NUTRITION
10th book
Unit – 14 TRANSPORTATION IN PLANTS

Introduction

- Multicellular organisms possess millions of cells in their body. Every cell needs a constant supply of essential substances like nutrients and oxygen to maintain life and survival. Food is the only source of energy and every cell gets its energy by the breakdown of glucose. The cells utilise this energy and govern various vital activities of life.

- Have you ever wondered how water and nutrients absorbed by the root are transported to the leaves? How is the food prepared by the leaves carried to the other parts of the plant? Do you know how water reaches the top of tall plants inspite of not having a circulatory system like animals? Water absorbed by the roots have to reach entire plant and the food synthesised by the leaves have to be distributed to all the parts of the plant. To understand this we need to recall the anatomy of the plants. Water and mineral salts absorbed by the roots reach all parts of the plant through the xylem. The food synthesised by the leaves are translocated to all parts of the plant through the phloem. The bulk movement of substances through the vascular tissue is called Translocation.

- 'Transport' means to carry things from one place to another. Have you ever wondered how in animals the useful substances are transported to other cells and toxic substances are removed? In larger organisms transport of nutrients, salts, oxygen, hormones and waste products around the body are performed by the **'Circulatory system'**. The circulatory system consists of the circulating fluids, **the blood and lymph** and **the heart and blood vessels** which form the collecting and transporting system.

Means of Transport in Plants

- The transport of materials in and out of the cells is carried out by diff usion and active transport in plants.

Diffusion

- The movement of molecules in liquid and solids from a region of higher concentration to a region of their lower concentration without the utilization of energy is called **diffusion**. Th is is a passive process.

Active Transport

- Active transport utilizes energy to pump molecules against a concentration gradient. Active transport is carried out by membrane bound proteins. Th ese proteins use energy to carry substances across the cell membrane hence they are oft en referred to as **pumps**. Th ese pumps can transport substances from a low concentration to a high concentration (**'uphill' transport**).

Osmosis

- Osmosis is the **movement of solvent** or water molecules from the **region of higher concentration** to the region of lower concentration through a semi-permeable membrane. Th is process is carried out till an equilibrium is reached. Osmosis is the passive movement of water or any other solvent molecules.

Plasmolysis

- It occurs when water moves out of the cell and resulting in the shrinkage of cell membrane away from the cell wall.

Imbibition

- Imbibition is a type of diffusion in which a solid absorbs water and gets swelled up. eg. absorption of water by seeds and dry grapes. If it were not for imbibition, seedlings would not have been able to emerge out of the soil.

Root Hair-Water Absorbing Unit

- There are millions of root hairs on the tip of the root which absorb water and minerals by diffusion. Root hairs are thin walled, slender extension of epidermal cell that increase the surface area of absorption.

Pathway of Water Absorbed by Roots

- Once the water enters the root hairs, the concentration of water molecules in the root hair cells become more than that of the cortex. Thus water from the root hair moves to the cortical cells by osmosis and then reaches the xylem. From there the water is transported to the stem and leaves.

Types of Movement of Water into the Root Cells

- Once water is absorbed by the root hairs, it can move deeper into root layers by two distinct pathways:

Apoplast pathway
Symplast pathway

Apoplast Pathway

- The **apoplastic** movement of water occurs exclusively through the intercellular spaces and the walls of the cells. Apoplastic movement does not involve crossing the cell membrane. This movement is dependent on the gradient.

_Symplast Pathway

- In **symplastic** movement, the water travels through the cells i.e. their cytoplasm; intercellular movement is through the plasmodesmata. Water enter the cells through the cell membrane, hence the movement is relatively slower. Movement is again down a potential gradient.

Transpi.ration

- Transpiration is the evaporation of water in plants through stomata in the leaves. Stomata are open in the day and closed at night. The opening and closing of the stomata is due to the change in turgidity of the guard cells. When water enters into the guard cells, they become turgid and the stoma open. When the guard cells lose water, it becomes flaccid and the stoma closes.

- Water evaporates from mesophyll cells of leaves through the open stomata, this lowers water concentration in mesophyll cells. As a result, more water is drawn into these cells from the xylem present in the veins through the process of osmosis. As water is lost from the leaves, pressure is created at the top to pull more water from the xylem to the mesophyll cells, this process is called **transpiration pull**. This extends up to the roots causing the roots to absorb more water from the soil to ensure continuous flow of water from the roots to the leaves.

- Transpiration is affected by several external factors such as temperature, light, humidity, and wind speed. Internal factors that affect transpiration include number and distribution of stomata, percentage of open stomata, water status of the plant, canopy structure etc.

Importance of Transpiration

❖ Creates transpirational pull for transport of water
❖ Supplies water for photosynthesis

- Transports minerals from soil to all parts of the plant
- Cools the surface of the leaves by evaporation.
- Keeps the cells turgid; hence, maintains their shape

Root Pressure

- As ion from the soil are actively transported into the vascular tissue of the root, water moves along and increases the pressure inside the xylem. This pressure is called root pressure and is responsible for pushing water to smaller height of the stem.

Uptake of Minerals

- Plants depend on minerals from soil for its nutritional requirements. All minerals cannot be passively absorbed by the roots. Two factors account for this: (i) minerals are present in the soil as charged particles (ions) that cannot move across cell membranes and

- (ii) the concentration of minerals in the soil is usually lower than the concentration of minerals in the root. Therefore, most minerals enter the root by active absorption through the cytoplasm of epidermal cells. This needs energy in the form of ATP. Then it is transported to all parts by transpiration pull.

Translocation of Mineral Ions

- Minerals are remobilised from older dying leaves to younger leaves. This phenomenon can be seen in deciduous plants. Elements like phosphorus, sulphur, nitrogen and potassium are easily mobilised, while elements like calcium are not remobilised. Small amounts of material exchange takes place between xylem and phloem.

Phloem Transport

- The food synthesised by the leaves are transported by the phloem either to the area of requirement or stored. Phloem tissue is composed of sieve tubes which have sieve plates. Cytoplasmic strands pass through the pores in the sieve plates.

- Phloem transports food (sucrose) from a source to a sink. The source is part of the plant that synthesize food, i.e., the leaf, and sink, is the part that needs or stores the food. But, the source and sink may be reversed depending on the season, or the plant's need.

- Since the source-sink relationship is variable, the direction of movement in the phloem can be upwards or downwards, i.e., **bidirectional**. In contrast, the movement is always **unidirectional** in xylem i.e., upwards.

Translocation of Sugars

- The mechanism of translocation of sugars from source to sink is through pressure flow hypothesis Glucose prepared at source (by photosynthesis) is converted to sucrose. Sucrose moves into the companion cells, then into the living phloem sieve tube cells by active transport. This process produces a hypertonic condition in the phloem. Water in the adjacent xylem moves into the phloem by osmosis. As osmotic pressure builds up, the phloem sap moves to areas of lower pressure. By active transport sucrose moves into the cells where it is utilised or stored. As sugars are removed, the osmotic pressure decreases and water moves out of the phloem.

Ascent of Sap and its Events – An Overview

- The upward movement of water and minerals from roots to different plant parts is called ascent of sap. A number of factors play a role in ascent of sap and it takes places in fol

Root Pressure: Water from soil enters the root hairs due to osmosis. Root pressure is responsible for movement of water up to the base of the stem.

Capillary Action: Water or any liquid rises in a capillary tube because of physical forces, this phenomenon is called capillary action. In the same way, in stem water rises up to certain height because of capillary action.

Adhesion-cohesion of Water Molecules: Water molecules form a continuous column lowing steps in the xylem because of forces of adhesion and cohesion among the molecules.

Cohesion: The force of attraction between molecules of water is called cohesion.

Adhesion: The force of attraction between molecules of different substances is called adhesion.Water molecules stick to a xylem because of force of adhesion.

Transpiration Pull: Transpiration through stomata creates vacuum which creates a suction. called transpiration pull. The transpiration pull sucks the water column from the xylem tubes and thus water is able to rise to great heights even in the tallest plants.

11^{th} Botany
Unit – 11 Transport in Plants

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. The following chart illustrate the various types of cell to cell transport:

Cell to cell transport

Passive Transport **Active**
Transport

Channel
Protein Carrier Diffusion **Facilitated**
Diffusion **Protein Pumps**

Channel Protein **Carrier**
Protein

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.

Characteristics of diffusion

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

Significance of diffusion in Plants

1. Gaseous exchange of O2 and CO2 between the atmosphere and stomata of leaves takes place by the process of diffusion. O2 is absorbed during respiration and CO2 is absorbed during photosynthesis.
2. In transpiration, water vapour from intercellular spaces diffuses into atmosphere through stomata by the process of diffusion.
3. The transport of ions in mineral salts during passive absorption also takes place by this process.

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,

  1. Size of molecule: Smaller molecules diffuse faster.
  2. 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.

- 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.

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 protein create larger pores in the outer membrane. Example: Porin and Aquaporin.

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.

Aquaporin

- Aquaporin is a water channel protein embedded in the plasma membrane. It regulates the massive amount of water transport across the membrane. 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.

Carrier protein

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

- There are 3 type of carrier proteins classified on the basis of handling of molecules and direction of transport. They are

1. **Uniport**
2. **Symport**
3. **Antiport**

Uniport

- In this molecule of a single type move across a membrane independent of other molecules in one direction.

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.

Antiport or Counter Transport:

- An antiport is an integral membrane transport protein that simultaneously transports two different molecules, in opposite directions, across the membrane.

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 gradientwith the expenditure of cellular energy asan activeprocess. Pumps use a source of free energy such as ATP or light to drive the thermodynamically uphill transportof ions or molecules. The pump action is an example of active transport. Example: Na^+-K^+-ATPase pump.

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.

Imbibition

- Colloidal systems such as gum, starch, proteins, cellulose, agar, gelatine 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 duringthe rainy season.

Significance of imbibition

1) During germination of seeds, imbibitionincreases the volume of seed enormously and leads to bursting of the seed coat.

2) It helps in the absorption of water by roots at the initial level.

Water Potential

- The concept of water potential wasintroduced 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 bythe 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 decreasesthe 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 (ΨS)

2) Pressure potential (ΨP) By correlating two factors, water potential is written as,

ΨW = ΨS + ΨP Water Potential = Solute potential + Pressure potential

1. Solute Potential (ΨS)

- Solute potential, otherwise known asosmotic 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 (ΨW= ΨS).

2. Pressure Potential (ΨP)

- Pressure potential is a mechanical forceworking 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 (ΨM)

- Matric potential represents the attractionbetween 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.

Osmotic Pressure and Osmotic Potential

- When a solution and its solvent (purewater) 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 asthe 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.

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 turgorpressure 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.

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

- Pure solvent (hypotonic) has higherdiffusion 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.

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

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 onlyin comparison with another solution.

Types of osmosis

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

i. Endosmosis:

- Endosmosis is defined asthe 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 asthe 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.

Plasmolysis (Plasma = cytoplasm; lysis = breakdown)

- When a plant cell is kept in a hypertonicsolution, 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:

1) Incipient plasmolysis

2) Evident plasmolysis and iii) Final plasmolysis. Differences among them are given in table

Significance

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

Deplasmolysis

- The effect of plasmolysis can be reversed,by transferring them back into water orhypotonic 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.

Reverse Osmosis

- Reverse Osmosis follows the sameprinciples 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

- Uses: Reverse osmosis is used forpurification of drinking water and desalination of seawater.

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.

Water Absorbing Organs

- Usually, absorption of water occurs inplants 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.

Path of Water Across Root Cells

- Water is first absorbed by root hairand 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 ofwater. They are

i) Apoplast
ii) Symplast
iii) Transmembrane route.

Apoplast

- The apoplast (Greek: apo = away; plast = cell) consists of everything externalto 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.

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.

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 twomembranes for each cell. Transport across the tonoplast is also involved.

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) passiveabsorption.

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.

Osmotic active absorption

- The theory of osmotic activeabsorption was postulated by Atkins (1916) andPreistley (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, pericycleand finally reaches protoxylem. As thesap reaches the protoxylem a pressure is developed known as root pressure. This theory involves the symplastic movement of water.

Objections to osmotic theory:

1. 1.Thecell sap concentration in xylem is not always high.
2. Root pressure is not universal in all plants especially in trees.

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 decreasein the rate of respiration and also the rate of absorption of water.

Passive Absorption

- In passive absorption, roots do not playany role in the absorption of water andis regulated by transpiration only. Due totranspiration, water is lost from leaf cellsalong with a drop in turgor pressure. Itincreases DPD in leaf cells and leads towithdrawal of water from adjacent xylemcells. In xylem, a tension is developedand is transmitted downward up to rootresulting in the absorption of water fromthe soil.

- In passive absorption the path of water may be symplastic orapoplastic. It accounts for about 98% ofthe total water uptake by plants.

Differences between Active Absorption and Passive Absorption

Active absorption	**Active absorption Passive absorption**
Active absorption takes place by the activity of root and root hairs	The pressure forabsorption is not developed in rootsand 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 symplasticmovement of water	Both symplast and apoplastmovement of water involved

Ascent of Sap

- In the last chapter, we studied about waterabsorption 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 withdissolved minerals from roots is called sap and its upward transport is called ascent of sap.

The Path of Ascent of Sap

- There is no doubt; water travels up along thevascular 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. 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 underthe microscope. Only xylem element iscolouredred, which indicates the pathof water is xylem. Phloem is not colored indicating that it has no role in the ascent of sap.

Mechanism of Ascent of Sap

- In ascent of sap, the biggest challenge is theforce 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.

Vital Force Theories

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

Relay pump theory of Godlewski (1884)

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

Pulsation theory of J.C.Bose (1923)

- Bose invented an instrument calledCrescograph, which consists of an electric probe connected to a galvanometer. When a probe is insertedinto 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.

Objections to vital force theories

- 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.

- Pumping action of living cells shouldbe in between two xylem elements (vertically) and not on lateral sides.

Root Pressure Theory

- If a plant which is watered well is cut a fewinches 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:

- ❖ Root pressure is totally absent in gymnosperms, which includes some of the tallest plants.
- ❖ There is no relationship between the ascent of sap and root pressure. Forexample, 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.
- ❖ Ascent of sap continues even in the absence of roots
- ❖ 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.

Physical Force Theory

- Physical force theories suggest that ascentof sap takes place through the dead xylemvessel and the mechanism is entirely physical and living cells are not involved.

Capillary theory

- Boehm (1809) suggested that the xylemvessels 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.

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.

Cohesion-tension or Cohesion andtranspiration pull theory

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

Strong cohesive force or tensile strength of water

- Water molecules have the strongmutual 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.

Continuity of the water column in the plant

- An important factor which can breakthe 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.

Transpiration pull or Tension in the unbroken water column

- The unbroken water column from leafto 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 adecrease in water potential. So, water movesas 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.

Transpiration

- Water absorbed by roots ultimatelyreaches 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 formof 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. The water may move through the xylem at a rate as fast as 75cm /min.

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

Types of Transpiration

Transpiration is of following three types:

Stomatal transpiration

- Stomata are microscopic structures presentin 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.

Lenticular transpiration

- In stems of woody plants and trees, theepidermis is replaced by periderm becauseof secondary growth. In order to providegaseous exchange between the living cellsand outer atmosphere, some pores whichlooks like lens-shaped raised spots arepresent on the surface of the stem calledLenticels. The loss of water from lenticelsis very insignificant as it amounts to only0.1% of the total.

Cuticular transpiration

- The cuticle is a waxy or resinous layerof cutin, a fatty substance covering theepidermis of leaves and other plant parts.Loss of water through cuticle is relativelysmall and it is only about 5 to 10 % of thetotal transpiration. The thickness of cuticleincreases in xerophytes and transpirationis very much reduced or totally absent.

Structure of Stomata

- The epidermis of leaves and green stemspossess 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 mm2. 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. The stoma opens to the interior into a cavity called sub-stomatalcavity which remains connected with the intercellular spaces.

Mechanism of Stomatal Movement

- Stomatal movements are regulated by thechange 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 proposedregarding opening and closing of stomata. The important theories of stomatalmovement are as follows,

  1. Theory of Photosynthesis in guard cells
  2. Starch – Sugar interconversion theory

3. Active potassium transport ion concept

Theory of Photosynthesis in guard cells

- Von Mohl (1856) observed that stomataopen 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.

Starch – Sugar Interconversion theory

- According to Lloyd (1908), turgidityof 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.

- Sayre (1920) observed that theopening 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 CO2by 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 CO2 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.

- The discovery of enzymephosphorylase 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.

- Steward (1964) proposed aslightly modified scheme of starch-sugar interconversion theory. According to him, Glucose-1-phosphate is osmoticallyinactive. 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.

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 changein pH from 5 to 7 by change of CO2.

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:

In light

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

2. Malic acid in guard cell dissociatesto malate anion and proton (H+).

3. 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.

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

5. Increased K+ ions in the guard cell are balanced by Cl– ions. Increase in solute concentration decreases the water potential in the guard cell.

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

7. Increased turgor pressure due to the entry of water opens the stomatal pore.

In Dark

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

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

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

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

5. Loss of water from guard cell reduces turgor pressure and causes closure of stomata

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.

External or Environmental factors

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.

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.

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.

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.

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.

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.

Internal factors

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

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.

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:

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.

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.

Guttation

- 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. 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.

Measurement of Transpiration

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. 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.

- 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 ($CoCl_2.2H_2O$ or $CoCl_2.4H_2O$) 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.

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 relay on the transpiration. Moreover plants withstand against scorching sunlight due to transpiration. Hence the transpiration is a "necessary evil" as stated by Curtis.

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.

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.

Ringing or girdling 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. 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.

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.

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.

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.

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

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

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

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.

Mechanism of Translocation

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

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.

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.

Electro-Osmotic theory

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

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.

- 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,

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

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

    3. 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.

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

    5. 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.

II. However, bidirectional movement of solute is commonly observed in plants.

III. Osmotic pressure of mesophyll cells and that of root hair do not confirm the requirements. This theory gives passive role to sieve tube and protoplasm, while some workers demonstrated the involvement of ATP.

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).

Passive Absorption

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:

    Contact exchange and ii. Carbonic acid exchange.

- 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.

Carbonic Acid Exchange Theory:

- According to this theory, soil solution plays an important role by acting as a medium for ion exchange. The CO2 released during respiration of root cells combines with water to form carbonic acid (H2CO3). Carbonic acid dissociates into H+ and HCO3 – 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.

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. The concept can be explained using two theories:

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:

    1. The mechanism of anion and cation absorption are different.
    2. Anions are absorbed through cytochrome chain by an active process, cations are absorbed passively.
    3. 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.

- 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:

1. Cations also induce respiration.
2. Fails to explain the selective uptake of ions.
3. It explains absorption of anions only.

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 Lecithinion 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. ATP is required for regeneration of lecithin.

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.

Unit -12- Mineral Nutrition

Classification of minerals

Classification of minerals based on their quantity

- Essential elements are classified as Macronutrients, Micronutrients and Unclassified minerals based on their requirements. Essential minerals which are required in higher concentration are called Macronutrients. Essential minerals which are required in less concentration called are as Micronutrients.

- Minerals like Sodium, Silicon, Cobalt and Selenium are not included in the list of essential nutrients but are required by some plants, these minerals are placed in the list of unclassified minerals. These minerals play specific roles for example, Silicon is essential for pest resistance, prevent water lodging and aids cell wall formation in Equisetaceae (Equisetum), Cyperaceae and Gramineae.

Mineral Types		
Macro nutrients	**Micro nutrients**	**Unclassified minerals**
Excess than 10 mmole Kg-1 in tissue concentration or 0.1 to 10 mg per gram of dry weight.	Less than 10 mmole Kg-1 in tissue concentration or equal or less than 0.1 mg per gram of dry weight.	Required for some plants in trace amounts and have some specific functions.
Example: C, H, O, N, P, K, Ca, Mg and S	Example: Fe, Mn, Cu, Mo, Zn, B, Cl and Ni	Example: Sodium, Cobalt, Silicon and Selenium

Classification of minerals based on mobility

- If you observe where the deficiency symptoms appear first, you can notice differences in old and younger leaves. It is mainly due to mobility of minerals. Based on this, they are classified into

1. Actively mobile minerals and
2. Relatively immobile minerals

Actively mobile minerals

- Nitrogen, Phosphorus, Potassium, Magnesium, Chlorine, Sodium, Zinc and Molybdenum. Deficiency symptoms first appear on old and senescent leaves due to active movement of minerals to younger leaves.

Relatively immobile minerals

- Calcium, Sulphur, Iron, Boron and Copper shows deficiency symptoms first that appear on young leaves due to the immobile nature of minerals

Classification of minerals based on their functions

a. Structural component minerals: Minerals like Carbon, Hydrogen, Oxygen and Nitrogen

b. Enzyme function: Molybdenum (Mo) is essential for nitrogenase enzyme during reduction of atmospheric nitrogen into ammonia. Zinc (Zn) is an important activator for alcohol dehydrogenase and carbonic anhydrase. Magnesium (Mg) is the activator for RUBP carboxylaseoxygenase and PEP carboxylase. Nickel (Ni) is a constituent of urease and hydrogenase.

c. Osmotic Potential: Potassium (K) plays a key role in maintaining osmotic potential of the cell. The absorption of water, movement of stomata and turgidity are due to osmotic potential.

d. Energy components: Magnesium (Mg) in chlorophyll and phosphorous (P) in ATP.

