Chapter 11

Unit V: Plant Physiology (Functional Organisation)

Transport in Plants

Learning Objectives

The learner will be able to,

- *Recall knowledge of basic physical and biological processes studied in previous classes.*
- *Classify, differentiate and compare the process of active and passive transport.*
- *Understand the mechanism of absorption of water.*
- *Analyse the various theories in ascent of sap.*
- *Understand the process of transpiration and Compare the various types of transpiration.*
- *Discuss the mechanism of phloem translocation.*
- *Understand the process behind mineral absorption.*

Chapter Outline

11.1 Types of transport
11.2 Cell to Cell transport
11.3 Plant water relations
11.4 Absorption of water
11.5 Ascent of Sap
11.6 Transpiration
11.7 Translocation of organic solutes
11.8 Mineral absorption

CHE4VV

Over 450 million years ago (the Ordovician period in Paleozoic era) plants migrated from their own sophisticated water world to newly formed land. The land had harsh environment; water availability was deeper and so plants struggled for getting water for their very existence. Some of them failed to survive and rest adopted themselves to the new world. The biggest adaptations followed for their survival was building their own water absorbing systems to draw water from deep inside the land. The creation and updating of water absorbing system (vascular tissues) led to the diversity of the plant kingdom. The gregarious growth of prehistoric pteridophytes, gymnosperms and present-day flowering plants led to the biggest challenge in the transport of water from root to several meters high trees against gravity. In this chapter, we will study the events taking place between the gain of water in roots and loss in leaves and the mechanisms behind the basic physical and biological processes in the movement of water, gases and minerals in plants. Further, we study how food material synthesized in the leaf can be transported to various utilizing and storage areas against struggles and challenges.

11.1 Types of Transport

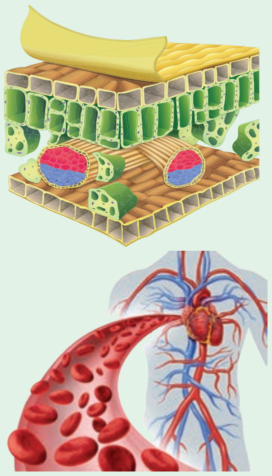
Transport is the process of moving water, minerals and food to all parts of the plant body. Conducting tissues such as xylem and phloem play an important role in this.

What is the need for transport? Water absorbed from roots must travel up to leaves by xylem for food preparation by photosynthesis. Likewise, food prepared from leaves has to travel to all parts of the plant including roots. Both the processes are interconnected and depend on each other.

❖ Based on the distance travelled by water (sap) or food (solute) they are classified as

(a) Short distance (Cell to cell transport) and (b) Long distance transport.

The Plumbing system of Plants and Humans



Plants and animals evolved separately but developed comparable structures to control transport of water and dissolved chemicals. But whose transport system is optimally designed to offer selective advantage? In plants, transport through xylem has allowed growth in height and colonization of diverse habitats and the system has to be extensive as Photosynthesis requires water. Murray's law predicts the thickness of branches in transport networks, such that the cost for transport and maintenance of the transport medium is minimized. This law is observed in the vascular and respiratory systems of animals, xylem in plants, and the respiratory system of insects. Further research in this area will improve our understanding of natural world.

i. **Short-distance (Cell to cell transport):** Involvement of few cells, mostly in the lateral direction. They are the connecting link to xylem and phloem from root hairs or leaf tissues respectively. Examples: Diffusion, Imbibition, and Osmosis.

ii. **Long-distance transport:** Transport within the network of xylem or phloem is an example for long-distance transport. Examples: Ascent of Sap and Translocation of Solutes.

❖ Based on energy expenditure during transport, they are classified as **(a) passive transport and (b) active transport.**

i. **Passive transport:** It is a downhill process which utilizes physical forces like gravity and concentration. No energy expenditure is required. It includes diffusion, facilitated diffusion, imbibition, and osmosis.

ii. **Active transport:** It is a biological process and it runs based on the energy obtained from respiration. It is an uphill process.

11.2 Cell to Cell Transport

Cell to cell or short distance transport covers the limited area and consists of few cells. They are the facilitators or tributaries to the long-distance transport. The driving force for the cell to cell transport can be passive or active (Figure 11.1). The following chart illustrate the various types of cell to cell transport:

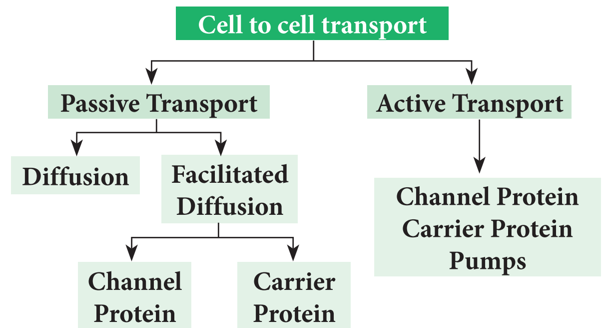


Figure 11.1: Cell to cell transport

11.2.1 Passive Transport

1. Diffusion

When we expose a lightened incense stick or mosquito coil or open a perfume bottle in a closed room, we can smell the odour everywhere in the room. This is due to the even distribution of perfume molecules throughout the room. This process is called **diffusion**.

In **diffusion**, the movement of molecules is continuous and random in order in all directions (Figure 11.2).

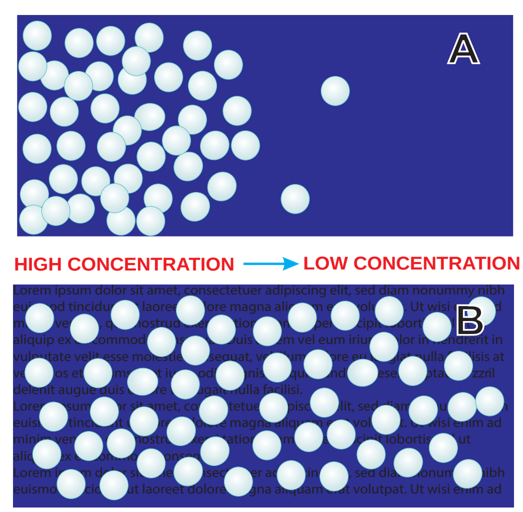


Figure 11.2: Distribution of molecules in diffusion (A) Initial stage (B) Final stage

Diffusion: The net movement of molecules from a region of their higher concentration to a region of their lower concentration along a concentration gradient until an equilibrium is attained.

Characteristics of diffusion

i. It is a passive process, hence no energy expenditure involved.
ii. It is independent of the living system.
iii. Diffusion is obvious in gases and liquids.
iv. Diffusion is rapid over a shorter distance but extremely slow over a longer distance.
v. The rate of diffusion is determined by temperature, concentration gradient and relative density.

Significance of diffusion in Plants

i. Gaseous exchange of O_2 and CO_2 between the atmosphere and stomata of leaves takes place by the process of diffusion. O_2 is absorbed during respiration and CO_2 is absorbed during photosynthesis.
ii. In transpiration, water vapour from intercellular spaces diffuses into atmosphere through stomata by the process of diffusion.
iii. The transport of ions in mineral salts during passive absorption also takes place by this process.

DO YOU KNOW?

Diffusion for sterilization in surgical theatres

Surgical theatres must be free from germs to prevent infection during surgeries. A mixture of Formalin and Potassium permanganate produces enormous fumes which will kill all pathogens in an enclosed area. This method is known as **fumigation** and operates by diffusion.

2. Facilitated Diffusion

Cell membranes allow water and nonpolar molecules to permeate by simple diffusion. For transporting polar molecules such as ions, sugars, amino acids, nucleotides and many cell metabolites is not merely based on concentration gradient. It depends on,

i. ***Size of molecule***: Smaller molecules diffuse faster.
ii. ***Solubility of the molecule***: Lipid soluble substances easily and rapidly pass through the membrane. But water soluble substances are difficult to pass through the membrane. They must be facilitated to pass the membrane.

Types of Membrane Permeability

A solution is made up of solute particles dissolved in a solvent and the permeability of the above components depends on the nature of cell membranes, which is given below:

Impermeable: Inhibit the movement of both solvent and solute molecules. Example: Suberised, cutinised or liginifid cell walls.

Permeable: They allow diffusion of both solvent and solute molecules through them. Example: Cellulosic cell wall.

Semi permeable: Semi permeable allow diffusion of solvent molecules but do not allow the passage of solute molecule. Example: Parchment paper.

Selectively permeable: All bio membranes allow some solutes to pass in addition to the solvent molecules. Example: Plasmalemma, tonoplast, and membranes of cell organelles.

In facilitated diffusion, molecules cross the cell membrane with the help of special membrane proteins called transport proteins, without the expenditure of ATP.

There are two types of transport proteins present in the cell membrane. They are channel protein and a carrier protein.

I. Channel Protein

Channel protein forms a channel or tunnel in the cell membrane for the easy passage of molecules to enter the cell. The channels are either open or remain closed. They may open up for specific molecules. Some channel proteins create larger pores in the outer membrane. Examples: Porin and Aquaporin.

i. **Porin**

Porin is a large transporter protein found in the outer membrane of plastids, mitochondria and bacteria which facilitates smaller molecules to pass through the membrane.

ii. **Aquaporin**

Aquaporin is a water channel protein embedded in the plasma membrane. It regulates the massive amount of water transport across the membrane (Figure 11.3). Plants contain a variety of aquaporins. Over 30 types of aquaporins are known from maize. Currently, they are also recognized to transport substrates like glycerol, urea, CO_2, NH_3, metalloids, and **Reactive Oxygen Species** (ROS) in addition to water. They increase the permeability of the membrane to water. They confer drought and salt stress tolerance.

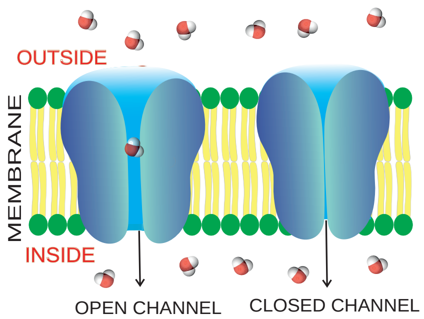


Figure 11.3: Aquaporin

II. Carrier Protein

Carrier protein acts as a vehicle to carry molecules from outside of the membrane to inside the cell and vice versa (Figure 11.4). Due to association with molecules to be transported, the structure of carrier protein gets modified until the dissociation of the molecules.

