Chapter 10

Anabolic, Endergonic (requiring energy), Oxido-Reduction Process, Physico-chemical Process.

Photosynthesis in Higher Plants

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

Chapter Contents

Introduction

It is a process in which green parts of the plants synthesize or manufacture complex organic food substances (carbohydrates) using carbon dioxide and water in the presence of sunlight and release oxygen as a by-product. In this process, energy from the sun is converted into chemical energy. It is an anabolic, endergonic (requiring energy) and oxido-reduction process.

Sunlight plays a much larger role in our sustenance than we may expect, as all the food we eat and all the fossil fuels we use, the air we breathe, they are all products or by-products of photosynthesis. Photosynthesis converts the radiant energy to forms of energy that can be used by the biological systems.

A simple equation representing the process is:

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

This chapter focuses on the metabolic machinery of the photosynthetic plants and the various phases and reactions involved that transform the light energy into chemical energy. We will also study the factors governing the rate of the photosynthetic process.

Let us explore the photosynthetic process which, if rightly said, supports life on earth.

IMPORTANCE OF PHOTOSYNTHESIS

The use of energy from sunlight by plants for photosynthesis is the basis of life on earth. Food represents the stored energy of sun rays and is manufactured by green plants with the aid of sunlight during photosynthesis. Photosynthesis is important due to two reasons :

(i) It is the primary source of food on earth.

(ii) It is also responsible for the release of oxygen into the atmosphere by the green plants which is needed by mostly all life forms.

Did You Know?

According to former estimates, only 10% of dry matter is produced by land plants while 90% of it is formed in oceans. However, the present estimates put the productivity of land plants to be 68% of the total.

WHAT DO WE KNOW?

Study on photosynthesis started around 300 years ago. On the basis of what we have studied in our earlier classes, simple experiments have shown that chlorophyll (green pigment of the leaf), light and CO_2 are required for photosynthesis to occur.

Experiment to demonstrate light & chlorophyll is necessary for photosynthesis : Take a destarched potted plant having variegated leaves and cover 2-3 leaves with the black paper. Expose the potted plant to sunlight for 1-2 hours. Pluck one covered leaf and one exposed leaf and test them for starch. The covered leaf does not show positive starch test showing that photosynthesis cannot occur in the absence of light. The exposed leaf shows blue and yellow parts where the blue colour or positive starch test occurs in the chlorophyll-containing parts.

Experiment to demonstrate CO_2 is necessary for photosynthesis (Moll's Half leaf experiment) : A part of leaf was enclosed in a test tube containing some KOH soaked cotton (which absorbs CO_2), while the other half of leaf was exposed to air. When the two halves of leaf were tested for starch, it was found that only the exposed part of leaf tested positive for starch. This showed us that CO_2 is required for photosynthesis.

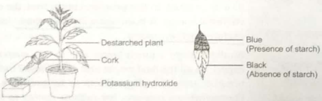


Fig. : Half leaf experiment

HISTORICAL ACCOUNT – EARLY EXPERIMENTS

There have been several simple experiments done which led to a gradual development in our understanding of photosynthesis.

(i) **Joseph Priestley (1733-1804)** in 1770 revealed the essential role of air in the growth of green plants through several experiments. He discovered oxygen in 1774. In an experiment done, Priestley observed that a candle burning in a closed space *i.e.*, a bell jar, soon gets extinguished. Similarly, a mouse would die of suffocation in a closed space (as shown in figure (a)&(b)). Through his experiment, he concluded that both, the burning candle and the mouse damage the air they use. But, when a mint plant was placed in the same bell jar, the mouse stayed alive and the candle continued to burn (as shown in figure (c)&(d)). Thus, Priestley concluded that the plants restore to the air whatever the breathing mouse and the burning candle remove.

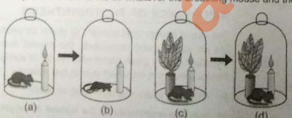


Fig. : Priestley's experiment

(ii) **Jan Ingenhousz (1730–1799)** through his experiments showed that sunlight is essential for the plant process that helps to somehow purify the air fouled by the breathing mouse and the burning candle. In another experiment, with an aquatic plant (*Hydrilla*) he showed that in bright sunlight, small bubbles were formed around the green parts of plant while in the dark, no bubbles were formed. He identified those bubbles to be of oxygen. Therefore, he showed that in the presence of sunlight it is only the green parts of the plants that could release oxygen.

(iii) **Julius von Sachs (1854)** found that the green parts in plants is where glucose is made and glucose is usually stored as starch. Later, he showed that the green substance in plants (now called chlorophyll) is located in special bodies (now called chloroplasts) within the plant cells.

(iv) **T.W. Engelmann (1843–1909)** experimented on *Cladophora*. Using a prism he split light into its spectral components and then he illuminated a green alga, *Cladophora*, placed in a suspension of aerobic bacteria. The bacteria were used to detect the sites of oxygen evolution. He found that the bacteria accumulated mainly in the region of blue and red light of the split spectrum. And thus, the first action spectrum of photosynthesis was described.

The empirical equation representing the total process of photosynthesis for organisms evolving oxygen was understood as :

$$CO_2 + H_2O \xrightarrow{\text{Light}} [CH_2O] + O_2$$

where $[CH_2O]$ represented a carbohydrate.

(v) **Cornelius van Niel (1897–1985)** a microbiologist, based on his studies of purple and green sulphur bacteria demonstrated that during photosynthesis, hydrogen released from a suitable oxidisable compound reduces carbon dioxide to carbohydrates and he inferred that oxygen evolved by the green plants comes from H_2O (water) and not from carbon dioxide. This hypothesis was later proved by using radioisotopic techniques.

$$2H_2A + CO_2 \xrightarrow{\text{Light}} 2A + CH_2O + H_2O$$

where H_2A is the oxidisable compound (H_2O or H_2S).

The correct equation to represent the overall process of photosynthesis could thus be summed as:

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

where $C_6H_{12}O_6$ is glucose and O_2 is released from water.

Ruben, Kamen *et.al.* used heavy but non-radioactive, stable isotope of oxygen ^{18}O to prove that O_2 evolve during light reaction comes from H_2O and not from CO_2.

Light : Sunlight is like a rain of photons of different frequencies. Visible light consists of radiations having a wavelength between 390–760 nm. Part of spectrum used in photosynthesis has a wavelength between 400–700 nm. It is called **photosynthetically active radiation (PAR)**.

WHERE DOES PHOTOSYNTHESIS TAKE PLACE?

Photosynthesis takes place in the green leaves of plants and other green parts of plants like stem etc. The most active photosynthetic tissue in higher plants is the mesophyll of leaves. Mesophyll cells have many chloroplasts, which contain the specialised light-absorbing green pigments, the **chlorophylls**.

Chloroplasts

In photosynthetic eukaryotes, photosynthesis occurs in the subcellular organelle known as the chloroplast. This double membrane-enclosed organelle possess a **third system** of membranes called **thylakoids**.

A stack of thylakoids forms a **granum**. Adjacent grana are connected by unstacked membranes called **stroma lamellae**. The fluid compartment surrounding the thylakoids, called the **stroma**.

There is a clear division of labour within the chloroplast.

