**II MSc; III SEMESTER**

**18MBO32C: PAPER-VIII PLANT PHYSIOLOGY**

## Unit –III

Photosynthesis: Organization of photosynthetic apparatus and light absorbing antenna systems; Absorption and transformation of radiant energy; Photosynthetic Electron transport and Photophosphorylation; Photooxidation of water; C3, C4 and CAM pathways and their efficiencies; Photorespiration and its regulation; Inorganic carbon concentrating mechanisms; RUBISCO and PEPC.

Notes:-

Photosynthesis is by far the most significant biological process on the planet earth. Photosynthesis can be defined as the anabolic process during which complex energy-richorganic molecules/compounds are synthesized by organisms from CO2 and H2O using solar energy.

Every day, the radiant energy of the sun that bombards the earth equals nearly a million Hiroshima-sized atomic bombs. Out of the total supply of solar energy received by the earth, only 1–2 per cent is utilized by photosynthesis.

In higher and other non-flowering plants, the photosynthetic reactions occur in the '**chloroplast – an incredible thermodynamic machine**'.

Photosynthesis occurs in three steps (Figure 7.1):

1. To harness solar energy by the chloroplasts
2. Using this solar energy to produce ATP and NADPH in the light reaction
3. Using the ATP and NADPH to power the synthesis of complex organic molecules using atmospheric CO2 during the dark reaction.

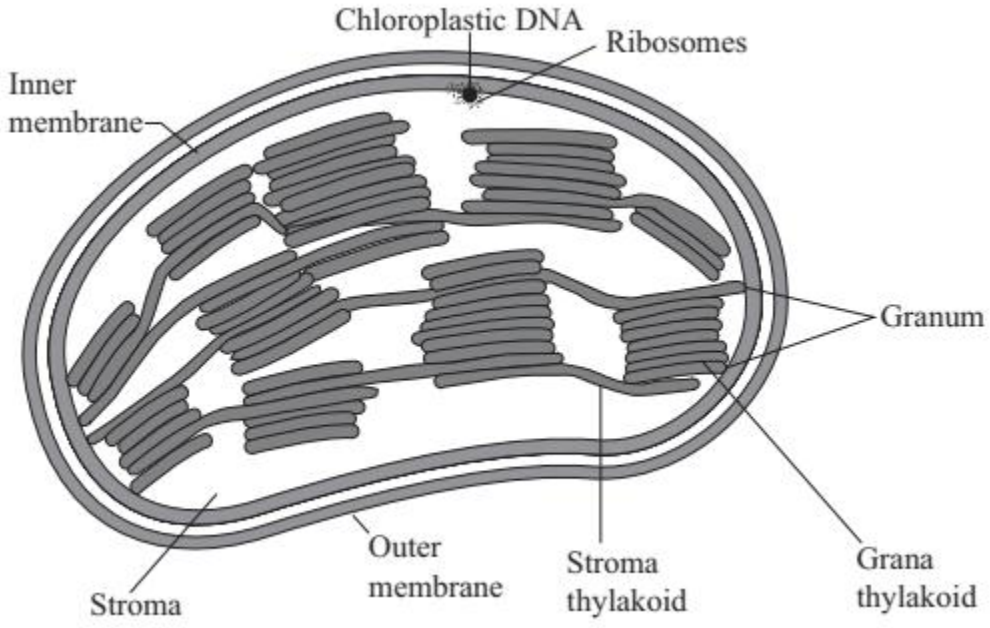
The following equation summarizes the overall process:

$$6CO_2 + 12H_2O \xrightarrow[\text{Chlorophyll}]{\text{673 Kcal of light energy}} \underset{\text{Carbohydrates}}{C_6H_{12}O_6} + 6O_2 + 6H_2O$$

Pigments in green plants have been categorized into two groups:

1. Vital (essential) pigments – Chl a ($C_{55}H_{72}O_5N_4Mg$)
2. Accessory pigments – Chl b, c, d, e, carotenoids, phycobilins

A typical chloroplast illustrating the major compartments. Grana are linked together by intergranal or stromal lamellae (also called frets). Chloroplasts contain their own DNA and ribosomes. The chloroplast envelope, with its numerous transporters, represents the essential interface in the complex metabolic network that link the chloroplast with other compartments.



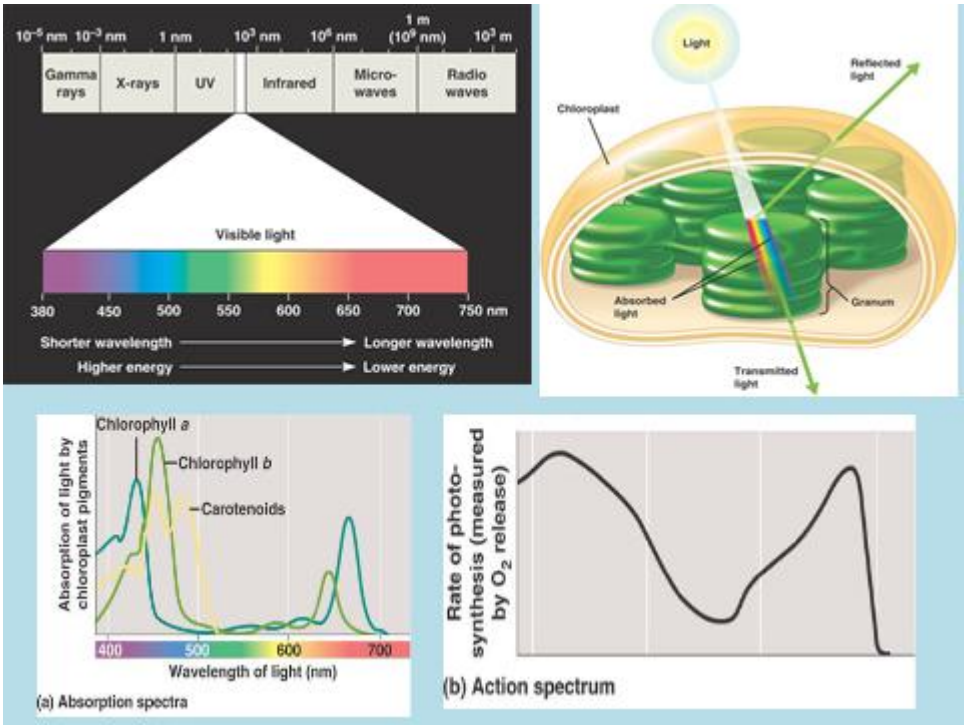

Chloroplast is a large organelle with a complex structure harboring two outer membranes called the chloroplast envelope and a third extensively folded internal membrane system called thylakoid.

The thylakoid membrane is composed of two morphologically distinct domains:-

The grana domain which is characterized by 5–20 layers of cylindrical stacks of thylakoid membrane disks and the stroma lamellae domain which are stroma-exposed membrane pairs connecting the grana stacks

