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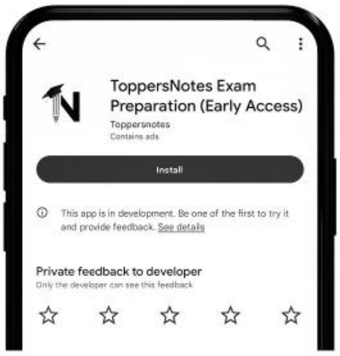

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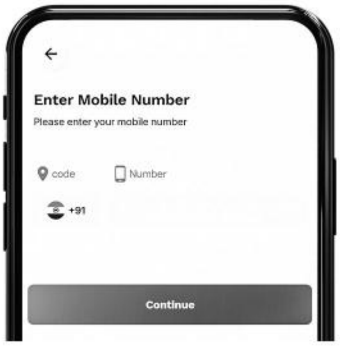

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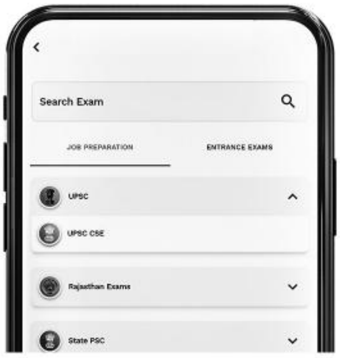

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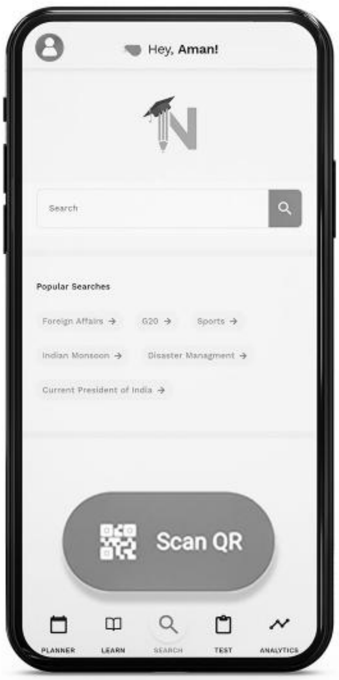

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CHAPTER 1

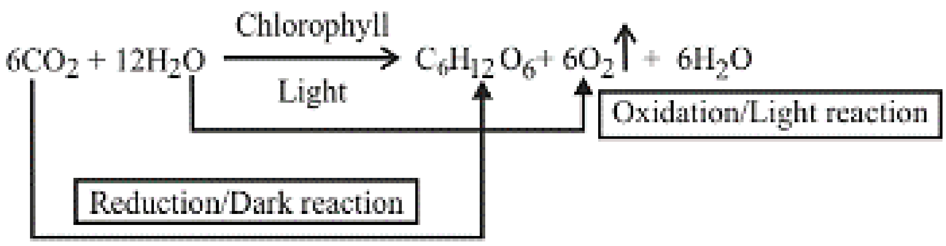
Photosynthesis in Higher Plants

CHAPTER OUTLINE

- Introduction
- Where does photoshynthesis takes place?
- Cyclic Electron Transport System
- CAM (Crassulacean Acid Metabolism) Plants
- Factors affecting Photosynthesis
- Significance of Photosynthesis
- Historical Background
- Mechanism of Photosynthesis
- Chemiosmotic Hypothesis
- Photorespiration/ Glycolate Pathway
- Bacterial Photosynthesis

INTRODUCTION

- All living beings require energy to perform their many life functions. This energy is derived directly or indirectly from the sun.
- **Green plants** are remarkable in that they **generate food** from simple components such as carbon dioxide and water in the presence of sunlight.
- **Photosynthesis** is the only biologically significant mechanism that can harvest this energy.
- **Photosynthesis** stores **energy** as **chemical energy** in food (carbohydrates, lipids, and proteins), which is released in living cells during **respiration** and used to generate heat or transformed into energy-rich substances (e.g., ATP and NADP).
- **Photosynthesis** is a **biochemical process** (both **anabolic** and **endergonic**) that produces organic compounds (carbohydrates) from inorganic raw materials (H_2O and CO_2) in the presence of light and pigments. As a **byproduct, O_2 is formed**.



- Aquatic plants perform 90% of total photosynthesis.
- Cyanobacteria (blue-green algae) pioneered true and oxygenic photosynthesis.
- Photosynthesis is lacking in *Cuscuta* (parasitic) and fungi (achlorophyllous).
- *Euglena* is a photosynthetic organism that connects mammals and plants.
- Though photosynthetic in the presence of sunlight, they operate as heterotrophs in the absence of sunshine, predating on other smaller organisms.
- *Tinospora* and *Trapa* roots are assimilatory or photosynthetic.

HISTORICAL BACKGROUND

Plants were thought to get food from the soil before the seventeenth century.

- **Van Helmont** (1648) concluded that "all **plant food is derived from water and not from soil**."
- According to **Stephen Hales** (1727), plants acquire a portion of their food from air, and light may also play a role in this process.
- **Joseph Priestly** conducted some intriguing experiments around 1772. He grabbed a half-full pot of water, centered it with a blazing candle, and covered it with a bell jar. The candle was eventually extinguished. Priestly kept a live mouse under the jar and observed how quickly it died.
- Later, he placed a mouse and a potted mint plant beneath the bell-jar and discovered that the mouse survived over an extended period of time. He also discovered that if a mint plant was put beneath a bell-jar for an extended period of time and then a lit candle was placed under the jar, it continued to burn for an extended period of time. Based on his findings, he concluded that **"plants have the ability to purify** foul air."

