Semester	Course	Hours	Credit	Sub. Code	Marks		
					Internal	External	Total
II	CC 7	6	5	18KP2B07	25	75	100

PLANT PHYSIOLOGY AND BIOCHEMISTRY

UNIT I: PHYSIOLOGY

Water relations of plants, Osmosis –Osmotic pressure, diffusion –diffusion pressure deficit, chemical and water potential in plants, water and salt stress, root pressure, Ascent of sap, Mineral nutrition in plants , Modern concepts of mineral salt absorption and its translocation. Transpiration, Stomatal physiology and regulation.

UNIT II:

PHOTOSYNTHESIS - Photosynthetic apparatus, Pigments, Red Drop and Emerson's Enhancement effect. Photosynthesis Mechanism – Light reactions; Cyclic, Non-cyclic and Pseudocyclic reaction. Dark reaction – C3 & C4 cycle. Photorespiration and Glycolate metabolism (C2 Cycle) Factors affecting and significance of photosynthesis. CAM cycle.

Source of Study Material

1. Pandey,S.N.,& Sinha., 1972, Plant Physiology, Vikas Publishing , New Delhi.
2. Salisbury, F.B.&Ross, CN.,1955.Plant Physiology, CBS Publishers, New Delhi.

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Unit – I

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UNIT I: PHYSIOLOGY

Water Relation in Plants

Plant–water relations concern how plants control the hydration of their cells, including the collection of water from the soil, its transport within the plant and its loss by evaporation from the leaves. The water status of plants is usually expressed as ‘water potential’, which has units of pressure, is always negative, and in simple form is the algebraic sum of the hydrostatic pressure and the osmotic pressure of water. Flow of water through plant and soil over macroscopic distances is driven by gradients in hydrostatic pressure. Over microscopic distances (e.g. across semipermeable membranes) it is driven by gradients in water potential. Evaporation of water from leaves is primarily controlled by stomata, and if not made good by the flow of water from soil through the plant to the leaves, results in the plants wilting.

Osmosis

“Osmosis is a process by which the molecules of a solvent pass from a solution of low concentration to a solution of high concentration through a semi-permeable membrane.”

Osmotic Solutions

There are three different types of solutions:

- Isotonic Solution
- Hypertonic Solution
- Hypotonic Solution

An isotonic solution is one that has the same concentration of solutes both inside and outside the cell.

A hypertonic solution is one that has a higher solute concentration outside the cell than inside.

A hypotonic solution is the one that has a higher solute concentration inside the cell than outside.

Types of Osmosis

Osmosis is of two types:

- **Endosmosis**– When a substance is placed in a hypotonic solution, the solvent molecules move inside the cell and the cell becomes turgid or undergoes deplasmolysis. This is known as endosmosis.
- **Exosmosis**– When a substance is placed in a hypertonic solution, the solvent molecules move outside the cell and the cell becomes flaccid or undergoes plasmolysis. This is known as exosmosis.

Osmotic Pressure

Osmotic pressure is the pressure required to stop water from diffusing through a membrane by osmosis. It is determined by the concentration of the solute. Water diffuses into the area of higher concentration from the area of lower concentration. When the concentration of the substances in the two areas in contact is different, the substances will diffuse until the concentration is uniform throughout.

Osmotic pressure can be calculated using the equation:

$$\Pi = MRT$$

Where,

Π denotes the osmotic pressure,
M is the molar concentration of the solute,
R is the gas constant,
T is the temperature

Diffusion

“Diffusion is the movement of molecules from a region of higher concentration to a region of lower concentration down the concentration gradient.”

Diffusion pressure deficit

Diffusion pressure deficit (DPD) is the amount by which two solutions differ in their diffusion pressure. It is defined as the amount by which the diffusion pressure of water or solvent in a solution is lower than that of pure water or solvent. It allows easy absorption of water due to diffusion pressure gradient.

chemical potential

In thermodynamics, chemical potential of a species is energy that can be absorbed or released due to a change of the particle number of the given species, e.g. in a chemical reaction or phase transition. The chemical potential of a species in a mixture is defined as the rate of change of free energy of a thermodynamic system with respect to the change in the number of atoms or molecules of the species that are added to the system. Thus, it is the partial derivative of the free energy with respect to the amount of the species, all other species' concentrations in the mixture remaining constant. The molar chemical potential is also known as partial molar free energy. When both temperature and pressure are held constant, chemical potential is the partial molar Gibbs free energy. At chemical equilibrium or in phase equilibrium the total sum of the product of chemical potentials and stoichiometric coefficients is zero, as the free energy is at a minimum.

Water Potential

Water potential is a measure of the energy state of water. This is a particularly important concept in plant physiology because it determines the direction and movement of water. Equation for water potential (must account for the factors that influence the diffusion of water):

$$\Psi_w = \Psi_p + \Psi_s + \Psi_g$$

Where, Ψ_w = water potential; Ψ_p = pressure potential; Ψs = solute or osmotic potential; and Ψ_g = gravity potential.

1. Solute (or osmotic) potential (Ψ_s)

This is the contribution due to dissolved solutes. Solutes always decrease the free energy of water, thus there contribution is always negative. The solute potential of a solution can be calculated with the van't Hoff equation: $\Psi_s = - miRT$ where m = molality (moles/1000 g); i = ionization constant (often 1.0); R = gas constant (0.0083 liter x MPa/mol deg); and T = temperature (K).

2. Pressure (or Pressure Potential; Ψ_p)

Due to the pressure build up in cells thanks to the wall. It is usually positive, although may be negative (tension) as in the xylem. Pressure can be measured with an osmometer.

3. Matric potential

This is the contribution to water potential due to the force of attraction of water for colloidal, charged surfaces. It is negative because it reduces the ability of water to move. In large volumes of water it is very small and usually ignored. However, it can be very important in the soil, especially when referring to the root/soil interface.

4. Gravity (Ψ_g)

Contributions due to gravity which is usually ignored unless referring to the tops of tall trees.

The water potential of pure water is zero. Water potentials in intact plant tissue are usually negative (because of the large quantities of dissolved solutes in cells).

Water potential is the sum of the contributions of the various factors that influence water potential

where: $\Psi_w = \Psi_p + \Psi_s + \text{etc.}$

Water stress

Water stress adversely impacts many aspects of the physiology of plants, especially photosynthetic capacity. If the stress is prolonged, plant growth, and productivity are severely diminished. Plants have evolved complex physiological and biochemical adaptations to adjust and adapt to a variety of environmental stresses. The molecular and physiological mechanisms associated with water-stress tolerance and water-use efficiency have been extensively studied.