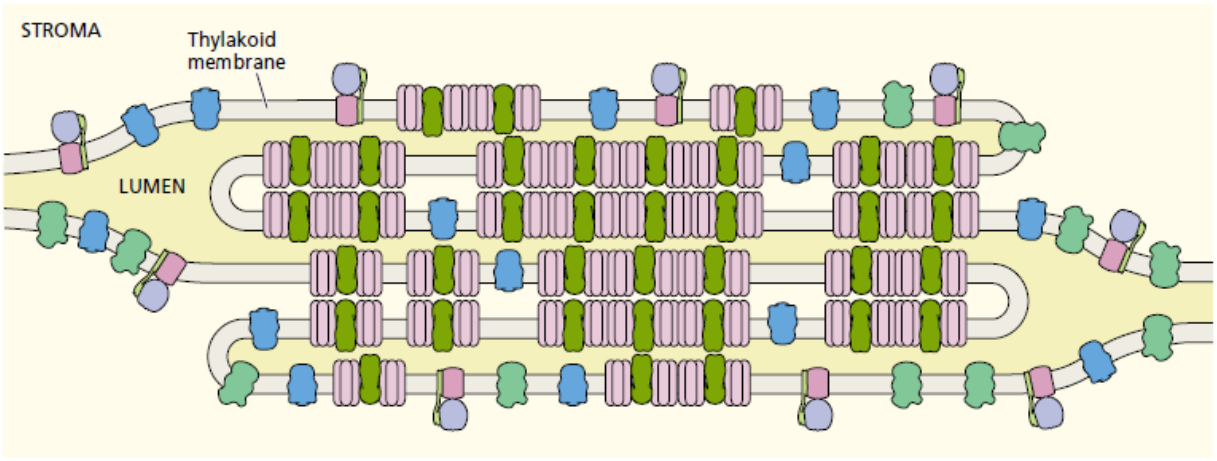
The chlorophyll molecule has a cyclic tetrapyrrolic structure – a porphyrin head with an isocyclic ring containing a magnesium atom at its centre. The phytol chain of the chlorophyll molecule extends from one of the pyrrole rings into the thylakoid membrane. The structure of the chlorophyll molecule roughly resembles a ‘tennis racket’ having a large flat head (the porphyrin ring) and a long handle (the

phytol tail). The angle between head and tail is 45°. Chlorophyll molecules preferentially absorb the blue (400–500 nm) and red (600–700 nm) wavelengths of the electromagnetic spectrum and reflect the green wavelengths (500–600 nm). Hence, leaves look green in color.




All light absorption and energy-transducing processes take place at the thylakoid membranes. The pH difference between the thylakoid space and the stroma is about 2 to 3. Thylakoid membranes contain ion channels besides proteins that are directly involved in the energy transduction processes. These ion channels lower the membrane potential and thus the energy required to transfer a proton across the membrane. The lipid composition of thylakoid membranes differs from that of other plant membranes. Besides lipids that are unique to thylakoid membranes, it contains polyunsaturated fatty acids to an exceptional large amount, which makes the thylakoid membranes highly fluid allowing a rapid diffusion of membrane protein complexes.

## Photosystems I and II Are Spatially Separated in the Thylakoid Membrane



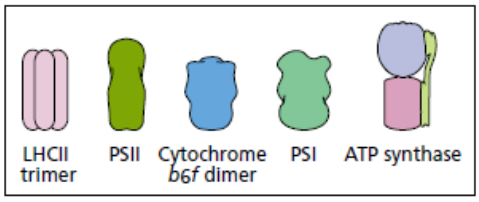
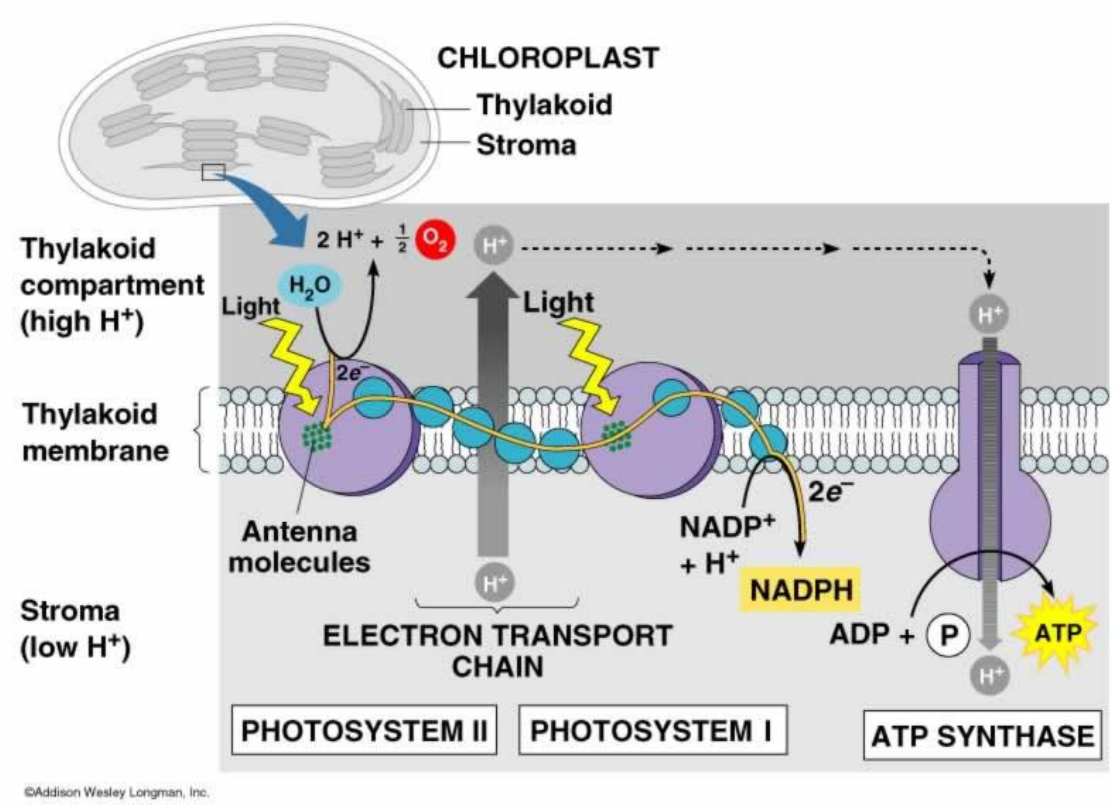
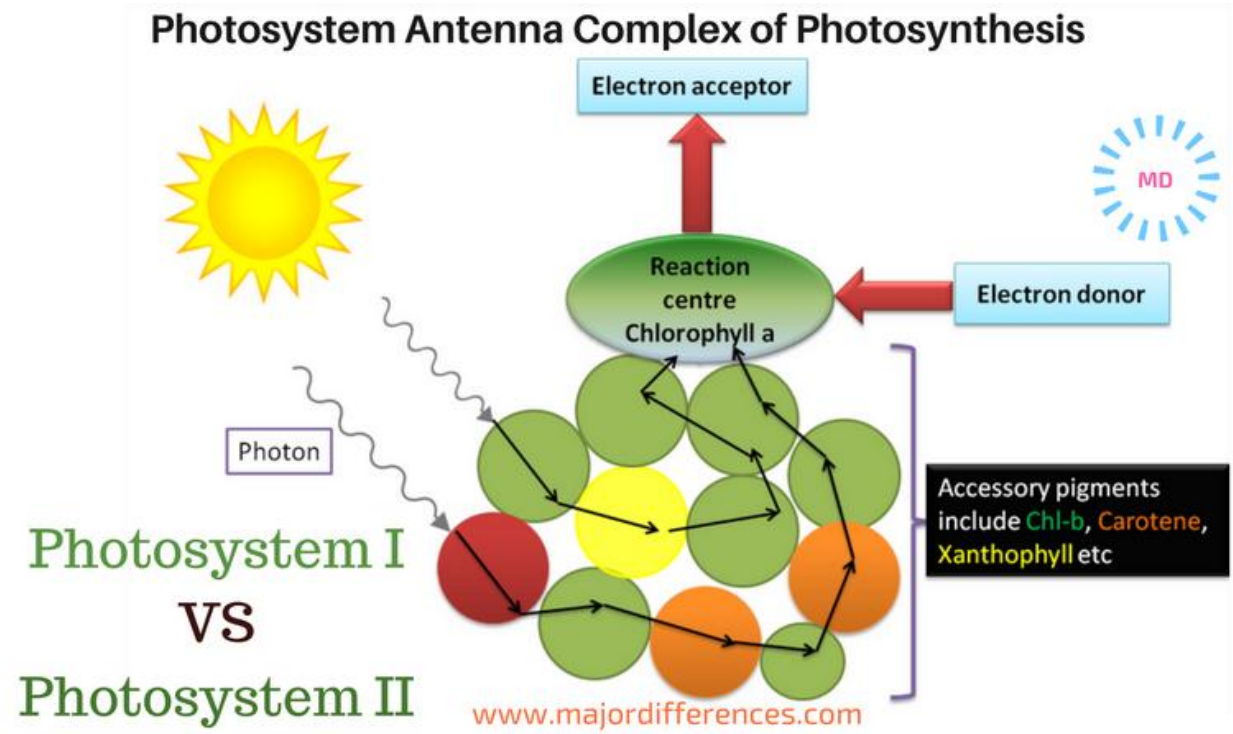
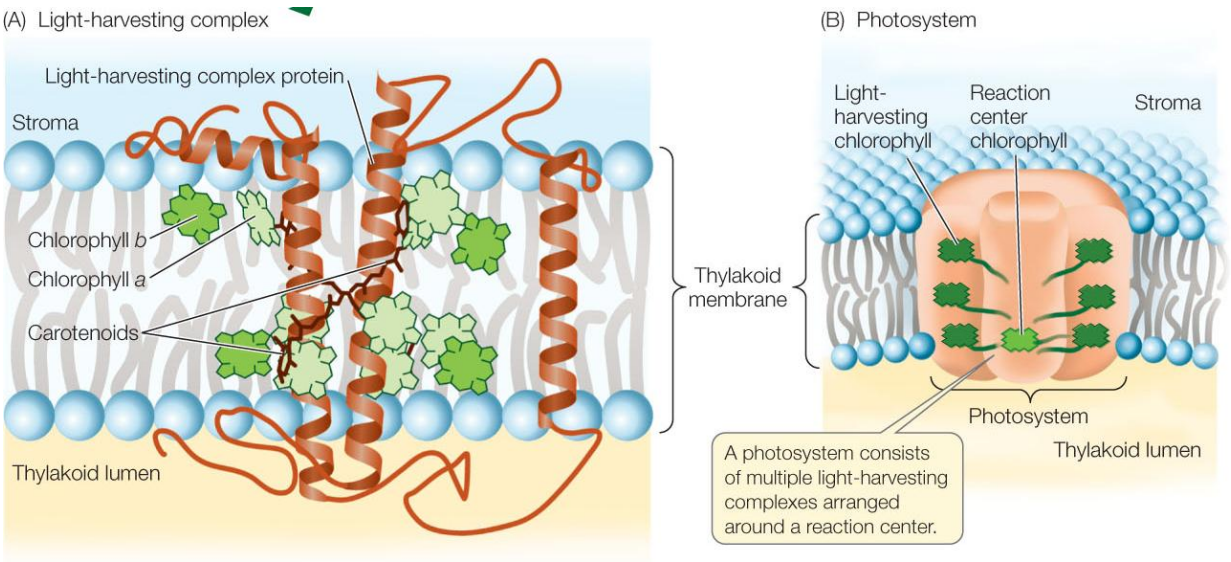