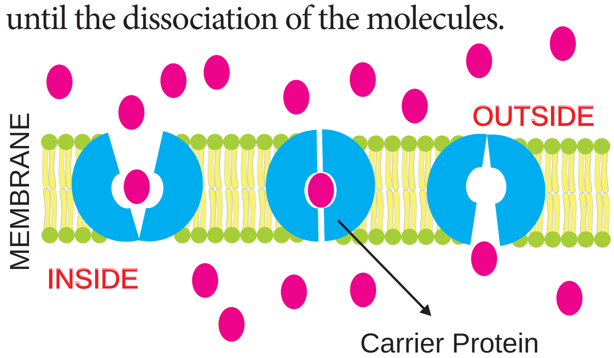


Figure 11.4: Carrier Protein

There are 3 types of carrier proteins classified on the basis of handling of molecules and direction of transport (Figure 11.5). They are, i) **Uniport** ii) **Symport** iii) **Antiport.**

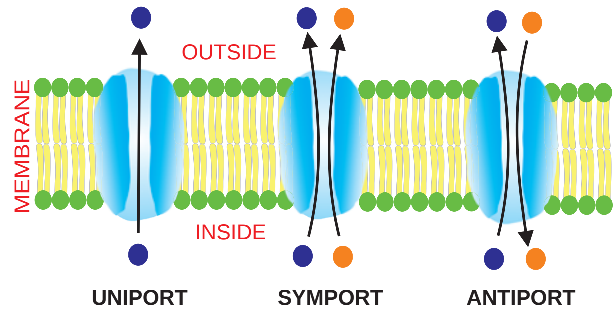


Figure 11.5: Direction of transport

i. ***Uniport***: In this molecule of a single type move across a membrane independent of other molecules in one direction.

ii. ***Symport or co-transport***: The term **symport** is used to denote an integral membrane protein that simultaneously transports two types of molecules across the membrane in the same direction.

iii. ***Antiport or Counter Transport***: An **antiport** is an integral membrane transport protein that simultaneously transports two different molecules, in opposite directions, across the membrane.

Discovery of Aquaporin

Peter Agre, discovered the "Water Pore" Aquaporin in RBC and received Nobel Prize for chemistry in 2003.

11.2.2 Active Transport

The main disadvantage of passive transport processes like diffusion is the lack of control over the transport of selective molecules. There is a possibility of harmful substances entering the cell by a concentration gradient in the diffusion process. But selective permeability of cell membrane has a great control over entry and exit of molecules. Active transport is the entry of molecules against a concentration gradient and an uphill process and it needs energy which comes from ATP. Passive transport uses kinetic energy of molecules moving down a gradient whereas, active transport uses cellular energy to move them against a gradient. The transport proteins discussed in facilitated diffusion can also transport ions or molecules against a concentration gradient with the expenditure of cellular energy as an active process. Pumps use a source of free energy such as ATP or light to drive the thermodynamically uphill transport of ions or molecules. The pump action is an example of active transport. Example: Na^+-K^+-ATPase pump (Table 11.1).

Table 11.1 Comparison of different transport mechanisms

Property	Passive transport		Active transport
	Simple diffusion	Facilitated diffusion	
Nature of process	Physical	Biological	Biological
Requirement for presence of membrane protein	No	Yes	Yes
Selectivity of molecule	No	Yes	Yes
Saturation of transport	No	Yes	Yes
Uphill transport	No	No	Yes
Energy requirement (ATP)	No	No	Yes
Sensitivity to inhibitors	No	Yes	Yes

Check your grasp!

What are the similarities and differences between co- transport and counter transport?

Solution:

Similarity: In both system two molecules are involved for the unidirectional transport.

Difference: In co-transport, two molecules are transported together whereas, in counter transport two molecules are transported in opposite direction to each other.

11.3 Plant Water Relations

Water plays an essential role in the life of the plant. The availability of water influences the external and internal structures of plants as protoplasm is made of 60-80% water. Water is a **universal solvent** since most of the substances get dissolved in it and the high tensile strength of water molecule is helpful in the ascent of sap. Water maintains the internal temperature of the plant as well as the turgidity of the cell.

11.3.1 Imbibition

Colloidal systems such as **gum, starch, proteins, cellulose, agar, gelatin** when placed in water, will absorb a large volume of water and swell up. These substances are called **imbibants** and the phenomenon is **imbibition**.

Examples: 1. The swelling of dry seeds 2. The swelling of wooden windows, tables, doors due to high humidity during the rainy season.

DO YOU KNOW?

The Power of Imbibition

In olden days, small wooden pegs were inserted into crevices of rocks followed by continuous hydration. Due to imbibition the volume of wooden peg increases and cuts off rocks precisely.

The gluten from wheat can take as much as 300% of its own weight

Significance of imbibition

i. During germination of seeds, imbibition increases the volume of seed enormously and leads to bursting of the seed coat.
ii. It helps in the absorption of water by roots at the initial level.

Activity

Imbibition experiment

Collect 5 gm of gum from Drumstick tree or Babool tree or Almond tree. Immerse in 100ml of water. After 24 hours observe the changes and discuss the results with your teacher.

11.3.2 Water Potential (Ψ)

The concept of water potential was introduced in 1960 by **Slatyer** and **Taylor**. Water potential is potential energy of water in a system compared to pure water when both temperature and pressure are kept the same. It is also a measure of how freely water molecules can move in a particular environment or system. Water potential is denoted by the Greek symbol **Ψ** (psi) and measured in **Pascal** (Pa). At standard temperature, the water potential of pure water is **zero**. Addition of solute to pure water decreases the kinetic energy thereby decreasing the water potential. Comparatively a solution always has low water potential than pure water. In a group of cells with different water potential, a water potential gradient is generated. Water will move from higher water potential to lower water potential.

Water potential (**Ψ**) can be determined by,

1. Solute concentration or Solute potential (Ψ_S)
2. Pressure potential (Ψ_P)

By correlating two factors, water potential is written as,

$$\Psi_W = \Psi_S + \Psi_P$$

Water Potential = Solute potential + Pressure potential

1. Solute Potential (Ψ_S)

Solute potential, otherwise known as **osmotic potential** denotes the effect of dissolved solute on water potential. In pure water, the addition of solute reduces its free energy and lowers the water potential value from zero to negative. Thus the value of solute potential is always negative. In a solution at standard atmospheric pressure, water potential is always equal to solute potential ($\Psi_W = \Psi_S$).

2. Pressure Potential (Ψ_P)

Pressure potential is a mechanical force working against the effect of solute potential. Increased pressure potential will increase water potential and water enters cell and cells become **turgid**. This **positive hydrostatic pressure** within the cell is called **Turgor pressure**. Likewise, withdrawal of water from the cell decreases the water potential and the cell becomes **flaccid**.

3. Matric Potential (Ψ_M)

Matric potential represents the attraction between water and the **hydrating colloid or gel-like organic molecules in the cell wall** which is collectively termed as **matric potential**. Matric potential is also known as **imbibition pressure**. The matric potential is maximum (most negative value) in a dry material. **Example**: The swelling of soaked seeds in water.

11.3.3 Osmotic Pressure and Osmotic Potential

When a solution and its solvent (pure water) are separated by a semipermeable membrane, a pressure is developed in the solution, due to the presence of dissolved solutes. This is called **osmotic pressure** (**OP**). Osmotic pressure is increased with the increase of dissolved solutes in the solution. More concentrated solution (low **Ψ** or Hypertonic) has high osmotic pressure. Similarly, less concentrated solution (high **Ψ** or Hypotonic) has low osmotic pressure. The osmotic pressure of pure water is always **zero** and it increases with the increase of solute concentration. Thus osmotic pressure always has a positive value and it is represented as π.

Osmotic potential is defined as the ratio between the number of solute particles and the number of solvent particles in a solution. Osmotic potential and osmotic pressure are numerically equal. Osmotic potential has a negative value whereas on the other hand osmotic pressure has a positive value.

11.3.4 Turgor Pressure and Wall Pressure

When a plant cell is placed in pure water (hypotonic solution) the diffusion of water into the cell takes place by endosmosis. It creates a positive hydrostatic pressure on the rigid cell wall by the cell membrane. Henceforth the pressure exerted by the cell membrane towards the cell wall is **Turgor Pressure (TP).**

The cell wall reacts to this turgor pressure with **equal and opposite force**, and the counter-pressure exerted by the cell wall towards cell membrane is **wall pressure (WP).**

Turgor pressure and wall pressure make the cell fully turgid.

TP + WP = Turgid.

Activity

Find the role of turgor pressure in sudden closing of leaves when we touch the 'touch me not' plant.

11.3.5 Diffusion Pressure Deficit (DPD) or Suction Pressure (SP)

Pure solvent (hypotonic) has higher diffusion pressure. Addition of solute in pure solvent lowers its diffusion pressure. The difference between the diffusion pressure of the solution and its solvent at a particular temperature and atmospheric pressure is called as **Diffusion Pressure Deficit (DPD)** termed by **Meyer (1938**). DPD is increased by the addition of solute into a solvent system. Increased DPD favours endosmosis or it sucks the water from hypotonic solution; hence **Renner** (1935) called it as **Suction pressure**. It is equal to the difference of osmotic pressure and turgor pressure of a cell. The following three situations are seen in plants:

- **DPD in normal cell:** DPD = OP – TP.
- **DPD in fully turgid cell**: Osmotic pressure is always equal to turgor pressure in a fully turgid cell.
- OP = TP or OP-TP =0. Hence DPD of fully turgid cell is zero.
- **DPD in flaccid cell**: If the cell is in flaccid condition there is no turgor pressure or TP=0. Hence DPD = OP.

11.3.6 Osmosis

Osmosis (Latin: *Osmos*-impulse, urge) is a **special type of diffusion**. It represents the movement of **water or solvent molecules** through a selectively permeable membrane **from the place of its higher concentration (high water potential) to the place of its lower concentration (low water potential).**

Types of Solutions based on concentration

i. ***Hypertonic*** (*Hyper* = High; *tonic* = solute): This is a strong solution (low solvent/ high solute / low **Ψ**) which **attracts solvent** from other solutions.

ii. ***Hypotonic*** (*Hypo* = low; *tonic* = solute): This is a weak solution (high solvent /low or zero solute / high **Ψ**) and it **diffuses water** out to other solutions (Figure 11.7).

iii. ***Isotonic*** (*Iso* = identical; *tonic* = soute): It refers to two solutions having same concentration. In this condition the net movement of water molecule will be zero.

The term hyper, hypo and isotonic are **relative terms** which can be used only in comparison with another solution.

Thistle funnel experiment

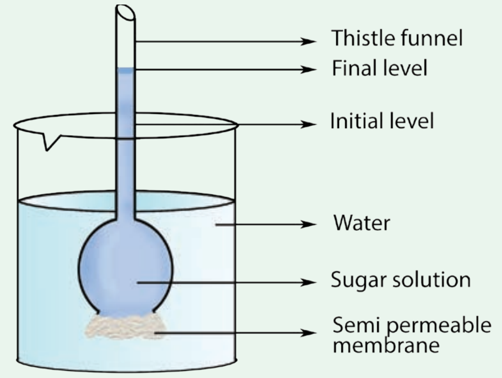


Figure 11.6: Thistle Funnel Experiment

Mouth of a thistle funnel is tied with goat bladder. It acts as a semipermeable membrane. Pour concentrated sugar solution in the thistle funnel and mark the level of solution. Place this in a beaker of water. After some time, water level in the funnel rises up steadily. This is due to the inward diffusion of water molecules through the semipermeable membrane (Figure 11.6).