The systems that regulate plant adaptation to water stress through a sophisticated regulatory network are the subject of the current review. Molecular mechanisms that plants use to increase stress tolerance, maintain appropriate hormone homeostasis and responses and prevent excess light damage, are also discussed. An understanding of how these systems are regulated and ameliorate the impact of water stress on plant productivity will provide the information needed to improve plant stress tolerance using biotechnology, while maintaining the yield and quality of crops.

Salt stress in plants

Soil salinization, the accumulation of water-soluble salts to levels that negatively impact plant production, is a global phenomenon affecting approximately 831 million hectares of land. More specifically, the phenomenon threatens 19.5% of the world's irrigated agricultural land and 2.1% of the world's non-irrigated (dry-land) agricultural lands. High soil salinity content can be harmful to plants because water-soluble salts can alter osmotic potential gradients and consequently inhibit many cellular functions. For example, high soil salinity content can inhibit the process of photosynthesis by limiting a plant's water uptake; high levels of water-soluble salts in the soil can decrease the osmotic potential of the soil and consequently decrease the difference in water potential between the soil and the plant's roots, thereby limiting electron flow from H_2O to P680 in Photosystem II's reaction center.

Over generations, many plants have mutated and built different mechanisms to counter salinity effects. A good combatant of salinity in plants is the hormone ethylene. Ethylene is known for regulating plant growth and development and dealing with stress conditions. Many central membrane proteins in plants, such as ETO2, ERS1 and EIN2, are used for ethylene signaling in many plant growth processes. Mutations in these proteins can lead to heightened salt sensitivity and can limit plant growth. The effects of salinity has been studied on Arabidopsis plants that have mutated ERS1, ERS2, ETR1, ETR2 and EIN4 proteins. These proteins are used for ethylene signaling against certain stress conditions, such as salt and the ethylene precursor ACC is used to suppress any sensitivity to the salt stress.

Root pressure

Root pressure is the transverse osmotic pressure within the cells of a root system that causes sap to rise through a plant stem to the leaves.

Root pressure occurs in the xylem of some vascular plants when the soil moisture level is high either at night or when transpiration is low during the day. When transpiration is high, xylem sap is usually under tension, rather than under pressure, due to transpirational pull. At night in some plants, root pressure causes guttation or exudation of drops of xylem sap from the tips or edges of leaves. Root pressure is studied by removing the shoot of a plant near the soil level. Xylem sap will exude from the cut stem for hours or days due to root pressure. If a pressure gauge is attached to the cut stem, the root pressure can be measured.

Root pressure is caused by active distribution of mineral nutrient ions into the root xylem. Without transpiration to carry the ions up the stem, they accumulate in the root xylem and lower the water potential. Water then diffuses from the soil into the root xylem due to osmosis. Root pressure is caused by this accumulation of water in the xylem pushing on the rigid cells. Root pressure provides a force, which pushes water up the stem, but it is not enough to account for the movement of water to leaves at the top of the tallest trees. The maximum root pressure measured in some plants can raise water only to 6.87 meters, and the tallest trees are over 100 meters tall.

Ascent of sap

The ascent of sap in the xylem tissue of plants is the upward movement of water and minerals from the root to the crown. Xylem is a complex tissue consisting of living and non-living cells. The conducting cells in xylem are typically non-living and include, in various groups of plants, vessels members and tracheids. Both of these cell types have thick, lignified secondary cell walls and are dead at maturity. Although several mechanisms have been proposed to explain the phenomenon, the cohesion-tension mechanism[1] has the most evidence and support. Although cohesion-tension has received criticism, for example due to the apparent existence of large negative pressures in some living plants, experimental and observational data favor this mechanism.

The more recently proposed compensating pressure (CP) theory favors a version of vital theory proposed by Jagdish Chandra Bose. However, experimental evidence has not supported it.

An alternative theory based on the behavior of thin films has been developed by Henri Gouin, a French professor of fluid dynamics.[5] The theory is intended to explain how water can reach the uppermost parts of the tallest trees, where the applicability of the cohesion-tension theory is debatable.

The theory assumes that in the uppermost parts of the tallest trees, the vessels of the xylem are coated with thin films of sap. The sap interacts physically with the walls of the vessels: as a result of van der Waals forces, the density of the film varies with distance from the wall of a vessel. This variation in density, in turn, produces a "disjoining pressure", whose value varies with distance from the wall. (Disjoining pressure is a difference in pressure from that which prevails in the bulk of a liquid; it is due to the liquid's interaction with a surface. The interaction may result in a pressure at the surface that is greater or less than that which prevails in the rest of the liquid.) As a tree's leaves transpire, water is drawn from the xylem's vessels; hence, the thickness of the film of sap varies with height within a vessel. Since the disjoining pressure varies with the thickness of the film, a gradient in the disjoining pressure arises during transpiration: the disjoining pressure is greater at the bottom of the vessel (where the film is thickest) and less at the top of the vessel (where the film is thinner). This spatial difference in pressure within the film results in a net force that pushes the sap upwards towards the leaves.

Mineral Nutrition in Plants

Mineral Nutrition is defined as the naturally occurring inorganic nutrient found in the soil and food that is essential for the proper functioning of animal and plant body. Minerals are vital elements necessary for the body. Both the plants and animals require minerals essentially. For example, Zinc is necessary for the manufacture of protein and for cell division.

Nutrients which are required by plants in very small amounts are termed as Micro Elements or macronutrients. Some of them include boron, copper, manganese, iron, chlorine, and molybdenum.

Nutrients which are required by plants in larger amounts are termed as Macronutrients. Some of them include sulfur, nitrogen, carbon, phosphorus, calcium, potassium and magnesium.

Role of Nutrients

- **Balancing function:** Some salts or minerals act against the harmful effects of the other nutrients thus balancing each other.
- **Maintenance of osmotic pressure:** Several minerals cell sap is present in organic or inorganic form to regulate the organic pressure of the cell.
- **Influencing the pH of the cell sap:** Different anions and cations has an influence on the pH of the cell sap.
- **Construction of the plant body:** Carbon, Hydrogen, and Oxygen are elements that help to construct the plant body by entering protoplasm and constitution of the wall.
- **Catalysis of the biochemical reaction:** Certain elements like zinc, magnesium, calcium and copper act as metallic catalysts in biochemical reactions.
- **Effects of Toxicity:** Certain minerals like arsenic and copper has a toxic effect on the protoplasm under specific conditions.

