\text{Phosphorylase} \\ \text{Night pH } 4.5-5}}{\overset{\text{Day pH } 7.5}{\rightleftharpoons}} \text{Glucose} - 1 - \text{Phosphate}$$

$\Rightarrow$ Conc. of cell of sap of guard cell increased → Entry of H_2O in guard cell → Guard cell turgid → Stomata open.

Stewards Modification : According to Steward (1964), appreciable change in O.P. of guard cells is possible after the conversion of glucose -1 – phosphate into glucose & pi (inorganic phosphate)

(i) Glucose-1-Phosphate $\xrightarrow{\text{Mutase}}$ Glucose-6-Phosphate

(ii) Glucose-6-Phosphate $\xrightarrow{\text{Phosphatase}}$ $\underbrace{\text{Glucose + pi}}$

$\Downarrow$

Conc. of guard cell increases

$\downarrow$

Stomata open $\leftarrow$ Guard cell turgid $\leftarrow$ osmotic entry of H_2O

(iii) Glucose + ATP $\xrightarrow{\text{Hexokinase}}$

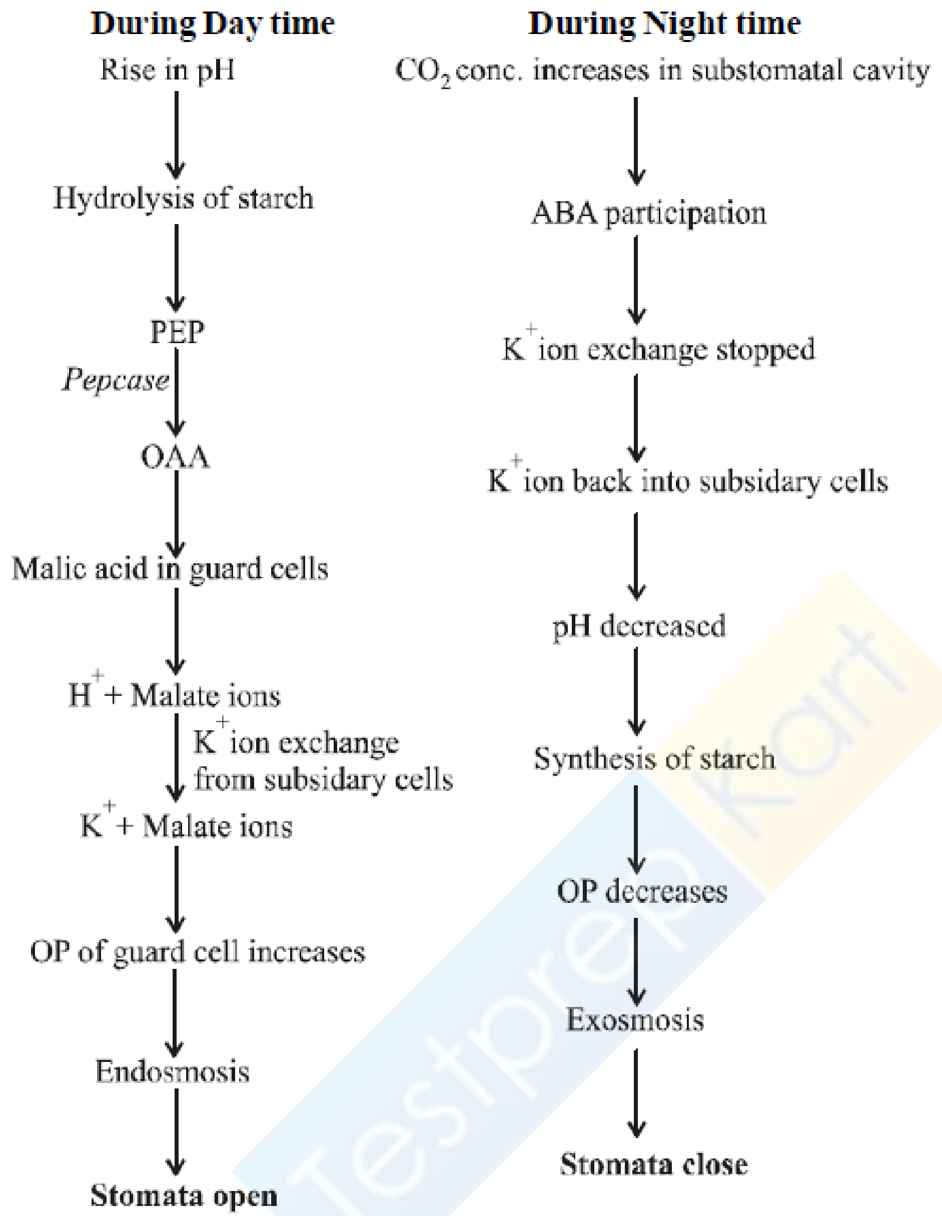
Glucose – 1 – Phosphate $\rightarrow$ Starch $\rightarrow$ Stomata closed

Objections

- Starch is absent in guard cells of some monocots like onion.
- Formation of organic acids is observed during stomatal opening.

(3) Malate or K^+ ion pump theory

Proposed by Levitt (1974) and elaborated by Raschke (1975) and Bowling (1976).



Factors affecting stomatal opening and closing :

- **Light** : In most of the plants, stomata open during the day (except succulent xerophytic plants) and close during the dark.
- **Temperature** : Loftfield showed temperature quotient of opening stomata is $[Q_{10}] = 2$
- CO_2 Concentration : Stomata opens at low concentration of CO_2 while remains closed at high concentration of CO_2.
- **Growth Hormones** :
  - Cytokinin hormone induces opening of stomata. It increases the influx of K^+ ions and stimulates the stomata for opening. While, ABA stimulates the stomata for closing. This hormone opposes the induction effect of cytokinins.
  - ABA affects the permeability of the guard cells. It prevents the outflux of H^+ ions and increases the outflux of K^+ ions. Because of this, pH of the guard cells decreases.
  - Cl^- ions also play an important role in stomatal movement.
  - ABA is formed due to high water stress in chloroplast of leaves.