Conversely, if water in the beaker is replaced by a sugar solution and sugar solution in the thistle funnel replaced by water, what will be happen?

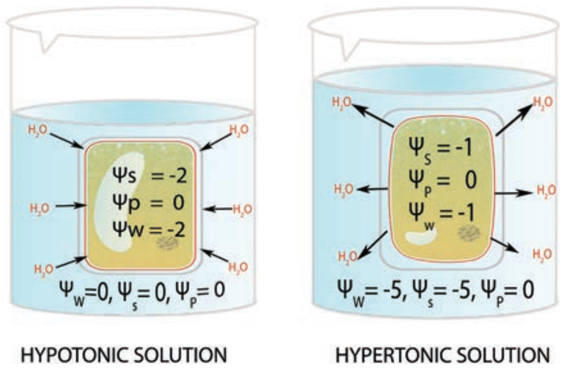


Figure 11.7: Types of solution based on concentration

1. Types of osmosis

Based on the direction of movement of water or solvent in an osmotic system, two types of osmosis can occur, they are ***Endosmosis*** and ***Exosmosis***.

i. Endosmosis: Endosmosis is defined as the osmotic entry of solvent into a cell or a system when it is placed in a pure water or hypotonic solution.
For example, dry raisins (high solute and low solvent) placed in the water, it swells up due to turgidity.

ii. Exosmosis: Exosmosis is defined as the osmotic withdrawal of water from a cell or system when it is placed in a hypertonic solution. Exosmosis in a plant cell leads to **plasmolysis**.

2. Plasmolysis (*Plasma* = cytoplasm; *lysis* = breakdown)

When a plant cell is kept in a hypertonic solution, water leaves the cell due to **exosmosis**. As a result of water loss, protoplasm shrinks and the cell membrane is pulled away from the cell wall and finally, the cell becomes **flaccid**. This process is named as **plasmolysis**.

Wilting of plants noticed under the condition of water scarcity is an indication of plasmolysis. Three types of plasmolysis occur in plants: i) ***Incipient plasmolysis ii) Evident plasmolysis*** **and *iii) Final plasmolysis***. Differences among them are given in table 11.2.

Significance

Plasmolysis is exhibited only by living cells and so it is used to test whether the cell is living or dead.

3. Deplasmolysis

The effect of plasmolysis can be reversed, by transferring them back into water or **hypotonic solution**. Due to endosmosis, the cell becomes turgid again. It regains its original shape and size. This phenomenon of the revival of the plasmolysed cell is called **deplasmolysis**. Example: Immersion of dry raisin in water.

Potato Osmoscope

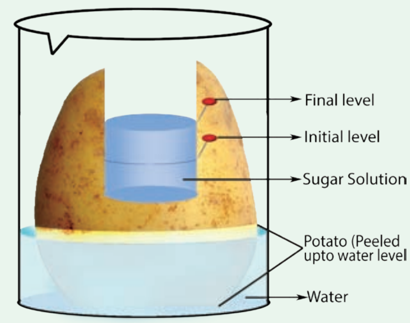


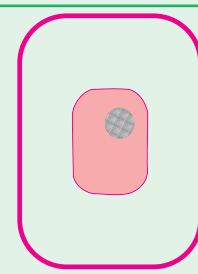
Figure 11.8: Demonstration of Endosmosis by Potato Osmoscope

i. Take a peeled potato tuber and make a cavity inside with the help of a knife.
ii. Fill the cavity with concentrated sugar solution and mark the initial level.
iii. Place this setup in a beaker of pure water.
iv. After 10 minutes observe the sugar solution level and record your findings (Figure 11.8).
v. With the help of your teacher discuss the results.

Instead of potato use beetroot or bottle-guard and repeat the above experiment. Compare and discuss the results.

4. Reverse Osmosis

Reverse Osmosis follows the same principles of osmosis, but in the reverse direction. In this process movement of water is reversed by applying pressure to force the water against a concentration gradient of the solution. In regular osmosis, the water molecules move from the higher concentration (pure water = hypotonic) to lower concentration (salt water = hypertonic). But in reverse osmosis, the water molecules move from the lower concentration (salt water = hypertonic) to higher concentration (pure water = hypotonic) through a selectively permeable membrane (Figure 11.9).

Table 11.2: Difference between plasmolysis types.		
Incipient plasmolysis	**Evident plasmolysis**	**Final plasmolysis**
No morphological symptoms appear in plants.	Wilting of leaves appear.	Severe wilting and drooping of leaves appear.
The plasma membrane separates only at the corner from the cell wall of cells.	Plasma membrane completely detaches from the cell wall.	Plasma membrane completely detaches from cell wall with maximum shrinkage of volume.
It is reversible.	It is reversible.	It is irreversible.
		

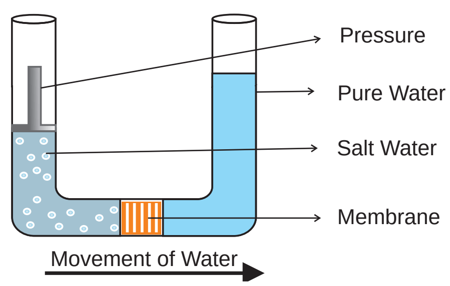


Figure 11.9: Reverse Osmosis

Uses: Reverse osmosis is used for purification of drinking water and desalination of sea water.

Check your grasp!

If a cell in the cortex with DPD of 5atm is surrounded by hypodermal cells with DPD of 2atm, what will be direction of movement of water?

Solution: Water will move from low DPD to high DPD (hypodermis 2 atm to cortex 5 atm).

11.4 Absorption of Water

Terrestrial plants have to absorb water from the soil to maintain turgidity, metabolic activities and growth. Absorption of water from soil takes place in two steps:

1. From soil to root hairs – either actively or passively.

2. From root hairs further transport in the lateral direction to reach xylem, the superhighway of water transport.

11.4.1 Water Absorbing Organs

Usually, absorption of water occurs in plants through young roots. The zone of rapid water absorption is **root hairs**. They are delicate structures which get continuously replaced by new ones. Root hairs are unicellular extensions of epidermal cells without cuticle. Root hairs are extremely thin and numerous and they provide a large surface area for absorption (Figure 11.10).

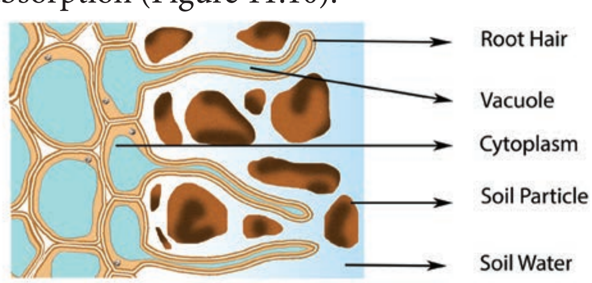


Figure 11.10: Structure of Root Hair

11.4.2 Path of Water Across Root Cells

Water is first absorbed by root hair and other epidermal cells through imbibition from soil and moves radially and centripetally across the cortex, endodermis, pericycle and finally reaches xylem elements osmotically.

There are three possible routes of water (Figure 11.11). They are i) **Apoplast** ii) **Symplast** iii) **Transmembrane route**.

1. Apoplast

The **apoplast** (Greek: ***apo*** = away; ***plast*** = cell) consists of everything external

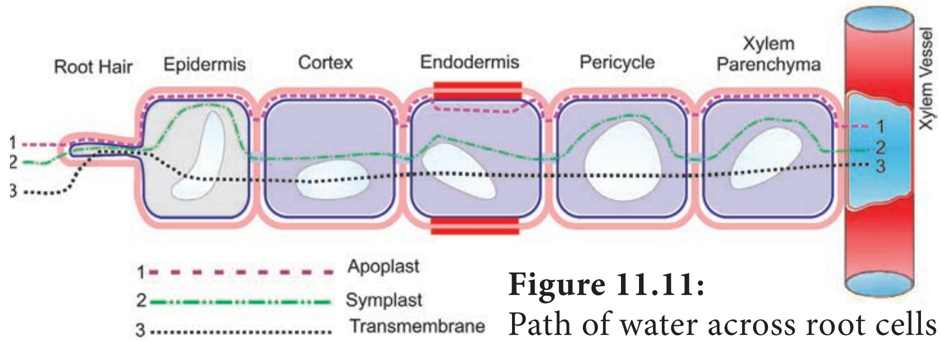


Figure 11.11:
Path of water across root cells

to the plasma membrane of the living cell. The apoplast includes cell walls, extra cellular spaces and the interior of dead cells such as vessel elements and tracheids. In the apoplast pathway, water moves exclusively through the cell wall or the non-living part of the plant without crossing any membrane. The apoplast is a continuous system.

2. Symplast

The **symplast** (Greek: ***sym*** = within; ***plast*** = cell) consists of the entire mass of cytosol of all the living cells in a plant, as well as the **plasmodesmata**, the cytoplasmic channel that interconnects them.

In the symplastic route, water has to cross plasma membrane to enter the cytoplasm of outer root cell; then it will move within adjoining cytoplasm through plasmodesmata around the vacuoles without the necessity to cross more membrane, till it reaches xylem.

3. Transmembrane route

In transmembrane pathway water sequentially enters a cell on one side and exits from the cell on the other side. In this pathway, water crosses at least two membranes for each cell. Transport across the **tonoplast** is also involved.

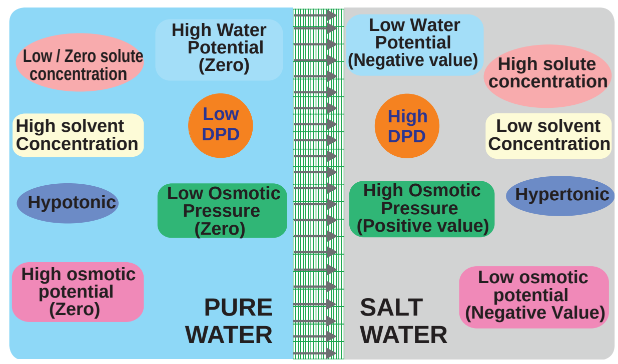
11.4.3 Mechanism of Water Absorption

Kramer (1949) recognized two distinct mechanisms which independently operate in the absorption of water in plants. They are, i) active absorption ii) passive absorption.