(i) Proteins and pigments (chlorophylls and carotenoids) that function in the photochemical events of photosynthesis, *i.e.*, trapping the light energy and synthesis of ATP and NADPH, are embedded in the thylakoid membrane.

(ii) In stroma, enzymatic reactions incorporate CO_2 into the plant leading to the synthesis of sugar, which in turn forms starch. : CO_2 Assimilation ⇒ Dark Reaction [C3 cycle or Calvin Cycle]

The former set of reactions, since they are directly light-driven are called **light reactions**. The latter are not directly light-driven but are dependent on the products of light reactions (ATP and NADPH). Hence, to distinguish the latter they are called by convention, as **dark reactions**. However, this should not be construed to mean that they occur in darkness or that they are not light-driven.

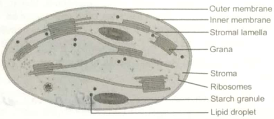


Fig. : Diagrammatic representation of an electron micrograph of a section of chloroplast

PHOTOSYNTHETIC PIGMENTS

Pigments are substances that have an ability to absorb light, at specific wavelengths.

A chromatographic separation of the leaf pigments shows that the colour of leaves is due to four pigments :

(i) **Chlorophyll a** – Bright or blue green in the chromatogram.

(ii) **Chlorophyll b** – Yellow-green

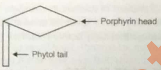
(iii) **Xanthophylls** – Yellow

(iv) **Carotene** – Yellow to yellow-orange

Of these, **chlorophyll-a is the primary photosynthetic pigment**.

Chlorophyll Pigments

Chlorophyll has a tadpole like structure. It consists of a porphyrin head and a phytol tail.



Porphyrin head :

(i) All chlorophylls have a complex ring structure chemically related to the **porphyrin**-like groups found in haemoglobin and cytochromes.

(ii) Site of the electrons rearrangements when the chlorophyll is excited.

(iii) A cyclic tetrapyrrolic structure with non-ionic magnesium atom.

Phytol tail :

(i) A long hydrocarbon tail is almost always attached to the ring structure.

(ii) Anchors the chlorophyll to the hydrophobic portion of the thylakoids.

Major types of chlorophylls are chlorophyll a, b, c, d, e; bacteriochlorophyll a and b etc.

Accessory Pigments

All pigments other than chlorophyll *a* are called accessory pigments.

These have two major roles in photosynthesis :

(i) They absorb light of different wavelengths and transfer the energy to chlorophyll molecules, thus they are also called **antenna molecules**. This enables a wider range of wavelength of incoming light to be utilised for photosynthesis. Chlorophyll b accounts for about one-fourth of total chlorophyll content.

(ii) Carotenoids protect plant from excessive heat and prevent photo-oxidation (oxidative destruction by light) of chlorophyll pigments. Thus, they are also called **"Shield Pigments"**.

Let us study the graph showing ability of pigments to absorb lights of different wavelengths.

Absorption spectrum : The graphic curve showing the amount of energy of different wavelengths of light absorbed by a substance/pigments.

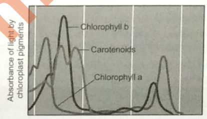


Fig. : Graph showing the absorption spectrum of chlorophyll a, b and the carotenoids

Action spectrum : The graphic curve showing the relative rates of photosynthesis at different wavelengths of light.

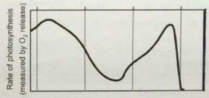


Fig. : Graph showing action spectrum of photosynthesis

Action spectrum of photosynthesis corresponds closely to absorption spectra of chlorophyll a showing that chlorophyll a is the chief pigment associated with photosynthesis.

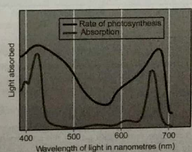


Fig. : Graph showing action spectrum of photosynthesis superimposed on absorption spectrum of chlorophyll a

These graphs, together, show that most of the photosynthesis takes place in the blue and red regions of the spectrum, some photosynthesis does take place at the other wavelengths of the visible spectrum. These graphs depict that maximum photosynthesis occurs at the wavelength at which there is maximum absorption by chlorophyll *a i.e.*, in the blue and red regions.

Example 1 : *Why do chloroplasts align themselves along the walls of the mesophyll cells?*

Solution : Chloroplasts align themselves along the walls of the mesophyll cells for the following two reasons.

(i) For easy diffusion of gases.

(ii) To receive optimum quantity of incident light.

Example 2 : *Why do chloroplast align themselves in vertical position along the lateral walls of the mesophyll cells?*

Solution : Chloroplast align themselves in vertical position along the lateral walls under high light intensities. This is to protect themselves or pigment system against destruction by light.

Try Yourself

1. On which green alga, action spectrum of photosynthetic pigments was studied by Engelmann?
   (1) *Nostoc* (2) *Cladophora*
   (3) *Chlorella* (4) *Scenedesmus*
2. Dark reactions of photosynthesis occur in
   (1) Grana (2) Thylakoid
   (3) Stroma lamellae (4) Stroma

FACT FILE

1. Both red and blue light are equally effective in photosynthesis but red light is more efficient.
2. For biosynthesis of chlorophyll, raw material required are succinyl Co-A and glycine.

WHAT IS LIGHT REACTION?

Light reactions or the 'Photochemical' phase is thought to be responsible for the formation of high-energy chemical intermediates, ATP and NADPH, and it includes light absorption, water splitting and release of oxygen. Several complexes are involved in this process which are discussed below :

THE PHOTOSYNTHETIC UNITS / PIGMENT SYSTEMS

These are group of pigments molecules which take part in the conversion of light energy into the chemical energy. The photosynthetic units are called **Photosystem I (PS-I)** and **Photosystem II (PS-II)**. Each unit has a **reaction centre** of a specific chlorophyll *a* molecule which absorbs light energy of long wavelength. These center can release electron upon absorption of energy. In PS-I, the reaction centre chlorophyll *a* has an

absorption peak at 700 nm, hence is called P_{700}, while in PS-II, reaction centre has an absorption maxima at 680 nm and is called P_{680}.

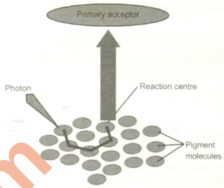


Fig. : The light harvesting complex

Reaction centre is surrounded by number of light harvesting pigment (LHP) molecules. These are also called **antenna molecules**. These absorb photons of different wavelength and transfer this energy to reaction centre. Harvesting molecules occur in form of specific complexes called **light-harvesting complexes** (LHC) called LHC-I and LHC-II. The pigment molecules of these complexes are bound to proteins. These help to make photosynthesis more efficient. LHP molecules also called Antenna Molecules.

PS-I → Reaction centre (P_{700}); LHC-I → LHP, Proteins

PS-II → Reaction centre (P_{680}); LHC-II → LHP, Proteins

Some of the important differences between the two photosystems are :

Photosystem I / Pigment system I	Photosystem II / Pigment system II
1. The reaction centre is P_{700} of chl a	1. The reaction centre is P_{680} of chl a
2. PS I lies on the outer surface of the thylakoids.	2. PS II occurs on the inner surface of the thylakoids.
3. Found in both grana and stroma lamellae.	3. Found in grana lamellae only.
4. Participates in both cyclic as well as non-cyclic flow of electrons.	4. It is involved only in non-cyclic flow of electrons.
5. Not associated with splitting of water.	5. Associated with splitting of water and release of O_2.

