Chapter 13

# PHOTOSYNTHESIS IN HIGHER PLANTS


**13.1 What do we Know?**
**13.2 Early Experiments**
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## 13.1 WHAT DO WE KNOW?

Sunlight is an inexhaustible form of energy called **solar energy**. Out of the total solar energy emitted by the sun, some part reaches the earth. Out of this, green plants are able to trap fraction of energy and convert it into chemical energy by synthesizing organic matter such as **carbohydrates**.

**Definition of photosynthesis** (Gr. Photon = Light, Synthesis = Putting together)
Photosynthesis is defined as, "*an intracellular, anabolic process in which glucose is synthesized using simple inorganic substances like $CO_2$ and $H_2O$ as raw material ,in the presence of light and chlorophyll-a and with the release of oxygen as a by-product*".

The overall reaction is:

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

Photosynthesis is a mechanism of energy input into the living world. It is a **redox reaction** where $CO_2$ is **reduced** to carbohydrate and $H_2O$ is **oxidized** to $O_2$.
The **oxidation of water** ($H_2$ removed) depends on light and is called **light reaction.**
The **reduction of $CO_2$** ($H_2$ is added) that does not depend on light is called **dark or light independent reaction.**

**Autotrophs:**

The organisms which are able to synthesize organic matter (food material) are called autotrophs. They are of two types:

**I. Photosynthetic autotrophs:**

- They contain chlorophyll photosynthetic pigments and prepare organic substances by obtaining solar energy
  e.g. All green plants, protists like diatoms, prokaryotes like **Cyanobacteria**, few bacteria like purple sulphur bacteria-**Chromatium** and green sulphur bacteria-**Chlorobium**

**II. Chemosynthetic autotrophs:**

- They obtain energy by oxidation of certain substances such as hydrogen sulphide ($H_2S$), ammonia ($NH_3$) etc. By using this energy these organisms prepare organic matter.
- They do not have photosynthetic pigments.
- Eg. Nitrifying bacteria **Nitrosomonas,** Sulphur bacteria like **Thiobacillus** and iron bacteria **Ferrobacillus**.

## 13.2 EARLY EXPERIMENTS:-

**I. Priestley:** He carried out very interesting **experiment on Bell jar**, Rat, Pudina & Candle. He came to conclude that plants purify air (burning of candles) and gaseous exchange occurs during photosynthesis.

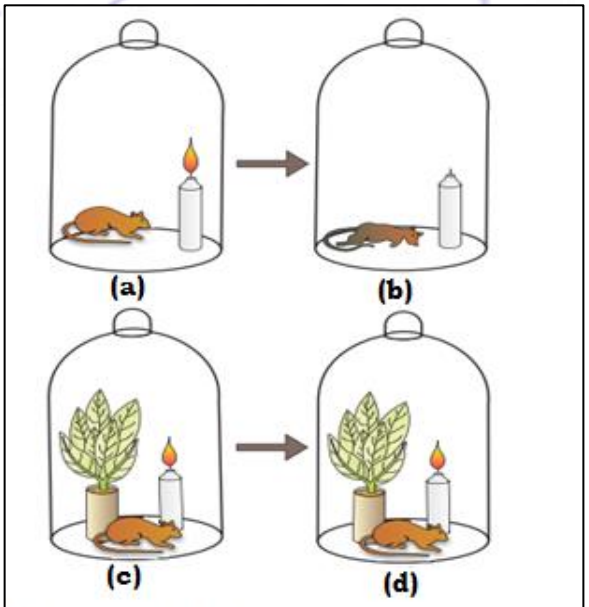


**Figure 13.1:** Priestley's experiment

Priestley observed that a candle burning in a closed space – a bell jar, soon gets extinguished (Figure 13.1 a, b, c, d). Similarly, a mouse would soon suffocate in a closed space. He concluded that a burning candle or an animal that breathe the air, both somehow, damage the air. But when he placed a mint plant in the same bell jar, he found that the mouse stayed alive and the candlecontinued to burn. Priestley hypothesised as follows: Plants restore to the air whatever breathing animals and burning candles remove.

II. **Jan Ingenhousz:** Using a similar setup as the one used by Priestley, but by placing it once in the dark and once in the sunlight, Jan Ingenhousz (1730-1799) showed that sunlight is essential to the plant process that somehow purifies the air fouled by burning candles or breathing animals. Ingenhousz in an elegant experiment with an aquatic plant showed that in bright sunlight, small bubbles were formed around the green parts while in the dark they did not. Later he identified these bubbles to be of oxygen. Hence he showed that it is only the green part of the plants that could release oxygen.

III. **Julius von Sachs:** Recognised the relation among photosynthesis, chloroplast and starch. It was not until about 1854 that provided evidence for production of glucose when plants grow. Glucose is usually stored as starch. His later studies showed that the green substance in plants (chlorophyll as we know it now) is located in special bodies (later called chloroplasts) within plant cells. He found that the green parts in plants is where glucose is made, and that the glucose is usually stored as starch.

IV. **Englemann:** Now consider the interesting experiments done by T.W Engelmann (1843 – 1909). Using a prism he split light into its spectral components and then illuminated a green alga, Cladophora, placed in a suspension of aerobic bacteria. The bacteria were used to detect the sites of $O_2$ evolution. He observed that the bacteria accumulated mainly in the region of blue and red light of the split spectrum. A first action spectrum of photosynthesis was thus described. It resembles roughly the absorption spectra of chlorophyll a and b.

V. **Formerly**, it was believed that oxygen evolved in photosynthesis comes from $CO_2$. $CO_2$ splits into C and $O_2$. C combines with $H_2O$ to form glucose and $O_2$ is evolved.

$$CO_2 + H_2O \longrightarrow (CH_2O) + 6O_2\uparrow$$

**Van Niel** in **1930**

- He first demonstrated that photosynthesis is essentially a light dependant reaction in which hydrogen from a suitable oxidisable compound reduces $CO_2$ to carbohydrates.
- He studied the process in purple and green sulphur bacteria which use **$H_2S$** instead of $H_2O$. He observed that $H_2S$ splits into $H_2$ and S. $H_2$ is used to reduce $CO_2$ to $CH_2O$ and sulphur is the by-product.
- Then he suggested that even during photosynthesis $H_2O$ molecule splits up into $H_2$ and $O_2$. Hence $O_2$ evolved by green plants comes from $H_2O$ and not from $CO_2$.
- The equation for bacterial photosynthesis is (Chemosynthesis)

$$6\ CO_2 + 12\ H_2S \xrightarrow[\text{Bacteriochlorophyll}]{\text{Sunlight}} C_6H_{12}O_6 + 6H_2O + 12S \uparrow$$

**VI. Hill's Reaction or Photolysis of Water**

- In 1937 a British biochemist called Robert Hill proved that $O_2$ evolved during photosynthesis came from $H_2O$ and not from $CO_2$.
- **Hills experiment:** Hill suspended isolated chloroplast from spinach leaves in water without $CO_2$. He added $Fe^{3+}$(Ferric) salts as hydrogen acceptor and placed it in light. He observed that Ferric salts got reduced into $Fe^{2+}$ (Ferrous) and $O_2$ bubbles evolve.
- Thus he proved that water splits.
- **Hill's Reaction → Photolysis**

$$H_2O \xrightarrow{\text{Light}} H^+ + OH^-$$

He thus summarized the process as:

$$2H_2O + 2A \xrightarrow[\text{Chlorophyll}]{\text{Light}} 2AH_2 + O_2$$

where A was the unknown hydrogen acceptor in plant chloroplasts.

**VII.** In **1941**, Scientists named **Ruben** and **Kamen confirmed** Hill's reaction. They carried out photosynthesis by taking $CO_2$ containing normal $O_2$ and water containing $\mathbf{O^{18}}$ isotope of $O_2$ and found that the $O_2$ released contained the isotope $O^{18}$ but when $CO_2$ containing the isotope $O^{18}$ of $O_2$ was used, the $O_2$ evolved did not contain the isotope.

$$6CO_2 + 12\ H_2O^{18} \longrightarrow C_6H_{12}O_6 + 6H_2O + 6O_2^{18}$$

**VIII.** In **1954, Dr. Arnon** found that the Hydrogen acceptor in plants is a **coenzyme NADP** (Nicotinamide Adenine Dinucleotide Phosphate). The above equation can hence be written as

$$2H_2O + 2NADP \xrightarrow[\text{Chlorophyll}]{\text{Light}} 2NADPH_2 + O_2$$

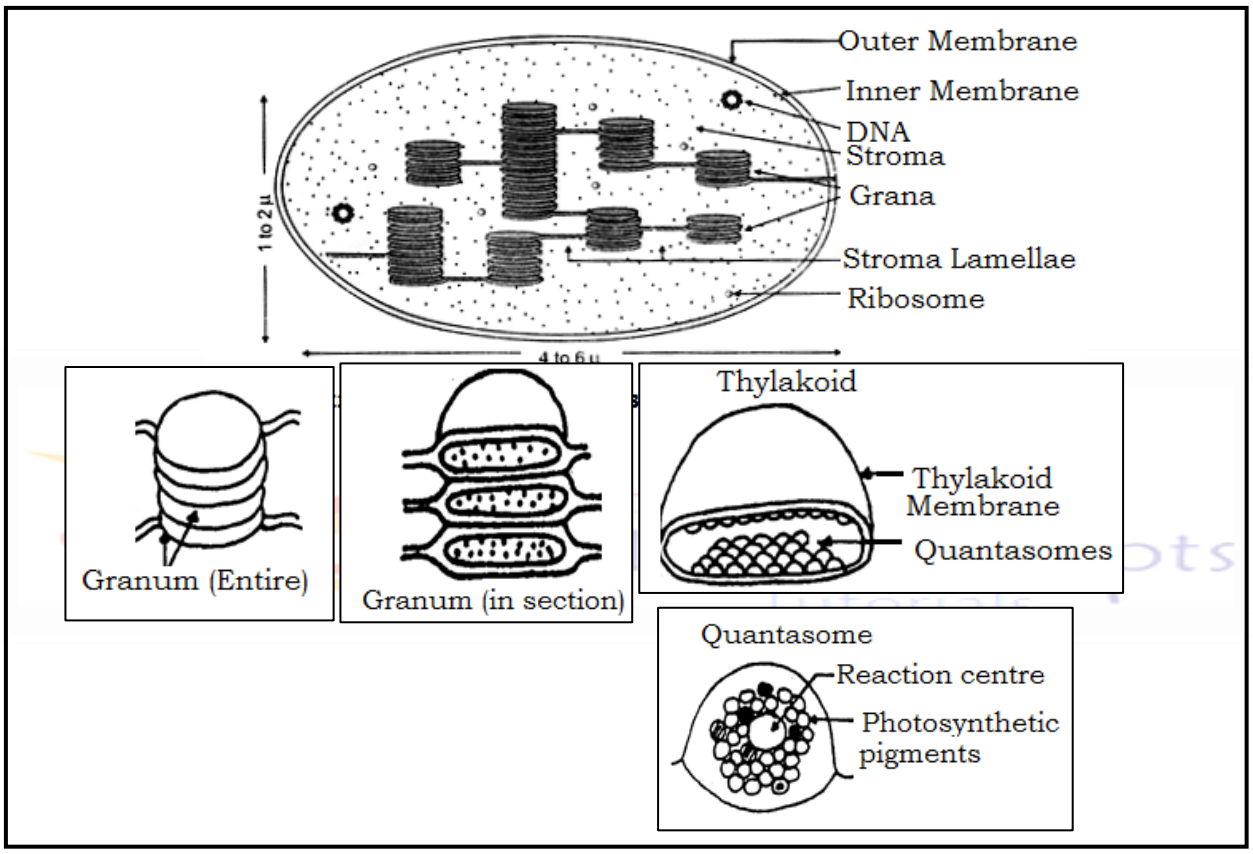
This $NADPH_2$ is used in the reduction of $CO_2$ during dark reaction.

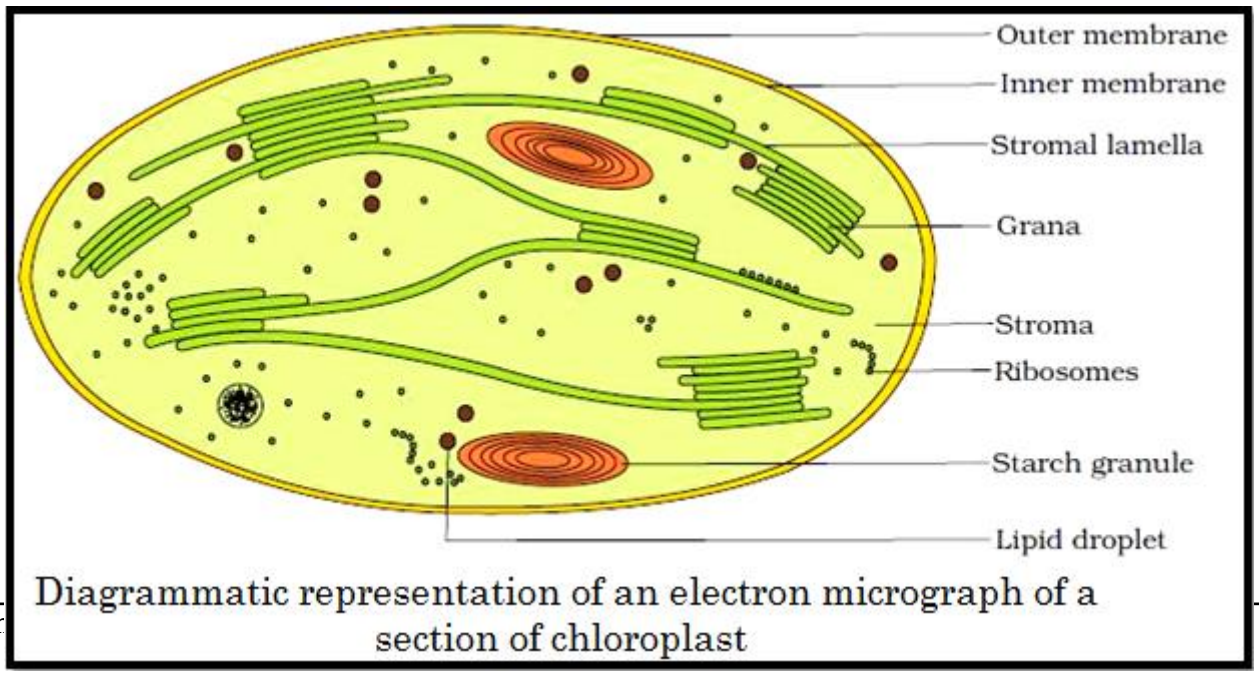
$$6CO_2^{18} + 12\ H_2O \longrightarrow C_6H_{12}O_6^{18} + 6H_2O^{18} + 6O_2$$

Thus it was proved that the source of $O_2$ during photosynthesis was $H_20$ & not $CO_2$.