**FIGURE 7.18** Organization of the protein complexes of the thylakoid membrane. Photosystem II is located predominantly in the stacked regions of the thylakoid membrane; photosystem I and ATP synthase are found in the unstacked regions protruding into the stroma. Cytochrome $b_6f$ complexes are evenly distributed. This lateral separation of the two photosystems requires that electrons and protons produced by photosystem II be transported a considerable distance before they can be acted on by photosystem I and the ATP-coupling enzyme. (After Allen and Forsberg 2001.)



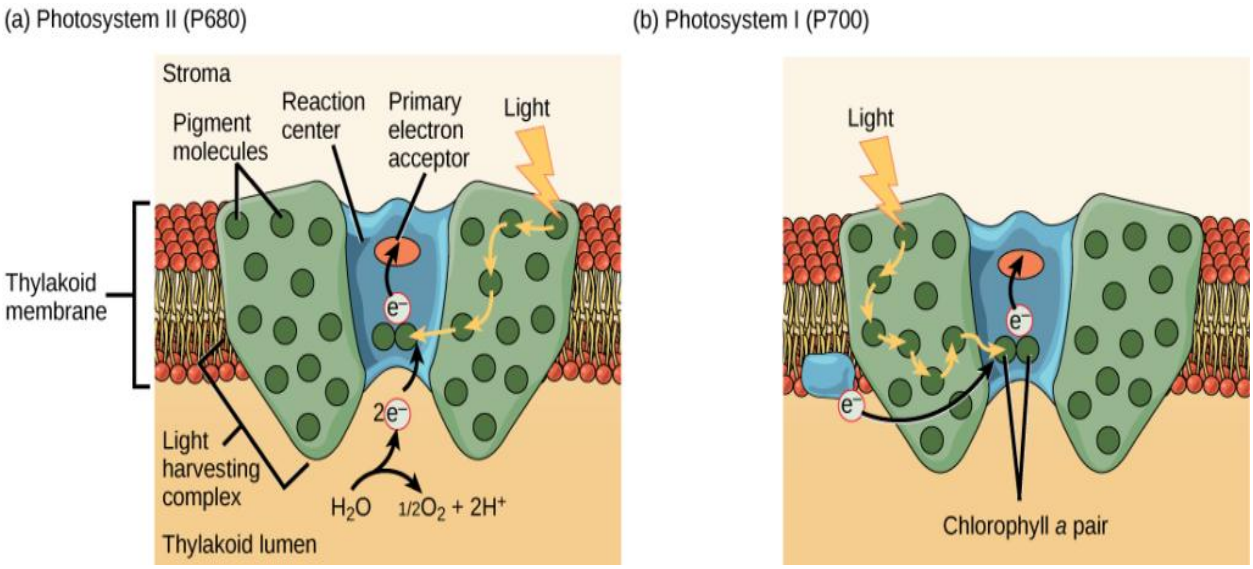
## PHOTOSYSTEM ORGANIZATION




The molecular structure of a single light-harvesting complex shows the polypeptide in brown with three helices that span the thylakoid membrane. Pigment molecules (carotenoids and chlorophylls a and b) are bound to the polypeptide. (B) Light-harvesting complexes are organized into large photosystems that span the thylakoid membrane and have a centrally placed reaction center. The

light-harvesting chlorophylls absorb light and pass the energy on to a chlorophyll in the reaction center.




**The complete photosynthetic reactions in cyanobacteria, algae and higher plants are executed by four major protein supercomplexes :-**

- **PSI,**
- **PSII,**
- **cytochrome b6f (plastoquinone-plastocyanin oxidoreductase) and**
- **F-ATPase (proton-motive force-driven ATP synthase)**

The transfer of electrons and protons in the thylakoid membrane is carried out vectorially by four protein complexes. Water is oxidized and protons are released in the lumen by PSII. PSI reduces NADP+ to NADPH in the stroma, via the action of ferredoxin (Fd) and the flavoprotein ferredoxin–NADP reductase (FNR). Protons are also transported into the lumen by the action of the cytochrome *b*6 *f* complex and contribute to the electrochemical proton gradient. These protons must then diffuse to the ATP synthase enzyme, where their diffusion down the electrochemical potential gradient is used to synthesize ATP in the stroma. Reduced plastoquinone (PQH2) and plastocyanin transfer electrons to cytochrome

*b*6 *f* and to PSI, respectively.Dashed lines represent electron transfer; solid lines represent proton movement.

**Electron and proton transfer in Thylakoid membrane involves:-**

**i) Four membrane-spanning proteins such as**

1. **photosystem II,**
2. **cytochrome *b*6 *f* ,**
3. **photosystem I,**
4. **ATP-Synthase), one protein that is associated to the**

ii) **Two soluble proteins (plastocyanin, ferredoxin)**

**iii) ATP-synthase uses the pH gradient to form an ATP from ADP and inorganic phosphate.**

The general pathway of the electron flow from the primary donor (water) to the final acceptor (NADPH) is known in detail, while much less is known about the cyclic electron flow. It is not clear whether ferredoxin interacts with cytochrome *b6 f* or not. Both PSI and PSII Supercomplexes bind chlorophyll molecules to sense different spectrums and intensities of light. Light harvested by the chlorophylls and other pigments in PSI and PSII is transferred to the photosynthetic reaction center (RC), further inducing the excitation of chlorophylls known as P680 for PSII and P700 for PSI to initiate the proton translocation across the membrane.