The NADP reductase enzyme is located on Stroma side (fluid compartment)

Production of Assimilatory Powers in Photosynthesis Stroma lamella lack PS II & NADP reductase enzyme

Arnon used the term assimilatory powers to refer ATP and NADPH.

The process of reduction of NADP into NADPH + H⁺ may be denoted as electron transport system (ETS) in photosynthesis while the process of formation of ATP from ADP and inorganic phosphate (iP) utilising light energy is called **photophosphorylation**.

The flow of electrons through ETS is linked to photophosphorylation.

THE ELECTRON TRANSPORT

Electron transport chain is a series of electron carriers over which electrons pass in a downhill journey releasing energy at every step that is used in generating an electrochemical proton gradient which helps in synthesising ATP.

> **Note :** ***Redox potential :*** *It is the measure of the tendency of a chemical species to acquire electrons and thereby get reduced. Also, called oxidation-reduction potential, it is measured in volts (V) or milli volts (mV).*

Based on path of electron, associated photophosphorylation can be identified as non-cyclic and cyclic photophosphorylation.

Non-Cyclic Photophosphorylation

Both PS I & PS II | Z-Scheme | In Grana lamellae

It involves both Photosystem I and Photosystem II. These two photosystems work in series, first PS II and then PS I. The two photosystems are connected through an electron transport chain. Both ATP and NADPH + H^+ are synthesised by this kind of electron flow.

First in PS II, the P_{680} molecule absorbs 680 nm wavelength of red light causing electrons to become excited and jump into an orbit which is farther from the atomic nucleus.

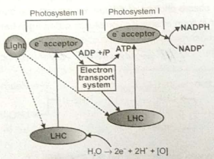


Fig. : Z scheme of light reaction

These electrons are picked up by an electron acceptor which passes them to an **electron transport system of cytochromes**. This movement of electrons is downhill on redox potential scale. The electrons are then passed onto the pigments of PS I, without being used as they pass through the electron transport chain. Simultaneously, electrons in the reaction center of PS I (P_{700}) are excited when they receive light of wavelength 700 nm and these electrons are transferred to another acceptor molecule that has a greater redox potential. These electrons are then moved downhill again to a molecule of $NADP^+$. The addition of these electrons reduces the $NADP^+$ to NADPH + H^+.

The whole scheme of transfer of electrons, starting from the PS II, uphill to the acceptor, down the electron transport chain to PS I, excitation of electrons, transfer to another acceptor and finally downhill to $NADP^+$ causing it to be reduced to NADPH + H^+ is called **Z-scheme**. This shape is formed when all the carriers are placed in a sequence on a redox potential scale.

Splitting of Water

The electrons that were removed from PS II must be replaced. This is achieved by electrons available due to splitting of water. The water splitting complex is associated with the PS II, which itself is physically located on the inner side of the membrane of the thylakoid. Water is split into H^+, [O] and electrons. The protons and oxygen formed by splitting of water is released within the lumen of the thylakoids. The oxygen produced is released as one of the net products of photosynthesis.

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

Cyclic Photophosphorylation

Only PS I | In Stroma lamellae

The process of cyclic photophosphorylation involves only PS I and this process takes place in the stroma lamellae membrane. When only PS I is functional, the electron is circulated within the photosystem and the phosphorylation occurs, due to cyclic flow of electrons.

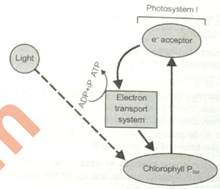


Fig. : Cyclic photophosphorylation

The membrane or lamella of the grana have both PS I and PS II, the stroma lamella membranes lack PS II as well as NADP reductase enzyme. The excited electron does not pass on to $NADP^+$ and is cycled back to the PS I complex through the electron transport chain. Cyclic photophosphorylation also occurs when only light of wavelength beyond 680 nm are available for excitation.

> **Knowledge Cloud**
>
> **Hill** and **Bendall** proposed Z-scheme. Reaction centre is involved in "quantum conversion" where energy of light is converted to chemical energy possessed by excited electron.

Some important differences between Cyclic and Non-cyclic photophosphorylation are as follows :

Cyclic Photophosphorylation	Non-cyclic Photophosphorylation
1. It is performed by photosystem I independently.	1. It is performed by collaboration of both photosystems II and I.
2. An external source of electrons is not required.	2. The process requires an external electron donor.
3. It is not connected with photolysis of water. Therefore, no oxygen is evolved.	3. It is connected with photolysis of water and liberation of oxygen occurs.
4. It synthesises ATP only.	4. It is not only connected with ATP synthesis, but also with production of NADPH. ATP & NADPH used in C_3 cycle.
5. It operates under low light intensity, anaerobic conditions or when CO_2 availability is poor.	5. Non-cyclic photophosphorylation takes place under optimum light, aerobic conditions and in the presence of carbon dioxide.
6. The system does not take part in photosynthesis except in certain bacteria.	6. The system is connected with CO_2 fixation in green plants.
7. It occurs mostly in stroma lamellae membrane. (membrane)	7. It occurs in the granal thylakoids.

Chemiosmotic Hypothesis

Chemiosmotic hypothesis was explained by P. Mitchell. This mechanism explains how ATP is synthesised in the chloroplast. ATP synthesis is linked to the development of a proton gradient across the membrane of the thylakoid and the proton accumulation is towards the inside of the membrane *i.e.*, in the lumen.

There are several processes that take place during activation of electrons and their transport which lead to the development of a proton gradient :

(a) **Photolysis of water towards thylakoid lumen :** The splitting of the water molecule takes place on the inner side of the membrane and so the hydrogen ions (protons) that are produced, they accumulate within the lumen of the thylakoids.

(b) **Transfer of H^+ from stroma to lumen as electrons move through photosystems :** The primary acceptor of electron located towards the outer side of the membrane transfers its electron to a H^+ carrier, and this molecule then removes a proton from the stroma while transporting an electron. When this H^+ carrier molecule passes on its electron to an electron carrier present on the inner side of the membrane, the H^+ is released into the lumen of the membrane.

(c) **NADPH reductase reaction occur towards stroma :** The NADP reductase enzyme is located on the stroma side of the membrane. Protons are necessary for the reduction of $NADP^+$ to NADPH + H^+ and these protons are removed from the stroma.

So, within the chloroplast, protons in the stroma decrease in number, while in the lumen there is accumulation of protons. This causes a decrease in pH in the lumen and creates a proton gradient across the thylakoid membrane.

This gradient is important because the breakdown of this gradient leads to release of energy. The gradient is broken down due to the movement of protons across the membrane to the stroma through the transmembrane channel of the F_0 of the ATPase. The **ATPase enzyme** consists of two parts: one called the F_0 is embedded in the membrane and forms a transmembrane channel that carries out facilitated diffusion of protons across the membrane. The other portion is called F_1 and protrudes on the outer surface of the thylakoid membrane on the side that faces the stroma. The breakdown of this gradient provides enough energy to cause a conformational change in the F_1 part of the ATPase, which makes the enzyme synthesise several molecules of ATP.