1. Active Absorption

The mechanism of water absorption due to forces generated in the root itself is called **active absorption**. Active absorption may be osmotic or non-osmotic.

Concept Map - Movement of water in an osmotic system based on various parameters



i. Osmotic active absorption

The theory of osmotic active absorption was postulated by **Atkins** (1916) and **Preistley** (1923). According to this theory, the first step in the absorption is soil water imbibed by cell wall of the root hair followed by osmosis. The soil water is hypotonic and cell sap is hypertonic. Therefore, soil water diffuses into root hair along the concentration gradient (endosmosis). When the root hair becomes fully turgid, it becomes hypotonic and water moves osmotically to the outer most cortical cell. In the same way, water enters into inner cortex, endodermis, pericycle and finally reaches protoxylem. As the sap reaches the protoxylem a pressure is developed known as **root pressure**. This theory involves the symplastic movement of water.

Objections to osmotic theory: 1.The cell sap concentration in xylem is not always high. 2. Root pressure is not universal in all plants especially in trees.

ii. Non-Osmotic active absorption

Bennet-Clark (1936), **Thimann** (1951) and **Kramer** (1959) observed absorption of water even if the concentration of cell sap in the root hair is lower than that of the soil water. Such a movement requires an expenditure of energy released by respiration (ATP). Thus, there is a link between water absorption and respiration. It is evident from the fact that when respiratory inhibitors like KCN, Chloroform are applied there is a decrease in the rate of respiration and also the rate of absorption of water.

2. Passive Absorption

In passive absorption, roots do not play any role in the absorption of water and is regulated by transpiration only. Due to transpiration, water is lost from leaf cells along with a drop in turgor pressure. It increases DPD in leaf cells and leads to withdrawal of water from adjacent xylem cells. In xylem, a tension is developed and is transmitted downward up to root resulting in the absorption of water from the soil.

In passive absorption (Table 11.3), the path of water may be symplastic or apoplastic. It accounts for about 98% of the total water uptake by plants.

Table: 11.3 Differences between Active Absorption and Passive Absorption

Active absorption	Passive absorption
Active absorption takes place by the activity of root and root hairs	The pressure for absorption is not developed in roots and hence roots play passive role
Transpiration has no effect on active absorption	Absorption regulated by transpiration
The root hairs have high DPD as compared to soil solution and therefore water is taken by tension	The absorption occurs due to tension created in xylem sap by transpiration pull, thus water is sucked in by the tension
Respiratory energy needed	Respiratory energy not required
It involves symplastic movement of water	Both symplast and apoplast movement of water involved

11.5 Ascent of Sap

In the last chapter, we studied about water absorption from roots to xylem in a lateral direction and here we will learn about the mechanism of distribution of water inside the plant. Like tributaries join together to form a river, millions of root hairs conduct a small amount of water and confluence in xylem, the superhighway of water conduction. Xylem handles a large amount of water to conduct to many parts in an upward direction.

The water within the xylem along with dissolved minerals from roots is called **sap** and its upward transport is called **ascent of sap.**

11.5.1 The Path of Ascent of Sap

There is no doubt; water travels up along the vascular tissue. But vascular tissue has two components namely Xylem and Phloem. Of these two, which is responsible for the ascent of sap? The following experiment will prove that xylem is the only element through which water moves up.

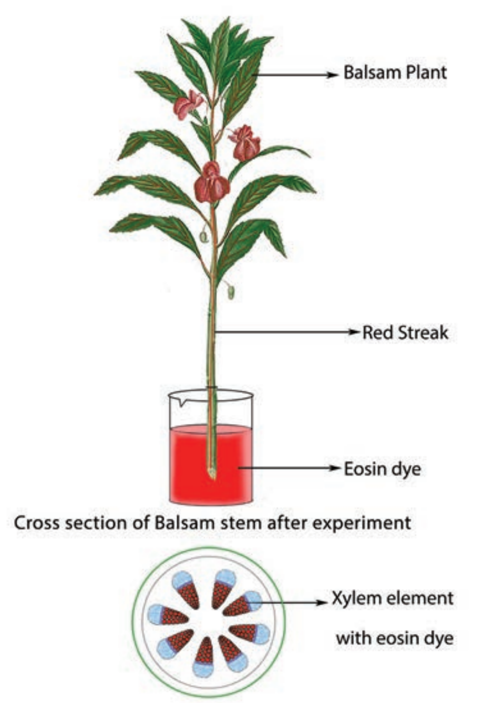


Figure 11.12: Balsam plant and eosin dye experiment

Cut a branch of balsam plant and place it in a beaker containing **eosin** (red colour dye) water. After some time, a red streak appears on the stem indicating the ascent of water. Remove the plant from water and cut a transverse section of the stem and observe it under the microscope. Only xylem element is coloured red, which indicates the path of water is xylem. Phloem is not colored indicating that it has no role in the ascent of sap (Figure 11.12).

Mechanism of Ascent of Sap

In ascent of sap, the biggest challenge is the force required to lift the water to the top of the tallest trees. A number of theories have been put forward to explain the mechanism of the ascent of sap. They are, A. Vital force theories, B. Root pressure theory, and C. Physical force theory.

11.5.2 Vital Force Theories

According to vital force theories, living cells are mandatory for the ascent of sap. Based on this the following two theories derived:

1. Relay pump theory of Godlewski (1884)

Periodic changes in osmotic pressure of living cells of the xylem parenchyma and medullary ray act as a pump for the movement of water.

2. Pulsation theory of J.C.Bose (1923)

Bose invented an instrument called **Crescograph**, which consists of an electric probe connected to a galvanometer (Figure 11.13). When a probe is inserted into the inner cortex of the stem, the galvanometer showed high electrical activity. Bose believed a rhythmic pulsating movement of inner cortex like a pump (similar to the beating of the heart) is responsible for the ascent of sap. He concluded that cells associated with xylem exhibit pumping action and pumps the sap laterally into xylem cells.

Figure 11.13: J. C. Bose

Objections to vital force theories

i. **Strasburger** (1889) and **Overton** (1911) experimentally proved that living cells are not mandatory for the ascent of sap. For this, he selected an old oak tree trunk which when immersed in **picric acid** and subjected to excessive heat killed all the living cells of the trunk. The trunk when dipped in water, the ascent of sap took place.

ii. Pumping action of living cells should be in between two xylem elements (vertically) and not on lateral sides.

11.5.3 Root Pressure Theory

If a plant which is watered well is cut a few inches above the ground level, sap exudes out with some force. This is called **sap exudation** or **bleeding**. **Stephen Hales**, father of plant physiology observed this phenomenon and coined the term '**Root Pressure**'. **Stoking** (1956) defined root pressure as "*a pressure developing in the tracheary elements of the xylem as a result of metabolic activities of the root*". But the following objections have been raised against root pressure theory:

i. Root pressure is totally absent in gymnosperms, which includes some of the tallest plants.

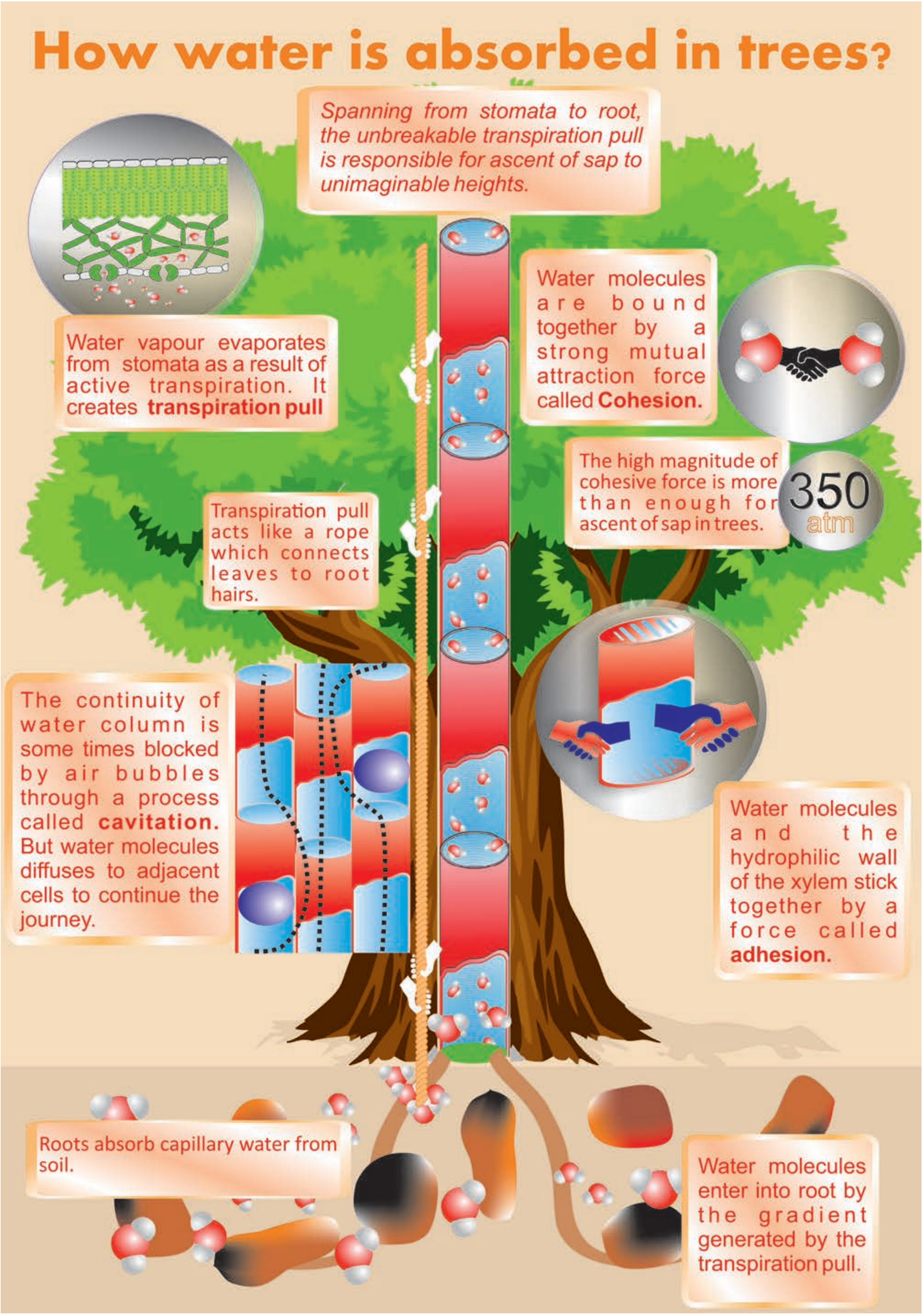
ii. There is no relationship between the ascent of sap and root pressure. For example, in summer, the rate of the ascent of sap is more due to transpiration in spite of the fact that root pressure is very low. On the other hand, in winter when the rate of ascent of sap is low, a high root pressure is found.

iii. Ascent of sap continues even in the absence of roots

iv. The magnitude of root pressure is about 2atm, which can raise the water level up to few feet only, whereas the tallest trees are more than 100m high.