## 13.3 WHERE DOES PHOTOSYNTHESIS TAKE PLACE?

- Chloroplasts are an important type of **plastid** which **contains** a green pigment called **chlorophyll**. They form the **structural** and **functional unit** of photosynthesis.
- About **20-100 chloroplasts** are uniformly distributed throughout the cytoplasm of cell or form clusters near nucleus or below the cell wall.




Diagrammatic representation of an electron micrograph of a section of chloroplast

- Chloroplasts are **lens** shaped.
- **Size:** Chloroplast has a diameter of **1 to 2** μ and the length is **4 to 6 μ**
- Each chloroplast has a double membrane called **peristromium**. Each one of them is a unit membrane and made up of lipoproteins.
- It encloses a colourless, colloidal, hydrophilic matrix called as **stroma** which is made up of carbohydrates, proteins, lipids, photosynthetic enzymes for dark reaction, 70 S ribosomes, DNA and RNA.
- DNA is circular, closed, naked ring and is called plastidome. Due to the presence of its own DNA, they are self duplicating and semi-autonomous cell organelles.
- Embedded in the stroma are **40-60** membranous stacks called **grana** (singular-granum). Each granum is made up to 5-50 disc-shaped membranous sacs/ lamellae called **thylakoids** which are placed one above the other like a stack of coins. Grana is the site of light reaction and ATP synthesis.
- The grana are connected to each other by inter-granal lamellae/ stromal lamellae/ **fret membranes**. They help in the rapid transport of materials.
- Each thylakoid is covered by a thylakoid membrane or grana lamellae and contains small, ultramicroscopic flattened spheres called **quantasomes**. Hence, they appear **granular.**
- According to Park and Biggins, pigments are located within quantasomes. Each quantasome is a photosynthetic unit and contains about 200-250 molecules of pigment system (Chlorophyll a, b, c, d, e, Carotenoids and Phycobillins) with a **reaction centre** in the middle. They act as photosynthetic units converting a quantum of light energy (photon) into chemical energy (ATP).
- Emerson established the presence of 2 distinct groups- PS-I and PS-II.
- In prokaryotes, chloroplasts are absent and pigments are located in lamellae ie. Thylakoids.

**Function:**

(i) **Chloroplast** is the site of **photosynthesis.**

(ii) **Light reaction** of photosynthesis takes place in **grana** part of chloroplast.

(iii) The **dark reaction** of photosynthesis occurs in **stroma.**

(iv) The **enzymes** necessary for dark reaction are present in **stroma.**

(v) (Thus the entire process of photosynthesis occurs in chloroplast. Hence chloroplast is also known as photosynthetic apparatus/ food producer/ food production centre of cell/ photosynthetic factory.)

## 13.4 HOW MANY PIGMENTS ARE INVOLVED IN PHOTSYNTHESIS?

- The photosynthetic pigments are placed in the quantasome of chloroplasts. They absorb light of certain wavelengths and reflect light of other wavelengths.
- **Anthocyanin,** is a purple coloured, non-photosynthetic pigment present in the flower.
- Photosynthetic pigementsare of three types:

  Chlorophylls - essential

  Carotenoids } Accessory
  Phycobillins }

### 1. CHLOROPHYLLS:

- They are the most important and abundant of all pigments.
- Green pigments.
- They are insoluble in water but soluble in organic solvents.
- All higher plants have chlorophyll a and b while others are found in lower plants.
- They are of the following 7 types:
  - Chlorophyll a, b,
  - Chlorophyll c, d, e- in brown and red algae along with Chlorophyll a
  - Bacterioviridin
  - Bacterio chlorophyll
- Chlorophyll- a and b show maximum absorption in blue-violet and red regions of visible light.

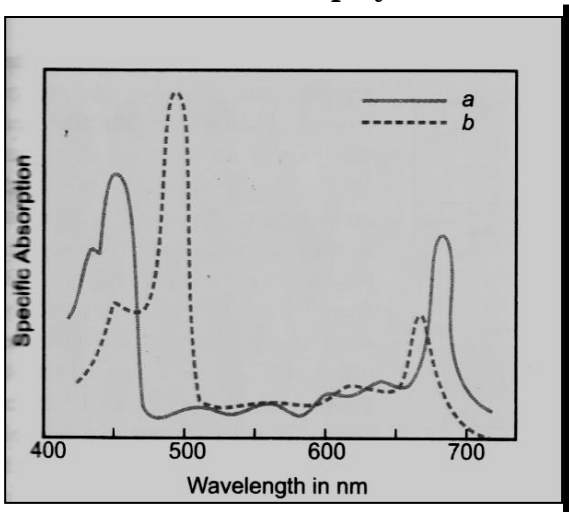
#### I. CHLOROPHYLL –A

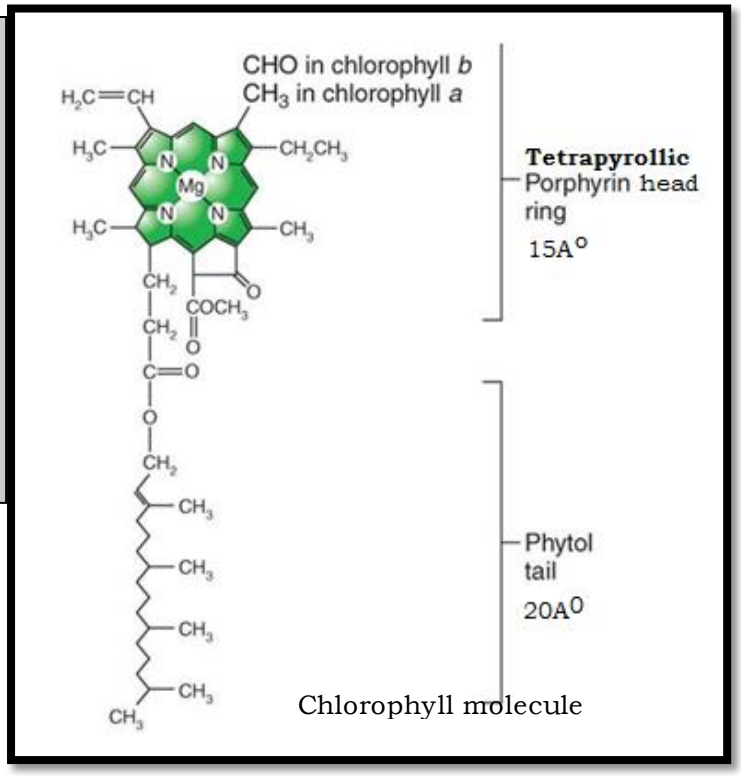
- It is present in all photosynthetic organisms (except photosynthetic bacteria.)
- Chlorophyll - a: $C_{55}\ H_{72}\ O_5\ N_4\ Mg$
- It is blue green
- Essential reaction centre

#### II. CHLOROPHYLL –B

- It is found in green algae, bryophytes and all vascular plants.
- Chlorophyll - b: $C_{55}\ H_{70}\ O_6\ N_4\ Mg$. It is similar to chlorophyll –a except that the –CH3 group in chlorophyll-a is replaced with –CHO in chlorophyll-b.
- It is yellow green

**Structure of chlorophyll:**




- Chlorophyll molecule is polar and has a chemical structure resembling a kite with a tetrapyrolporphyrin head and a phytol tail.
- The rhomboid, hydrophilic **head** consists of 4 pyrole rings with non-ionic magnesium at the centre. The head is embedded in the protein part of thylakoid membrane.
- To the 4th rings the phytol tail is attached. It is lipophilic and extends in the lipid layer of thylakoid membrane.

**Chlorophyll Synthesis:**

Succinyl CoA + Glycine →Protochlorophyll (Protochlorophyllide) $\frac{\text{Light}}{2H}$ Chlorophyll.

**2. CAROTENOIDS:**

- Carotenoids are widely distributed in chloroplasts and chromoplasts.
- They show wide range in colour, from yellow, orange to red.
- They are insoluble in water but soluble in organic solvents.
- They mainly absorb **blue-violet** region of visible light.

They are lipids. They are of two types:

**I. Carotenes**

- $C_{40}$ $H_{56}$: They are hydrocarbons.
- They have a deep orange colour.

- They are of two types α -carotenes and β -carotenes. Major carotene is β -carotenes.

**II. Xanthophylls**

- $C_{40}$ $H_{56}$ $O_2$:They are oxygenated hydrocarbons
- They are **yellow** in colour.
- Lutein is the major xanthophyll present in plants.

**3. Phycobillins:**

They are chromo proteins in red algae and cyanobacteria. Their types are:

- **Phycoerythrin**- It is found in **red algae**
- **Phycocyanin**- It is found in **blue green algae**.

**Role of Pigments:**

**PHOTO EXCITATION OF CHLOROPHYLL A:**

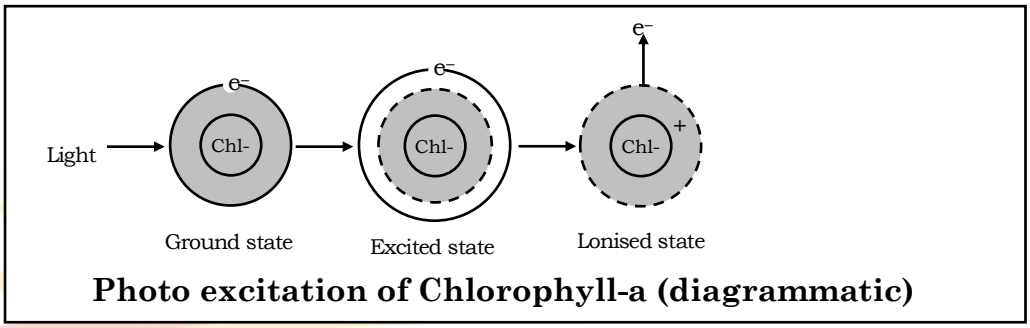
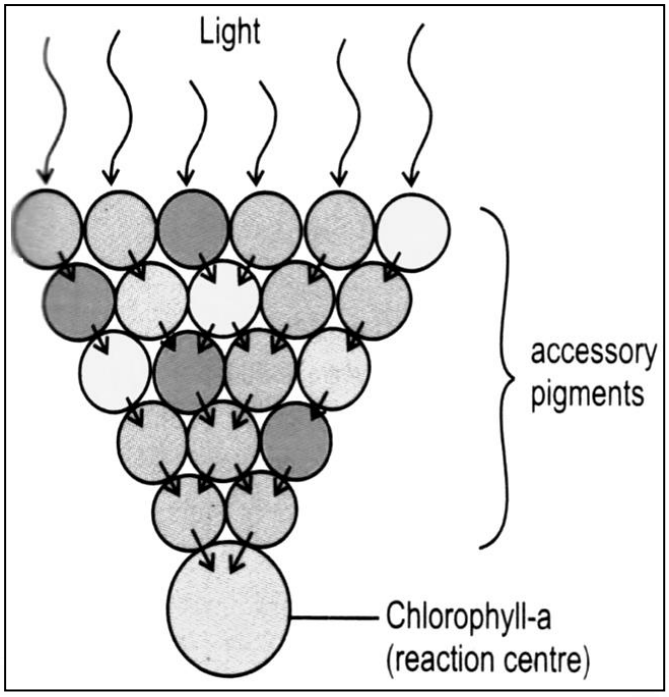



**Photo excitation of Chlorophyll-a (diagrammatic)**

- **Chlorophyll-a** is the only pigment that absorbs and converts light energy into chemical energy hence it is called **essential pigment** or reaction centre or master molecule.
- Chlorophyll-a also absorbs light energy of specific wavelength. Chlorophyll-a, is present in different forms. Among them there are two special forms of Chlorophyll-a, which are **Chlorophyll-a 680 & Chlorophyll-a 700.**
- **Stages :**
  - **(i)** Initially chlorophyll – a is at the **ground state.**
  - **(ii)** When chlorophyll-a (reaction centre) receives light energy in the form of photons then it becomes energy rich and gets activated. This is called **excited state** of chlorophyll.
  - **(iii)** Excited chlorophyll-a emits out light/ radiation energy rich electron.With the loss of one electron chlorophyll molecule develops positive charge. This is called **ionized** chlorophyll $a^+$. This energy rich electron is accepted by by many electron carriers during the transfer and the energy released is used to generate ATP. Thus light energy is converted to chemical energy.Chlorophyll a molecule cannot remain in this state for more than $\mathbf{10^{-9}}$ seconds. Thus photochemical reaction i.e. electron transfer is very fast.