On absorbing light, PSII produces a very high oxidizing potential (about +1.2 Volts) sufficient to split water into its elemental constituents. In contrast, PSI produces a very low redox potential (about –1.0 Volts), which provides the energy to reduce NADP+ to NADPH.

- In PSII, P680 undergoes charge separation and the generated electrons are transferred to the quinone acceptor pheophytin and plastoquinone sequentially.
- Meanwhile, water molecule, the authentic electron donor, is oxidized to molecular oxygen and P680 is eventually reduced. After the reaction, the electrons are ultimately transferred to the thylakoid-embedded cytochrome b6f, which oxidizes plastoquinols to plastoquinones and reduces plastocyanins.

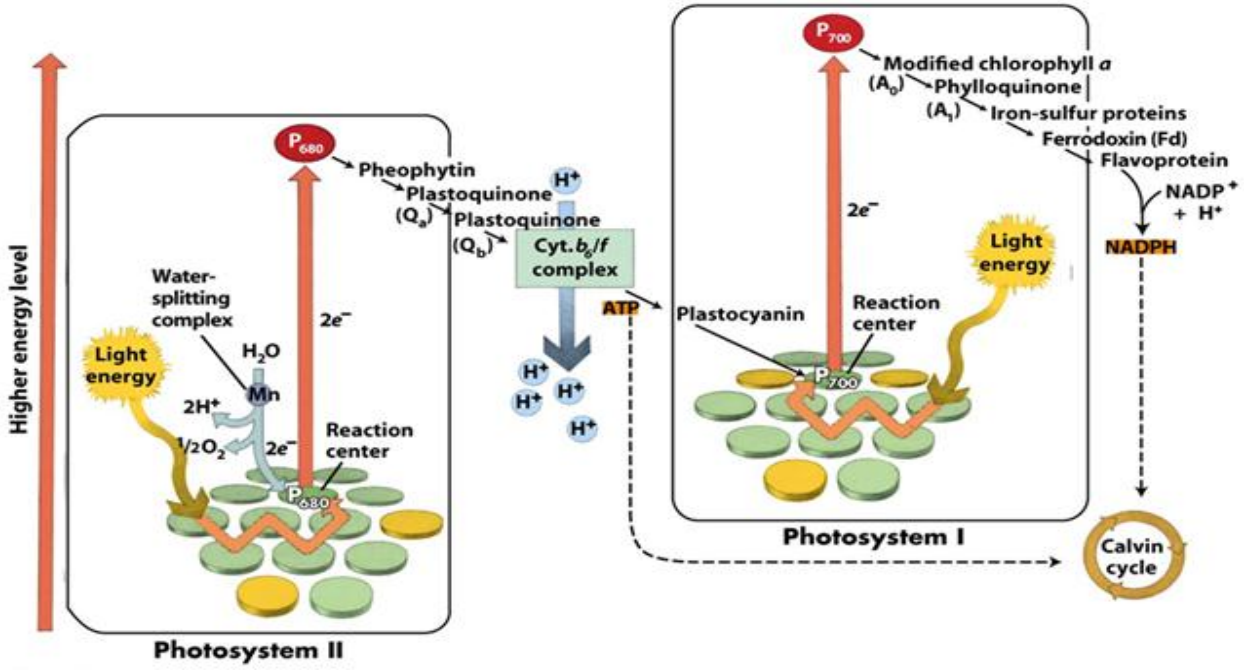
- And then, the plastocyanin is oxidized by PSI, during which the reduced electron carrier protein ferredoxin, is used to reduce NADP to NADPH by ferredoxin–NADP+ reductase (FNR) enzyme.
- Together, PSII generates the most positive redox potential, while PSI generates the powerful naturally occurring reductant NADPH.

The photocatalytic activity of PSII and PSI is linked by the cytochrome b6f complex, and the proton-motive force generated during the process are utilized by the F-ATPase to generate ATP, which together with NADPH are supplied as energy compounds for sugar synthesis from carbon dioxide by the dark reaction.

Photooxidation of water:-

During photosynthesis, water oxidation happens in the oxygen-evolving complex (OEC), which comprises the Mn4CaO5 cluster as the catalytic center. Water splitting is a process fulfilled in five consecutive stages named S0 to S4. It has been a model system for synthesizing catalysts for inorganic water oxidation and dioxygen evolution.

**LIGHT REACTIONS OF OXYGENIC PHOTOSYNTHESIS**




The Z scheme showing the relative energy of molecules in the photosynthetic electron transport of the Light-dependent reactions of Photosynthesis.

A chlorophyll molecule has a heme containing a mg+ (magnesium) atom in the center. It also has a long tail.\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\When light is absorbed by chlorophyll, an electron in the magnesium atom jumps from the ground state to an excited state. This electron is farther away from the center of the atom.

The chlorophyll molecule is right next to another molecule which grabs electrons. When the electron gets far enough away from the center of the atom, this molecule steals the electrons and passes it from molecule to molecule.

The energy of the electron transfer is used to pump hydrogen atoms across the thylakoid membrane.

A high H+ concentration is made in the inner thylakoid space. This high H+ concentration is used to make ATP using the proton channel ATP synthase.

- **There are two chlorophyll reactive centers that absorb chlorophyll at different wavelengths.**
- **One reactive center dumps the electrons on the other, and the second one finally dumps the electrons on the high energy molecule NADP which forms NADPH+H.**
- **NADP is the final electron acceptor in photosynthesis.**
- **The magnesium ion that lost the electron in the chlorophyll atom at the beginning is now a very unhappy ion.**
- **It steals an electron from water to get back to a normal state.**
- **Water breaks apart into hydrogen ions and oxygen gas. This is why plants release oxygen.**
- **Water is the initial electron donor in photosynthesis.**

**PRODUCTION of ATP**

**• The concentration of H+ ions inside the thylakoid membrane becomes much higher than the concentration outside.**

**• H+ ions rush out through membrane protein called ATP synthase.**

**• The ATP synthase spins like a turbine and the energy is used to bind ADP and P together to form ATP.**

PHOTOPHOSPHORYLATION

**Photophosphorylation is the process of utilizing light energy from photosynthesis to convert ADP to ATP.**

**It is the process of synthesizing energy-rich ATP molecules by transferring the phosphate group into ADP molecule in the presence of light.**

**Photophosphorylation is of two types:**

- **Cyclic Photophosphorylation**
- **Non-cyclic Photophosphorylati**

**CYCLIC PHOTOPHOSPHORYLATION:-**

Under certain conditions, the photoexcited electrons take an alternative path called cyclic electron flow which uses photosystem I (P700) but not photosystem II (P680).

