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STUDY MATERIAL

Photosynthesis in Higher plants

ENGLISH MEDIUM

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PHOTOSYNTHESIS IN HIGHER PLANTS

- Introduction
- What do we Know?
- Early Experiments
- Where does Photosynthesis take place?
- How many Pigments are Involved in Photosynthesis?
- What is Light Reaction?
- The Electron Transport/Photophosphorylation
- Where are the ATP and NADPH Used?/Dark reaction/Biosynthetic phase
- Photorespiration
- Factors affecting Photosynthesis

01. INTRODUCTION

- **"Photosynthesis is a Physico - chemical or photo–biochemical process in which the organic compounds (carbohydrates) are synthesised from the inorganic raw material (H_2O & CO_2) in the presence of light & pigments. O_2 is evolved as by product or one of the net products".**

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

- Light energy is converted into chemical energy by photosynthesis.
- Photosynthesis is a **redox reaction** during which **oxidation of H_2O** occurs (as it provides H^+ and e^-) during light reaction and **reduction of CO_2** occurs (as it accepts H^+ & e^-) during dark reaction (biosynthetic phase)
- Photosynthesis is an **Anabolic** (synthesising) & **Endergonic** (Energy absorbing) process.

02. WHAT DO WE KNOW?

- Some simple experiments show that chlorophyll (green pigment of the leaf), light and CO_2 are required for photosynthesis to occur.
- Look for starch formation in two leaves – **a variegated leaf or a leaf that was partially covered with black paper and one that was exposed to light.** On testing these leaves for starch it was clear that **photosynthesis occurred only in the green parts of the leaves in the presence of light.**
- Another experiment is the **Moll's half-leaf experiment,** where a part of a leaf is enclosed in a test tube containing some KOH soaked cotton (which absorbs CO_2), while the other half is exposed to air. The setup is then placed in light for some time. On testing for starch later in the two halves of the leaf, the exposed part of the leaf tested positive for starch while the portion that was in the tube, tested negative. This **shows that CO_2 is required for photosynthesis.**

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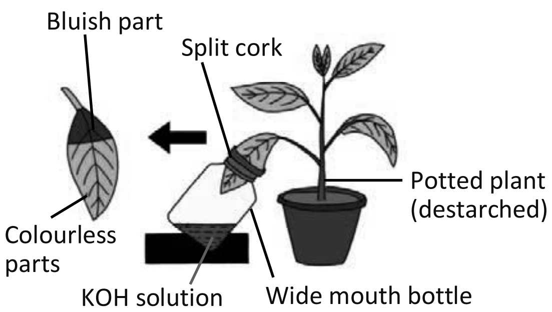
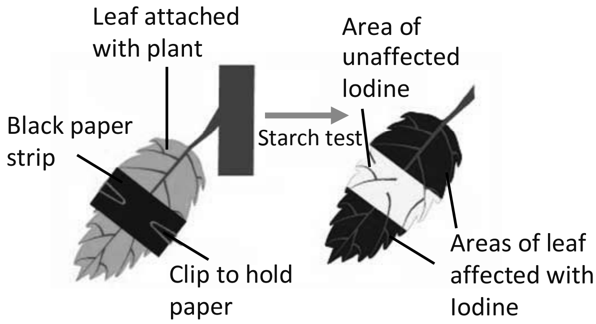


Moll's Half leaf experiment

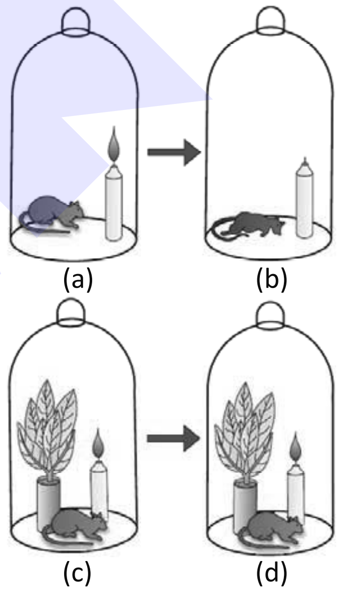


Variegated leaf experiment

03. EARLY EXPERIMENTS

(1) J. PRIESTLEY

- Joseph Priestley (1733-1804) in 1770 performed a series of experiments that revealed the essential role of air in the growth of green plants.
- Priestley observed that a candle burning in a closed space – a bell jar, soon gets extinguished. 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 candle continued to burn.
- **Prisetley hypothesised as follows : plants restore to the air whatever breathing animals and burning candles remove.**



Priestley's experiment

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(2) JAN INGENHOUSZ (1779)

- 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.**

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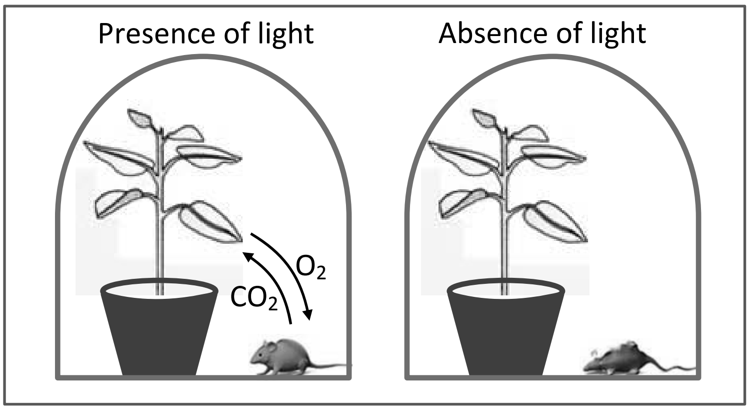
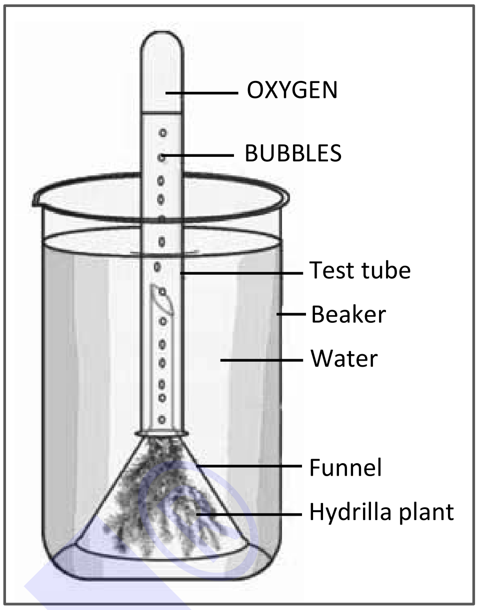




(3) J. V. SACHS (1854)

It was not until about 1854 that Julius von Sachs 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.

(4) VAN NIEL (1897-1985)

A milestone contribution to the understanding of photosynthesis was that made by a microbiologist, Cornelius van Niel, who, based on his studies of purple and green bacteria, demonstrated that photosynthesis is essentially a light-dependent reaction in which hydrogen from a suitable oxidisable compound reduces carbon dioxide to carbohydrates.

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

H_2A = suitable oxidisable compound or H-Donor

In green plants H_2O is the hydrogen donor and is oxidised to O_2. Some organisms do not release O_2 during photosynthesis. When H_2S, instead is the hydrogen donor for purple and green sulphur bacteria, the 'oxidation' product is sulphur or sulphate depending on the organism and not O_2. Hence, he inferred that the O_2 evolved by the green plant comes from H_2O, not from carbon dioxide.

(5) RUBEN & KAMEN (1941)

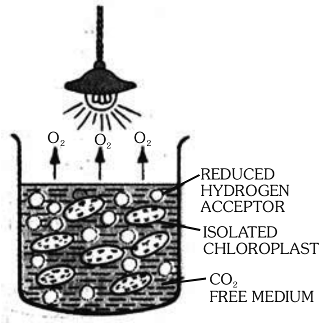
Used O^{18} (radioisotopic technique) to show experimentally that O_2 in photosynthesis released from water.

$$\boxed{6CO_2 + 12H_2O^{18} \xrightarrow[\text{Chlorophyll}]{\text{Light}} C_6H_{12}O_6 + 6H_2O + 6O_2^{18}}$$

(6) ROBERT HILL AND BENDALL

They are credited for :

- Detailed study of light reaction and proposed **Z scheme.**
- Detailed study of light reaction in isolated chloroplast of *Stellaria* plant. He illuminated the isolated chloroplasts of *Stellaria media* in the presence of hydrogen acceptors (ferricyanides) in the absence of carbon dioxide. The chloroplasts evolved oxygen



$$2A + 2H_2O \xrightarrow[\text{Hill reagent}]{\text{Sunlight}} 2AH_2 + O_2$$

A = Hydrogen acceptor (Hill reagent)

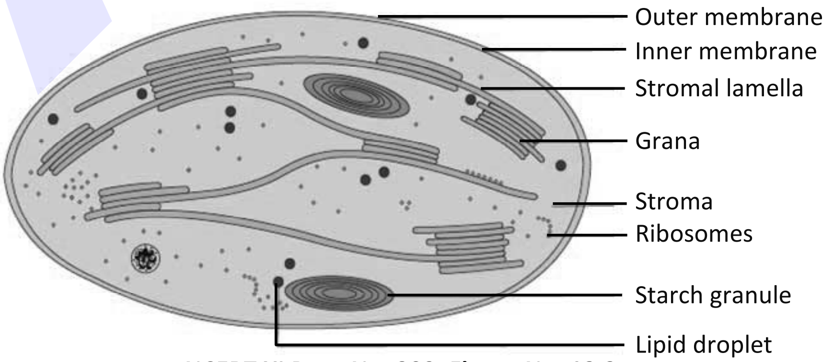
Hill reagent

Natural	Artificial
eg. NADP	eg. Potassium ferricyanide, Benzoquinone, chromate and DCPIP etc.

DCPIP (Dichlorophenol indophenol) is a blue colour dye, which become colourless on reduction.

04. WHERE DOES PHOTOSYNTHESIS TAKE PLACE?

- **Photosynthesis** does take place in the **green leaves** of plants but it does so also in **other green parts** of the plants.
- Within the chloroplast there is the membranous system consisting of grana, the stroma lamellae, and the matrix stroma. There is a clear division of labour within the chloroplast. The membrane system is responsible for trapping the light energy and also for the synthesis of ATP and NADPH. In stroma, enzymatic reactions synthesise sugar, which in turn forms starch. The former set of reactions, since they are directly light driven are called light reactions (photochemical 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 (carbon reactions).