11.5.4 Physical Force Theory

Physical force theories suggest that ascent of sap takes place through the dead xylem vessel and the mechanism is entirely physical and living cells are not involved.


How water is absorbed in trees?
Spanning from stomata to root, the unbreakable transpiration pull is responsible for ascent of sap to unimaginable heights.
Water vapour evaporates from stomata as a result of active transpiration. It creates transpiration pull
Water molecules are bound together by a strong mutual attraction force called Cohesion.
The high magnitude of cohesive force is more than enough for ascent of sap in trees.
350 atm
Transpiration pull acts like a rope which connects leaves to root hairs.
The continuity of water column is some times blocked by air bubbles through a process called cavitation. But water molecules diffuses to adjacent cells to continue the journey.
Water molecules and the hydrophilic wall of the xylem stick together by a force called adhesion.
Roots absorb capillary water from soil.
Water molecules enter into root by the gradient generated by the transpiration pull.

1. **Capillary theory**

Boehm (1809) suggested that the xylem vessels work like a capillary tube. This capillarity of the vessels under normal atmospheric pressure is responsible for the ascent of sap. This theory was rejected because the magnitude of capillary force can raise water level only up to a certain height. Further, the xylem vessels are broader than the tracheid which actually conducts more water and against the capillary theory.

2. **Imbibition theory**

This theory was first proposed by **Unger** (1876) and supported by **Sachs** (1878). This theory illustrates, that water is imbibed through the cell wall materials and not by the lumen. This theory was rejected based on the ringing experiment, which proved that water moves through the lumen of the cell and not by a cell wall.

3. **Cohesion-tension or Cohesion and transpiration pull theory**

Cohesion-tension theory was originally proposed by **Dixon** and **Jolly** (1894) and again put forward by **Dixon** (1914, 1924). This theory is based on the following features:

i. **Strong cohesive force or tensile strength of water**

Water molecules have the strong mutual force of attraction called **cohesive force** due to which they cannot be easily separated from one another. Further, the attraction between a water molecule and the wall of the xylem element is called **adhesion**. These cohesive and adhesive force works together to form an unbroken continuous water column in the xylem. The magnitude of the cohesive force is much high (350 atm) and is more than enough to ascent sap in the tallest trees.

ii. **Continuity of the water column in the plant**

An important factor which can break the water column is the introduction of air bubbles in the xylem. Gas bubbles expanding and displacing water within the xylem element is called **cavitation** or **embolism**. However, the overall continuity of the water column remains undisturbed since water diffuses into the adjacent xylem elements for continuing ascent of sap.

iii. **Transpiration pull or Tension in the unbroken water column**

The unbroken water column from leaf to root is just like a rope. If the rope is pulled from the top, the entire rope will move upward. In plants, such a pull is generated by the process of transpiration which is known as **transpiration pull.**

Water vapour evaporates from mesophyll cells to the intercellular spaces near stomata as a result of active transpiration. The water vapours are then transpired through the stomatal pores. Loss of water from mesophyll cells causes a decrease in water potential. So, water moves as a pull from cell to cell along the water potential gradient. This tension, generated at the top (leaf) of the unbroken water column, is transmitted downwards from petiole, stem and finally reaches the roots. The cohesion theory is the most accepted among the plant physiologists today.

11.6 Transpiration

Water absorbed by roots ultimately reaches the leaf and gets released into the atmosphere in the form of vapour. Only a small fraction of water (less than 5%) is utilized in plant development and metabolic process.

The loss of excess of water in the form of vapour from various aerial parts of the plant is called **transpiration**. Transpiration is a kind of evaporation but differs by the involvement of biological system. The amount of water transpired is astounding (Table 11.4). The water may move through the xylem at a rate as fast as 75cm /min.

Table: 11.4 Rate of Transpiration in some plants

Plant	Transpiration per day
Corn plant	2 Litres
Sunflower	5 Litres
Maple tree	200 Litres
Date palm	450 Litres

> **Activity**
> Select a leafy twig of fully grown plant in your school campus. Cover the twig with a transparent polythene bag and tie the mouth of the bag at the base of the twig. Observe the changes after two hours and discuss with your teacher

11.6.1 Types of Transpiration

Transpiration is of following three types:

1. Stomatal transpiration

Stomata are microscopic structures present in high number on the lower epidermis of leaves. This is the most dominant form of transpiration and being responsible for most of the water loss (90 - 95%) in plants.

2. Lenticular transpiration

In stems of woody plants and trees, the epidermis is replaced by periderm because of secondary growth. In order to provide gaseous exchange between the living cells and outer atmosphere, some pores which looks like lens-shaped raised spots are present on the surface of the stem called **Lenticels**. The loss of water from lenticels is very insignificant as it amounts to only 0.1% of the total.

3. Cuticular transpiration

The cuticle is a waxy or resinous layer of **cutin**, a fatty substance covering the epidermis of leaves and other plant parts. Loss of water through cuticle is relatively small and it is only about 5 to 10 % of the total transpiration. The thickness of cuticle increases in xerophytes and transpiration is very much reduced or totally absent.

11.6.2 Structure of Stomata

The epidermis of leaves and green stems possess many small pores called **stomata**. The length and breadth of stomata is about 10-40μ and 3-10μ respectively. Mature leaves contain between 50 and 500 stomata per square mm. Stomata are made up of two **guard cells**, special semi-lunar or kidney-shaped living epidermal cells in the epidermis. Guard cells are attached to surrounding epidermal cells known as **subsidiary cells** or **accessory cells**. The guard cells are joined together at each end but they are free to separate to form a pore between them. The inner wall of the guard cell is thicker than the outer wall (Figure 11.14). The stoma opens to the interior into a cavity called **sub-stomatal cavity** which remains connected with the intercellular spaces.

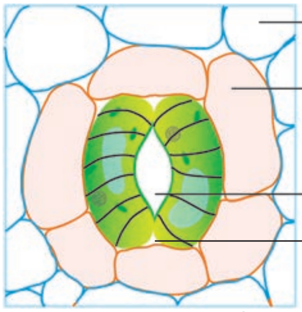


Figure 11.14: Structure of Stomata

11.6.3 Mechanism of Stomatal Movement

Stomatal movements are regulated by the change of turgor pressure in guard cells. When water enters the guard cell, it swells and its unevenly thickened walls stretch up resulting in the opening of stomata. This is due to concave non-elastic nature of inner wall pulled away from each other and stretching of the convex elastic natured outer wall of guard cell.

Different theories have been proposed regarding opening and closing of stomata. The important theories of stomatal movement are as follows,

1. *Theory of Photosynthesis in guard cells*
2. *Starch – Sugar interconversion theory*
3. *Active potassium transport ion concept*

1. Theory of Photosynthesis in guard cells

Von Mohl (1856) observed that stomata open in light and close in the night. According to him, chloroplasts present in the guard cells photosynthesize in the presence of light resulting in the production of carbohydrate (Sugar) which increases osmotic pressure in guard cells. It leads to the entry of water from other cell and stomatal aperture opens. The above process *vice versa* in night leads to closure of stomata.

Demerits

1. Chloroplast of guard cells is poorly developed and incapable of performing photosynthesis.

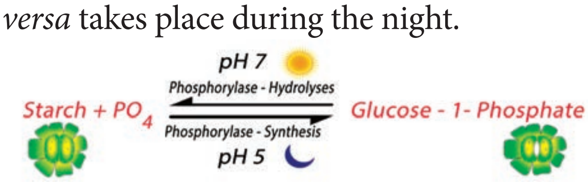
2. The guard cells already possess much amount of stored sugars.

2. Starch – Sugar Interconversion theory

i. According to **Lloyd** (1908), turgidity of guard cell depends on interconversion, of starch and sugar. It was supported by **Loftfield** (1921) as he found guard cells containing sugar during the daytime when they are open and starch during the night when they are closed.

ii. **Sayre** (1920) observed that the opening and closing of stomata depends upon change in pH of guard cells. According to him stomata open at high pH during day time and become closed at low pH at night. Utilization of CO_2 by photosynthesis during light period causes an increase in pH resulting in the conversion of starch to sugar. Sugar increase in cell favours endosmosis and increases the turgor pressure which leads to opening of stomata. Likewise, accumulation of CO_2 in cells during night decrease the pH level resulting in the conversion of sugar to starch. Starch decreases the turgor pressure of guard cell and stomata close.

iii. The discovery of enzyme **phosphorylase** in guard cells by **Hanes** (1940) greatly supports the starch-sugar interconversion theory. The enzyme *phosphorylase* hydrolyses starch into sugar and high pH followed by endosmosis and the opening of stomata during light. The *vice versa* takes place during the night.



iv. **Steward** (1964) proposed a slightly modified scheme of starch-sugar interconversion theory. According to him, Glucose-1-phosphate is osmotically inactive. Removal of phosphate from Glucose-1-phosphate converts to Glucose which is osmotically active and increases the concentration of guard cell leading to opening of stomata (Figure 11.15).

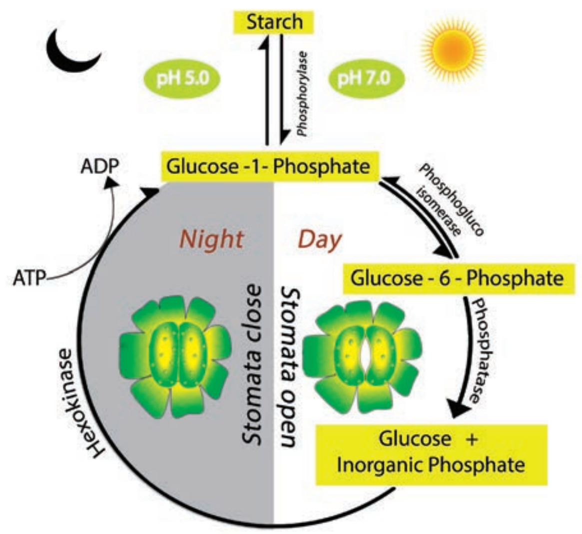


Figure 11.15: Steward Scheme

Objections to Starch-sugar interconversion theory

i. In monocots, guard cell does not have starch.

ii. There is no evidence to show the presence of sugar at a time when starch disappears and stomata open.

iii. It fails to explain the drastic change in pH from 5 to 7 by change of CO_2.