**Role of Accessory Pigments:**

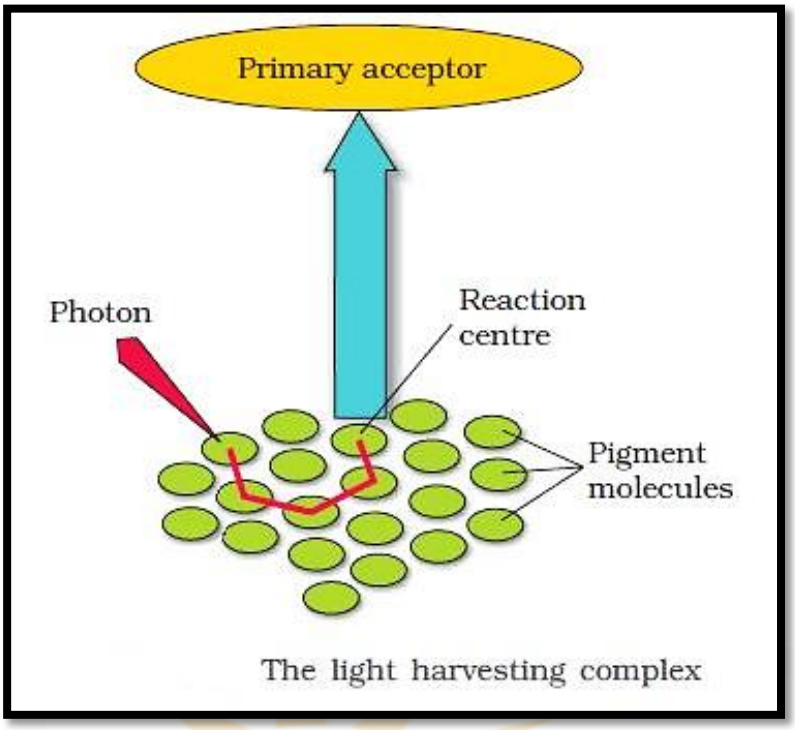



- Chlorophyll - b and carotenoids absorb light energy of different wavelengths and transfer it to the chlorophyll - a by **resonance**.
- They broaden the spectrum of light absorbed and help in absorbing light energy more efficiently; hence they are called accessory pigments.
- These pigments act as **antenna complexes** and harvest light from different regions of the spectrum than the chlorophyll. The light (radiation energy) captured by these pigments is **funneled** into the reaction centre for conversion into the chemical energy.
- Carotenoids also protect the essential pigment chlorophyll a, from photo-oxidation.

**Concept of Photo pigment systems:**

- Each photo system consists of reaction centre and accessory pigments.
- In the thylakoid membranes, chloroplast shows two kinds of photo systems namely Photo system I and Photosystem II also called PS-I and PS-II, respectively. Each photo system has its own set of chlorophyll molecules.
- In **PS I,** chlorophyll-a with maximum absorption at 700nm **($P_{700}$)** is the **reaction centre**while in **PS II**, chlorophyll-a with peak absorption at 682nm **($P_{680}$)** is the **reaction centre**. (The letter P stands for pigment and 680 or 700 for the wavelengths of light at or below which these molecules absorb light.)
- Chlorophyll-a exists in different forms, which show maximum absorption at different wavelengths of light, such as chl-a 650, chl-a 673, chl-a 680, chl-a 700, etc.
- In **PS-II**, manganese, calcium and chloride ions are present in addition to the electron carriers. These ions play important role in **Photolysis of water**.

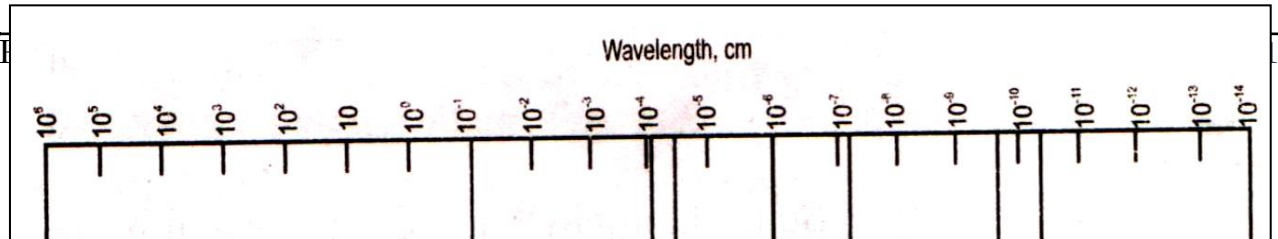
- Each photo system is with Core Complex (CC) and Light harvesting complex (LHC).




a) **Core Complex-CC** is composed of single specific chlorophyll-a molecule as reaction centre and few other Chlorophyll-a molecules and **electron carriers.**

b) **Light harvesting complex-LHC** is composed of about 200 chlorophyll-a, few chlorophyll-b and 50 carotenoid molecules.

## 13.5 WHAT IS LIGHT REACTION?- NATURE OF LIGHT:



Electromagnetic Spectrum of Light

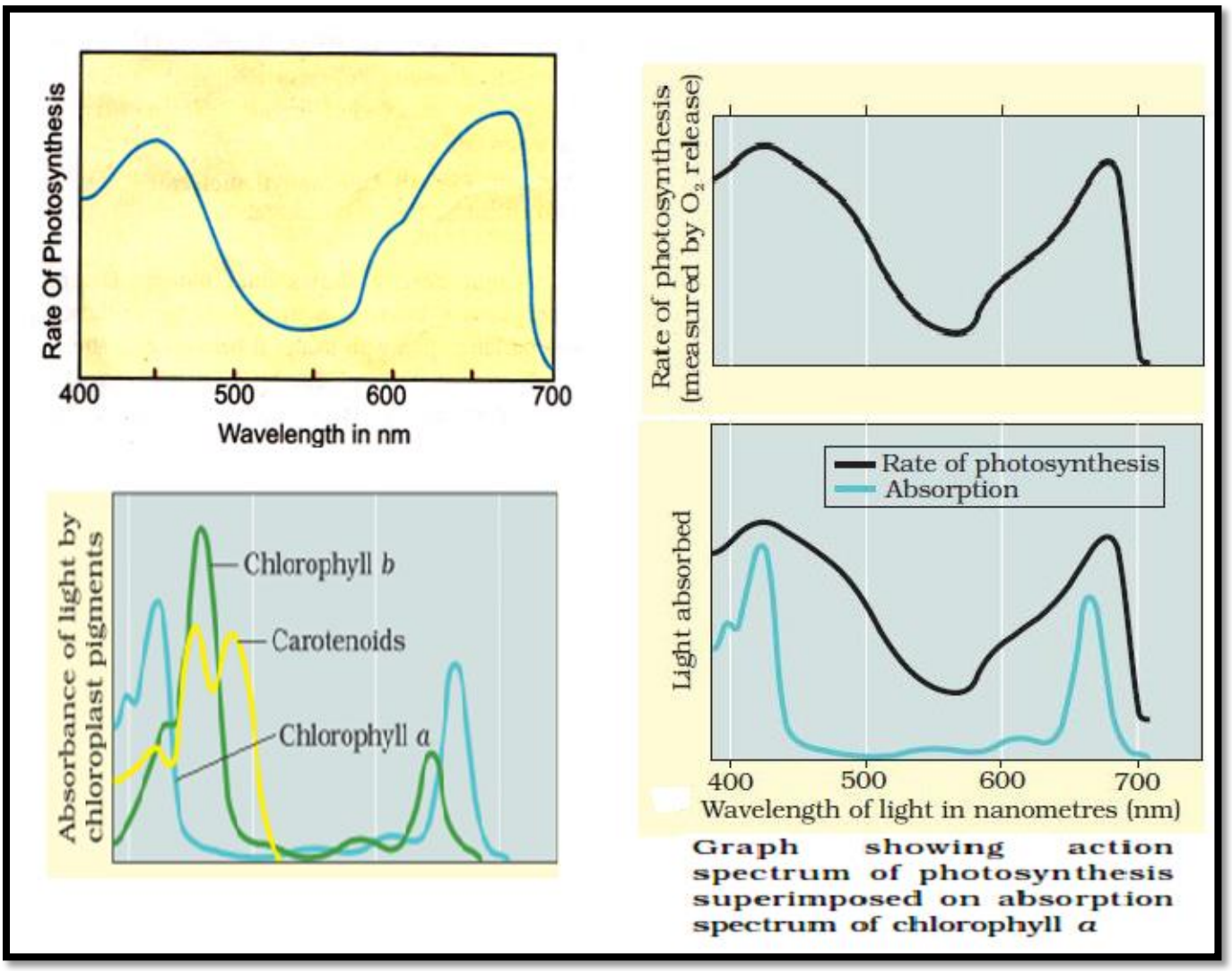
(i) Photosynthesis is influenced by quality (wavelength) and quantity (intensity) of light.

(ii) Dual nature of light:

a) **Wave theory**- during propagation.

b) **Corpuscular theory**: on interaction with matter, it behaves like a stream of discrete packets of energy known as photons. Each photon contains definite amount of energy called **quantum**. Thus each quantum represents a unit of energy which is absorbed by pigments. Amount of energy contained in a photon is inversely proportional to the wavelength of light i.e. long wavelength has less amount of energy and short wavelength has more energy.)

$$\textbf{quantum} \alpha \frac{1}{\lambda}$$




(iii) **Sun** is the only naturalsource of light for photosynthesis. The radiations of sun consist of two parts: visible light and invisible light.

(iv) Photosynthetic pigments absorb light energy only in visible part. Qualitatively visible light consists of **seven colours** of different wavelengths.

(v) **Visible spectrum** is present between the wavelength of **390 nm** (violet) to **760 nm** (red).It is also referred to as **PAR** -Photosynthetically active radiation.

(vi) Maximum absorption takes place in red and blue rays. There is slight absorption in yellow and orange colour. Therefore the rate of photosynthesis is **maximum** in **red** and next in **blue light** and negligible in green light.

(vii) The action peak shows highest peak in the red region and another smaller peak in the blue region.

**LIGHT REACTION**

- It is a light trapping **photo-chemical** reaction which takes place in the **grana** of the chloroplast. It is the 1st phase of photosynthesis.
- In light reaction two important events take place. They are **Photo-oxidation or photolysis** of water and **Photophosphorylation**.
- **Photolysis of water:** In presence of light chlorophyll– a brings about splitting of water into $H_2$ and $O_2$ ($H^+$ and $OH^-$). As a result $O_2$ is evolved as free gas and $H_2$ is accepted by NADP to form $NADPH_2$.
- In this reaction, absorption of light energy by pigments and conversion into chemical energy in the form of **ATP**occurs.

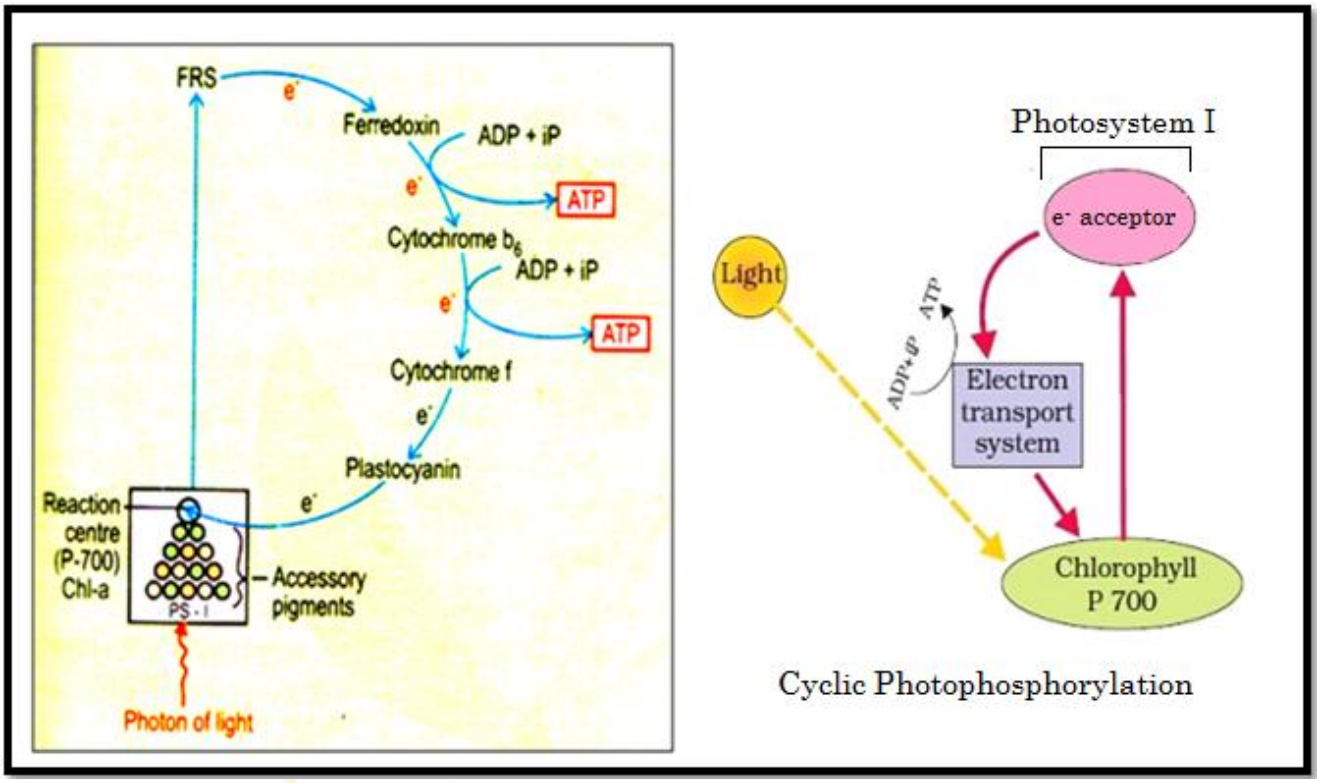
**Photophosphorylation:**

- It is a process in which ATP is synthesized during photosynthesis using solar energy.
- Addition of phosphate to a compound is called as Phosphorylation. When phosphate is added to ADP with the help of energy from light, it is called as photophosphorylation.
- The light energy excites chl-a of the photo systems to release high energy electrons. The electrons pass through a series of electron acceptors which is made up of cytochromes.
- As the electron passes through the cytochromes its energy is used to bind adenosine diphosphate (ADP) with inorganic phosphate to form ATP.

  i.e. $ADP + iP \xrightarrow{Light\,Energy} ATP$

  Since the electron is transferred through the cytochrome system, this process is also called as Electron Transfer System.
- According to Dr. Arnon, there are two ways in which photophosphorylation takes place. They are Cyclic photophosphorylation and Non-cyclic photophosphorylation.