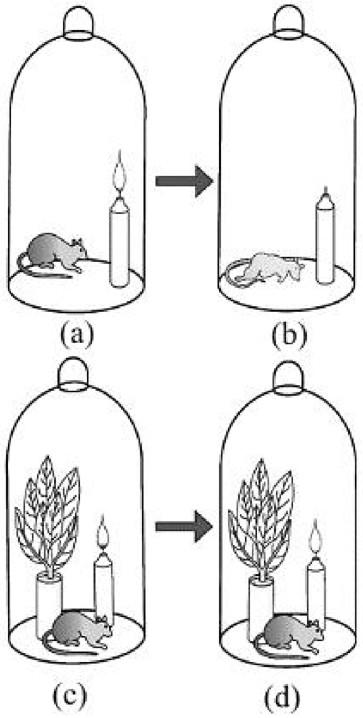


Figure: Priestley's Experiment

- **Jan Ingen-Housz** (1779) concluded from his experiment that **air cleansing** was only **accomplished by green plant parts** in the **presence of sunlight**.
- **Jean Senebier** (1782) demonstrated that in the presence of light, plants absorb CO_2 and emit O_2. He also demonstrated that the rate of O_2 evolution is proportional to the rate of CO_2 consumption.
- **Nicolus de Saussure** (1804) demonstrated the necessity of water in the photosynthetic process. He also demonstrated that the amount of CO_2 absorbed equals the amount of O_2 emitted.
- **Julius Robert Mayer** (1845) claimed that light has radiant energy, which plants convert to chemical energy, which serves to sustain the existence of plants and animals.
- **Julius Von Sachs** (1862) demonstrated that starch is the first observable result of photosynthesis. He also demonstrated the concept of photosynthesis.
- **T.W. Engelmann** (1843-1909) conducted an experiment in which he separated light into its spectrum components and then illuminated a green alga, *Cladophora*, suspended in an aerobic bacteria culture using a prism. The bacteria were employed to identify O_2 evolution locations.
- He discovered that bacteria accumulated primarily in the blue and red-light regions of the split spectrum. As a result, a first action spectrum of photosynthesis was characterized. It is similar to the absorption spectra of chlorophylls a and b.
- **C.B. van Niel** disproved Nicolas de Saussure's discovery in 1930. He demonstrated that sulphur bacteria manufacture carbohydrates using H_2S (instead of water) and CO_2 as follows;

$$6CO_2 + 12H_2S \longrightarrow C_6H_{12}O_6 + 6H_2O + 12S$$

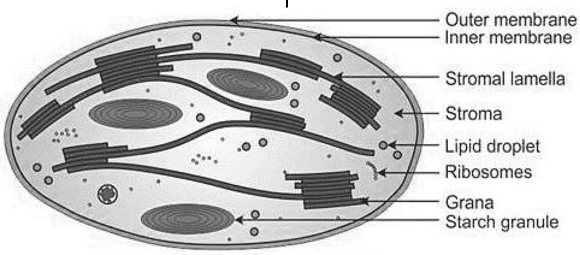
This led van Niel to the postulation that in green plants, water (H_2O) is utilized in place of $H_2\,S$ and O_2 is evolved in place of sulphur (S).

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

- **Ruben and Kamen validated van Niel's discover**y in 1941 by employing *Chlorella*, a green alga. He employed water (H_2O) with a heavy isotope of oxygen (O^{18}), oxygen with an atomic weight of 18 (regular oxygen has an atomic weight of 16), and discovered that the oxygen emitted during photosynthesis was of the O^{18} type (i.e., heavy oxygen). When CO_2^{18} was employed, however, the released oxygen was of the typical form, i.e., O_2^{16}. This implies that the **oxygen generated by green plants is the result of water splitting (oxidation).**
- **Huber, Michel, and Deisenhofer** (1985) crystallized the photosynthetic reaction center of *Rhodopseudomonas viridis*, a purple photosynthetic bacterium. They used the X-ray diffraction technique to examine its structure. For their achievement, they were awarded the Nobel Prize in Chemistry in 1988.

WHERE DOES PHOTOSYNTHESIS TAKE PLACE

- Photosynthesis occurs primarily in specialized cells termed mesophyll cells of leaves in higher plants.
- These cells include **chloroplasts**, which are **actual photosynthesis sites**. It converts CO_2 into carbohydrates.
- Chloroplasts are organelles with a **double membrane**. The **stroma** is the space defined by the **chloroplast's inner membrane**.
- The stroma contains a number of organized flattened membrane sacs (called **thylakoids**). Thylakoids are stacked in stacks similar to **grana**, which are currency piles.
- The chloroplast's **thylakoids** hold the majority of the machinery for the **photochemical** reaction of **photosynthesis**. They contain pigments that **absorb sun energy**.