Functions, mode of absorption and deficiency symptoms of macronutrients

- Macronutrients, their functions, their mode of absorption, deficiency symptoms and deficiency diseases are discussed here:

1. Nitrogen (N):

- It is required by the plants in greatest amount. It is an essential component of proteins, nucleic acids, amino acids, vitamins, hormones, alkaloids, chlorophyll and cytochrome. It is absorbed by the plants as nitrates (NO_3). Deficiency symptoms: Chlorosis, stunted growth, anthocyanin formation.

2. Phosphorus (P):

- Constituent of cell membrane, proteins, nucleic acids, ATP, NADP, phytin and sugar phosphate. It is absorbed as H_2PO_4 and HPO_4 ions. Deficiency symptoms: Stunted growth, anthocyanin formation, necrosis, inhibition of cambial activity, affect root growth and fruit ripening.

3. Potassium (K):

- Maintains turgidity and osmotic potential of the cell, opening and closure of stomata, phloem translocation, stimulate activity of enzymes, anion and cation balance by ion-exchange. It is absorbed as K_1 ions. Deficiency symptoms: Marginal chlorosis, necrosis, low cambial activity, loss of apical dominance, lodging in cereals and curled leaf margin.

4. Calcium (Ca):

- It is involved in synthesis of calcium pectate in middle lamella, mitotic spindle formation, mitotic cell division, permeability of cell membrane, lipid metabolism, activation of phospholipase, ATPase, amylase and activator of adenyl kinase. It is absorbed as Ca_{21} exchangeable ions.

5. **Deficiency symptoms:**

- Chlorosis, necrosis, stunted growth, premature fall of leaves and flowers, inhibit seed formation, Black heart of Celery, Hooked leaf tip in Sugar beet, Musa and Tomato.

6. **Magnesium (Mg):**

- It is a constituent of chlorophyll, activator of enzymes of carbohydrate metabolism (RUBP Carboxylase and PEP Carboxylase) and involved in the synthesis of DNA and RNA. It is essential for binding of ribosomal sub units. It is absorbed as Mg_{21} ions. Deficiency symptoms: Inter veinal chlorosis, necrosis, anthocyanin (purple) formation and Sand drown of tobacco.

7. **Sulphur (S):**

- Essential component of amino acids like cystine, cysteine and methionine, constituent of coenzyme A, Vitamins like biotin and thiamine, constituent of proteins and ferredoxin.plants utilise sulphur as sulphate (SO_4) ions.

Deficiency symptoms:

- Chlorosis, anthocyanin formation, stunted growth, rolling of leaf tip and reduced nodulation in legumes.

NPK Fertilizers

It consists of nitrogen, phosphate with potassium in different proportions. The number labelled on the bags as 15-15-15 indicates N, P & K in equal proportions.

Functions, mode of absorption and deficiency symptoms of micronutrients

- Micronutrients even though required in trace amounts are essential for the metabolism of plants. They play key roles many plants. Example: Boron is essential for translocation of sugars, molybdenum is involved in nitrogen metabolism and zinc is needed for biosynthesis of auxin. Here, we will study about the role of micro nutrients, their functions, their mode of absorption, deficiency symptoms and deficiency diseases.

1. Iron (Fe):

- Iron is required lesser than macronutrient and larger than micronutrients, hence, it can be placed in any one of the groups. Iron is an essential element for the synthesis of chlorophyll and carotenoids. It is the component of cytochrome, ferredoxin, flavoprotein, formation of chlorophyll, porphyrin, activation of catalase, peroxidase enzymes. It is absorbed as ferrous (Fe21) and ferric (Fe31) ions. Mostly fruit trees are sensitive to iron.

Deficiency:

- Interveinal Chlorosis, formation of short and slender stalk and inhibition of chlorophyll formation.

2. Manganese (Mn):

- Activator of carboxylases, oxidases, dehydrogenases and kinases, involved in splitting of water to liberate oxygen (photolysis). It is absorbed as manganous (Mn21) ions. Deficiency: Interveinal chlorosis, grey spot on oats leaves and poor root system.

3. Copper (Cu):

- Constituent of plastocyanin, component of phenolases, tyrosinase, enzymes involved in redox reactions, synthesis of ascorbic acid, maintains carbohydrate and nitrogen balance, part of oxidase and cytochrome oxidase. It is absorbed as cupric (Cu21) ions.

Deficiency:

- Die back of citrus, Reclamation disease of cereals and legumes, chlorosis, necrosis and Exanthema in Citrus.

4. **Zinc (Zn):**

- Essential for the synthesis of Indole acetic acid (Auxin) activator of carboxylases, alcohol dehydrogenase, lactic dehydrogenase, glutamic acid dehydrogenase, carboxy peptidases and tryptophan synthetase. It is absorbed as Zn21 ions.

Deficiency:

- Little leaf and mottle leaf due to deficiency of auxin, Inter veinal chlorosis, stunted growth, necrosis and Khaira disease of rice.

5. **Boron (B):**

- Translocation of carbohydrates, uptake and utilisation of Ca11, pollen germination, nitrogen metabolism, fat metabolism, cell elongation and differentiation. It is absorbed as borate BO32 ions. Deficiency: Death of root and shoot tips, premature fall of flowers and fruits, brown heart of beet root, internal cork of apple and fruit cracks.

6. **Molybdenum (Mo):**

- Component of nitrogenase, nitrate reductase, involved in nitrogen metabolism, and nitrogen fixation. It is absorbed as molybdate (Mo21) ions.

Deficiency:

- Chlorosis, necrosis, delayed flowering, retarded growth and whip tail disease of cauliflower.

7. **Chlorine (Cl):**

- It is involved in Anion – Cation balance, cell division, photolysis of water. It is absorbed as Cl2 ions.

Deficiency:

- Wilting of leaf tips

8. **Nickel (Ni):**

- Cofactor for enzyme urease and hydrogenase.

Deficiency: Necrosis of leaf tips.

Calmodulin
Calmodulin is a Ca21 modulating protein in eukaryotic cells. It is a heat stable protein involved in fine metabolic regulations.

Deficiency diseases and symptoms

The following table (Table 12.2) gives you an idea about Minerals and their Deficiency symptoms:

Deficiency diseases and Symptoms	
Name of the deficiency disease and symptoms	Deficiency minerals
1. Chlorosis (Overall)	Nitrogen, Potassium, Magnesium, Sulphur,Iron, Manganese, Zinc and Molybdenum.
a. Interveinal chlorosis	Magnesium, Iron, Manganese and Zinc
b. Marginal chlorosis	Potassium
2. Necrosis (Death of the tissue)	Magnesium, Potassium, Calcium, Zinc, Molybdenum and Copper.
3. Stunted growth	Nitrogen, Phosphorus, Calcium, Potassium and Sulphur.
4. Anthocyanin formation	Nitrogen, Phosphorus, Magnesium and Sulphur
Delayed flowering	Nitrogen, Sulphur and Molybdenum
6. Die back of shoot, Reclamation disease, Exanthema in citrus (gums on bark)	Copper
7. Hooked leaf tip	Calcium

8. Little Leaf	Zinc
9. Brown heart of turnip and Internal cork of apple	Boron
10. Whiptail of cauliflower and cabbage	Molybdenum
11. Curled leaf margin	Potassium

Mineral Toxicity

a. Manganese toxicity

- Increased Concentration of Manganese will prevent the uptake of Fe and Mg, prevent translocation of Ca to the shoot apex and cause their deficiency. The symptoms of manganese toxicity are appearance of brown spots surrounded by chlorotic veins.

b. Aluminium Toxicity

- Aluminium toxicity causes precipitation of nucleic acid, inhibition of ATPase, inhibition of cell division and binding of plasma membrane with Calmodulin.

Hydroponics and Aeroponics

1. Hydroponics or Soilless culture:

- Von Sachs developed a method of growing plants in nutrient solution. The commonly used nutrient solutions are Knop solution (1865) and Arnon and Hoagland Solution (1940). Later the term Hydroponics was coined by Goerick (1940) and he also introduced commercial techniques for hydroponics. In hydroponics roots are immersed in the solution containing nutrients and air is supplied with help of tube (Figure 12.3).

Aeroponics:

- This technique was developed by Soifer Hillel and David Durger. It is a system where roots are suspended in air and nutrients are sprayed over the roots by a motor driven rotor.

Nitrogen Fixation

- Inspiring act of nature is self-regulation. As all living organisms act as tools for bio geo chemical cycles, nitrogen cycle is highly regulated. Life on earth depends on nitrogen cycle. Nitrogen occurs in atmosphere in the form of N2 (N≡N), two nitrogen atoms joined together by strong triple covalent bonds.

- The process of converting atmospheric nitrogen (N2) into ammonia is termed as nitrogen fixation. Nitrogen fixation can occur by two methods: 1. Biological; 2. Non-Biological.

Non – Biological nitrogen fixation

- ❖ Nitrogen fixation by chemical process in industry.
- ❖ Natural electrical discharge during lightening fixes atmospheric nitrogen.

Biological nitrogen fixation

- Symbiotic bacterium like Rhizobium fixes atmospheric nitrogen. Cyanobacteria found in Lichens, Anthoceros, Azolla and coralloid roots of Cycas also fix nitrogen. non-symbiotic (free living bacteria) like Clostridium also fix nitrogen.

Symbiotic nitrogen fixation

Nitrogen fixation with nodulation

- Rhizobium bacterium is found in leguminous plants and fix atmospheric nitrogen. This kind of symbiotic association is beneficial for both the bacterium and plant. Root nodules are formed due to bacterial infection. Rhizobium enters into the host cell and proliferates, it remains separated from the host cytoplasm by a membrane.

Stages of Root nodule formation:

1. Legume plants secretes phenolics which attracts Rhizobium.
2. Rhizobium reaches the rhizosphere and enters into the root hair, infects the root hair and leads to curling of root hairs.
3. Infection thread grows inwards and separates the infected tissue from normal tissue.
4. A membrane bound bacterium is formed inside the nodule and is called bacteroid.
5. Cytokinin from bacteria and auxin from host plant promotes cell division and leads to nodule formation

Non-Legume

- Alnus and Casuarina contain the bacterium Frankia. Psychotria contains the bacterium Klebsiella.
- Nitrogen fixation without nodulation The following plants and prokaryotes are involved in nitrogen fixation.

Lichens - Anabaena and Nostoc
Anthoceros - Nostoc
Azolla - Anabaena azollae
Cycas - Anabaena and Nostoc

Non-symbiotic Nitrogen fixation

- Free living bacteria and fungi also fix atmospheric nitrogen.

Aerobic	Azotobacter, Beijerneckia and Derxia
Anaerobic	Clostridium
Photosynthetic	Chlorobium and Rhodospirillum
Chemosynthetic	Disulfovibrio
Free living fungi	Yeast and Pullularia

Cyanobacteria	Nostoc, Anabaena and Oscillatoria.

Nitrogen cycle and nitrogen metabolism

Nitrogen cycle

- This cycle consists of following stages:

Fixation of atmospheric nitrogen

- Di-nitrogen molecule from the atmosphere progressively gets reduced by addition of a pair of hydrogen atoms. Triple bond between two nitrogen atoms (N N) are cleaved to produce ammonia.

- Nitrogen fixation process requires Nitrogenase enzyme complex, Minerals (Mo, Fe and S), anaerobic condition, ATP, electron and glucose 6 phosphate as H1 donor. Nitrogenase enzyme is active only in anaerobic condition. To create this anaerobic condition a pigment known as leghaemoglobin is synthesized in the nodules which acts as oxygen scavenger and removes the oxygen. Nitrogen fixing bacteria in root nodules appears pinkish due to the presence of this leghaemoglobin pigment.

Nitrification

- Ammonia (NH_3^+) is converted into Nitrite (NO_2^-) by Nitrosomonas bacterium. Nitrite is then converted into Nitrate (NO_3^-) by Nitrobacter bacterium. Plants are more adapted to absorb nitrate (NO_3^-) than ammonium ions from the soil.

Nitrate Assimilation

- The process by which nitrate is reduced to ammonia is called nitrate assimilation and occurs during nitrogen cycle.

Ammonification

- Decomposition of organic nitrogen (proteins and amino acids) from dead plants and animals into ammonia is called ammonification.

Organisim involved in this process are Bacillus ramosus and Bacillus vulgaris.

Denitrification

- Nitrates in the soil are converted back into atmospheric nitrogen by a process called denitrification. Bacteria involved in this process are Pseudomonas, Thiobacillus and Bacillus subtilis.

Nitrogen Metabolism

Ammonium Assimilation (Fate of Ammonia)

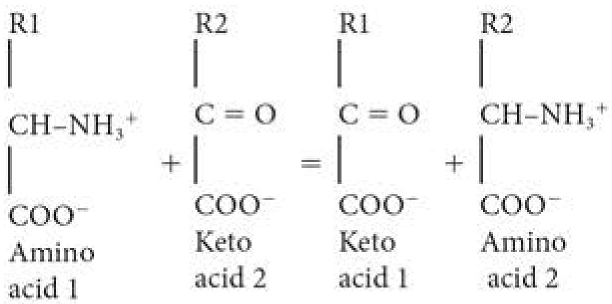
- Ammonia is converted into amino acids by the following processes:

Reductive amination

- Glutamic acid or glutamate is formed by reaction of ammonia with α-ketoglutaric acid.

Transamination

- Transfer of amino group (NH3+) from glutamic acid glutamate to keto group of keto acid. Glutamic acid is the main amino acid from which other amino acids are synthesised by transamination. Transamination requires the enzyme transaminase and co enzyme pyridoxal phosphate (derivative of vitamin B6-pyridoxine)



Catalytic Amination: (GS/GOGAT Pathway)

- Glutamate amino acid combines with ammonia to form the amide glutamine.

$$\text{Glutamate} + NH_4^+ \xrightarrow[\text{ATP} \;\to\; \text{ADP + Pi}]{\text{Glutamine Synthetase (GS)}} \text{Glutamine.}$$

- Glutamine reacts with α ketoglutaric acid to form two molecules of glutamate.

$$\text{Glutamine} + \alpha \text{ Ketoglutaric acid (2- oxoglutarate)} \xrightarrow[\text{NADH+H}^+ \;\to\; \text{NAD}^+]{\text{GOGAT (enzyme)}} 2 \text{ Glutamate}$$

- Glutamine reacts with α ketoglutaric acid to form two molecules of glutamate.

Special modes of nutrition

- Nutrition is the process of uptake and utilization of nutrients by living organisms. There are two main types such as autotrophic and heterotrophic nutrition. Autotrophic nutrition is further divided into photosynthetic and chemosynthetic nutrition. Heterotrophic nutrition is further divided into saprophytic, parasitic, symbiotic and insectivorous type. In this topic you are going to learn about special mode of nutrition.

Saprophytic mode of nutrition in angiosperms

- Saprophytes derive nutrients from dead and decaying matter. Bacteria and fungus are main saprophytic organisms. Some angiosperms also follow saprophytic mode of nutrition. Example: Neottia. Roots of Neottia (Bird's Nest Orchid) associate with mycorrhizae and absorb nutrients as a saprophyte. Monotropa (Indian Pipe) grow on humus rich soil found in thick forests. It absorbs nutrient through mycorrhizal association.

Parasitic mode of nutrition in angiosperms

- Organisms deriving their nutrient from another organism (host) and causing disease to the host are called parasites.

a. Obligate or Total parasite – Completely depends on host for their survival and produces haustoria.

1. Total stem parasite: The leafless stem twine around the host and produce haustoria. Example: Cuscuta (Dodder), a rootless plant growing on Zizyphus, Citrus and so on.
2. Total root parasite: They do not have stem axis and grow in the roots of host plants produce haustoria. Example: Rafflesia, Orobanche and Balanophora.

b. Partial parasite - Plants of this group contain chlorophyll and synthesize carbohydrates. Water and mineral requirements are dependent on host plant.

1. Partial Stem Parasite: Example: Loranthus and Viscum (Mistletoe) Loranthus grows on fig and mango trees and absorb water and minerals from xylem.

2. Partial root parasite: Example: Santalum album (Sandal wood tree) in its juvenile stage produces haustoria which grows on roots of many plants.

Symbiotic mode of Nutrition

a. **Lichens:**

- It is a mutual association of Algae and Fungi. Algae prepares food and fungi absorbs water and provides thallus structure.

b. **Mycorrhizae:**

- Fungi associated with roots of higher plants including Gymnosperms. Example: Pinus.

c. **Rhizobium and Legumes:**

- This symbiotic association fixes atmospheric nitrogen

d. **Cyanobacteria and Coralloid Roots:**

- This association is found in Cycas where Nostoc associates with its coralloid roots.

Symbiotic mode of nutrition

Insectivorous mode of nutrition

- Plants which are growing in nitrogen deficient areas develop insectivorous habit to resolve nitrogen deficiency.

a. **Nepenthes (Pitcher plant):**

- Pitcher is a modified leaf and contains digestive enzymes. Rim of the pitcher is provided with nectar glands and acts as an attractive lid. When insect is trapped, proteolytic enzymes will digest the insect.

b. **Drosera (Sundew):**

- It consists of long club shaped tentacles which secrete sticky digestive fluid which looks like a sundew.

c. **Utricularia (Bladder wort):**

- Submerged plant in which leaf is modified into a bladder to collect insect in water.

d. **Dionaea (Venus fly trap):**

- Leaf of this plant modified into a colourful trap. Two folds of lamina consist of sensitive trigger hairs and when insects touch the hairs it will close

Lichens are indicators of SO2 pollution and a pioneer species in xeric succession.

Check your grasp! Mineral X required for the activation of enzyme nitrogenase, Mineral Y involved in transport of sugar and Mineral Z required for maintaining ribosome structure. Identify X, Y and Z.

Chapter 13
Photosynthesis

- Life on earth is made up of organic compounds. How do we get these organic compounds? Ultimately, plants are the main source of all kinds of carbon compounds in this planet. We directly or indirectly depend on plants for this. Plants are the major machinery which produce organic compounds like carbohydrates, lipids, proteins, nucleic acids and other biomolecules.

- Though man has reached the glory of achievements still he is not able to imitate the metabolic activities of plants which produces energy resources and other biomolecules.

A quest for future energy

Hydrogen is considered as a promising energy vector for the next generation. It can be used for "green" electricity production or developing cogeneration systems such as fuel cells. The sustainability of its employment depends on the energy source used to synthesize it from hydrogen-rich compounds such as water or biomass. The splitting of water in hydrogen and oxygen by means of solar radiation in Photolysis is common in plants. Water splitting is not an easy process to mimic artificially but preliminary success is achieved so far. If young minds take up this as their research ambition a revolution can be made in green energy.

- The plants get energy from sun by converting solar or radiant energy into chemical energy by the process of Photosynthesis, which acts as a driving force for both biotic and abiotic world. Photosynthesis produces 1700 million tonnes of dry matter per year by fixing 75 × 1012 Kg of carbon every year. Photosynthetic organisms use only 0.2 % of incident solar light on earth. Carbohydrates produced by photosynthesis are the basic raw material for respiration and also to produce many organic compounds. It maintains atmospheric oxygen and carbon dioxide level. Photosynthesis consumes atmospheric carbon dioxide which is continuously added by the respiration of organisms. Photosynthesis is the major endergonic reaction. In this chapter, we will study about the energy yielding process of photosynthesis and various types of energy utilization processes to produce carbohydrates.

Historical Events in Photosynthesis

- ❖ Van Helmont (1648) – Increase in organic substances comes from water alone by growing a Willow tree that gains weight but soil loses only 2 ounces of the original weight.

- ❖ Stephen Hales (1727) – Father of Plant Physiology, Plants obtain nourishment from air and light.

- ❖ Joseph Priestley (1772) – Performed experiments with candle, mice and Mint plant and concluded that vegetation purifies the air.

- ❖ Jean-Ingen-Housz (1779) – Confirmed Priestley's experiment that oxygen released by the plants is possible only in light.

- ❖ Lavoisier (1783) – Purifying gas produced by plants in sunlight is Oxygen (Phlogiston) and noxious gas produced by burning of candle (de Phlogiston) is Carbon di oxide.

- ❖ Desaussure (1804)- Explained the importance of water in the process of photosynthesis.

- ❖ Dutrochet (1837) – Explained the importance of Chlorophyll in Photosynthesis.

- ❖ Von Mayer (1845) – Green plants convert solar energy into chemical energy of organic matter. CO2 1 H2O Organic matter 1 O2

- ❖ Liebig (1845) – Organic matter of plants was derived from CO2.

- ❖ Julius Von Sachs (1854) – Discovered that product of photosynthesis was starch. Green substance (chlorophyll) is located in special structures (Chloroplast).

- T.W. Engelmann (1888)- Plotted action spectrum of photosynthesis

- Blackman (1905) – Proposed Law of Limiting factors.

- Warburg (1920) – Used unicellular green algae Chlorella for the study of Photosynthesis.

- Van Neil (1931) – Oxygen released during photolysis comes from water and not from CO2. He also conducted experiments in Purple green bacteria and demonstrated Photosynthesis. In Green Sulphur bacteria H2S is the Hydrogen donor which releases Sulphur instead of oxygen.

$$2H_2A + CO_2 \xrightarrow[Chlorophyll]{Light} (CH_2O)_n + H_2O + 2A$$

- Emerson and Arnold (1932) – Existence of light and dark reaction by flashing light experiments.

- R. Hill (1937) – Explained photolysis with the help of isolated chloroplasts and electron acceptors in the presence of light.

