Photosynthesis

- Photosynthesis is the synthesis of carbohydrate from sunlight, water and CO₂ by the green plants. It is an endergonic and anabolic process. Bacteria shows anoxygenic photosynthesis as they do not use water and do not evolve oxygen. Cyanobacteria (blue green algae) evolved oxygen first time in evolution as they show oxygenic photosynthesis.

HISTORY

1648. Van Helmont. He found that in five years as a willow plant increased its weight to 33 times, the soil lost only 56.7 gm of matter. Van Helmont, therefore, thought that vegetation is only water.

1772. Joseph Priestley. Foul air or phlogiston produced during burning of candles or animal (mice) respiration could be converted into pure air or phlogiston by plants (mint).

1779. Jan Ingenhousz. Purification of air or formation of phlogiston is carried out by green plants only in the presence of sunlight.


1888. Englemann. Discovered the effect of different wavelengths of light on photosynthesis and plotted the action spectrum.

1905. Blackmann. Propounded the ‘law’ or principle of limiting factors. He also proposed the occurrence of a dark phase in photosynthesis.

1920. Warburg. First employed Chlorella, an unicellular nonmotile green alga, for study of photosynthesis. He studied the effect of high O₂ concentration, poisons like cyanide and light flashes on photosynthesis.

1939. Robin Hill. Demonstrated photosynthesis (light reaction) by isolated chloroplast in presence suitable electron acceptor.

1941. Ruben, Kamen and Hassid. Used heavy isotope ¹⁸O and proved that in photosynthesis, oxygen comes from water.

1954. Arnon et. al. Discovered photophosphorylation. Also showed fixation of CO₂ by previously illuminated isolated chloroplasts by using radioactive carbon ¹⁴C in their carbon dioxide.

1957. Emerson. Found red drop and photosynthetic enhancement or Emerson effect.

1985. Huber, Michel and Deisenhofer. Crystallised the photosynthetic reaction centre from purple bacterium Rhodopseudomonas viridis. In 1988 they were awarded the Nobel Prize in Chemistry.

RAW MATERIALS

1. Carbon Dioxide. In land plants, carbon dioxide is obtained from the atmosphere through the stomata. Hydrophytes get their carbon dioxide supply from the aquatic environment as bicarbonates. Bicarbonates are absorbed by the hydrophytes through their general surface.

2. Water. Van Niel (1931), while working on a type of photosynthetic bacteria, found that they required hydrogen sulphide for their carbon fixation. There was no evolution of oxygen. Obviously in these photosynthetic bacteria carbon dioxide did not split up as there was no evolution of oxygen.

\[
6\text{CO}_2 + 12\text{H}_2\text{S} \rightarrow \text{C}_6\text{H}_{12}\text{O}_6 + 6\text{H}_2\text{O} + 12\text{S}
\]

He also propounded that oxygen is evolved from water.

3. Light. Light is the visible part of electromagnetic radiations. Electromagnetic spectrum consists of 8 types of radiations – cosmic rays, gamma rays, X-rays, ultra-violet radiations, light spectrum, infra-red rays, and radio waves. Visible light consists of radiations having a wavelength 390–760 nm (or 3900 – 7600 Å). Photosynthetically Active Radiation (PAR) is 400 – 700 nm...
Photosynthesis

Longer than those of red are called infra-red. They have wave length of more than 760 nm. Sunlight or solar radiations reaching the earth have wavelength between 300 nm (in the ultraviolet range) to 2600 nm (in the infra-red range).

**Chloroplasts (Chloroplasts)**

Chloroplasts were first observed by N. Grew (1682) but were studied by Dutrochet (1837), Sachs, Mayer and then by Schimper.

**Chemical Composition : Proteins, 50-60%, Lipids, 20 – 30%, Chlorophylls, 5 – 10%, Carotenoids, 1 – 2%, RNA 2 – 3%, DNA. 0.5%, Quinones, Vitamin K, Vitamin E, Traces. Minerals (Fe, Mg, Mn, P, Co, Cl, Cu). Traces. Chloroplast is surrounded by a double membrane envelope. Internally it has matrix and thylakoids.