Chloroplast

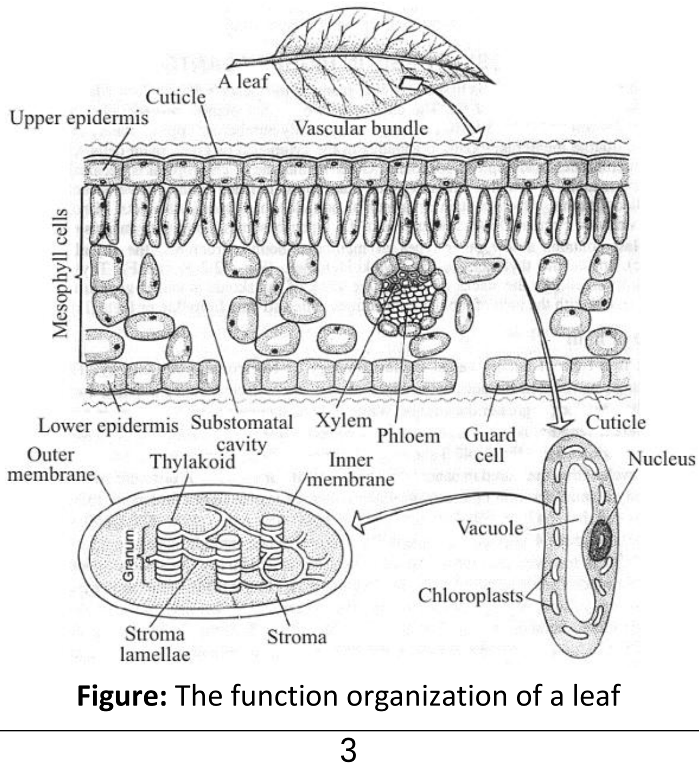


Figure: The function organization of a leaf

Photosynthetic Pigments

- **Pigments** are organic compounds that, due to the presence of conjugated double bonds in their structures, absorb light of specific wavelengths in the visible spectrum.
- There are numerous pigments found in photosynthetic cells.
- **PSU (Photosynthetic units)** present in **thylakoid membranes** are composed of 230-400 molecules of diverse pigments, which Park and Biggins refer to as **Quantasomes**. Chlorophylls are tetrapyrrolic magnesium (Mg) porphyrin complexes.
- The molecule of **chlorophyll** has a **Mg-porphyrin head** and an **alcoholic phytol tail**. The **phytol head** is **hydrophilic**, while the **phytol tail** is **hydrophobic**.
  - Chlorophyll - $a - C_{55}H_{72}O_5\ N_4Mg(CH_3$ group at $III^{rd}C$ of IInd pyrrole ring)
  - Chlorophyll $b - C_{55}H_{70}O_6\ N_4Mg$ (CHO group at IIIrd C of Ind pyrrole)
  - Chlorophyll $c - C_{55}H_{32}O_5\ N_4Mg$
  - Chlorophyll $d - C_{54}H_{70}O_6\ N_4Mg$
  - Carotenes $-C_{40}H_{56}$
  - Xanthophylls $-C_{40}H_{56}O_2$
- **Chl-a** and **carotenes** are **ubiquitous pigments** found in all **oxygen-producing cells**.
- **Chlorophylls** are only **soluble** in **organic solvents** such as ketones, ethers, and so on.
- PS II and the enzyme NADP reductase are absent in **Stroma lamellae/stroma thylakoids**.
- **By paper chromatography/chromatogram, different pigment colours are appear -**
  - Chlorophyll a-blue-green.
  - Chlorophyll b-yellow green.
  - Xanthophyll - yellow
  - Carotenoids - yellow to yellow - orange
- Carotenoids absorb light energy and transfer it to Chl a, so serving as **accessory pigments.** They shield chlorophyll molecules from photo-oxidation by absorbing nascent oxygen and converting it to a harmless molecular state.
- Carotenoids are divided into two groups: **carotenes and xanthophyll**.
  (i) Carotenes are orange-red pigments with the typical formula $C_{40}H_{56}$. They are separated from the carrot. They are found in all plant groupings, from algae to angiosperms. Common carotenes include, and carotene; phytotene, lycopene, neurosporene, and others. Lycopene is a red pigment found in tomatoes and red peppers. Because β-carotene is converted to vitamin A when hydrolyzed, carotenes are also known as provitamin A. β-carotene is a dark yellow pigment found in carrot roots.
  (ii) Xanthophylls: These are yellow carotenoid compounds that are also known as **xanthols or carotenols.** They have the general formula $C_{40}H_{56}O_2$ and contain oxygen in addition to carbon and hydrogen.
- **Lutein** ($C_{40}H_{56}O_2$) is a widely dispersed xanthophyll that contributes to the golden color of autumn leaves. Another major xanthophyll found in Phaeophyceae (brown algae) is fucoxanthin ($C_{40}H_{56}O_6$).
- **Phycobilins**: Blue-green algae (Cyanobacteria) and red algae are the primary sources of these colours. These pigments feature an open tetrapyrrolic structure with no magnesium or phytol chain.
- Blue-green algae contain more phycocyanin, while red algae include more phycoerythrin.
- Phycobilins are formed when phycocyanin and phycoerythrin combine. These water-soluble pigments are assumed to be linked to tiny granules connected by lamellae. Phycobilins, like carotenoids, are accessory pigments that absorb light and transfer it to chlorophyll a.

Absorption and Action Spectra

- The **absorption spectrum** is the curve that represents the **amount of light** absorbed by pigment at each wavelength.
- The action spectrum is the curve that shows the **rate of photosynthesis** at different wavelengths of light.

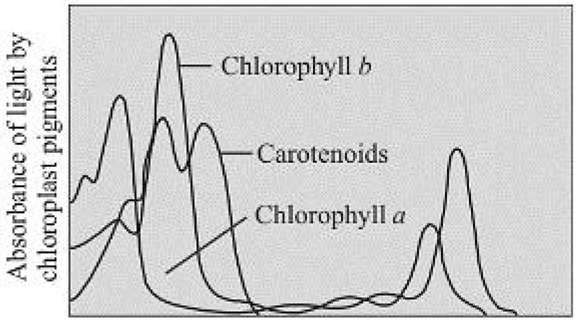


Figure: Graph showing the absorption spectrum of chlorophyll a and b

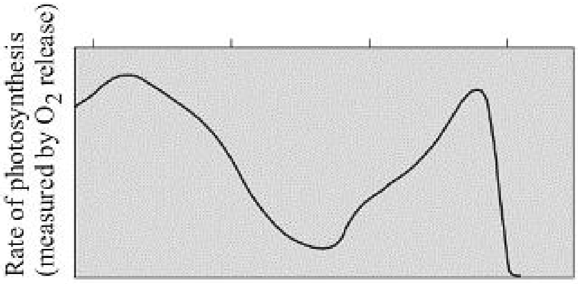
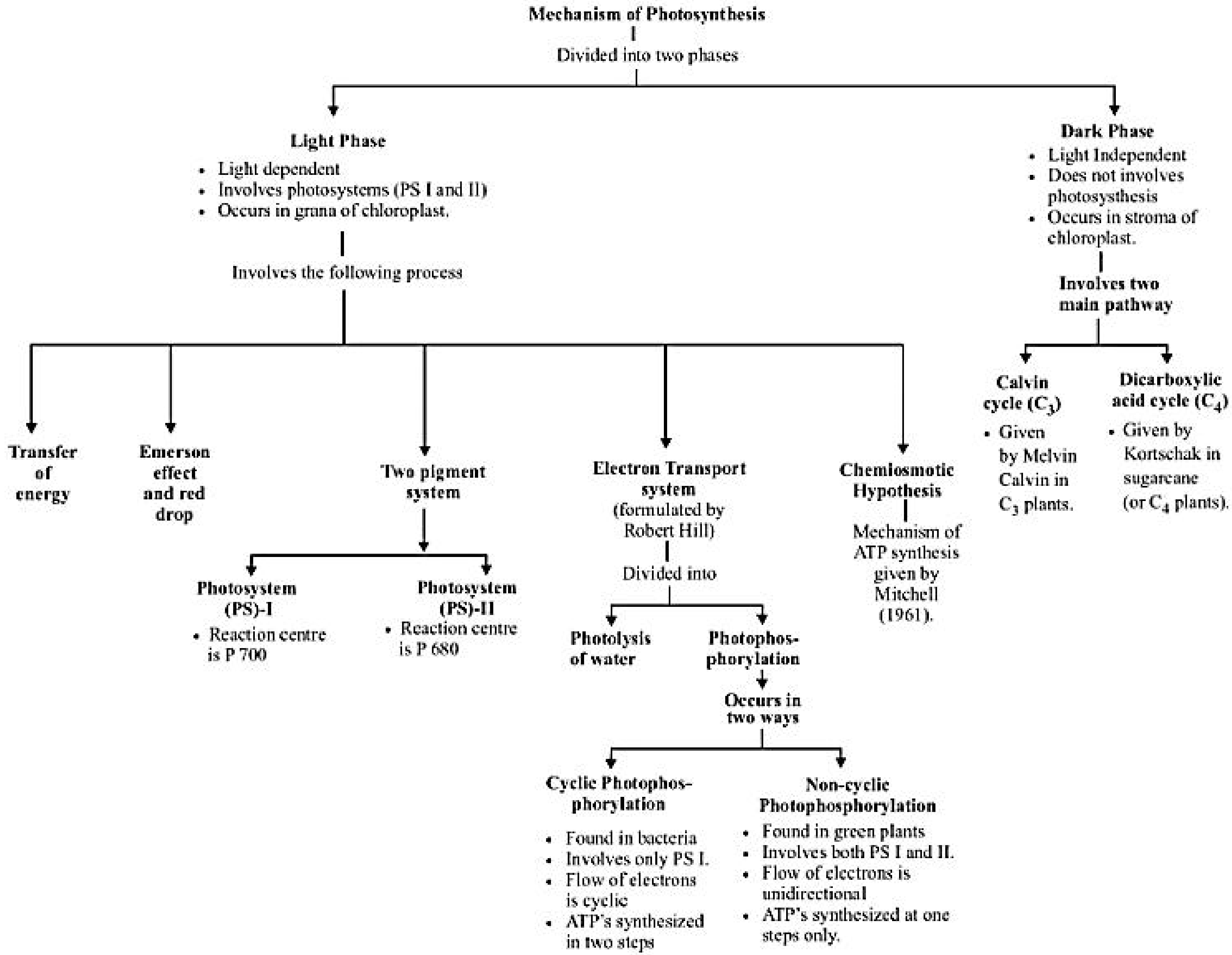