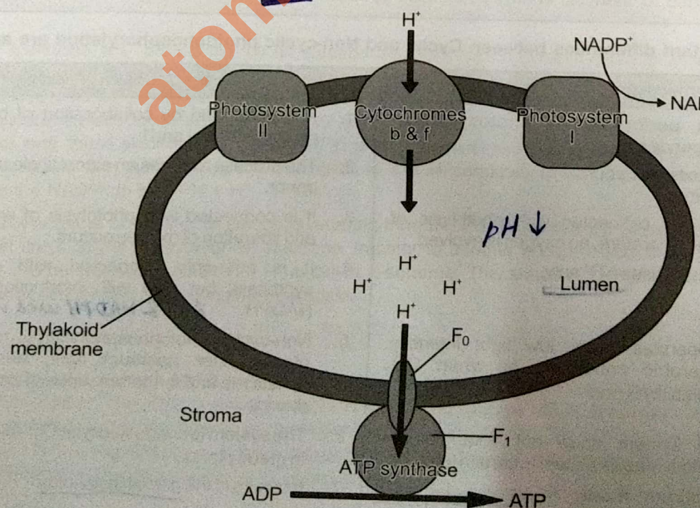


Fig. : ATP synthesis through chemiosmosis

Chemiosmosis process requires a membrane, a proton pump, a proton gradient and ATPase enzyme. Energy is used to pump protons across the membrane into the lumen, which creates a proton gradient across the membrane. ATPase enzyme has transmembrane channel that allows diffusion of protons back across the membrane, this releases energy to activate ATPase enzyme which catalyses the formation of ATP.

Along with the NADPH produced, the ATP is used in the biosynthetic reaction taking place in the stroma, responsible for the fixation of carbon dioxide and synthesis of sugars.

Example 3 : *Which molecule in non-cyclic photophosphorylation donates electron to PS II?*

Solution : Water, via water splitting complex donate electron to PS II in non-cyclic photophosphorylation.

Example 4 : *Cyclic photophosphorylation occurs when only light of wavelengths ________ are available.*

(i) Below 680 nm (ii) Beyond 680 nm

(iii) 400 nm and below (iv) Beyond 400 nm

Solution : Beyond 680 nm.

Example 5 : *Why NADPH + H^+ is not synthesized during the cyclic photophosphorylation?*

Solution : Cyclic photophosphorylation involves only the PS I and this process takes place in the stroma lamella membrane, which lacks PS II and NADP reductase enzyme. Thus, it results only in the synthesis of ATP and not of NADPH + H^+.

Try Yourself

3. Mark out the incorrect statement.
   (1) PS II is found in both grana and stroma lamellae
   (2) PS II is involved in photolysis of water
   (3) PS I participates in both cyclic as well as non-cyclic flow of electrons
   (4) The reaction centre in PS II is P_{680}
4. An external source of electrons is not required in
   (1) Cyclic photophosphorylation (2) Non-cyclic photophosphorylation
   (3) Z-scheme of flow of electrons (4) All of these

EXERCISE

1. Select the incorrect statement w.r.t. photosynthesis.
   (1) Anabolic, endergonic and redox process
   (2) Physico-chemical process using light energy to drive the synthesis of organic compounds
   (3) Of the total world's photosynthesis, 90% is carried out by fresh water plants
   (4) Annually 4 × 10^{13} kg of carbon is fixed through photosynthesis in biosphere

2. Action spectrum of photosynthetic pigments was studied by Englemann on Cladophora in the presence of Aerobic bacteria.
(1) *Spirogyra*, Anaerobic (2) *Cladophora*, Aerobic
(3) *Chlorella*, Aerobic (4) *Scenedesmus*, Anaerobic

3. Anoxygenic and oxygenic photosynthesis are respectively shown by
(1) Green algae & red algae
(2) Red algae & monocots
(3) Pigmented sulphur bacteria & cyanobacteria
(4) BGA & higher plants

4. OEC is located in/on
(1) Outer surface of granal membrane (2) Lumen of stroma lamellae
(3) Inner surface of thylakoid membrane (4) Stroma

5. Pigments are organised into two discrete photochemical light harvesting complexes within the PS I and PS II. These are named in
(1) The sequence of discovery
(2) Which they function in light reaction
(3) The sequence of arrangement of chlorophylls
(4) More than one option is correct

6. Select incorrect statement
(1) Each photosystem has all the pigments except one molecule of chlorophyll a
(2) Action spectra is greater in blue and red light
(3) Chlorophyll a & b are primary pigments associated with photosynthesis
(4) PS II is involved in evolution of O_2

7. Primary electron acceptor in cyclic photophosphorylation is
(1) Phaeophytin (2) Fe-S
(3) PC (4) Cyt-b_6-f complex

8. Whole scheme of transfer of electrons, starting from the PS II, uphill to the acceptor, down the electron transport chain to PS I, excitation of electrons, transfer to another acceptor, and finally down hill to $NADP^+$ causing it to be reduced to NADPH + H^+ is called
(1) Oxidative phosphorylation (2) Cyclic photophosphorylation
(3) PCR cycle (4) Z-scheme

9. Which of the following is **not** a requirement of chemiosmosis?
(1) RuBisCO (2) Membrane
(3) ATPase enzyme (4) Proton pump

10. Stroma lamellae membrane lacks
(1) PS I only (2) PS II only
(3) PS I and electron carriers (4) PS II and NADP reductase

WHERE ARE ATP AND NADPH USED?

Dark Reaction or Biosynthetic Reaction

The products of light reaction *i.e.*, ATP and NADPH are essential for assimilation of CO_2 to carbohydrates. **This is the biosynthetic phase of photosynthesis**. These reactions take place in the **stroma** of chloroplast where all the enzymes required are present. This process does not depend directly on the presence of light but is dependent on the products of light reaction *i.e.*, ATP and NADPH. This could also be verified as immediately after light becomes unavailable, this biosynthetic process continues for some time and then stops. But, if then, light is made available again, the synthesis starts again. Hence, calling the biosynthetic phase as the dark reaction is a misnomer. The dark reaction occurs through Calvin cycle. Calvin cycle may be supported by C_4 cycle or Crassulacean Acid Metabolism (CAM) in certain plants.

Calvin Cycle or C_3 Cycle

Melvin Calvin used radioactive ^{14}C in algal photosynthesis studies. This led to the discovery that the first CO_2 fixation product was a three-carbon organic acid. He also helped to mark out the complete biosynthetic pathway, hence it is called **Calvin Cycle**. The first stable product identified was 3-phosphoglyceric acid (PGA), hence it is named C_3 pathway. Calvin cycle occurs in **all photosynthetic plants** whether they have C_3 or C_4 pathway. Radioactive C^{14} was used.

Primary Acceptor of CO_2

The primary acceptor molecule during the C_3 cycle is a five-carbon ketose sugar–Ribulose bisphosphate (RuBP). The enzyme for CO_2 fixation is RuBisCO (Ribulose Bisphosphate Caboxylase Oxygenase). It is the **most abundant** enzyme on earth. It is characterised by the fact that its active site can bind to both CO_2 and O_2, hence the name. RuBisCO has a much greater affinity for CO_2 than for O_2 and the binding is competitive. It is the relative concentration of O_2 and CO_2 that determines which of the two will bind to the enzyme. Before the scientists discovered the 5-carbon ketose sugar as primary acceptor it was believed that since the first product was a C_3 acid, the primary acceptor would be a 2-carbon compond.

