Photosynthesis

Definition :

The synthesis of complex organic material using carbon dioxide, water, inorganic salts, and light energy (from sunlight) captured by light-absorbing pigments, such as chlorophyll and other accessory pigments.

Origin

Greek 'photos' means 'Light' and 'Synthesis' means 'to produce'. It means formation / production of something in presence of light.

Photosynthetic Organism

1.Photosynthetic Plants : Some types of bacteria, algae, and higher plants who posses photosynthetic pigment (like chlorophyll), they are capable of photosynthesis.

1.Photosynthetic root : i)*Trapa natans*-is an aquatic plant with green submerged roots.

ii)*Tinospora cordifolia*-has long , slender, hanging aerial adventitiuos roots. These roots are green and photosynthetic.

2.Photosynthetic stem : i) **Cladodes or cladophylls**-are flat, leaf-like stems modified for photosynthesis.

3.Photosynthetic animals : *Euglena* and *Crysamoeba*

4.Plants unable to photosynthesis : *Mucor* and *Yeast*

Photosynthetic Pigments

Green plants have six closely related photosynthetic pigments (in order of increasing polarity):

- Carotene - an orange pigment
- Xanthophyll - a yellow pigment
- Phaeophytin *a*- a gray-brown pigment
- Phaeophytin *b*- a yellow-brown pigment
- Chlorophyll *a*- a blue-green pigment
- Chlorophyll *b*- a yellow-green pigment

Chlorophyll a is the most common of the six, present in every plant that performs photosynthesis. The reason that there are so many pigments is that each absorbs light more efficiently in a different part of the electromagnetic spectrum. Chlorophyll a absorbs well at a wavelength of about 400-450 nm and at 650-700 nm; chlorophyll b at 450-500 nm and at 600-650 nm. Xanthophyll absorbs well at 400-530 nm. However, none of the pigments absorbs well in the green-yellow region, which is responsible for the abundant green we see in nature.

Albinism and Chlorosis

In plants, **albinism** is characterized by partial or complete loss of chlorophyll pigments and incomplete differentiation of chloroplast membranes. Albinism in plants interferes with photosynthesis which can reduce survivability.Some plant variations may have white flowers or other parts. However, these plants are not totally devoid of chlorophyll. Terms associated with this phenomenon are "hypochromia" and "albiflora".

chlorosis is a condition in which leaves produce insufficient chlorophyll. As chlorophyll is responsible for the green color of leaves, chlorotic leaves are pale, yellow, or yellow-white. The affected plant has little or no ability to manufacture carbohydrates through photosynthesis and may die unless the cause of its chlorophyll insufficiency is treated, although some chlorotic plants, such as the albino *Arabidopsis thaliana* mutant *ppi2*, are viable if supplied with exogenous sucrose.Chlorosis is derived from the word Chloris or from the Greek *khloros* meaning 'greenish-yellow', 'pale green', 'pale', 'pallid', or 'fresh'.