- Ruben and Kamen (1941) – Used 18O radioactive Oxygen to prove that oxygen evolves from water.

- Arnon, Allen and Whatley (1954) – Used radioactive 14CO2 to show fixation of CO2 by isolated chloroplast.

- Melvin Calvin (1954) – Used radioactive 14CO2 and traced path of carbon in the dark phase of photosynthesis or C3 Cycle.

- Emerson et al., (1957) – Reported existence of two photosystems

- Hatch and Slack (1965) – Reported C4 pathway and CO2 fixation in C4 plants

- Huber, Michel and Dissenhofer (1985) – Crystalized photosynthetic reaction centre of Rhodobacter and received the Nobel Prize in 1988.

Definition, Significance and Site of Photosynthesis

Definition of Photosynthesis

- Photosynthesis is referred as photochemical oxidation and reduction reactions carried out with help of light, converting solar energy into Chemical energy. It is the most important anabolic process. Plants and photosynthetic bacteria use simple raw materials like carbon dioxide water and with the help of light energy synthesize carbohydrates and evolve oxygen. The overall chemical equation for photosynthesis is:

$$6CO_2 + 6H_2O \xrightarrow[\text{Chlorophyll}]{\text{Light}} C_6H_{12}O_6 + 6O_2\uparrow$$

- Ruben and Kamen (1941) demonstrated six molecules of water as insufficient for the evolution of 6 molecules of O2 and modified the equation as:

$$6CO_2 + 12H_2O \xrightarrow[\text{Chlorophyll}]{\text{Light}} C_6H_{12}O_6 + 6\,H_2O + 6O_2\uparrow$$

- Photosynthesis is a collection of oxidation and reduction reactions (Redox reaction). Oxidation- Water is oxidised into oxygen (loss of electrons).

  Reduction – CO2 is reduced into Carbohydrates (gain of electrons).

- In some bacteria, oxygen is not evolved and is called as non-oxygenic and aerobic photosynthesis. Examples: Green sulphur, Purple sulphur and green filamentous bacteria.

Significance of Photosynthesis

1. Photosynthetic organisms provide food for all living organisms on earth either directly or indirectly.

2. It is the only natural process that liberates oxygen in the atmosphere and balances the oxygen level.

3. Photosynthesis balances the oxygen and carbon cycle in nature.

4. Fuels such as coal, petroleum and other fossil fuels are from preserved photosynthetic plants.
5. Photosynthetic organisms are the primary producers on which all consumers depend for energy.

6. Plants provide fodder, fibre, fire wood, timber, useful medicinal products and these sources come by the act of photosynthesis.

Site of Photosynthesis

- Chloroplasts are the main site of photosynthesis and both energy yielding process (Light reaction) and fixation of carbon dioxide (Dark reaction)that takes place in chloroplast. It is a double wall membrane bounded organelle, discoid or lens shaped, 4–10 µm in diameter and 1–33 µm in thickness. The membrane is a unit membrane and space between them is 100 to 200 Å. A colloidal and proteinaceous matrix called stroma is present inside.

- A sac like membranous system called thylakoid or lamellae is present in stroma and they are arranged one above the other forming a stack of coin like structure called granum (plural grana). Each chloroplast contains 40 to 80 grana and each granum consists of 5 to 30 thylakoids.

- Thylakoids found in granum are called grana lamellae and in stroma are called stroma lamellae. Thylakoid disc size is 0.25 to 0.8 micron in diameter. A thinner lamella called Fret membrane connects grana. Pigment system I is located on outer thylakoid membrane facing stroma and Pigment system II is located on inner membrane facing lumen of thylakoid. Grana lamellae have both PS I and PS II whereas stroma lamellae have only PS I. Chloroplast contains 30–35% Proteins, 20–30% phospholipids, 5–10% chlorophyll, 4–5% Carotenoids, 70S ribosomes, circular DNA and starch grains. Inner surface of lamellar membrane consists of small spherical structure called as Quantasomes. Presence of 70S ribosome and DNA gives them status of semi-autonomy and proves endosymbiotic hypothesis which says chloroplast evolved from bacteria. Thylakoid contains pigment systems which produces ATP and NADPH $+H^+$ using solar energy. Stroma contains enzyme which reduces carbondioxide into carbohydrates. In Cyanobacteria thylakoid lies freely in cytoplasm without envelope.

Photosynthetic Pigments

- A photosynthetic pigment is a pigment that is present in chloroplasts or photosynthetic bacteria which captures the light energy necessary for photosynthesis.

Types of Photosynthetic pigments		
Chlorophyll	**Carotenoids**	**Phycobilins**
1. Chlorophyll 'a' (C55H72O5N4Mg) – Green plants and Cyanobacteria	1. Carotene (C40H56) – Lycopene (Red)	1. Phycocyanin – Cyanobacteria
2. Chlorophyll 'b' (C55H70O6N4Mg) – Green algae and all higher plants	2.Xanthophyll (C40H56O2)- Yellow colour – Violaxanthin, Fucoxanthin (Brown Algae) and Lutein	2. Phycoerythrin – Red Algae
3. Chlorophyll 'c' (C55H32O5N4Mg) – Dinoflagellates, Diatoms and Brown Algae		
4. Chlorophyll 'd' – Red Algae		
5. Chlorophyll 'e' – Xathophycean Algae		
6. Bacteriochlorophyll 'a'		
7. Bacteriochlorophyll 'b'		
8. Chlorobium Chlorophyll 650		
9. Chlorobium Chlorophyll 666		

Chlorophyll

- Chlorophyll 'a' is the primary pigment which acts as a reaction centre and all other pigments act as accessory pigments and trap solar energy and then transfer it to chlorophyll 'a'. Chlorophyll molecules have a tadpole like structure. It consists of Mg-Porphyrin head (Hydrophilic Head) and (Lipophilic tail) Phytol tail. The Porphyrin head consists of four pyrrol rings linked together by C-H bridges. Each pyrrole ring comprises of four carbons and one nitrogen atom. Porphyrin ring has several side groups which alter the properties of the pigment. Different side groups are indicative of various types of chlorophyll. The Phytol tail made up of 20 carbon alcohol is attached to carbon 7 of the Pyrrole ring IV. It has a long propionic acid ester bond. Long lipophilic tail helps in anchoring chlorophyll to the Lamellae.

I. Biosynthesis of Chlorophyll

- Chlorophyll is synthesized from intermediates of respiration and photosynthesis. Succinic acid an intermediate of Krebs cycle is activated by the addition of coenzyme A and it reacts with a simple amino acid glycine and the reaction goes on to produce chlorophyll 'a'. Bio synthesis of chlorophyll 'a' requires Mg, Fe, Cu, Zn, Mn, K and nitrogen. The absence of any one of these minerals leads to chlorosis (Recall what you have studied in 'Mineral Nutrition').

II. Comparison of Chlorophyll – 'a' with other pigments

1. Chlorophyll 'b' differs from Chlorophyll 'a' in having CHO (aldehyde)group instead of CH3(Methyl) group at the 3rd C atom in II Pyrrol ring (Figure 13.2).

2. Chlorophyll 'c' differs from Chlorophyll 'a' by lacking phytol tail.

3. Chlorophyll 'd' differs from Chlorophyll 'a' in having O-CHO group instead of CH-CH2 group at 2nd Carbon in the 1st Pyrrol ring.

4. Pheophytin resembles Chlorophyll 'a' except that it lacks Mg atom. Instead it has two H atoms.

5. Phycobilins have open tetra pyrrols and they have neither Mg nor phytol chain.

Carotenoids

- Carotenoids are yellow to orange pigments, mostly tetraterpens and these pigments absorb light strongly in the blue to violet region of visible spectrum. These pigments protect chlorophyll from photooxidative damage. Hence, they are called as shield pigments. These pigments absorb light and transfer these to chlorophyll. Almost all carotenoid pigments have 40 carbon atoms. Ripening of fruits, floral colours and leaf colour change during autumn is due to Carotenoids (Carotene and Xanthophyll) (Figure 13.3).

I. Carotenes:

- Orange, Red, Yellow and Brownish pigments, hydrocarbons (Lipids) and most of them are tetraterpenes $(C_{40}H_{56})$. Carotene is the most abundant Carotene in plants and it is a precursor of Vitamin A. Lycopene is the red pigment found in the fruits of tomato, red peppers and roses.

II. Xanthophylls:

- Yellow $(C_{40}H_{56}O_2)$ pigments are like carotenes but contain oxygen. Lutein is responsible for yellow colour change of leaves during autumn season. Examples: Lutein, Violaxanthin and Fucoxanthin

Phycobilins

- They are proteinaceous pigments, soluble in water, and do not contain Mg and Phytol tail. They exist in two forms such as

1. Phycocyanin found in cyanobacteria
2. Phycoerythrin found in rhodophycean algae (Red algae).

Spectrum of Electromagnetic Radiation

- In the total electromagnetic spectrum, visible light is the smallest part. The entire life on earth depends on light and is the driving force for all organisms. Plants have natural potential to utilize solar energy directly. In the given picture electromagnetic radiation spectrum and components of visible spectrum are mentioned. The wavelength of solar radiation which reaches the earth is between 300 to 2600 nm. The visible spectrum ranges between 390 to 763 nm (3900 å to 7630 å). The colour of the light is determined by the wavelength. Energy of the quantum is inversely proportional to wavelength. Shorter wavelength has more energy than longer wavelength. Electromagnetic spectrum consists of 8 types of radiations such as cosmic rays, gamma rays, X rays, U-V rays, Visible light spectrum, infrared rays, electric rays and radio rays.

Light is extremely variable and if radiation is evenly distributed over the globe it is sufficient to melt 35 m thick ice layer.

Properties of Light

1. Light is a transverse electromagnetic wave.

2. It consists of oscillating electric and magnetic fields that are perpendicular to each other and perpendicular to the direction of propagation of the light.

3. Light moves at a speed of 3 × 108 ms–1
4. Wavelength is the distance between successive crests of the wave.

5. Light as a particle is called photon. Each photon contains an amount of energy known as quantum.

6. The energy of a photon depends on the frequency of the light.

Photosynthetic Unit (Quantasome)

- Quantasomes are the morphological expression of physiological photosynthetic units, located on the inner membrane of thylakoid lamellae. Each quantasome measures about 180 å × 160 å and 100 å thickness. In 1952, Steinman observed granular structures in chloroplast lamellae under electron microscope. Later, Park and Biggins (1964) confirmed these granular structures as physiological units of photosynthesis and coined the term Quantasome. According to them one quantasome contains about 230 chlorophyll molecules. A minimum number of chlorophyll and other accessory pigments act together in a photochemical reaction to release one oxygen or to reduce one molecule of CO_2. It constitutes a photosynthetic unit. (Figure 13.7) Emerson and Arnold (1932) based on flashing light experiment found 2500 chlorophyll molecules are required to fix one molecule of CO_2. However, the reduction or fixation of one CO_2 requires 10 quanta of light and so each unit would contain 1/10 of 2500 i.e. 250 molecules. Usually 200 to 300 chlorophyll molecules are considered as a physiological unit of photosynthesis. According to Emerson 8 quanta of light are required for the release of one oxygen molecule or reduction of one Carbon dioxide molecule. The quantum yield is 1/8 or 12 %.

Absorption Spectrum and Action Spectrum

Absorption Spectrum

- The term absorption refers to complete retention of light, without reflection or transmission. Pigments absorb different wavelengths of light. A curve obtained by plotting the amount of absorption of different wavelengths of light by a pigment is called its absorption spectrum.

- Chlorophyll 'a' and chlorophyll 'b' absorb quanta from blue and red region
- Maximum absorption peak for different forms of chlorophyll 'a' is 670 to 673, 680 to 683 and 695 to 705nm.
- Chlorophyll 'a' 680 (P680) and Chlorophyll 'a' 700 (P700) function as trap centre for PS II and PS I respectively.

Action Spectrum

- The effectiveness of different wavelength of light on photosynthesis is measured by plotting against quantum yield. The curve showing the rate of photosynthesis at different wavelengths of light is called action spectrum. From the graph showing action spectrum, it can be concluded that maximum photosynthesis takes place in blue and red region of the spectrum. This wavelength of the spectrum is the absorption maxima for Chlorophyll (a) and Chlorophyll (b). The Action Spectrum is instrumental in the discovery of the existence of two photosystems in O2 evolving photosynthesis (Figure 13. 8).

Emerson's Experiments and Hill's Reaction

Red Drop or Emerson's First Effect

- Emerson conducted experiment in Chlorella using only one wavelength of light (monochromatic light) at a time and he measured quantum yield. He plotted a graph of the quantum yield in terms of O2 evolution at various wavelengths of light. His focus was to determine at which wavelength the photochemical yield of oxygen was maximum. He found that in the wavelength of 600 to 680 the yield was constant but suddenly dropped in the region above 680 nm (red region). The fall in the photosynthetic yield beyond red region of the spectrum is referred as Red drop or Emerson's first effect.

Emerson's Enhancement Effect

- Emerson modified his first experiment by supplying shorter wavelength of light (red light) along with longer wavelength of light (far red light). He found that the monochromatic light of longer wavelength (far red light) when supplemented with shorter wavelength of light (red light) enhanced photosynthetic yield and recovered red drop. This enhancement of photosynthetic yield is referred to as Emerson's Enhancement Effect

Photosynthetic rate at far red light (710 nm) = 10
Photosynthetic rate at red light (650 nm) = 43.5
Photosynthetic rate at red + far red (650 1 710 nm) 5 72.5 (Enhancement effect).

Hill's Reaction

- R. Hill (1937) isolated chloroplasts and when they were illuminated in the presence of suitable electron acceptors such as ferricyanide, they were reduced to ferrocyanide and oxygen is evolved. Hill's Reaction is now considered to be equivalent to Light Reaction.

Conclusions of Hill's Reaction:

1. During photosynthesis oxygen is evolved from water.
2. Electrons for the reduction of CO_2 are obtained from water.
3. Reduced substance produced, later helps to reduce CO_2

$$2H_2O \ 1 \ 2A \rightarrow 2 \ AH_2 \ 1 \ O_2$$

- A is the Hydrogen acceptor, the common in vitro hydrogen acceptors are ferricyanide, benzoquinone and Di Chloro Phenol Indole Phenol (DCPIP).

13.8 Modern Concept of Photosynthesis

- Photosynthesis is an Oxidation and Reduction process. Water is oxidised to release O_2 and CO_2 is reduced to form sugars. The first phase requires light and is called light reaction or Hill's reaction.

1. Light reaction: It is a photochemical reaction whereas dark reaction is a thermochemical reaction. Solar energy is trapped by chlorophyll and stored in the form of chemical energy (assimilatory power) as ATP and reducing power NADPH + H^1. NADPH + H^1 alone are known as reducing powers. This reaction takes place in thylakoid membrane of the chloroplast. Oxygen is evolved as a result of splitting of water molecules by light. Light reaction is discussed in two phases:

i. Photo-oxidation Phase:

• Absorption of light energy.
• Transfer of energy from accessory pigments to reaction centre.
• Activation of Chlorophyll 'a' molecule.

ii. Photo Chemical Phase:

• Photolysis of water and oxygen evolution
• Electron transport and synthesis of assimilatory power.

2. Dark reaction (Biosynthetic phase):

- Fixation and reduction of CO_2 into carbohydrates with the help of assimilatory power produced during light reaction. This reaction does not require light and is not directly light driven. Hence, it is called as Dark reaction or Calvin-Benson cycle (Figure 13.10).

Photo-Oxidation Phase of Light Reaction

- The action of photon plays a vital role in excitation of pigment molecules to release an electron. When the molecules absorb a photon, it is in excited state. When the light source turned off, the high energy electrons return to their normal low energy orbitals as the excited molecule goes back to its original stable condition known as ground state. When molecules absorb or emit light they change their electronic state. Absorption of blue light excites the chlorophyll to higher energy state than absorption of Red light, because the energy of photon is higher when their wavelength is shorter. When the pigment molecule is in an excited state, this excitation energy is utilised for the phosphorylation. Phosphorylation takes place with the help of light generated electron and hence it is known as photophosphorylation.

Fluorescence and Phosphorescence

- Normal state of an atom or molecule is called ground state. When a photon of light collides with the chlorophyll molecule, an electron from outer most orbit is moved to higher energy orbit causing excitation of chlorophyll. This is known as excited state. There are three excited states such as:

1. First singlet state (S1)
2. Second singlet state (S2)
3. First Triplet Sate (T1)

- When a red light strikes chlorophyll molecule, one electron is released from its ground level (S0) to first singlet state (S1). It is in unstable state having half-life period of 10-9 seconds. When a blue light strikes chlorophyll molecule, one electron is released from its ground level (S0) to second singlet state (S2). It is because blue light has shorter wavelength and more energy than red light. This state is also unstable having half-life period of less than 10–12 seconds. Both S1 and S2 states being unstable move to ground state S0 by releasing energy through the several possible ways.

i. Fluorescence

- The electron from first singlet state (S1) returns to ground state (S0) by releasing energy in the form of radiation energy (light) in the red region and this is known as fluorescence. Fluorescence is the immediate emission of absorbed radiations (Figure 13.11). Pathway of electron during fluorescence: $S_1 \rightarrow S_0$

ii. Phosphorescence

- Electron from Second Singlet State (S2) may return to next higher energy level (S1) by losing some of its extra energy in the form of heat. From first singlet state (S1) electron further drops to first triplet state (T1). Triplet State is unstable having half life time of 10-3 seconds and electrons returns to ground state with emission of light in red region called as phosphorescence (Figure 13.11). Phosphorescence is the delayed emission of absorbed radiations. Pathway of electron during Phosphorescence:

Photosystem and Reaction Centre

- ❖ Thylakoid membrane contains Photosystem I (PS I) and Photosystem II (PS II).
- ❖ PS I is in un stacked region of granum facing stroma of chloroplast.
- ❖ PS II is found in stacked region of thylakoid membrane facing lumen of thylakoid.
- ❖ Each Photosystem consists of central core complex (CC) and light harvesting Complex (LHC) or Antenna molecules (Figure 13.12)
- ❖ The core complex consists of respective reaction centre associated with proteins, electron donors and acceptors.

❖ PS I – CC I consists of reaction centre P700 and LHC I

❖ PS II – CC II consists of reaction centre P680 and LHC II (Table 13.2).

❖ Light Harvesting Complex consists of several chlorophylls, carotenoids and xanthophyll molecules.

❖ The main function of LHC is to harvest light energy and transfer it to their respective reaction centre.

Photosystem I	Photosystem II
1. The reaction centre is P700	1. Reaction centre is P6890
2. PS I is involved in both cyclic and non-cyclic.	2. PS II participates in Non – cyclic pathway
3. Not involved in photolysis of water and evolution of oxygen	3. Photolysis of water and evolution of oxygen take place.
4. It receives electrons from PS II during non-cyclic photophosphorylation	4. It receives electrons by photolysis of water
5. Located in un stacked region granum facing chloroplast stroma	5. Located in stacked region of thylakoid membrane facing lumen of thylakoid.
6. Chlorophyll and Carotenoid ratio is 20 to 30: 1	6. Chlorophyll and Carotenoid ratio is 3 to 7:1

Photochemical phase of light reaction

- In this phase electrons pass through electron carrier molecules and generate assimilatory powers ATP and NADPH 1 H1. Splitting of water molecule generates electrons replacing electrons produced by the light.

Photolysis of Water

- The process of Photolysis is associated with Oxygen Evolving Complex (OEC) or water splitting complex in pigment system II and is catalysed by the presence of Mn^{++} and Cl^{-}. When the pigment system II is active it receives light and the water molecule splits into OH^{-} ions and H1 ions. The OH^{-}ions unite to form water molecules again and release O2 and electrons. Photolysis of water is due to strong oxidant which is yet unknown and designated as Z or Yz. Widely accepted theory proposed by Kok et al.,(1970) explaining photo-oxidation of water is water oxidizing clock (or) S′ State Mechanism. It consists of a series of 5 states called as S_0, S_1, S_2, S_3 and S_4. Each state acquires positive charge by a photon (hv) and after the S4 state it acquires 4 positive charges, four electrons and evolution of oxygen. Two molecules of water go back to the S0. At the end of photolysis 4 H^+,4 e^- and O2 are evolved from water (Figure 13.13).

Oxygen Evolving Comlplex (OEC)

$$4\,H_2O \longrightarrow 4\,H^+ + 4\,OH^-$$
$$4\,OH^- \longrightarrow 2\,H_2O + O_2 + 4\,e^-$$
$$2H_2O \longrightarrow 4\,H^+ + O_2 + 4\,e^-$$

Electron Transport Chain of Chloroplast

Electron transport chain in each photosystem involves four complexes:

- ❖ Core Complex (CC): CC I in PS I the reaction centre is P700, CC II in PS II the reaction centre is P680
- ❖ Light Harvesting Complex or Antenna complex (LHC):
- ❖ Two types: LHC I in PS I and LHC II in PS II.
- ❖ Cytochrome b6 f complex: It is the non-pigmented protein complex connecting PS I and PS II. Plastoquinone (PQ) and Plastocyanin (PC) are intermediate complexes acting as mobile or shuttle electron carriers of Electron Transport Chain. PQ acts as utilizes energy from ETC and converts ADP and inorganic phosphate (Pi) into ATP (Figure 13.14).