## CYCLIC PHOTOPHOSPHORYLATION:



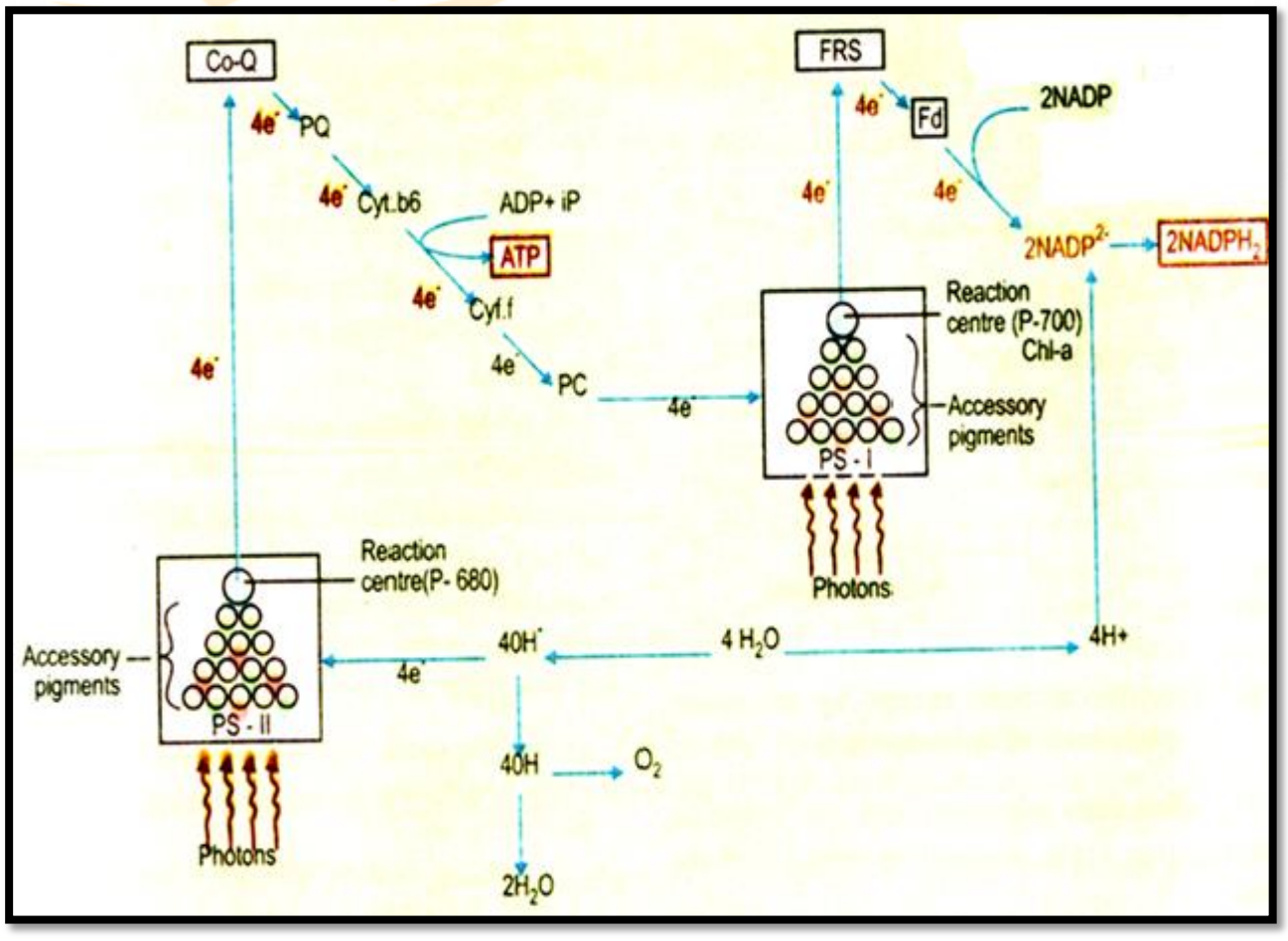

- In cyclic photophosphorylation, the energy rich **electron** released **by chlorophyll-a returns back** to the same reaction centre and hence the name.
- Here, light of wavelength **700 nm** or less strikes the chlorophyll-a molecule due to which **only PS-I** operates.
- The pigments in PS-I absorb energy of different wavelengths of light, which is funneled to the reaction centre, a specific molecule of chl-a ie.$P_{700}$.
- When chlorophyll-a ($P_{700}$.) gets excited, it gives out an energy rich electron. This electron is accepted by an unknown electron acceptor **FRS** – Ferredoxin Reducing Substance, which passes the electron to an iron containing red pigment **ferredoxin**. Due to this, $P_{700}$ becomes positively charged or left ionized.
- These electrons roll down the energy gradient through a series of electron carriers.
- Ferredoxin then passes the electron to **Cytochrome-$b_6$** .During this transfer some of the electron's energy is used to bind ADP and iP to form one molecule of ATP.
- From Cytochrome-$b_6$ the electron is then transferred to **Cytochrome-f** where one more molecule of ATP is formed.
- From Cytochrome-f it is transferred to **plastocyanin.** During this electron transfer, the electron is a ground state as it has lost almost all its energy.

- Then from plastocyanin it is passed back to chlorophyll-a. Since the electron is returned back to chlorophyll-a where it originated, it is known as **cyclic photophosphorylation** or cyclic electron transfer.

**Significance:**

- It occurs in all photo-autotrophs along with non-Cyclic Photophosphorylation.
- In Cyclic photophosphorylation, **two** energy rich **ATP** molecules are produced **perelectron** released.
- Only one pigment system is required (PSI).
- It is a **major** pathway of light reaction.
- It does not require an electron donor like water.
- When $CO_2$ fixation is stopped or $CO_2$ concentration is low and NADP is not available, electrons from Fd come back to PS-I.
- Reducing agent in the form of **$NADPH_2$ is not released** and photolysis of water does not take place. Therefore, this mechanism is considered to be a **non-efficient one**.

## 2. NON-CYCLIC PHOTOPHOSPHORYLATION:



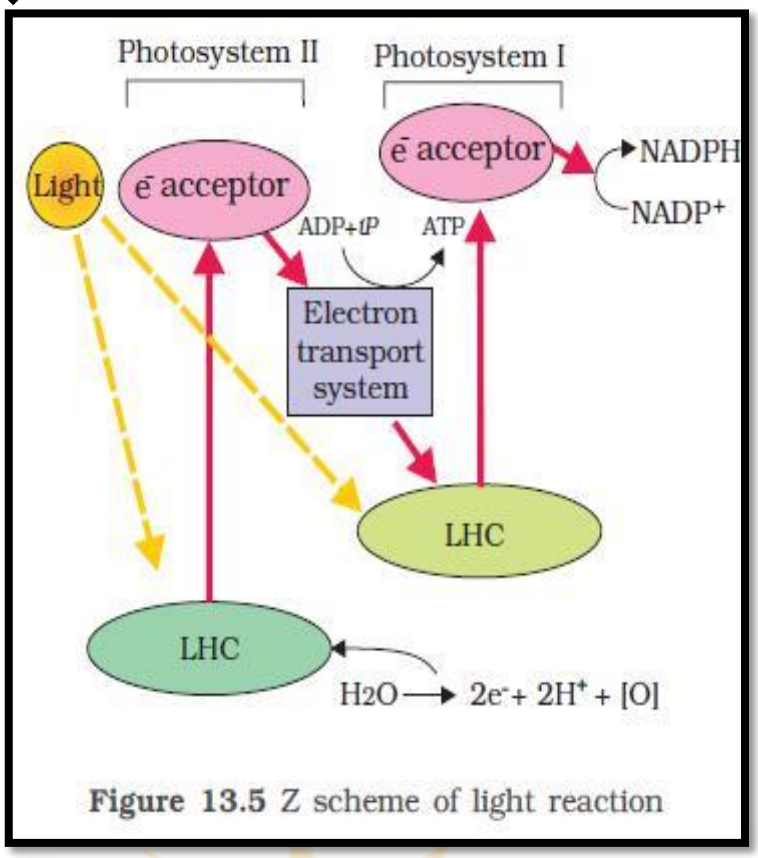



**Figure 13.5** Z scheme of light reaction

- 'In the non-cyclic photo-phosphorylation, the energy rich electron released by chlorophyll-a does not return back to the same chl-a molecule. The electrons flow from $H_2O$ to PS-II, from PS-II via cytochromes to PS-I and finally to NADP.
- It occurs under aerobic conditions, high $CO_2$ concentration and enough light intensity.
- In this **both** the **photosystems** operate.

**A. EVENTS AT PS-II:**

**(i)** The pigments in PS-II absorb energy of different wavelengths of light which is funneled to the reaction centre.

**(ii)** When chlorophyll-a (P-680) of photosystem-II is energized by light energy, it gives out energy rich electrons.

**(iii)** These electrons are accepted by the electron acceptor 'coenzyme Q and then passed on to the cytochrome member **plastoquinone**. This leaves the reaction centre ionized or positively charged and PQ gets reduced.

**(iv)** The electrons from **plastoquinone** roll down a series of electron acceptors, **cytochrome-$b_6$, cytochrome-f** and **plastocyanin**and finally the de-energised electrons return to chlorophyll-a of photo system-I.

**(v)** The loss of electrons of chlorophyll-a 680 is compensated by the electrons during photolysis of water. Here **water acts** as **an electron donor**.

**(vi)** Thus PS-II replaces the lost electrons in PS-I.

**(vii)** When from Cytochrome-$b_6$ the electrons are transferred to **Cytochrome-f**, one molecule of ATP is formed.

**B. EVENTS AT PS-I:**

**(i)** The pigments in PS-I absorb energy of different wavelengths of light which is funneled to the reaction centre.

**(ii)** When chlorophyll-a (P-700) of photo system-I is energized by light, its electrons are **raised to a higher level** and **released**.

**(iii)** The electrons are captured by **electron acceptor** FRS-ferredoxin reducing substance and then passed to iron containing pigment called ferredoxin.

**(iv)** From reduced ferredoxin, these electrons are taken up by NADP (Nicotinamide adenine dinucleotide phosphate) and become negatively charged.

**(v)** NADP also receives 4($H^+$) from the photo-oxidation of water and gets reduced to $NADPH_2$.

**(vi)** PS-II replaces the lost electrons in PS-I.

**C. PHOTO-OXIDATION OF WATER (OR PHOTOLYSIS OF WATER):**

**(i)** It is a process in which under the influence of light and strong oxidizing agent $P_{680}$+, the water splits into $H^+$ and $OH^-$.

**(ii)** This is initiated by the transfer of 4 charges.

**(iii)** The (OH-) so formed, then reacts to form $H_2O$ and $O_2$ is given out as a gas. The electrons from $OH^-$ are passed to the excited chlorophyll molecule to stabilize it.

**(iv)** The reaction is dependent on $Mn^{++}$, $Ca^{++}$ and $Cl^-$ and initiated by Chlorophyll$^-$a of P.S. -II.

**(v)** Water acts as a reducing agent.

**(vi)** It donates $4H^+$ to 2NADP and reduces it to $2NADPH_2$ in presence of enzyme ferredoxin DADP reductase which in turn reduces other compounds during photosynthesis.

The reaction takes place in the following manner,

$4H_2O \rightarrow 4\ H^+ + 4\ e^- + 2H_20 + O_2$

**(vii)** 4 electrons are accepted by oxidized $P_{680}$.

**(viii)** Since the electron given out by chlorophyll-a **does not return** back to it, this process is called as **Non-cyclic photophosphorylation** or non-cyclic electron transfer. E.g. It is seen in all green plants.

**Significance:**

- Non-cyclic photophosphorylation produces **ATP** which provides energy for dark reaction.
- It also produces **$NADPH_2$** which reduces **$CO_2$** to **carbohydrates.**
- It involves **photolysis** of water, where water acts as a hydrogen donor.
- It releases **$O_2$** as a byproduct, essential for life.
- It is **a major pathway** of light reaction. (Photosynthesis requires both, reducing agent as well as light energy for the reduction of $CO_2$ to carbohydrates. Both these forms are available in non-cyclic photophosphorylation and hence it is considered to be a **more efficient process**)
- Dr. Arnon called ATP + $NADPH_2$ as**assimilatory power** for dark reaction

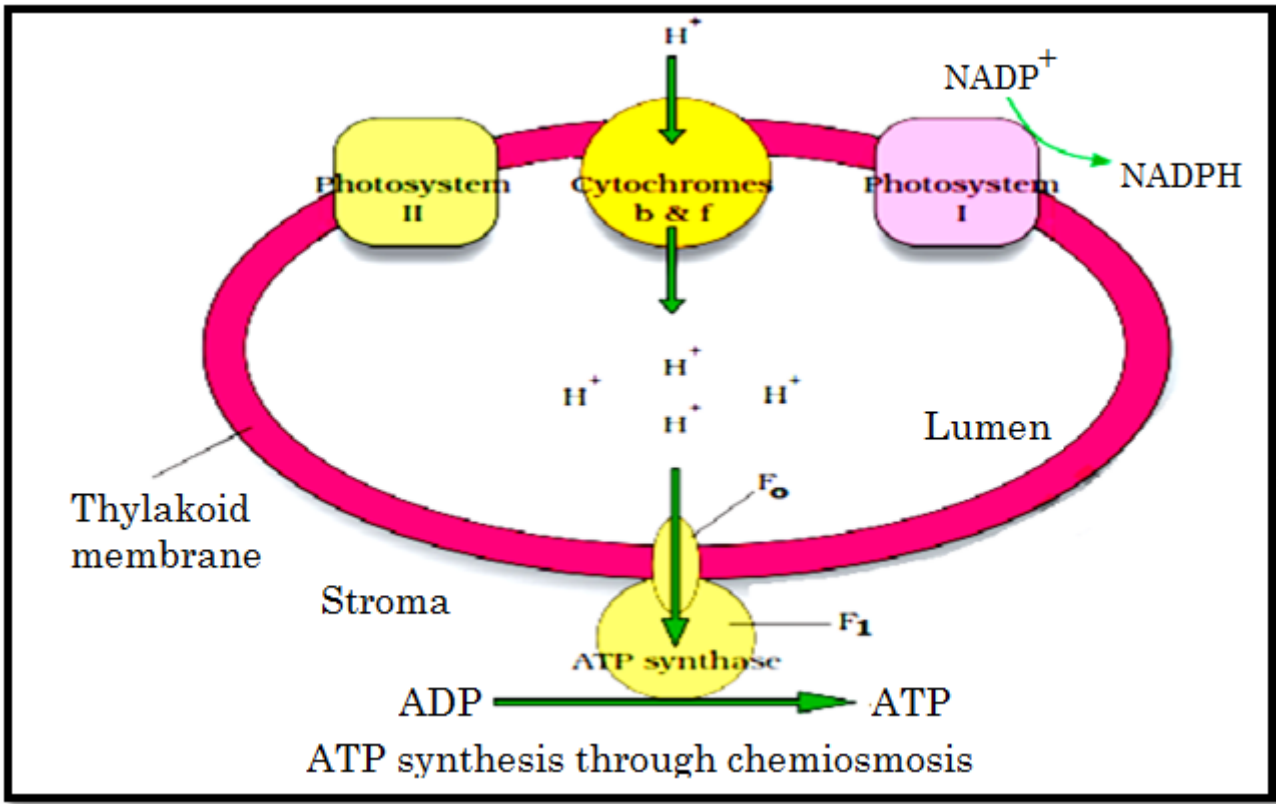
**Quantum requirement:** The number of light Quanta or photons required for the evolution of 1 mol. Of $O_2$ in photosynthesis. Emerson calculated that the quantum requirement is 8.