FACTORS AFFECTING THE RATE OF TRANSPIRATION

It is of two types :

- External factors (environmental factors)
- Internal factors

(A) EXTERNAL FACTORS OR ENVIRONMENTAL FACTORS

- **Atmospheric humidity**

$$T_r \propto \frac{1}{\text{Relative humidity}}$$

- The rate of transpiration (T_r) is higher in low atmospheric humidity while at higher atmospheric humidity, the atmosphere is moistened, decreasing the rate of transpiration.
- Therefore, the rate of transpiration is high during the summer and low in rainy season.

- **Temperature**

$T_r \propto$ Temperature

- The value of Q_{10} for transpiration is 2. It means by increasing 10°C temperature, the rate of transpiration is approximately double. (By Loftfield)
- Water vapour holding capacity of air increases at high temperature, resulting in an increase in the rate of transpiration.

- **Light**
  - Light stimulates the rate of transpiration.
  - Rate of transpiration is faster in blue-light than that of red light, because stomata are completely opened at their full capacity in the blue light.

- **Wind velocity**

$T_r \propto$ Wind velocity

- Transpiration is less in constant air but if wind velocity is high, the rate of transpiration is also high because wind removes humid air (saturated air) around the stomata.

- **Atmospheric Pressure**
  - The speed of the air increases at low atmospheric pressure. As a result, the rate of the diffusion increases which in turn increases the rate of transpiration.
  - The rate of transpiration is found to be maximum in the high intensity of light at high range of hills.

- **Anti-transpirants**

Chemical substances which reduce the rate of transpiration are known as anti-transpirants. Anti-transpirants are as follows :
Phenyl mercuric acetate (PMA), Aspirin (Salicylic acid), Abscisic acid (ABA), Oxi-ethylene, Silicon oil, CO_2 and low viscous wax.

(B) INTERNAL FACTORS

- **Leaf area** : If leaf area is more, transpiration is faster. However, the rate of transpiration per unit area is more in smaller leaves than in larger leaves due to high number of stomata in a small leaf. Number of stomata per unit area of leaf is called stomatal frequency.

$$I = \frac{S}{E + S} \times 100 \text{ here,}$$

I = Stomatal index.
S = No. of stomata per unit area.
E = No. of epidermal cells in unit area.

- **Leaf structure** : The anatomical features of leaves like sunken or vestigial stomata, presence of hair, cuticle or waxy layer on the epidermis, presence of hydrophilic substances such as gums, mucilage etc. in the cells; compactly arranged mesophyll cells etc. help in reducing the rate of transpiration.
- **Root-shoot ratio** : The rate of transpiration is directly proportional to the root-shoot ratio.

- **Age of plants** : Germinating seeds show a slow rate of transpiration. It becomes maximum at maturity. However, it decreases at senescence.
- **Orientation of leaves** : If the leaves are arranged transversely on the shoot, they lose more water because they are exposed to direct sunlight. If placed perpendicular, they transpire at slower rate.

ADVANTAGES OF TRANSPIRATION

- Transpiration influences the absorption of water from the soil.
- Transpiration exerts a tension or pull on water column in xylem which is responsible for the ascent of sap.
- Transpiration helps in the movement of water and minerals absorbed by the roots to the other parts of the plant.
- The evaporation of water during transpiration contributes to the cooling of leaves (and also the surrounding air) and protects leaves from heat injury particularly under conditions of high temperature and intense sunlight.

DISADVANTAGES OF TRANSPIRATION

Transpiration often results in water deficit which causes injury to the plants by desiccation.

WILTING

- A plant usually fails to survive if it is conditioned to water deficiency. The symptoms appear in the plant, plant parts or in the cells due to scarcity of water are termed as **wilting**. It is loss of turgidity causing folding and drooping of leaves and other soft aerial parts of the plant.
- Rapid transpiration causes mid-day leaf water deficit (**temporary wilting**). If such condition continues for some time, permanent water deficit (**permanent wilting**) may develop, which causes injury to plants.
- Since approximately 90 percent of absorbed water is lost through transpiration, the energy used in absorption and conduction of water is wasted.

GUTTATION

- Loss of water from the aerial parts or leaves of the plant in the form of water droplets is called guttation.
- The term guttation was coined by Burgerstein.
- Exuded liquid of guttation along with water contains some organic and inorganic (dissolved) substances. It means it is not pure water.
- Normally, guttation process is found in herbaceous plants like grasses, tomato, Balsam, Colocasia, Saxifraga and in some of the plants of Cucurbitaceae family.
- Guttation occurs from the margins of the leaves through the special pore (always open) like structure are called **Hydathodes** or **Water stomata**.
- Generally guttation occurs during night or early morning.
- The process of guttation takes place due to the root pressure, developed in cortex cells of root.

Table : Differences between Transpiration and Guttation.

S. No.	Transpiration	Guttation
1.	It normally occurs in day time.	It occurs during cooler periods of night and early morning.
2.	Water comes out in the form of vapour.	Water is lost in the form of droplets.
3.	Released water vapour is in the pure form.	Water which is exuded, is a mixture of organic and inorganic substances.
4.	It occurs through stomata, cuticles and lenticles.	It occurs through hydathodes.
5.	It occurs through aerial parts of plant.	It occurs through leaves.
6.	It becomes very slow and even stops in humid conditions.	It occurs in humid conditions.