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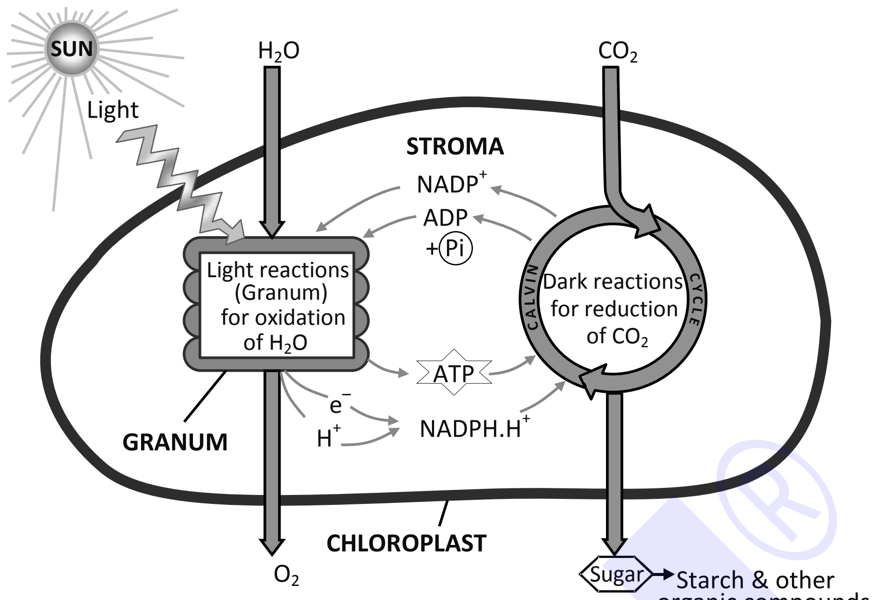
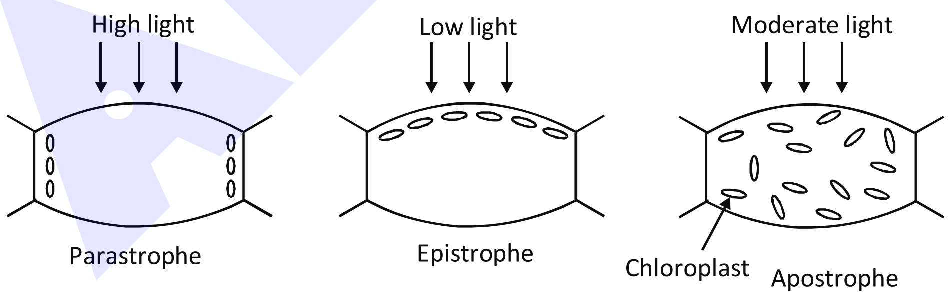


Division of labour in chloroplast

- **Alignment of chloroplasts :**

  Usually the chloroplasts align themselves along the walls of the mesophyll cells, such that they get the optimum quantity of the incident light.

Conditions	Alignment of chloroplasts
High light intensity	Parallel to the incident light/Lateral walls **(Parastrophe)**
Low light intensity	Perpendicular to the incident light **(Epistrophe)**
Moderate light intensity	Random **(Apostrophe)**



Various kinds of alignment of chloroplasts

Q. When do you think the chloroplasts will be aligned with their flat surface parallel to the walls ?

Ans. Under **high** light conditions, this is called **parastrophe.**

Q. When do you think chloroplast will be perpendicular to the incident light ?

Ans. Under **low** light conditions, this is called **epistrophe.**

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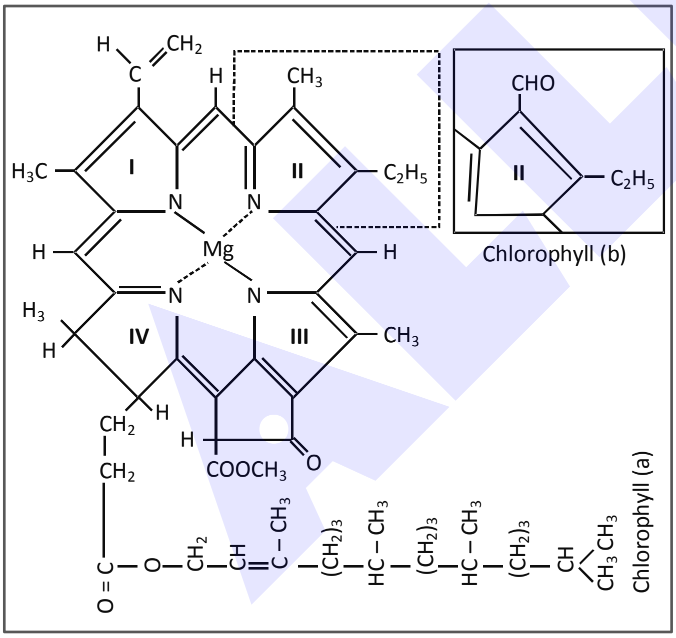
05. HOW MANY PIGMENTS ARE INVOLVED IN PHOTOSYNTHESIS?

- Photosynthetic pigments are special molecules those absorb, transmit and reflect different colours of light from the visible spectrum of sunlight. Pigment appears in the colour which it reflect and uses the colour which it absorbs.
- **Photosynthetic pigments are of following types :–**
  1. Chlorophylls **2. Carotenoids** **3. Phycobilins**
- Leaf pigments can be separated through paper chromatography technique and the result of this separation is called chromatogram.

(1) CHLOROPHYLLS

- Green colored pigment
- Light is required for their synthesis
- Soluble in organic solvents
  - Chlorophylls are of following types –
    Chl. – a, **Chl – b**, Chl. – c, Chl. – d, Chl. – e
  - **Chl – a** is universal pigment, which is found in all O_2 liberating photosynthetic organisms. Its color is **blue green** in chromatogram.
  - **Chl – b** is accessory photosynthetic pigment found in euglenoids, green algae and higher plants. Its color is **yellow green** in chromatogram

(A) **Structure of Chlorophyll :** Structure of chlorophyll look like **tadpole.**



Chlorophyll

Porphyrin Head	**Phytol Tail ($C_{20}H_{39}OH$)**
• Size = 15 × 15 Å	• Size = 20 Å long
• It is hydrophilic	• It is hydrophobic
• It is a tetrapyrole structure with Mg present in the centre.	• Tail remain embedded in lipid bilayer of thylakoid membrane.

- **Chlorophyll – a** $C_{55}H_{72}O_5N_4Mg$ ⟶ CH_3 group in II[nd] pyrrol ring.
- **Chlorophyll – b** $C_{55}H_{70}O_6N_4Mg$ ⟶ CHO group in II[nd] pyrrol ring.

(B) Chlorophyll Synthesis :

$$\text{Succinyl CoA + Glycine} \longrightarrow \text{Protochlorophyll} \xrightarrow[2H]{light} \text{Chlorophyll}$$

- This reaction is catalysed by **iron (Fe)**

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(2) CAROTENOIDS

- The first carotenoid was discovered in carrot and was named carotene. Carotenes are the first type of carotenoids. These are yellow orange in colour. It contains carbon and hydrogen.
- Another carotenoid is xanthophyll that contains carbon, hydrogen and oxygen. These are usually yellow in colour.
- Among carotenoids, β – carotene (type of carotene) and lutein (type of xanthophyll) are common in plants.

Functions of carotenoids :

(1) They are **accessory pigments** and make photosynthesis more efficient by absorbing different wavelengths of light.

(2) They protect chl-a from photo oxidation and they also protect photosynthetic machinery by converting **lethal nascent oxygen** into unharmful **molecular oxygen,** thus called **shield pigments.**

$$-CH=CH-CH=CH- + [O] \rightarrow -\underset{\diagdown O \diagup}{CH-CH}-\underset{\diagdown O \diagup}{CH-CH}- \rightarrow -CH=CH-CH=CH- + O_2$$

(3) PHYCOBILLINS

- They are hot water soluble pigment.
- They lack Mg and phytol tail.

Types :

(i) Phycocyanin – Blue (ii) Phycoerythrin – Red (iii) Allophycocyanin – Light blue

They occur exclusively in BGA and Red algae as an accessory pigments.

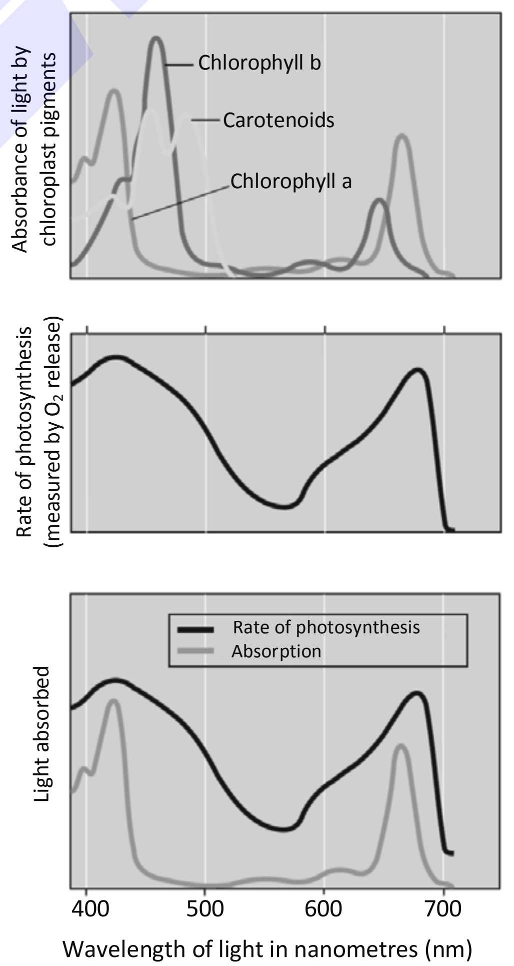
PAR (Photosynthetic Active radiation) – 400–700 nm

(4) ABSORPTION SPECTRUM

- **Graphical presentation of the absorption of different wavelenght of light by a particular pigment.**
- Figure (a) showing the ability of pigments to absorb lights of different wavelengths (absorption spectrum). **Chl. a shows maximum absorption at blue light. It shows another absorption peak at red light.**

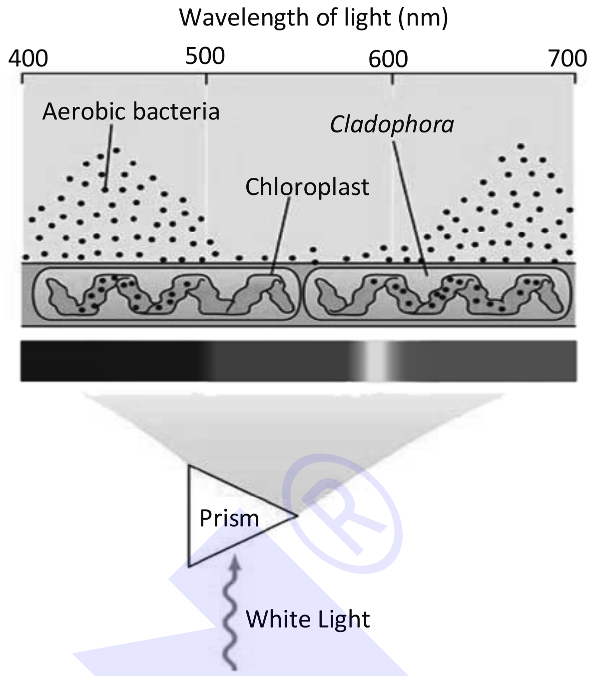
(5) ACTION SPECTRUM

- **The graphic curve depicting the relative rates of photosynthesis at different wavelengths of light is called action spectrum**
- Figure (b) showing the wavelengths at which photosynthesis occurs in a plant (Action spectrum). Figure (c) show that the wavelengths at which there is maximum absorption by chlorophyll a, i.e., in the blue and the red regions, also show higher rate of photosynthesis. Hence, **we can conclude that chlorophyll-a is the chief pigment associated with photosynthesis.**



NCERT XI Page No. 210, Figure No. 13.3

Now consider the interesting experiment done by T.W Engelmann. 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.