**Quantum Yield:** The number of oxygen molecule evolved by one quantum of light in photosynthesis is called as **Quantum yield.** Hence the quantum yield is 0.125 or 12.5%.

## 13.6 CHEMIOSMOTIC HYPOTHESIS: (Proton Pump)

- **Dr. Peter Mitchell** proposed The Chemiosmotic hypothesis in 1961 and was awarded the **Nobel Prize** in chemistry for this in 1978.
- The movement of ions across a selectively permeable membrane, down their electrochemical gradient is called **chemiosmosis.** (Just as movement of water/solvent across the membrane is osmosis).

- More specifically it relates to generation of **ATP** by the movement of **hydrogen** ions across a membrane during cellular respiration in mitochondria and during photosynthesis in chloroplasts.
- In photosynthesis, these membranes are thylakoids and the protons accumulate in the lumen. (In respiration, protons accumulate in the inter membrane space of the mitochondria).
- When hydrogen ions (protons) **diffuse** from an area of higher proton concentration to an area of lower proton concentration, **an electrochemical concentration gradient** of protons is developed. Dr. Peter Mitchell proposed that this electrochemical concentration gradient of protons across a membrane could be harnessed to make ATP. **ATP synthase** is the enzyme that makes ATP by **Chemiosmosis.**



ATP synthesis through chemiosmosis

- The gradient allows protons to pass through the membrane. This gradient produces the kinetic energy for H+ and eventually that energy will be used to phosphorylate ADP to ATP.
- Due to splitting of water molecule on the inner side of the membrane, hydrogen ions accumulate within the lumen of thylakoids. The **NADP reductase enzyme** is located in the stoma side of the membrane. For reduction of NADP to $NADPH_2$ protons are required along with electrons that come from ferredoxin. Hence, within the chloroplast, protons in the stoma decrease in number of protons. This creates a **proton gradient** across the thylakoid membrane. There is subsequent

spontaneous movement of protons generating energy which is used for the synthesis of ATP.

- 1 NADP uses 7.5 times more light energy to be converted to NADPH2 than when ADP is converted to ATP.
- This gradient is important because it is the breakdown of this gradient that 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 the gradient provides enough energy to cause a conformational change in the $F_1$ particle of the ATPase, which makes the enzyme synthesis several molecules of energy-packed ATP.

## 13.7 WHERE ARE THE ATP AND NADPH USED?

### LIGHT – INDEPENDENT REACTIONS/DARK REACTION/ BLACKMAN'S REACTION

- This is the second phase of photosynthesis in which $CO_2$ is fixed or reduced to glucose. It occurs in the stroma of chloroplast. It is independent of light (does not require direct light) hence called dark reaction. The products of light reaction namely, ATP and $NADPH_2$ are used here.
- The presence of dark reaction was first established by **Blackman** hence also called **'Blackman's reaction'.**

$$CO_2 + 2NADPH_2 + 2ATP \longrightarrow (CH_2O) + H_2O + 2NADP + 2ADP + 2iP$$

### CALVIN CYCLE ($C_3$ PATHWAY):

- The well-known plant physiologist **Dr. Melvin Calvin** in 1954 discovered the correct "path of carbon" in photosynthesis, i.e. sequence of biochemical reactions of $CO_2$ fixation into glucose. He carried out experiments on unicellular green algae like **Chlorella** and **Scenedesmus**, and used radioactive isotope of carbon. **$C^{14}$**, as a tracer.
- $^{14}CO_2$ was fed to photosynthesizing algal cells for definite time in seconds. The algal cells were then killed by dropping the suspension in hot methanol. The technique of **paper chromatography** was used to separate the intermediates formed and the technique of **radio-autography** was used to find out compounds with $^{14}CO_2$.
- Dr. Calvin showed and experimentally proved that these biochemical reactions leading to synthesis of glucose take place in cyclic manner. A substance (initial

acceptor) present in the stroma accepts atmospheric $CO_2$ and forms first stable product of photosynthesis. This substance undergoes many changes and final product, glucose is produced in **90 seconds**. Simultaneously, the initial accepter is regenerated so that it can accept $CO_2$ again and keep the process going.

- The first stable product is a 3-carbon compound, hence, Dr. Calvin called it $C_3$ cycle, or $C_3$ pathway, but is more popularly known as **Calvin cycle** or **Calvin-Benson cycle.** For this work, he was awarded a Nobel Prize in 1961, in association with his co-worker Dr. Benson.
- **The cycle involves following three main steps:**

1. Carboxylation
2. Reduction

3A. Synthesis

3B. Regeneration

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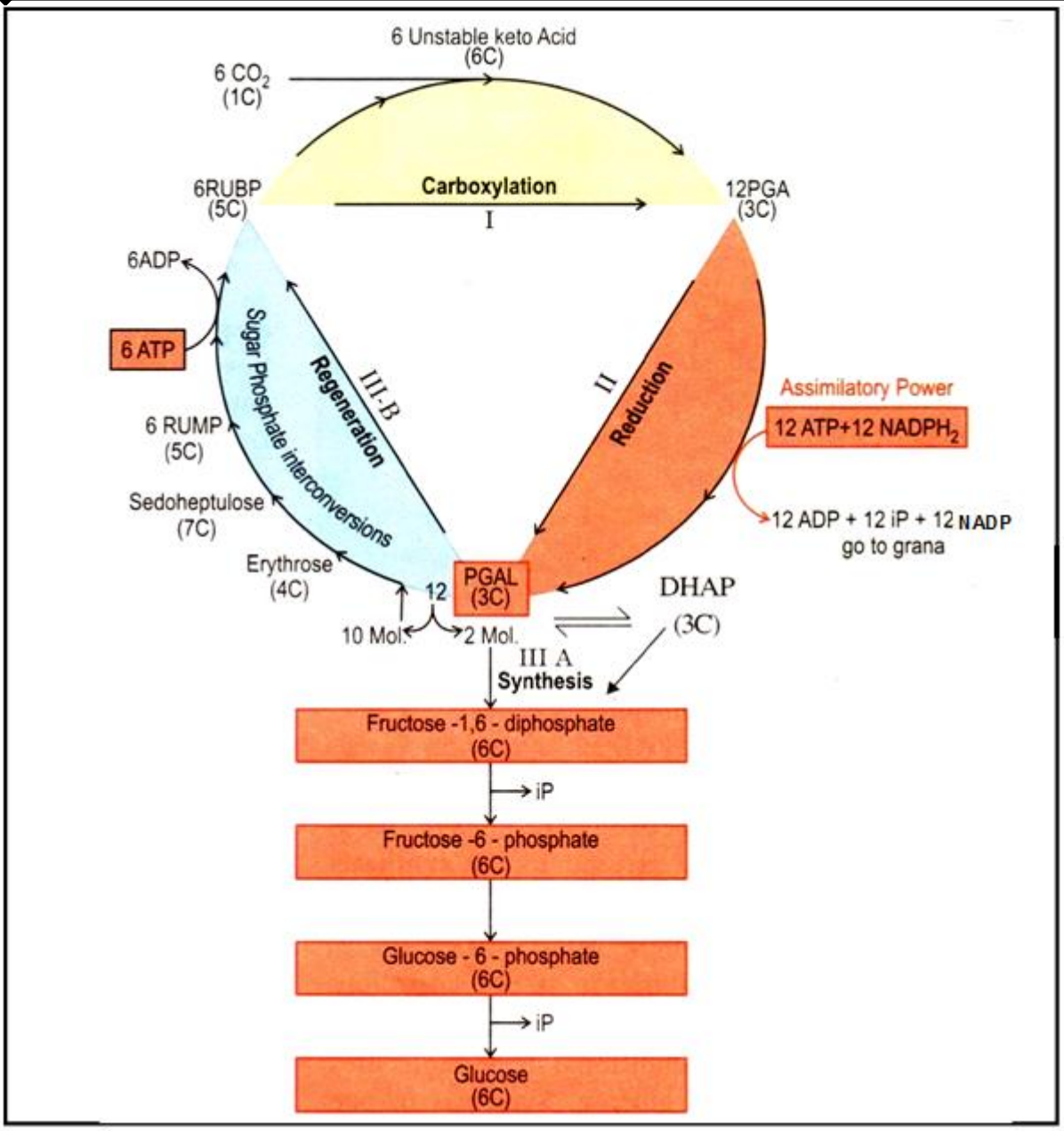



**1. Carboxylation:**

Atmospheric $CO_2$ is accepted by a 5-carbon compound called Ribulose-1-5-di-phosphate (RUDP) or Ribulose –1-5 bisphosphate (**RUBP)** in presence of enzyme RUDP carboxylase or **RUBP carboxylase (RuBisCO)** to form a 6-carbon unstable compound. Immediately it splits by hydrolysis into two molecules of 3-carbon compound called phosphoglyceric acid (**PGA),** in the presence of same enzyme.

$$\text{RUBP (5C)} + CO_2\,(1C) \xrightarrow[\text{RUBP Carboxylase}]{Mg^{+}} \text{unstable compound (6C)}$$

$$\text{Unstable compound (6C)} + H2O \xrightarrow[\text{RUBP Carboxylase}]{Mg^{++}} 2,\ 3PGA\ (3C)$$

**2. Reduction: (Utilization of Assimilatory Power)**

The Phosphoglyceric acid molecules are first phosphorylated by using ATP to produce 1,3-di-phosphogylceric acid which is then reduced using $NADPH_2$ to produce phospho-glyceraldehyde (PGAL) and inorganic phosphate is released.

$$3PGA + ATP \longrightarrow 1, 3 \text{ di-PGA} + ADP$$

$$1, 3 \text{ di-PGA} + NADPH_2 \longrightarrow 3PGAL + NADP + iP$$

Some part of 3PGAL is converted into its isomer Dihydroxyacetone phosphate (DHAP) in the presence of enzyme triose-phosphate isomerase.

**3A. Synthesis:**

For the synthesis of one glucose molecule, six turns of Calvin cycle are required or six molecules of RUBP and six molecules of $CO_2$ are required.

1/6 part of PGAL i.e. out of 12 molecules, 2 are used for synthesis of glucose.

**2(3C) = 1 (6C).** One molecule of PGAL and one molecule of DHAP combine together to form one molecule of fructose 1, 6-diphosphate.

$$3PGAL\ (3C) + DHAP \xrightarrow{(3C)} \text{Fructose 1, 6-diphosphate } (6C)$$

By dephosphorylation it produces fructose-6-phosphate which then isomerizes into glucose-6-phospahte. Glucose-6-phospate loses a phosphate group (dephosphorylation) to produce glucose. Glucose is either utilized or stored as starch.

(During glycolysis, glucose splits into DHAP & PGAL, then PGAL gets oxidized to PGA, hence this part of Calvin cycle i.e. **reduction and synthesis** is called reverse of glycolysis or **glycolytic reversal)**.

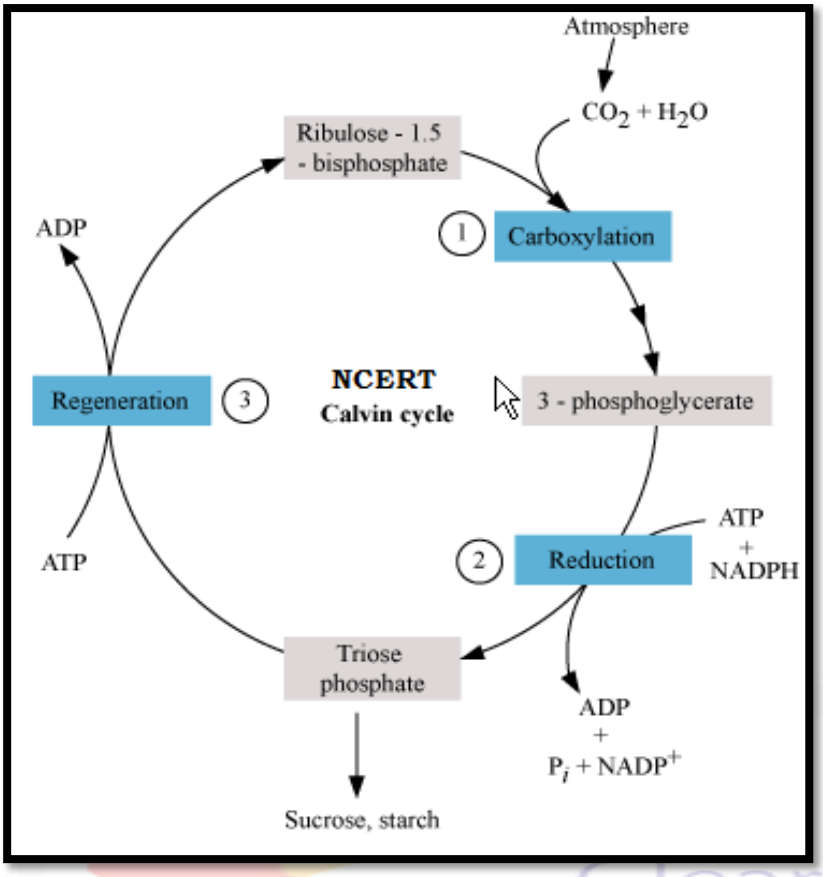
**3B. Regeneration:**

RUBP gets regenerated though several biochemical reactions. These reactions are called sugar phosphate interconversions. All the compounds/ intermediates formed are sugar phosphates, for example erythrose-4-phosphate (4-C), xylulose-5-phosphate (5-C), Ribose-5-phosphate (5-C), Sedoheptulose-7-phosphate (7-C) etc.