- **Matrix or Stroma.** It is a protein colloidal complex that fills the interior of the chloroplast. In the matrix are embedded a number of granules, enzymes, DNA, mRNA, tRNA, rRNA, ribosomes. Ribosomes are 70S type. Thylakoids are structural and functional elements of chloroplasts which are embedded throughout the matrix or stroma. Each thylakoid is a flattened sac lined by a membrane specialised in harvesting light energy. Thylakoid membranes are about 7 nm thick while the lumen can be 5 - 70 nm in width. In Red Algae, thylakoids occur singly. In green algae, thylakoids occur in groups of 2-20. The grouped thylakoids are called lamellae. Grana are closely packed stacks of disc-shaped thylakoids. 40 - 100 grana are found in chloroplast. Thylakoids present in a granum are called granal thylakoids. Grana are connected to one another by means of stroma thylakoid or intergranal lamellae or frets.

Thylakoid membranes possess chlorophylls, carotenoids, cytochromes, quinones, ATP-synthetase, etc.

- **Photosystem I** The pigment system (light harvesting system) is more abundant in membranes of stroma thylakoids and non-appressed parts of granal thylakoids.

- **Photosystem II** The pigment system is more abundant in the appressed parts of granal thylakoids.

- **ATP-Synthetase** It is more commonly present in non-appressed membranes of granal thylakoids and in stroma thylakoids.

**Photosynthetic Pigments**

Chloroplasts have two types of photosynthetic pigments, chlorophylls and carotenoids. Bacteria possess bacteriochlorophylls instead of chlorophylls. Phycobilins occur in some algae.

- **Chlorophyll a:** The chlorophyll a has molecular formula as $\text{C}_{55}\text{H}_{72}\text{O}_{5}\text{N}_{4}\text{Mg}$ and the molecular weight is 893. The molecule is distinguishable into a 'head' of size 15 x 15 A and a 'tail' of 20 A length. The 'head' is made up of porphyrin, a tetrapyrrole closed ring derivative and the 'tail' of phytol ($\text{C}_{20}\text{H}_{39}\text{OH}$). There is a 5th isocyclic ring of cyclopentanone. A non-ionic magnesium atom is held within tetrapyrrole ring by two covalent and two co-ordinate bonds. The chlorophyll a absorbs blue, yellow and red wavelengths of the spectrum.

- **Chlorophyll b:** Its molecular formula is $\text{C}_{55}\text{H}_{72}\text{O}_{5}\text{N}_{4}\text{Mg}$ and the molecular weight is 907. It is similar to chlorophyll a except in having a formyl (CHO) group instead of methyl (CH$_3$) at carbon-3 position of the second pyrrole ring. It absorbs blue and red wavelengths.

- **Chlorophyll c:** Its molecular formula is probably $\text{C}_{35}\text{H}_{42}\text{O}_{4}\text{N}_{4}\text{Mg}$ and the molecular weight is 712. It is found in brown algae, diatoms and also in Pyrrophyta and Cryptophyta.

- **Chlorophyll d:** Its molecular formula is $\text{C}_{54}\text{H}_{70}\text{O}_{4}\text{N}_{4}\text{Mg}$ the molecular weight is 895. It absorbs blue, yellow and red wavelengths of light. It is reported in red algae.

- **Chlorophyll e:** The molecular formula and structure of this chlorophyll is not known. It has been reported from Xanthophyta.

- **Carotenoids:** The carotenoids are unsaturated polyhydrocarbons. Light is not necessary for their biosynthesis. The carotenoid pigments include two classes of compounds namely carotenes and xanthophylls.

(i) **Carotenes:** Since they were first isolated from the roots of carrot by Wakenroder, hence the name carotene. These are orange coloured pigments having empirical formula as $\text{C}_{40}\text{H}_{56}$ and molecular weight, 536. They are found in all groups of plants i.e., from algae to Angiosperms. The β-carotene on hydrolysis produce vitamin A hence the carotenes are also called provitamin A.

\[
\text{C}_{40}\text{H}_{56} + 2\text{H}_2\text{O} \xrightarrow{\text{Carotene}} 2\text{C}_{20}\text{H}_{20}\text{OH} \ (\text{Vitamin A})
\]
(ii) Xanthophylls: They are yellow coloured carotenoid also called xanthins or carotenols. These are oxygen containing carotenoids and are more abundant in nature. The ratio of xanthophyll to carotene in nature is 2:1 in young leaves. The most common xanthophyll in green plants is lutein \((C_{40}H_{56}O_2)\). In brown algae the brown pigment is fucoxanthin.