Micronutrients

Functions of some of the Micronutrients are stated below:

Copper

- It is a component of oxidase, cytochrome oxidase, phenolases and ascorbic acid oxidase that is responsible for activating the enzymes.
- Copper plays a vital role in photophosphorylation.
- It also helps to balance carbohydrate-nitrogen regulation.

Manganese

- It is necessary for photosynthesis during the photolysis of water.
- The mineral is required for the synthesis of chlorophyll.
- It acts as an activator of nitrogen metabolism.

Zinc

- It is essential for the synthesis of tryptophan, metabolism of carbohydrates and phosphorus.
- It is a constituent of enzymes like alcohol dehydrate-gas, carbonic anhydrase, lactic dehydrogenase, hexokinase, and carboxypeptidase.

Macronutrients

Functions of certain macronutrients are stated below:

Phosphorous

- Phosphorous boosts fruit ripening and root growth in a healthy manner by helping translocation of carbohydrates.
- They are found abundantly in fruits and seeds.
- Deficiency of Phosphorus leads to premature fall of leaves and they turn purplish or dark green in color.

Nitrogen

- It is present in various coenzymes, hormones, and ATP etc.
- Nitrogen is a vital constituent of vitamins, nucleic acids, proteins and many others.
- Deficiency of nitrogen leads to the complete suppression of flowering and fruiting, impaired growth, and development of anthocyanin pigmentation in stems.

Potassium

Potassium is the only monovalent cation that is necessary for plants. It acts as an enzyme activator including DNA polymerase. The deficiency of potassium leads to Mottled chlorosis.

Mechanism of Mineral Salt Absorption:

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

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

Plasma membrane of the root cells is not permeable to all the ions. It is selectively permeable. All the ions of the same salt are not absorbed at equal rate but there is unequal absorption of ions. First step in the absorption of mineral salts is the process of Ion-Exchange which does not require metabolical energy but greatly facilitates mineral salt absorption.

Ion-Exchange:

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

(i) Contact Exchange Theory:

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

(ii) Carbonic Acid Exchange Theory:

According to this theory, the CO_2 released during respiration of root cells combines with water to form carbonic acid (H_2CO_3). Carbonic acid dissociates into H^+ and an anion HCO_3^- in soil solution. These H^+ ions may be exchanged for cations adsorbed on clay particles.

The cations thus released into the soil solution from the clay particles, may be adsorbed on root cells in exchange for H^+ ions or as ion pairs with bicarbonate. Thus, soil solution plays an important role in carbonic acid exchange theory.

Absorption of mineral salts may be of two types:

(1) Passive and

(2) Active

(1) Passive Absorption of Mineral Salts:

When the concentration of mineral salts is higher in the outer solution than in the cell sap of the root cells, the mineral salts are absorbed according to the concentration gradient by simple process of diffusion. This is called as passive absorption because it does not require expenditure of metabolic energy.

It is now known that during passive absorption, the mineral salts may diffuse through cell membranes directly through lipid bilayer but mainly through trans-membrane ion-selective protein channels or trans-membrane carrier proteins. Carrier or channel mediated passive transport of mineral salts across the membrane is also called as facilitated diffusion.

(2) Active Absorption of Mineral Salts:

It has often been observed that the cell sap in plants accumulates large quantities of mineral salts ions against the concentration gradient. For example in alga Nitella the cell sap accumulated K^+ and phosphate ions to such an extent that their concentrations were thousands and hundreds times greater than in the pond water in which the plant was growing.

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

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

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

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

The Carrier Concept:

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

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

(i) Isotopic Exchange:

Several times, it has been found that actively absorbed radioactive ions (such as $^{35}S0_4$) cannot diffuse back or be exchanged with other ions in the outer solution indicating thereby that the plasma membrane is not permeable to free ions.

(ii) Saturation Effects:

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

(iii) Specificity:

Active sites on carrier compound may be specific which can bind only some specific ions. This also explains the selective and unequal absorption of ions by the plants. There are two common hypotheses based on the carrier concept to explain the mechanism of active salt absorption, although they are not universally accepted.

(1) Lundegardh’s Cytochrome Pump Theory:

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

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

(i) The mechanism of anion and cation absorption is different.

(ii) Anions are absorbed through cytochrome chain by an active process.

(iii) Cations are absorbed passively.

(2) Bennet-Clark’s Protein-Lecithin Theory:

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

According to this theory,

(i) the phosphate group in the phosphatide is regarded as the active centre binding the cations, and the basic choline group as the anion binding centre.

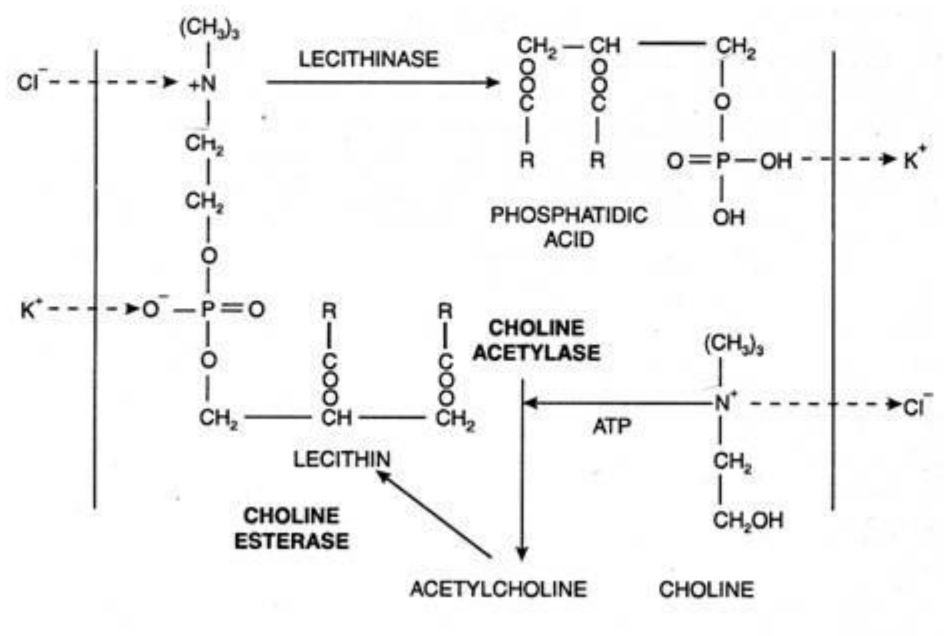

Fig. 7.4. Diagrammatic representation of the Bennet-Clark's Protein-Lecithin theory.