5/6 part of PGAL i.e. out of 12 molecules, remaining 10 molecules are used for regeneration of 6 molecules of ribulose mono-phosphate (RUMP). **10(3C) = 6 (5C)**

RUMP is phosphorylated to RUBP using ATP. For regeneration of 6 RUBP. 6 ATPs are required. Thus the initial acceptor of $CO_2$ gets regenerated and keeps the process going. ($12NADPH_2$ and 18 ATP are required for synthesis of one glucose molecule).

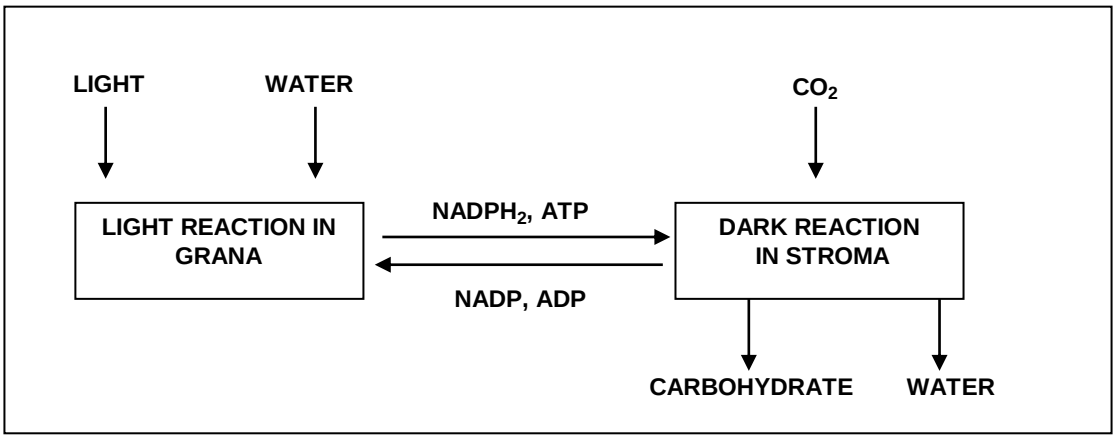
**Significance of dark reaction:**




- In dark reaction $CO_2$, is absorbed and fixed to form carbohydrates.
- ATP acts as an energy and phosphate donor and gets converted to ADP which is utilized in light reaction in the synthesis of ATP.
- $NADPH_2$ acts as a hydrogen donor and gets converted into NADP which is utilized in the light reaction for synthesis of $NADPH_2$.
- Other than glucose, various sugars are formed as by-products

| In | Out |
|---|---|
| Six $CO_2$ | One glucose |
| 18 ATP | 18 ADP |
| 12 NADPH | 12 NADP |

**INTERDEPENDENCE OF LIGHT AND DARK REACTION:**




The light and dark reactions are the two phases of photosynthesis and are interdependent.

**A.** The light reaction takes place in the presence of **sunlight**. It produces **ATP** and **$NADPH_2$**. ATP molecules provide energy and phosphate for the phosphorylation of RuMP to RuDP and 3PGA to 1, 3 DPGA. $NADPH_2$ provides hydrogen for the reduction of 1, 3 diphosphoglyceric acid to 3 phosphoglyceraldehyde during dark reaction. Thus, **dark reaction is dependent on light reaction.**

**B.** Thus, the dark reaction converts ATP to ADP and $NADPH_2$ to NADP. The ADP and NADP are necessary for light reaction where they get converted from ADP to ATP and NADP to $NADPH_2$ during electron transfer. Thus, **light reaction is dependent on dark reaction**.

## 13.8 ALTERNATIVE PATHWAYS OF DARK REACTION

At high temperature, high light intensity and low $CO_2$ concentration, plants cannot perform the standard dark reaction-C3 cycle. Such plants opt for

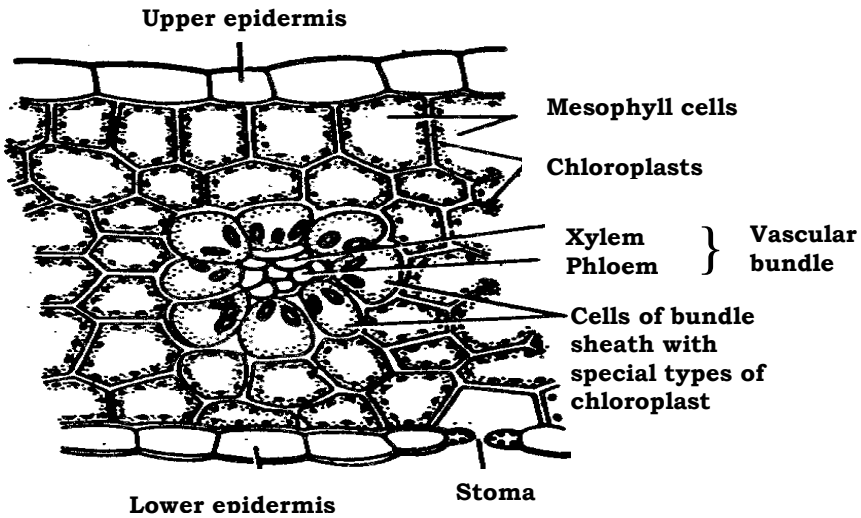
1. C4 pathway
2. CAM pathway.

### 1. $C_4$ PATHWAY OR DICARBOXYLIC ACID PATHWAY:

- There exists an **alternative** pathway which uses **Phosphoenol pyruvic acid (PEP)** as a substrate and the first stable product is a 4C compound called **Oxalo acetic acid (OAA).** This alternative pathway is called as **$C_4$ pathway**.
- The plants like maize, sugarcane, jowar, Amaranthus, etc. have this $C_4$ pathway, hence all such plants are called $C_4$ plants.
- H.P. Kortshak reported this alternative method of $CO_2$ fixation for the first time (in 1965) in sugarcane. In 1970 M.D. Hatch and C.R. Slack outlined the entire series of reactions; hence it is called Hatch and Slack pathway or HSK pathway.

**Characteristics of $C_4$ Plants:**

- They are adapted to **hot** and humid **conditions** of the tropics with **low $CO_2$**content.
- $CO_2$ is not directly absorbed by RuBisCO.
- **Efficiency** of $CO_2$ absorption and assimilation is **higher** than $C_3$ plants.
- They can perform photosynthesis in **high temperatures** and **intense light**. (Optimum temperature for photosynthesis is 30 – 35°C).
- Their overall **yield is more**.
- Their leaves show typical Kranz Anatomy.



**Leaf showing kranz anatomy**

**Kranz anatomy:** (Kranz, meaning wreath or necklace)

- $C_4$ plants show Kranz anatomy.
- The mesophyll is not differentiated into palisade and spongy tissue. It is homogenous.

- The chloroplasts in **mesophyll** cells contain **granal**chloroplasts. They are smaller in size more in number with abundant grana and very less stroma. The enzyme, PEP carboxylase is present in mesophyll chloroplast.

- Each vascular bundle is surrounded by a ring or wreath of radially arranged large **bundle sheath cells**. These cells contain **agranal** chloroplasts, i.e. chloroplasts are without grana. These chloroplasts are bigger in size, less in number and are with only stroma. RUBP carboxylase (RuBisCO) in bundle sheath chloroplast.
- Thus chloroplasts show **dimorphism** in C-4 plants.

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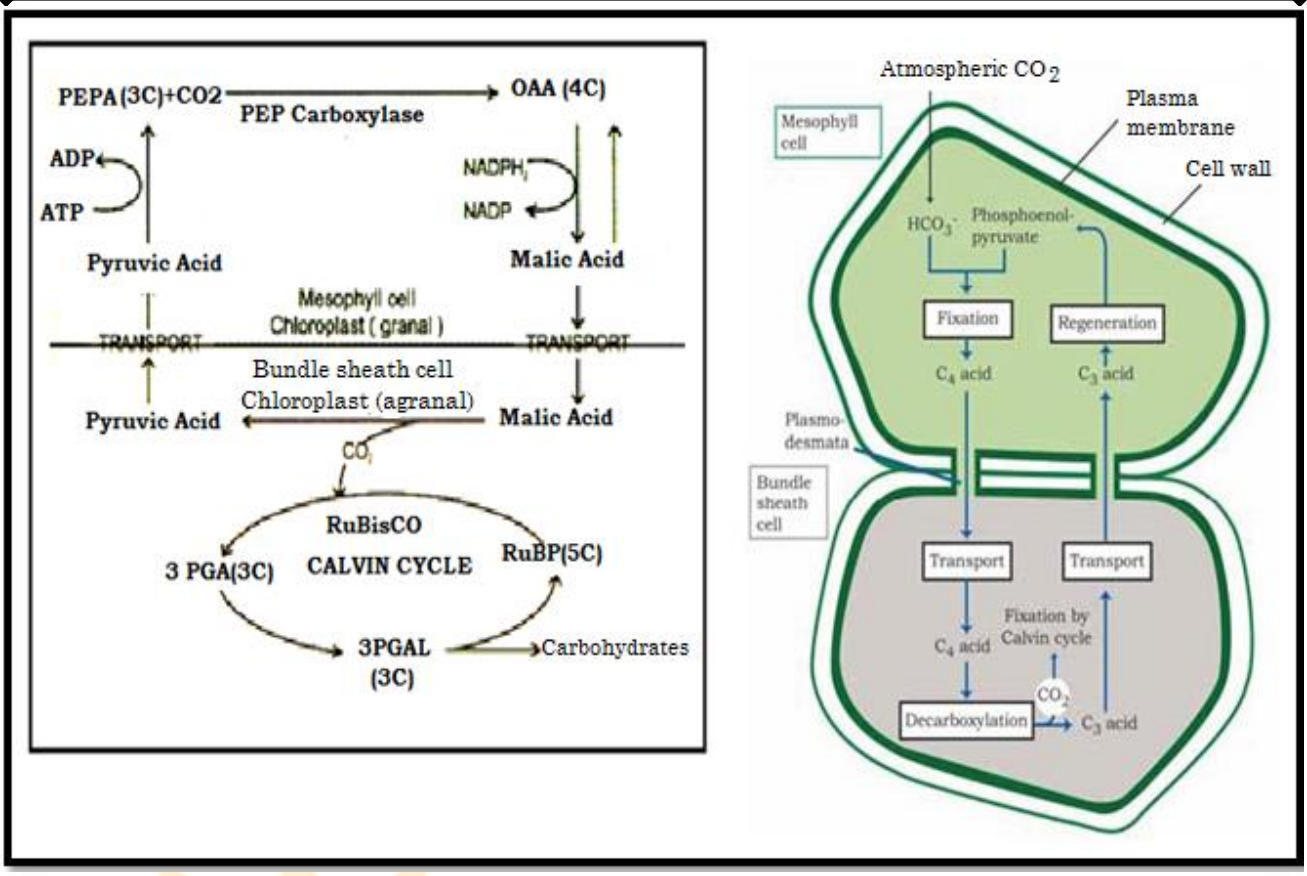
**Mechanism of HSK or $C_4$ pathway:**




## $C_4$ Pathway

The reactions occurring in this pathway are completed in two parts and at two different sites.

**Part I (Reactions in Mesophyll cells)**

**(i) Carboxylation (First $CO_2$ fixation):**

Atmospheric $CO_2$ entering through stomata is accepted by phospho-enol pyruvic acid (PEPA), a three carbon compound, present in the mesophyll cells. In the presence of water and enzyme PEP carboxylase, PEPA gets carboxylated to form oxaloacetic acid (OAA), a four-carbon compound. The enzyme PEP carboxylase can function even if the concentration of $CO_2$ in atmosphere is as low as 2 ppm (parts per million)

$$PEPA(3C) + CO_2\ (1C) + H_2O \xrightarrow{\text{Pep carboxylase}} OAA(4C) + H_3PO_4.$$

**(ii) Reduction:** Oxalo-acetic acid is reduced to malic acid in the presence of $NADPH_2$ and an enzyme malate dehydrogenase. (Or changed to aspartic acid by amination in the presence of $NADPH_2$ and an enzyme transaminase).

$$OAA\ (4C) + NADPH_2 \xrightarrow{\text{Malate dehydrogenase}} Malate\ (4C) + NADP$$

$$[OAA\ (4C) + NADPH_2 + NH_3 \xrightarrow{\text{Transaminase}} Aspartic\ acid\ (4C) + NADP + H_2O]$$

**Part – II (Reactions in Bundle sheath cells)**

**(i) Decarboxylation:**

Malic acid (or aspartic acid) is transported to chloroplasts of bundle sheath cells. In these agranal chloroplasts, malic acid undergoes decarboxylation in the presence of NADP to form pyruvic acid and $CO_2$ is released. Hydrogen removed at this step forms $NADPH_2$.

$$\text{Malate (4C)} + \text{NADP} \xrightarrow{\text{Malate dehydrogenase}} \text{Pyruvate (3C)} + CO_2 + NADPH_2$$

(If aspartic acid is formed, it undergoes deamination to form pyruvic acid)

**(ii) Second $CO_2$ fixation:**

The $CO_2$ released in accepted by a second $CO_2$ acceptor RUBP and is fixed by $C_3$ pathway (Calvin cycle) in the agranal chloroplast of bundle sheath cells. Thus glucose is formed by Calvin cycle and is transported through phloem.