Figure: Graph showing action spectrum of photosynthesis

- The absorption spectrum is investigated using a **spectrophotometer**. Chlorophyll a and chlorophyll b absorption spectra show that these pigments mostly absorb blue and red light (430 nm and 662 nm for chlorophyll a, 455 nm and 644 nm for chlorophyll b).
- Maximum photosynthesis occurs in the blue and red parts of the spectrum, according to the action spectrum. **T.W. Engelmann** (1882) investigated the first photosynthetic action spectrum utilizing the green alga *Spirogyra* and oxygen-seeking bacteria.

MECHANISM OF PHOTOSYNTHESIS

Flow chart : Mechanism of Photosynthesis



- **Photosynthesis** is an **oxidation-reduction** reaction in which water is oxidized to produce O_2 and CO_2 is reduced to produce starch and sugars.
- Photosynthesis is accomplished in two stages, according to scientists:
  (1) Light phase or Photochemical reactions or Light dependent processes or Hill's reactions: During this stage, energy from sunlight is absorbed and converted to chemical energy, which is stored in ATP and NADPH +H^+.
  (2) Dark phase or Chemical dark reactions or Light independent reactions or Blackman reaction or Biosynthetic phase: Carbohydrates are produced from carbon dioxide during this stage using the energy stored in the ATP and NADPH created in light dependent reactions.

S. No.	**Light reaction**	**Dark reaction**
1.	It is a light dependent process.	It does not require light.
2.	Involves photosystems – I and II.	No photosystem is required.
3.	Photolysis of water takes place and O_2 is liberated	Photolysis of water does not take place and CO_2 is absorbed.
4.	Occurs within the grana of the chloroplast.	Occurs within the stroma of the chloroplast.
5.	ATP and NADPH produced and they are used to drive the dark reaction.	Glucose is produced and Reduced NADP is oxidized.

Light phase or photochemical reactions or light dependent reactions or Hill's reactions.

- Light reactions occur in the **grana fraction of chloroplasts,** and these reactions include light-dependent activities. This light reaction mostly generates assimilatory powers (ATP and $NADPH_2$).
- **Robin Hill (1939) first demonstrated** that oxygen is released due to photochemical splitting of water when chloroplasts extracted from Stellaria media and *Lamium album* leaves are suspended in a test tube containing suitable electron acceptors, such as potassium ferroxalate (Some plants require only this chemical) and potassium ferricyanide.
- Under these conditions, no CO_2 was consumed and no carbohydrate was generated, but O_2 evolution accompanied light-driven reduction of electron acceptors.

$$\underset{\text{Electron acceptor}}{4Fe^{3+}} + \underset{\text{Electron donor}}{2H_2O} \longleftrightarrow \underset{\text{Reduced Product}}{4Fe^{2+}} + 4H^+ + O_2 \uparrow$$

- **Photolysis** is the **splitting of water** during photosynthesis. This reaction is known as the Hill reaction after its discoverer.
- The Hill Reaction demonstrates that
  (1) Oxygen is liberated from water during photosynthesis.
  (2) Water is used to obtain electrons for CO_2 reduction [i.e., a reduced substance (hydrogen donor) is generated, which later reduces CO_2].
- The dye used by Hill for his renowned Hill reaction is **2,6-dichlorophenolindophenol** (DCPIP), a blue chemical compound used as a redox dye.
- When exposed to light in a photosynthetic system, this dye changes color (or becomes colorless if decreased).

- According to Arnon (1961), light energy is transformed to chemical energy during this process. This energy is stored in ATP (the process of ATP formation in chloroplasts is known as photophosphorylation), and NADPH is generated as a hydrogen donor from the electron acceptor $NADP^+$, which is found in all living things.
- Photoreduction, or the creation of reducing power NADPH, is the formation of hydrogen donor NADPH from electron acceptor.

Quantum Yield

(i) Photosynthesis rate or yield can be measured in terms of quantum yield or O_2 evolution, which can be described as **"Number of O_2 molecules evolved per quantum of light absorbed in photosynthesis."**

(ii) Photosynthesis quantum requirement = 8, i.e., 8 quanta of light are required to evolve one molecule of O_2.

(iii) As a result, quantum yield = **1/8 = 0.125** (a fraction of 1) as **12%**.

- **R. Emerson and C.M. Lewis (1943)** discovered that the **quantum yield of photosynthesis** declines towards the **extreme red end** of the spectrum (or longer). Because this decrease in quantum yield is detected in the distant area or beyond the red portion of the spectrum, it is referred to as **red drop.**
- **Emerson et al. (1957)** discovered that supplying light of shorter wavelengths (less than 680 nm) simultaneously increases photosynthetic efficiency of light of 680 nm or longer. The quantum yield of photosynthesis was larger when both short and long wavelengths were provided together than when both wavelengths were given separately. **The Emerson effect** or Emerson enhancement effect refers to this improvement in photosynthetic efficiency (or quantum yield).

$$E = \frac{\text{Quantum yield in combined beam} - \text{Quantum yield in red beam}}{\text{Quantum yield in far red beam}}$$

Pigment Systems

- Within Photosystem I (PS I) and Photosystem II (PS II), the pigments are organized into two distinct **photochemical light harvesting complexes (LHC).**
- By absorbing different wavelengths of light, these pigments contribute to improve photosynthetic efficiency.
- The reaction center is formed by a single chlorophyll a molecule. In each photosystems, the reaction center is different.
- The reaction center chlorophyll an in PS I has an absorption peak at 700 nm and is thus known as **P700**, but in PS II it has an absorption peak at 680 nm and is known as **P680.**
  - **(i) Pigment system I or Photosystem I (PSI)**: This system's key pigments are chlorophyll a 670, chlorophyll a 683, chlorophyll a 695, and P700. Carotenes and chlorophyll b are also included in pigment system 1 by certain physiologists. As a result, this system absorbs both shorter and longer wavelengths than 680 nm.
  - **(ii) Pigment system II (PSII):** This system's primary pigments include chlorophyll a 673, P680, chlorophyll b, and phycobilins. Only wavelengths shorter than 680nm are absorbed by this pigment system.