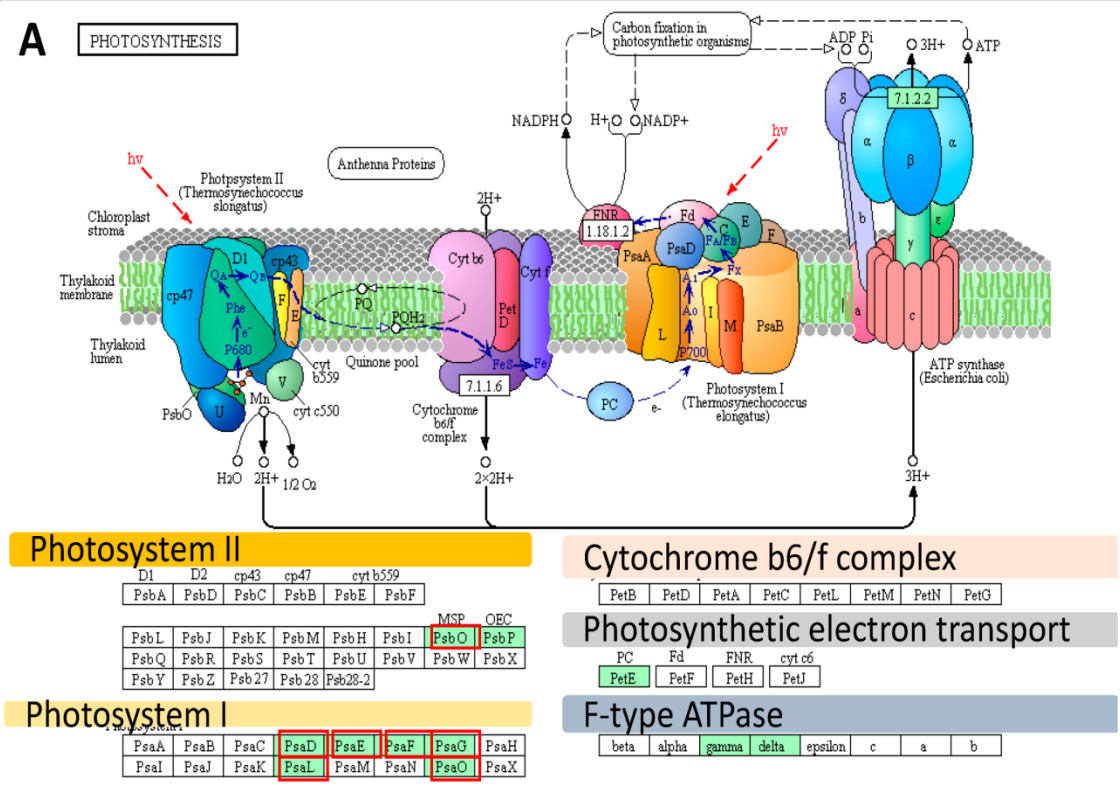
*This process produces no NADPH and no $O_2$, but it does make ATP.*

The chloroplast shifts to this process when the ATP supply drops and the level of NADPH rises. Often the amount of ATP needed to drive the Calvin cycle exceeds what is produced in non-cyclic photophosphorylation. Without sufficient ATP, the Calvin cycle will slow or even stop.

**Comparison of Cyclic Photophosphorylation and Non-cyclic Photophosphorylation.**

| **Cyclic Photophosphorylation** | **Non-Cyclic Photophosphorylation** |
|---|---|
| **Only Photosystem I is involved.** | **Both Photosystem I and II are involved.** |
| **P700 is the active reaction centre.** | **P680 is the active reaction centre.** |
| **Electrons travel in a cyclic manner.** | **Electrons travel in a non – cyclic manner.** |
| **Electrons revert to Photosystem I** | **Electrons from Photosystem I are accepted by NADP.** |
| **ATP molecules are produced.** | **Both NADPH and ATP molecules are produced.** |
| **Water is not required.** | **Photolysis of water is present.** |
| **NADPH is not synthesized.** | **NADPH is synthesized.** |

| Oxygen is not evolved as the by-product | Oxygen is evolved as a by-product. |
|---|---|
| This process is predominant only in bacteria. | This process is predominant in all green plants. |



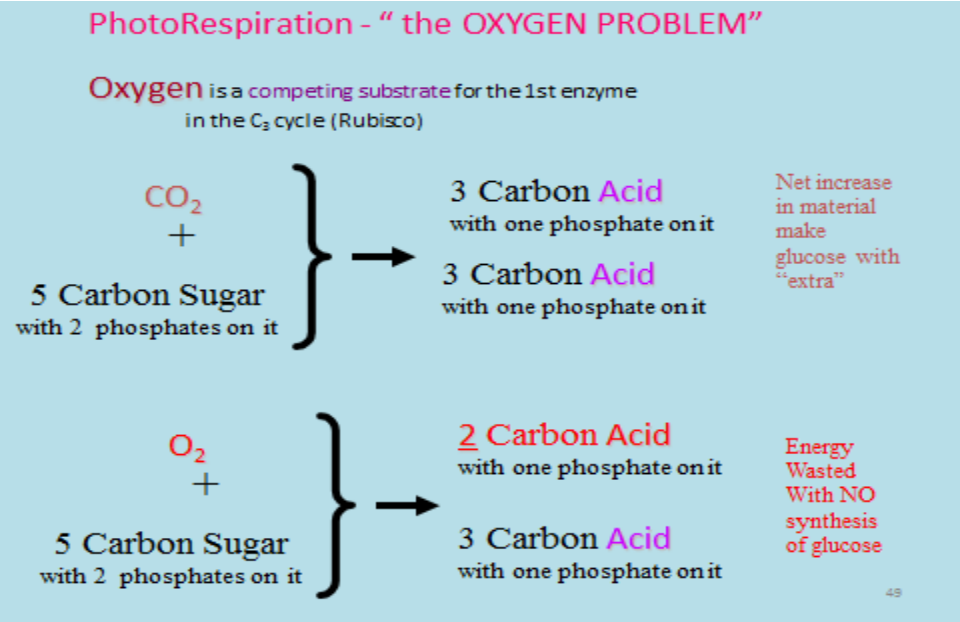

## Rubisco (Ribulose-1,5-bisphosphate carboxylase/oxygenase)

Rubisco, a dual functional enzyme, is found in all the green tissues of the leaves of C3 or Calvin– Benson cycle plants and also in the parenchymatous bundle sheath cells surrounding the vascular tissues of C4 or Hatch and Slack cycle plants. It shows different physiological functions, depending upon the levels of $CO_2$/ $O_2$. At high levels of $CO_2$ ($CO_2$ > $O_2$), the enzyme has carboxylase activity while in high concentrations of oxygen ($O_2$ > $CO_2$) it has oxygenase activity, producing one molecule each of phosphoglyceric acid (3C fragment) and phosphoglycolic acid (2C fragment), evolved during photorespiration in C3 plants.

From this, it is evident that oxygen can replace $CO_2$ as a substrate for the enzyme, i.e., $O_2$is a competitive inhibitor with respect to $CO_2$.

Rubisco, indeed the world's most abundant protein on the earth (~50 per cent of all the protein in the stroma), is present in green tissues of the leaf.

Rubisco has been isolated and purified in crystalline form, from the leaves of several species (Lorimer and Andrews, 1981). It is composed of about 16 pairs of 2 kinds of subunits.