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

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

Once inside the epidermal cells of the root, the mineral salts in their ionic form move from one cell to another by:

(i) Apoplastic pathway (i.e., through cell walls and intercellular spaces),

(ii) Trans membrane pathway (i.e., by crossing the membranes) and

(iii) Symplastic pathway (i.e., through plasmodesmata), and ultimately reach to xylem vessels and tracheids from where they are carried to different parts of the shoot along with ascent of sap.

Translocation

Translocation is the movement of materials in plants from the leaves to other parts of the plant. Nutrients, mainly sugars, are created in the leaves during photosynthesis. These are then transported throughout the plant through phloem, which are a long series of connected cells.

The Pressure-Flow Mechanism

The rate of translocation in angiosperms (flowering plants) is approximately 1 meter per hour. In conifers it is generally much slower, but even so this is far too fast to be accounted for by diffusion. Instead, the sap flows, like a river of dilute syrup water. What is the force that drives the flow of material in the phloem? It is pressure, generated in the sieve elements and companion cells in source tissues. In leaves, sugar is synthesized in mesophyll cells (the middle layer of the leaf), and is then actively pumped into the phloem, using metabolic energy. By using energy, the sugar is not only transferred to the phloem but is also concentrated. When a solute such as sugar is concentrated inside cells, water enters the cells by osmosis. Since the plant cells have a rigid cell wall, this influx of water creates a great deal of internal pressure, over ten times the pressure in an automobile tire. The pressure causes sap to move out through the pores of the sieve element, down the tube.

At the other end of the transport stream, in the sinks, sugar is constantly leaving the phloem and being used by surrounding cells. Some is consumed as an energy source, some is stored as sugar or starch, and some is used to make new cells if the sink tissue is growing. Since sugar leaves the phloem in the sink, water exits too (again by osmosis) and the pressure goes down. Therefore, there is a difference in pressure between source and sink phloem. This causes the solution to flow, just as water flows along a pressure gradient in a garden hose. This process is known as the pressure-flow mechanism.

Transpiration

Plants also require an excretory system to discharge excess water from their body. This process of elimination of excess water from the plant body is known as transpiration. It is generally the evaporation of water from the surface of the leaves.

During the process of transpiration, water molecules in the plant tissues are removed from the aerial parts of the plants. Only a small amount of water absorbed by the plants is utilised in growth and development. The rest is eliminated in the form of transpiration.

Types of Transpiration

There are three different types of transpiration in plants:

Stomatal Transpiration

It is the evaporation of water from the stomata of the plants. Most of the water from the plants is transpired this way. The water near the surface of the leaves changes into vapour and evaporates when the stomata are open.

Lenticular Transpiration

Lenticels are minute openings in the bark of branches and twigs. Evaporation of water from the lenticels of the plants is known as lenticular transpiration.

Lenticels are not present in all the plants. A minimal amount of water is lost through lenticels.

Cuticular Transpiration

It is the evaporation of water from the cuticle of the plants. The cuticle is a waxy covering on the surface of the leaves of the plants. About 5-10% of the water from the leaves is lost through cuticular transpiration. During dry conditions when the stomata are closed, more water is transpired through the cuticles.

Opening and Closing of Stomata

Stomata consist of a pair of guard cells with an aperture in between. It remains open during the daytime and is closed at night. The reason for the opening and closing of this structure is the turgidity of guard cells.

The interior wall of the guard cells present towards the aperture is dense and flexible. The stomata open when the turgidity of the guard cells increases. The exterior walls bulge out, and the interior walls form a crescent shape.

The orientation of the microfibrils in the guard cells also plays an important role in the opening of the stomata. The radial orientation of the microfibrils makes it easier for the stomata to open. The stomata close when the turgidity of the guard cells decreases due to the water loss and the interior walls form a crescent shape retrieve their original shape.

In dicots, the lower side of leaves have more stomata while in monocots, both the sides have an equal number of stomata.

Stomatal Physiology

The epidermal surface of a leaf has several tiny pores called stomata which are microscopic and are surrounded by two guard cells which control their opening and closing. Cell wall of the guard cells adjacent to the stomatal pore is thicker and more inelastic than the wall adjacent to the surrounding epidermal cells. An increase in turgor pressure will cause the more elastic part of the guard cell wall to stretch considerably.

The cell wall bordering the stomatal pore is thicker than that next to the surrounding cells. The guard cells contain chloroplast, while the inelastic thicker part of the wall encloses the pore. When the water is lost, the guard cells decrease in volume; their walls straighten and the aperture is closed.

In some plants, the guard cells are accompanied by epidermal cells which are different from the rest of the epidermal cells. These cells are called subsidiary or accessory cells. The guard cells possess chloroplasts but the eidermal cells lack them. Photosynthesis in the guard cells is at a reduced rate.

Types of Stomata:

Morphologically, four types of stomata are distinguished in the dicots and this classification is based on the arrangement of the epidermal cells adjacent to the guard cells.

i. Anomocytic type:

These are also called ranunculaceous types. In this type the guard cells are surrounded by some cells which do not differ from the other epidermal cells.

ii. Anisocytic type:

These are also called cruciferous types. In this type the guard cells are surrounded by three unequally sized subsidiary cells.

iii. Paracytic type:

This is also called rubiaceous type. Here each guard cell is accompanied by one or more subsidiary cells which are parallel to the long axis of the epidermal cell.

iv. Diacytic type:

This is also called caryophyllaceous type. Here the stoma is surrounded by two subsidiary cells.

v. Actinocytic type:

In this type the stomata are surrounded by a circle of radiating cells.

In the monocots as many as 4 types are distinguished on the basis of number of subsidiary cells surrounding the guard cells.

Some of the recent workers have distinguished as many as 15 main types of stomata in ferns, gymnosperms and angiosperms and for details reference may be made to any textbook on plant anatomy.

3. Distribution of Stomata:

Stomata are more frequent on the lower surface of the leaves but their occurrence on both the surfaces has also been commonly noted.

They are distributed only on the lower surface e.g. in oak, apple and orange; more on lower surface than on the upper surface e.g. in bean, maize, and sunflower and equally on both the surfaces e.g., in maize, oats; only on the upper surface e.g. water lily and absent or functionless e.g. in submerged water plants.