Photophosphorylation

- Phosphorylation taking place during respiration is called as oxidative phosphorylation and ATP produced by the breakdown of substrate is known as substrate level phosphorylation. In this topic, we are going to learn about phosphorylation taking place in chloroplast with the help of light. During the movement of electrons through carrier molecules ATP and NADPH + H^+ are produced. Phosphorylation is the process of synthesis of ATP by the addition of inorganic phosphate to ADP. The addition of phosphate here takes place with the help of light generated electron and so it is called as photophosphorylation. It takes place in both cyclic and non-cyclic electron transport.

Cyclic Photophosphorylation

- Cyclic photophosphorylation refers to the electrons ejected from the pigment system I (Photosystem I) and again cycled back to the PS I. When the photons activate P700 reaction centre photosystem II is activated. Electrons are raised to the high energy level. The primary electron acceptor is Ferredoxin Reducing Substance (FRS) which transfers electrons to Ferredoxin (Fd), Plastoquinone (PQ), cytochrome b6-f complex, Plastocyanin (PC) and finally back to chlorophyll P700 (PS I). During this movement of electrons Adenosine Di Phosphate (ADP) is phosphorylated, by the addition of inorganic phosphate and generates Adenosine Tri Phosphate (ATP). Cyclic electron transport produces only ATP and there is no NADPH + H+ formation. At each step of electron transport, electron loses potential energy and is used by the transport chain to pump H1 ions across the thylakoid membrane. The proton gradient triggers ATP formation in ATP synthase enzyme situated on the thylakoid membrane. Photosystem I need light of longer wave length (> P700 nm). It operates under low light intensity, less CO2 and under anaerobic conditions which makes it considered as earlier in evolution (Figure 13.15).

Non-Cyclic Photophosphorylation

- When photons are activated reaction centre of pigment system II(P680), electrons are moved to the high energy level. Electrons from high energy state passes through series of electron carriers like pheophytin, plastoquinone, cytochrome complex, plastocyanin and finally accepted by PS I (P700). During this movement of electrons from PS II to PS I ATP is generated (Figure 13. 16). PS I (P700) is activated by light, electrons are moved to high energy state and accepted by electron acceptor molecule ferredoxin reducing Substance (FRS). During the downhill movement through ferredoxin, electrons are transferred to NADP1 and reduced into NADPH 1 H1 (H1 formed from splitting of water by light).

- Electrons released from the photosystem II are not cycled back. It is used for the reduction of NADP1 in to NADPH 1 H1. During the electron transport it generates ATP and hence this type of photophosphorylation is called non-cyclic photophosphorylation. The electron flow looks like the appearance of letter 'Z' and so known as Z scheme. When there is availability of NADP1 for reduction and when there is splitting of water molecules both PS I and PS II are activated (Table 13.3). Non-cyclic electron transport PS I and PS II both are involved co-operatively to transport electrons from water to NADP1 (Figure 13.6). In oxygenic species non-cyclic electron transport takes place in three stages.

i. **Electron transport from water to P680:** Splitting of water molecule produce electrons, protons and oxygen. Electrons lost by the PS II (P680) are replaced by electrons from splitting of water molecule.

ii. **Electron transport from P680 to P700**: Electron flow starts from P680 through a series of electron carrier molecules like pheophytin, plastoquinone (PQ), cytochrome b6-f complex, plastocyanin (PC) and finally reaches P700 (PS I).

iii. **Electron transport from P700 to $NADP^+$**: PS I(P700) is excited now and the electrons pass to high energy level. When electron travels downhill through ferredoxin, $NADP^+$ is reduced to $NADPH + H^+$.

Bio energetics of light reaction

- To release one electron from pigment system it requires two quanta of light.

- One quantum is used for transport of electron from water to PS I.

❖ Second quantum is used for transport of electron from PS I to $NADP^+$

❖ Two electrons are required to generate one $NADPH + H^+$.

❖ During Non-Cyclic electron transport two $NADPH + H^+$ are produced and it requires 4 electrons.

❖ Transportation of 4 electrons requires 8 quanta of light.

Cyclic Photophosphorylation	Non-Cyclic Photophosphorylation
1. PS I only involved	1. PS I and PS II involved
2. Reaction centre is P700	2. Reaction centre is P680
3. Electrons released are cycled back	3. Electron released are not cycled back
4. Photolysis of water does not take place	4. Photolysis of water takes place
5. Only ATP synthesized	5. ATP and NADPH + H+ are synthesized
6. Phosphorylation takes place at two places	6. Phosphorylation takes place at only one place
7. It does not require and external electron donor	7. Requires external electron donor like H2O or H2S
8. It is not sensitive to dichloro dimethyl urea (DCMI)	8. It is sensitive to DCMI and inhibits electron flow

Chemiosmotic Theory

- Chemiosmotic theory was proposed by P. Mitchell (1966). According to this theory electrons are transported along the membrane through PS I and PS II and connected by Cytochrome b6-f complex. The flow of electrical current is due to difference in electrochemical potential of protons across the membrane. Splitting of water molecule takes place inside the membrane. Protons or H^+ ions accumulate within the lumen of the thylakoid (H+ increase 1000 to 2000 times). As a result, proton concentration is increased inside the thylakoid lumen. These protons move across the membrane because the primary acceptor of electron is located outside the membrane. Protons in stroma less in number and creates a proton gradient. This gradient is broken down due to the movement of proton across the membrane to the stroma through CF_O of the ATP synthase enzyme. The proton motive force created inside the lumen of thylakoid or chemical gradient of H^+ ion across the membrane stimulates ATP generation (Figure 13.17).

- The evolution of one oxygen molecule (4 electrons required) requires 8 quanta of light. C_3 plants utilise 3 ATPs and 2 NADPH + H^+ to evolve one Oxygen molecule. To evolve 6 molecules of Oxygen 18 ATPs and 12 NADPH + H^+ are utilised. C_4 plants utilise 5 ATPs and 2 NADPH + H^+ to evolve one oxygen molecule. To evolve 6 molecules of Oxygen 30 ATPs and 12 NADPH + H^+ are utilised.

Dark Reaction or C3 Cycle or Biosynthetic phase or Photosynthetic Carbon Reduction (PCR) cycle

- Biosynthetic phase of photosynthesis utilises assimilatory powers (ATP and NADPH + H^+) produced during light reaction are used to fix and reduce carbon dioxide into carbohydrates. This reaction does not require light. Therefore, it is named Dark reaction. Ribulose 1,5 bisphosphate (RUBP) act as acceptor molecule of carbon dioxide and fix the CO2 by RUBISCO enzyme. The first product of the pathway is a 3- carbon compound (Phospho Glyceric Acid) and so it is also called as C3 Cycle. It takes place in the stroma of the chloroplast. M. Melvin Calvin, A.A. Benson and their co-workers in the year 1957 found this path way of carbon fixation. Melvin Calvin was awarded Nobel Prize for this in 1961 and this pathway named after the discoverers as Calvin-Benson Cycle. Dark reaction is temperature dependent and so it is also called thermo-chemical reaction. Dark reaction consists of three phases: (Figure 13.18).

1. Carboxylation (fixation)
2. Reduction (Glycolytic Reversal)
3. Regeneration

Phase 1- Carboxylation (Fixation)

- The acceptor molecule Ribulose 1,5 Bisphosphate (RUBP) a 5 carbon compound with the help of RUBP carboxylase oxygenase (RUBISCO) enzyme accepts one molecule of carbon dioxide to form an unstable 6 carbon compound. This 6C compound is broken down into two molecules of 3-carbon compound phosphor glyceric acid (PGA) (Figure 13.19).

$$RUBP + CO_2 \xrightarrow{\text{Rubisco}} \text{2 molecules PGA}$$

Phase 2 – Glycolytic Reversal /Reduction

- Phospho glyceric acid is phosphorylated by ATP and produces 1,3 bis phosphor glyceric acid by PGA kinase. 1,3 bis phosphor glyceric acid is reduced to glyceraldehyde 3 Phosphate (G-3-P) by using the reducing power NADPH 1 H1. Glyceraldehyde 3 phosphate is converted into its isomeric form dihydroxy acetone phosphate (DHAP).

$$PGA \xrightarrow[\text{ATP} \rightarrow \text{ADP}]{\text{PGA Kinase}} \text{1,3 bisphosphoglyceric acid}$$

$$\text{1,3 bisphosphoglceric acid} \xrightarrow{NADPH + H^+ \rightarrow NADP^+} \text{Glyceraldehyde-3-Phosphate}$$

Phase 3 – Regeneration

- Regeneration of RUBP involves the formation of several intermediate compounds of 6-carbon, 5-carbon, 4-carbon and 7- carbon skeleton. Fixation of one carbon dioxide requires 3 ATPs and 2 NADPH 1 H1, and for the fixation of 6 CO2 requires 18 ATPs and 12 NADPH 1 H1 during C3 cycle. One 6 carbon compound is the net gain to form hexose sugar.

$$RU5P \xrightarrow{ATP \rightarrow ADP} RUBP$$

Overall equation for dark reaction:

$$6CO_2 + 18ATP + 12NADPH + H^+ \longrightarrow C_6H_{12}O_6 + 6H_2O + 18ADP + 18Pi + 12NADP^+$$

RUBISCO – RUBP
Carboxylase Oxygenase enzyme, is the most abundant protein found on earth. It constitutes 16 % of the chloroplast protein. It acts as carboxylase in the presence of CO^2 and oxygenase in the absence of CO^2.

Hatch & Slack Pathway or C_4 Cycle or Dicarboxylic Acid Pathway or Dicarboxylation Pathway

- Till 1965, Calvin cycle is the only pathway for CO_2 fixation. But in 1965, Kortschak, Hart and Burr made observations in sugarcane and found C_4 or dicarboxylic acid pathway. Malate and aspartate are the major labelled products. This observation was confirmed by Hatch & Slack in 1967. This alternate pathway for the fixation of CO_2 was found in several tropical and sub-tropical grasses and some dicots. C_4 cycle is discovered in more than 1000 species. Among them 300 species belong to dicots and rest of them are monocots. C_4 plants represent about 5% of Earth's plant biomass and 1% of its known plant species. Despite this scarcity, they account for about 30% of terrestrial carbon fixation. Increasing the proportion of C_4 plants on earth could assist bio sequestration of CO_2 and represent an important climate change avoidance strategy.
- C_4 pathway is completed in two phases, first phase takes place in stroma of mesophyll cells, where the CO_2 acceptor molecule is 3-Carbon compound, phosphor enol pyruvate (PEP) to form 4-carbon Oxalo acetic acid (OAA). The first product is a 4-carbon and so it is named as C_4 cycle. oxalo acetic acid is a dicarboxylic acid and hence this cycle is also known as dicarboxylic acid pathway (Figure 13.20). Carbon dioxide fixation takes place in two places one in mesophyll and another in bundle sheath cell (dicarboxylation pathway). It is the adaptation of tropical and sub-tropical plants growing in warm and dry conditions. Fixation of CO_2 with minimal loss is due to absence of photorespiration. C_4 plants require 5 ATP and 2 NADPH + H^+ to fix one molecule of CO_2.

Stage: I Mesophyll Cells

$$\text{Phosphoenol Pyruvate (PEP) (3C)} + CO_2 \xrightarrow{\text{PEP carboxylase}} \text{Oxaloacetic acid (OAA) (4C)}$$

- Oxaloacetic acid (OAA) is converted into malic acid or aspartic acid and is transported to the bundle sheath cells through plasmodesmata.

Stage: II Bundle Sheath Cells

- Malic acid undergoes decarboxylation and produces a 3 carbon compound Pyruvic acid and CO2. The released CO2 combines with RUBP and follows the calvin cycle and finally sugar is released to the phloem. Pyruvic acid is transported to the mesophyll cells.

$$\underset{(5C)}{\text{RUBP}} + CO_2 \xrightarrow{\text{Rubisco}} \underset{(3C)}{\text{2 PGA}}$$

- **Kranz Anatomy:** It is the German term meaning a halo or wreath. In C_4 plants vascular bundles are surrounded by a layer of bundle sheath. Bundle sheath is surrounded by a ring of mesophyll cells. The characteristic feature of C_4 plants is the presence of dimorphic chloroplast:
- **Bundle sheath chloroplast**: Larger chloroplast, thylakoids not arranged in granum and rich in starch.
- **Mesophull Chloroplast**: Smaller chloroplast, thylakoids arranged in granum and less starch.

Differences between C_3 and C_4 plants	
C_3 Plants	**C_4 Plants**
1. Co^2 fixation takes place in mesophyll cells only	1. CO^2 fixation takes place mesophyll and bundle sheath
2. CO^2 acceptor is RUBP only	2. PEP in mersophyll and RUBP in bundle sheath cells
3. First product is 3C - PGA	3. First product is 4C – OAA
4. Kranz anatomy is not present	4. Kranz anatomy is present

5. Granum is present in mesophyll cells	5. Granum present in mesophyll cells and absent in bundle sheath
6. Normal Chloroplast	6. Dimorphic chloroplast
7. Optimum temperature 20° to 25° C	7. Optimum temperature 30° to 45°C
8. Fixation of CO^2 at 50 ppm	8. Fixation of CO^2 even less than 10 ppm
9. Less efficient due to higher photorespiration	9. More efficient due to less photorespiration
10. RUBP carboxylase enzyme used for fixation	10. Pep carboxylase and RUBP carboxylase used
11. 18 ATPs used to synthesize one glucose	11. Consumes 30 ATPs to produce one glucose.
12. Efficient at low CO^2	12. Efficient at higher CO^2
13. Example: Paddy, Wheat, Potato and so on	Example: Sugar cane, Maize, Sorghum, Amaranthus and so on

Significance of C4 cycle

1. Plants having C_4 cycle are mainly of tropical and sub-tropical regions and
2. are able to survive in environment with low CO_2 concentration.
3. C_4 plants are partially adapted to drought conditions.
4. Oxygen has no inhibitory effect on C_4 cycle since PEP carboxylase is insensitive to O_2.
5. Due to absence of photorespiration, CO_2 Compensation Point for C_4 is lower than that of C_3 plants.

- Differences between C_3 Plants (C_3 cycle) and C_4 Plants (C_4 Cycle) are given in table 13.4.

Crassulacean Acid Metabolism or CAM cycle

- It is one of the carbon pathways identified in succulent plants growing in semi-arid or xerophytic condition. This was first observed in crassulaceae family plants like Bryophyllum, Sedum, Kalanchoe and is the reason behind the name of this cycle. It is also noticed in plants from other families Examples: Agave, Opuntia, Pineapple and

Orchids. The stomata are closed during day and are open during night (Scotoactive).

- This reverse stomatal rhythm helps to conserve water loss through transpiration and will stop the fixation of CO_2 during the day time. At night time CAM plants fix CO_2 with the help of Phospho Enol Pyruvic acid (PEP) and produce oxalo acetic acid (OAA).

- Subsequently OAA is converted into malic acid like C4 cycle and gets accumulated in vacuole increasing the acidity. During the day time stomata are closed and malic acid is decarboxylated into pyruvic acid resulting in the decrease of acidity. CO2 thus formed enters into Calvin Cycle and produces carbohydrates (Figure13.21).

Significance of CAM Cycle

1. It is advantageous for succulent plants to obtain CO_2 from malic acid when stomata are closed.
2. During day time stomata are closed and CO_2 is not taken but continue their photosynthesis.
3. Stomata are closed during the day time and help the plants to avoid transpiration and water loss.

Photorespiration or C_2 Cycle or Photosynthetic Carbon Oxidation (PCO) Cycle

- Respiration is a continuous process for all living organisms including plants. Decker (1959) observed that rate of respiration is more in light than in dark. Photorespiration is the excess respiration taking place in photosynthetic cells due to absence of CO_2 and increase of O_2 (Table 13.5).

- with the help of Phospho Enol Pyruvic acid (PEP) and produce oxalo acetic acid (OAA). Subsequently OAA is converted into malic acid like C4 cycle and gets accumulated in vacuole increasing the acidity. During the day time stomata are closed and malic acid is decarboxylated into pyruvic acid resulting in the decrease of acidity. CO2 thus formed enters into Calvin Cycle and produces carbohydrates (Figure13.21).

Significance of CAM Cycle

1. It is advantageous for succulent plants to obtain CO2 from malic acid when stomata are closed.
2. During day time stomata are closed and CO2 is not taken but continue their photosynthesis.
3. Stomata are closed during the day time and help the plants to avoid transpiration and water loss.

Photorespiration or C^2 cycle or Photosynthetic Carbon Oxidation (PCO) Cycle

- Respiration is a continuous process for all living organisms including plants. Decker (1959) observed that rate of respiration is more in light than in dark. Photorespiration is the excess respiration taking place in photosynthetic cells due to absence of CO_2 and increase of O_2. This condition changes the carboxylase role of RUBISCO into oxygenase. C_2 Cycle takes place in chloroplast, peroxisome and mitochondria. RUBP is converted into PGA and a 2C-compound phosphoglycolate by Rubisco enzyme in chloroplast. Since the first product is a 2C-compound, this cycle is known as C_2 Cycle. Phosphoglycolate by loss of phosphate becomes glycolate. Glycolate formed in chloroplast enters into peroxisome to form glyoxylate and hydrogen peroxide. Glyoxylate is converted into glycine and transferred into mitochondria.

- In mitochondria, two molecules of glycine combine to form serine. Serine enters into peroxisome to form hydroxy pyruvate. Hydroxy pyruvate with help of NADH + H^+ becomes glyceric acid. Glyceric acid is cycled back to chloroplast utilising ATP and becomes Phosphoglyceric acid (PGA) and enters into the Calvin cycle (PCR cycle). Photorespiration does not yield any free energy in the form of ATP. Under certain conditions 50% of the photosynthetic potential is lost because of Photorespiration (Figure 13.22).

Significance of photorespiration

1. Glycine and Serine synthesised during this process are precursors of many biomolecules like chlorophyll, proteins, nucleotides.
2. It consumes excess NADH 1 H1 generated.

3. Glycolate protects cells from Photo oxidation.

Carbon Dioxide Compensation Point

- When the rate of photosynthesis equals the rate of respiration, there is no exchange of oxygen and carbon dioxide and this is called as carbon dioxide compensation point. This will happen at particular light intensity when exchange of gases becomes zero. When light is not a limiting factor and atmospheric CO_2 concentration is between 50 to 100 ppm the net exchange is zero.

Differences between Photorespiration and Dark Respiration	
Photorespiration	**Dark respiration**
1. It takes place in photosynthetic green cells	1. It takes place in all living cells
2. It takes place only in the presence of light	2. It takes place all the time
3. It involves chloroplast, peroxisome and mitochondria	3. It involves only mitochondria
4. It does not involve Glycolysis, Kreb's Cycle and ETS	4. It involves glycolysis, Kreb's Cycle and ETS
5. Substrate is glycolic acid	5. Substrate is carbohydrates, protein or fats
6. It is not essential for survival	6. Essential for survival
7. No phosphorylation and yield of ATP	7. Phosphorylation produces ATP energy
8. $NADH_2$ is oxidized to NAD^+	8. NAD^+ us reduced to $NADH^2$
9. Hydrogen peroxide is produced	9. Hydrogen peroxide is not produced
10. End products are CO_2 and PGA	10. End products are CO_2 and water

Factors affecting Photosynthesis

- In 1860, Sachs gave three cardinal points theory explaining minimum, optimum and maximum factors that control photosynthesis. In 1905, Blackman put forth the importance of smallest factor. Blackman's law of limiting factor is actually a modified Law proposed by Liebig's Law of minimum. According to Blackman, "When a process is conditioned as to its rapidity by a number of separate factors, the rate of the process is limited by the pace of the lowest factor". To conclude in an easy way "at any given point of time the lowest factor among essentials will limit the rate of photosynthesis". For example, when even sufficient light intensity is available, photosynthesis may be low due to low CO_2 in the atmosphere. Here, CO_2 acts as a limiting factor. If CO_2 is increased in the atmosphere the rate of photosynthesis also increases. Further increase in photosynthesis is possible only if the available light intensity is also increased proportionately (Figure 13.23).

- Factors affecting photosynthesis are further grouped into External or Environmental factors and Internal factors.

I. External factors: Light, carbon dioxide, temperature, water, mineral and pollutants.

II. Internal factors: Pigments, protoplasmic factor, accumulation of carbohydrates,
anatomy of leaf and hormones.

External factors

1. Light: Energy for photosynthesis comes only from light. Photooxidation of water and excitation of pigment molecules are directly controlled by light. Stomatal movement leading to diffusion of CO_2 is indirectly controlled by light.

a. **Intensity of Light:** Intensity of light plays a direct role in the rate of photosynthesis. Under low intensity the photosynthetic rate is low and at higher intensity photosynthetic rate is higher. It also depends on the nature of plants. Heliophytes (Bean Plant) require higher intensity than Sciophytes (Oxalis).

b. **Quantity of Light:** In plants which are exposed to light for longer duration (Long day Plants) photosynthetic rate is higher.

c. **Quality of light:** Different wavelengths of light affect the rate of photosynthesis because pigment system does not absorb all the rays equally. Photosynthetic rate is maximum in blue and red light. Photosynthetically Active Radiation (PAR) is between 400 to

700 nm. Red light induces highest rate of photosynthesis and green light induces lowest rate of photosynthesis.