Comparison of Photosystem I and Photosystem II.

S. No.	Photosystem I	Photosystem II
1.	PS I lies on the outer surface of the thylakoids.	PS II lies on the inner surface of the thylakoids.
2.	In this system, molecular oxygen is not evolved.	As the result of photolysis of water, molecular oxygen is evolved.
3.	Its reaction center is P700.	Its reaction center is P680.
4.	NADPH is formed in this reaction.	NADPH is not formed in this reaction.
5.	It participates both in cyclic and non-cyclic photophosphorylation.	It participates only in non-cyclic photophosphorylation.
6.	It receives electrons from photosystem II.	It receives electrons from photolytic dissociation of water.
7.	It is not related with photolysis of water.	It is related with photolysis of water.

- Antennas and accessory pigments absorb radiant energy and distribute it among themselves. This type of energy transfer is known as **resonance transfer.**
- The antenna then excites molecules, which send their energy to the chlorophyll 'a' molecule in the reaction center.
- **Inductive resonance** is the term for this phenomenon.
- Finally, chl.'a' molecule convert light energy into electrical energy via electric charge separation.

CYLIC ELECTRON TRANSPORT SYSTEM

(I) Cyclic Photophosphorylation

- The process by which ATP is synthesized by cell (in mitochondria and chloroplast) is called as phosphorylation.
- **Only PS-I (LHC-I)** works in cyclic photophosphorylation.

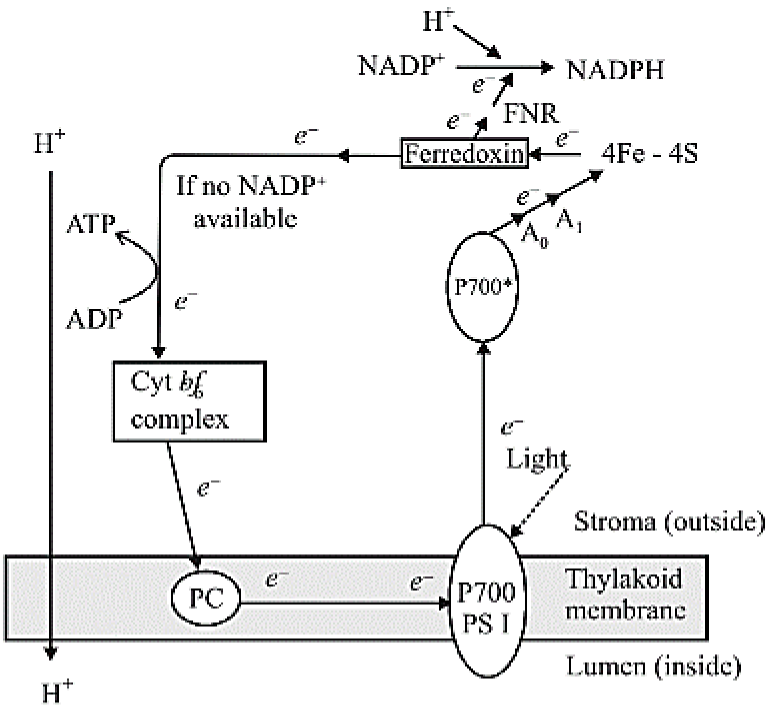


Figure: Cyclic Photo-phosphorylation

- Light with a wavelength greater than 680 nm activates cyclic ETS or PS-I.
- It can be found in **grana thylakoids** and **stroma thylakoids**.
- During cyclic ETS, the electron expelled from PS-I's reaction center returns to its reaction center.
- Because photolysis of water is missing in cyclic ETS, no oxygen evolution occurs.
- Because phosphorylation occurs twice, each cyclic ETS generates two ATP.
- **The cyclic process does not produce $NADPH_2$ (reducing power).**
- In cyclic ETS, **plastocyanin (PC)** is a **Cu-containing blue protein**.
- According to recent studies, the first e-acceptor is FRS (Ferredoxin Reducing Substance), a Fe-S containing protein. Previously, fd (**Ferredoxin**) was **thought** to be the **first e-acceptor**.)

(II) Z-Scheme/Non-Cyclic Electron Transport System/Non Cyclic Photophosphorylation

- In non-cyclic ETS, both PS-I and PS-II are involved.
- It occurs at **grana thylakoids only**.

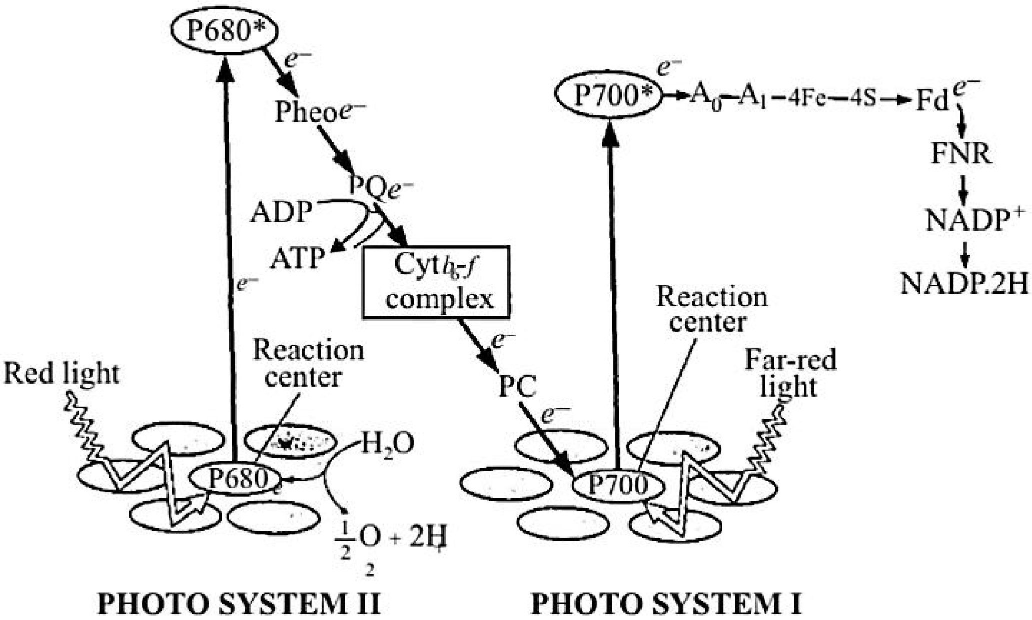


Figure: Non-Cyclic Photo-Phosphorylation

- The e^- ejected from PS-II never returns to chla-680 (reaction center) and is eventually captured by NADP.
- During this process, oxygen is produced as a result of water photolysis, and the synthesis of $NADPH_2$ and ATP happens.
- Each non-cyclic ETS turn generates 1 ATP and 2 $NADPH_2$ (4 molecules of H_2O are photolyzed and 1 molecule of O_2 is liberated).
- **PQ, or plastoquinone**, is the **primary e-acceptor in non-cyclic reactions**.
- Pheophytin (structure similar to chl a but lacking Mg) has recently been identified as the first e-acceptor in the Z-scheme.
- In non-cyclic ETS, plastocyanin (a Cu-containing pigment) connects PS-I and PS-II.
- In **the Z-scheme**, **the last e-acceptor is $NADP^+$ (Hill reagent)**.
- Energy flows from PS II to PS I under non-cyclic ETS.