When fully opened, the stomatal pore has a width of 3 to 12 μ and a length of 10 to 40 μ. The number of stomata range from 100 to 60,000 per square centimetre.

Mechanism of Stomatal Physiology:

(i) Starch-sugar hypothesis:

Lloyd, Doftified and Sayre observed that starch content of guard cells is high in the dark and low in light. This is unlike the other epidermal cells and mesophyll cells where opposite effect is observed. It is also noted that a high pH favours opening and a low pH the closure of stomata.

In light CO_2 concentration of guard cells and neighbouring cells is lowered being consumed in photosynthesis; hence the rise in pH.

In the dark, CO_2 of respiration accumulates in the guard cells; hence there is fall in pH of the guard cells.

A high pH favours conversion of starch into osmotically active reducing sugars, resulting in an increase of turgor in the guard cells and stomata open. The reverse reaction occurs when pH is lowered.

The enzyme phosphorylase, present in the chloroplasts catalyzes this reaction in the presence of inorganic phosphate as follows:

$$\text{Starch} + \text{Pi} \xrightleftharpoons[\text{(pH 5.0)}]{\text{Phosphorylase (pH 7.0)}} \text{Glucose 1 – Phosphate}$$

Steward (1964) criticized the above scheme and pointed out that unless glucose 1-phosphate was further converted to glucose and inorganic phosphate, no appreciable change in osmotic potential can be obtained.

Inorganic phosphate on the left side of the above equation is just as osmotically active as glucose 1 -phosphate on the right.

At high pH starch is converted to glucose in the following way to make the stomata open:

$$\text{Starch} \xrightarrow[\text{Phosphoglucomutase}]{\text{Phosphorylase}} \text{G 1} - PO_4 \text{ (Glucose 1 – phosphate)}$$

$$\text{G 1}-PO_4 \xrightarrow{\text{Phosphatase}} \text{G6-}PO_4 \text{ (Glucose 6 – phosphate)}$$

$$\text{G6}-PO_4 \longrightarrow \text{Glucose} + \text{Pi}$$

The closing of stomata requires metabolic energy in the form of ATP. With the help of ATP and in the presence of oxygen, the enzyme hexokinase converts glucose to glucose 1 -phosphate. The latter is then converted to starch.

There are several drawbacks of the starch hydrolysis theory. For instance, the increase of the osmotic potential of the guard cells during stomatal opening cannot be explained by the formation of glucose from starch in its entirety.

It also does not account for the extra-effectiveness of blue light during the opening of stomata. In some plants there is no starch present in the guard cells (e.g., Allium sp.).

Inter-conversion of starch-sugar is very slow and does not satisfactorily explain the quick stomatal movement or responses to water levels.

(ii) Glycolic acid hypothesis:

Zalitch (1963) has proposed that glycolic acid plays an important role in stomatal opening. He has suggested the formation of carbohydrates from glycolic acid, thus increasing the osmotic value.

The general assumption is that ATP produced in this mechanism furnishes the required energy needed for the opening and closing of stomata.

It is believed that energy possibly participates in the active pumping of water into the guard cells.

The main objection against this theory is the speculative nature of the role of energy in ‘pumping’ of water.

(iii) Several recent studies have demonstrated the occurrence of ATP and glycolate in the guard cells through photosynthesis. Studies of Rama Das and Raghvendra (1976) using inhibitors of Photosystem 1 and Photosystem II, have provided unequivocal support to this view point.

Their studies have further revealed that in vivo the process of photophosphorylation possibly satisfies the energy requirements for stomatal movements. Thus, the dependency of light for the opening of stomata lay in the energy matabolism rather than in carbon metabolism.

Using isolated epidermal strips of Commelinabengalensis it was shown that the opening of stomata in light was under the control of cyclic photophosphorylation. When the inhibitors of cyclic photophosphorylation were added to the epidermal strips, stomata closed rapidly while the inhibitors of non-cyclic photophosphorylation did not influence the stomatal aperture.

Similarly the catalysts of the cyclic and not the noncyclic photophosphorylation promoted stomatal opening. Further the involvement of ATP in the enhancement of stomatal opening in the presence of K^+ was also confirmed through the addition of the inhibitors like, 2, 4-dinitrophenol which caused the closure of the stomata.

On the other hand, the addition of HCO_3^- ions in the medium caused the closure of stomata. These authors also speculated a mechanochemical system operating in the stomatal movement, thus explaining the requirement of energy.

(iv) Adenosine triphosphate (ATP) is also produced during respiration for the dark opening of stomata. Recent studies have also demonstrated that stomatal movement was also regulated by the hormones. For instance, the stomata were opened by the cytokinins either directly or by functioning as metabolic sinks.

On the other hand, several inhibitors like ABA caused their closure. It may also be mentioned that ABA functions in the presence of CO_2 only. In fact, ABA was produced in the leaf cells under stress conditions and antagonises the cytokinin action. This inhibitor is also shown to change the diffusion and permeability of the guard cells. In this way K^+ influx is inhibited.

Thus, K^+ from guard cells passes into the epidermal or subsidiary cells and the guard cells collapse resulting in the closure of the stomata. In this efflux of H+ ions is also avoided. In the guard cells the acidity is raised or pH becomes acidic or low. Similar situation prevails with excessive CO_2. It is well accepted that low pH and excessive organic acids stimulate starch synthesis.

Raschke (1979) has proposed a scheme based on interaction of the feedback and feed-forward pathways (see above) (Fig. 8-6). According to him stomatal movements can be considered manifestations of a central system optimizing gas exchange and employing feedback and feed forward methods of control.

UNIT II

Photosynthesis

Photosynthesis, the process by which green plants and certain other organisms transform light energy into chemical energy. During photosynthesis in green plants, light energy is captured and used to convert water, carbon dioxide, and minerals into oxygen and energy-rich organic compounds.

Photosynthetic Apparatus

Photosynthetic cells contain special pigments that absorb light energy. Different pigments respond to different wavelengths of visible light. **Chlorophyll**, the primary pigment used in photosynthesis, reflects green light and absorbs red and blue light most strongly. In plants, photosynthesis takes place in chloroplasts, which contain the chlorophyll. Chloroplasts are surrounded by a double membrane and contain a third inner membrane, called the **thylakoid membrane**, that forms long folds within the organelle. In electron micrographs, thylakoid membranes look like stacks of coins, although the compartments they form are connected like a maze of chambers. The green pigment chlorophyll is located within the thylakoid membrane, and the space between the thylakoid and the chloroplast membranes is called the **stroma**.