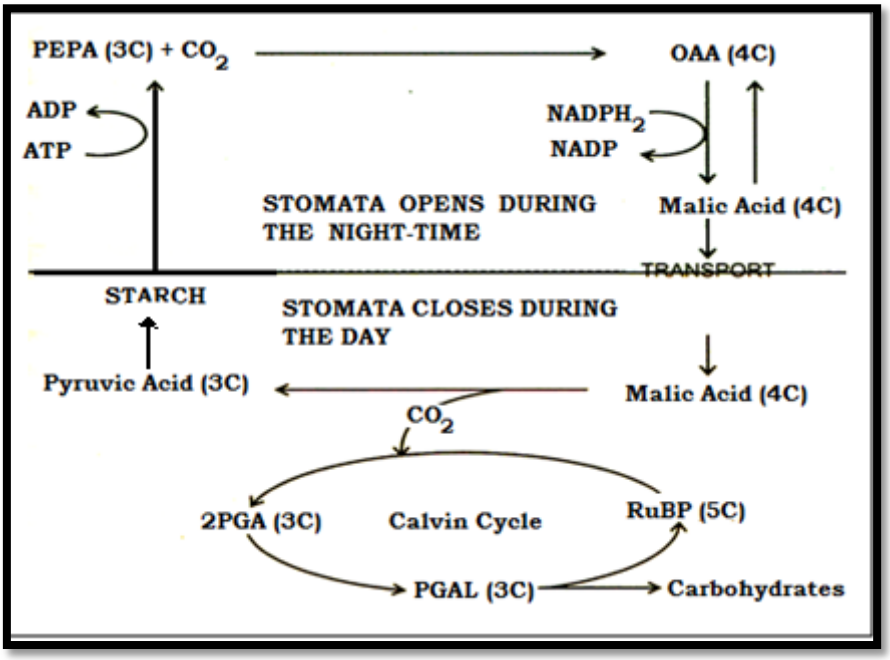
**(iii)** Pyruvic acid produced due to decarboxylation of malic acid is transported back to mesophyll cells and is **phosphorylated** by ATP to form PEPA. PEPA, the initial acceptor is thus regenerated to continue the pathway.

$$\text{Pyruvic acid (3C)} + \text{ATP} \longrightarrow \text{PEPA (3C)} + \text{ADP}$$

**Significance**:

- In $C_4$ plants, $CO_2$ fixation takes place twice, in two different cells during day.
- PEP carboxylase can pick up $CO_2$ at very low concentration and $C_4$ plants can photosynthesize in high light intensity, high temperature and less amount of water.
- Thus C-4 pathway has evolved in arid plants to maintain efficiency of photosynthesis under adverse conditions.
- In $C_4$ plants, PEP carboxylase (PEPCase) fixes $CO_2$ at low $CO_2$ concentration in the mesophyll cells. In the bundle sheath cells, $CO_2$ concentration is more, so that RUBISCO functions as carboxylase and **photorespiration is avoided.** C-4 pathway is therefore also referred to as $CO_2$ concentrating meschanism. Due to this some $C_4$ plants, such as maize, sugarcane and jowar are more productive. In $C_4$ plants light reaction takes place in mesophyll cells (granal chloroplasts) while dark reaction (Calvin cycle) in bundle sheath cells (agranal chloroplasts).
- The rate of $CO_2$**absorption** and **fixation** is very **rapid**.
- Carboxylation of PEP takes place very rapidly due to the **high efficiency** of the enzyme PEP case.
- It is an **adaptation** seen in plants growing in tropical conditions, i.e. in regions with high temperature and low $CO_2$ content.
- It helps in getting a **higher yield** in agricultural crops.

## 2. CAM-PLANTS/CRASSULACEAN ACID METABOLISM / DARK $CO_2$ FIXATION / DARK ACIDIFICATION:




- It is seen in members of **Crassulaceae** family with succulent xerophytic plants which grow in dry conditions (xerophytic).
- Eg. **Kalanchoe,** etc.
- In CAM plants stomata are of scotoactive type-they open at night and close during the day to check the water loss due to transpiration.
- Diurnal fluctuation of acids occur in CAM plants.
- **At night**,
  - **a.** PEPA gets regenerated from starch.
  - **b.** when the stomata opens, the primary acceptor of $CO_2$ is **PEPA** (Phosphoenol pyruvate).
  - **c.** oxaloacetic acid is the first product of carboxylation reaction in the presence of **PEP caboxylase**.
  - **d.** OAA in the presence of enzyme malate dehydrogenase gets reduced to malic acid.
  - **e.** Malate accumulates at night and acid concentration increases.
  - **f.** $C_4$ cycle occurs.
- **During the day,**
  - **a.** When the stomata are closed, malate undergoes decarboxylation gradually and gets converted to pyruvate.
  - **b.** $CO_2$ released enters $C_3$ cycle to produce sugars which gets converted to starch
  - **c.** Pyruvate also gets converted to starch. Thus acid concentration decreases and starch accumulates during the day.

**d.** $C_3$ cycle occurs

- **PEP caboxylase&Rubisco** present in mesophyll cells.(**No Kranz- anatomy)**
- In CAM plants 30 ATP and 12 $NADPH_2$ are required as assimilatory power for 1 glucose synthesis.

- **Oleary** and **Rouhani** discovered CAM-process
- **Eg.** Of CAM are Bryophyllum, Sedum, Kleinia, Opuntia, Crassula, Agave, Aloe, Euphorbiasps, Pineapple, Welwitschia(Gymnosperm).

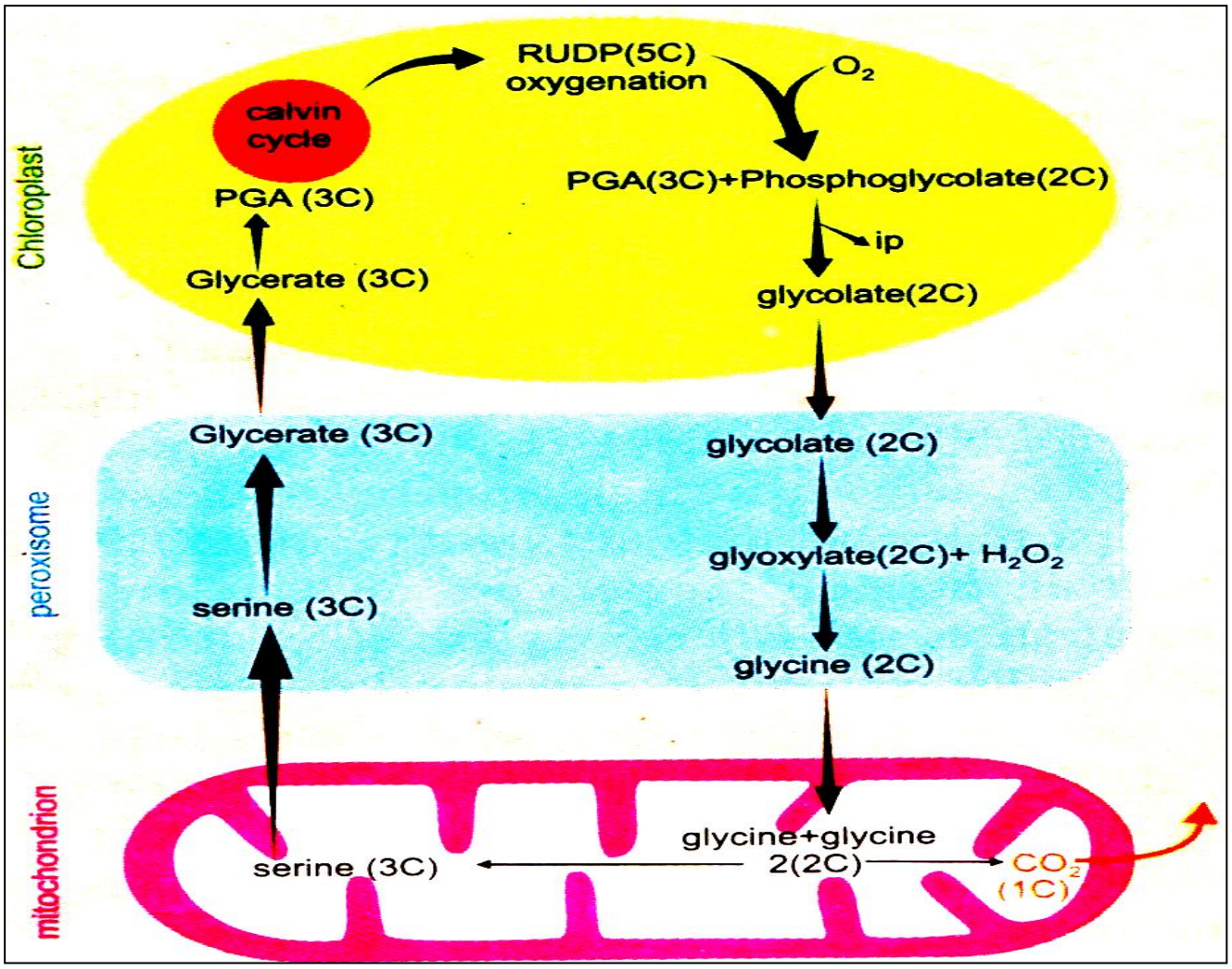
| **Characteristics** | **$C_3$ Plants** | **$C_4$ Plants** | **Choose from** |
|---|---|---|---|
| Cell type in which the Calvin cycle takes place | Mesophyll | Bundle sheath | Mesophyll/Bundle sheath / both |
| Cell type in which the initial carboxylation reaction occurs | Mesophyll | Mesophyll | Mesophyll / Bundle sheath / both |
| How many cell types does the leaf have that fix $CO_2$. | One | Two | Two: Bundle sheath and mesophyll<br>One: Mesophyll<br>Three: Bundle sheath, palisade, spongy mesophyll |
| Which is the primary $CO_2$ acceptor | RuBP | PEP | RuBP / PEP / PGA |
| Number of carbons in the | 5 | 3 | 5 / 4 / 3 |
| Primary $CO_2$ acceptor Which is the primary $CO_2$ fixation product | PGA | OAA | PGA / OAA / RuBP / PEP |
| No. of carbons in the primary $CO_2$ fixation product | 3 | 4 | 3 / 4 / 5 |
| Does the plant have RuBisCO? | Yes | Yes | Yes / No / Not always |
| Does the plant have PEP Case? | Yes | Yes | Yes / No / Not always |
| Which cells in the plant have Rubisco? | Mesophyll | Bundle sheath | Mesophyll/Bundle sheath/none |
| $CO_2$ fixation rate under high light conditions. | Medium | High | Low/high/medium |

| | | | |
|---|---|---|---|
| Whether photorespiration is present at low light intensities | Negligible | Negligible | High / negligible / sometimes |
| Whether photorespiration is present at high light intensities | High | Negligible | High / negligible / sometimes |
| Whether photorespiration would be present at low $CO_2$ concentrations. | High | Negligible | High/negligible/sometimes |
| Whether photorespiration would be present at high $CO_2$ concentrations. | Negligible | Negligible | High/negligible/sometimes |
| Temperature optimum | 20-25$^oC$ | 30-40$^oc$ | 30-40 C/20-25C/above 40C |
| Examples | Wheat Rice | **Maize Sugarcane Sorghum** | |

## 13.9 PHOTORESPIRATION/ PHOTOSYNTHETIC CARBON OXIDATION CYCLE:

- The process of respiration (oxidation) that is initiated in the chloroplast and takes place only during day is called photorespiration.
- For photorespiration to occur, RuBisCO is the key enzyme.
- **RuBisCO** is the most abundant enzyme in the world and its active site can bind to both $CO_2$ and $O_2$. This binding is competitive.
- However, RuBisCO is thermolabile and requires higher concentration of $CO_2$ for its activity.

- At high temperature the stomata close partially so that availability of $CO_2$ falls. Moreover, at high temperature and at low $CO_2$ concentration, RUBP carboxylase, (i.e. RuBisCO-Ribulose Bis phosphate Carboxylase Oxygenase), functions as oxygenase and brings about oxidation of RUBP instead of carboxylation. Due to this a considerable (approximately 25%) part of photosynthetically fixed $CO_2$ goes back to atmosphere. This is called **photorespiration.**




- At high temperature, high light intensity and low $CO_2$, concentration, oxidation of RUBP by $O_2$ takes place, which results in the formation of one molecule of 2-C compound, phosphoglycolate and one molecule of PGA.
- PGA gets incorporated in Calvin cycle while the phosphoglycolate gets dephosphorylated to form glycolate within the chloroplast.
- The glycolate then gets diffused into peroxisomes where it is oxidized to glyoxylate and then gets converted into an amino acid glycine (2C).