Comparison of Cyclic Photophosphorylation and Non-Cyclic Photophosphorylation

S. No.	Cyclic photophosphorylation	Non-cyclic photophosphorylation
1.	It involves photosystem I.	It involves both PS I and PS II.
2.	It is not connected with photolysis of water, so no oxygen is evolved.	It is connected with photolysis of water and liberation of oxygen.
3.	Electrons move in a closed circle. Electron expelled from P700 return to it after passing through different electron acceptors.	Electrons do not move in a closed circle. Electrons expelled by the reaction centre P680 does not returned it, Here water donate the electrons to P680.
4.	In each flow of electrons, 2 molecules of ATP are synthesized.	In each flow of electron, 1 molecule of ATP is synthesized.
5.	NADPH is not produced.	NADPH is produced.
6.	It is not inhibited by DCMU.	It is inhibited by DCMU.

CHEMIOSMOTIC HYPOTHESIS

- Mitchell (1961) proposed the chemiosmotic theory to explain the mechanism of ATP synthesis.
- Protons build inside the thylakoid membranes as electrons are transferred by the electron transport system (ETS).
- Due to photolytic splitting of water, the lumen of a thylakoid becomes enriched with H^+ ion.
- The **primary electron acceptor** is found on the **thylakoid membrane's outer surface**. It moves an electron to an H-carrier. The carrier takes a proton from the matrix while transferring an electron to the membrane's inner side. While the electron moves to the next carrier, the proton is discharged into the lumen.
- **NADP reductase** is found on the stroma side of membrane. It gets electrons from PSI and protons from the matrix to convert $NADP^+$ to NADP + H^+.
- The passage of protons through transmembrane channels, **F_0 of ATPase, breaks down the proton gradient.**
- Therefore, within the lumen there is accumulation of protons whereas in chloroplast's stroma proton no. decreases.
- The ATPase enzyme is composed of two parts: **F_0 and F_1 particles.**
- F_0 is embedded in thylakoid membrane whereas F_1 protrudes on outer surface of thylakoid membrane.
- The remaining membrane is impervious to H^+.
- F_0 facilitates the diffusion of H^+ or protons. Protons moving to the outer side of ATP cause conformational changes in the F_1 particle of ATPase or coupling factor.
- The ATPase enzyme's transitory F_1 particle generates ATP from ADP and inorganic phosphate.
- When **$2H^+$ pass through ATPase, one molecule of ATP is generated.**

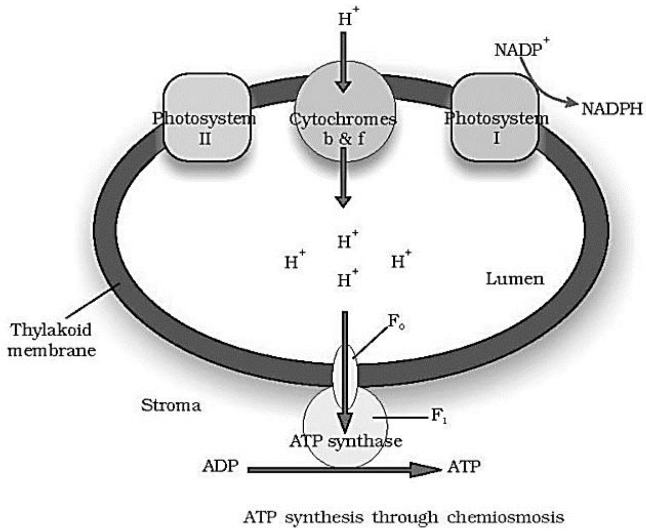


Figure: ATP synthesis through chemiosmosis

Dark phase or Chemical dark reactions or Light independent reactions or Blackman reaction or Biosynthetic phase.

- **Carbon fixation**, also known as the **photosynthetic carbon reduction (PCR)** cycle or dark reactions, is the process by which all photosynthetic eukaryotic organisms eventually assimilate CO_2 into carbohydrate.
- The dark reactions are temperature sensitive yet independent of light, hence the name, however they rely on the products of photosynthesis's light reactions, namely NADP. H_2 and ATP.
- Carbon dioxide fixation occurs in the stroma of chloroplasts because it contains enzymes required for CO_2 fixing and sugar production.

(i) Calvin cycle/ C_3-cycle

- In this approach, Calvin and Benson found the carbon route.
- Calvin cycle is known as the C_3 cycle because the first stable molecule is 3C-PGA **(Phosphoglyceric acid)**.
- Calvin investigated *Chlorella* and *Scenedesmus* (microscopic unicellular algae that may be easily maintained in a laboratory).
- During his work, he used chromatography and radioactive tracer (C^{14}) techniques to detect C_3 cycle reactions.
- **RuBisCO** (Ribulose bis-phosphate carboxylase oxygenase) is the major enzyme in the C_3-cycle, which is found in the stroma and accounts for 16% of chloroplast protein. RuBisCO is the most common enzyme on the planet.
- Ribulose 1,5-diphosphate (RuBp) is the CO_2-acceptor in the C_3 cycle. RuBisCO catalyzes this carboxylation process.
- Temperate species *Atriplex hastata* and *Atriplex patula* are C_3 plants.
- **One glucose requires six Calvin cycle turns to be formed.**
- In this cycle, **18ATP and 12NADPH₂** are used to generate one mole of hexose sugar (glucose).