- 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. It happens because other thylakoid pigments like chlorophyll-b, xanthophylls and carotenoids, which are called accessory pigments, also absorb light and transfer the energy to chlorophyll a. Indeed, they not only enable a wider range of wavelength of incoming light to be utilised for photosynthesis but also protect chlorophyll a from photo-oxidation.

Golden Key Points

- Light energy is converted into chemical energy by photosynthesis.
- Photosynthesis is a **redox reaction** and is an **anabolic** (synthesising) & **endergonic** (Energy absorbing) process.
- There is a clear division of labour within the chloroplast. The membrane system is responsible for trapping the light energy and also for the synthesis of ATP and NADPH. In stroma, enzymatic reactions synthesise sugar, which in turn forms starch.
- Leaf pigments can be separated through paper chromatography technique and the result of this separation is called chromatogram.
- **Chl-a** is universal pigment, which is found in all O_2 liberating photosynthetic organisms. Its color is **blue green** in chromatogram.
- Phycobillins are hot water soluble pigment.
- **Chl-a shows maximum absorption at blue light. It shows another absorption peak at red light.**

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BEGINNER'S BOX INTRODUCTION, WHAT DO WE KNOW?, EARLY EXPERIMENTS, WHERE DOES PHOTOSYNTHESIS TAKE PLACE?, HOW MANY PIGMENTS ARE INVOLVED IN PHOTOSYNTHESIS?

1. Photosynthesis :-
(1) is a physio-chemical process (2) is a redox reaction
(3) is an anabolic process (4) all of the above

2. Variegated leaf experiment shows that :-
(1) water is essential for photosynthesis (2) CO_2 is essential for photosynthesis
(3) O_2 is essential for photosynthesis (4) Chlorophyll is essential for photosynthesis

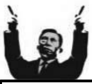
3. The oxidation product in photosynthesis of higher plants, is :-
(1) Oxygen (2) Starch (3) Glucose (4) Sulphate

4. ATP and NADPH forming reactions of photosynthesis are :-
(1) not directly light driven (2) directly light driven
(3) indirectly light dependent (4) light independent

5. Action spectrum of photosynthesis resembles roughly the absorption spectrum of :-
(1) Carotenoid (2) Chlorophyll-b (3) Chlorophyll-a (4) Both (2) and (3)

06. WHAT IS LIGHT REACTION ?

- Light reactions or the 'Photochemical' phase include **light absorption, water splitting, oxygen release and formation of high energy chemical intermediates like ATP and NADPH.**
- Photosystems are required for this process.
- Emerson & Arnold worked on *Chlorella* and gave concept of two photosystem or two pigment system.



- **Emerson effect and Red drop :**
  Emerson and **Arnold** experimented upon ***Chlorella***.
- **Observation :**
  - Reported minimum photosynthetic yield, when supplied monochromatic beam of 700 nm or > 680 nm only. **(Red drop)**
  - Reported enhancement in photosynthetic yield, when both 700 nm and 680 nm supplied together **(Enhancement effect or Emerson effect)**
- **Conclusion :**
  Two types of photosystems (PS-I and PS-II) exist in photosynthetic units. They operate simultaneously and their operation / activation required 700 nm and 680 nm radiation.

- **The groups of photosynthetic pigments in thylakoid membranes are known as photosystems.**
- The pigments are organised as two discrete photochemical light harvesting complexes (LHC) within the Photosystem I (PS I) and Photosystem II (PS II).

Photosystem = Reaction centre + LHC

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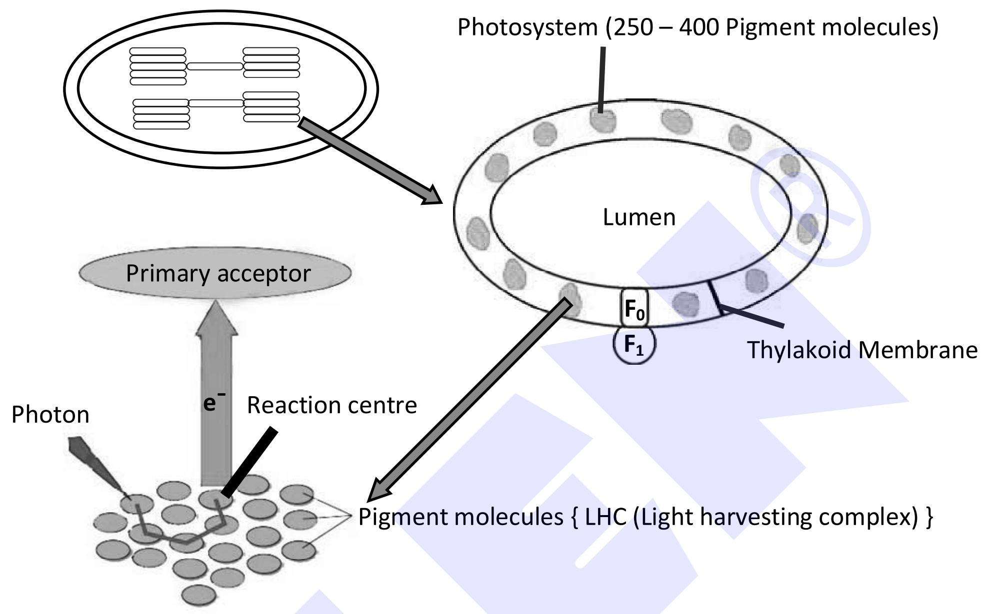
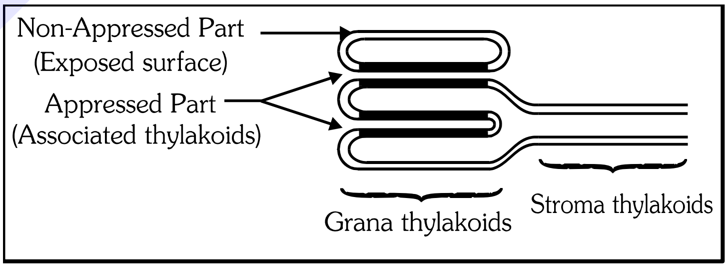
- In every photosystem there is a reaction centre (molecule of chlorophyll-a) surrounded by accessory pigments. The accessory pigments absorb light energy and transfer it to the reaction centre. These pigments help to make photosynthesis more efficient by absorbing different wavelengths of light. These molecules are known as antenna molecules or LHC. The LHC are made up of hundreds (250 - 400 molecules) of pigment molecules bound to proteins.



NCERT XI Page No. 211, Figure No. 13.4

- The reaction centre is different in both the photosystems. In **PS-I the reaction centre chlorophyll-a has an absorption peak at 700 nm, hence is called P700, while in PS-II it has absorption peak at 680 nm, and is called P680.**
- These are named in the sequence of their discovery, and not in the sequence in which they function during the light reaction.
- **The PS-II is located in the appressed region of granal thylakoids and PS-I in non appressed region of grana and in stroma thylakoids. (In the other way we can say that granal thylakoids have both PS-I and PS-II whereas stroma thylakoids have only PS-I).**



- **Granal thylakoids have PS-I, PS-II and FNR (Ferredoxin NADP reductase) enzyme whereas stroma thylakoids have only PS-I.**

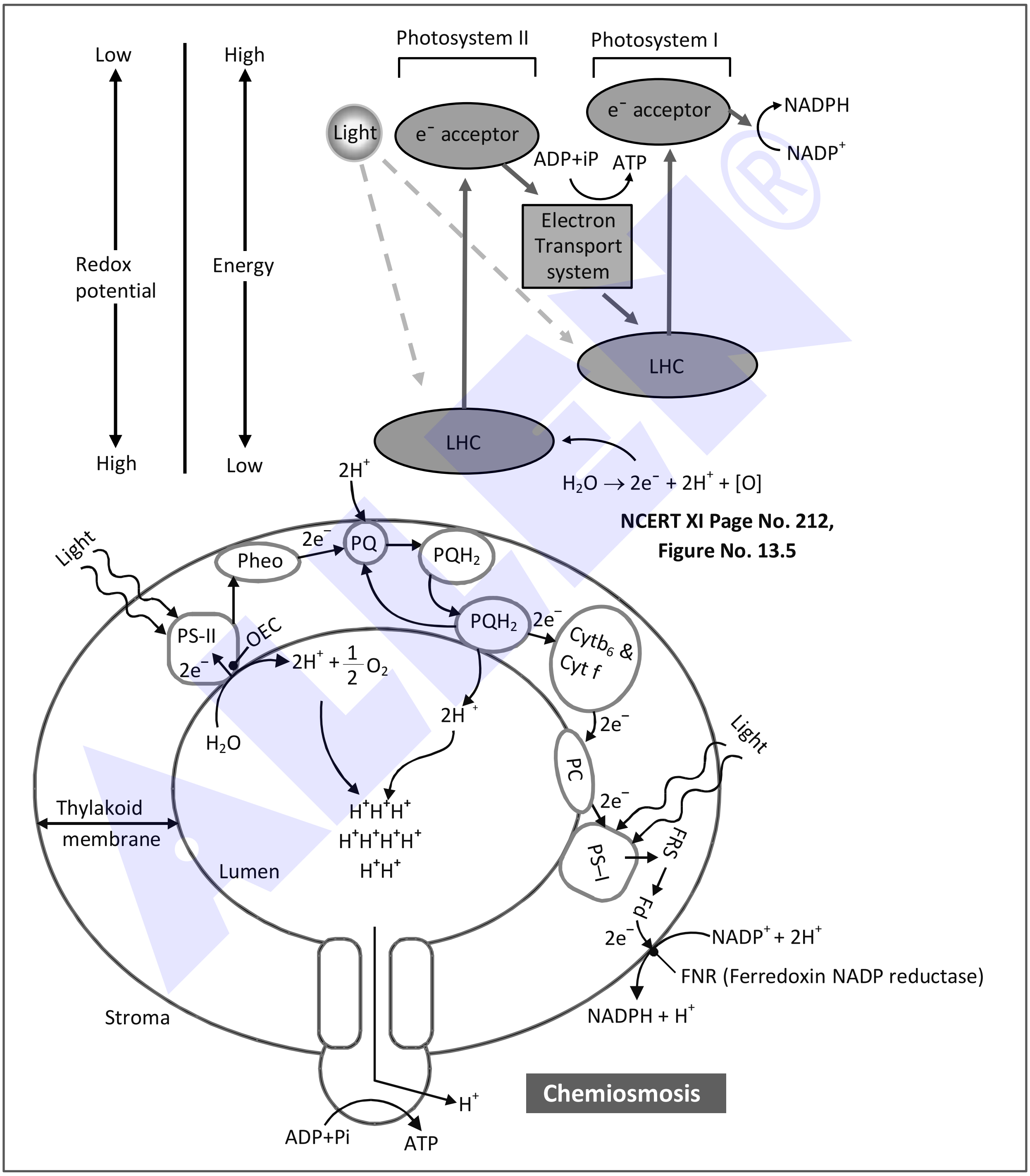
07. THE ELECTRON TRANSPORT

OR

PHOTOPHOSPHORYLATION

- Synthesis of ATP from ADP and inorganic phosphate (iP) with the help of light energy is known as **photophosphorylation.** It is of two types :-

(1) NON-CYCLIC PHOTOPHOSPHORYLATION / Z-SCHEME AND SPLITTING OF WATER



NCERT XI Page No. 212, Figure No. 13.5

Chemiosmosis

- Both PS–I and PS–II are involved in non cyclic photophosphorylation. So it occurs at grana thylakoids only, not in stroma thylakoids because stroma thylakoids lack PS - II as well as NADP reductase enzyme.