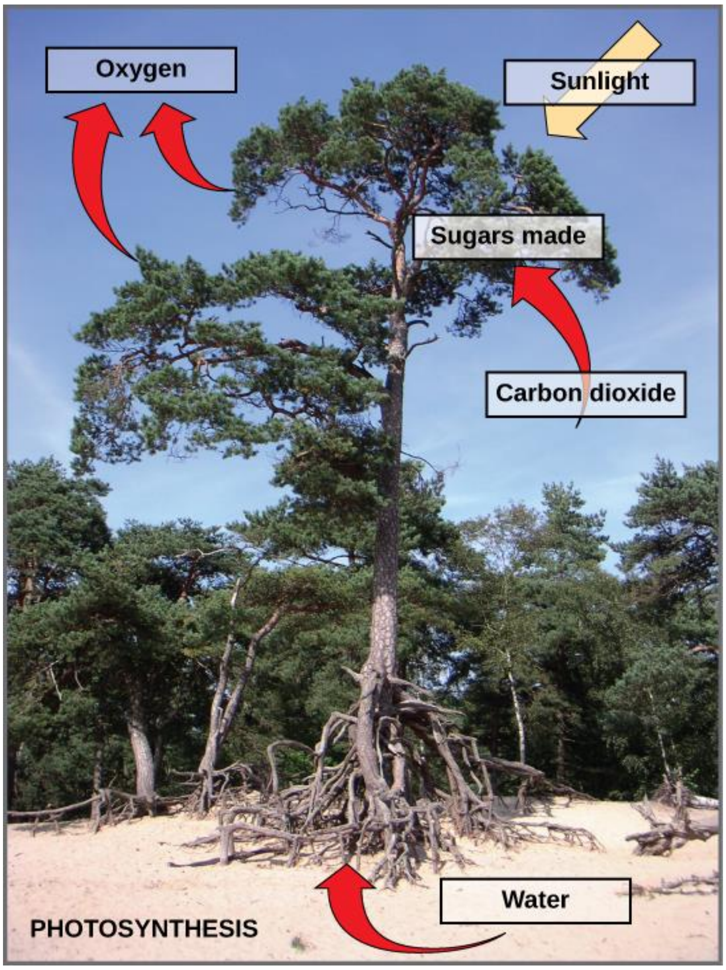
Difference Between Chlorophyll a Chlorophyll b

Chlorophyll-a	***Chlorophyll-b***
1.It is the principal photosynthetic pigment.	*1.It is the accessory photosynthetic pigment.*
2.It is present in all phototrophs except bacteria.	*2.It is present in all phototrophs other than Diatoms, Cyanobacteria, red and brown algae.*
3.Blue-green in pure state.	*3.Olive green in pure state.*
4.Empirical formula is $C_{55}H_{77}O_5N_4Mg$.	*4.Empirical formula is $C_{55}H_{70}O_6N_4Mg$.*
5.The third carbon of the side is methyl group(-CH_3).	*5.Side group at the third carbon is aldehyde group(-CHO).*
6.Molecular weight is 873.	*6.Molecular weight is 907.*

Overview

In multicellular autotrophs, the main cellular structures that allow photosynthesis to take place include chloroplasts, thylakoids, and chlorophyll.
Mesophyll : A layer of cells that comprises most of the interior of the leaf between the upper and lower layers of epidermis.Stoma :A pore in the leaf and stem epidermis that is used for gaseous exchange.

Photosynthesis is a multi-step process that requires sunlight, carbon dioxide, and water as substrates. It produces oxygen and glyceraldehyde-3-phosphate (G3P or GA3P), simple carbohydrate molecules that are high in energy and can subsequently be converted into glucose, sucrose, or other sugar molecules. These sugar molecules contain covalent bonds that store energy. Organisms break down these molecules to release energy for use in cellular work.



Photosynthesis

Photosynthesis uses solar energy, carbon dioxide, and water to produce energy-storing carbohydrates. Oxygen is generated as a waste product of photosynthesis.

The energy from sunlight drives the reaction of carbon dioxide and water molecules to produce sugar and oxygen, as seen in the chemical equation for photosynthesis. Though the equation looks simple, it is carried out through many complex steps. Before learning the details of how photoautotrophs convert light energy into chemical energy, it is important to become familiar with the structures involved.