Photosynthetic Pigments

There are four different types of pigments present in leaves:

1. Chlorophyll a
2. Chlorophyll b
3. Xanthophylls
4. Carotenoids

Chlorophyll is a green pigment found in the chloroplasts of the **plant cell** and in the mesosomes of cyanobacteria. This green colour pigment plays a vital role in the process of photosynthesis by permitting plants to absorb energy from sunlight. Chlorophyll is a mixture of chlorophyll-a and chlorophyll-b.

Besides green plants, other organisms that perform photosynthesis contain various other forms of chlorophyll such as chlorophyll-c1, chlorophyll-c2, chlorophyll-d and chlorophyll-f.

Red Drop and Emerson’s Enhancement Effect

The **Emerson effect** is the increase in the rate of photosynthesis after chloroplasts are exposed to light of wavelength 680 nm (deep red spectrum) and more than 680 nm (far red spectrum). When simultaneously exposed to light of both wavelengths, the rate of photosynthesis is far higher than the sum of the red light and far red light photosynthesis rates. The effect was early evidence that two photosystems, processing different wavelength.

When Emerson exposed green plants to differing wavelengths of light, he noticed that at wavelengths of greater than 680 nm the efficiency of photosynthesis decreased abruptly despite the fact that this is a region of the spectrum where chlorophyll still absorbs light (chlorophyll is the green pigment in plants - it absorbs mainly the red and blue wavelengths from light). When the plants were exposed to short-wavelength light, (less than 660 nm), the efficiency also decreased. Emerson then exposed the plants to both short and long wavelengths at the same time, causing the efficiency to increase greatly. He concluded that there must be two different photosystems involved in photosynthesis, one driven by short-wavelength light and one driven by long-wavelength (PS1 and PS2). They work together to enhance efficiency and convert the light energy to forms that can be absorbed by the plant.

The light excites the chlorophyll molecules at the reaction centre and causes an increase in energy. As the molecule becomes less excited, its energy is transported through a chain of electron carriers to the next photosystem which does much the same thing and produces energy-carrying organic molecules.

Mechanism of Photosynthesis

The **process of photosynthesis** occurs in two stages:

- Light-dependent reaction or light reaction
- Light independent reaction or dark reaction

Light-dependent reaction or light reaction

In the process of photosynthesis, the phosphorylation of ADP to form ATP using the energy of sunlight is called **photophosphorylation**. Cyclic photophosphorylation occurs in both aerobic and anaerobic conditions. Only two sources of energy are available to living organisms: sunlight and reduction-oxidation (redox) reactions. All organisms produce ATP, which is the universal energy currency of life. In photosynthesis this commonly involves photolysis, or photodissociation, of water and a continuous unidirectional flow of electrons from water to photosystem II.

In photophosphorylation, light energy is used to create a high-energy electron donor and a lower-energy electron acceptor. Electrons then move spontaneously from donor to acceptor through an electron transport chain..

Cyclic Photophosphorylation

This form of photophosphorylation occurs on the stroma lamella or fret channels. In cyclic photophosphorylation, the high energy electron released from P700 of PS1 flow down in a cyclic pathway. In cyclic electron flow, the electron begins in a pigment complex called photosystem I, passes from the primary acceptor to ferredoxin and then to plastoquinone, then to cytochrome b_6f (a similar complex to that found in mitochondria), and then to plastocyanin before returning to Photosystem-1. This transport chain produces a proton-motive force, pumping H^+ ions across the membrane; this produces a concentration gradient that can be used to power ATP synthase during chemiosmosis. This pathway is known as cyclic photophosphorylation, and it produces neither O_2 nor NADPH. Unlike non-cyclic photophosphorylation, NADP+ does not accept the electrons; they are instead sent back to cytochrome b_6f complex.

In bacterial photosynthesis, a single photosystem is used, and therefore is involved in cyclic photophosphorylation. It is favored in anaerobic conditions and conditions of high irradiance and CO_2 compensation points.

Non-Cyclic Photophosphorylation

The other pathway, non-cyclic photophosphorylation, is a two-stage process involving two different chlorophyll photosystems. Being a light reaction, non-cyclic photophosphorylation occurs in the thylakoid membrane. First, a water molecule is broken down into $2H^+ + 1/2\ O_2 + 2e^-$ by a process called photolysis (or light-splitting). The two electrons from the water molecule are kept in photosystem II, while the $2H^+$ and $1/2O_2$ are left out for further use. Then a photon is absorbed by chlorophyll pigments surrounding the reaction core center of the photosystem. The light excites the electrons of each pigment, causing a chain reaction that eventually transfers energy to the core of photosystem II, exciting the two electrons that are transferred to the primary electron acceptor, pheophytin. The deficit of electrons is replenished by taking electrons from another molecule of water. The electrons transfer from pheophytin to plastoquinone, which takes the $2e^-$ from Pheophytin, and two H^+ Ions from the stroma and forms PQH_2, which later is broken into PQ, the $2e^-$ is released to Cytochrome b_6f complex and the two H^+ ions are released into thylakoid lumen. The electrons then pass through the Cyt b_6 and Cyt f. Then they are passed to plastocyanin, providing the energy for hydrogen ions (H^+) to be pumped into the thylakoid space. This creates a gradient, making H^+ ions flow back into the stroma of the chloroplast, providing the energy for the regeneration of ATP.

The photosystem II complex replaced its lost electrons from an external source; however, the two other electrons are not returned to photosystem II as they would in the analogous cyclic pathway. Instead, the still-excited electrons are transferred to a photosystem I complex, which boosts their energy level to a higher level using a second solar photon. The highly excited electrons are transferred to the acceptor molecule, but this time are passed on to an enzyme called Ferredoxin-$NADP^+$ reductase which uses them to catalyse the reaction

$$NADP^+ + 2H^+ + 2e^- \rightarrow NADPH + H^+$$

This consumes the H^+ ions produced by the splitting of water, leading to a net production of $1/2O_2$, ATP, and $NADPH+H^+$ with the consumption of solar photons and water.

The concentration of NADPH in the chloroplast may help regulate which pathway electrons take through the light reactions. When the chloroplast runs low on ATP for the Calvin cycle, NADPH will accumulate and the plant may shift from noncyclic to cyclic electron flow.

Pseudocyclic Photophosphorylation

Another way to make up the deficit is by a process called pseudocyclic photophosphorylation in which some of the electrons passing to ferredoxin then reduce molecular oxygen back to H_2O instead of reducing $NADP^+$ to NADPH.