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- Primary electron acceptor from PS-II is pheophytin, which passes electrons to an electrons transport system (ETS) consisting of cytochromes. **This movement of electrons is downhill, in terms of an oxidation- reduction or redox potential scale.** The electrons emitted from PS II pass through the electron transport chain to the pigments of PS I. Simultaneously, electrons in the reaction centre of PS I are also excited when they receive red light of wavelength 700 nm and are transferred to another accepter molecule (FRS) and then to Fd. These electrons then move downhill again, this time to a molecule of energy rich $NADP^+$.

- The electrons that were moved from photosystem II must be replaced. This is achieved by electrons available due to splitting of water. The splitting of water is associated with the PS II; water is split into H^+, [O] and electrons. This creates oxygen, one of the net products of photosynthesis. The electrons needed to replace those removed from photosystem I are provided by photosystem II.

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

  We need to emphasise here that 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.**

- The addition of these electrons reduces $NADP^+$ to NADPH + H^+ (protons from stroma). At every step oxidation/reduction of electron carrier take place and energy is released which is utilized in creation of proton gradient to form ATP.

- **This 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 accepter, and finally down hill to $NADP^+$ is called the Z scheme, due to its characteristic shape.**

- **This Z shape is formed when all the carriers are placed in a sequence on a redox potential scale.**

- **Quantum requirement –**

  The number of light quanta or photons required for the evolution of 1 molecule of O_2 in photosynthesis. Emerson calculated that the quantum requirement is 8.

- **Quantum Yield –**

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

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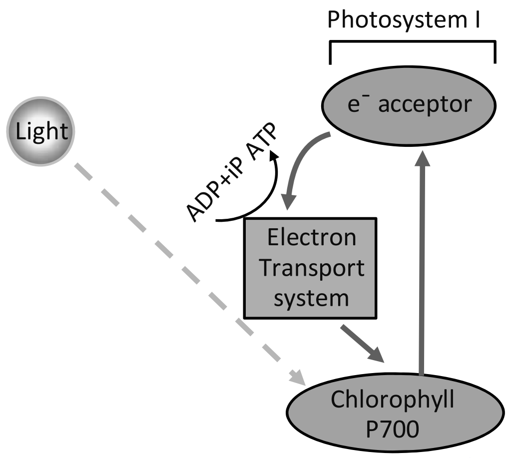
(2) CYCLIC PHOTOPHOSPHORYLATION

- In cyclic photophosphorylation, **only PS-I works.**
- A possible location where this could be happening is in the stroma lamellae/thylakoid.
- During cyclic ETS, the electron ejected from reaction centre of PS-I, returns back to its reaction centre. At every step oxidation and reduction of each electron carrier take place which release the energy and this energy is utilized in creation of proton gradient to form ATP.
- In cyclic ETS, no oxygen evolution occurs because photolysis of water is absent.
- **NADPH + H^+ (Reducing power) is not formed in cyclic process. There is formation of only ATP.**



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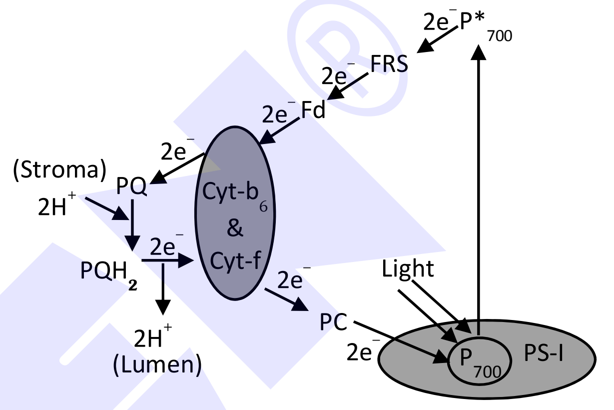

Cyclic Photophosphorylation

(3) CHEMIOSMOTIC HYPOTHESIS

- **Proposed by Peter Mitchell (1961) to explain the mechanism of ATP formation (Phosphorylation) in chloroplast (During photosynthesis) and in mitochondria (During respiration).**
- According to this hypothesis **ATP synthesis is linked to development of a proton gradient (Difference of proton (H^+) concentration) across a membrane. In chloroplast these are membranes of the thylakoid.**
- The steps that cause a proton gradient to develop –
  (a) Since **splitting of the water molecule** takes place on the inner side of the membrane, the **hydrogen ions** that are produced by the splitting of water **accumulate within the lumen of the thylakoids.**
  (b) As electron move through the photosystems, protons are transported across the membrane. This happens because the **primary accepter of electron (Pheophytin**) which is located towards the outer side of the membrane transfers its electron not to an electron carrier but to an **H carrier (Plastoquinone).** Hence this molecule removes a proton from the stroma while transporting an electron. When Plastoquinone passes on its electron to the **electron carrier (FeS protein 'or' Cytochrome)** on the inner side of the membrane, the proton is released into the inner side of the membrane or the lumen side of the membrane.

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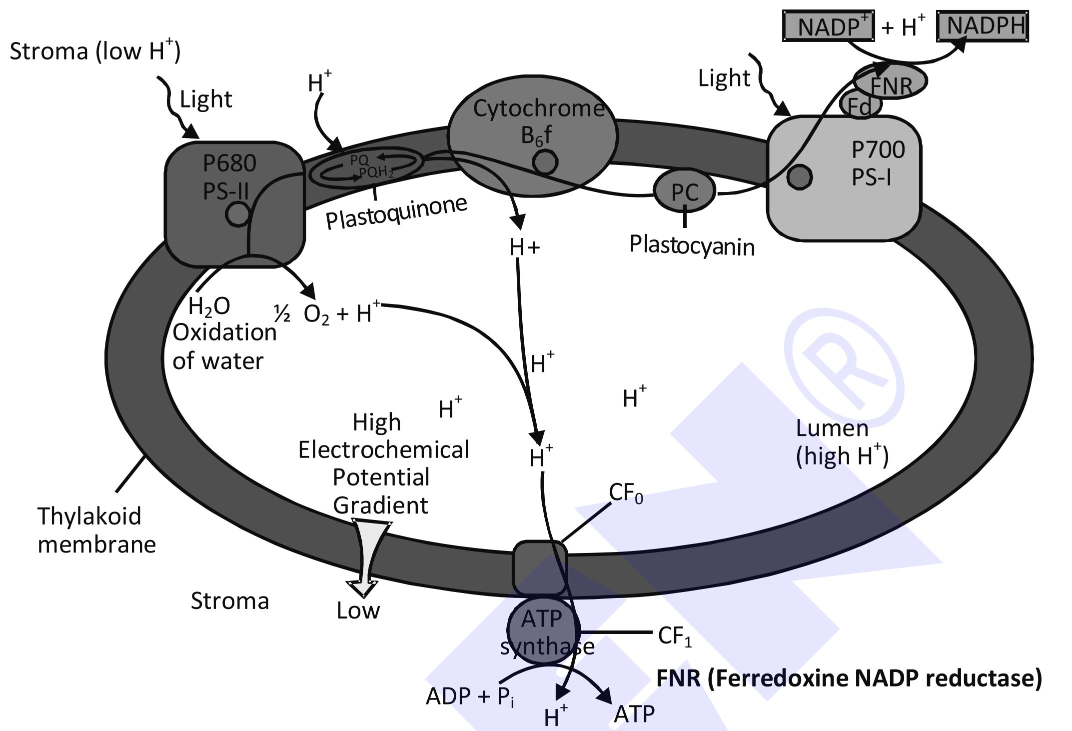
(c) **The NADP reductase enzyme is located on the stroma side of the membrane.** Along with electrons that come from the acceptor of electrons of PS I, **protons are necessary for the reduction of $NADP^+$ to $NADPH^+$ + H^+. These protons are also removed from the stroma.**



ATP synthesis through chemiosmosis

NCERT XI Page No. 214, Figure No. 13.7

- Hence, **within the chloroplast,** protons in the **stroma decrease** in number, while in the **lumen** there is **accumulation of protons.** This creates a **proton gradient** across the thylakoid membrane as well as a measurable decrease in pH in the lumen.
- **The ATP synthase enzyme consists of two parts: one called the CF_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 CF_1 and protrudes on the outer surface of the thylakoid membrane on the side that faces the stroma.**
- **This gradient is important because it is 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 CF_0 of the ATP synthase.**
- **The break down of the gradient provides enough energy to cause a conformational change in the CF_1 particle of the ATP synthase, which makes the enzyme synthesise several molecules of energy-packed ATP."**
- **"Chemiosmosis requires a membrane, a proton pump, a proton gradient and ATP synthase. Energy is used to pump protons across a membrane, to create a gradient or a high concentration of protons within the thylakoid lumen. ATP synthase has a channel that allows diffusion of protons back across the membrane; this releases enough energy to activate ATP synthase enzyme that catalyses the formation of ATP."**

Golden Key Points

- Light reactions or the 'Photochemical' phase include **light absorption, water splitting, oxygen release and formation of high energy chemical intermediates like ATP and NADPH.**
- **Granal thylakoids have PS-I, PS-II and FNR (Ferredoxin NADP reductase) enzyme whereas stroma thylakoids have only PS-I.**
- **Water splitting complex is associated with the PS-II, which itself is physically located on the inner side of the membrane of the thylakoid.**
- **NADPH + H^+ (Reducing power) is not formed in cyclic process. There is formation of only ATP.**
- **"Chemiosmosis requires a membrane, a proton pump, a proton gradient and ATP synthase.**

BEGINNER'S BOX

WHAT IS LIGHT REACTION?, THE ELECTRON TRANSPORT (PHOTOPHOSPHORYLATION)

1. 'Red drop' phenomenon is plants occur due to decrease in activity of :-
(1) Phycobilin pigment
(2) Photosystem-I
(3) Photosystem-II
(4) Both (2) and (3)

2. Which of the following is a correct sequence of electron transfer in z-scheme of photosynthesis?
(1) $H_2O \rightarrow$ PS-I $\rightarrow$ PS-II $\rightarrow$ $NADP^+$
(2) PS-I $\rightarrow$ H_2O $\rightarrow$ $NADP^+$ $\rightarrow$ PS-II
(3) PS-II $\rightarrow$ $NADP^+$ $\rightarrow$ H_2O $\rightarrow$ PS-I
(4) $H_2O \rightarrow$ PS-II $\rightarrow$ PS-I $\rightarrow$ $NADP^+$

3. Which of the following is the location of NADPH + H^+ formation in the chloroplast during light reaction of photosynthesis?
(1) At the stroma thylakoid membrane
(2) At the grana thylakoid membrane
(3) At the outer membrane of chloroplast
(4) At the inner membrane of chloroplast

4. Alongwith electrons, protons are necessary for the reduction of $NADP^+$. Source of these protons is :-
(1) Stroma of chloroplast
(2) Lumen of stroma thylakoid
(3) Cytoplasm
(4) Space between both the membranes of chloroplast

5. During creation of proton gradient in chloroplast, which of the following is correct ?
(1) Stroma – High pH, Thylakoid lumen – Low pH
(2) Stroma – Low pH, Thylakoid lumen – High pH
(3) Stroma – Low pH, Thylakoid lumen – Low pH
(4) Stroma – High pH, Thylakoid lumen – High pH

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08. WHERE ARE THE ATP AND NADPH USED?