2. Carbon dioxide

- CO_2 is found only 0.3 % in the atmosphere but plays a vital role. Increase in concentration of CO2 increases the rate of photosynthesis (CO_2 concentration in the atmosphere is 330 ppm). If concentration is increased beyond 500ppm, rate of photosynthesis will be affected showing the inhibitory effect.

3. Oxygen: The rate of photosynthesis decreases when there is an increase of oxygen concentration. This Inhibitory effect of oxygen was first discovered by Warburg (1920) using green algae Chlorella.

4. Temperature: The optimum temperature for photo synthesis varies from plant to plant. Temperature is not uniform in all places. In general, the optimum temperature for photosynthesis is 25oC to 35°C. This is not applicable for all plants. The ideal temperature for plants like Opuntia is 55oC, Lichens 20oC and Algae growing in hot spring photosynthesis is 75°C. Whether high temperature or low temperature it will close the stomata as well as inactivate the enzymes responsible for photosynthesis (Figure 13. 24).

5. Water: Photolysis of water provides electrons and protons for the reduction of NADP, directly. Indirect roles are stomatal movement and hydration of protoplasm. During water stress, supply of NADPH 1 H1 is affected.

6. Minerals: Deficiency of certain minerals affect photosynthesis e.g. mineral involved in the synthesis of chlorophyll (Mg, Fe and N), Phosphorylation reactions (P), Photolysis of water (Mn and Cl), formation of plastocyanin (Cu).

7. Air pollutants: Pollutants like SO2, NO2, O3 (Ozone) and Smog affects rate of photosynthesis.

Internal Factors

1. Photosynthetic Pigments: It is an essential factor and even a small quantity is enough to carry out photosynthesis.

2. Protoplasmic factor: Hydrated protoplasm is essential for photosynthesis. It also includes enzymes responsible for Photosynthesis.

3. Accumulation of Carbohydrates : Photosynthetic end products like carbohudrates are accumulated in cells and if translocation of carbohudrates is slow then this will affect the rate of photosynthesis.

4. Anatomy of leaf: Thickness of cuticle and epidermis, distribution of stomata, presence or absence of Kranz anatomy and relative proportion of photosynthetic cells affect photosynthesis.

5. Hormones: Hormones like gibberellins and cytokinin increase the rate of photosynthesis.

Difference between photosynthesis in plants and photosynthesis in bacteria	
Photosynthesis in Plants	**Photosynthesis in Bacteria**
1. Cyclic and non – cycle phosphorylation	1. Only cyclic phosphorylation takes place
2. Photosystem I and II involved	2. Photosystem I only involved
3. Electron donor is water	3. Electron donor is H2S
4. Oxygen is evolved	4. Oxygen is not evolved
5. Reaction centres are P700 and P680	5. Reaction centre is P_{870}
6. Reducing agent is NADPH+H+	6. Reducing agent is NADH + H+
7. PAR is 400 to 700 nm	7. PAR is above 700 nm
8. Chlorophyll, carotenoid and xanthophyll	8. Bacterio chlorophyll and bacterio viridin
9. Photosynthetic apparatus – chloroplast	9. It is chlorosomes and chromatophores

Photosynthesis in bacteria

- Though we study about bacterial photosynthesis as the last part, bacterial photosynthesis formed first and foremost in evolution. Bacteria does not have specialized structures like chloroplast. It has a simple type of photosynthetic apparatus called chlorosomes and chromatophores (Table 13.6). Van Neil (1930) discovered a bacterium that releases sulphur instead of oxygen during photosynthesis. Here, electron donor is hydrogen sulphide (H2S) and only one photosystem is involved (PS I) and the reaction centre is P870. Pigments present in bacteria are bacteriochlorophyll a, b, c, d, e and g and carotenoids. Photosynthetic bacteria are classified into three groups:

1. Green sulphur bacteria. Example: Chlorobacterium and Chlorobium.

2. Purple sulphur bacteria. Example: Thiospirillum and Chromatium.

3. Purple non-sulphur bacteria. Example: Rhodopseudomonas and Rhodospirllum.

Summary

- Photosynthesis is an oxidation and reduction process. It has two phases: the light reaction and dark reaction. During light reaction water is oxidised to release O2 and during dark reaction $CO^2$is reduced to form sugars. Solar energy is trapped by pigment system I and pigment system II. P700 and P680 act as reaction centres for PS I and PS II respectively. Splitting of water molecule (Photolysis) produces electrons, protons and oxygen. Photophosphorylation takes place through cyclic and non-cyclic mechanisms and generates energy and reducing power. Dark reaction or biosynthetic phase of photosynthesis use the products of light energy (ATP and NADPH 1 H1) and carbon dioxide is reduced to Carbohydrates. Carbon pathway in C3 cycle has RUBP as the acceptor molecule and the first product is PGA (3C). Carbon pathway in C4 plants involves mesophyll and bundle sheath cells, Kranz anatomy. Dimorphic chloroplast, no photorespiration, acceptor molecule as PEP and first product as OAA (4C) are some of the unique characters of C4 cycle. C2 Cycle or photorespiration is operated when less amount of CO2 is used for reduction and O2 increases.

- Rubisco starts to play oxygenase role. Succulent and xerophytic plants show reverse stomatal rhythm as they open during night time and close during day time and follow CAM cycle. Night time produces malic acid and during day time malate is converted into pyruvate and produces CO2 which is reduced to carbohydrates.

- Photosynthesis is affected by internal and external factors. Bacterial photosynthesis is the primitive type of photosynthesis and it involves only photosystem I.

Unit V Plant Physiology (Functional Organisation)

14. Respiration

Plant and Animal Interdependence

In biosphere, plants and animals are complementary systems which are integrated to sustain life. In plants, oxygen enters through the stomata and it is transported to cells, where oxygen is utilized for energy production. Plants require carbon dioxide to survive, to produce carbohydrates and to release oxygen through photosynthesis. These oxygen molecules are inhaled by human through the nose, which reaches the lungs where oxygen is transported through the blood and it reaches cells. Cellular respiration takes place inside the cell. A specialized respiratory system is present in animals but is absent in plants for delivering oxygen inside the cell. But the cellular respiration stages are similar in both plants and animals which hint at evolutionary divergence.

- If you are sleeping under a tree during night time you will feel difficulty in breathing. During night, plants take up oxygen and release carbon dioxide and as a result carbon dioxide will be abundant around the tree. This process of CO_2 evolution is called respiration. This process takes place during day time also (Figure 14.1). It is accompanied by breakdown of substrates and release of energy. In this chapter, respiration process in plants at cellular level will be dealt with.

Gaseous Exchange

Respiration

- The term respiration was coined by Pepys (1966). Respiration is a biological process in which oxidation of various food substances like carbohydrates, proteins and fats take place and as a result of this, energy is produced where O_2 is taken in and CO_2 is liberated. The organic substances which are oxidized during respiration are called respiratory substrates. Among these, glucose is the commonest respiratory substrate. Breaking of C-C bonds of complex organic compounds through oxidation within the cells leads to energy release. The energy released during respiration is stored in the form of ATP (Adenosine Tri Phosphate) as well as liberated heat. Respiration occurs in all the living cells of organisms. The overall process of respiration corresponds to a reversal of photosynthesis.

$$C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O + \text{Energy}$$
$$\text{(686 K cal or 2868 KJ)}$$

- Depending upon the nature of respiratory substrate, Blackman divided respiration into,

1. Floating respiration
2. Protoplasmic respiration

- When carbohydrate or fat or organic acid serves as respiratory substrate and it is called floating respiration. It is a common mode of respiration and does not produce any toxic product. Whereas respiration utilizing protein as a respiratory substrate, it is called protoplasmic respiration. Protoplasmic respiration is rare and it depletes structural and functional proteins of protoplasm and liberates toxic ammonia.

Compensation point

- At dawn and dusk the intensity of light is low. The point at which CO_2 released in respiration is exactly compensated by CO_2 fixed in photosynthesis that means no net gaseous exchange takes place, it is called compensation point. At this moment, the amount of oxygen released from photosynthesis is equal to the amount of oxygen utilized in respiration.

- The two common factors associated with compensation point are CO_2 and light (Figure 14.2). Based on this there are two types of compensation point. They are CO_2 compensation point and light compensation point. C_3 plants have compensation points ranging from 40-60 ppm (parts per million) CO_2 while those of C_4 plants ranges from 1-5 ppm CO_2.

Structure of ATP

- Respiration is responsible for generation of ATP. The discovery of ATP was made by Karl Lohman (1929). ATP is a nucleotide consisting of a base-adenine, a pentose sugar-ribose and three phosphate groups. Out of three phosphate groups the last two are attached by high energy rich bonds (Figure 14.3). On hydrolysis, it releases energy (7.3 K cal or 30.6 KJ/ATP) and it is found in all living cells and hence it is called universal energy currency of the cell. ATP is an instant source of energy within the cell. The energy contained in ATP is used in synthesis carbohydrates, proteins and lipids. The energy transformation concept was established by Lipman (1941).

ATP is not only higher energy compound present in a cell. There are other higher energy compounds also present. Example GTP (Guanosine Tri Phosphate) and UTP (Uridine Tri Phosphate).

Redox Reactions

$NAD^{+} + 2e^{-} + 2H^{+} \rightarrow NADH + H+$

$FAD + 2e^{-} + 2H^{+} \rightarrow FADH^{2}$

- When NAD+ (Nicotinamide Adenine Dinucleotide-oxidised form) and FAD (Flavin Adenine Dinucleotide) pick up electrons and one or two hydrogen ions (protons), they get reduced to NADH 1 H1 and FADH2 respectively. When they drop electrons and hydrogen off they go back to their original form. The reaction in which NAD1 and FAD gain (reduction) or lose (oxidation) electrons are called redox reaction (Oxidation reduction reaction). These reactions are important in cellular respiration.

Types of Respiration: Respiration is classified into two types as aerobic and anaerobic respiration (Figure 14.4)

14.4.1 Aerobic respiration

- Respiration occurring in the presence of oxygen is called aerobic respiration. During aerobic respiration, food materials like carbohydrates, fats and proteins are completely oxidised into CO_2,

H_2O and energy is released. Aerobic respiration is a very complex process and is completed in four major steps:

1. Glycolysis
2. Pyruvate oxidation (Link reaction)
3. Krebs cycle (TCA cycle)
4. Electron Transport Chain (Terminal oxidation).

Anaerobic respiration

- In the absence of molecular oxygen glucose is incompletely degraded into either ethyl alcohol or lactic acid (Table 14.1). It includes two steps:

1. Glycolysis
2. Fermentation

Stages of Respiration

1. Glycolysis-conversion of glucose into pyruvic acid in cytoplasm of cell.
2. Link reaction-conversion of pyruvic acid into acetyl coenzyme-A in mitochondrial matrix.
3. Krebs cycle-conversion of acetyl coenzyme A into carbon dioxide and water in the mitochondrial matrix.
4. Electron transport chain and oxidative phosphorylation remove hydrogen atoms from the products of glycolysis, link reaction and Krebs cycle release water molecule with energy in the form of ATP in mitochondrial inner membrane (Figure 14.5).

Differences between aerobic and anaerobic respiration	
Aerobic respiration	**Anaerobic Respiration**
1. It occurs in all living cells of higher organisms.	1. It occurs yeast and some bacteria.
2. It requires oxygen for breaking the respiratory substrate.	2. Oxygen is not required from breaking the respiratory substrate.
3. The end products are CO2 and H2O	3. The end products are alcohol, and CO2 (or) lactic acid.
4. Oxidation of one molecule of	4. Only 2 ATP molecules are

glucose produces, 36 ATP molecules.	produced.
5. It consists of four stages – glycolysis, link reaction, TCA cycle and electron	5. It consists of two stages- glycolysis and fermentation.
6. It occurs in cytoplasm and mitochondria.	6. It occurs only in cytoplasm.

Glycolysis (Gr: Glykos 5 Glucose, Lysis 5 Splitting)

- ❖ Glycolysis is a linear series of reactions in which 6-carbon glucose is split into two molecules of 3-carbon pyruvic acid. The enzymes which are required for glycolysis are present in the cytoplasm (Figure 14.6).
- ❖ The reactions of glycolysis were worked out in yeast cells by three scientists Gustav Embden (German), Otto Meyerhoff (German) and J Parnas (Polish) and so it is also called as EMP pathway. It is the first and common stage for both aerobic and anaerobic respiration. It is divided into two phases.

1. **Preparatory phase** or endergonic phase or hexose phase (steps 1-5).

2. **Pay off phase** or oxidative phase or exergonic phase or triose phase (steps 6-10).

1. Preparatory phase

- Glucose enters the glycolysis from sucrose which is the end product of photosynthesis. Glucose is phosphorylated into glucose-6-phosphate by the enzyme hexokinase, and subsequent reactions are carried out by different enzymes (Figure 14.6). At the end of this phase fructose-1, 6 - bisphosphate is cleaved into glyceraldehyde-3-phosphate and dihydroxy acetone phosphate by the enzyme aldolase. These two are isomers. Dihydroxy acetone phosphate is isomerised into glyceraldehyde-3- phosphate by the enzyme triose phosphate isomerase, now two molecules of glyceraldehyde 3 phosphate enter into pay off phase. During preparatory phase two ATP molecules are consumed in step-1 and step-3 (Figure 14.6).

2. Pay off phase

- Two molecules of glyceraldehyde-3- phosphate oxidatively phosphorylated into two molecules of 1,3 - bisphospho glycerate. During this reaction 2NAD+ is reduced to 2NADH + H+ by glyceraldehyde- 3- phosphate dehydrogenase at step 6. Further reactions are carried out by different enzymes and at the end two molecules of pyruvate are produced. In this phase, 2ATPs are produced at step 7 and 2 ATPs at step10 (Figure 14.6). Direct transfer of phosphate moiety from substrate molecule to ADP and is converted into ATP is called substrate phosphorylation or direct phosphorylation or trans phosphorylation. During the reaction at step 9, 2phospho glycerate dehydrated into Phospho enol pyruvate a water molecule is removed by the enzyme enolase. As a result, enol group is formed within the molecule. This process is called Enolation.

3. Energy Budget

- In the payoff phase totally 4ATP and 2NADH 1 H1 molecules are produced. Since 2ATP molecules are already consumed in the preparatory phase, the net products in glycolysis are 2ATPs and 2NADH $+H^+$.

The overall net reaction of glycolysis

$C_6 H_{12}O_6$ + 2ADP + 2Pi + $2NAD^+$

2x $CH_3COCOOH$ + 2ATP +2NADH $+2H^+$

Pyruvate Oxidation (Link reaction)

- Two molecules of pyruvate formed by glycolysis in the cytosol enters into the mitochondrial matrix. In aerobic respiration this pyruvate with coenzyme A is oxidatively decarboxylated into acetyl CoA by pyruvate dehydrogenase complex.

- This reaction is irreversible and produces two molecules of NADH 1 H1 and 2CO2. It is also called transition reaction or Link reaction. The reaction of pyruvate oxidation is

$$2x\ CH_3COCOOH + 2NAD^+ + 2CoA$$

$$\downarrow \text{Pyruvate dehydrogenase complex/ } Mg^{++}$$

$$2xCH_3CO.CoA + 2NADH + 2H^+ + 2CO_2\uparrow$$

Pyruvate dehydrogenase complex consist of three distinct enzymes, such as 1. Pyruvate dehydrogenase 2. Dihydrolipoyil transacetylase 3. Dihydrolipoyil dehydrogenase and five different coenzymes, TPP (Thymine Pyro Phosphate), NAD^+, FAD, CoA and lipoate.

Krebs cycle or Citric acid cycle or TCA cycle:

- Two molecules of acetyl CoA formed from link reaction now enter into Krebs cycle. It is named after its discoverer, German Biochemist Sir Hans Adolf Krebs (1937). The enzymes necessary for TCA cycle are found in mitochondrial matrix except succinate dehydrogenase enzyme which is found in mitochondrial inner membrane (Figure 14.7).

Sir Hans Adolf Krebs was born in Germany on 25th August 1900. He was awarded Nobal Prize for his discovery of Citric acid cycle in Physiology in 1953.

- TCA cycle starts with condensation of acetyl CoA with oxaloacetate in the presence of water to yield citrate or citric acid. Therefore, it is also known as Citric Acid Cycle (CAC) or Tri Carboxylic Acid (TCA) cycle. It is followed by the action of different enzymes in cyclic manner. During the conversion of succinyl CoA to succinate by the enzyme succinyl CoA synthetase or succinate thiokinase, a molecule of ATP synthesis from substrate without entering the electron transport chain is called substrate level phosphorylation. In animals a molecule of GTP is synthesized from GDP+Pi. In a coupled reaction GTP is converted to GDP with simultaneous synthesis of ATP from ADP+Pi. In three steps (4, 5, 9) in this cycle NAD+ is reduced to NADH1 H1 and at step 7 (Figure14.8) where FAD is reduced to FADH2. The summary of link reaction and Krebs cycle in Mitochondria is

$$\text{Pyruvic acid} + 4NAD^+ + FAD + 4H_2O + ADP + Pi \xrightarrow{\text{Mitochondrial matrix.}} 3CO_2 + 4NADH + 4H^+ + FADH_2 + H_2O + ATP.$$

- Two molecules of pyruvic acid formed at the end of glycolysis enter into the mitochondrial matrix. Therefore, Krebs cycle is repeated twice for every glucose molecule where two molecules of pyruvic acid produces six molecules of CO2, eight molecules of NADH 1 H1, two molecules of FADH2 and two molecules of ATP.

1. Significance of Krebs cycle:

1. TCA cycle is to provide energy in the form of ATP for metabolism in plants.
2. It provides carbon skeleton or raw material for various anabolic processes.
3. Many intermediates of TCA cycle are further metabolised to produce amino acids, proteins and nucleic acids.
4. Succinyl CoA is raw material for formation of chlorophylls, cytochrome, phytochrome and other pyrrole substances.
5. α-ketoglutarate and oxaloacetate undergo reductive amination and produce amino acids.
6. It acts as metabolic sink which plays a central role in intermediary metabolism.

2. Amphibolic nature

- Krebs cycle is primarily a catabolic pathway, but it provides precursors for various biosynthetic pathways there by an anabolic pathway too. Hence, it is called amphibolic pathway. It serves as a pathway for oxidation of carbohydrates, fats and proteins. When fats are respiratory substrate they are first broken down into glycerol and fatty acid. Glycerol is converted into DHAP and acetyl CoA. This acetyl CoA enters into the Krebs cycle. When proteins are the respiratory substrate they are degraded into amino acids by proteases. The amino acids after deamination enter into the Krebs cycle through pyruvic acid or acetyl CoA and it depends upon the structure. So respiratory intermediates form the link between synthesis as well as breakdown. The citric acid cycle is the final common pathway for oxidation of fuel molecules like amino acids, fatty acids and carbohydrates. Therefore, respiratory pathway is an amphibolic pathway (Figure 14.9).

The synthesis of glucose from certain non-carbohydrate carbon substrates such as proteins and lipids are called gluconeogenesis.

Electron Transport Chain (ETC) (Terminal oxidation)

- During glycolysis, link reaction and Krebs cycle the respiratory substrates are oxidized at several steps and as a result many reduced coenzymes NADH + H^+ and $FADH_2$ are produced. These reduced coenzymes are transported to inner membrane of mitochondria and are converted back to their oxidized forms produce electrons and protons. In mitochondria, the inner membrane is folded in the form of finger projections towards the matrix called cristae. In cristae many oxysomes (F_1 particles) are present which have electron transport carriers are present. According to Peter Mitchell's Chemiosmotic theory this electron transport is coupled to ATP synthesis.

- Electron and hydrogen (proton) transport takes place across four multi-protein complexes (I-IV). They are

1. Complex-I (NADH dehydrogenase).

- It contains a flavoprotein(FMN) and associated with non-heme iron Sulphur protein (Fe-S). This complex is responsible for passing electrons and protons from mitochondrial NADH (Internal) to Ubiquinone (UQ).

$$NADH + H+ +UQ \rightleftharpoons NAD^{+} +UQH_2$$

- In plants, an additional NADH dehydrogenase (External) complex is present on the outer surface of inner membrane of mitochondria which can oxidise cytosolic NADH + H^+. Ubiquinone (UQ) or Coenzyme Quinone (Co Q) is a small, lipid soluble electron, proton carrier located within the inner membrane of mitochondria.

2. Complex-II (Succinic dehydrogenase)

- It contains FAD flavoprotein is associated with non-heme iron Sulphur (Fe-S) protein. This complex receives electrons and protons from succinate in Krebs cycle and is converted into fumarate and passes to ubiquinone.

$$Succinate + UQ \rightarrow Fumarate + UQH_2$$

3. Complex-III (Cytochrome bc_1 complex)

- This complex oxidises reduced ubiquinone (ubiquinol) and transfers the electrons through Cytochrome bc_1 Complex (Iron Sulphur center bc_1 complex) to cytochrome c. Cytochrome c is a small protein attached to the outer surface of inner membrane and act as a mobile carrier to transfer electrons between complex III to complex IV.

$$UQH_2 + 2Cyt\ c_{oxidised} \rightleftharpoons UQ + 2Cyt\ c_{reduced} + 2H^+$$

(A and B) and cytochromes a and a_3. Complex IV is the terminal oxidase and brings about the reduction of 1/2 O_2 to H_2O.Two protons are needed to form a molecule of H_2O (terminal oxidation).

$$2Cyt\ c_{oxidised} + 2H^+ + 1/2\ O_2 \rightleftharpoons 2Cyt\ c_{reduced} + H_2O$$

- The transfer of electrons from reduced coenzyme NADH to oxygen via complexes I to IV is coupled to the synthesis of ATP from ADP and inorganic phosphate (Pi) which is called Oxidative phosphorylation. The F_0F_1-ATP synthase (also called complex V) consists of F0 and F_1. F_1 converts ADP and Pi to ATP and is attached to the matrix side of the inner membrane. F_0 is present in inner membrane and acts as a channel through which protons come into matrix.