3. Theory of K^+ transport

This theory was proposed by **Levit** (1974) and elaborated by **Raschke** (1975). According to this theory, the following steps are involved in the stomatal opening:

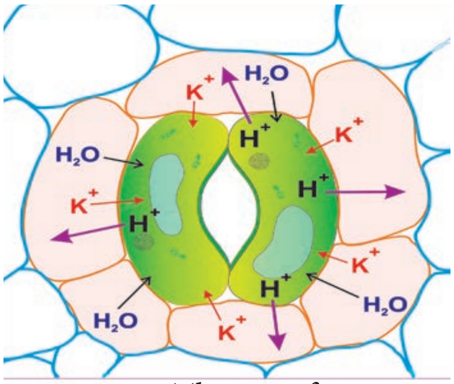


Figure 11.16: Theory of K^+ transport Opening of stomata

In light

i. In guard cell, starch is converted into organic acid (malic acid).

ii. Malic acid in guard cell dissociates to malate anion and proton (H^+).

iii. Protons are transported through the membrane into nearby subsidiary cells with the exchange of K^+ (Potassium ions) from subsidiary cells to guard cells. This process involves an electrical gradient and is called **ion exchange**.

iv. This ion exchange is an active process and consumes ATP for energy.

v. Increased K^+ ions in the guard cell are balanced by Cl^- ions. Increase in solute concentration decreases the water potential in the guard cell.

vi. Guard cell becomes hypertonic and favours the entry of water from surrounding cells.

vii. Increased turgor pressure due to the entry of water opens the stomatal pore (Figure 11.16).

In Dark

i. In dark, photosynthesis stops and respiration continues with accumulation of CO_2 in the sub-stomatal cavity.

ii. Accumulation of CO_2 in cell lowers the pH level.

iii. Low pH and a shortage of water in the guard cell activate the stress hormone **Abscisic acid** (ABA).

iv. ABA stops further entry of K^+ ions and also induce K^+ ions to leak out to subsidiary cells from guard cell.

v. Loss of water from guard cell reduces turgor pressure and causes closure of stomata (Figure 11.17).

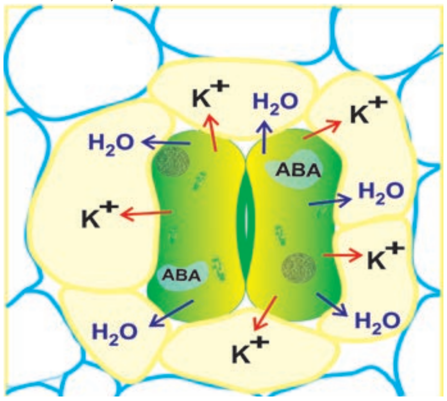


Figure 11.17: Theory of K^+ transport Closing of stomata

11.6.4 Factors Affecting Rate of Transpiration

The factors affecting the rate of transpiration can be categorized into two groups. They are 1. External or Environmental factors and 2. Internal or plant factors.

1. External or Environmental factors

i. Atmospheric humidity: The rate of transpiration is greatly reduced when the atmosphere is very humid. As the air becomes dry, the rate of transpiration is also increased proportionately.

ii. Temperature: With the increase in atmospheric temperature, the rate of transpiration also increases. However, at very high-temperatures stomata closes because of flaccidity and transpiration stop.

iii. Light: Light intensity increases the temperature. As in temperature, transpiration is increased in high light intensity and is decreased in low light intensity. Light also increases the permeability of the cell membrane, making it easy for water molecules to move out of the cell.

iv. Wind velocity: In still air, the surface above the stomata get saturated with water vapours and there is no need for more water vapour to come out. If the wind is breezy, water vapour gets carried away near leaf surface and DPD is created to draw more vapour from the leaf cells enhancing transpiration. However, high wind velocity creates an extreme increase in water loss and leads to a reduced rate of transpiration and stomata remain closed.

Activity

What will happen if an indoor plant is placed under fan and AC?

v. Atmospheric pressure: In low atmospheric pressure, the rate of transpiration increases. Hills favour high transpiration rate due to low atmospheric pressure. However, it is neutralized by low temperature prevailing in the hills.

vi. Water: Adequate amount of water in the soil is a pre-requisite for optimum plant growth. Excessive loss of water through transpiration leads to wilting. In general, there are three types of wilting as follows,

a. Incipient wilting: Water content of plant cell decreases but the symptoms are not visible.

b. Temporary wilting: On hot summer days, the freshness of herbaceous plants reduces turgor pressure at the day time and regains it at night.

c. Permanent wilting: The absorption of water virtually ceases because the plant cell does not get water from any source and the plant cell passes into a state of permanent wilting.

2. Internal factors

i. Leaf area: If the leaf area is more, transpiration is faster and so xerophytes reduce their leaf size.

ii. Leaf structure: Some anatomical features of leaves like sunken stomata, the presence of hairs, cuticle, the presence of hydrophilic substances like gum, mucilage help to reduce the rate of transpiration. In xerophytes the structural modifications are remarkable. To avoid transpiration, as in ***Opuntia*** the stem is flattened to look like leaves called **Phylloclade**. **Cladode** or **cladophyll** in ***Asparagus*** is a modified stem capable of limited growth looking like leaves. In some plants, the petioles are flattened and widened, to become **phyllodes** example ***Acacia melanoxylon.***

11.6.5 Plant Antitranspirants

The term **antitranspirant** is used to designate any material applied to plants for the purpose of retarding transpiration. An ideal antitranspirant checks the transpiration process without disturbing the process of gaseous exchange. Plant antitranspirants are two types:

1. To act as a physical barrier above the stomata

Colourless plastics, Silicone oil and **low viscosity waxes** are sprayed on leaves forming a thin film to act as a physical barrier (for transpiration) for water but permeable to CO_2 and O_2. The success rate of a physical barrier is limited.

2. Induction of Stomata closure

Carbon-di-oxide induces stomatal closure and acts as a natural antitranspirant. Further, the advantage of using CO_2 as an antitranspirant is its inhibition of photorespiration. **Phenyl Mercuric Acetate** (PMA), when applied as a foliar spray to plants, induces partial stomatal closure for two weeks or more without any toxic effect. Use of **abscisic acid** highly induces the closing of stomata. **Dodecenyl succinic acid** also effects on stomatal closure.

Uses:

- Antitranspirants reduce the enormous loss of water by transpiration in crop plants.
- Useful for seedling transplantations in nurseries.

11.6.6 Guttation

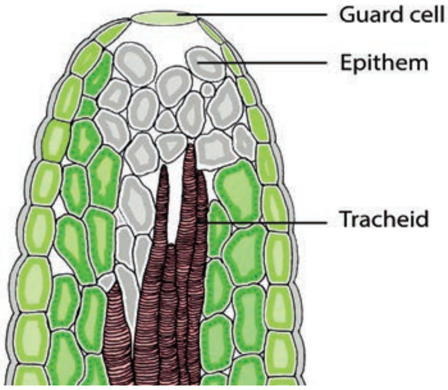


Figure 11.18: Structure of Hydathode

During high humidity in the atmosphere, the rate of transpiration is much reduced. When plants absorb water in such a condition root pressure is developed due to excess water within the plant. Thus excess water exudates as liquid from the edges of the leaves and is called **guttation**. Example: Grasses, tomato, potato, brinjal and *Alocasia*. Guttation occurs through stomata like pores called **hydathodes** generally present in plants that grow in moist and shady places. Pores are present over a mass of loosely arranged cells with large intercellular spaces called **epithem**

(Figure 11.18). This mass of tissue lies near vein endings (xylem and Phloem). The liquid coming out of hydathode is not pure water but a solution containing a number of dissolved substances.

11.6.7 Measurement of Transpiration

1. Ganongs potometer

Ganongs potometer is used to measure the rate of transpiration indirectly. In this, the amount of water absorbed is measured and assumed that this amount is equal to the amount of water transpired.

Apparatus consists of a horizontal graduated tube which is bent in opposite directions at the ends. One bent end is wide and the other is narrow. A reservoir is fixed to the horizontal tube near the wider end. The reservoir has a stopcock to regulate water flow. The apparatus is filled with water from reservoir. A twig or a small plant is fixed to the wider arm through a split cock. The other bent end of the horizontal tube is dipped into a beaker containing coloured water. An air bubble is introduced into the graduated tube at the narrow end (Figure 11.19). keep this apparatus in bright sunlight and observe.As transpiration takes place, the air bubble will move towards the twig. The loss is compensated by water absorption through the xylem portion of the twig. Thus, the rate of water absorption is equal to the rate of transpiration.

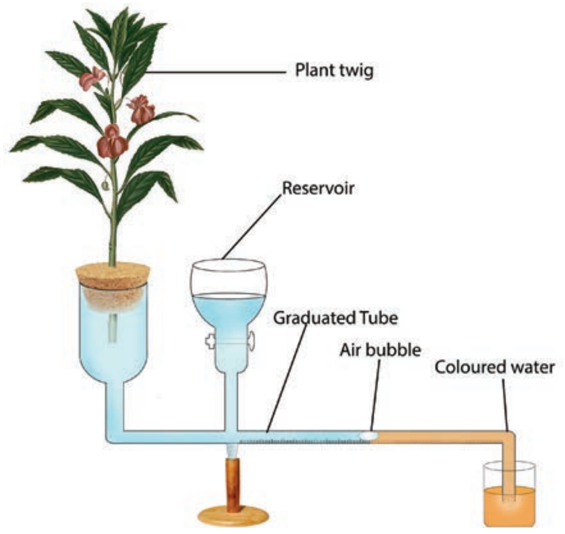


Figure 11.19: Ganongs Potometer

2. Cobalt chloride ($CoCl_2$) paper method

Select a healthy dorsiventral leaf and clean its upper and lower surface with dry cotton. Now place a dry Cobalt chloride (**$CoCl_2$**) strips on both surface and immediately cover the paper with glass slides and immobilize them. It will be observed after some time that the $CoCl_2$ strip of lower epidermis turns pink. This indicates that $CoCl_2$ becomes hydrated ($CoCl_2 \cdot 2H_2O$ or $CoCl_2 \cdot 4H_2O$) due to water vapours coming out through stomata. The rate of transpiration is more on the lower surface than in the upper surface of the dorsiventral leaf.

11.6.8 Significance of transpiration

Transpiration leads to loss of water, as stated earlier in this lesson 95% of absorbed water is lost in transpiration. It seems to be an evil process to plants. However, number of process like absorption of water, ascent of sap and mineral absorption directly rely on the transpiration. Moreover plants withstand against scorching sunlight due to transpiration. Hence the transpiration is a "**necessary evil**" as stated by **Curtis**.

11.7 Translocation of Organic Solutes

Leaves synthesize food material through photosynthesis and store in the form of starch grains. When required the starch is converted into simple sugars. They must be transported to various parts of the plant system for further utilization. However, the site of food production (leaves) and site of utilization are separated far apart. Hence, the organic food has to be transported to these areas.

The phenomenon of food transportation from the site of synthesis to the site of utilization is known as **translocation of organic solutes**. The term **solute** denotes food material that moves in a solution.