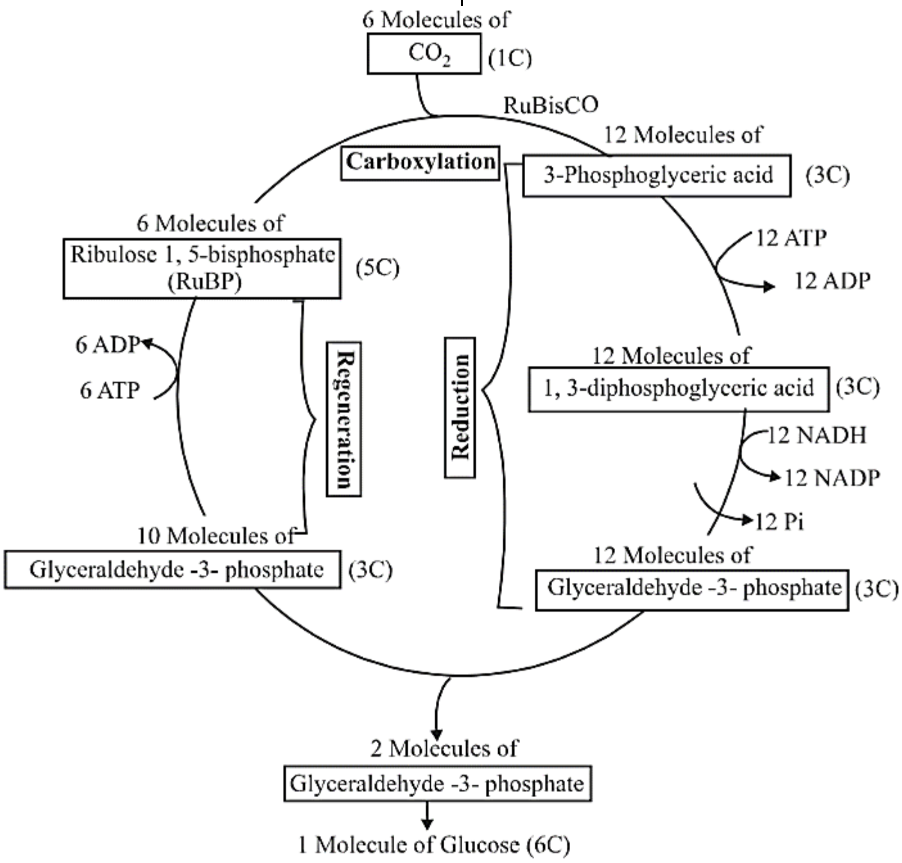


Figure: Calvin cycle

Calvin cycle is divided into three distinct phases:

(a) Carboxylation

(b) Glycolytic reversal

(c) Regeneration of RuBP

1. 6mol. of RuBP + 6mol. of $CO_2 \left(HCO_3^-\right) \xrightarrow[\text{[Carboxyldismutase]}]{\text{RuBisCO}} + 6H_2O$

   6C unstable comp. $\rightarrow$ 12 mol. of 3-phosphoglyceric acid (PGA)

Glycolytic Reversal:

2. 12 mol. of $3-\text{PGA}+12\text{ATP}\xrightarrow{\text{Triokinase}}12$, mol. of I, 3-bisphosphoglycericacid (1, 3 BiPGA)

3. $12 \text{ mol. of } 1,3\text{-BiPGA} \xrightarrow[12NADPH_2 \rightarrow 12NADP^+]{\textit{Dehydrogenase}}$

   12 mol. of 3-phosphoglyceraldehyde (3-PGAL) (Triose phosphate) $+12H_3PO_4$

- After a series of complex reactions, two of these 12 molecules are recycled to produce sugar, starch, and other carbohydrates, while the remaining ten molecules are recycled to renew six molecules of Ribulose-5-phosphate.

4. Out of **2 molecules of PGAL** one mol is converted to its isomer 3-**hydroxy acetone phosphate**.

   $\underset{(9C)}{1\text{mol.of PGAL}}+\underset{(9C)}{1\text{mol.of DHAP}} \xrightarrow{\textit{Aldolase}} \underset{(18C)}{1\text{ mol.of Fructose1,6 Biphosphate}}$

   [1 mol. fructose $\xrightarrow{\textit{Isomerase}}$ $[C_6H_{12}O_6]$ Glucose $\longrightarrow$ Sucrose/Starch]

Regeneration of Ribulose 1, 5 biphosphate

5. $\underset{(12C)}{2\text{mol.of Fructose-6-P}}+\underset{(6C)}{2\text{mol.of PGAL}} \xrightarrow{\text{Transketolase}} \underset{(8C)}{2\text{mol.of Erythrose-4-P}}+\underset{(10C)}{2\text{mol.of Xylulose-5P}}$

6. $\underset{(8C)}{2\text{mol.of Erythrose-4-P}}+\underset{(6C)}{2\text{mol.of DHAP}} \xrightarrow{\textit{Aldolase}} \underset{(14C)}{2\text{mol.of Sedoheptulose1,7-BiP}}$

7. $\underset{(14C)}{2\text{mol.of Sedoheptulose-P}}+\underset{(6C)}{2\text{mol.of PGAL}} \xrightarrow{\textit{Transketolase}} \underset{(14C)}{2\text{mol.of Xylulose-5-P}}+\underset{(10C)}{2\text{mol.of Ribose-5-P}}$

8. 2 × 2 mol. of Xylusose-P $\xrightarrow{\text{Epimerase}}$ 4 mol. of Ribulose-5P (20C)

9. 2 mol. of Ribose-5P $\xrightarrow{\text{Isomerase}}$ 2 mol. of Ribulose-5P (10C)

10. 6 mol. of Ribulose-5P + 6ATP $\xrightarrow{\text{Kimase}}$ 6 mol. Ribulose-1,5-BiP(CO_2 acceptor) + 6 ADP

C_4 cycle (Hatch and Slack Pathway)

- Kortschak and Hartt discovered the formation of **4C-compound OAA (Oxalo Acetic Acid)** during a **dark reaction in sugarcane leaves**.
- Hatch and Slack (1967) investigated and proposed a mechanism for dark reactions in sugarcane and maize leaves in great detail.
- The **first stable result** of this reaction is **OAA,** which is a **4C molecule** and a dicarboxylic substance; consequently, the **Hatch and Slack pathway** is known as the **C_4 cycle** or **dicarboxylic acid cycle (DCA).**