OR

(DARK REACTION/BIOSYNTHETIC PHASE)

- **This process does not directly depend on the presence of light but is dependent on the products of the light reaction like ATP and NADPH so immediately after light becomes unavailable, the biosynthetic process continues for some time and then stops. If then light is made available, the synthesis starts again.**
- It was of interest to scientists to find out how this reaction proceeded, or rather what was the first product formed when CO_2 is taken into a reaction or fixed. Just after world war II, among the several efforts to put radioisotopes to beneficial use, the work of Melvin Calvin is exemplary. The use of radioactive ^{14}C by him in algal photosynthesis studies led to the discovery that the first CO_2 fixation product was a 3-carbon organic acid. He also contributed to working out the complete biosynthetic pathway; hence it was called Calvin cycle after him. The first product identified was 3-phosphoglyceric acid or in short PGA.
- Scientists also tried to know whether all plants have PGA as the first product of CO_2 fixation, or whether any other product was formed in other plants. Experiments conducted over a wide range of plants led to the discovery of another group of plants, where the first stable product of CO_2 fixation was again an organic acid, but one which had 4 carbon atoms in it. This acid was identified to be oxaloacetic acid or OAA. Since then CO_2 assimilation during photosynthesis was said to be of two main types: those plants in which the first product of CO_2 fixation is a C_3 acid (PGA), i.e., the C_3 pathway, and those in which the first product was a C_4 acid (OAA), i.e., the C_4 pathway.
- The CO_2 fixation into glucose in all photosynthetic plants take place by Calvin cycle.
- In C_3 pathway, biosynthetic phase has only Calvin cycle. In C_4 pathway, some additional reactions also occur before Calvin cycle, during biosynthetic phase.

(I) THE CALVIN CYCLE OR C_3–PATHWAY

- **In C_3–plants, Calvin cycle occurs in stroma of chloroplast of mesophyll cells.**
- I[st] stable compound of Calvin cycle is 3 carbon compound–**PGA** (Phosphoglyceric acid or phosphoglycerate) thus Calvin cycle is called **C_3–cycle.** (First compound is unstable, 6C keto acid–carboxy ketoribitol bisphosphate).

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- Calvin studied the dark reaction in green algae ***Chlorella* & *Scenedesmus*.** During his experiment he used **radioisotopy** (C^{14} radioisotope) and **chromatography** techniques for identification and separation of intermediates of C_3–cycle.
- **RuBisCO (Ribulose-1,5-bis-Phosphatecarboxylase-oxygenase) is main enzyme in C_3–cycle which is present in stroma. RuBisCO is the most abundant enzyme and protein on earth.**
- For ease of understanding, the Calvin cycle can be described under three stages: carboxylation, reduction and regeneration.

(1) Carboxylation :

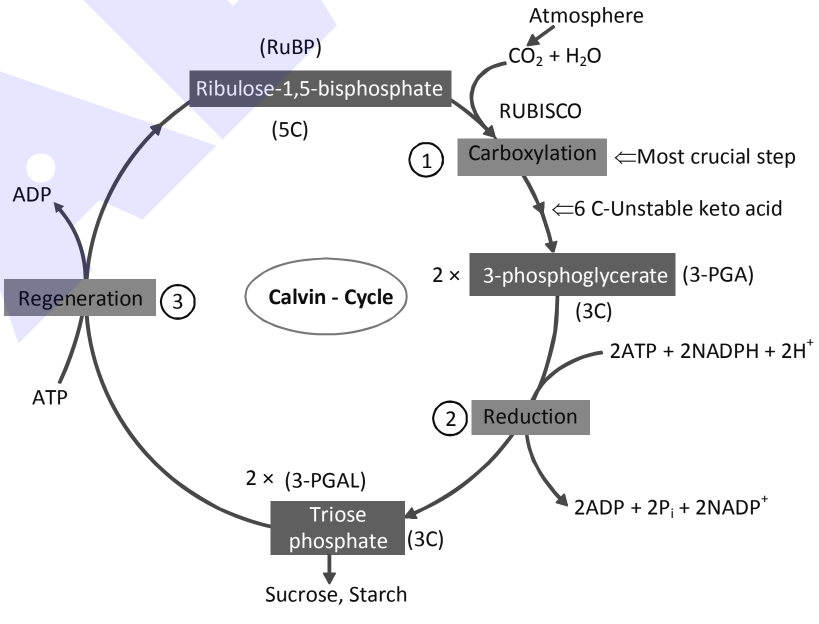
Carboxylation is the fixation of CO_2 into a stable organic intermediate. Carboxylation is the most crucial step of the Calvin cycle where CO_2 is utilised for the carboxylation of RuBP (Ribulose bisphosphate – 5 carbon ketose sugar). This reaction is catalysed by the enzyme RuBP carboxylase which results in the formation of two molecules of 3-PGA. Since this enzyme also has an oxygenation activity it would be more correct to call it RuBP carboxylase-oxygenase or RuBisCO.

(2) Reduction :

These are a series of reactions that lead to the formation of glucose. The steps involve utilisation of 2 molecules of ATP for phosphorylation and two of NADPH for reduction per CO_2 molecule fixed. The fixation of six molecules of CO_2 and 6 turns of the cycle are required for the formation of one molecule of glucose from the pathway.

(3) Regeneration :

Regeneration of the CO_2 acceptor molecule RuBP is crucial if the cycle is to continue uninterrupted. The regeneration steps require one ATP for phosphorylation to form RuBP.



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- Hence for every CO_2 molecule entering the Calvin cycle, 3 molecules of ATP and 2 of NADPH are required. It is probably to meet this difference in number of ATP and NADPH used in the dark reaction that the cyclic phosphorylation takes place.
- **6 turns of Calvin cycle are required for the formation of one glucose.**
- **12 NADPH + H^+ & 18 ATP are required as assimilatory power to produce one glucose in dark reaction in C_3 cycle.**

Calvin cycle	
In	**Out**
Six CO_2 18 ATP 2 NADPH	One glucose 18 ADP 12NADP

(II) C_4 PATHWAY/ HATCH & SLACK PATHWAY

OR

CO_2 CONCENTRATING MECHANISM / CO-OPERATIVE PHOTOSYNTHESIS/ DICARBOXYLIC ACID CYCLE (DCA CYCLE)

- **Hatch** & **Slack** (1967), studied it in detail in sugarcane and maize leaves and proposed a new pathway for dark reactions.
- First stable product of this pathway is **OAA,** which is a **4C, DCA** (Dicarboxylic Acid), thus Hatch & Slack pathway is also called **C_4 pathway** or **DCA cycle.**
- **Most of the C_4 plants are monocots (Tropical grasses), which belong to Gramineae & Cyperaceae families. C_4 plants are adapted to hot and dry environment.**
- E.g. of C_4 plants – **Sugarcane, Maize, Sorghum.**
- **Wheat, Rice and Barley (monocot) are C_3 species.**
- **Kranz (Wreath) Anatomy –** Present in leaves of C_4 plants. In these plants special green large cells are found around the vascular bundles in leaves, these are called bundle sheath cells, and the leaves which have such anatomy are said to have 'Kranz anatomy'. **'Kranz' means 'wreath' and is reflection of the arrangement of cells.**

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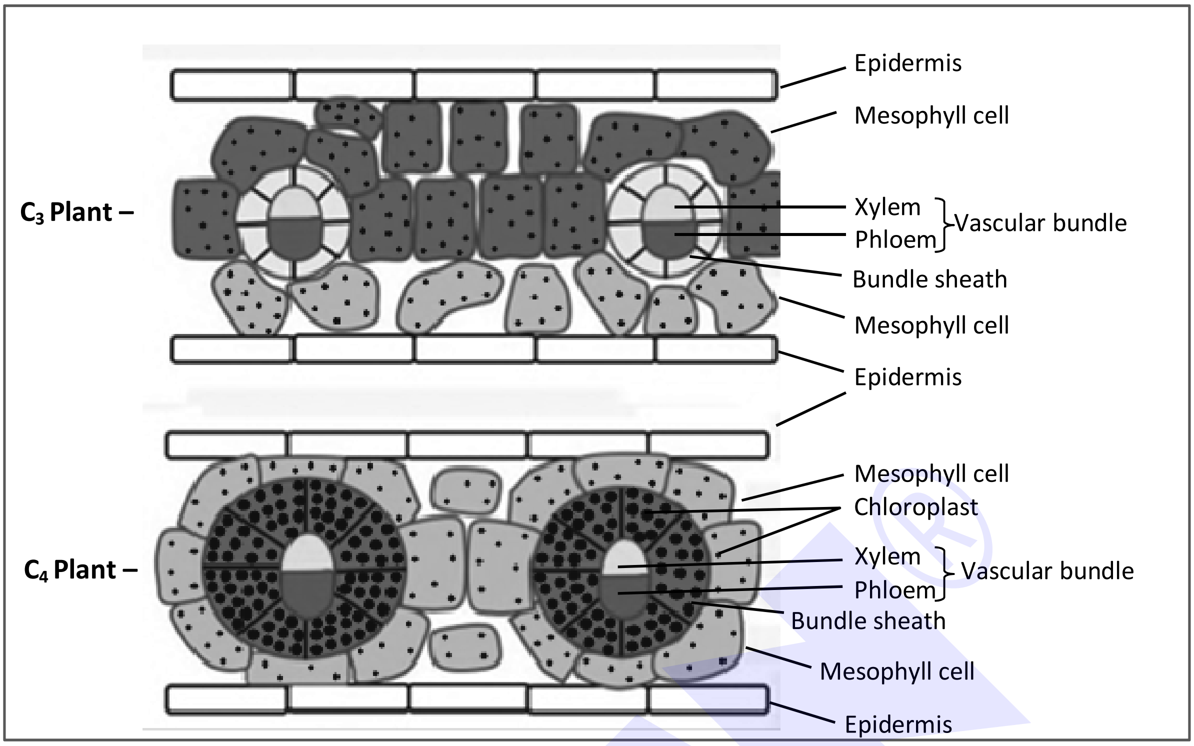

- The bundle sheath cells may form several layers around the vascular bundles, they are characterised by -
  - **having a large number of chloroplasts**
  - **thick walls impervious to gaseous exchange**
  - **no intercellular spaces**
- **Dimorphic chloroplasts** are present in leaf cells of C_4 plants. Chloroplast of bundle sheath cells or **Kranz cells** are **large** and **without grana** (Agranal i.e. the thylakoids are present only as stroma lamellae). Mesophyll chloroplast are **small** and **with grana** (Granal chloroplast i.e. both grana and stroma thylakoid are present).
- **First CO_2 acceptor in C_4 plants is PEP (Phosphoenol Pyruvate) (3C–compound) in mesophyll cells, while second CO_2 acceptor is RuBP (5C–compound), in bundle sheath cells.**
- **Initial fixation of CO_2 in mesophyll cells is catalysed by PEPcase (PEP carboxylase), which results in the formation of OAA(4C).**
- Then reduction of OAA take place by NADPH results in formation of malic Acid (4C) or transamination of OAA resulting in formation of aspartic acid (4C).
- The malic acid or aspartic acid (4C) formed in mesophyll cells are transported to bundle sheath cells. In bundle sheath cells the decarboxylation of malate takes place and CO_2 is released along with pyruvic acid (3C).