- Phycobilins (biliprotein): The phycobilins or more appropriately called phycobiliproteins comprise a bile pigment or phycocyanin attached to a protein. The bile pigment shows an open chain tetrapyrrole structure. Three classes of biliproteins are recognised namely the phycocerythrin (red) phycocyanin (blue) and allophycocyanin (light blue). They are mainly found in red \((Rhodophyceae)\) and blue-green \((Cyanophyceae)\) algae.

- Emerson Effect. While studying the effect of monochromatic light of different wavelengths on photosynthesis in \(Chlorella\). Emerson (1957) found a sharp fall in quantum yield at wavelength more than 680 nm. The reduction in the rate of photosynthesis in monochromatic light of more than 680 nm is called red drop. The two types of monochromatic beams (Red light of wavelength shorter than 680 nm and red light more than 680 nm) were then applied simultaneously or in quick succession. The rate of photosynthesis was found to be quite high as compared to the sum of the rates of photosynthesis obtained with single beams. This is called Enhancement Effect.

- Photosynthetic Units. They are groups of pigment molecules which take part in photoconversion or change of light energy into chemical energy. Each photosynthetic unit has a reaction centre of special chlorophyll a molecule which absorbs long wave light energy. It is surrounded by a number of light harvesting pigment molecules. Harvesting pigment molecules are of two types, antenna and core molecules. (i) Antenna Molecules. They are pigment molecules that occur on the side of photosynthetic unit. Antenna molecules absorb photons of different wavelengths. They get excited. Energy is transferred to core molecules by electron spin resonance. (ii) Core Molecules are pigment molecules which lie around the trap centre. They take part in both direct light harvesting as well as transfer of energy from the antenna molecules. The energy gained by core molecules is passed on to reaction or trap centre. With the gain of energy, the reaction centre extrudes an electron.

**Pigment Systems or Photosystems**

Photosynthetic units occur in the form of two distinct groups called photosystems or pigment systems. Green plants and cyanobacteria possess two photosystems, I and II. But bacteria possess only one photosystem.

**Photosystem I (PS I)**. It is a photosynthetic pigment system along with some electron carriers that is located on both the non appressed parti of grana thylakoids as well as stroma thylakoids. PS I has more of chlorophyll a. Chlorophrill b and carotenoids are comparatively less. Its photocentre has a special chlorophyll a molecule called \(P_{700}\) \((P_{703})\). It is surrounded by other chlorophyll a molecules, followed by chlorophyll b and carotenoids. Photosystem I has FeS, ferredoxin, plastoquinone, cytochrome complex and plastocyanin. It takes part in both cyclic and non-cyclic photophosphorylation. PSI can carry on cyclic photophosphorylation independently. Normally it drives an electron from photosystem II to NADP⁺.

**Photosystem II (PS II)**. It is a photosynthetic pigment system along with some electron carriers that is located in the appressed part of the grana thylakoids. PS II has chlorophyll a, b and carotenoids. Chl a and chl b contents are almost equal. Carotenoid content is higher as compared to that of PS I. The photocentre is a special chlorophyll a molecule called \(P_{680}\) \((P_{683})\). It is surrounded by other chlorophyll a molecules, chlorophyll b molecules. PS II also contains Mn²⁺, Cl⁻, quencher molecule Q, plastoquinone (PQ), cytochrome complex and plastocyanin. It picks up electron released during photolysis of water. The same is extruded on absorption of light energy. As the extruded electron passes over cytochrome complex, sufficient energy is released to take part in the synthesis of ATP from ADP and inorganic phosphate. This photophosphorylation is non-cyclic. PS II can operate only in conjunction with PS I.

**Quantum Requirement and Quantum Yield**

The rate or yield of photosynthesis is measured as number of oxygen molecules produced per quantum of light absorbed. This is called quantum yield.

The number of photons or quanta required to release one molecule of oxygen in photosynthesis is called quantum requirement.

Emerson showed that reduction of one molecule of \(CO_2\) to carbohydrates and liberation of one molecule of oxygen required a minimum of 8 quanta of light. Thus quantum requirement of photosynthesis is 8 and quantum yield is 1/8 or 12.5%.
**Absorption Spectrum**

Graphic representation of degree and portions of light wavelengths absorbed by a substance is called absorption spectrum. Recording of wavelengths of light absorbed by a substance is made with the help of an instrument called spectrophotometer. In an absorption spectrum the height of curve at a given wavelength gives the relative absorbance at that wavelength. Absorption spectra of chlorophylls \( a \) and \( b \) show that the two pigments absorb maximum in blue-violet and red parts of light. It has been found that chlorophyll \( a \) has several forms which show maximum absorbance in red region at different wavelengths like 660–670, 670–680, 690–700, etc.