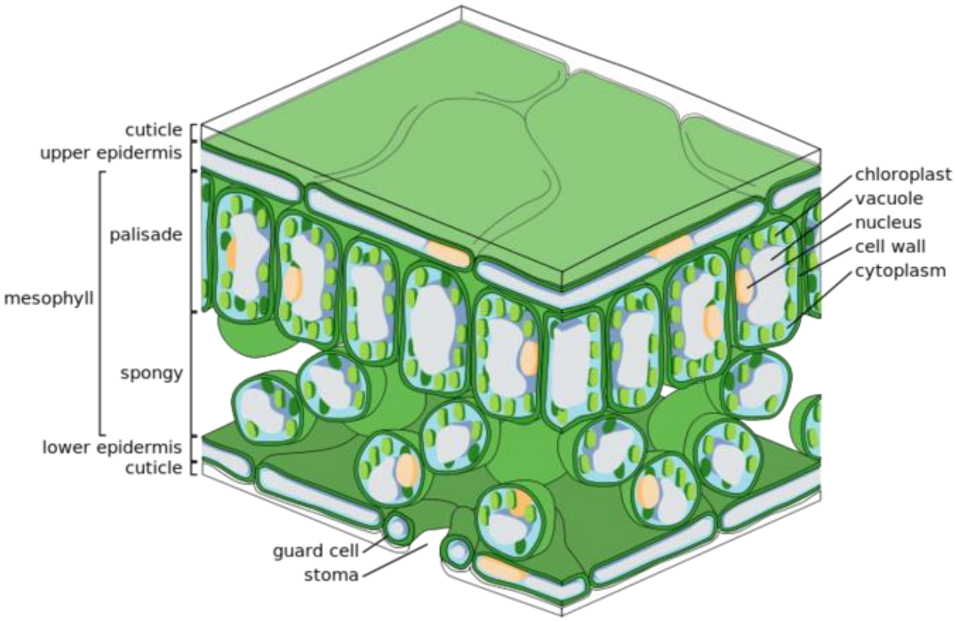
Photosynthesis Equation			
Carbon dioxide +	Water SUNLIGHT →	Sugar +	Oxygen
$6CO_2$	$6H_2O$	$C_6H_{12}O_6$	$6O_2$

Chemical equation for photosynthesis

The basic equation for photosynthesis is deceptively simple. In reality, the process includes many steps involving intermediate reactants and products. Glucose, the primary energy source in cells, is made from two three-carbon GA3P molecules.

Photosynthesis and the Leaf

In plants, photosynthesis generally takes place in leaves, which consist of several layers of cells. The process of photosynthesis occurs in a middle layer called the mesophyll. The gas exchange of carbon dioxide and oxygen occurs through small, regulated openings called stomata (singular: stoma), which also play a role in the plant's regulation of water balance. The stomata are typically located on the underside of the leaf, which minimizes water loss. Each stoma is flanked by guard cells that regulate the opening and closing of the stomata by swelling or shrinking in response to osmotic changes.



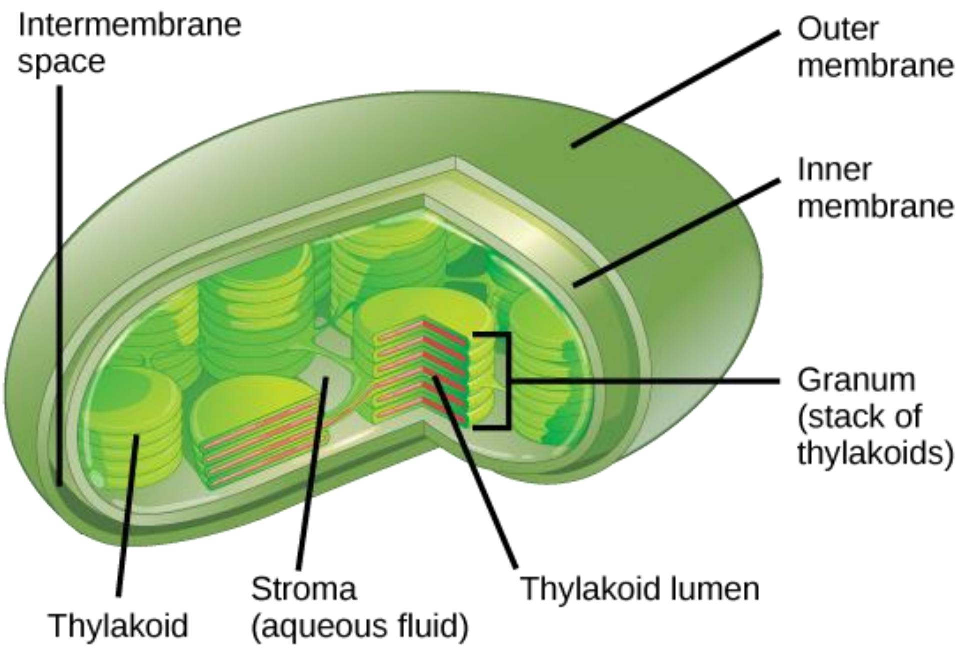
Structure of a leaf (cross-section)

Photosynthesis takes place in the mesophyll. The palisade layer contains most of the chloroplast and principal region in which photosynthesis is carried out. The airy spongy layer is the region of storage and gas exchange. The stomata regulate carbon dioxide and water balance.