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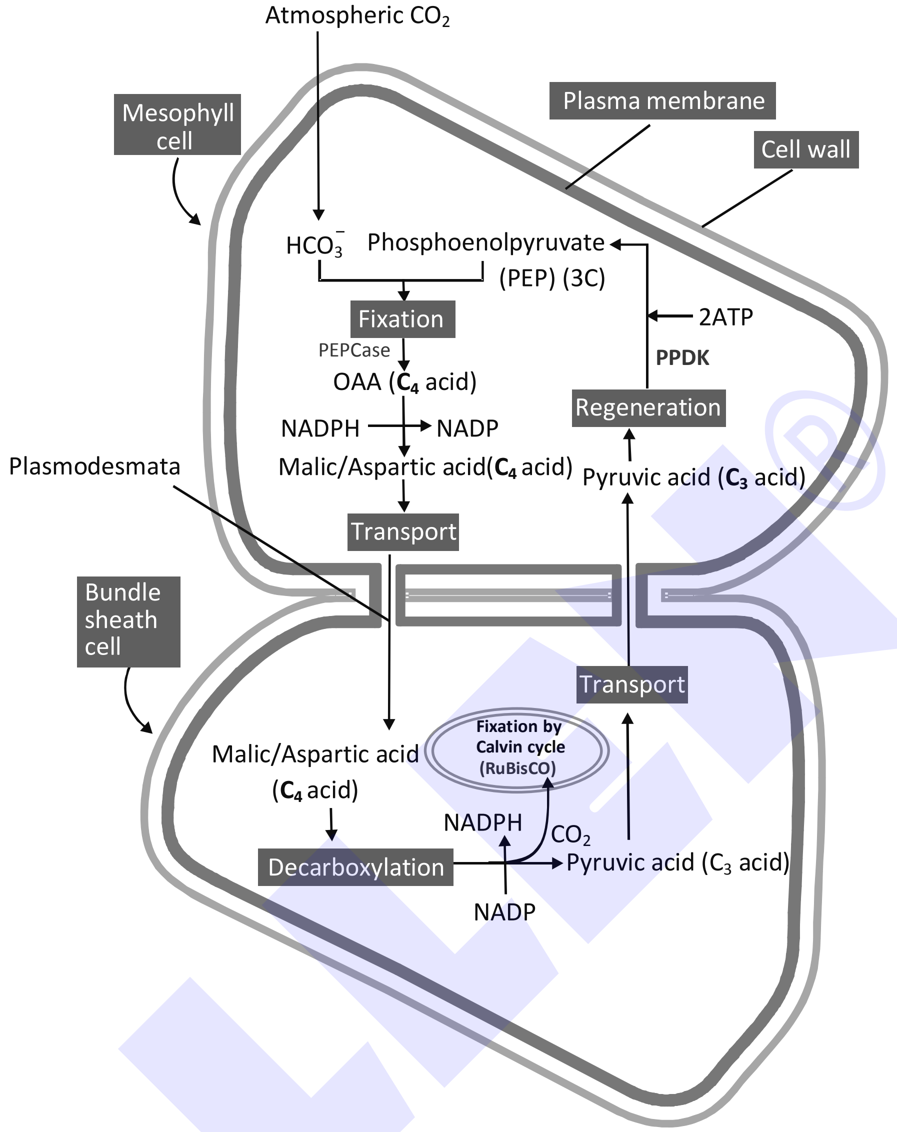
Diagrammatic representation of the Hatch and Slack Pathway



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- Released CO_2 in bundle sheath cells is accepted by RUBP, catalysed by RuBisCO. The C_3 cycle/Calvin cycle operates in bundle sheath cells with utilization of assimilatory power (18 ATP & 12 NADPH) resulting in formation of glucose.
- Pyruvic acid from bundle sheath cells return to mesophyll cells. It regenerate the PEP (primary CO_2 acceptor) by utilization of 12 ATP, catalysed by enzyme PPDK (Pyruvate phosphate dikinase). So in **C_4 plants total 30 ATP and 12 NADPH are utilized for synthesis of one glucose.**
- C_4 plants are special because :
  - **They have a special type of leaf anatomy (Kranz anatomy)**
  - **They tolerate higher temperature**
  - **They show a response to high light intensities**
  - **They lack a process called photorespiration so have greater productivity of biomass.**

- **In C_4 plants photorespiration does not occur.** This is because they have a mechanism that increases the concentration of CO_2 at the RuBisCO enzyme site. This takes place when the C_4 acid (malic or aspartic acid) from the mesophyll cell is broken down in the bundle sheath cells to release CO_2 (CO_2 pumping), this results in increasing the intracellular concentration of CO_2. In turn, this ensures that the RuBisCO functions as a carboxylase minimising the oxygenase activity.
- **In addition, in C_4 plants, site of O_2 evolution (mesophyll cell) and site of RuBisCO activity (Bundle sheath cell) are different.**
- The evolution of the C_4 photosynthetic system is probably one of the strategies for maximising the availability of CO_2 while minimising water loss. C_4 plants are twice as efficient as C_3 plants in terms of fixing carbon (making sugar). However, a C_4 plant loses only half as much water as a C_3 plant for the same amount of CO_2 fixed.

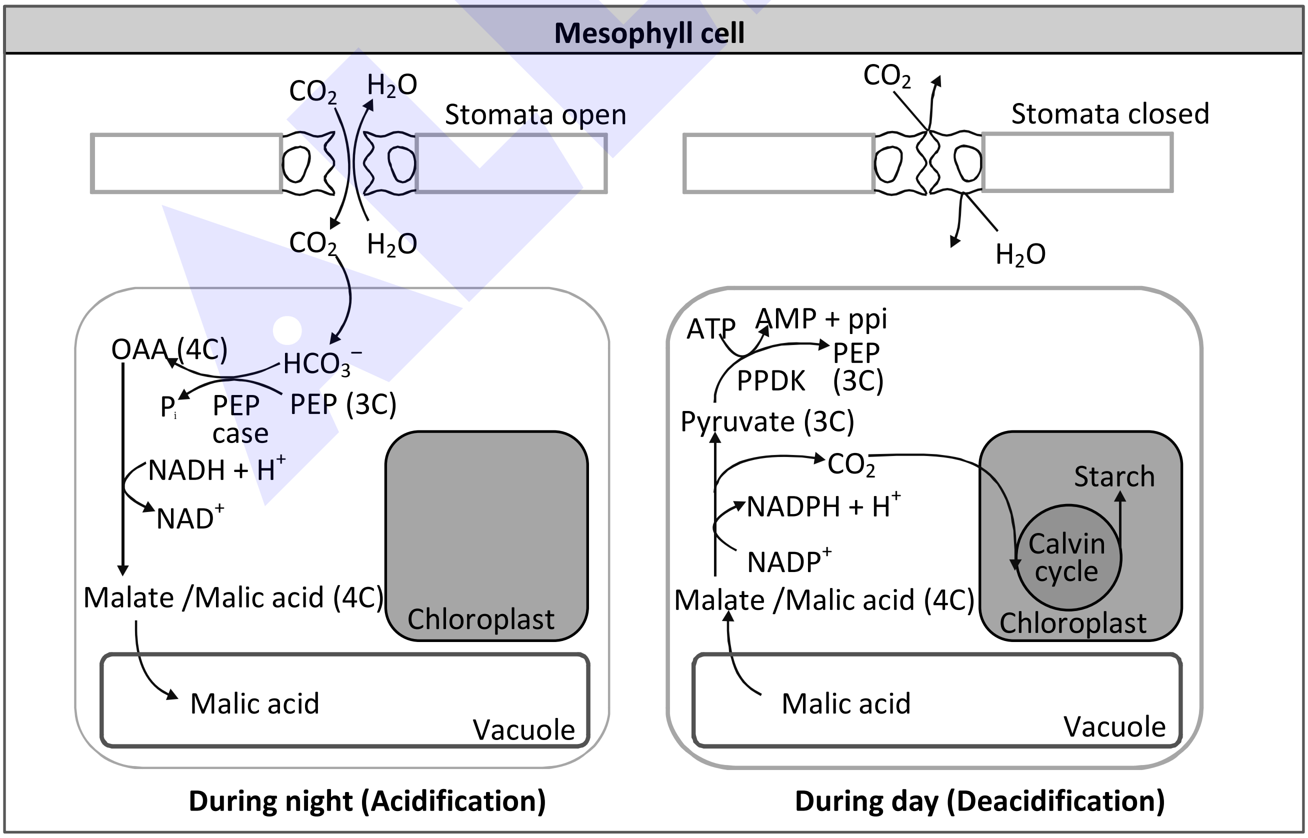
(III) CAM Pathway / Crassulacean Acid Metabolism / Dark CO_2 fixation

- CAM pathway was discovered by **Oleary** and **Rouhani.**
- They observed that CO_2 fixation occurs during night in members of **Crassulaceae family (succulent xerophytes)**. Succulents or CAM plants are characterised by **scotoactive stomata** (stomata open during night and remain closed during day time).

Example of some CAM Plants : ***Kalanchoe, Bryophyllum, Opuntia, Agave, Aloe, Euphorbia,*** **Pineapple**, ***Welwitschia*** (Gymnosperm)

- These plants are adapted to water conservation.
- Primary acceptor of CO_2 is PEP and **OAA is the first product.**
- **PEPcase and RuBisCO both are present in mesophyll cells.**

CAM Pathway



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Golden Key Points

- **Dark reaction of photosynthesis does not directly depend on the presence of light but is dependent on the products of the light reaction like ATP and NADPH.**
- The CO_2 fixation into glucose in all photosynthetic plants take place by Calvin cycle.
- Calvin studied the dark reaction in green algae ***Chlorella*** **&** ***Scenedesmus*****.** During his experiment he used **radioisotopy** (C^{14} radioisotope).
- **RuBisCO is the most abundant enzyme and protein on earth.**
- **First CO_2 acceptor in C_4 plants is PEP (Phosphoenol Pyruvate) (3C–compound) in mesophyll cells, while second CO_2 acceptor is RuBP (5C–compound), in bundle sheath cells.**
- In **C_4 plants total 30 ATP and 12 NADPH are utilized for synthesis of one glucose.**
- **In C_4 plants photorespiration does not occur.** This is because they have a mechanism that increases the concentration of CO_2 at the RuBisCO enzyme site.