Stages of Calvin Cycle

Calvin cycle can be described under three stages :

(i) **Carboxylation :** It is the fixation of CO_2 into a stable organic intermediate. In this, CO_2 is utilised for the carboxylation of RuBP. This reaction is catalysed by the enzyme RuBisCO and it results in the formation of two molecules of 3-PGA (3-Phosphoglyceric acid).

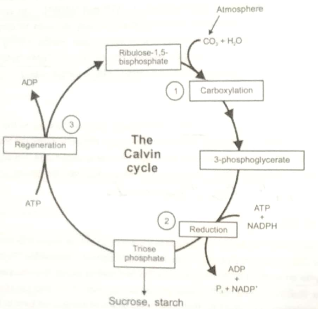
(ii) **Reduction :** These reactions lead to the formation of glucose. The steps involve utilisation of two molecules of ATP for phosphorylation and two of NADPH for reduction, per molecule of CO_2 fixed. The fixation of six molecules of CO_2 and six turns of the cycle are required for the removal of one molecule of glucose from the pathway.

(iii) **Regeneration :** For the cycle to continue uninterrupted, regeneration of the CO_2 acceptor molecule is crucial. This step requires one ATP for phosphorylation to form RuBP. To make one molecule of glucose six turns of the cycle are required. 18 ATP and 12 NADPH molecules are used to make a molecule of glucose. Hence, for every CO_2 molecule entering the Calvin cycle, three molecules of ATP and two molecules of NADPH are required.

For every CO_2 molecule entering Calvin cycle, three molecules of ATP and two molecules of NADPH are required. It is to meet this difference in number of ATP and NADPH that the cyclic phosphorylation takes place.

FACT FILE

RuBisCO and many other enzymes of Calvin cycle are regulated by light.



Summary of Calvin cycle :

In	Out
6 CO_2	1 Glucose
18 ATP	18 ADP
12 NADPH	12 NADP

THE C_4 PATHWAY (HATCH AND SLACK PATHWAY)

Most of the plants that are adapted to dry tropical regions have the C_4 pathway, e.g., Sugarcane, Maize, *Sorghum*, *Amaranthus* etc. In these plants, **double fixation** of carbon dioxide occurs. The initial or the first product of this pathway is a four carbon compound–Oxaloacetic acid (OAA) and hence the name. Two Australian botanists **Hatch** and **Slack** discovered that tropical plants are much more efficient in CO_2 utilization. Hence, Hatch-Slack cycle was named.

C_4 plants are special as they have a special type of leaf anatomy, they can tolerate higher temperatures, they show a response to high intensities of light, they lack a wasteful process called photorespiration, thus they show greater productivity and higher yield as compared to the C_3 plants.

The C_4 pathway requires the presence of two types of cells *i.e.*, **mesophyll cells** and **bundle sheath cells**. The particularly large cells around the vascular bundles of C_4 plants are called bundle sheath cells, these cells may form several layers around the vascular bundles, they are characterised by having large number of chloroplasts, grana are absent, thick walls impervious to gaseous exchange and no intercellular spaces. This special anatomy of leaves of the C_4 plants is called **'Kranz' anatomy**. 'Kranz' means wreath and is a reflection of the arrangement of cells.

Process of Hatch-Slack Pathway

It is a cyclic process. The primary CO_2 acceptor is a three-carbon molecule **phosphoenol pyruvate (PEP)** and it is present in mesophyll cells. The enzyme that catalyses this CO_2 fixation is **PEP carboxylase or PEPcase**. The mesophyll cells of C_4 plants lack the enzyme RuBisCO. The 4-carbon oxaloacetic acid (OAA) is formed in the mesophyll cells. It is then converted to other four-carbon compounds like malic acid or aspartic acid in the mesophyll cells itself, these are then transported to the bundle sheath cells. In the bundle sheath cells, these C_4 acids are broken down to release CO_2 and a three-carbon molecule. The CO_2 released in the bundle sheath cells enters the C_3 or the Calvin pathway.

The bundle sheath cells are rich in an enzyme RuBisCO, but lacks PEPcase. The three-carbon molecule is transported back to the mesophyll cells where it is converted to PEP again with the help of a **cold sensitive enzyme**, called PEP synthetase, thus completing the cycle.

Thus, the basic pathway that results in the formation of the sugars, the Calvin pathway is common to the C_3 and C_4 plants.

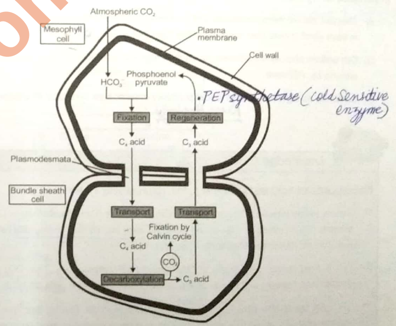


Fig. : Diagrammatic representation of the Hatch and Slack Pathway

Regeneration of PEP from C_3 acid requires 2 ATP equivalent. However, there is no net gain or loss of NADPH in **C_4 cycle**.

ATP consumed in C_4 plants :

C_4 cycle – 2 ATP per CO_2 fixed

C_3 cycle – 3 ATP per CO_2 fixed

Total – 5 ATP per CO_2 fixed

Thus, to form a hexose or to fix 6 CO_2, 6 × 5 ATP = 30 ATP are consumed.

Some major differences between C_3 pathway and C_4 pathway are :

C_3 pathway	C_4 pathway
1. The primary acceptor of CO_2 is RuBP – a five carbon compound.	1. The primary acceptor of CO_2 is PEP – a three carbon compound.
2. The first stable product is 3-phosphoglycerate (3C-compound).	2. The first stable product is oxaloacetic acid (4C-compound).
3. It occurs in the mesophyll cells of the leaves.	3. It occurs in the mesophyll and bundle-sheath cells of the leaves.
4. It is a slower process of carbon fixation.	4. It is a faster process of carbon fixation.
5. 3ATP are consumed to fix one CO_2.	5. 2ATP are consumed to fix one CO_2.

Importance of C_4 Plants

(i) They can tolerate saline conditions due to abundant occurrence of organic acids (malic and oxaloacetic acid) in them which lowers their water potential than that of soil. so water moves in.

(ii) Can perform photosynthesis even when their stomata are closed due to the presence of strong CO_2 fixing enzyme *i.e.* PEPcase.

(iii) Concentric arrangement of cells in leaf produces smaller area in relation to volume for better water utilisation. Kranz Anatomy

Knowledge Cloud

CRASSULACEAN ACID METABOLISM (CAM) (Diurnal acid cycle) :

(i) Certain plants called CAM plants (with Crassulacean Acid Metabolism – CAM) have **scotoactive stomata**. These plants fix CO_2 during night but form sugars only during day (when RuBisCO is active), *e.g.*, *Sedum*, *Kalanchoe*, Pineapple, *Opuntia*.

(ii) CO_2 is fixed during night (dark) to OAA using PEP carboxylase. This CO_2 comes from respiration (breakdown of starch) and also from the atmosphere. Malic acid gets stored in **vacuoles**.

(iii) The CAM plants also contain the enzymes of Calvin cycle. During day time, malic acid breaks into pyruvate and CO_2. While CO_2 enters the Calvin cycle, pyruvate is used up to regenerate PEP.