At first glance, this might seem a fruitless undoing of all the hard work of photosynthesis. But look again. Although the electrons cycle from water to ferredoxin and back again, part of their pathway is through the chemiosmosis-generating stem of cytochrome b_6/f.

Here, then, is another way that simply by turning on a light, enough energy is imparted to electrons that they can bring about the synthesis of ATP.

Dark Reaction

The **Calvin cycle, light-independent reactions**, **bio synthetic phase, dark reactions**, or **photosynthetic carbon reduction (PCR) cycle** of photosynthesis are the chemical reactions that convert carbon dioxide and other compounds into glucose. These reactions occur in the stroma, the fluid-filled area of a chloroplast outside the thylakoid membranes. These reactions take the products (ATP and NADPH) of light-dependent reactions and perform further chemical processes on them. The Calvin cycle uses the reducing powers ATP and NADPH from the light dependent reactions to produce sugars for the plant to use. These substrates are used in a series of reduction-oxidation reactions to produce sugars in a step-wise process. There is no direct reaction that converts CO2 to a sugar because all of the energy would be lost to heat. There are three phases to the light-independent reactions, collectively called the Calvin cycle: carboxylation, reduction reactions, and ribulose 1,5-bisphosphate (RuBP) regeneration.

Steps

In the first stage of the Calvin cycle, a CO_2 molecule is incorporated into one of two three-carbon molecules (glyceraldehyde 3-phosphate or G3P), where it uses up two molecules of ATP and two molecules of NADPH, which had been produced in the light-dependent stage. The three steps involved are:

1. The enzyme RuBisCO catalyses the carboxylation of ribulose-1,5-bisphosphate, RuBP, a 5-carbon compound, by carbon dioxide (a total of 6 carbons) in a two-step reaction.[5] The product of the first step is enediol-enzyme complex that can capture CO_2 or O_2. Thus, enediol-enzyme complex is the real carboxylase/oxygenase. The CO_2 that is captured by enediol in second step produces an unstable six-carbon compound called 2-carboxy 3-keto 1,5-biphosphoribotol (CKABP) (or 3-keto-2-carboxyarabinitol 1,5-bisphosphate) that immediately splits into 2 molecules of 3-phosphoglycerate (also written as 3-phosphoglyceric acid, PGA, 3PGA, or 3-PGA), a 3-carbon compound.
2. The enzyme phosphoglycerate kinase catalyses the phosphorylation of 3-PGA by ATP (which was produced in the light-dependent stage). 1,3-Bisphosphoglycerate (1,3BPGA, glycerate-1,3-bisphosphate) and ADP are the products. (However, note that two 3-PGAs are produced for every CO_2 that enters the cycle, so this step utilizes two ATP per CO_2 fixed.)
3. The enzyme glyceraldehyde 3-phosphate dehydrogenase catalyses the reduction of 1,3BPGA by NADPH (which is another product of the light-dependent stage). Glyceraldehyde 3-phosphate (also called G3P, GP, TP, PGAL, GAP) is produced, and the NADPH itself is oxidized and becomes $NADP^+$. Again, two NADPH are utilized per CO_2 fixed.

The next stage in the Calvin cycle is to regenerate RuBP. Five G3P molecules produce three RuBP molecules, using up three molecules of ATP. Since each CO_2 molecule produces two G3P molecules, three CO_2 molecules produce six G3P molecules, of which five are used to regenerate RuBP, leaving a net gain of one G3P molecule per three CO_2 molecules (as would be expected from the number of carbon atoms involved).

The regeneration stage can be broken down into steps.

1. Triose phosphate isomerase converts all of the G3P reversibly into dihydroxyacetone phosphate (DHAP), also a 3-carbon molecule.
2. Aldolase and fructose-1,6-bisphosphatase convert a G3P and a DHAP into fructose 6-phosphate (6C). A phosphate ion is lost into solution.

3. Then fixation of another CO_2 generates two more G3P.
4. F6P has two carbons removed by transketolase, giving erythrose-4-phosphate (E4P). The two carbons on transketolase are added to a G3P, giving the ketose xylulose-5-phosphate (Xu5P).
5. E4P and a DHAP (formed from one of the G3P from the second CO_2 fixation) are converted into sedoheptulose-1,7-bisphosphate (7C) by aldolase enzyme.
6. Sedoheptulose-1,7-bisphosphatase (one of only three enzymes of the Calvin cycle that are unique to plants) cleaves sedoheptulose-1,7-bisphosphate into sedoheptulose-7-phosphate, releasing an inorganic phosphate ion into solution.
7. Fixation of a third CO_2 generates two more G3P. The ketose S7P has two carbons removed by transketolase, giving ribose-5-phosphate (R5P), and the two carbons remaining on transketolase are transferred to one of the G3P, giving another Xu5P. This leaves one G3P as the product of fixation of 3 CO_2, with generation of three pentoses that can be converted to Ru5P.
8. R5P is converted into ribulose-5-phosphate (Ru5P, RuP) by phosphopentose isomerase. Xu5P is converted into RuP by phosphopentose epimerase.
9. Finally, phosphoribulokinase (another plant-unique enzyme of the pathway) phosphorylates RuP into RuBP, ribulose-1,5-bisphosphate, completing the Calvin cycle. This requires the input of one ATP.

Thus, of six G3P produced, five are used to make three RuBP (5C) molecules (totaling 15 carbons), with only one G3P available for subsequent conversion to hexose. This requires nine ATP molecules and six NADPH molecules per three CO_2 molecules.

C4 Pathway (Hatch and Slack Pathway)

Every photosynthetic plant follows Calvin cycle but in some plants, there is a primary stage to the Calvin Cycle known as C4 pathway. Plants in tropical desert regions commonly follow the C4 pathway. Here, a 4-carbon compound called oxaloacetic acid (OAA) is the first product by carbon fixation. Such plants are special and have certain adaptations as well.

The C4 pathway initiates with a molecule called phosphoenolpyruvate (PEP) which is a 3-carbon molecule. This is the primary CO_2 acceptor and the carboxylation takes place with the help of an enzyme called PEP carboxylase. They yield a 4-C molecule called oxaloacetic acid (OAA).

Eventually, it is converted into another 4-carbon compound known as malic acid. Later, they are transferred from mesophyll cells to bundle sheath cells. Here, OAA is broken down to yield carbon dioxide and a 3-C molecule.

The CO_2 thus formed is utilized in the Calvin cycle whereas 3-C molecule is transferred back to mesophyll cells for regeneration of PEP.