BEGINNER'S BOX

WHERE ARE THE ATP AND NADPH USED? (DARK REACTION/BIOSYNTHETIC PHASE)

1. In C_3 plants, RuBisCO enzyme is found :-
(1) on the grana thylakoid of chloroplast of mesophyll cell
(2) in the stroma of chloroplast of mesophyll cell
(3) on the stroma thylakoid of chloroplast of mesophyll cell
(4) in the stroma of chloroplast of bundle sheath cell

2. For every CO_2 molecule entering the calvin cycle __'A'__ molecules of ATP and __'B'__ of NADPH are required. Choose the correct one for A and B from the following :-
(1) A = 18, B = 12 (2) A = 12, B = 18 (3) A = 2, B = 3 (4) A = 3, B = 2

3. For utilisation of one CO_2 molecule in Hatch and slack pathway __'A'__ molecules of NADPH and __'B'__ of ATP are required.
Choose the correct one for A and B from the following :.
(1) A = 2, B = 5 (2) A = 5, B = 2 (3) A = 12, B = 30 (4) A = 30, B = 12

4. In C_4 plants site of RuBisCO activity and site of O_2 evolution respectively are :-
(1) mesophyll cell and mesophyll cell (2) mesophyll cell and bundle sheath cell
(3) bundle sheath cell and mesophyll cell (4) bundle sheath cell and bundle sheath cell

5. The primary acceptor of CO_2 in CAM pathway is :-
(1) PEP (2) OAA (3) RuBP (4) PGA

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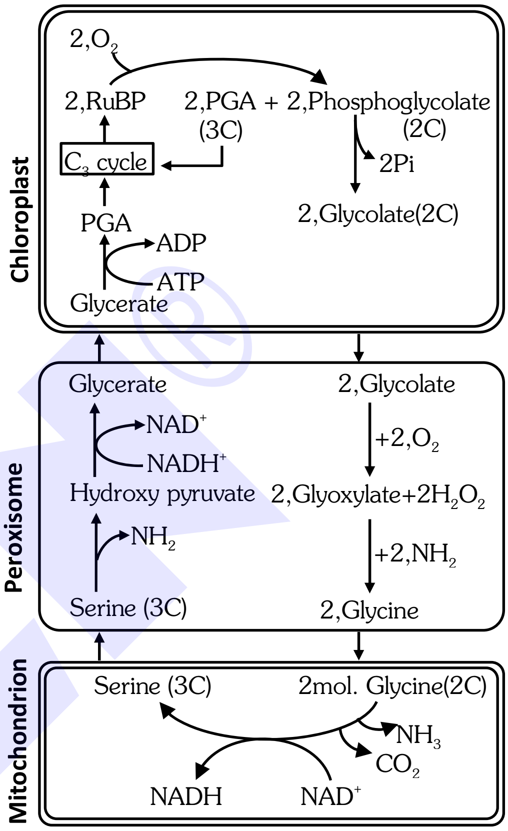
09. PHOTORESPIRATION

OR

PHOTOSYNTHETIC CARBON OXIDATION (PCO) CYCLE/C_2 CYCLE/ GLYCOLATE METABOLISM

- **The light dependent uptake of O_2 & release of CO_2 in green cells of C_3 plants is called Photorespiration. This process create an important difference between C_3 and C_4 plant.**
- It occurs in **chloroplast, peroxisome & mitochondria.**
- RuBisCO is characterised by the fact that its active site can bind to both CO_2 and O_2 – hence the name. This 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. **(Usually RuBisCO has a much greater affinity for CO_2 than for O_2).**
- Conditions for photorespiration – **High light intensity (High O_2, Low CO_2) and high temperature.**



Photorespiration/Photosynthetic carbon oxidation cycle

- When O_2 concentration is higher than CO_2 concentration then RuBisCO perform oxygenation of RuBP, which leads to phenomenon of photorespiration. Here the RuBP instead of being converted to 2 molecules of PGA, binds with O_2 to form one molecule of phosphoglycerate (3C) and one molecule of phosphoglycolate (2C).
- **In the photorespiratory pathway there is neither synthesis of sugars, nor of ATP and NADPH. Rather it results in the release of CO_2 with the utilisation of ATP. The biological function of photorespiration is not known yet.**

Warburg effect :

The Warburg's effect is the decrease in the rate of photosynthesis by high oxygen concentrations. Oxygen is a **competitive inhibitor** of the carbondioxide fixation by RuBisCO. Furthermore, oxygen promotes **photorespiration** which **reduces** photosynthetic output.

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 One: Mesophyll Three: Bundle sheath, palisade, spongy mesophyll
Which is the primary CO_2 acceptor	RuBP	PEP	RuBP/PEP/PGA
Number of carbons in the primary CO_2 acceptor	5	3	5/4/3
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 PEPCase?	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°C	30-40°C	30-40 C/20-25C/above 40 C
Examples	**Wheat** **Rice**	**Maize** **Sugarcane** **Sorghum**	

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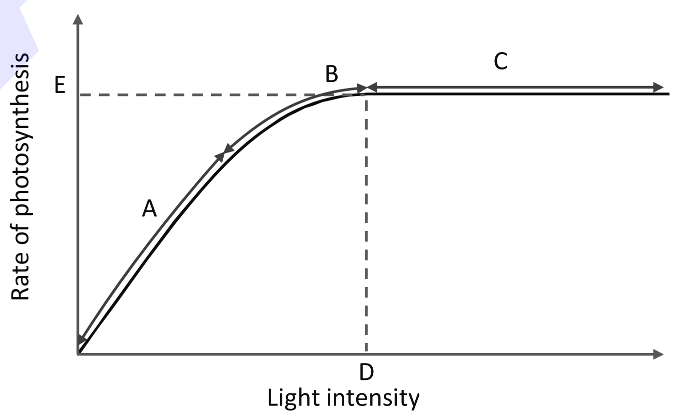
10. FACTORS AFFECTING PHOTOSYNTHESIS

- An understanding of the factors that affect photosynthesis is necessary. The rate of photosynthesis is very important in determining the yield of plants including crop plants. Photosynthesis is under the influence of several factors, both internal (plant) and external. **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.**
- The external factors would include the **availability of sunlight, temperature, CO_2 concentration and water.** As a plant photosynthesises, all these factors will simultaneously affect its rate. Hence, though several factors interact and simultaneously affect photosynthesis or CO_2 fixation, usually one factor is the major cause or is the one that limits the rate. Hence, at any point the rate will be determined by the factor available at sub-optimal levels.
- When several factors affect any [bio] chemical process, Blackman's (1905) Law of Limiting factors comes into effect. This states the following:
- 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.
- For example, despite the presence of a green leaf and optimal light and CO_2 conditions, the plant may not photosynthesise if the temperature is very low. This leaf, if given the optimal temperature, will start photosynthesising.
- CO_2 is limiting in clear sky but light becomes limiting in cloudy days and in dense forest or for plants growing in shade.

(1) LIGHT

- We need to distinguish between **light quality**, **light intensity** and **the duration of exposure to light**, while discussing light as a factor that affects photosynthesis. There is a linear relationship between incident light and CO_2 fixation rates at low light intensities. At higher light intensities, gradually the rate does not show further increase as other factors become limiting.



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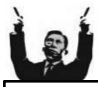
- **Light saturation occurs at 10% of full sunlight.**
- **Except for plants in shade or in dense forests, light is rarely a limiting factor in nature. Increase in incident light beyond a point causes the breakdown of chlorophyll and a decrease in photosynthesis.**

(2) CO_2

- **Carbon dioxide is the major limiting factor for photosynthesis. The concentration of CO_2 is very low in the atmosphere (between 0.03 and 0.04 percent). Increase in concentration upto 0.05 percent can cause an increase in CO_2 fixation rate, beyond this the levels can become damaging over longer periods.**
- 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.
- **C_4–Plants show saturation at about 360 $\mu L L^{-1}$ (0.036% or 360 ppm) while C_3 responds to increased CO_2 concentration and saturation is seen only beyond 450 $\mu L L^{-1}$ (0.045% or 450 ppm). Thus, current availability of CO_2 levels is limiting to the C_3 plants not for C_4 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 fertilizing effect).**
- **Atmospheric CO_2 is not limiting factor for C_4 plants and Submerged hydrophytes.**



CO_2 compensation point : It is the point where rate of photosynthesis become equal to the rate of respiration (NPP is zero).

CO_2 compensation point for C_4 plants is **0-10 ppm.**

CO_2 compensation point for C_3 plants is **25-100 ppm.**

(3) TEMPERATURE

- **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 **(30°– 40°C)** and show higher rate of photosynthesis while C_3 plants have a much lower temperature optimum **(20° – 25° C).**
- 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.

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(4) WATER

- Even though water is one of the reactants in the light reaction, the effect of water as a factor is more through its effect on the plant, rather than directly on photosynthesis. Water stress causes the stomata to close hence reducing the CO_2 availability. Besides, **water stress also makes leaves wilt, thus, reducing the surface area of the leaves and their metabolic activity as well.**

Inhibitors :

They are used as **weedicides** or **herbicides.**

- DCMU (Dichlorophenyl Dimethyl urea) / Diuron, CMU / Monouron and PAN (peroxy acetyl nitrates) inhibit photosynthesis by blocking PS-II as they stop electron flow between P 680 and PQ.
- Diquat, Paraquat, (viologen dyes) inhibit cyclic photophosphorylation by blocking electron flow between P 700 and Fd.

	Bacterial Photosynthesis		Plant Photosynthesis
1.	Pigment containing structures are chromatophores	1.	Pigment containing structures are thylakoids inside chloroplasts
2.	Pigments are bacteriochlorophyll and bacterioviridin	2.	Pigments are chlorophylls and carotenoids
3.	Its anoxygenic because PS II is absent. (O_2 evolution is absent).	3.	Its oxygenic because PS II is present which can photolyse the H_2 O. (O_2 evolved)
4.	Only one pigment system is present whose photocenter is B-890 (PS-II absent)	4.	Two pigments system PS-I (P 700) and PS-II (P 680) are present.
5.	Action spectrum is infra red.	5.	Action spectrum is blue-red
6.	During light reaction NAD^+ being reduced to NADH	6.	During light reaction $NADP^+$ being reduced to NADPH.

Golden Key Points

- **The light dependent uptake of O_2 & release of CO_2 in green cells of C_3 plants is called Photorespiration.**
- Conditions for photorespiration – **High light intensity (High O_2, Low CO_2) and high temperature.**
- **The biological function of photorespiration is not known yet.**
- **The plant or internal factors are dependent on the genetic predisposition and the growth of the plant.**
- CO_2 is limiting in clear sky but light becomes limiting in cloudy days and in dense forest or for plants growing in shade.
- **Light saturation occurs at 10% of full sunlight.**
- **Current availability of CO_2 levels is limiting to the C_3 plants not for C_4 plants.**
- **The dark reactions being enzymatic are temperature controlled. Though the light reactions are also temperature sensitive they are affected to a much lesser extent.**

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BEGINNER'S BOX — PHOTORESPIRATION, FACTORS AFFECTING PHOTOSYNTHESIS

1. Which of the following conditions favour photorespiration?
(1) High light intensity (2) High temperature
(3) Low CO_2 concentration (4) All of the above

2. Which of the following is synthesised during photorespiration?
(1) Phosphoglycerate (2) ATP
(3) NADPH (4) Sugar

3. Which of the following is the major limiting factor for photosynthesis?
(1) Light (2) Water
(3) CO_2 (4) Temperature

4. Which of the following is not correct?
(1) Light is rarely a limiting factor for photosynthesis
(2) Current availability of atmospheric CO_2 levels is limiting for C_4 plants
(3) Law of limiting was given by Blackman
(4) Water stress indirectly reduces the CO_2 availability for plants

5. Which of the following is an inhibitor of photosystem-II ?
(1) DCMU (2) ATP (3) AMP (4) Diquat

BEGINNER'S BOX — ANSWER KEY

INTRODUCTION, WHAT DO WE KNOW?, EARLY EXPERIMENTS, WHERE DOES PHOTOSYNTHESIS TAKE PLACE?, HOW MANY PIGMENTS ARE INVOLVED IN PHOTOSYNTHESIS?