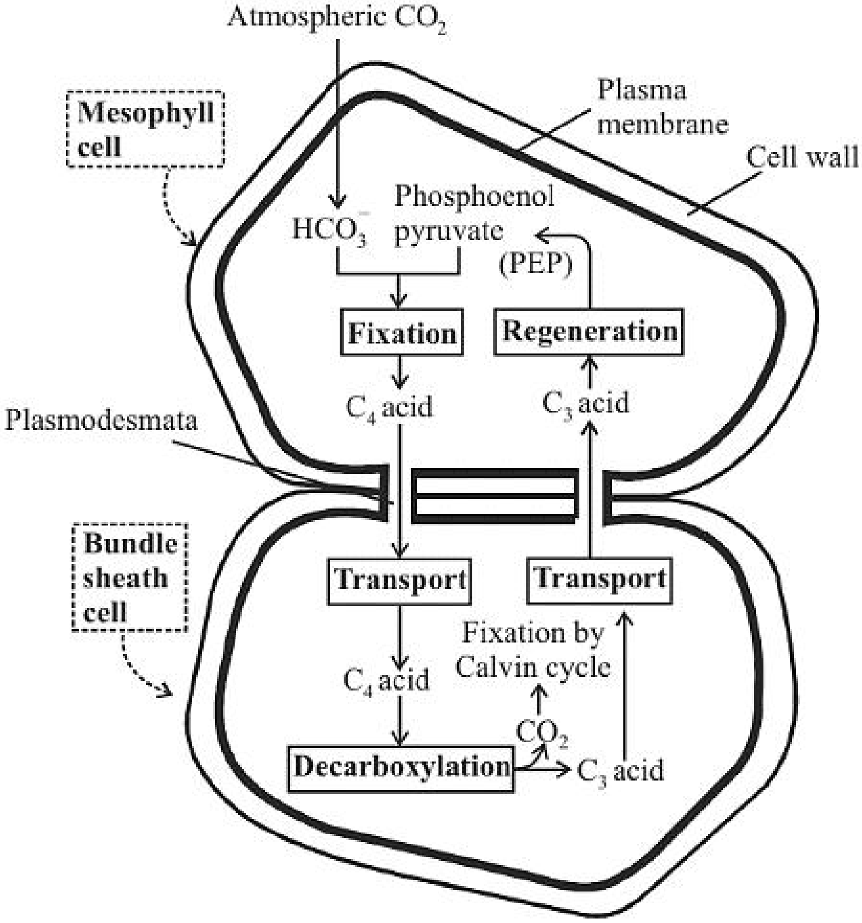


Figure: Diagrammatic representation of the Hatch and Slack Pathway

- The C_4-cycle occurs in 1500 species from 19 angiosperm families, however the majority of the plants are monocots from the Graminae and Cyperaceae families (sugarcane, maize, sorghum, oat, chloris, sedges, bajra, *Panicum*, *Alloteropsis*, and so on).
- *Euphorbia* spp., *Amaranthus*, *Chenopodium*, *Boerhavia*, *Atriplex rosea*, *Portulaca*, *and Tribulus* are C_4-cycle dicots.
- *Kranz (Wreath) Anatomy* - Present in leaves of C_4 plants.
  The following are some of the characteristics of kranz anatomy:
  (i) Green bundle sheath cells (BS cells) are found around vascular bundles.
  (ii) Leaf cells have dimorphic chloroplasts. Bundle sheath or Kranz cell chloroplasts are bigger and lack grana. Mesophyll chloroplasts are tiny and covered in grana.

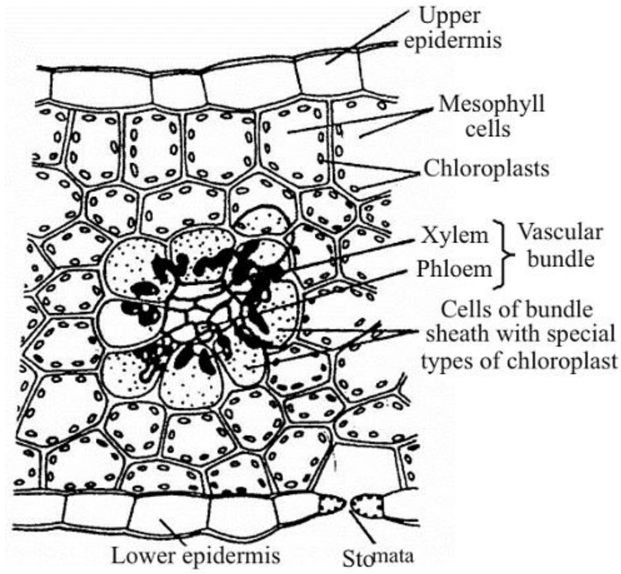


Figure: Cross section of leaf showing "Kranz" type of anatomy

- C_3-cycle occurs in bundle sheath cells, while C_4 cycle occurs in mesophylls cells in the C_4-Plant.
- Hatch and Slack route operation necessitates the collaboration of both photosynthetic cells, namely **mesophyll cells and bundle sheath cells.**

- C_4 plants are more efficient photosynthetically because there is **no Warburg effect** or **photorespiration** in C_4 plants since less O_2 is present at the location of RuBisCO (BS cells) (mesophyll cells pump more CO_2 for C_3 cycle).
- C_4 plants are found in tropical environments and have evolved to high temperatures, limited water supply, and intense light. As a result, they are better developed and adapted than C_3 plants.
- They have no effect on photorespiration.
- Photorespiration can begin in C_4 plants if the content of O_2 is artificially increased.
- PEPcase performs the first carboxylation in the C_4 cycle in mesophyll chloroplast, while bundle sheath cells perform the second carboxylation or ultimate CO_2 fixation in the C_3 cycle.
- PEP case is a carboxylase enzyme that catalyzes the binding of one molecule of CO_2 to the 3C chemical phosphoenol pyruvate to create the 4-C compound oxaloacetate.
- **Phosphoenol pyruvate (PEP), a 3C-** compound, is **the CO_2 acceptor in C_4 mesophyll cells, while RuBp is the acceptor in bundle sheath cells.**
- 12NADPH₂ (=36 ATP) +30 ATP =66 ATP required for C_4 -plants to produce 1 hexose (Glucose).
- Pyruvate phosphate dikinase (PPDK) (convert ATP into AMP) is a temperature sensitive enzyme found in C_4 and CAM plants, which allows C_4 plants to photosynthesize more efficiently at high temperatures.

C_4 Plant Characteristics

(i) At the current CO_2 concentration, C_4 plants are more efficient.

(ii) The current level of atmospheric CO_2 is not a limiting factor for C_4 plants.

(iii) C_4 plants have low CO_2 compensation points. (8-10 ppm)

(iv) When CO_2 concentration increases, productivity (fertility) does not increase in C_4 plants because-

(a) Mesophyll cells provide more CO_2 for Calvin cycle.

(b) The concentration of CO_2 surrounding the RuBisCO site is higher in C_4 plants, implying that photorespiration is unlikely.

Comparison of C_3 plants and C_4 plants

S. No.	C_3 Plants	C_4 Plants
1.	CO_2 fixation one time.	CO_2 fixation occurs two times, one in mesophyll cells to form oxaloacetic acid and another in bundle sheath cells to form 3-phosphoglyceric acid.
2.	RuBP (5-C compound) is CO_2 acceptor. It is a weak CO_2 acceptor.	PEP in mesophyll cells and RuBP in bundle sheath cells function as CO_2 acceptor. PEP is a very strong CO_2 acceptor as compared to RuBP.
3.	First product of CO_2 fixation is PGA (3-C compound).	It is oxaloacetic acid (4-C compound) in mesophyll cells and PGA in bundle sheath cells.
4.	Leaf anatomy not Kranz type. Only one type of chloroplasts are found.	Kranz type of leaf anatomy. The mesophyll is undifferentiated and its cells occur in concentric layers around vascular bundles. C_4 plants possess dimorphic chloroplasts.