Photosynthesis within the Chloroplast

In all autotrophic eukaryotes, photosynthesis takes place inside an organelle called a chloroplast. For plants, chloroplast-containing cells exist in the mesophyll. Chloroplasts have a double membrane envelope composed of an outer membrane and an inner membrane. Within the double membrane are stacked, disc-shaped structures called thylakoids.

Embedded in the thylakoid membrane is chlorophyll, a pigment that absorbs certain portions of the visible spectrum and captures energy from sunlight. Chlorophyll gives plants their green color and is responsible for the initial interaction between light and plant material, as well as numerous proteins that make up the electron transport chain. The thylakoid membrane encloses an internal space called the thylakoid lumen. A stack of thylakoids is called a granum, and the liquid-filled space surrounding the granum is the stroma or "bed."



Structure of the Chloroplast

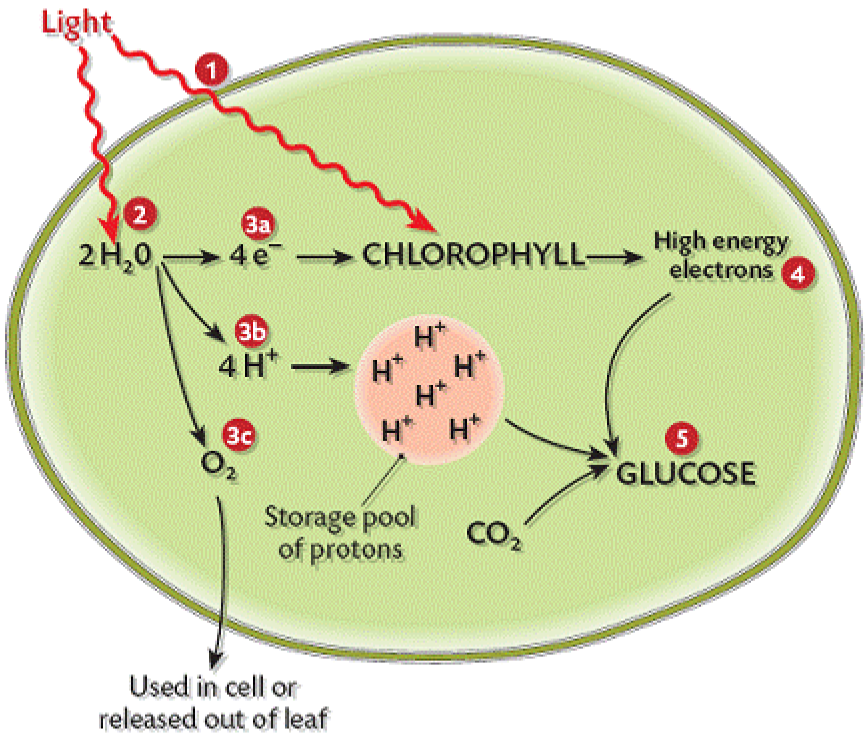
Photosynthesis takes place in chloroplasts, which have an outer membrane and an inner membrane. Stacks of thylakoids called grana form a third membrane layer.

Main components of photosynthesis

1.Light : Source- Light supplies the required energy for the process of photosynthesis. The main source of this light is the sun.The pigments absorbs the blue, violet and red light most out of seven lights of the visible white light. The Photons (an invisible high energy containing molecule of the sun) contains Quantum (the enclosed energy of photons) which is the chief source of energy of the whole photosynthesis process. Chlorophylls absorbs these photons molecule and get transformed into activated chlorophyll.