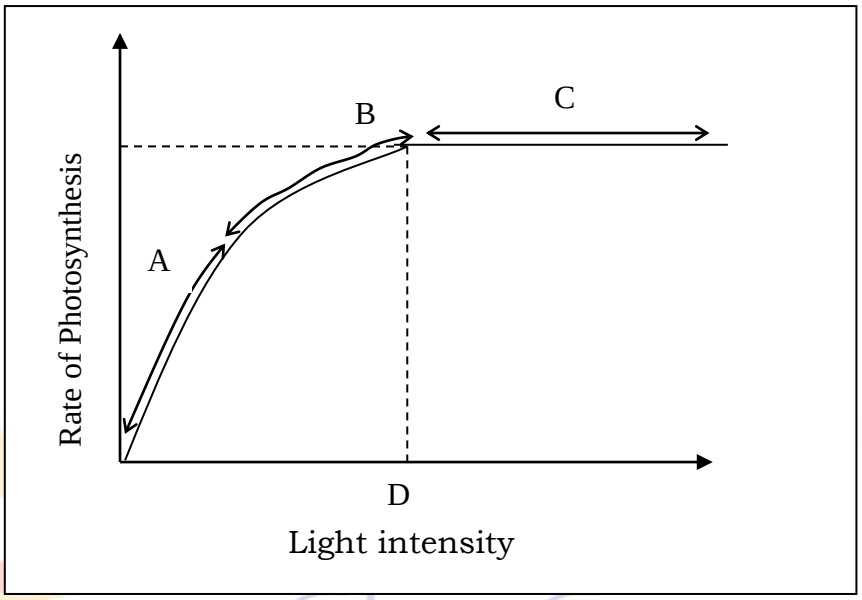
- Glycine enters mitochondria and two molecules of glycine give rise to one molecule of serine (3C) and one $CO_2$. The serine is taken up by peroxisome and gets converted into glycerate.
- The glycerate enters the chloroplast, gets phosphorylated to form PGA and enters the Calvin cycle.
- Thus 75% of the carbon lost by oxygenation of RUBP is recovered but 25% is lost as release of one molecule of $CO_2$.
- It protects the $C_3$ plants from photo-oxidative damage.
- RuBisCO has a much greater affinity for CO than for O2. This binding is competitive. It is the relative concentration of O2 and CO2 that determines which of the two will bind to the enzyme.
- In C3 plants some O2 does bind to RuBisCO, and hence CO2 fixation is decreased.
- In the photorespiratory pathway, there is neither synthesis of sugars, nor of ATP. Rather it results in the release of CO2 with the utilisation of ATP. In the photorespiratory pathway there is no synthesis of ATP or NADPH. Therefore, photorespiration is a **wasteful** process.
- In C4 plants photorespiration does not occur. This is because they have a mechanism that increases the concentration of CO2 at the enzyme site. This takes place when the C4 acid from the mesophyll is broken down in the bundle sheath cells to release CO2 – this results in increasing the intracellular concentration of CO2. In turn, this ensures that the RuBisCO functions as a carboxylase minimising the oxygenase activity.

## 13.10 FACTORS AFFECTING PHOTOSYNTHESIS:

**Law of limiting factors: (Blackman):** "When a process is conditioned to its rapidity by a number of factors, then rate of process is limited by the pace of the slowest factor" ($CO_2$, light, chlorophyll, water, temp.) $CO_2$ becoming limiting in clear sky, but light limiting in cloudy days and in dense forest. Atmospheric $CO_2$ is not limiting factor for $C_4$ plants & submerged hydrophytes.

**1. LIGHT:**

At low light intensity there is a linear relationship between light intensity and rate of photosynthesis**.** But at high light interbity there is no farther increase in rate of photosynthesis. At very high light intensity **Photooxidation (solarization)** of photosynthetic pigments may occur.



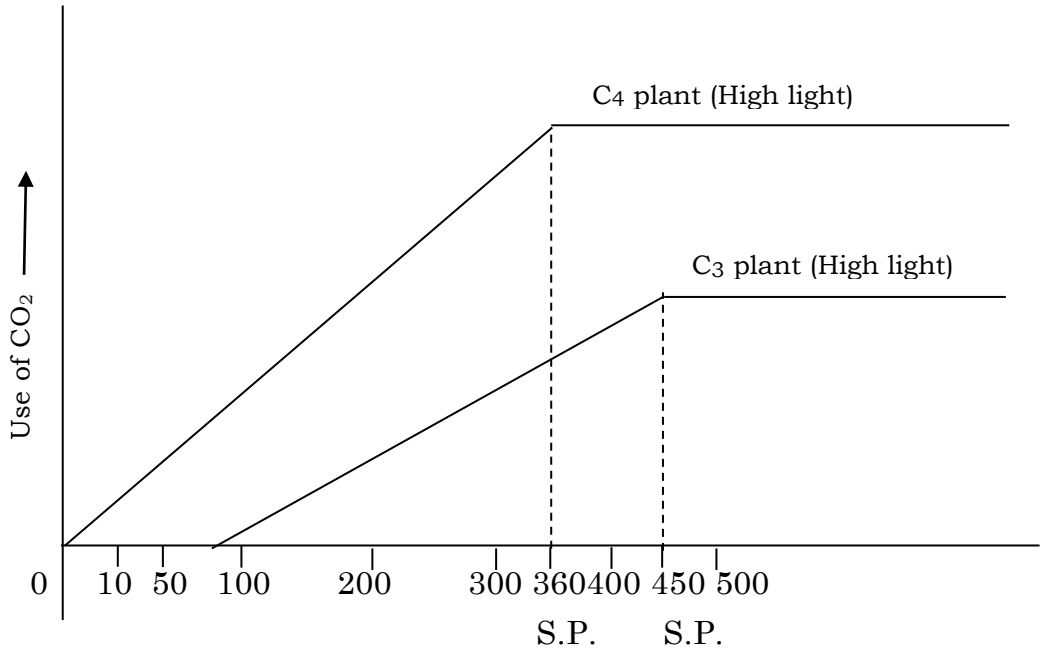

Intensity of light, at which rate of photosynthesis, becomes equal (or compensate) with the rate of respiration in plants is known as **light compensation point** (Net photosynthesis or net primary productivity at this point is zero and no gaseous exchange between plant and atmosphere)

**2. TEMPERATURE:**

- Optimum temp. for photosynthesis is **20-25$^{o}$C for $C_3$ plants and 30-40$^{o}$C for $C_4$ plants**.
- At high temp. rate of photosynthesis decreases due to denaturation of enzymes.
- The dark reactions being enzymatic are temperature controlled. Though the light reactions are also temperature sensitive they are affected to a much lesser extent. The $C_4$ plants respond to higher temperatures and show higher rate of photosynthesis while C3 plants have a much lower temperature optimum.
- 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.

**3. $CO_2$ (between 0.03 and 0.04 percent)**

- **An increase in CO2 concn, upto 0.05% rate of photosynthesis is increased.** Higher $CO_2$ concentration is toxic to plant & also closed stomata.
- "CO2 concn at which CO2 fixation in photosynthesis is equal to volume of $CO_2$ released in respiration **"$CO_2$ compensation point"** (when plant saturated with full light).
- $CO_2$ compensation point for $C_4$ plants is 0-10 ppm, while for $C_3$ plants it is 25-100 ppm.
- The $C_3$ and $C_4$ plants respond differently to $CO_2$ concentrations. At low light conditions neither group responds to high $CO_2$ conditions. At high light intensities, both $C_3$ and $C_4$ plants show increase in the rates of photosynthesis. What is important to note is that the $C_4$ plants show saturation at about 360 µlL-1 while $C_3$ responds to increased $CO_2$ concentration and saturation is seen only beyond 450 µlL-1. Thus, current availability of $CO_2$ levels is limiting to the $C_3$ plants.
- The fact that $C_3$ plants respond to higher $CO_2$ concentration by showing increased rates of photosynthesis leading to higher productivity has been used for some greenhouse crops such as tomatoes and bell pepper. They are allowed to grow in carbon dioxide enriched atmosphere that leads to higher yields.



$CO_2$ in ppm ⟶ (S.P. = Saturation point)

**4. WATER:**

Less availability of water reduces the rate of photosynthesis (stomata get closed, leaves become wilted and slow enzymatic activities.)

**Plant Factors:**

(i) **Amount of Chlorophyll**

**(ii) Leaf:** Various lepaf factors like leaf number, size, age and leaf orientation affect the photosynthesis

**5. INHIBITORS:**

DCMU (Diuron/ Dichlorophenyl Dimethyl Urea), CMU (Monuron), PAN inhibit the photosynthesis by blocking PS – II They stop e-flow between P-680 & PQ.

In cyclic ETS diquat, paraquat (Viologen dyes) inhibit e-flow between P-700 &Fd.

All these chemicals are used **as weedicides or herbicides.**

**SIGNIFICANCE OF PHOTOSYNTHESIS:**

- Photosynthesis is the most important biological process in which **food** is **prepared** by plants, which is used by plants themselves as a source of energy as well as by animals/heterotrophs either directly or indirectly (except chemo-autotrophs).
- **Conversion of radiant energy:** Photosynthesis converts radiant energy into chemical energy. All organisms use chemical energy for their activities.
- **Carbohydrate**s formed, are the **chief source of energy**. Besides, they are converted into fats, proteins etc. and are stored in the plant body which are then consumed by animals.
- Photosynthesis being greater than respiration increases the biomass and provides feeding, hiding, nesting places for animals.
- In photosynthesis, **carbon dioxide** is **absorbed** and **oxygen is released** which is used by all living organisms during respiration. Thus photosynthesis **purifies air** and prevents green house effect produced due to $CO_2$. It is the only process which replenishes atmospheric oxygen. Molecules of Oxygen ($O_2$) evolved during photosynthesis combine with atoms of Oxygen (O) in the atmosphere and form **Ozone ($O_3$).** It forms a layer between 15 km to 35 km above the earth surface and absorbs harmful ultra violet (UV) radiation which would otherwise reach earth's surface and cause mutations, ailments like skin cancer and rise in earth's temperature.

- **Purification of atmosphere:** Photosynthesis consumes atmospheric carbon dioxide which is being continuously added by the respiration or organisms and burning of organic fuels. Thus, photosynthesis acts as Purifier of atmosphere.
- Timber, cotton, alkaloids, gum, resins, tannins, steroids, rubber, oils etc. are indirect products of photosynthesis.
- **Fossil fuels:** Fossil fuels such as coal, natural gas and petroleum are also products of photosynthetic organisms which lived in the remote past some millions of years ago.

### 1. Comparison between Photosynthesis and Chemosynthesis

| | Photosynthesis | Chemosynthesis |
|---|---|---|
| 1. | In photosynthesis, energy is derived from light | In chemosynthesis, energy is derived from oxidation of some chemical compounds. |
| 2. | They require presence of light | They do not require presence of light. |
| 3. | Donor of hydrogen in photosynthesis is water. | Donor of hydrogen in chemosynthesis is some chemical compound other than water. |
| 4. | It occurs in all green plants and some bacteria. | It occurs only in some bacteria. |
| 5. | They have photosynthetic pigments. | They do not have photosynthetic pigments. |

### 2. Comparison between Grana and Stroma

| | Grana | Stroma |
|---|---|---|
| 1. | The grana consist of quantasomes containing the pigment chlorophyll. | The stroma does not consist of quantasomes containing the pigment chlorophyll. |
| 2. | The grana contain the enzymes necessary for the formation of ATP molecules. | The stroma contains the enzymes necessary for the formation of carbohydrate from carbon dioxide. |
| 3. | The chemical reactions occurring in grana require the presence of light. (Light reaction takes place) | The chemical reactions occurring in stroma do not require the presence of light. (Dark reaction takes place) |
| 4. | The grana play a vital role in the generation of ATP, $NADPH_2$ and | The stroma plays a vital role in the synthesis of glucose from carbon dioxide. |

| | | |
|---|---|---|
| | evolution of oxygen, during the process of photosynthesis | |

### 3. PS I and PSII

| | PS I | PS II |
|---|---|---|
| 1. | It has p 700 as reaction centre | It has p 680 as reaction center. |
| 2. | It has more of carotenes. | It has more of xanthophylls. |
| 3. | It carries out cyclic photophosphorylation independently | It carries out non-cyclic photophosphorylation in association with PS I |
| 4. | It is not involved in photolysis of water. | It causes photolysis of water |

### 4. Cyclic Photophosphorylation and Non-Cyclic Photophosphorylation

| | Cyclic Photophosphorylation | Non-Cyclic Photophosphosphorylation |
|---|---|---|
| 1. | Emitted electron return back to the reaction centre. | Emitted electron does not return back to the reaction centre. |
| 2. | Only PS I works. | Both PS I and PS II works. |
| 3. | Only ATP is formed. | ATP and $NADPH_2$ are formed. |
| 4. | Does not involve photolysis of $H_2O$ | Photolysis of $H_2O$ takes place |
| 5. | No evolution of oxygen. | Oxygen is evolved. |
| 6. | Comparatively less energy is produced. | Comparatively more energy is produce. |

### 5. Comparison between Light and Dark reaction

| | Light Reaction | Dark Reaction |
|---|---|---|
| 1. | It is a photochemical reaction | It is a synthetic reaction |
| 2. | It requires presence of light | It does not require presence of light |
| 3. | It takes place in the grana of chloroplast | It takes place in the stroma of chloroplast. |
| 4. | It produces ATP and $NADPH_2$ | It utilizes ATP and $NADPH_2$ |
| 5. | It involves photolysis of water and release of $O_2$. | It involves fixation of $CO_2$ and formation of carbohydrate. |

## Theory Questions

### Q.1. Long Answer Questions:

1. Define photophosphorylation and describe non-cyclic photophosphorylation.
2. Give an account of Calvin cycle.
3. Distinguish between $C_3$ and $C_4$ pathway.
4. Describe $C_4$ pathway with examples.
5. Describe different types of photosynthetic pigments and explain their role.

### Q.2. Short Answer Questions:

1. Define photosynthesis. Why is it a redox reaction?
2. Write briefly about significance of photosynthesis.
3. Draw a well labelled diagram showing ultra-structure of chloroplast.
4. Distinguish between cyclic and non-cyclic photophosphorylation.
5. Give diagrammatic representation of non-cyclic photophosphorylation.
6. Explain how photosynthesis takes place during day in spite of stomata being closed, in certain plants.
7. Explain how photorespiration is avoided in C-4 plants.
8. "Hill's experiment does not prove that the source of oxygen evolved during photosynthesis, is water." This statement is true or false? Explain
9. Write a note on nature of light and its role in photosynthesis

### Q.3. Very Short Answer Questions:

1. Why is chlorophyll-a called essential pigment?
2. Under which conditions cyclic photophosphorylation will take place?
3. Which substance acts as hydrogen accepter in plants when photolysis of water takes place?
4. What was used to prove that source of oxygen evolved during photosynthesis is water
5. What are cytochromes?
6. Why light independent reactions cannot take place during night?
7. In CAM plants, why dopes acid concentration increase during night?
8. How many $NADPH_2$ and ATP are required for synthesis of one molecule of glucose?