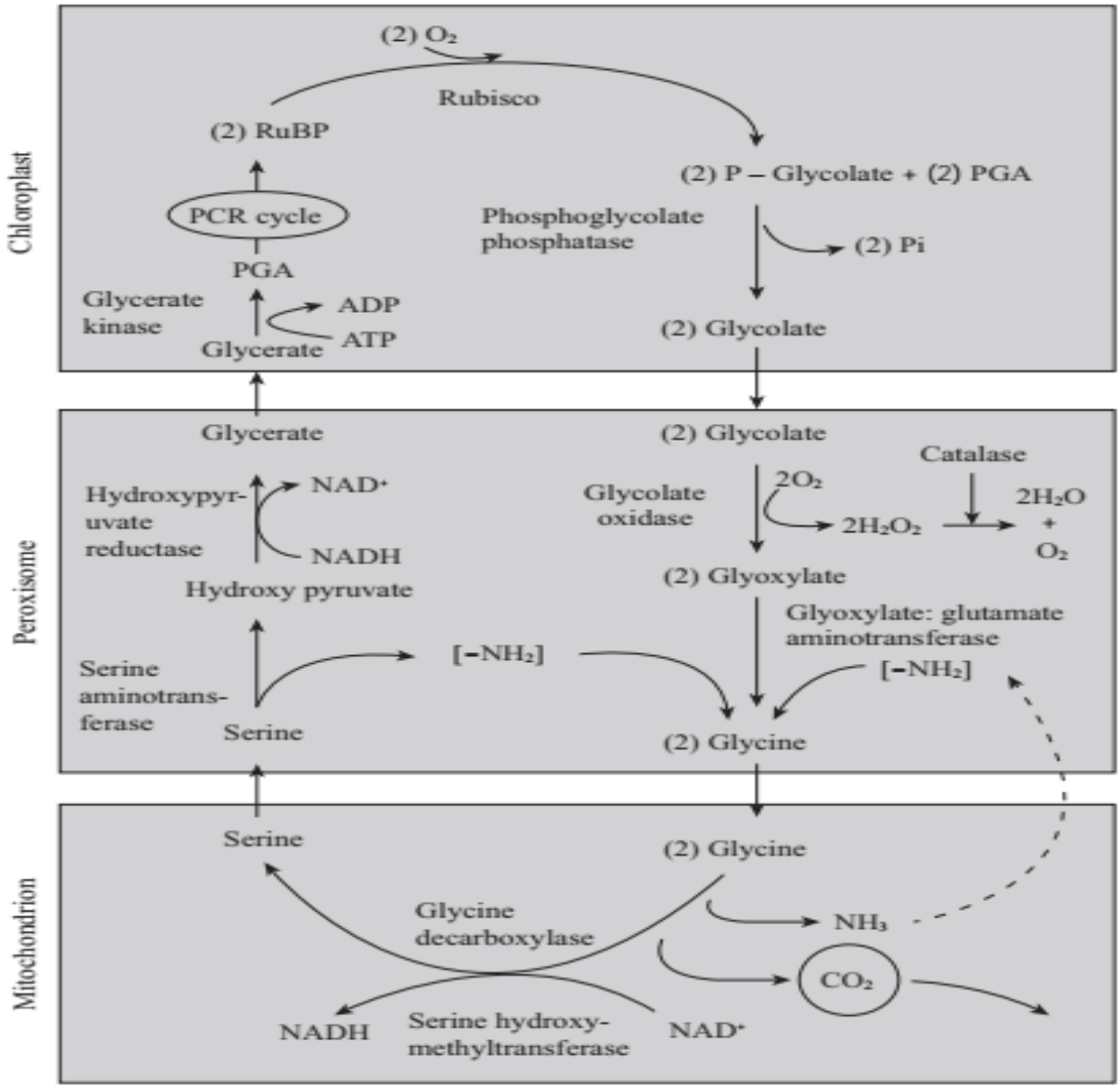

Plants that exhibit Calvin cycle exclusively for $CO_2$fixation also display a competing process of light and oxygen-dependent evolution of $CO_2$ referred to as photorespiration or the PCO cycle (Photosynthetic Carbon Oxidation cycle).

This cycle also starts with Rubisco, which under excess of oxygen concentration (5–21 % and beyond) catalyzes the oxidation as well as carboxylation of RuBP. Thus, O2competes with $CO_2$ for binding at the catalytic site of Rubisco and often splits RuBP into phosphoglycolate (2-C compound) and 3-phosphoglycerate.

The oxygenase activity of Rubisco is very significant because $O_2$ molecules in nature are many times more than $CO_2$. Photosynthesis can result in accumulation of even higher concentration of $O_2$ inside the leaf than is found in the atmosphere. Phosphoglycolate is transported from the chloroplast and oxidized through a sequence of reactions within peroxisomes to form glycine. Glycine next moves to the mitochondrion where through a complicated reaction, the enzyme glycine decarboxylase, with its cofactor tetrahydrofolate (THF), catalyzes the NAD–dependent oxidative conversion of a molecule of glycine to one each of $CO_2$, NH3

and CH2-THF (methylene tetrahydrofolate). Glycine decarboxylase complex has four enzyme subunits, and pyridoxal phosphate, FAD and lipoamide cofactors, in addition to THF. Reaction of CH2 – THF with a second glycine molecule, catalyzed by serine hydroxymethyltransferase, regenerates THF and produces serine which goes back to the peroxisome.

Ammonia, a product of glycine decarboxylation in the mitochondria is efficiently reassimilated in the chloroplast via glutamine synthetase – glutamate α-ketoglutarate aminotransferase (GS-OGAT) pathway through a series of reactions.




Photorespiratory glycolate pathway or C2 pathway or photosynthetic carbon oxidation (PCO) pathway

**Significance of photorespiration**

As much as 30 per cent of the photosynthetically fixed carbon may be lost (recycled to $CO_2$) through the glycolate pathway of photorespiration, and it contributes directly to a reduction in dry matter accumulation and ultimately in yield. The energy that was expended to fix it ($CO_2$) is thus wasted. However, it may be wrong to assume that photorespiration is an entirely wasteful process.

The useful function of photorespiration is that it plays a necessary role in themetabolism or intraorganellar transport of nitrogen compounds by virtue of glycolate–glycine–serine transformation. Amino acids, glycine and serine serve as precursors for many important metabolites such as proteins, chlorophylls, nucleotides, and so on.

Moreover, 020xxin volved in dissipating excess reducing power of too much (NADPH) generated in the light reactions of photosynthesis. Returning to the evolutionary significance, it may be stated that eon's ago there was no $O_2$ in the earth's atmosphere, so there was no production of phosphoglycolate by RuBP carboxylase.

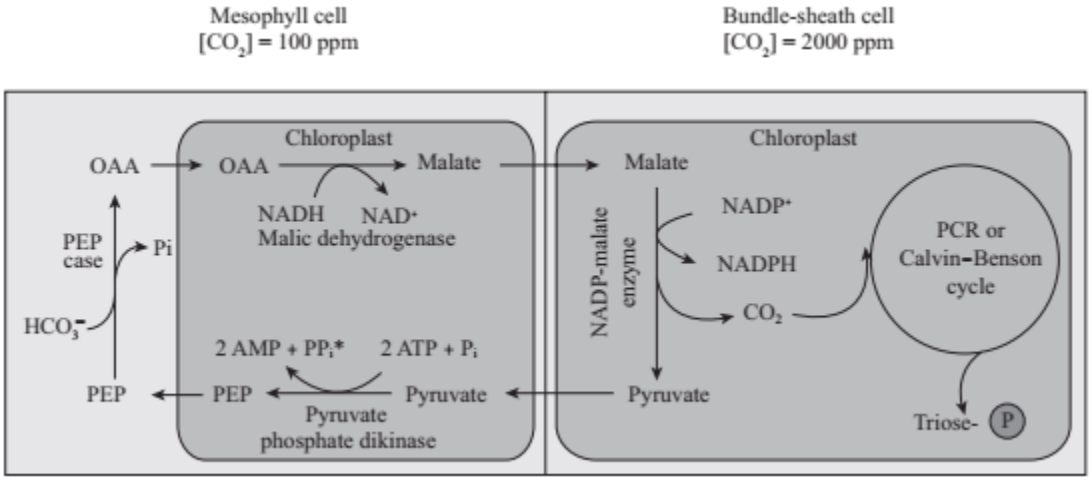
As oxygen, produced by photosynthesis, accumulated in the atmosphere, the RuBP carboxylase started exhibiting 'oxygenase' activity and thus the process of photorespiration began.

## Hatch–Slack Pathway

C4 plants exhibit 'Kranz' (from the German, 'Wreath like') anatomy. Each vascular bundle in the leaves is covered by a layer of large, prominent parenchymatous cells – chlorophyllous parenchymatous cells known as **bundle sheath cells**. C4 plants exhibit 'Kranz' (from the German, 'Wreath like') anatomy. Each vascular bundle in the leaves is covered by a layer of large, prominent parenchymatous cells – chlorophyllous parenchymatous cells known as bundle sheath cells, which in turn are surrounded by loosely organized spongy, undifferentiated mesophyll cells. Cells of the leaves of C4 plants possess dimorphic chloroplasts, mesophyll chloroplasts and bundle sheath chloroplasts.

These in turn are surrounded by loosely organized spongy, undifferentiated esophyll cells. Cells of the leaves of C4 plants possess dimorphic chloroplasts, mesophyll chloroplasts and bundle sheath chloroplasts.