**Action Spectrum**

It is a graph that depicts the effectiveness of light of various wavelengths in performing a particular function. The first action spectrum of photosynthesis was studied by T.W. Engelmann (1882) using green alga *Spirogyra* and aerobic bacteria. Engelmann employed a prism to break sunlight into rainbow of different colours that fell over the aquatic alga. Oxygen seeking bacteria were found to accumulate around regions of alga according to the amount of photosynthesis performed and oxygen evolved. They were regions which received blue and red lights.

**Fluorescence**

It is almost instant re-radiation of light energy by a substance after having absorbed the same. Fluorescence stops immediately after the withdrawal or source of illumination. All types of photosynthetic pigments are fluorescent. However, most of the fluorescence produced by green parts are due to chlorophyll \( a \) as all other pigments hand over absorbed energy to it through resonance. On absorption of light energy, a fluorescent substance gets excited. In the excited state an outer electron moves to a higher orbital. It is called excited singlet state. Liberation of unutilised absorbed energy is called fluorescence. Chlorophyll emits red fluorescence though it absorbs both blue and red wavelengths of light. It has two peaks, one in the red region below 700 nm and the other in the far-red above 720 nm. The out burst of fluorescence on initial few seconds of illumination is called as Kutinsky effect.

**Phosphorescence**

Fluorescence is almost immediate. If whole of absorbed energy is not lost in fluorescence, the excited molecule loses a small amount of energy and comes to lie in triplet excited state. Afterwards it loses the remaining energy and comes to ground state. The delayed re-radiation of absorbed energy is called phosphorescence.

**The Light Reaction (Hill Reaction)**

In the light reaction of photosynthesis, two important products are formed, NADPH\(_1\) (properly expressed as NADPH + H\(^+\)) and ATP. Besides, there is evolution of oxygen as a by-product. There is experimental evidence to prove it.

**Experiments with isolated chloroplasts:** Hill (1937-39) conducted an experiment with isolated chloroplasts from *Stellaria media* and used some oxidants like ferricyanides and benzoquinone (Hill reagents). By placing them in sun light, he notice evolution of oxygen from water. Hill, therefore, concluded that if there was hydrogen acceptor in the medium, it would have been reduced. Arnon, (1951-1954) repeated the experiment with isolated chloroplasts and concluded that:

(i) The hydrogen acceptor present in plants is NADP (Nicotinamide Adenine Dinucleotide Phosphate), earlier called as TPN (Triphospho Pyridine Nucleotide), also called as Co II (Coenzyme II). It is reduced to NADPH\(_2\).

(ii) An ADP molecule is converted to ATP in light by utilizing inorganic phosphate. This phenomenon is called photophosphorylation.

\[ ADP + {\text{i}}PO_4 \xrightarrow{\text{Photophosphorylation}} ATP \]

*Arnon, 1959,* observed that isolated chloroplasts are capable of fixing CO\(_2\) resulting in the formation of carbohydrates. He suggested that the light reaction occurs in the granum of the chloroplast and the dark reaction in stroma.

**Photophosphorylation**

It is formation of ATP from ADP and inorganic phosphate with the help of solar energy. It was discovered by Arnon *et al.* It is of two types, cyclic and non-cyclic.
Cyclic photophosphorylation
Here electron extruded by the reaction centre of photosystem I (P_{700}), returns back to reaction centre after passing over a number of electron carriers. It is performed by photosystem I independently. After gaining photon energy, the electron is extruded from the reaction centre. It is picked up by FeS and then passes over to ferredoxin (Fd), cytochrome b_{6}, cytochrome f. From Cyt. f electron moves to plastocyanin from where it becomes available to P_{700} again.

- Noncyclic Photophosphorylation (Z - scheme; proposed by Hill and Bendall)
Both photosystems are involved here. Electron extruded by P_{680} or PS II does not return to it but is passed on to NADP^{+} with the help of PS I. P_{680} after gaining photon energy extrudes an electron which is picked up by phlophyrin, a non Mg chlorophyll a from which electron passes on to another electron acceptor Q and then to plastquinone. The electron is picked up by cytochrome f complex and then passes to plastocyanin. PC hands over the electron to P_{700} or PS I. Reaction centre of PS I extrudes the electron which passes through FeS, Fd and then to NADP^{+}.