11.7.1 Path of Translocation

It has now been well established that phloem is the path of translocation of solutes. Ringing or girdling experiment will clearly demonstrate the translocation of solute by phloem.

11.7.2 Ringing or girdling experiment

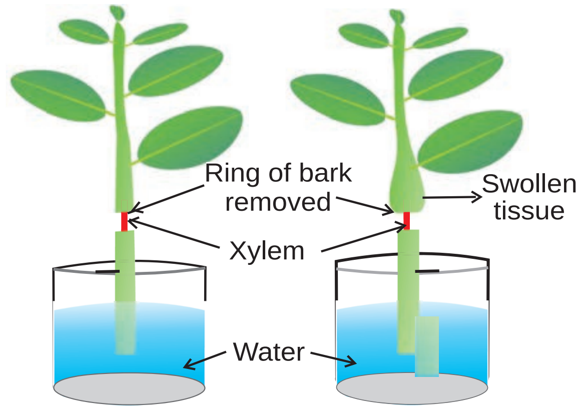


Figure 11.20: Ringing experiment

The experiment involves the removal of all the tissue outside to vascular cambium (bark, cortex, and phloem) in woody stems except xylem. Xylem is the only remaining tissue in the girdled area which connects upper and lower part of the plant. This setup is placed in a beaker of water. After some time, it is observed that a swelling on the upper part of the ring appears as a result of the accumulation of food material (Figure 11.20). If the experiment continues within days, the roots die first. It is because, the supply of food material to the root is cut down by the removal of phloem. The roots cannot synthesize their food and so they die first. As the roots gradually die the upper part (stem), which depends on root for the ascent of sap, will ultimately die.

11.7.3 Direction of Translocation

Phloem translocates the products of photosynthesis from leaves to the area of growth and storage, in the following directions,

Downward direction: From leaves to stem and roots.

Upward direction: From leaves to developing buds, flowers, fruits for consumption and storage. Germination of seeds is also a good example of upward translocation.

Radial direction: From cells of pith to cortex and epidermis, the food materials are radially translocated.

11.7.4 Source and Sink

Source is defined as any organ in plants which are capable of exporting food materials to the areas of metabolism or to the areas of storage. Examples: Mature leaves, germinating seeds.

Sink is defined as any organ in plants which receives food from source.Example: Roots, tubers, developing fruits and immature leaves (Figure 11.21).

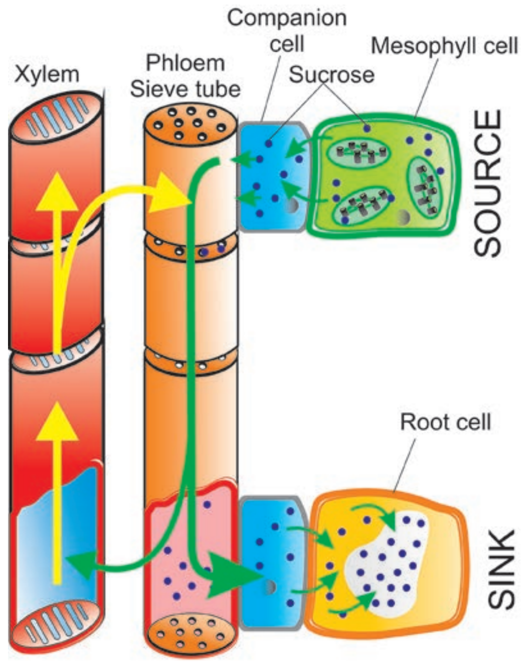


Figure 11.21: Source and Sink

11.7.5 Phloem Loading

The movement of ***photosynthates*** (products of photosynthesis) from mesophyll cells to phloem sieve elements of mature leaves is known as **phloem loading**. It consists of three steps.

i. Sieve tube conducts **sucrose** only. But the *photosynthate* in chloroplast mostly in the form of starch or triose-phosphate which has to be transported to the cytoplasm where it will be converted into sucrose for further translocation.

ii. Sucrose moves from mesophyll to nearby sieve elements by short distance transport.

iii. From sieve tube to sink by long-distance transport.

Why plants transport sugars as sucrose and not as starch or glucose or fructose?

Glucose and Fructose are simple monosaccharides, whereas, Sucrose is a disaccharide composed of glucose and fructose. Starch is a polysaccharide of glucose. Sucrose and starch are more efficient in energy storage when compared to glucose and fructose, but starch is insoluble in water. So it cannot be transported via phloem and the next choice is sucrose, being water soluble and energy efficient, sucrose is chosen as the carrier of energy from leaves to different parts of the plant. Sucrose has low viscosity even at high concentrations and has no reducing ends which makes it inert than glucose or fructose.During photosynthesis, starch is synthesized and stored in the chloroplast stroma and sucrose is synthesized in the leaf cytosol from which it diffuses to the rest of the plant.

11.7.6 Phloem Unloading

From sieve elements sucrose is translocated into sink organs such as roots, tubers, flowers and fruits and this process is termed as **phloem unloading**. It consists of three steps:

1. ***Sieve element unloading***: Sucrose leave from sieve elements.
2. ***Short distance transport***: Movement of sucrose to sink cells.
3. ***Storage and metabolism***: The final step when sugars are stored or metabolized in sink cells.

11.7.7 Mechanism of Translocation

Several hypotheses have been proposed to explain the mechanism of translocation. Some of them are given below:

1. Diffusion hypothesis

As in diffusion process, this theory states the translocation of food from higher concentration (from the place of synthesis) to lower concentration (to the place of utilization) by the simple physical process. However, the theory was rejected because the speed of translocation is much higher than simple diffusion and translocation is a biological process which any poison can halt.

2. Activated diffusion theory

This theory was first proposed by **Mason** and **Maskell** (1936). According to this theory, the diffusion in sieve tube is accelerated either by activating the diffusing molecules or by reducing the protoplasmic resistance to their diffusion.

3. Electro-Osmotic theory

The theory of electro osmosis was proposed by **Fenson** (1957) and **Spanner** (1958). According to this, an electric-potential across the sieve plate causes the movement of water along with solutes. This theory fails to explain several problems concerning translocation.

4. Munch Mass Flow hypothesis

Mass flow theory was first proposed by **Munch** (1930) and elaborated by **Crafts** (1938). According to this hypothesis, organic substances or solutes move from the region of high osmotic pressure (from mesophyll) to the region of low osmotic pressure along the turgor pressure gradient. The principle involved in this hypothesis can be explained by a simple physical system as shown in figure 11.22.

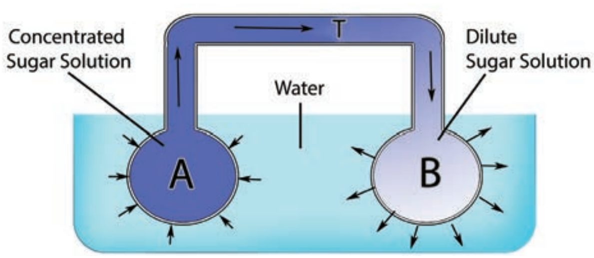


Figure 11.22: A model demonstrating the Mass flow hyphothesis

Two chambers "A" and "B" made up of semipermeable membranes are connected by tube "T" immersed in a reservoir of water. Chamber "A" contains highly concentrated sugar solution while chamber "B" contains dilute sugar solution. The following changes were observed in the system,

i. The high concentration sugar solution of chamber "A" is in a hypertonic state which draws water from the reservoir by endosmosis.

ii. Due to the continuous entry of water into chamber "A", turgor pressure is increased.

iii. Increase in turgor pressure in chamber "A" force, the mass flow of sugar solution to chamber "B" through the tube "T" along turgor pressure gradient.

iv. The movement of solute will continue till the solution in both the chambers attains the state of isotonic condition and the system becomes inactive.

v. However, if new sugar solution is added in chamber "A", the system will start to run again.

A similar analogous system as given in the experiment exists in plants:

Chamber "A" is analogous to mesophyll cells of the leaves which contain a higher concentration of food material in soluble form. In short "A" is the production point called "**source**".

Chamber "B" is analogous to cells of stem and roots where the food material is utilized. In short "B" is consumption end called "**sink**".

Tube "T" is analogous to the sieve tube of phloem.

Mesophyll cells draw water from the xylem (reservoir of the experiment) of the leaf by endosmosis leading to increase in the turgor pressure of mesophyll cell. The turgor pressure in the cells of stem and the roots are comparatively low and hence, the soluble organic solutes begin to flow *en masse* from mesophyll through the phloem to the cells of stem and roots along the gradient turgor pressure.

In the cells of stem and roots, the organic solutes are either consumed or converted into insoluble form and the excess water is released into xylem (by turgor pressure gradient) through cambium.

Merits:

i. When a woody or herbaceous plant is girdled, the sap contains high sugar containing exudates from cut end.

ii. Positive concentration gradient disappears when plants are defoliated.

Objections:

i. This hypothesis explains the unidirectional movement of solute only. However, bidirectional movement of solute is commonly observed in plants.

ii. Osmotic pressure of mesophyll cells and that of root hair do not confirm the requirements.

iii. This theory gives passive role to sieve tube and protoplasm, while some workers demonstrated the involvement of ATP.

11.8 Mineral Absorption

Minerals in soil exist in two forms, either dissolved in soil solution or adsorbed by colloidal clay particle. Previously, it was mistakenly assumed that absorption of mineral salts from soil took place along with absorption of water. But absorption of minerals and ascent of sap are identified as two independent processes. Minerals are absorbed not only by root hairs but also by the cells of epiblema.

Plasma membrane of root cells are not permeable to all ions and also all ions of same salt are not absorbed in equal rate.
Penetration and accumulation of ions into living cells or tissues from surrounding medium by crossing membrane is called **mineral absorption**. Movement of ions into and out of cells or tissues is termed as transport or **flux**. Entry of the ion into cell is called **influx** and exit is called **efflux**. Various theories have been put forward to explain this mechanism. They are categorized under passive mechanisms (without the involvement of metabolic energy) and active mechanisms (involvement of metabolic energy).

11.8.1 Passive Absorption

1. Ion-Exchange:

Ions of external soil solution were exchanged with same charged (anion for anion or cation for cation) ions of the root cells. There are two theories explaining this process of ion exchange namely:

i. Contact exchange and ii. Carbonic acid exchange.

i. **Contact Exchange Theory:**

Figure 11.23: 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 a small volume of space called **oscillation volume**. Due to small space, both ions overlap each other's oscillation volume and exchange takes place (Figure 11.23).

ii. **Carbonic Acid Exchange Theory:**

According to this theory, soil solution plays an important role by acting as a medium for ion exchange. 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 HCO_3^- in the soil solution. These H^+ ions exchange with cations adsorbed on clay particles and the cations from micelles get released into soil solution and gets adsorbed on root cells (Figure 11.24).