(iv) The succulents, therefore synthesize plenty of organic acids from CO_2 during night (when stomata are open) and plenty of carbohydrates during the day (when stomata are closed).

(v) Like Calvin cycle, CAM cycle also operates in the mesophyll cell. None of these have shown chloroplast dimorphism as is found in C_4 plants.

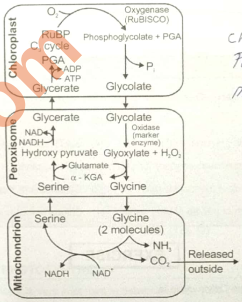
(vi) It should be remembered that the slow growing desert succulents exhibiting CAM cycle have the slowest photosynthetic rate, while the species possessing C_4 pathway possess the highest rates.

(vii) Thus, CAM plants are although not as efficient as C_4 plants, they are definitely better suited to the adverse conditions (*i.e.*, conditions of extreme desiccation).

PHOTORESPIRATION or C_2 cycle

Photorespiration is a process which involves loss of fixed carbon as CO_2 in plants in the presence of light. It is initiated in chloroplasts. This process does not produce ATP or NADPH and is a **wasteful process**.

Photorespiration occurs usually when there is high concentration of oxygen. Under such circumstances, RuBisCO, the enzyme that catalyses the carboxylation of RuBP during the first step of Calvin cycle, functions as an oxygenase. Some O_2 does bind to RuBisCO and hence CO_2 fixation is decreased. The RuBP binds with O_2 to form one molecule of PGA (3C compound) and phosphoglycolate (2C compound) in the pathway of photorespiration. There is neither the synthesis of sugar, nor of ATP. Rather, it results in the release of CO_2 with the utilisation of ATP. It leads to a 25 percent loss of the fixed CO_2. O_2 is first utilized in chloroplast and then in peroxisomes.



Reactions of C_2 pathway

Chloroplast, Peroxisomes } O_2 is utilised
Mitochondria → Loss of CO_2

Photorespiration or C_2 cycle involves three organelles viz., chloroplast, peroxisomes and mitochondria. Loss of CO_2 occurs in mitochondria.

In C_4 plants, photorespiration does not occur. **This is because these plants have a mechanism that increases the concentration of CO_2 at the enzyme site.** During the C_4 pathway, when the C_4 acid from the mesophyll cells is broken down in the bundle sheath cells, it releases CO_2 – this results in increasing the intracellular concentration of CO_2. This in turn, ensures that the RuBisCO functions as a carboxylase minimising the oxygenase activity.

Thus, the productivity and yields are better in C_4 plants as compared to C_3 plants. In addition, the C_4 plants show tolerance to higher temperature also.

Knowledge Cloud

Photorespiration is not related to aerobic respiration as aerobic respiration occurs throughout the day and night in all types of cells, but photorespiration occurs in presence of light in green cells only. ATP is produced in aerobic respiration unlike photorespiration where ATP is consumed. Photorespiration utilizes a part of light energy and saves the plant from photo-oxidative damage.

Example 6 : *Why do the C_4 plants show better yield and high productivity than C_3 plants?*

Solution : The C_4 plants have evolved a mechanism to avoid photorespiration which may otherwise lead to 25 percent loss of CO_2 fixed. These plants have a mechanism that increases the concentration of CO_2 at the RuBisCO site and thus minimising the oxygenase activity of the enzyme.

Example 7 : *What is the net consumption of ATP and NADPH for every CO_2 molecule fixed in C_4 plants?*

Solution : Five molecules of ATP and 2 molecules of NADPH are net consumed for every CO_2 molecule fixed in C_4 plants.

Try Yourself

5. Regeneration step in C_3 cycle per CO_2 fixation requires
   (1) 1 ATP (2) 6 ATP
   (3) 1 NADPH + H⁺ and 1 ATP (4) 3 ATP and 2 NADPH + H⁺
6. The primary enzyme necessary for carboxylation in C_4 plants is present in
   (1) Chloroplast of mesophyll cells (2) Cytoplasm of mesophyll cells
   (3) Cytoplasm of bundle sheath cells (4) Chloroplast of bundle sheath cells

EXERCISE

11. The most crucial step of the Calvin cycle is
    (1) Decarboxylation (2) Carboxylation
    (3) Reduction (4) Regeneration
12. Which one of the following statement is incorrect for carboxylating enzyme in C_3 plants?
    (1) Bifunctional nature
    (2) Can bind with CO_2 only
    (3) Its old name was carboxydismutase
    (4) Located in stroma or matrix of chloroplasts
13. ATP as well as NADPH + H⁺ both are required during the conversion of _______ in C_3 cycle.
    (1) RuBP + CO_2 → 2 × PGA (2) PGA → PGAL
    (3) PGAL → DHAP (4) Fructose 1, 6 biphosphate → Glucose
14. Regeneration of each RuBP in C_3 cycle requires
    (1) 1 ATP (2) 6 ATP
    (3) 1 ATP and 1 NADPH + H⁺ (4) 3 ATP and 2 NADPH + H⁺

15. Double carboxylation with spatial difference is characteristic of
    (1) *Triticum* (2) *Pisum*
    (3) *Saccharum* (4) *Bryophyllum*
16. Primary carboxylating enzyme in C_4 plants is found in
    (1) Chloroplast of mesophyll cells (2) Cytoplasm of mesophyll cells
    (3) Chloroplast of bundle sheath cells (4) Cytoplasm of bundle sheath cells
17. How many additional ATP are used during synthesis of two molecules of hexose sugar in maize than tomato?
    (1) 12 (2) 36
    (3) 24 (4) 8
18. In photorespiration, glycolate and glycine synthesis occurs respectively in
    (1) Chloroplast and mitochondria (2) Peroxisome and chloroplast
    (3) Chloroplast and peroxisome (4) Peroxisome and mitochondria
19. Photorespiration occurs in
    (1) Plants having dimorphic chloroplasts (2) Plants possessing Kranz anatomy
    (3) C_3 plants (4) Both C_4 and C_3 plants
20. The primary CO_2 acceptor molecule during the C_3 cycle is a
    (1) Ketose sugar (2) 5 C compound
    (3) PEP (4) Both (1) & (2)

FACTORS AFFECTING PHOTOSYNTHESIS

The rate of photosynthesis is very important in determining the yield of the plants including crop plants. An understanding of the factors that affects photosynthesis is very necessary. Photosynthesis is under the influence of both external and internal (plant) factors.

The **external factors** include the availability of sunlight, temperature, CO_2 concentration and water. Though several factors interact and simultaneously affect photosynthesis rate, at any point the rate is determined by the factors available at sub-optimal levels.

The **plant factors** include the number, size, age and orientation of leaves, mesophyll cells and chloroplasts, internal CO_2 concentration and amount of chlorophyll. The plant factors are dependent on the genetic predisposition and the growth of the plant.

In 1905, Blackman gave the **Law of Limiting factors**. When several factors affect any biochemical process, then this law comes into effect. This states that:

If a chemical process is affected by more than one factor, then its rate will be determined by the factor which is nearest to its minimal value. It is the factor which directly affects the process if its quantity is changed.