MECHANISM OF PHOTOSYNTHESIS
Photosynthesis occurs in two phases - Photochemical and Biochemical. Photochemical phase is also called light Reaction or Hill reaction. Biochemical phase is also termed as Dark reaction or Blackmann's reaction.

Light Reaction
This step occurs in presence of light. During this step ATP and NADPH are produced. ATP and NADPH are together known as Assimilatory Power. This phase involves photolysis of water and production of assimilatory power.

(a) Photolysis of H_{2}O: It is breaking up of H_{2}O into hydrogen and oxygen in the illuminated chloroplasts. A small complex of protein is attached to photosystem II. It is called oxygen evolving complex (OEC). OEC centre oxidises H_{2}O into oxygen, H^{+} and electrons. Cl^{-}, Ca^{2+} and Mn^{2+} is required during this process.

\[ 2H_{2}O \rightarrow 2H^{+} + \frac{1}{2}O_{2} + 2e^{-} \]

(b) Production of Assimilatory power: The electrons released during photolysis of H_{2}O are picked up by reaction centre (P_{680}) of PS II. On receiving a photon of light energy P_{680} expels an electron. It is primary reaction of photosynthesis which involves conversion of light energy into chemical energy (Quantum conversion). The electron extruded by P_{680} is picked up by phlophyrin, from where electron passes over a series of carriers. While passing over cytochrome complex, the electron loses sufficient energy for creation of proton gradient and synthesis of ATP (Photophosphorylation). From plastocyanin the electron is picked up by trap centre (P_{700}) of PS I. Electron is expelled by P_{700}. Which is picked up by FeS, ferredoxin and NADP - reductase. NADP reductase gives electrons to NADP^{+} for combining with H^{+} ions to produce NADPH.

Dark reaction
It does not require light. During this reaction or biosynthetic pathway assimilatory power is used in fixation and reduction of CO_{2}. The enzymes required for this reaction are present in matrix of chloroplast. There are two main pathways C_{3} or Calvin cycle and C_{4} or dicarboxylic acid cycle.
**CALVIN CYCLE OR C₃ CYCLE OR REDUCTIVE PENTOSE PATHWAY**

This path of C-assimilation was given by Calvin, Benson and Bassham (1949). They got the Nobel Prize for this work in the year 1961. This is also known as C₃ cycle because CO₂ reduction is cyclic process and first stable product in this cycle is a 3-C compound (i.e., 3-Phosphoglyceric acid or 3-PGA).

![Calvin cycle diagram](image)

**Fig. Calvin cycle (C₃ cycle)**

- In this cycle, CO₂ acceptor molecule is RuBP or RuDP (i.e., Ribulose 1, 5-biphosphate or Ribulose 1, 5-diphosphate).
- As Calvin cycle takes in only one carbon (as CO₂) at a time, so it takes six turns of the cycle to produce a net gain of six carbons (i.e., hexose or glucose).
- In this cycle, for formation of one mole of hexose sugar (Glucose), 18 ATP and 12 NADPH₂ are used.
- The plants in which this pathway of CO₂ reduction occurs, are called C₃ plants.
- Enzyme RUBISCO (RUBP carboxylase oxygenase) was also called earlier as carboxy dismutase.
- RUBISCO is most abundant protein on earth and its present on the outer surface of thylakoid membrane.

**PHOTOESPIRATION**

Photosynthetic Carbon Oxidation or PCO Cycle or C₂ cycle

It was discovered by Dicker and Tio (1959) in Tobacco leaves. Subsequently, photorespiration was found to be universal in C₃ plants. It involves three cell organelles - chloroplasts, peroxisomes and mitochondria. The various evidences in support of occurrence of photorespiration are

(i) Decrease in the rate of photosynthesis with the increase in light intensity.
(ii) Decrease in the rate of photosynthesis when O₂ concentration is raised from 2.5% to 21%.
Mechanism

- RUBP carboxylase function as RUBP oxygenase with the decrease in CO₂ : O₂ ratio
- In photorespiration two molecules of phosphoglycolate formed by oxygenation of RUBP is changed to one molecule of RUBP is changed to one molecule of phosphoglycerate (PGA) and one molecule of CO₂. Thus, 75% of carbon lost in oxygenation of RUBP is recovered by photorespiratory carbon oxygenation.
- Photo respiration do not give any energy or reducing power. It consumes energy. So its a wasteful process, especially in C₃ plants but negligible or absent in C₄ plants.
- Photo respiration also increases with temperature and age of the leaf.
- Glycine and serine are two amino acids formed in photorespiration or C₂ cycle.