C4 plants capture $CO_2$ through phosphoenolpyruvate carboxylase (PEP carboxylase or PEPcase). Upon entry into the mesophyll cells, $CO_2$ is hydrated to bicarbonate ions (HCO 3–) in a step catalyzed by carbonic anhydrase. $CO^2$ accepted by PEP is converted into a 4-carbon compound, oxaloacetic acid (OAA), which is immediately reduced to malic acid, using NADH. An interesting point about this process is that it is not completely independent of the Calvin cycle. Malic acid is carried to the bundle sheath cell by a transport protein that spans the membranes of the two adjacently placed cells, through a plasmodesmata. There it readily releases $CO_2$ to be refixed immediately by Rubisco via the Calvin cycle and gets oxidized to pyruvate, which is carried back to the mesophyll cell, through plasmodesmata. Pyruvate receives a phosphate group from ATP, thereby regenerating phosphoenolpyruvate (PEP). The C4 cycle has, therefore, to be viewed not as an independent cycle, but as an adjunct to the Calvin cycle. Nonetheless, C4 plants do not fix $CO_2$ by both C3 and C4 pathways in 'any one cell', rather, there is a 'spatial separation' (separated in space).




C4 Pathway or Hatch–Slack Pathway

Another interesting aspect is that PEP carboxylase has a much greater affinity for $CO_2$ and can fix $CO_2$ at extremely low $CO_2$ levels (<10 ppm) as compared to Rubisco, which can reduce $CO_2$ at much higher CO2 levels (50 ppm or above). It shows no obvious inhibition by O2 with the net result that $CO_2$ initially captured

over a large volume of leaf space is released into the relatively small volume of the bundle sheath. Consequently, the local $CO_2$ concentration in these cells is very high and refixed by Rubisco into the Calvin cycle. However, ATP is required to convert pyruvate to phosphoenolpyruvate (PEP) and perhaps also for the transport of organic acids to and from the mesophyll cells.

$$\text{Pyruvate} + \text{Pi} + \text{ATP} \xrightarrow[\text{(mesophyll cells)}]{\text{Pyruvate phosphate dikinase}} \text{PEP} + \text{AMP} + \text{PPi}$$

The location of bundle sheath cells close to vascular tissues also enables them to pass their final product of photosynthesis, i.e. sucrose, directly into the sieve tubes of phloem tissue for movement to other parts of the plant. Significance of C4 photosynthesis appears to be its mechanism to reduce photorespiration and maximize $CO_2$ assimilation.

Overall, the C4 cycle is an adaptive feature to enable plants to survive better under environments of higher temperatures, intense solar radiation and moisture stress (as water is not the reactant in $CO_2$ assimilation in mesophyll cells).

| **C3 Plant**<br>**C3 Plants (Calvin cycle)**<br><br>**s (Calvin cycle)** | **C4**<br>**C4 Plants (Hatch and Slack cycle)**<br><br>**Plants (Hatch and Slack cycle)** |
|---|---|
| 1. Calvin cycle is present in all the green cells of the leaf. | Hatch–Slack cycle is present in the mesophyll cells while C3cycle is restricted to the bundle sheath cells. |
| 2. Ribulose 1,5-bisphosphate is the initial carbon dioxide ($CO_2$) acceptor. | Two $CO_2$ acceptors are present– phos phoenolpyruvate in the mesophyll cells and RuBP in the bundle sheath cells. |
| 3. The first stable compound is a 3-carbon compound, i.e., phosphoglyceric acid. | The first stable product is a 4-carbon compound, i.e., oxaloacetic acid/malic acid. |
| 4. The leaves don't have 'Kranz anatomy'. The chloroplasts in the green cells are of one type. They are small with well-defined grana and have both, photosystems I and II. | The leaves have 'Kranz anatomy' (kranz = wreath, a German word). The vascular tissue is covered by a ring of large parenchyma cells – the bundle sheath. The chloroplasts are dimorphic. The cells of mesophyll have chloroplasts similar to those of C3 plants, accumulating very little starch while the chloroplasts of bundle-sheath (BS) cells are large and agranal and contain large starch grains. They are centripetally arranged and lack PS II, and therefore dependent on the chloroplasts of the mesophyll for the supply of NADPH. |
| 5. RuBP and other enzymes of the C3 pathway are found in the mesophyll cells. | RuBP and other enzymes of C3 pathway are present in the BS whereas the mesophyll cells contain the enzymes of C4 cycle. |

| | |
|---|---|
| 6. The optimum temperature range is between 10 and 25 °C. | The temperature optima for C4 species is much higher than those for C3 plants. The optimum temperature range is between 30 and 45°C. |
| 7. Because of lesser affinity of RuBP for $CO_2$, they best operate at high CO2 levels, i.e., 50 ppm. | PEP carboxylase has strong affinity for $CO_2$, which is why it can capture $CO_2$ at low concentration, i.e., 10 ppm or even lower. |
| 8. Photorespiration is present that further reduces the photosynthetic yield. C3 plants are thus less efficient photosynthetically and have low productivity. | Photorespiration is absent, which is way C4 plants are photosynthetically efficient showing high productivity as they waste none of their photosynthetically fixed $CO_2$. |

| | |
|---|---|
| 9. Oxygen has an inhibitory effect on photosynthesis. | Oxygen does not have any inhibitory effect. |
| 10. In the C3 cycle, 18 ATP are needed for the production of one glucose molecule,. | In the C4 cycle, 30 ATP are used up for producing one glucose molecule. |
| Examples are pulses, most of the cereals, oil seeds, temperate and tropical tree species. | Examples are sugarcane, maize, sorghum, grain amaranth. |

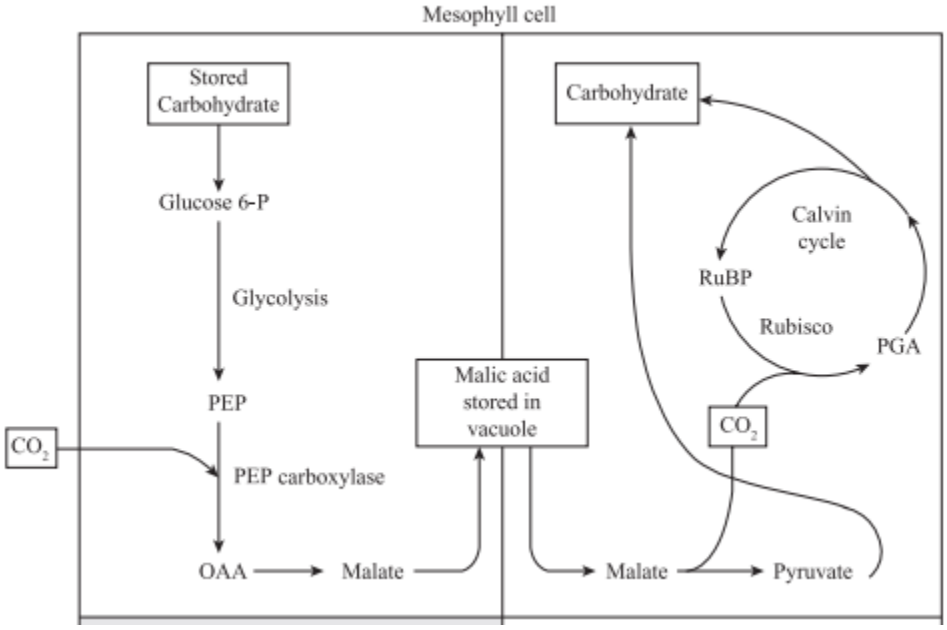
**CAM Pathway (Crassulacean Acid Metabolism)**

The dark uptake of CO2 by succulents was observed as early as 1810 by De Saussure while studying a cactus. In 1815, Heyne noted that the succulent Bryophyllum accumulated organic acids at night. In the 1960s, there was renewed interest in Crassulacean acid metabolism because of the similarity of carbon metabolism between C4 species and CAM species and the realization that CAM was an adaptive modification of basic photosynthetic metabolism. CAM pathway was named so, after the angiospermic family Crassulaceae in which it was first reported. CAM has been found in hundreds of species in 26 angiosperm families including the Cactaceae, Liliaceae, a few succulent members of Euphorbiaceae, epiphytic species of Orchidaceae and Bromeliaceae, non-epiphytic bromeliads (e.g.pineapple), in some pteridophytes and in a gymnosperm, Welwitschia mirabilis.