Role of sunlight in photosynthesis : Sunlight plays two major role in photosynthesis process-

A)After getting activated by absorbing the photons molecule, the activated chlorophyll breakdown the water into $H_2O= 2H^+ + 2e^- +1/2\ O_2$.



B) Helps in photosynthetic phosphorylation --- In the process of photosynthesis, the phosphorylation of ADP to form ATP using the energy of sunlight is called **photophosphorylation**. Only two sources of energy are available to living organisms: sunlight and reduction-oxidation (redox) reactions. All organisms produce ATP, which is the universal energy currency of life.In photophosphorylation, light energy is used to create a high-energy electron donor and a lower-energy electron acceptor. Electrons then move spontaneously from donor to acceptor through an electron transport chain.

2.Water : Source-Water from the soil is the major source. It is carried to the leaves in xylem tissue. Some water is also produced by the mitochondria of leaf cells during aerobic respiration.

Role of water : Water splits into oxygen, hydrogen ions, and electrons to replace the lost electrons of photosystem II in light-dependent reaction. Also, as hydrogen ions pass through ATP synthase, ATP is formed to use in the light-independent reaction. Reduces NADP INTO NADPH + H^{+}.

3.Carbon-dioxide : Source-Carbon dioxide in air is the major source for the leaves of plants. Also carbon dioxide produced by the mitochondria of the plant during aerobic respiration is a minor source. Carbon dioxide dissolved in water is the major source for aquatic plants.

Dual role of CO2 : Carbon dioxide, in its ionic form bicarbonate, has a regulating function in the splitting of water in photosynthesis. This means that carbon dioxide has an additional role to being reduced to sugar, according to scientists at Umea University in Sweden.Inorganic carbon in the form of carbon dioxide, CO2, is reduced in photosynthesis to organic compounds in the chloroplasts. Less well known is that inorganic carbon also affects the rate of the photosynthetic electron transport and thus the rate of photosynthetic oxygen production. This result was first published by the Nobel Prize winner Otto Warburg and his collaborator in the late 1950s.

Their explanation for the stimulating effect was logical at that time since they proposed that carbon dioxide was the source of the oxygen that plants produce.
Their idea was proven to be incorrect many years later and instead we now know that water, H2O, is the source of oxygen in the atmosphere. The observed stimulating effect by inorganic carbon on photosynthetic electron transport, has continued to cause an inflammatory debate among photosynthetic researchers around the world and resulted in hundreds of papers published on this issue."Our results will now put an end to this debate," says chemistry professor Johannes Messenger.His research group has developed a very sensitive techniques based on "Membrane Inlet Mass Spectroscopy" that can be used to measure the production of gases in photosynthetic samples under analytically controlled conditions.With this sensitive method they were able to test an earlier hypothesis that bicarbonate is acting as an acceptor for the protons that are produced when water is split in photosystem II. If so, a light driven production of carbon dioxide in addition to oxygen should be detected.They found they could detect relatively large amounts of carbon dioxide in the mass spectrometric experiments."Therefore, it seems as if two different carbon species, both derived from the carbonic acid cycle, have got the optimal chemical properties to be used as terminal electron acceptor (CO2) in the very end of the photosynthetic reaction and at the same time as proton acceptor (HCO3-) in the very beginning of the photosynthetic reaction", says Johannes Messinger.The results open up a new research field where researchers can investigate possible biological and ecological consequences of the dual role of carbon dioxide.
In the search for a clean and renewable energy source researchers at Umeå University are studying photosynthesis with the purpose to create artificial photosynthesis devices. Their aim is to understand and model the complex reactions that take place in plant chloroplasts during photosynthesis in order to mimic natural photosynthesis in an "artificial leaf", an integrated unit that connects all important processes. If successful, it will be possible to convert sunlight directly into environmentally friendly energy carriers, for example into hydrogen gas.