- Oxidation of one molecule of NADH + H^+ gives rise to 3 molecules of ATP and oxidation of one molecule $FADH_2$ produces 2 molecules of ATP within a mitochondrion. But cytoplasmic NADH + H^+ yields only two ATPs through external NADH dehydrogenase. Therefore, two reduced coenzyme (NADH + H^+) molecules from glycolysis being extra mitochondrial will yield 2× 2 = 4 ATP molecules instead of 6 ATPs (Figure 14.10). The Mechanism of mitochondrial ATP synthesis is based on Chemiosmotic hypothesis. According to this theory electron carriers present in the inner mitochondrial membrane allow for the transfer of protons (H^+).For the production of single ATP, 3 protons (H^1) are needed. The terminal oxidation of external NADH bypasses the first phosphorylation site and hence only two ATP molecules are produced per external NADH oxidised through mitochondrial electron transport chain. However, in those animal tissues in which malate shuttle mechanism is present, the oxidation of external NADH will yield almost 3 ATP molecules.

- Complete oxidation of a glucose molecule in aerobic respiration results in the net gain of 36 ATP molecules in plants as shown in table 14.2. Since huge amount of energy is generated in mitochondria in the form of ATP molecules they are called 'power house of the cell'. In the case of aerobic prokaryotes due to lack of mitochondria each molecule of glucose produces 38 ATP molecules.

Abnormal rise in respiratory rate of ripening in fruits is called Climacteric. Examples are apple, banana, mango, papaya, pear.

Recent view

- When the cost of transport of ATPs from matrix into the cytosol is considered, the number will be 2.5 ATPs for each NADH + H+ and 1.5 ATPs for each FADH2 oxidised during electron transport system. Therefore, in plant cells net yield of 30 ATP molecules for complete aerobic oxidation of one molecule of glucose. But in those animal cells (showing malate shuttle mechanism) net yield will be 32 ATP molecules.

Peter Mitchel, a British Biochemist received Nobel prize for Chemistry in 1978 for his work on the coupling of oxidation and phosphorylation in mitochondria.

Electron transport chain inhibitors

1. 2, 4 DNP (Dinitrophenol) - It prevents synthesis of ATP from ADP, as it directs
2. electrons from Co Q to O_2
3. Cyanide - It prevents flow of electrons from Cytochrome a3 to O2
4. Rotenone - It prevents flow of electrons from NADH + H^+/$FADH_2$ to Co Q
5. Oligomycin – It inhibits oxidative phosphorylation

Cyanide resistant respiration is believed to be responsible for the climacteric in fruits Cyanide resistant respiration is known to generate heat in thermogenic tissues. The amount of heat produced in thermogenic tissues may be as high as 51° C.

Respiratory Quotient (RQ)

- The ratio of volume of carbon dioxide given out and volume of oxygen taken in during respiration is called Respiratory Quotient or Respiratory ratio. RQ value depends upon respiratory substrates and their oxidation.

$$RQ = \frac{\text{Volume of } CO_2 \text{ liberated}}{\text{Volume of } O_2 \text{ consumed}}$$

1. The respiratory substrate is a carbohydrate, it will be completely oxidised in aerobic respiration and the value of the RQ will be equal to unity.

$$\underset{\text{Glucose}}{C_6H_{12}O_6} + 6O_2 \longrightarrow 6CO_2\uparrow + 6H_2O + \text{Energy}$$

$$\text{RQ of glucose} = \frac{6 \text{ molecules of } CO_2}{6 \text{ molecules of } O_2}$$

$$= 1 \text{ (unity)}$$

2. If the respiratory substrate is a carbohydrate it will be incompletely oxidised when it goes through anaerobic respiration and the RQ value will be infinity.

$$\underset{\text{Glucose}}{C_6H_{12}O_6} \longrightarrow 2CO_2\uparrow + \underset{\text{Ethyl alcohol}}{2C_2H_5OH} + \text{Energy}$$

$$\left.\begin{matrix}\text{RQ of glucose} \\ \text{Anaerobically}\end{matrix}\right\} = \frac{2 \text{ molecules of } CO_2}{\text{zero molecule of } O_2}$$

$$= \infty \text{ (infinity)}$$

3. In some succulent plants like Opuntia, Bryophyllum carbohydrates are partially oxidised to organic acid, particularly malic acid without corresponding release of CO_2 but O_2 is consumed hence the RQ value will be zero.

$$\underset{\text{Glucose}}{2C_6H_{12}O_6} + 3O_2 \longrightarrow \underset{\text{Malic acid}}{3C_4H_6O_5} + 3H_2O + \text{Energy}$$

$$\begin{matrix}\text{RQ of glucose} \\ \text{in succulents}\end{matrix} = \frac{\text{zero molecule of } CO_2}{3 \text{ molecules of } O_2}$$

$$= 0 \text{ (zero)}$$

Net Products gained during aerobic respiration per glucose molecule					
Stages	**CO_2**	**ATP**	**Reduced NAD^+**	**Reduced FAD**	**Total ATP Production**
Glycolysis	0	2	2 (2 × 2 = 4)	0	6
Link reaction	2	0	2 (2 × 3 = 6)	0	6
Krebs cycle	4	2	6	2	24

			(6 × 3 = 18)	(2 × 2 = 4)	
Total	**6**	**4ATPs**	**28 ATPs**	**4 ATPs**	**36 ATPs**

4. When respiratory substrate is protein or fat, then RQ will be less than unity.

$$\underset{\text{Tripalmitin(Fat)}}{2(C_{51}H_{98}O_6)} + 145O_2 \longrightarrow 102CO_2\uparrow + 98H_2O + \text{Energy}$$

$$\text{RQ of Tripalmitin} = \frac{102 \text{ molecules of } CO_2}{145 \text{ molecules of } O_2}$$

$$= 0.7 \text{ (less than unity)}$$

5. When respiratory substrate is an organic acid the value of RQ will be more than unity.

$$\underset{\text{Malic acid}}{C_4H_6O_5} + 3O_2 \longrightarrow 4CO_2\uparrow + 3H_2O + \text{Energy}$$

$$\text{RQ of malic acid} = \frac{4 \text{ molecules of } CO_2}{3 \text{ molecules of } O_2}$$

$$= 1.33 \text{ (more than unity)}$$

Significance of RQ

1. RQ value indicates which type of respiration occurs in living cells, either aerobic or anaerobic.
2. It also helps to know which type of respiratory substrate is involved.

Red colour in various parts of plants is due to the presence of anthocyanin, synthesis of which require more O_2 than CO_2 evolved. RQ will be less than one.

Respiratory quotients of some other substances

Proteins	:	0.8 – 0.9
Oleic acid (Fat)	:	0.71
Palmitic acid (Fat)	:	0.36
Tartaric acid	:	1.6
Oxalic acid	:	4.0

Experiment to demonstrate the production of CO_2 in aerobic

respiration
Take small quantity of any seed (groundnut or bean seeds) and allow them to germinate by imbibing them. While they are germinating place them in a conical flask. A small glass tube containing 4 ml of freshly prepared

Potassium hydroxide (KOH) solution is hung into the conical flask with the help of a thread and tightly close the one holed cork (Figure 14.11). Take a bent glass tube, the shorter end of which is inserted into the conical flask through the hold in the cork, while the longer end is dipped in a beaker containing water. Observe the position of initial water. Observe the position of initial water level in bent glass tube. This experimental setup is kept for two hours and the seeds were allowed to germinate. After two hours, the level of water rises in the glass tube. It is because, the CO_2 evolved during aerobic respiration by KOH solution and the level of water will rise in the glass tube.

$$CO_2 + 2KOH -> K_2CO_3 + H_2O$$

In the case of groundnut or bean seeds, the rise of water is relatively lesser because these seeds use fat and proteins as respiratory substrate and release a very small amount of CO_2 But in the case of wheat grains, the rise in water level is greater because they use carbohydrate as respiratory substrate. When carbohydrates are used as substrate, equal amounts of CO_2 and O_2. But in the case of wheat grains, the rise in water levelis greater because they use carbohydrate are used as substrate, equal amounts of CO_2 and O_2 are evolved and consumed.

Anaerobic Respiration

Fermentation

- Some organisms can respire in the absence of oxygen. This process is called fermentation or anaerobic respiration (Figure 14.12). There are three types of fermentation:

1. Alcoholic fermentation
2. Lactic acid fermentation
3. Mixed acid fermentation

1. Alcoholic fermentation

- The cells of roots in water logged soil respire by alcoholic fermentation because of lack of oxygen by converting pyruvic acid into ethyl alcohol and CO2. Many species of yeast (Saccharomyces) also respire anaerobically. This process takes place in two steps:

$$\text{(i) } 2CH_3COCOOH \xrightarrow[\text{TPP}]{\text{Pyruvate decarboxylase}} 2CH_3CHO + 2CO_2\uparrow$$

Pyruvic acid → Acetaldehyde

$$\text{(ii) } 2CH_3CHO + 2NADH + 2H^+ \xrightarrow{\text{Alcohol dehydrogenase}} 2CH_3CH_2OH + 2NAD^+$$

Acetaldehyde → Ethyl alcohol

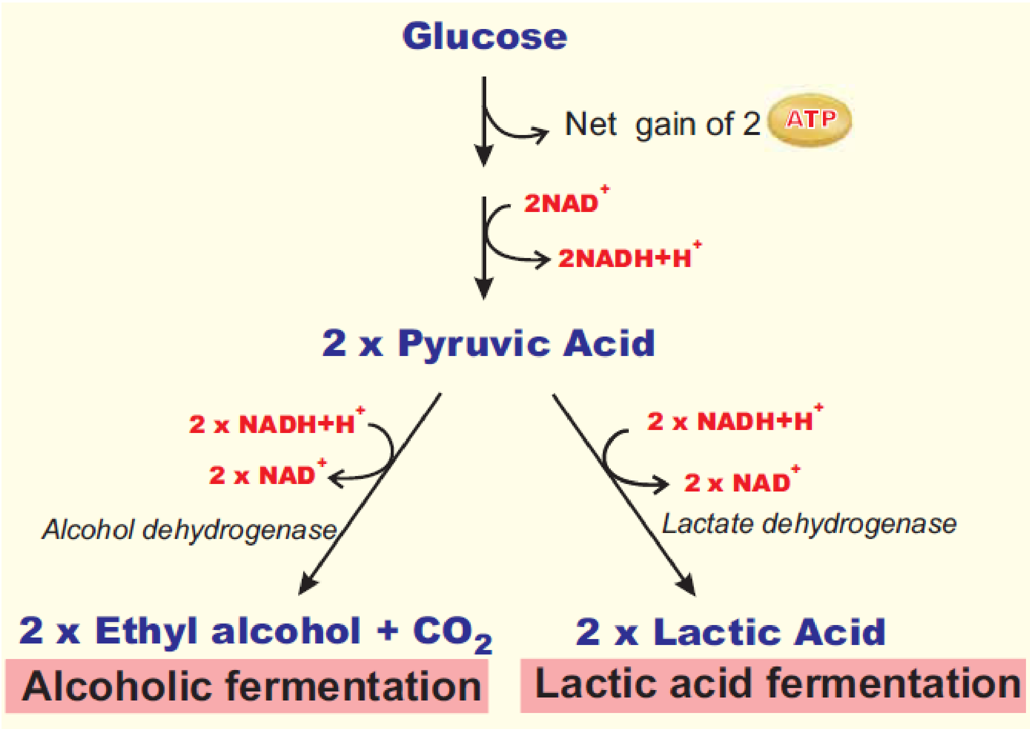


Figure 14.12: Anaerobic Respiration

Comparison of alcoholic fermentation and lactic acid fermentation	
Alcoholic fermentation	**Lactic acid fermentation**
1. It produces alcohol and releases CO_2 from pyruvic acid	1. It produces lactic acid and does not releases CO_2 from pyruvic acid.
2. It takes place in two steps.	2. It takes place in single step.
3. It involves two enzymes, pyruvate decarboxylase with	3. It uses one enzyme lactate dehydrogenase with Zn^{++}.

Mg++ and alcohol dehydrogenase.	
4. It forms acetaldehyde as intermediate compound.	4. Does not form any intermediate compound.
5. It commonly occurs in yeast.	5. Occurs in Bacteria, some fungi and vertebrate muscles.

Industrial uses of alcoholic fermentation:

1. In bakeries, it is used for preparing bread, cakes, biscuits.
2. In beverage industries for preparing wine and alcoholic drinks.
3. In producing vinegar and in tanning, curing of leather.
4. Ethanol is used to make gasohol (a fuel that is used for cars in Brazil).

2. Lactic acid fermentation

- Some bacteria (Bacillus), fungi and muscles of vertebrates produce lactic acid from pyruvic acid (Table 14.3)

$$\underset{\text{Pyruvic acid}}{2CH_3COCOOH} + 2NADH + 2H^+ \xrightarrow{\text{Lactate dehydrogenase}} \underset{\text{Lactic acid}}{2CH_3CHOHCOOH} + 2NAD^+$$

3. Mixed acid fermentation

- This type of fermentation is a characteristic feature of Enterobacteriaceae and results in the formation of lactic acid, ethanol, formic acid and gases like CO_2 and H_2.

Characteristics of Anaerobic Respiration

1. Anaerobic respiration is less efficient than the aerobic respiration (Figure 14. 12) (Table 14.4).
2. Limited number of ATP molecules is generated per glucose molecule (Table 14.5).
3. It is characterized by the production of CO_2 and it is used for Carbon fixation in photosynthesis.

Comparison between glycolysis and fermentation	
Glycolysis	**Fermentation**
1. Glucose is converted into pyruvic acid.	1. Starts from pyruvic acid and is converted into alcohol or lactic acid.
2. It takes place in the presence or absence of oxygen.	2. It takes places in the absence of oxygen.
3. Net gain is 2 ATP.	3. No net gain of ATP molecules.
4. 2NADH + H^+ molecules are produced.	4. 2NADH+ H^+ molecules are utilised.

Stage	Substrate level ATP production	Reduced NAD^+	Total ATP
Glycolysis	2	2*	8
Anaerobic respiration	2	2 reduced NAD^+ re-oxidised	2

*One reduced NAD^+ equivalent to 2 ATPs

Demonstration of alcoholic fermentation

Take a Kuhne's fermentation tube which consists of an upright glass tube with side bulb. Pour 10% sugar solution mixed with baker's yeast into the fermentation tube the side tube is filled plug the mouth with lid. After some time, the glucose solution will be fermented. The solution will give out an alcoholic smell and level of solution in glass column will fall due to the accumulation of CO_2 gas. It is due to the presence of zymase enzyme in yeast which converts the glucose solution into alcohol and CO_2 . Now introduce a pellet of KOH into the tube, the level of solution will rise in upright tube Figure 14.13.

Figure 14.13Kuhne's fermentation experiment

How alcoholic beverages like beer and wine is made?

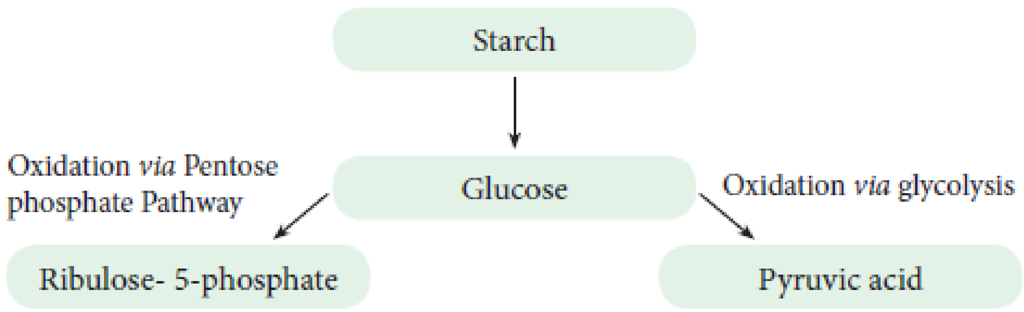
The conversion of pyruvate to ethanol takes place in malted barley and grapes through fermentation. Yeasts carryout this process under anaerobic conditions and this conversion increases ethanol concentration. If the concentration. If the concentration increases, it's toxic effect kills yeast cells and left out is called beer and wine respectively.

Pentose Phosphate Pathway (Phospho Gluconate Pathway)

- During respiration breakdown of glucose in cytosol occurs both by glycolysis (about 2/3) as well as by oxidative pentose phosphate pathway (about 1/3). Pentose phosphate pathway was described by Warburg, Dickens and Lipmann (1938). Hence, it is also called Warburg-Dickens- Lipmann pathway. It takes place in cytoplasm of mature plant cells. It is an alternate way for breakdown of glucose (Figure 14.15). It is also known as Hexose monophosphate shunt (HMP Shunt) or Direct Oxidative Pathway. It consists of two phases, oxidative phase and non-oxidative phase. The oxidative events convert six molecules of six carbon Glucose-6-phosphate to 6 molecules of five carbon sugar Ribulose-5 phosphate with loss of 6CO2 molecules and generation of 12 NADPH 1 H1 (not NADH). The remaining reactions known as non-oxidative pathway, convert Ribulose-5-phosphate molecules to various intermediates such as Ribose-5- phosphate(5C), Xylulose-5-phosphate(5C), Glyceraldehyde-3-phosphate(3C), Sedoheptulose-7-Phosphate(7C), and Erythrose-4-phosphate(4C). Finally, five molecules of glucose-6-phosphate is regenerated (Figure 14.16). The overall reaction is:

$$6 \times \text{Glucose-6-Phosphate} + 12NADP^{1} + 6H_2O$$
$$\downarrow$$
$$5 \times \text{Glucose-6-Phosphate} + 6CO_2\ 1\ Pi + 12NADPH + 12H^{1}$$

- The net result of complete oxidation of one glucose-6-phosphate yield $6CO_2$ and 12NADPH + H^+. The oxidative pentose phosphate pathway is controlled by glucose-6-phosphate dehydrogenase enzyme which is inhibited by high ratio of NADPH to $NADP^+$.



Significance of pentose phosphate pathway

1. HMP shunt is associated with the generation of two important products, NADPH and pentose sugars, which play a vital role in anabolic reactions.

2. Coenzyme NADPH generated is used for reductive biosynthesis and counter damaging the effects of oxygen free radicals
3. Ribose-5-phosphate and its derivatives are used in the synthesis of DNA, RNA, ATP, NAD1, FAD and Coenzyme A.

4. Erythrose is used for synthesis of anthocyanin, lignin and other aromatic compounds.

Unit – 15 - Plant Growth and Development

- The Banyan tree continues to grow for thousands of years and some others particularly annual plants cease growth within a season or within a year. Can you understand the reasons? How does a zygote give rise to an embryo and an embryo to a seedling? How does a new plant structure arise from the pre-existing structure? Growth is defined as an irreversible permanent increase in size, shape, number, volume and dry weight. Plant growth occurs by cell division, cell enlargement, differentiation and maturation.

Bamboos are evergreen grasses and certain species of it can grow at the rate of growth 91 cm per day. The Saguaro Cactus is a tree like cactus and is a slow growing plant. The rate of growth is one inch in the first ten years and it does not begin to flower until it is about 60 years old. It's lifespan exceeds 150 years and takes 75–100 years to grow a side arm

Characteristics of Growth

- Growth increases in protoplasm at cellular level.

- Stem and roots are indeterminate in growth due to continuous cell division and is called open form of growth.

- The primary growth of the plant is due to the activity of apical meristem where, new cells are added to root and shoot apex causing linear growth of plant body.

- The secondary vascular cambium and cork cambium add new cells to cause increase in girth.

- Leaves, flowers and fruits are limited in growth or of determinate or closed form growth.

- Monocarpic annual plants produce flowers only once during lifetime and dies. Example: Paddy and Bean

- Monocarpic perennials produce flowers only once during life time but the plants survive for many years.

  Example: Bamboo.

- Polycarpic perennials produce flowers every year during life time. Example: Coconut

Growth is measurable, it is amazing to know that one single maize root apical meristem can give rise to more than 17,500 new cells per hour and cells in a watermelon may increase in size upto 3,50,000 times.

Indication of growth

Growth in plants can be measured in terms of,

1. Increase in length or girth (roots and stems)
2. Increase in fresh or dry weight
3. Increase in area or volume (fruits and leaves)
4. Increase in number of cells produced

Phases of growth

There are three phases of growth,

1. Formative phase
2. Elongation phase
3. Maturation phase

Formative phase

- Growth in this phase occurs in meristematic cells of shoot and root tips. These cells are small in size, have dense protoplasm, large nucleus and small vacuoles. Cells divide continuously by mitotic cell division. Some cells retain capability of cell division while other cells enter the next phase of growth.

Elongation phase

- Newly formed daughter cells are pushed out of the meristematic zone and increases the volume. It requires auxin and food supply, deposition of new cell wall materials (intussusception), addition of protoplasm and development of central vacuole take place.

Maturation phase

- During this stage cells attain mature form and size. Thickening and differentiation takes place. After differentiation, the cells do not grow further.