CAM is also a means of maintaining higher photosynthetic rates in high water-stressed environments. CAM plants exhibit an inverted stomatal cycle – open at night for $CO_2$ uptake, when moisture deficit is less and close during the day time, when moisture stress is more. $CO_2$ is stored overnight as organic acids (malate) in the vacuolar sap, again through the action of PEP carboxylase. Decarboxylation of malate to pyruvate during the day provides the required $CO_2$ for photosynthesis.

Both carboxylation and decarboxylation occur in same cells, i.e., mesophyll cells but there is temporal separation (separated in time) of the two reactions. In CAM plants, closed cycle of carbon intermediates does not exist as there is in C4 plants. Thus CAM is cyclic in time only.

Although the ability of a plant to perform CAM is genetically determined, it is also environmentally controlled. In general, CAM is favoured by hot days with high irradiance levels, cool nights, dry soils, and high salt concentrations.




Crassulacean acid metabolism (CAM) in the light and dark.

**Inorganic carbon concentrating mechanisms; RUBI**SCO **and PEP**

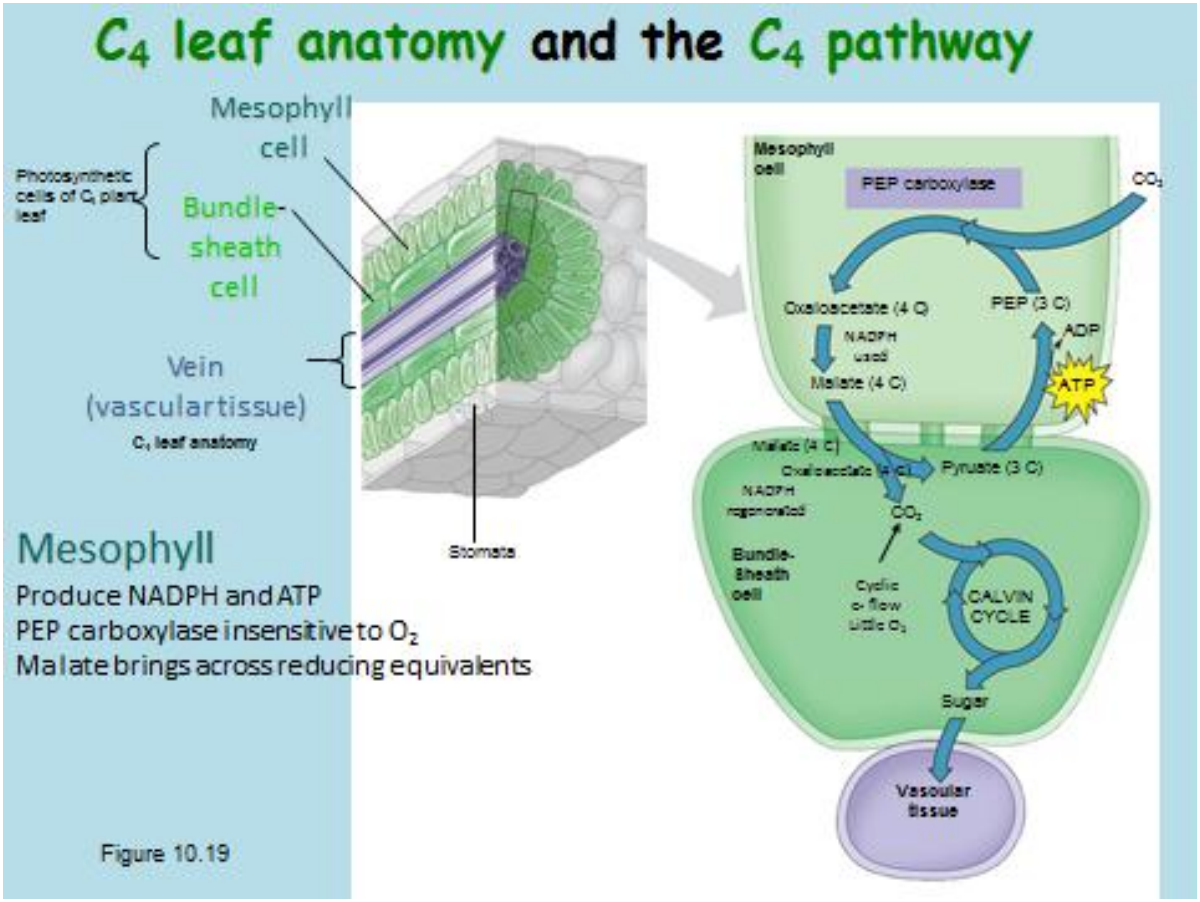
Mechanisms for concentrating carbon around the Rubisco enzyme, which drives the carbon-reducing steps in photosynthesis, are widespread in plants; in vascular plants they are known as crassulacean acid metabolism (CAM) and C4 photosynthesis. CAM is common in desert succulents, tropical epiphytes, and aquatic plants and is characterized by nighttime fixation of $CO_2$. The proximal selective factor driving the evolution of this $CO_2$-concentrating pathway is low daytime $CO_2$, which results from the unusual reverse stomatal behavior of terrestrial CAM species or from patterns of ambient $CO_2$ availability for aquatic CAM species.

Inorganic carbon concentrating mechanisms (CCMs) catalyse the accumulation of $CO_2$ around rubisco in all cyanobacteria, most algae and aquatic plants and in C4

and crassulacean acid metabolism (CAM) vascular plants. CCMs are polyphyletic (more than one evolutionary origin) and involve active transport of Inline Formula, $CO_2$ and/or H+, or an energized biochemical mechanism as in C4 and CAM plants. While the CCM in almost all C4 plants and many CAM plants is constitutive, many CCMs show acclimatory responses to variations in the supply of not only $CO_2$ but also photosynthetically active radiation, nitrogen, phosphorus and iron. The evolution of CCMs is generally considered in the context of decreased $CO_2$ availability, with only a secondary role for increasing $O_2$. However, the earliest CCMs may have evolved in oxygenic cyanobacteria before the atmosphere became oxygenated in stromatolites with diffusion barriers around the cells related to UV screening. This would decrease $CO_2$ availability to cells and increase the $O_2$ concentration within them, inhibiting rubisco and generating reactive oxygen species, including $O_3$.

C4 photosynthesis is based on similar biochemistry but carboxylation steps are spatially separated in the leaf rather than temporally as in CAM. This biochemical pathway is most commonly associated with a specialized leaf anatomy known as Kranz anatomy; however, there are exceptions. The ultimate selective factor driving the evolution of this pathway is excessively high photorespiration that inhibits normal C3 photosynthesis under high light and high temperature in both terrestrial and aquatic habitats. CAM is an ancient pathway that likely has been present since the Paleozoic era in aquatic species from shallow-water palustrine habitats. Molecular phylogenies indicate C4 is a more recent innovation than CAM and that it originated in the mid-Tertiary, 20–30 Ma, although some data support an earlier origin.

A largely unexplored hypothesis is that climatic changes in late Miocene altered disturbance regimes, in particular the incidence of fires, which today are often associated with maintenance of C4 grasslandsCAM and C4 evolution required coupling of biochemical pathways with structural changes in photosynthetic tissues, succulence in CAM and Kranz in C4. Equally important is the fact that the selective environments are quite different, with CAM evolution thriving on stressful sites inhospitable to C3 species whereas C4 evolution has selected for rapid growth capable of outcompeting associated C3 plants.




Reference: - Plant Physiology: Theory and Applications by S. L. Kochhar and Sukhbir Kaur Gujral, Cambridge CB2 8BS, UK (2020).