To illustrate the law, suppose light intensity supplied to a leaf is just sufficient to utilize 5 mg of CO_2 per hour in photosynthesis. As the CO_2 supply is increased, the rate also increases till 5 mg of CO_2 enters the leaf per hour. After that, any further increase in the supply of CO_2 does not have any affect upon the rate. Light has now become the limiting factor and further increase in rate of photosynthesis will occur only by increasing the intensity of light.

(A) External factors affecting photosynthesis

Light : It is an essential factor for photosynthesis. It affects the rate of photosynthesis as :

(i) **Light intensity :** There is a linear relationship between incident light and CO_2 fixation at low light intensities. At higher light intensities, gradually the rate does not show further increase as other factors become limiting. The light saturation occurs at 10 percent of the total sunlight available to plants. Increase in incident light beyond a point causes the breakdown of chlorophyll and thus resulting in decrease in photosynthesis. Hence, except for plants in shade or in dense forests, light rarely becomes a limiting factor.

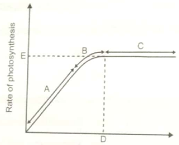


Fig. : Graph of light intensity on the rate of photosynthesis

(ii) **Light quality :** Light between 400–700 nm wavelength constitute the photosynthetically active radiation (PAR). Maximum photosynthesis takes place in red and blue light of the visible spectrum and minimum photosynthesis takes place in green light.

(iii) **Duration of light :** Light duration does not affect the rate of photosynthesis, but it affects the overall photosynthesis.

Carbon Dioxide Concentration

It is a **major limiting factor** influencing the rate of photosynthesis. The concentration of CO_2 is very low in the atmosphere (between 0.03 percent and 0.04 percent). This level of carbon dioxide is far below the requirement for optimum photosynthesis. Increase in concentration up to 0.05 percent can cause an increase in the rate of photosynthesis but beyond this level, it becomes damaging over longer periods.

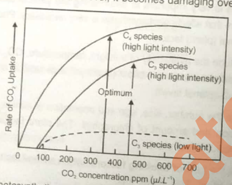


Fig. : Photosynthetic response of C_3 and C_4 plants to CO_2 concentration

The C_3 and C_4 plants respond differently to CO_2 concentration. At low light intensities neither type responds to high CO_2 concentration. At high light intensities, both C_3 and C_4 plants show increase in the rate of photosynthesis. The C_4 plants show saturation at about 360 μlL^{-1} (ppm), while C_3 plants show saturation only beyond 450 μlL^{-1} (ppm), thus, the current concentration of CO_2 is limiting for C_3 plants.

As C_3 plants respond to higher CO_2 concentration by showing increased rate of photosynthesis, leading to higher productivity, this has been used for the production of greenhouse crops like tomatoes and bell pepper. These crops are allowed to grow in CO_2 enriched atmosphere that leads to higher yields (CO_2 fertilization effect).

Temperature : Photosynthesis can take place over a wide range of temperatures. The light reactions are temperature senstive but they are affected to a much lesser extent. The dark reactions being enzymatic are temperature controlled. Again, the temperature optimum for photosynthesis of different plants also depends on the habitat that they are adapted to. Tropical plants have a higher temperature optimum than the plants adapted to temperate climates.

The C_4 plants respond to higher temperatures and they show higher rate of photosynthesis, while C_3 plants have much lower temperature optimum. Optimum temperature in C_3 plant is 20–25°C and for C_4 plant is 30–45°C.

Did You Know?

The minimum temperature at which most plants starts photosynthesis is 0–5°C. It is as low as – 35°C for gymnosperms. Maximum temperature at which photosynthesis can occur is 50–55°C for desert plants and 70–75°C for hot spring algae.

Water : Water is one of the raw materials utilized for the process of photosynthesis. Photosynthetic process utilizes less than 1% of the water absorbed by a plant, hence it is rarely a limiting factor in photosynthesis. Water stress causes the stomata to close, hence reducing the CO_2 availability as gaseous exchange could not occur. Also, water stress makes leaves wilt, thus reducing the surface area of the leaves and the metabolic activity reduces as well. Thus, the effect of water as a factor is more through its effect on the plant, rather than directly on photosynthesis.

(B) Internal factors affecting photosynthesis

Photosynthesis is under the influence of several internal (plant) factors. The plant factors include the number, size, age and orientation of leaves, mesophyll cells and chloroplasts, internal CO_2 concentration and the amount of chlorophyll. The plant or internal factors are dependent on the genetic predisposition and the growth of the plant.

(1) **Chlorophyll :** Of the internal factors, chlorophyll is the most important because light energy is trapped by only this substance. There is no photosynthesis in the absence of chlorophyll. The non green parts of variegated leaves (*e.g.*, *Croton*), therefore, do not have starch. **Photosynthetic number** or **assimilation number** shows a relationship between the chlorophyll and photosynthesis. It is the amount of carbon dioxide (in gms) assimilated by one gram of chlorophyll in an hour. **Emerson** (1929) observed a direct relationship between the chlorophyll content of a leaf and the rate of photosynthesis. If all other factors are favourable, increased chlorophyll leads to an increase in photosynthesis.

(2) **Photosynthetic products :** With the accumulation of the end products of photosynthesis in mesophyll cells, there is decrease in their photosynthetic rate because concentration of these products in the cells increases the rate of respiration.

Example 8 : *How the light intensity affects the rate of photosynthesis?*

Solution : There is a linear relationship between the light intensity and CO_2 fixation rate at low light intensities. At higher light intensities, gradually the rate does not show further increase as other factors become limiting.

Example 9 : Define *the law of limiting factors.*

Solution : The law states that if a chemical process is affected by more than one factor, then its rate will be determined by the factor which is nearest to its minimal value; it is the factor which directly affects the process if its quantity is changed.

Try Yourself

7. Fill in the blank columns in the table to bring the differences between C_3 and C_4 plants.

Characteristics	C_3 plants	C_4 plants	Choose from
(i) Cell type in which the Calvin cycle takes place.			Mesophyll / Bundle sheath / both
(ii) Cell type in which the initial carboxylation reaction occurs.			Mesophyll / Bundle sheath / both
(iii) How many cell types, do the leaf have, that fix CO_2.			Two : Bundle sheath and mesophyll One : Mesophyll Three : Bundle sheath, palisade, spongy mesophyll
(iv) Which is the primary CO_2 acceptor?			RuBP / PEP / PGA
(v) Number of carbons in the primary CO_2 acceptor.			5 / 4 / 3
(vi) Which is the primary CO_2 fixation product?			PGA / OAA / RuBP / PEP
(vii) Number of carbons in the primary CO_2 fixation product.			3 / 4 / 5
(viii) Does the plant have RuBisCO?			Yes / No / Not always
(ix) Does the plant have PEP Case?			Yes / No / Not always
(x) Which cells in the plant have RuBisCO?			Mesophyll / Bundle sheath / none
(xi) CO_2 fixation rate under high light conditions.			Low / high / medium
(xii) Whether photorespiration is present at low light intensities.			High / negligible / sometimes
(xiii) Whether photorespiration is present at high light intensities.			High / negligible / sometimes
(xiv) Whether photorespiration would be present at low CO_2 concentrations.			High / negligible / sometimes
(xv) Whether photorespiration would be present at high CO_2 concentrations.			High / negligible / sometimes
(xvi) Temperature optimum			30–40°C / 20–25°C / above 40°C
(xvii) Examples			Cut vertical sections of leaves of different plants and observe under the microscope for Kranz anatomy and list them in the appropriate columns.