Hatch and Slack Cycle or C₄ Cycle

Kortschak, Hartt and Burr (1965) reported that rapidly photosynthesizing sugarcane leaves produced a 4-C compound like aspartic acid and malic acid as a result of CO₂-fixation. This was later supported by M.D. Hatch and C.R. Slack (1966) and they reported that a 4-C compound oxaloacetic acid (OAA) is the first product in CO₂ reduction process.

This led to an alternative pathway of CO₂ fixation, which is known as Hatch and Slack’s cycle or C₄ cycle (as 4-C compound is first stable product).

This pathway was first reported in members of family Gramineae (grasses) like sugarcane, maize, sorghum, etc., (Tropical grasses) but later on in other sub-tropical plants also like Atriplex and Amaranthus.

- Genera like Flaveria (Asteraceae) Punicum, Alternanthera and Atriplex contain both C₃ and C₄ species. These C₄ plants have a characteristic leaf anatomy called Krantz anatomy (German word meaning: Wreathe, Ring or Halo)
  Here vascular bundles are surrounded by sheath of large parenchymatous cells called bundle sheaths which are surrounded by mesophyll cells. Here two types of chloroplasts are present (Chloroplast Dimorphism)
  (i) Bundle sheath chloroplasts: Larger in size, lack grana (Agranal chloroplasts) and contain starch grains.
  (ii) Mesophyll chloroplasts: Similar in size, contain grana (Granal chloroplasts) and lack starch grains.

Bundle sheath cells and mesophyll cells are connected by plasmodesmata.

- CO₂ acceptor molecule here is PEP (Phospho Enol Pyruvate) and not RuBP. Further, PEP-carboxylase (PEPCO) is the key enzyme (RuBP-carboxylase enzyme is negligible or absent in mesophyll chloroplast, but present in bundle sheath chloroplast)
- In C₄ plants, for formation of one mole of hexose (glucose), 30 ATP and 12 NADPH are required
Significance of C₄ Cycle

This C₄ cycle is helpful to plants growing in dense tropical forests, where there is poor supply of CO₂. Because here there is internal supply of CO₂, so these plants can survive in poor CO₂ conditions. Photorespiration is negligible or absent in C₄ plants and present only in C₃ plants.

<table>
<thead>
<tr>
<th>Features</th>
<th>C₃</th>
<th>C₄</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cell type</td>
<td>One (mesophyll)</td>
<td>Two (mesophyll and bundle-sheath)</td>
</tr>
<tr>
<td>Kranz anatomy</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>Chloroplasts</td>
<td>One type (granal only)</td>
<td>Two types (granal and agranal)</td>
</tr>
<tr>
<td>CO₂ acceptor</td>
<td>RuBP</td>
<td>PEP</td>
</tr>
<tr>
<td>First CO₂ fixation product</td>
<td>3-PGA (3C compound)</td>
<td>Oxaloacetic acid (4C compound)</td>
</tr>
<tr>
<td>Carboxylase enzyme</td>
<td>Rubisco</td>
<td>PEPcase; Rubisco</td>
</tr>
<tr>
<td>CO₂ fixation rate</td>
<td>Low</td>
<td>High</td>
</tr>
<tr>
<td>O₂ inhibition of photosynthesis</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>Photorespiration</td>
<td>High</td>
<td>Negligible</td>
</tr>
<tr>
<td>Productivity</td>
<td>Low</td>
<td>High</td>
</tr>
<tr>
<td>CO₂ compensation point</td>
<td>High (25-100μ CO₂ l⁻¹)</td>
<td>Low (0-10 μl CO₂ l⁻¹)</td>
</tr>
<tr>
<td>Temperature optimum</td>
<td>20°C - 25°C</td>
<td>30°C - 45°C</td>
</tr>
<tr>
<td>Examples</td>
<td>Rice, wheat, potato</td>
<td>Maize, pearl millet, Amaranthus</td>
</tr>
</tbody>
</table>

CAM CYCLE (CRASSULACEAN ACID METABOLISM)

This metabolism was first of all reported in Bryophyllum, a member of family Crassulaceae and hence is called crassulacean acid metabolism.
This occurs in mostly succulents (xerophytes) like Opuntia, Agave, Aloe, Sedum, Kalanchoe, etc., But there occurs dark acidification, i.e., during night malic acid is formed. This malic acid breaks up into CO₂ and pyruvic acid in day time and CO₂ released is utilized in C₃ cycle.