Que.	1	2	3	4	5
Ans.	4	4	1	2	4

WHAT IS LIGHT REACTION? THE ELECTRON TRANSPORT (PHOTOPHOSPHORYLATION)

Que.	1	2	3	4	5
Ans.	3	4	2	1	1

WHERE ARE THE ATP AND NADPH USED?, (DARK REACTION/BIOSYNTHETIC PHASE)

Que.	1	2	3	4	5
Ans.	2	4	1	3	1

PHOTORESPIRATION, FACTORS AFFECTING PHOTOSYNTHESIS

Que.	1	2	3	4	5
Ans.	4	1	3	2	1

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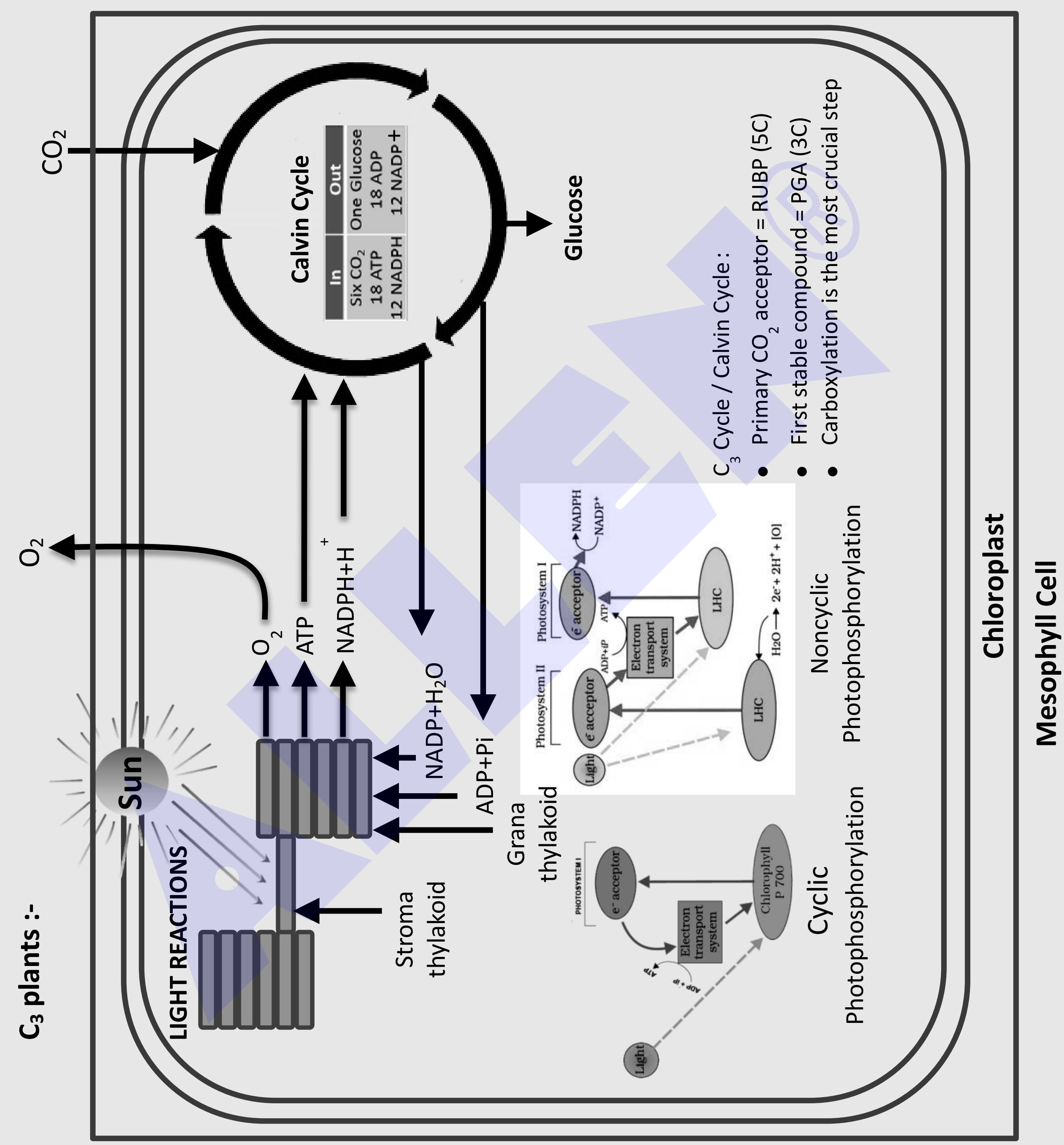
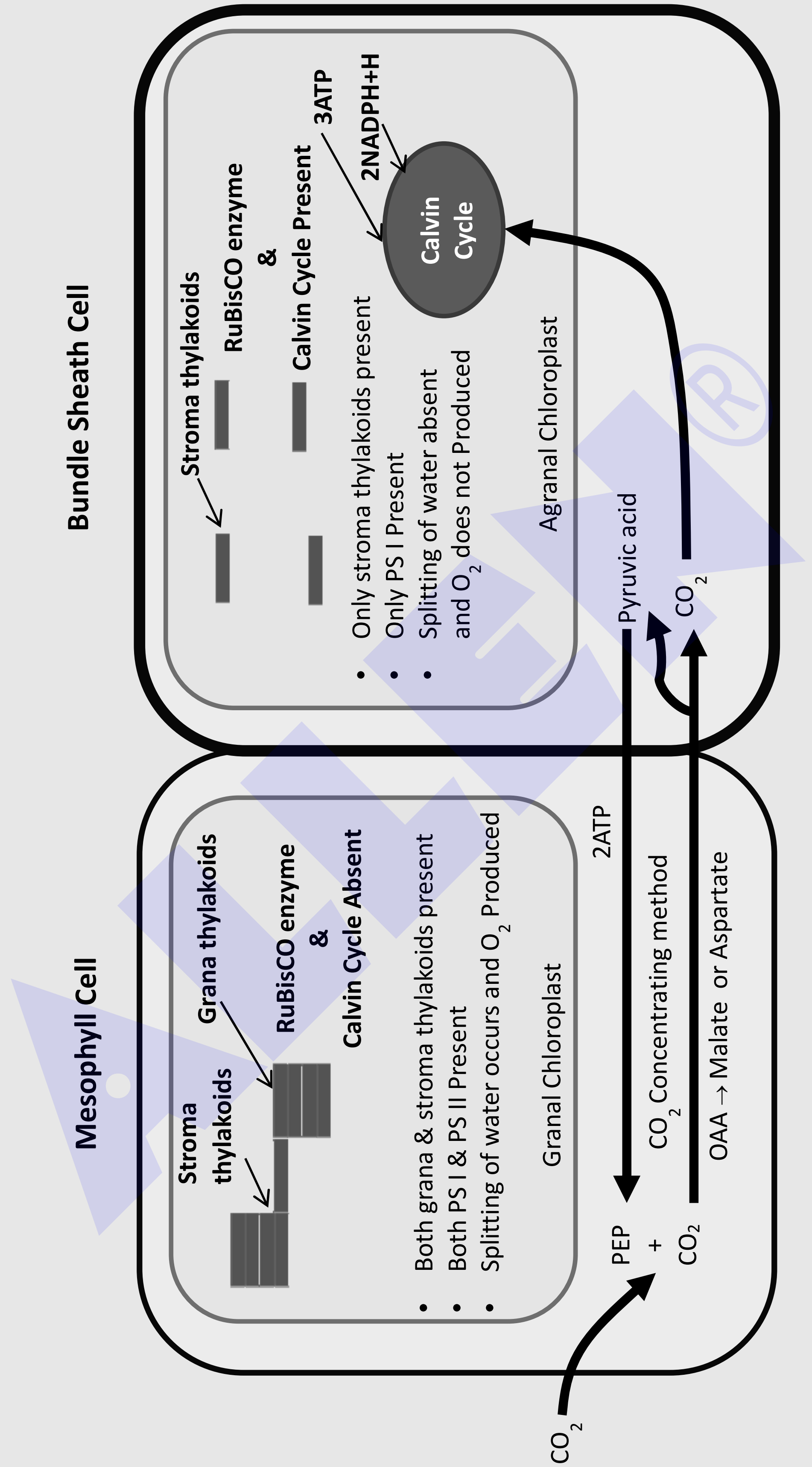
ESSENCE




Bundle Sheath Cell
Stroma thylakoids
RuBisCO enzyme
&
Calvin Cycle Present
3ATP
2NADPH+H
Calvin Cycle
• Only stroma thylakoids present
• Only PS I Present
• Splitting of water absent and O_2 does not Produced
Agranal Chloroplast
Pyruvic acid
CO_2
Mesophyll Cell
Stroma thylakoids
Grana thylakoids
RuBisCO enzyme
&
Calvin Cycle Absent
• Both grana & stroma thylakoids present
• Both PS I & PS II Present
• Splitting of water occurs and O_2 Produced
Granal Chloroplast
2ATP
CO_2 Concentrating method
OAA → Malate or Aspartate
PEP + CO_2
CO_2

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- In C_3 plants if O_2 bind to RuBisCO then RuBP form one molecule of phosphoglycerate (3 carbon) and one molecule of phosphoglycolate (2 carbon) in Chloroplast.
- Photorespiration or C_2 cycle occurs in chloroplast, peroxisome and mitochondria.
- In **photorespiration** neither synthesis of sugar nor of ATP and NADPH occurs.
- High light intensity favours photorespiration.
- In **C_4 plants, photorespiration does not occur** because they **increase the concentration of CO_2 in bundle sheath cells** (site of RuBisCO enzyme) by **pumping** it in the form of C_4 acid (malic acid or aspartic acid).
- **Law of limiting factor** – proposed by **Blackman.**
- Light saturation in plants occurs at 10 per cent of the full sunlight.
- **CO_2 is the major limiting factor for photosynthesis.**
- **CO_2 saturation** for **C_4 plants** – at **about 360 mlL^{-1} or PPM** concentration of CO_2.
- **CO_2 saturation** for **C_3 plants – at beyond 450 mlL^{-1} or PPM** concentration of CO_2.
- **Current** availability of **CO_2** levels is **limiting to the C_3 plants not for C_4 plants.**
- C_3 plants respond to higher CO_2 concentration by showing increase rate of photosynthesis (experiments on **green house crops** such as **tomatoes** and **bell pepper**), it is called **CO_2 fertilising effect.**
- For **plants in shade** or in **dense forest, light** may be the **limiting factor.**
- The dark reactions being enzymatic, are temperature controlled, **light reactions** are **less temperature sensitive.**