EXERCISE

21. Factors that affect the rate of photosynthesis in plants are dependent on the
    (1) Genetic predisposition (2) External factors
    (3) Growth of the plant (4) More than one option is correct
22. The C_3-plants show CO_2 saturation
    (1) At about 360 μL^{-1} (2) Only below 450 μL^{-1}
    (3) Only beyond 540 μL^{-1} (4) Only beyond 450 μL^{-1}
23. Plants show light saturation effect at ________ of full sunlight.
    (1) 10% (2) 50%
    (3) 70% (4) 100%
24. Mark the odd one (w.r.t internal factors affecting photosynthesis)
    (1) Amount of chlorophyll (2) Light intensity
    (3) Mesophyll cells (4) Orientation of leaves
25. Minimum photosynthesis takes place in
    (1) Green light (2) Red light
    (3) Blue light (4) White light
26. Major limiting factor for photosynthesis in C_3 plants is
    (1) CO_2 (2) Temperature
    (3) Light (4) Water
27. Optimum temperature for the photosynthetic process of C_3 plants is
    (1) 20-25°C (2) 10-20°C
    (3) 30-45°C (4) 45-55°C
28. Photosynthetic process utilizes ________ of water absorbed by a plant.
    (1) 10% (2) 15%
    (3) Less than 1% (4) 5%
29. Which of the following factor does not have direct effect on photosynthesis?
    (1) Temperature (2) Water
    (3) Atmospheric CO_2 concentration (4) Light
30. In *Zea mays*, optimum CO_2 concentration for photosynthesis is
    (1) 450 ppm (2) 360 ppm
    (3) 0-10 ppm (4) 10-20 ppm

ADDITIONAL INFORMATION

Oxygenic photosynthesis : In green plants and cyanobacteria water is used as a source of reducing power. Photolysis of water results in release of oxygen as by-product. This photosynthesis which involves oxygen release is called oxygenic photosynthesis.

Anoxygenic photosynthesis : In bacteria evolution of oxygen during photosynthesis has not been demonstrated as they are incapable of using H_2O as reducing power. Instead it is obtained from H_2S, thiosulphate etc.

Some Important Definitions

- **Photosynthesis :** It is an anabolic, endergonic and oxido-reductive process in which the green parts of plants synthesize the complex organic material using CO_2, H_2O and light energy captured by light-absorbing pigments such as chlorophyll.
- **Light reactions :** The membrane system of the chloroplast is responsible for trapping the light energy and also for the synthesis of ATP and NADPH. This is known as light reaction.
- **Dark reactions :** In stroma of the chloroplast, enzymatic reactions incorporate CO_2 into the plant leading to the synthesis of sugar, this reaction is not directly light driven but is dependent on the products of light reaction (ATP and NADPH), this is known as dark reaction.
- **Pigments :** These are substances that have an ability to absorb light at specific wavelength.
- **Light-harvesting complex :** Photosynthetic pigment molecules bound to proteins, also called **antenna** molecules, as they help to make photosynthesis more efficient by absorbing different wavelengths of light.
- **Reaction center :** Part of photosystem with single chlorophyll a molecule which is the chief pigment associated with photosynthesis. Only reaction centre can eject electrons to ETS.
- **Photophosphorylation :** It is the synthesis of ATP from ADP and inorganic phosphate in the presence of light.
- **Non-cyclic photophosphorylation :** When the two photosystems are connected through an electron transport chain, they work in a series, first PS II and then PS I, leading to the synthesis of both ATP and NADPH + H^+.
- **Cyclic photophosphorylation :** When only PS I is functional, the electron is circulated within the photosystem and the photophosphorylation occurs due to cyclic flow of electrons. NADPH + H^+ is not synthesised in the process, only ATP is synthesised.
- **C_3 pathway :** The process of CO_2 assimilation during photosynthesis, in which the first product of CO_2 fixation is a C_3 acid (PGA) is called the C_3 pathway.
- **C_4 pathway:** The process of CO_2 assimilation during photosynthesis, in which the first product of CO_2 fixation is a C_4 acid (OAA) is called the C_4 pathway.
- **RuBisCO :** Ribulose Bisphosphate Carboxylase Oxygenase. It catalyses the CO_2 fixation reaction during Calvin cycle.
- **Photoactive stomata :** Stomata which opens during day, *e.g.*, C_3 and C_4 plants.
- **Scotoactive stomata :** Stomata which opens during night, *e.g.*, CAM plants like *Sedum*, *Opuntia*.
- **OAA :** Oxaloacetic acid, the first stable product during C_4 pathway.
- **Photorespiration :** It is a process that involves oxidation of organic compounds in plants by oxygen in presence of light. No ATP is produced in this process. It is present in C_3 plants and absent in C_4 plants.

Quick Recap

1. Photosynthesis is a vital process among photoautotrophs.
2. Photosynthetic reaction can be simplified as :

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

3. Photosynthesis takes place only in the green parts of the plants mainly the leaves. Within the leaves mesophyll cells have a large number of chloroplasts that are responsible for fixation of carbon dioxide.
4. Photosynthesis occurs in two stages – light reaction and the dark reaction.
5. Within the chloroplast, the membrane system is responsible for trapping the light energy and synthesis of ATP and NADPH–**light reaction**.
6. In stroma of the chloroplast, enzymatic reactions incorporate CO_2 into the plant leading to the synthesis of sugar–**dark reaction**.
7. In the light reaction, the energy is absorbed by the **pigment systems** (photosystems).
8. There are two pigment systems – PS I and PS II. In a pigment system one molecule of chlorophyll a functions as reaction center and others as light-harvesting complexes or antenna molecules.
9. PS I has 700 nm absorbing chlorophyll a $\mathbf{P_{700}}$ molecule as its reaction center while PS II has a $\mathbf{P_{680}}$ reaction center that absorbs light at 680 nm.
10. After absorbing light, electrons become excited and transferred through PS II to the electron transport system consisting of cytochromes and then to PS I and finally to NADP forming NADPH.
11. Splitting of water molecules is associated with the PS II resulting in the release of O_2, protons and transfer of electrons to PS II.
12. During the transfer of electrons through electron transport chain, a proton gradient is created across the membrane of the thylakoid.
13. The breakdown of this gradient due to the movement of protons across the membrane to the stroma through the channel of F_0 of the ATPase results in release of enough energy for synthesis of ATP.
14. During the dark reactions (carbon fixation cycle), the enzyme RuBisCO catalyses the initial carboxylation reaction, where CO_2 combines with RuBP to form a three-carbon compound, 3-phosphoglycerate, thus this pathway is called C_3 pathway or Calvin cycle.
15. During this process, ATP and NADPH synthesised in the light reaction are utilised.
16. RuBisCO also catalyses a wasteful oxygenation reaction in C_3 plants called **photorespiration**.
17. There is another pathway of CO_2 fixation called as **C_4 pathway** in which the first product is a four-carbon compound *i.e.*, oxaloacetic acid.
18. In these plants (having C_4 pathway), Calvin cycle is carried out in the bundle-sheath cells for the synthesis of carbohydrates. Photorespiration is absent.
19. Both external & internal factors affect the rate of photosynthesis in plants.

❑ ❑ ❑