- In these plants, stomata open during night and close during day time (Scotocative stomata)
- In these plants carbon fixation at night is by PEPCO and during day is by RUBISCO.
- CAM plants lack Kranz anatomy.
- They are not resistant to photorespiration but minimise transpiration as stomata is closed during day time.

**FACTORS OF PHOTOSYNTHESIS**

- Blackmann's law of limiting factor: Rate of photosynthesis is affected by the pace of the slowest factor or limiting factor eg. light or CO₂.

Sach has determined three cardinal points for a factor; **Minimum, Optimum and Maximum.**

1. **Light**
   - No photosynthesis occurs in a very weak intensity of light. As the intensity of light increases, the process begins and picks up the pace. A very strong intensity of light causes solarization. During solarization, photo-oxidation occurs and if it continues for a few hours, the photosynthetic apparatus is destroyed. The photosynthesis begins in the morning hour, reaches its peak in the noon/afternoon and then its rate declines. The value of light at which further increase is not accompanied by an increase in CO₂ uptake is called light saturation point. A plant continues to respire almost at a uniform rate. During peak hour rate of photosynthesis is about twenty times faster than that of respiration. However, in the morning as well in the evening (twilight), photosynthesis equals the rate of respiration. It is called light compensation point.

2. **Temperature**
   - The plants can perform photosynthesis on a range of temperature. While some cryophytes can do photosynthesis at -35°C, some thermal algae can do this act even at 75°C. Usually the plants can perform photosynthesis between 10°C - 40°C. The optimum temperature ranges between 25°C - 30°C.

3. **CO₂**
   - The concentration of CO₂ in the atmosphere is 0.03% by volume. If this concentration is increased by 15 to 20 times, the photosynthetic rate increases, if no other factor becomes limiting. Still higher concentration of CO₂ is toxic to plant. However, the value of upper limit of CO₂ concentration is variable. A stage in CO₂ concentration where there is no net absorption of CO₂ by illuminated plant organ is called CO₂ compensation point or threshold value. Its less than 10 ppm for C₄ plants and 50 - 100 ppm for C₃ plants.

4. **Water**
   - It is a reactant in photosynthesis. A plant utilizes less than 1% water from its total absorption and the rest is transpired. A decrease in water contents cause loss of turgor thereby closing down the stomata. The effect of water is more indirect than direct.

5. **Oxygen**
   - The concentration of oxygen in the atmosphere is about 21% volume and it seldom fluctuates. An increase in oxygen concentration decreases photosynthesis and the phenomenon is called Warburg effect. The explanation to this problem lies in the phenomenon of photorespiration. In C-3 plants the rate of day (light) respiration is faster than the dark respiration. This enhanced rate of respiration is called photorespiration. It operates in high light intensity, high oxygen concentration and high temperature. Here oxygen competes with CO₂ for the oxidation of RuBP to phosphoglycolic acid, thus reducing the fixation of CO₂.

6. **Chemicals**
   - The chemicals, which act as enzyme inhibitor like all other vital processes, inhibit photosynthesis also. Such chemicals are cyanides, hydroxyl amine, H₂S, CO, iodoacetates etc. Besides, chloroform and ethers also inhibit photosynthesis. The herbicides dichlorophenyl dimethyl urea (DCMU) and chlorophenyl dimethyl urea (CMU) are also photosynthetic inhibitors. They inactivate PS II, thus inhibiting the Hill reaction.

7. **Minerals**
   - Mn²⁺, Cl⁻, Ca²⁺ ions help in photolysis of water. Mg and Fe in synthesis of chlorophyll. B and K help in translocation of solutes.