Kinetics of growth

- It is an analysis of the motion of cells or expansion.

Stages in Growth rate

- The total period from initial to the final stage of growth is called the grand period of growth. The total growth is plotted against time and 'S' shaped sigmoid curve (Grand period curve) is obtained. It consists of four phases.

They are:

1. Lag phase
2. Log phase
3. Decelerating phase
4. Maturation phase

Lag phase

- In this phase new cells are formed from pre-existing cells slowly. It is found in the tip of the stem, root and branches. It is the initial stage of growth. In other words, growth starts from this period.

Log phase or exponential growth

- Here, the newly formed cell increases in size rapidly by deposition of cell wall material. Growth rate is maximum and reaches top because of cell division and physiological processes are quite fast. The volume of protoplasm also increases. It results in rapid growth and causes elongation of internode in the stem.

Decelerating phase or Decline phase or slow growth phase

- The rate of growth decreases and becomes limited owing to internal and external or both the factors because the metabolic process becomes slow.

Steady state period or maturation phase

- In this phase cell wall thickening due to new particle deposition on the inner surface of the cell wall takes place. The overall growth ceases and becomes constant. The growth rate becomes zero.

Types of growth rate

- The increased growth per unit time is termed as growth rate. An organism or part of an organism can produce more cells through arithmetic growth or geometric growth or both.

Arithmetic Growth Rate

- If the length of a plant organ is plotted against time, it shows a linear curve and this growth is called arithmetic growth.

  ❖ The rate of growth is constant and it increases in an arithmetic manner.

  ❖ Only one cell is allowed to divide between the two-resulting progeny cell.

  ❖ One continues to divide but the other undergoes cell cycle arrest and begins to develop, differentiate and mature.

❖ After each round of cell division, only a single cell remains capable of division and one new body cell forms.

- For example, starting with a single cell after round 1 of cell division there is one dividing cell and one body cell. After round 2 there are two body cells, after round 3 there are three and so on

- The plants single dividing cell would undergo one million rounds of nuclear and cellular division. If each round requires one day, this type of arithmetic increase would require one million days or 2739.7 years. This arithmetic rate is capable of producing small number of cells present in very small parts of plants. For example the hair on many leaves and stems consists of just a single row of cells produced by the division of the basal cell, the cell at the bottom of the

- hair next to other epidermal cells. Hair may contain 5 to 10 cells by the division of the basal cell. So, all its cells could be produced in just five to ten days. In the figure 15.4, on plotting the hight of the plant against time a linear curve is obtained. Mathematically it is expressed as:

$L_t = L_o + rt$
L_t = length at time 't'
L_o = length at time zero
r = growth rate of elongation per unit

Geometric growth rate:

- This growth occurs in many higher plants and plant organs and is measured in size or weight. In plant growth, geometric cell division results if all cells of an organism or tissue are active mitotically. Example: Round three in the given figure 15.5, produces 8 cells as 23 5 8 and after round 20 there are 220 5 1,048,576 cells. The large plant or animal parts are produced this way. In fact, it is common in animals but rare in plants except when they are young and small. Exponential growth curve can be expressed as,

$W_1 = W0ert$
W_1 = Final size (weight, height and number)
W_0 = Initial size at the beginning of the period
r = Growth rate
t =Time of growth
e = Base of the natural logarithms

- Here 'r' is the relative growth rate and also a measure of the ability of the plant to produce new plant material, referred to as efficiency index. Hence, the final size of W_1 depends on the initial size W_0.

Arithmetic and Geometric Growth of Embryo

- Plants often grow by a combination of arithmetic and geometric growth patterns. A young embryonic plant grows geometrically and cell division becomes restricted to certain cells at the tips of roots and shoots. After this point, growth is of the slower arithmetic type, but some of the new cells that are produced can develop into their mature condition and begin carrying out specialized types of metabolism.

- Plants are thus a mixture of older, mature cells and young, dividing cells.

- Quantitative comparisons between the growth of living system can also be made in two ways and is explained in the table 1. In figure 15.7, two leaves A and B are drawn at a particular time. Then A1and B1 are drawn after a given time. A and B 5 Area of leaves at a particular time. A1 and B1 5 Area of leaves after a given time. (A1-A) and (B1-B) represents an absolute increase in area in the given time. Leaf A

Table 1: Comparison between absolute and relative growth rates

Absolute growth rate	Relative growth rate
Increase in total growth of two organs measured and compared per unit	The growth of the given system per unit time expressed per unit initial parameter

time is called absolute growth rate.	is called relative growth rate.

increases from 5 cm2 to 10 cm2; 5 cm2 in a given time. Leaf B increases from 50 cm2 to 55 cm2 ; 5 cm2 in a given time. Hence, both leaves A and B increase their area by 5 cm2 in a given time. This is absolute growth. Relative growth is faster in leaf A because of initial small size. It decreases with time

Conditions of growth

- Plant growth is influenced by a variety of external and internal factors. A brief account of these factors is given below:

External Factors

Water

- Water is essential for cell enlargement as well as growth in the size of the cell. Turgidity of cells helps in growth extension. Water provides the medium for enzymatic activities needed for growth.

Nutrition

- Nutrition plays an important role in the formation of protoplasm. Macro and micro elements are very important as sources of energy. For example, carbon and oxygen in carbon-di-oxide and hydrogen in water are assimilated in photosynthesis.

Temperature

- Temperature plays a significant role in the growth of the plant. Proper growth of a plant occurs at a about 28o C to 30o C temperature and above 45o C will damage the protoplasm and hinders the growth.

Oxygen

- Oxygen has a vital role in the growth of the plant. It helps in releasing metabolic energy essential for growth activities. It is necessary for respiration.

Light

- Light has its own contribution in the growth of the plant. Light is important for growth and photosynthesis. Light stimulates healthy growth. Absence of light may lead to yellowish in colour. This is called etiolation.

Internal Factors

a. Genes are intracellular factors for growth.
b. Phytohormones are intracellular factors for growth. Example: auxin, gibberellin, cytokinin.
c. C/N ratio.

- The ratio of carbohydrates and nitrogenous compounds regulate the specific pattern of growth in plants. For example, if a plant contains more nitrogenous compounds as compared to carbohydrates it produces more protoplasm less mechanical tissues and vigorous vegetative growth. On the other hand, less nitrogenous compounds and more carbohydrates favour the synthesis of more wall material, less protoplasm, and more mechanical tissues.

Experiment: 1. Arc auxanometer:

- The increase in the length of the stem tip can easily be measured by an arc auxanometer which consists of a small pulley to the axis of which is attached a long pointer sliding over a graduated arc. A thread one end of which is tied to the stem tip and another end to a weight passes over the pulley tightly. As soon as the stem tip increases in length, the pulley moves and the pointer slide over the graduated arc. The reading is taken. The actual increase in the length of the stem is then calculated by knowing the length of the pointer and the radius of the pulley. If the radius of the pulley is 4 inches and the length of pointer 20 inches the actual growth is measured as follows:

$$\text{Actual growth in length} = \frac{\text{Distance travelled by the pointer} \times \text{radius of the pulley}}{\text{Length of the pointer}}$$

$$\text{For example, actual growth in length} = \frac{10 \times 4 \text{ inches}}{20 \text{ inches}}$$

$$= 2 \text{ inches}$$

Differentiation

- The process of maturation of meristematic cells to specific types of cells performing specific functions is called differentiation.

Dedifferentiation

- The living differentiated cells which had lost capacity to divide, regain the capacity to divide under certain conditions. Hence, dedifferentiation is the regaining of the ability of cell division by the differentiated cells. Example: Interfascicular cambium and Vascular cambium.

Redifferentiation

- Differentiated cells, after multiplication again lose the ability to divide and mature to perform specific functions. This is called redifferentiation (Figure 15.9). Example: Secondary xylem and Secondary phloem.

Plasticity

- Plants follow different pathways in response to environment or phases of life to form different kinds of structures.

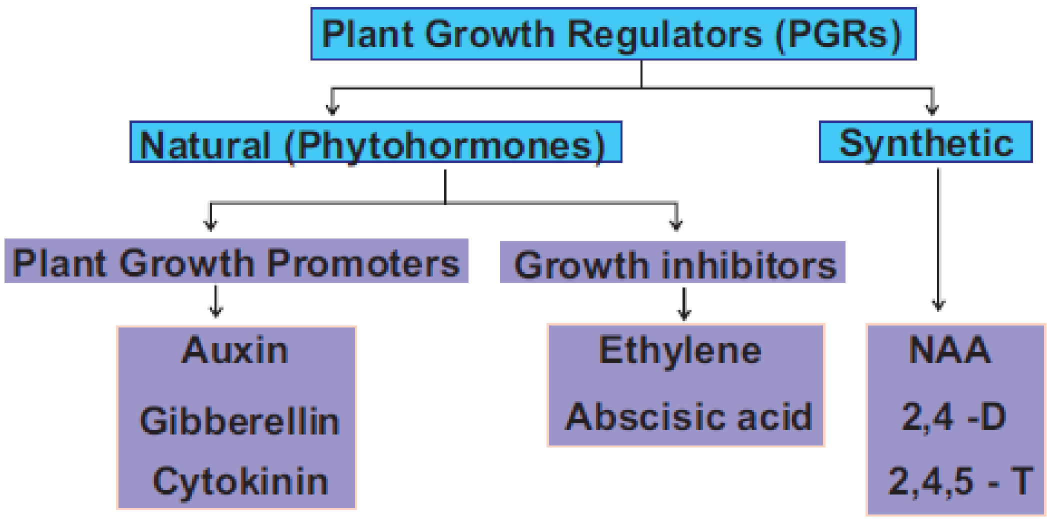
- This ability is called plasticity. Example: Heterophylly in cotton and coriander. In such plants, the leaves of the juvenile plant are different in shape from those in mature plants. On the other hand, the difference in shapes of leaves produced in air and those produced in water in buttercup also represent the heterophyllous development due to the environment. This phenomenon of heterophylly is an example of plasticity.

Plant Growth Regulators

- Plant Growth Regulators (chemical messenger) are defined as organic substances which are synthesized in minute quantities in one part of the plant body and transported to another part where they influence specific physiological processes. Five major groups of hormones viz., auxins, gibberellins, cytokinins, ethylene and abscisic acid are presently known to coordinate and regulate growth and development in plants. The term phytohormones is implied to those chemical substances which are synthesized by plants and thus, naturally occurring. On the other hand, there are several manufactured chemicals which often resemble the hormones in physiological action and even in molecular structure. Recently, another two groups, the brassinosteroids and polyamines were also known to behave like hormones.

Plant growth regulators – classification

- Plant Growth Regulators are classified as natural and synthetic based on their source and a detailed flow diagram is given in.



Classification of Plant Growth Regulators

Characteristics of phytohormones

1. Usually produced in tips of roots, stems and leaves.
2. Transfer of hormones from one place to another takes part through conductive systems.
3. They are required in trace quantities.
4. All hormones are organic in nature.
5. There are no specialized cells or organs for their secretion.
6. They are capable of influencing physiological activities leading to promotion, inhibition and modification of growth.

Synergistic and Antagonistic effects

I. Synergistic effects:

- The effect of one or more substance in such a way that both promote each others activity. Example: Activity of auxin and gibberellins or cytokinins.

II. Antagonistic effects:

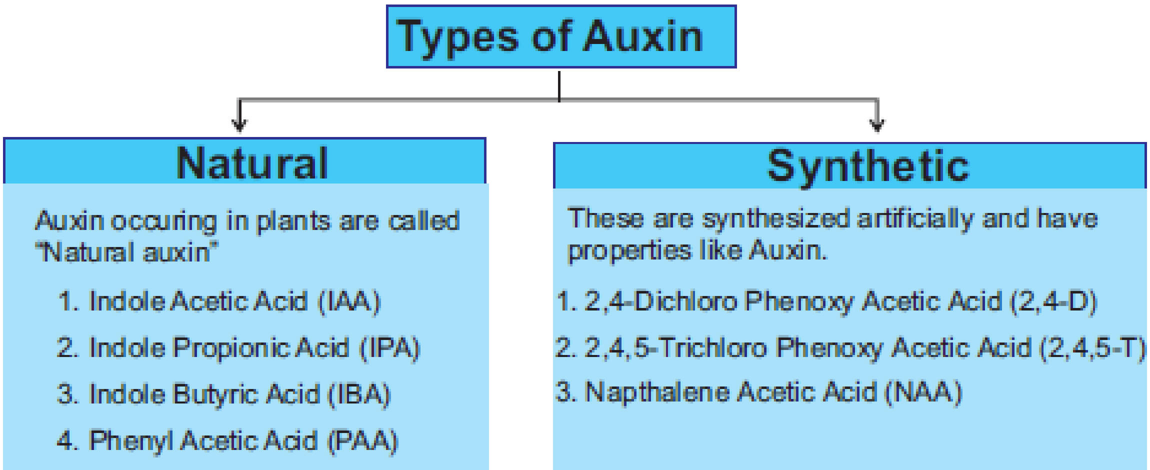
- The effect of two substances in such a way that they have opposite effects on the same process. One accelerates and other inhibits. Example: ABA and gibberellins during seed or bud dormancy. ABA induces dormancy and gibberellins break it.

Auxins

Discovery

- During 1880, Charles Darwin noted the unilateral growth and curvature of Canary grass (Phalaris canariensis) coleoptile to light. The term auxin (Greek: Auxin – to Grow) was first used by F. W. Went in 1926 using Oats (Avena) coleoptile and isolated the auxin. F.

W. Went in 1928 collected auxin in agar jelly. Kogl and Haugen Smith (1931) isolated Auxin from human urine, and called it as Auxin A. Later on in 1934, similar active substances was isolated from corn grain oil and was named as Auxin B. Kogl et al., (1934) found heteroauxin in the plant and chemically called it as Indole Acetic Acid (IAA)



Classification of Auxins

Occurrence

- Auxin is generally produced by the growing tips of the stem and root, from where they migrate to the region of the action.

Types of Auxin

- Auxins are divided into two categories Natural auxins and Synthetic auxins

> **Anti-auxins**
> Anti-auxin compounds when applied to the plant inhibit the effect of auxin. Example: 2, 4, 5-Tri Iodine Benzoic Acid (TIBA) and Napthylpthalamine.

Free auxin

- They move out of tissues as they are easily diffusible. Example: IAA.

Bound Auxin

- They are not diffusible. Example: IAAAspartic acid

Precursor

- The amino acid Tryptophan is the precursor of IAA and zinc is required for its synthesis.

Chemical structure

- Auxin has similar chemical structure of IAA.

Transport in Plants

- Auxin is polar in transport. It includes basipetal and acropetal transport. Basipetal means transport through phloem from shoot to root and acropetal means transport through xylem from root to shoot.

Bioassay (Avena Curvature Test / Went Experiment)

- Bioassay means testing of substances for their activity in causing a growth response in a living plant or its part.

The procedure involves the following steps:

- When the Avena seedlings have attained a height of 15 to 30 mm, about 1mm of the coleoptile tip is removed. This apical part is the source of natural auxin. The tip is now placed on agar blocks for few hours. During this period, the auxin diffuses out of these tips into the agar. The auxin containing agar block is now placed on one side of the decapitated stump of Avena coleoptile. The auxin from the agar blocks diffuses down through coleoptile along the side to which the auxin agar block is placed. An agar block without auxin is placed on another decapitated coleoptile. Within an hour, the coleoptiles with auxin agar block bends on the opposite side where the agar block is placed. This curvature can be measured placed on one side of the decapitated stump of Avena coleoptile. The auxin from the agar blocks diffuses down through coleoptile along the side to which the auxin agar block is placed. An agar block without auxin is placed on another decapitated coleoptile. Within an hour, the coleoptiles with auxin agar block bends on the opposite side where the agar block is placed. This curvature can be measured.

Physiological Effects

- They promote cell elongation in stem and coleoptile.
- At higher concentrations auxins inhibit the elongation of roots but induce more lateral roots. Promotes growth of root only at extremely low concentrations.
- Suppression of growth in lateral bud by apical bud due to auxin produced by apical bud is termed as apical dominance.
- Auxin prevents abscission.
- It is responsible for initiation and promotion of cell division in cambium, which is responsible for the secondary growth and tumor. This property of induction of cell division has been exploited for tissue culture techniques and for the formation of callus.
- Auxin stimulates respiration.
- Auxin induces vascular differentiation.

Agricultural role

- It is used to eradicate weeds. Example: 2,4-D and 2,4,5-T.
- Synthetic auxins are used in the formation of seedless fruits (Parthenocarpic fruit).
- It is used to break the dormancy in seeds. Induce flowering in Pineapple by NAA & 2,4-D.
- Increase the number of female flowers and fruits in cucurbits.

Gibberellins

1. Discovery

- The effect of gibberellins had been known in Japan since early 1800 where certain rice plants were found to suffer from 'Bakanae' or foolish seedling disease. This disease was found by Kurosawa (1926) to be caused by a fungus Gibberella fujikuroi. The active substance was separated from fungus and named as gibberellin by Yabuta (1935). These are more than 100 gibberellins reported from both fungi and higher plants. They are noted as GA1, GA2, GA3 and so on. GA3 is the first discovered gibberellin. In 1938, Yabuta and Sumiki isolated gibberellin in crystalline form. In1955, Brain et al., gave the name gibberellic acid. In 1961, Cross et al., established its structure.

2. Occurrence

- The major site of gibberellin production in plants is parts like embryo, roots and young leaves near the tip. Immature seeds are rich in gibberellins.

3. Precursors

- The gibberellins are chemically related to terpenoids (natural rubber, carotenoids and steroids) formed by 5-C precursor, an Isoprenoid unit called Iso Pentenyl Pyrophosphate (IPP) through a number of intermediates. The primary precursor is acetate.

4. Chemical structure

- All gibberellins have gibbane ring structure.

5. Transport in plants

- The transport of gibberellins in plants is non-polar. Gibberellins are translocated through phloem and also occur in xylem due to lateral movement between vascular bundles.

6. **Bioassay (Dwarf Pea assay)**

- Seeds of dwarf pea are allowed to germinate till the formation of the coleoptile. GA solution is applied to some seedlings. Others are kept under control. Epicotyle length is measured and as such, GA stimulating epicotyle growth can be seen.

7. **Physiological Effects**

❖ It produces extraordinary elongation of stem caused by cell division and cell elongation.

❖ Rosette plants (genetic dwarfism) plants exhibit excessive intermodal growth when they are treated with gibberellins. This sudden elongation of stem followed by flowering is called bolting.

❖ Gibberellin breaks dormancy in potato tubers.

❖ Many biennials usually flower during second year of their growth. For flowering to take place, these plants should be exposed to cold season. Such plants could be made to flower without exposure to cold season in the first year itself, when they are treated with gibberellins.

8. **agricultural role**

❖ Formation of seedless fruits without fertilization is induced by gibberellins Example: Seedless tomato, apple and cucumber.

❖ It promotes the formation of male flowers in cucurbitaceae. It helps in crop improvement.

❖ Uniform bolting and increased uniform seed production.

❖ Improves number and size of fruits in grapes. It increase yield.

❖ Promotes elongation of inter-node in sugarcane without decreasing sugar content.

- ❖ Promotion of flowering in long day plants even under short day conditions.
- ❖ It stimulates the seed germination.

Cytokinins (Cytos – cell, Kinesis – division)

Discovery

- The presence of cell division inducing substances in plants was first demonstrated by Haberlandt in 1913 in Coconut milk (liquid endosperm of coconut) which contains cell division inducing substances. In 1954, Skoog and Miller discovered that autoclaved DNA from herring sperm stimulated cell division in tobacco pith cells. They called this cell division inducing principle as kinetin (chemical structure: 6-Furfuryl Amino Acid). This does not occur in plants. In 1963, Lethan introduced the term cytokinin. In 1964, Lethan and Miller isolated and identified a new cytokinin called Zeatin from unripe grains of maize. The most widely occurring cytokinin in plants is Iso Pentenyl adenine (IPA).

Occurrence

- Cytokinin is formed in root apex, shoot apex, buds and young fruits.

Precursor

- Cytokinins are derivatives of the purine adenine.

Precursor

- Cytokinins are derivatives of the purine adenine.

Transport in plants

- The distribution of cytokinin in plants is not as wide as those of auxin and gibberellins but found mostly in roots. Cytokinins appear to be translocated through xylem.

Physiological effect

- ❖ Cytokinin promotes cell division in the presence of auxin (IAA).
- ❖ Induces cell enlargement associated with IAA and gibberellins
- ❖ Cytokinin can break the dormancy of certain light-sensitive seeds like tobacco and induces seed germination.
- ❖ Cytokinin promotes the growth of lateral bud in the presence of apical bud.
- ❖ Application of cytokinin delays the process of aging by nutrient mobilization.
  It is known as Richmond Lang effect.
- ❖ Cytokinin (i) increases rate protein synthesis (ii) induces the formation of inter-fascicular cambium (iii) overcomes apical dominance (iv) induces formation of new leaves, chloroplast and lateral shoots.
- ❖ Plants accumulate solutes very actively with the help of cytokinins.

Ethylene (Gaseous Phytohormone)

- Almost all plant tissues produce ethylene gas in minute quantities

Discovery

- In 1924, Denny found that ethylene stimulates the ripening of lemons. In 1934, R. Gane found that ripe bananas contain abundant ethylene. In 1935, Cocken et al., identified ethylene as a natural plant hormone

Occurrence

- Maximum synthesis occurs during climacteric ripening of fruits (see Box info) and tissues undergoing senescence. It is formed in almost all plant parts like roots, leaves, flowers, fruits and seeds.