Corn, sugarcane and some shrubs are examples of plants that follow the C4 pathway. Calvin pathway is a common pathway in both C3 plants and C4 plants but it takes place only in the mesophyll cells of the C3 Plants but not in the C4 Plants.

Photorespiration

Photorespiration (also known as the **oxidative photosynthetic carbon cycle**, or **C_2 photosynthesis**) refers to a process in plant metabolism where the enzyme RuBisCO oxygenates RuBP, wasting some of the energy produced by photosynthesis. The desired reaction is the addition of carbon dioxide to RuBP (carboxylation), a key step in the Calvin–Benson cycle, but approximately 25% of reactions by RuBisCO instead add oxygen to RuBP (oxygenation), creating a product that cannot be used within the Calvin–Benson cycle. This process reduces the efficiency of photosynthesis, potentially reducing photosynthetic output by 25% in C_3 plants.[1] Photorespiration involves a complex network of enzyme reactions that exchange metabolites between chloroplasts, leaf peroxisomes and mitochondria.

Glycolate pathway is also known as the C_2 cycle of photosynthesis or photorespiration or glycolate-glyoxylate metabolism. It reduces the photosynthesis efficiency of C_3 plants. Glycolate metabolism is also found in unicellular green algae.

This cycle helps in removing 2-phosphoglycolate, a toxic metabolite produced by the oxygenation reaction of RuBisCO. It produces PGA eventually but ~25% of C is released as CO_2 in the process and ATP is also utilised.

Glycolate Pathway (C2 Cycle)

- The process competes with the photosynthesis process. It wastes some of the energy produced by photosynthesis.
- It occurs in Chloroplast, Peroxisomes and Mitochondria.
- The main enzyme of the Calvin cycle RuBisCO has an affinity for both CO_2 and O_2 and they both compete for binding with RuBisCO. Their binding is dependent on the concentration of both the species. At mild temperatures, RuBisCO has a higher affinity for carbon dioxide.
- The process initiates when O_2 binds with RuBisCO. The enzyme adds oxygen to RuBP (Ribulose-1,5-bisphosphate), i.e. oxygenation of RuBPand forms 2-phosphoglycolate and 3PGA (3-phosphoglycerate). This occurs in the chloroplast.

- 3PGA produced at a reduced rate and enters the Calvin cycle.
- 2-phosphoglycolate is translocated to peroxisomes, where it is oxidised to glyoxylate by hydrogen peroxide (H_2O_2). The enzyme catalysing this reaction is Glycolate oxidase.
- Hydrogen peroxide is acted on by catalase, which breaks it to water and oxygen.
- Glyoxylate is converted to Glycine in peroxisomes by Glutamate-glyoxylate aminotransferase.
- Glycine is transported to mitochondria.
- In mitochondria, 2 Glycine molecules (2C) get converted to a Serine (3C). CO_2 and NH_3 are released in the process. This reaction is catalysed by an enzyme called Glycine decarboxylase.
- Serine is transported back to peroxisomes, where it is converted to Glycerate.
- Glycerate is transported back to the chloroplast, where it is phosphorylated to form 3PGA. ATP is used in this reaction. 3PGA enters the Calvin cycle.

It is important to note that RubisCO has a higher affinity for oxygen at increased temperatures. This results in a higher rate of photorespiration in hot and dry environments. To minimise photorespiration, C_4 plants and CAM plants have derived different mechanisms for carbon fixation. Carbon dioxide gets accumulated around RuBisCO in these plants to suppress its oxygenation activity.

CAM plants

Some plants that are adapted to dry environments, such as cacti and pineapples, use the **crassulacean acid metabolism** (**CAM**) pathway to minimize photorespiration. This name comes from the family of plants, the Crassulaceae, in which scientists first discovered the pathway.

Instead of separating the light-dependent reactions and the use of CO_2 in the Calvin cycle in space, CAM plants separate these processes in time. At night, CAM plants open their stomata, allowing CO_2 to diffuse into the leaves. This CO_2 is fixed into oxaloacetate by PEP carboxylase (the same step used by C4 plants), then converted to malate or another type of organic acid^33cubed.

The organic acid is stored inside vacuoles until the next day. In the daylight, the CAM plants do not open their stomata, but they can still photosynthesize. That's because the organic acids are transported out of the vacuole and broken down to release CO_2 which enters the Calvin cycle. This controlled release maintains a high concentration of CO_2 around rubisco.

The CAM pathway requires ATP at multiple steps (not shown above), so like C_4 photosynthesis, it is not an energetic "freebie." However, plant species that use CAM photosynthesis not only avoid photorespiration, but are also very water-efficient. Their stomata only open at night, when humidity tends to be higher and temperatures are cooler, both factors that reduce water loss from leaves. CAM plants are typically dominant in very hot, dry areas, like deserts.

Factors affecting photosynthesis

There are several ways of measuring the rate of photosynthesis in the laboratory. These include:

- the rate of oxygen output
- the rate of carbon dioxide uptake
- the rate of carbohydrate (glucose) production

These are not perfect methods as the plant will also be respiring, which will use up some oxygen and carbohydrate and increase carbon dioxide output.

Several factors can affect the rate of photosynthesis:

- light intensity
- carbon dioxide concentration
- temperature
- chlorophyll

The amount of chlorophyll also affects the rate of photosynthesis:

- plants in lighting conditions unfavourable for photosynthesis synthesise more chlorophyll, to absorb the light required
- the effects of some plant diseases affect the amount of chlorophyll, and therefore the ability of a plant to photosynthesise, such as downy mildew in grape vines

Significance of Photosynthesis

1. Photosynthesis is a source of all our food and fuel. It is the only biological process that acts as the driving vital force for the whole animal kingdom and for the non-photosynthetic organism.

2. It drives all other processes of biological and abiological world. It is responsible for the growth and sustenance of our biosphere.

3. It provides organic substances, which are used in the production of fats, proteins, nucleoproteins, pigments, enzymes, vitamins, cellulose, organic acids, etc. Some of them become structural parts of the organisms.

4. It makes use of simple raw materials such as CO2, H2O and inexhaustible light energy for the synthesis of energetic organic compounds.

5. It is significant because it provides energy in terms of fossil fuels like coal and petrol obtained from plants, which lived millions and millions of years ago.

6. Plants, from great trees to microscopic algae, are engaged in converting light energy into chemical energy, while man with all his knowledge in chemistry and physics cannot imitate them.