8. **Hormones**
   - Auxina Gibberellin and Cytokin in increase the photosynthesis. ABA decrease it.
**Translocation of Solute**

- A plant prepares food through its leaves. The leaves act as ‘supply end’ or source. It is then translocated to various parts of the plant body such as roots, tubers, fruits and other storage regions. These regions act as consumption end or sink.
- Czapek found that phloem is the pathway of translocation of organic nutrients.

**Girdling Experiments**

Malpighi performed girdling or ringing of stems. A narrow ring of bark is removed below the foliage. Bark swells up above the ring. It may also develop adventitious roots. The swelling is due to accumulation of nutrients above the ring. This experiment proves that nutrients pass through phloem and not through the xylem.

- Hartig (1837): Discovered Sieve Tubes in the Bark
- Autoradiography: Leaves were fed with radioactive $^{14}\text{CO}_2$. Sections were cut and autoradiographs were prepared. It was found that transport occured through the sieve tubes.
- Transported solutes: The food is generally translocated as carbohydrate. The most dominant carbohydrate is sucrose. In some plants phloem sap contains raffinose, stachyose and mannitol.
- Translocation rate: The sieve elements are 100 – 500 $\mu$m long and 20 – 40 $\mu$m in diameter. Average rate of translocation is 55 cms/hours.

**Mechanism of Translocation**

- Protoplasmic streaming hypothesis: It was proposed by Hugo de Vries. According to this theory the food is transported across by streaming current of protoplasm. This hypothesis explains the bidirectional movement of metabolites across a single sieve element.
- Electro-osmotic hypothesis: This theory was proposed by Spanner. According to him the solute particles move electro-osmotically across the sieve plate through sieve pores.
- Mass flow or pressure flow hypothesis:
  - It was first proposed by Hartig and later modified by Munch. According to this hypothesis organic substances flow in solution form in the sieve elements due to development of pressure gradient between source and sink ends.
  - In plants, organic nutrients are synthesised in the mesophyll cells. From these cells nutrients enter into sieve tube elements which absorb water from the near by xylem elements. It produces a high turgor pressure that causes flow of nutrient solution in the sieve elements, towards the region where turgor pressure is low. In the sink region water moves back to xylem as O.P. is low due to utilisation of food or conversion to starch, therefore low T.P. is maintained at the sink end.

**Factors Affecting Translocation**

(i) Temperature: The optimum temperature for translocation ranges between 20°C – 30°C. It increases with increase of temperature up to a maximum limit and then decreases.

(ii) Minerals: It has been demonstrated that boron enhanced translocation of labelled sucrose in tomato.

**Some important points to remember**

- The formation of ATP in photophosphorylation is explained by Mitchell’s chemiosmotic coupling hypothesis. For ATP synthesis a proton gradient develops across the thylakoid membrane.
- For every $3\text{H}^+$ which diffuse back to stroma via $\text{CF}_0 - \text{CF}_1$ particles on the thylakoid membrane one ATP is synthesized (coupling reaction).
- ATP synthetase enzyme has two components, $\text{CF}_0$ and $\text{CF}_1$ and it is located in the thylakoid membrane.
- Annually, about $75 \times 10^{12}$ kg of carbon (in the form of $\text{CO}_2$) is fixed through photosynthesis, producing about 1700 million tonnes of dry matter.
- About 90% of photosynthesis is carried out in the oceans (largely by the phytoplanktons and algae).
- During photosynthesis, 264 gms of CO₂ and 216 gms of water are utilised for producing 108 gms of water and 192 gms of O₂.
- The reaction centre in bacteria is B-890.
- Redox potential is the tendency of an atom/molecule having low redox potential to lose electrons (electron donors) while those with high redox potential to accept electron (gain electrons). Hence, electrons move from substances having low redox potentials to those having high redox potentials.
- DCMU (Dichlorophenyl dimethyl urea)—a herbicide—inhibits PSII and oxygen release in light phase.
- In C₃ plants, more CO₂ is released in light than in dark due to photorespiration.
- If the trunk of a tree is ringed, roots die first.
- Ringing experiments are not successful in monocots because of scattered vascular bundles.
- If ringing is done between fruit and leaves, fruit would be smaller in size.
- pH of the phloem sap varies between 7.5 to 8.6.
- *Atriplex roseus* shows Calvin cycle whereas *A. hastata* shows Hatch-Slack cycle.
- *Phaeophytin* is chlorophyll without Mg²⁺.
- PQ and PC are the mobile carriers of the electron transport chain of photophosphorylation.