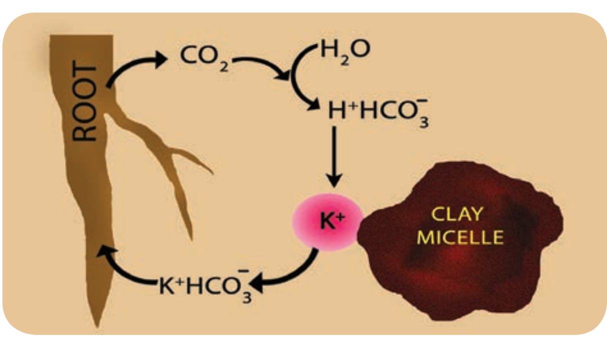


Figure 11.24: Carbonic Acid Exchange theory

11.8.2 Active Absorption

Absorption of ions against the concentration gradient with the expenditure of metabolic energy is called **active absorption**. In plants, the vacuolar sap shows accumulation of anions and cations against the concentration gradient which cannot be explained by theories of passive absorption. Mechanism of active absorption of salts can be explained through carrier concept.

Carrier Concept:

This concept was proposed by **Van den Honert** in 1937. The cell membrane is largely impermeable to free ions. However, the presence of **carrier molecules** in the membrane acts as a vehicle to pick up or bind with ions to form **carrier-ion-complex,** which moves across the membrane. On the inner surface of the membrane, this complex breaks apart releasing ions into cell while carrier goes back to the outer surface to pick up fresh ions (Figure 11.25).

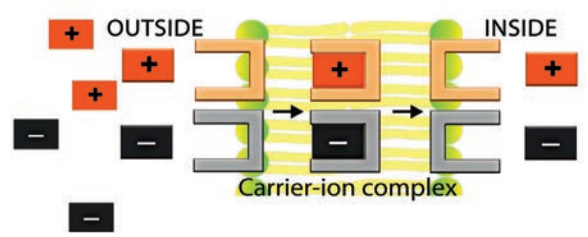


Figure 11.25: Carrier Concept

The concept can be explained using two theories:

1. Lundegardh's Cytochrome Pump Theory:

Lundegardh and **Burstrom** (1933) observed a correlation between respiration and anion absorption. When a plant is transferred from water to a salt solution the rate of respiration increases which is called as **anion respiration** or **salt respiration**. Based on this observation **Lundegardh** (1950 and 1954) proposed cytochrome pump theory which is based on the following assumptions:

i. The mechanism of anion and cation absorption are different.

ii. Anions are absorbed through cytochrome chain by an active process, cations are absorbed passively.

iii. An oxygen gradient responsible for oxidation at the outer surface of the membrane and reduction at the inner surface.

According to this theory, the enzyme *dehydrogenase* on inner surface is responsible for the formation of protons (H^+) and electrons (e^-). As electrons pass outward through electron transport chain there is a corresponding inward passage of anions. Anions are picked up by oxidized cytochrome oxidase and are transferred to other members of chain as they transfer the electron to the next component (Figure 11.26).

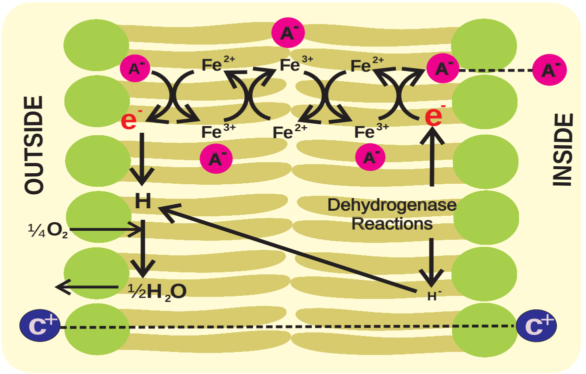


Figure 11.26: Cytochrome Pump theory

The theory assumes that cations (C^+) move passively along the electrical gradient created by the accumulation of anions (A^-) at the inner surface of the membrane.

Main defects of the above theory are:

(i) Cations also induce respiration.

(ii) Fails to explain the selective uptake of ions.

(iii) It explains absorption of anions only.

2. Bennet-Clark's Protein-Lecithin Theory:

In 1956, **Bennet-Clark** proposed that the carrier could be a protein associated with **phosphatide** called as **lecithin**. The carrier is **amphoteric** (the ability to act either as an acid or a base) and hence both cations and anions combine with it to form **Lecithin-ion complex** in the membrane. Inside the membrane, Lecithin-ion complex is broken down into **phosphatidic acid** and **choline** along with the liberation of ions. Lecithin again gets regenerated from *phosphatidic acid* and *choline* in the presence of the enzyme *choline acetylase* and *choline esterase* (Figure 11.27). ATP is required for regeneration of lecithin.

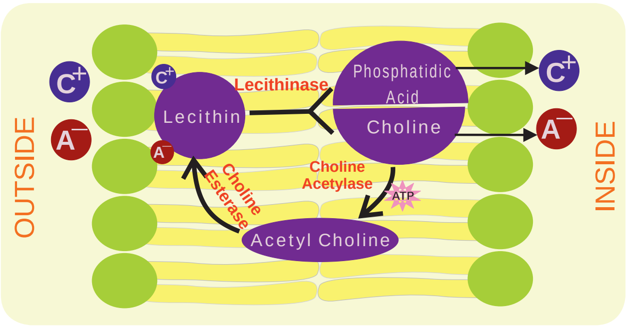


Figure 11.27: Protein-Lecithin theory

11.8.3 Donnan equilibrium

Within the cell, some of the ions never diffuse out through the membrane. They are trapped within the cell and are called fixed ions. But they must be balanced by the ions of opposite charge. Assuming that a concentration of fixed anions is present inside the membrane, more cations would be absorbed in addition to the normal exchange to maintain the equilibrium. Therefore, the cation concentration would be greater in the internal than in the external solution. This electrical balance or equilibrium controlled by electrical as well as diffusion phenomenon is known as the **Donnan equilibrium**.

Summary

There are two types of transports namely short and long distance in plants to translocate sap and solutes. Based on energy requirement, the transport may either be passive or active. The process of diffusion, facilitated diffusion, imbibition and osmosis are driven by concentration gradient like a ball rolling down to a slope and hence, no energy is needed. The water absorbed (either active or passive) from the soil by root hairs must reach the xylem for further transportation. There are three possible routes to reach the xylem from root hairs. They are i) apoplast ii) symplast and/or iii) transmembrane. Various theories explain the path of sap in the xylem and Dixon's Cohesion-tension theory is the most accepted one. Transpiration is mostly carried out by stomata, which has guard cells. The general mechanism of stomatal movement is based on entry and exit of water molecules in guard cells. Many theories are there to explain how water enters and exits from guard cells. The theory of potassium transport enumerates two different reactions separately run for opening and closing of stomata. Contrary to ascent of sap by xylem in an upward direction, the path of solute which consists of the photosynthetic products is always in phloem and translocate multidirectional. The point of origin of translocation is photosynthetic leaves which are the source. On the other hand, point of utilization is called sink. According to Munch mass flow hypothesis, the solutes move along the concentration gradient in a bulk flow.

Although minerals are dissolved in soil water, they do not tend together with water to enter the root hairs during absorption of water. Mineral absorption is independent of water absorption. Minerals are absorbed either actively or passively.

Evaluation

1. In a fully turgid cell
   a. DPD = 10 atm; OP = 5 atm; TP = 10 atm
   b. DPD = 0 atm; OP = 10 atm; TP = 10 atm
   c. DPD = 0 atm; OP = 5 atm; TP = 10 atm
   d. DPD = 20 atm; OP = 20 atm; TP = 10 atm

2. Which among the following is correct?
   i. apoplast is fastest and operate in nonliving part
   ii. Transmembrane route includes vacuole
   iii. symplast interconnect the nearby cell through plasmadesmata
   iv. symplast and transmembrane route are in living part of the cell

   a. i and ii b. ii and iii
   c. iii and iv d. i, ii, iii, iv

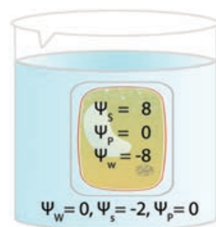
3. What type of transpiration is possible in the xerophyte *Opuntia*?
   a. Stomatal b. Lenticular
   c. Cuticular d. All the above

4. Stomata of a plant open due to
   a. Influx of K^+ b. Efflux of K^+
   c. Influx of Cl^- d. Influx of OH^-

5. Munch hypothesis is based on
   a. Translocation of food due to TP gradient and imbibition force
   b. Translocation of food due to TP
   c. Translocation of food due to imbibition force
   d. None of the above

6. If the concentration of salt in the soil is too high and the plants may wilt even if the field is thoroughly irrigated. Explain

7. How phosphorylase enzyme open the stomata in starch sugar interconversion theory?



8. List out the non-photosynthetic parts of a plant that need a supply of sucrose?

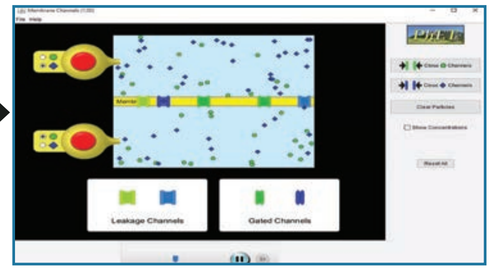
9. What are the parameters which control water potential?

10. An artificial cell made of selectively permeable membrane immersed in a beaker (in the figure). Read the values and answer the following questions?
    a. Draw an arrow to indicate the direction of water movement
    b. Is the solution outside the cell isotonic, hypotonic or hypertonic?
    c. Is the cell isotonic, hypotonic or hypertonic?
    d. Will the cell become more flaccid, more turgid or stay in original size?
    e. With reference to artificial cell state, is the process endosmosis or exosmosis? Give reasons

ICT Corner

Membrane transport

Let's play with **membrane proteins.**



Steps

- Open PhET:
  Method 1: By scanning the QR Code given
  Method 2: Through Google – Open PhET by typing PhET
- Select play with simulation & enter
- Click Biology – select Membrane Channels & run
- Select Membrane channel in PhET
- Select round molecule and pump it by pressing red button in one column
- Select square molecule and pump it by pressing the same action
- Observe the movement of molecules across membrane

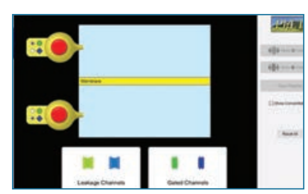
Activity

- Use leakage channel and gated channel in closed and open position and observe the molecules movement.

Step 1

Step 2

Step 3



Step 4

URL:

https://phet.colorado.edu/

* Pictures are indicative only

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