Transport in plants

- Ethylene can easily diffuse inside the plant through intercellular spaces.

Precursor

- It is a derivative of amino acid methionine, linolenic acid and fumaric acid.

Bioassay (Gas Chromatography)

- Ethylene can be measured by gas chromatography. This technique helps in the detection of exact amount of ethylene from different plant tissues like lemon and orange.

Physiological Effects

- ❖ Ethylene stimulates respiration and ripening in fruits.
- ❖ It stimulates radial growth in stem and root and inhibits linear growth.
- ❖ It breaks the dormancy of buds, seeds and storage organs.
- ❖ It stimulates formation of abscission zone in leaves, flowers and fruits. This makes the leaves to shed prematurely.
- ❖ Inhibition of stem elongation (shortening the internode).
- ❖ In low concentration, ethylene helps in root initiation.
- ❖ Growth of lateral roots and root hairs. This increases the absorption surface of the plant roots.
- ❖ The growth of fruits is stimulated by ethylene in some plants. It is more marked in climacteric fruits.
- ❖ Ethylene causes epinasty.

Agricultural role

- ❖ Ethylene normally reduces flowering in plants except in Pine apple and Mango.
- ❖ It increases the number of female flowers and decreases the number of male flowers.
- ❖ Ethylene spray in cucumber crop produces female flowers and increases the yield.

Abscisic Acid (ABA) (Stress Phyto Hormone)

Discovery

- In 1963, the hormone was first isolated by Addicott et al., from young cotton bolls and named as Abscission II. Eagles and Wareing during 1963–64 isolated a dormancy inducing substance from leaves of Betula and called it as dormin. In 1965, it was found by Cornsforth et al., that both dormin and abscission are chemically same compounds and called Abscisic Acid (ABA).

Occurrence

- This hormone is found abundantly inside the chloroplast of green cells.

Precursors

- The hormone is formed from mevalonic acid pathway or xanthophylls.

Transport in plants

- Abscisic acid is transported to all parts of the plant through diffusion as well as through phloem and xylem.

Chemical structure

- It has carotenoid structure.

Bioassay (Rice Coleoptile)

- The inhibition of IAA induces straight growth of rice seedling coleoptiles.

Physiological effects

- ❖ It helps in reducing transpiration rate by closing stomata. It inhibits K1 uptake by guard cells and promotes the leakage of malic acid. It results in closure of stomata.
- ❖ It spoils chlorophylls, proteins and nucleic acids of leaves making them yellow.
- ❖ Inhibition of cell division and cell elongation.
- ❖ ABA is a powerful growth inhibitor. It causes 50% inhibition of growth in Oat coleoptile.
- ❖ It induces bud and seed dormancy.
- ❖ It promotes the abscission of leaves, flowers and fruits by forming abscission layers.
- ❖ ABA plays an important role in plants during water stress and during drought conditions. It results in loss of turgor and closure of stomata. It has anti-auxin and anti-gibberellin property.
- ❖ Abscisic acid promotes senescence in leaves by causing loss of chlorophyll pigment decreasing the rate of photosynthesis and changing the rate of proteins and nucleic acid synthesis.

Agricultural Role

- ❖ In Cannabis sativa, induces male flower formation on female plants.
- ❖ Induction of flowers in short day plants.
- ❖ It promotes sprouting in storage organs like Potato.
- ❖ ABA plays an important role in plants during water stress drought conditions.
- ❖ It inhibits the shoot growth and promotes growth of root system. This character protect the plants from water stress. Hence, ABA is called as stress hormone.

Photoperiodism

- Trees take several years for initiation of flowering whereas an annual herb flowers within few months. Each plant requires a specific time period to complete their vegetative phase which will be followed by reproductive phase as per their internal control points through Biological Clock. The physiological mechanisms in relation to flowering are controlled by (i) light period (Photoperiodism) and (ii) temperature (Vernalization). The physiological change on flowering due to relative length of light and darkness (photoperiod) is called Photoperiodism. The term photoperiodism was coined by Garner and Allard (1920) when they observed this in 'Biloxi' variety of soybean (Glycine max) and 'Maryland mammoth' variety of tobacco (Nicotiana tabacum). The photoperiod required to induce flowering is called critical day length. Maryland mammoth (tobacco variety) requires 12 hours of light and cocklebur (Xanthium pensylvanicum) requires 15.05 hours of light for flowering.

Classification of plants based on Photoperiodism

- Depending upon the photoperiodic responses plants are classified as given in

1. **Long day plants:**

- The plants that require long critical day length for flowering are called long day plants or short night plants. Example: Pea, Barley and Oats.

2. **Short long day plants:**

- These are long day plants but should be exposed to short day lengths during early period of growth for flowering. Example: Wheat and Rye.

3. **Short day plants:**

- The plants that require a short critical day length for flowering are called short day plants or long night plants. Example: Tobacco, Cocklebur, Soybean, Rice and Chrysanthemum.

4. **Long short day plants:**

- These are actually short-day plants but they have to be exposed to long days during their early periods of growth for flowering. Example: Some species of Bryophyllum and Night jasmine

5. **Intermediate day plants**

- These require a photoperiod between long day and short day for flowering. Example: Sugarcane and Coleus.

6. **Day neutral plants:**

- There are a number of plants which can flower in all possible photoperiods. They are also called photo neutrals or indeterminate plants. Example: Potato, Rhododendron, Tomato and Cotton.

Photoperiodic induction

- An appropriate photoperiod in 24 hours' cycle constitutes one inductive cycle.

Plants may require one or more inductive cycles for flowering. The phenomenon of conversion of leaf primordia into flower primordia under the influence of suitable inductive cycles is called photoperiodic induction. Example: Xanthium (SDP) – 1 inductive cycle and Plantago (LDP) – 25 inductive cycles.

Site of Photoinductive perception

- Photoperiodic stimulus is perceived by the leaves. Floral hormone is synthesised in leaves and translocated to the apical tip to promote flowering. This can be explained by a simple experiment on Cocklebur (Xanthium pensylvanicum), a short day plant. Usually Xanthium will flower under short day conditions. If the plant is defoliated and kept under short day conditions it will not flower. Flowering will occur even when all the leaves are removed except one leaf. If a cocklebur plant is defoliated and kept under long day conditions, it will not flower. If one of its leaves is exposed to short day condition and rest are in long day condition, flowering will occur.

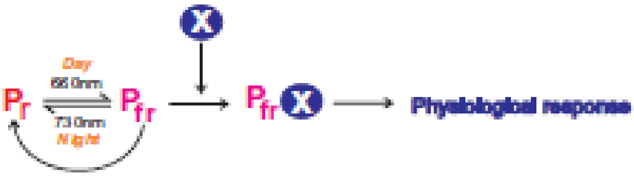
> The nature of flower producing stimulus has been elusive so far. It is believed by many physiologists that it is a hormone called florigen. The term florigen was coined by Chailakyan (1936) but it is not possible to isolate.

Importance of photoperiodism

1. The knowledge of photoperiodism plays an important role in hybridisation experiments.

2. Photoperiodism is an excellent example of physiological pre-conditioning that is using an external factor to induce physiological changes in the plant.

Phytochrome



- Phytochrome is a bluish biliprotein pigment responsible for the perception of light in photo physiological process. Butler et al., (1959) named this pigment and it exists in two interconvertible forms: (i) red light absorbing pigment which is designated as Pr and (ii) far red light absorbing pigment which is designated as Pfr. The Pr form absorbs red light in 660nm and changes to Pfr. The Pfr form absorbs far red light in 730nm and changes to Pr. The Pr form is biologically inactive and it is stable whereas Pfr form is biologically active and it is very unstable. In short day plants, Pr promotes flowering and Pfr inhibits the flowering whereas in long day plants flowering is promoted by Pfr and inhibited by Pr form. Pfr is always associated with hydrophobic area of membrane systems while Pr is found in diffused state in the cytoplasm. The interconversion of the two forms of phytochrome is mainly involved in flower induction and also additionally plays a role in seed germination and changes in membrane conformation.

Vernalization (Vernal – Spring Like)

- Besides photoperiod certain plants require a low temperature exposure in their earlier stages for flowering. Many species of biennials and perennials are induced to flower by low temperature exposure (0oC to 5oC). This process is called Vernalization. The term Vernalization was first used by T. D. Lysenko (1938).

Mechanism of Vernalization:

Two main theories to explain the mechanism of vernalization are:

1. Hypothesis of phasic development
2. Hypothesis of hormonal involvement

Hypothesis of phasic development

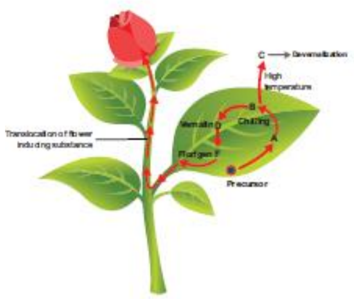
- According to Lysenko, development of an annual seed plant consists of two phases. First phase is thermostage, which is vegetative phase requiring low temperature and suitable moisture. Next phase is photo stage which requires high temperature for synthesis of florigen (flowering hormone).

Hypothesis of hormonal involvement

- According to Purvis (1961), formation of a substance A from its precursor, is converted into B after chilling. The substance B is unstable. At suitable temperature B is converted into stable compound D called Vernalin. Vernalin is converted to F (Florigen). Florigen induces flower formation. At high temperature B is converted to C and devernalization occur.

Technique of Vernalization:

- The seeds are first soaked in water and allowed to germinate at 10o C to 12o C. Then seeds are transferred to low temperature (3oC to 5oC) from few days to 30 days. Germinated seeds after this treatment are allowed to dry and then sown. The plants will show quick flowering when compared to untreated control plants.



Vernalization and Flowering

Devernalization

- Reversal of the effect of vernalization is called devernalization.

Parctical applications

1. Vernalization shortens the vegetative period and induces the plant to flower earlier.
2. It increases the cold resistance of the plants.
3. It increases the resistance of plants to fungal disease.
4. Plant breeding can be accelerated.

Seed Germination and Dormancy

Seed Germination

- The activation and growth of embryo from seed into seedling during favourable conditions is called seed germination.

Types of germination

- There are to methods of seed germination. Epigeal and hypogeal.

Epigeal germination

- During epigeal germination cotyledons are pushed out of the soil. This happens due to the elongation of the hypocotyl.

  Example : Castor and Bean.

Hypogeal germination

- During hypogeal germination cotyledons remain below the soil due to rapaid elongation of epicotyls.

Example : Maize

Factors affecting germination

- Seed germination is directly affected by external and internal factors:

External factors
Water:

- It activates the enzymes which digest the complex reserve foods of the seed. If the water content of the seed goes below a critical level, seeds fail to germinate.

Temperature:

- Seeds fails to germinate at very low and high temperature. The optimum temperature is 25^0 C to 35^0 C for most tropic species.

Oxygen:

- It is necessary for germination. Since aerobic respiration is a physiological requirement for germination most will germinate well in air contain 20% oxygen.

Light:

- There are many seeds which respond to light for germination and these seeds said to be photoblastic.

Soil conditions:

- Germination of seed in its natural habits it influenced by soil conditions such as water holding capacity, mineral composition and aeration of the soil.

Internal factors
Maturity of embryo:

- The seeds of some plants, when shed will contain immature embryo. Such seeds germinate only after maturation of embryo.

Viability:

- Usually seeds remain viable or living only for a particular period. Viability of seeds range from a few days (Example: Oxalis) to more than hundred years. Maximum viability (1000 years) has been recorded in lotus seeds. Seeds germinate only within the period of viability.

Dormancy:

- Seeds of many plants are dormant at the time of shedding. A detailed treatment is given below.

Seed Dormancy

- The seeds of most plants germinate under favourable environmental conditions but some seeds do not germinate when suitable conditions like water, oxygen and favourable temperature are not available. Germination of such seeds may be delayed for days, months or years. The condition of a seed when it fails to germinate even in suitable environmental condition is called seed dormancy. There are two main reasons for the development of dormancy: Imposed dormancy and innate dormancy. Imposed dormancy is due to low moisture and low temperature. Innate dormancy is related to the properties of seed itself.

Factors causing dormancy of seeds:

1. Hard, tough seed coat causes barrier effect as impermeability of water, gas and restriction of the expansion of embryo prevents seed germination.

2. Many species of seeds produce imperfectly developed embryos called rudimentary embryos which promotes dormancy.

3. Lack of specific light requirement leads to seed dormancy.

4. A range of temperatures either higher or lower cause dormancy.

5. The presence of inhibitors like phenolic compounds which inhibits seed germination cause dormancy.

Methods of breaking dormancy:

- The dormancy of seeds can be broken by different methods. These are:

Scarification:

- Mechanical and chemical treatments like cutting or chipping of hard tough seed coat and use of organic solvents to remove waxy or fatty compounds are called as Scarification.

Impaction:

- In some seeds water and oxygen are unable to penetrate micropyle due to blockage by cork cells. These seeds are shaken vigorously to remove the plug which is called Impaction.

Stratification:

- Seeds of rosaceous plants (Apple, Plum, Peach and Cherry) will not germinate until they have been exposed to well aerated, moist condition under low temperature (0^oC to 10^oC) for weeks to months. Such treatment is called Stratification.

Alternating temperatures:

- Germination of some seeds is strongly promoted by alternating daily temperatures. An alternation of low and high temperature improves the germination of seeds.

Light:

- The dormancy of photoblastic seeds can be broken by exposing them to red light.

Senescence

- Plant life comprises some sequential events, viz: germination, juvenile stage, maturation, old age and death. Old age is called senescence in plants. Senescence refers to all collective, progressive and deteriorative processes which ultimately lead to complete loss of organization and function. Unlike animals, plants continuously form new organs and older organs undergo a highly regulated senescence program to maximize nutrient export.

Types of Senescence

Leopold (1961) has recognised four types of senescence:

1. Overall senescence
2. Top senescence
3. Deciduous senescence
4. Progressive senescence

The branch of botany which deals with ageing, abscission and senescence is called Phytogerontology

Overall senescence:

- This kind of senescence occurs in annual plants when entire plant gets affected and dies. Example: Wheat and Soybean. It also occurs in few perennials also. Example: Agave and Bamboo.

Top senescence:

- It occurs in aerial parts of plants. It is common in perennials, underground and root system remains viable. Example: Banana and Gladiolus.

Deciduous senescence:

- It is common in deciduous plants and occurs only in leaves of plants, bulk of the stem and root system remains alive. Example: Elm and Maple.

Progressive senescence:

- This kind of senescence is gradual. First it occurs in old leaves followed by new leaves then stem and finally root system. It is common in annuals

Physiology of Senescence

- Cells undergo changes in structure.
- Vacuole of the cell acts as lysosome and secretes hydrolytic enzymes.
- The starch content is decreased in the cells.
- Photosynthesis is reduced due to loss of chlorophyll accompanied by synthesis and accumulation of anthocyanin pigments, therefore the leaf becomes red.

• There is a marked decrease in protein content in the senescing organ.

• RNA content of the leaf particularly rRNA level is decreased in the cells due to increased activity of the enzyme RNAase.

• DNA molecules in senescencing leaves degenerate by the increased activity of enzyme DNAase.

Factors affecting Senescence:

• ABA and ethylene accelerate senescence while auxin and cytokinin retard senescence.

• Nitrogen deficiency increases senescence whereas nitrogen supply retards senescence.

• High temperature accelerates senescence but low temperature retards senescence.

• Senescence is rapid in dark than in light.

• Water stress leads to accumulation of ABA leading to senescence.

Programmed cell death (PCD)

- Senescence is controlled by plants own genetic programme and death of the plant or plant part consequent to senescence is called Programmed Cell Death. In short senescence of an individual cell is called PCD. The proteolytic enzymes involving PCD in plants are phytaspases and in animals are caspases. The nutrients and other substrates from senescing cells and tissues are remobilized and reallocated to other parts of the plant that survives. The protoplasts of developing xylem vessels and tracheids die and disappear at maturity to make them functionally efficient to conduct water for transport. In aquatic plants, aerenchyma is normally formed in different parts of the plant such as roots and stems which encloses large air spaces that are created through PCD. In the development of unisexual flowers, male and female flowers are present in earlier stages, but only one of these two completes its development while other aborts through PCD

Abscission

- Abscission is a physiological process of shedding of organs like leaves, flowers, fruits and seeds from the parent plant body. When these parts are removed the plant seals off its vascular system to prevent loss of water and nutrients. Final stage of senescence is abscission. In temperate regions all the leaves of deciduous plants fall in autumn and give rise to naked appearance, then the new leaves are developed in the subsequent spring season. But in evergreen plants there is gradual abscission of leaves, the older leaves fall while new leaves are developed continuously throughout the year.

Morphological and Anatomical changes during abscission

- Leaf abscission takes place at the base of petiole which is marked internally by a distinct zone of few layers of thin walled cells arranged transversely. This zone is called abscission zone or abscission layer. An abscission layer is greenish-grey in colour and is formed by rows of cells of 2 to 15 cells thick. The cells of abscission layer separate due to dissolution of middle lamella and primary wall of cells by the activity of enzymes pectinase and cellulase resulting in loosening of cells. Tyloses are also formed blocking the conducting vessels. Degrading of chlorophyll occur leading to the change in the colour of leaves, leaf detachment from the plant and leaf fall. After abscission, outer layer of cells becomes suberized by the development of periderm

Hormones influencing abscission

- All naturally occurring hormones influence the process of abscission. Auxinsand cytokinins retard abscission, while abscisic acid (ABA) and ethylene induce it.

Significance of abscission

1. Abscission separates dead parts of the plant, like old leaves and ripe fruits.

2. It helps in dispersal of fruits and continuing the life cycle of the plant.

3. Abscission of leaves in deciduous plants helps in water conservation during summer.

4. In lower plants, shedding of vegetative parts like gemmae or plantlets help in vegetative reproduction

11th economics

Unit – 8 Indian Economy Before And After Independence.

Green Revolution

- The term Green Revolution refers to the technological breakthrough in of agricultural practices. During 1960s the traditional agricultural practices were gradually replaced by modern technology and agricultural practices in India. Initially the new technology was tried in 1960-61 as a pilot project in seven districts. It was called as the High Yielding Varieties Programme (HYVP).

Achievement of Green Revolution

1. The major achievement of the new strategy was to boost the production of major cereals viz., wheat and rice. India was depending on the US for the food grain. The US by using Public Law 480 (PL480) exported wheat to India. Indians were waiting for the ships to sip their food. On the other hand, India lost lots of minerals. The US could strategically exploit Indian mineral resources at cheapest price for manufacturing missiles and weapons, which gave job opportunity for larger US youth and largely contributed to US GDP. But now India is food surplus, exporting food grains to the European countries.

2. The Green revolution was confined only to High Yielding Varieties (HYV) cereals, mainly rice, wheat, maize and jowar.

3. This Strategy was mainly directed to increase the production of commercial crops or cash crops such as sugarcane, cotton, jute, oilseeds and potatoes.

4. Per hectare productivity of all crops had increased due to better seeds.

5. Green Revolution had positive effect on development of industries, which manufactured agricultural tools like tractors, engines, threshers and pumping sets.

6. Green Revolution had brought prosperity to rural people. Increased production had generated employment opportunities for rural masses. Due to this, their standard of living had increased.

7. Due to multiple cropping and more use of chemical fertilizers, the demand for labour increased.

8. Financial resources were provided by banks and co-operative societies. These banks provided loans to farmer on easy terms.

The New Agricultural strategy was also called by various names. Modern agricultural technology, seed - fertilizer - water technology, or simply green revolution.

Weaknesses of Green Revolution

1. Indian Agriculture was still a gamble of the monsoons.
2. This strategy needed heavy investment in seeds, fertilizers, pesticides and water.
3. The income gap between large, marginal and small farmers had increased. Gap between irrigated and rain fed areas had widened.
4. Except in Punjab, and to some extent in Haryana, farm mechanization had created widespread unemployment among agricultural labourers in the rural areas.
5. Larger chemical use and inorganic materials reduced the soil fertility and spoiled human health. Now organic farming is encouraged.

Rainbow Revolution	
1. Green revolution – Agriculture (Food grains productions)	7. White Revolution - Milk
2. Blue Revolution – Fish	8. Yellow Revolution – Oilseeds
3. Golden Revolution – Fruits / Apple	9. Black Revolution – Petroleum
4. Solver Revolution – Egg	10. Round Revolution – Potato
5. Red Revolution- Meat/Tomato	11. Grey Revolution – Fertilizes

6. Pink Revolution – Shrimp	12. Brown Revolution – Leather

Second Green Revolution

- The Government of India had implemented 'Second Green revolution' to achieve higher agricultural growth. The target of Second Green Revolution was to increase 400 million tons of food grain production as against about 214 million tons in 2006-07. This is to be achieved by 2020. In agricultural sector, the growth rate of 5% to 6% has to be maintained over next 15 years. There may be changes in these statistics.

Requirements of Second Green revolution:

- Introduction of Genetically Modified (GM) seeds which double the per acreage production.
- Contribution of private sector to market the usage of GM foods.
- Government can play a key role in expediting irrigation schemes and managing water resources.
- Linking of rivers to transfer surplus water to deficient areas.