Chemical Equation and description of the equation of photosynthesis

The most basic summary of the photosynthesis process can be shown with a net chemical equation

$$6CO_2(g) + 6H_2O(l) + h\nu \rightarrow C_6H_{12}O_6(s) + 6O_2(g)$$

The symbol $h\nu$ is used to depict the energy input from light (in the case of most plants, sunlight). This chemical equation, however, is a dramatic simplification of the very complicated series of chemical reactions that photosynthesis involves. It also implies that the only product is glucose , $C_6H_{12}O_6(s)$, which is also a simplification. Still, take a moment to look at this chemical equation. If one were to guess where the various atoms in the reactants end up when products are produced, it would be reasonable to suggest that the oxygen atoms in the $O_2(g)$ were those originally associated with carbon dioxide. Most scientists believed this to be true until the 1930s when experiments by American biologist Cornelius van Niel suggested that oxygen- hydrogen bonds in water must be broken in photosynthesis. Further research confirmed his hypothesis and ultimately revealed that many reactions are involved in photosynthesis. There are two major components of photosynthesis: the light cycle and the dark cycle. As implied by these names, the reactions in the light cycle require energy input from sunlight (or some artificial light source) to take place. The reactions in the dark cycle do not have to take place in the dark, but they can progress when sunlight is not present.

The critical step of the light cycle is the absorption of electromagnet radiation by a pigment molecule. The most famous pigment is chlorophyll , but other molecules, such as β- carotene, also absorb light (see Figure 1). Together, these pigment molecules form a type of light harvesting antennae that is more efficient at interacting with sunlight than would be possible with the pigments acting alone. When the light is absorbed, electrons in the pigment molecule are excited to high energy states. A series of enzymes called electron transport systems help channel the energy present in these electrons into reactions that store it in chemical bonds. For example, one major chemical reaction that results from the absorbed light energy (and excited electrons) involves water and nicotinamide adenine dinucleotide phosphate ($NADP^+$). The net reaction is shown by the chemical equation $2\ NADP^+ + 2\ H_2O \rightarrow NADPH + O_2 + 2H^+$

This is an example of an oxidation –reduction reaction, and it shows that the light cycle is the stage of photosynthesis when water breaks up. The amount of energy required to make this reaction proceed is greater than what can be provided by a single photon of visible light. Therefore, there must be at least two ways that plants harvest light energy in photosynthesis. These two systems are referred to as photosystem I (PSI) and photosystem II (PSII), although the numbers associated with these names do not imply which one happens "first." At the same time that NADPH is being produced, the combination of the photo systems also produces a concentration gradient of protons. Enzymes in the cell use this proton gradient to produce ATP from ADP. Thus, the light cycle produces two "high energy" molecules: NADPH and ATP.

With the high energy products provided by the light cycle, plants then use reactions that do not require light to actually produce carbohydrates. The initial steps in the dark cycle are collectively called the Calvin cycle, named after American chemist Melvin Calvin who along with his coworkers determined the nature of these reactions during the late 1940s and early 1950s. The Calvin cycle essentially has two stages. In the first part of the cycle, several enzymes act in concert to produce a molecule called glyceraldehyde-3-phosphate (GAP). Note in the illustration that this molecule has three carbon atoms. Each of these carbon atoms comes originally from carbon dioxide molecules—so photosynthesis completes the amazing task of manufacturing carbohydrates out of air (the source of the carbon dioxide). This stage of the Calvin cycle is sometimes called carbon fixing. In order to carry out this synthesis of GAP, the Calvin cycle consumes some of the NADPH and ATP that was produced during the light cycle. The carbon dioxide needed for this step enters through pores in the photosynthetic leaf (called stomata). Plants close these pores during hot, dry times of the day (to prevent water loss) so the details of carbon fixing vary for plants from different climates. In hot climates, where stomata are closed for a higher percentage of time, the trapping of carbon dioxide has to be more efficient than in cooler climates. This biochemical difference in photosynthesis helps explain why plants from one climate do not grow as well in warmer (or cooler) places. The second stage of the cycle builds even larger carbohydrate molecules. With more than half a dozen enzyme-catalyzed reactions in this portion of the dark cycle, five-and six-carbon carbohydrates are produced. The five-carbon molecules continue in the cycle to help produce additional GAP, thus perpetuating the cyclic process. Photosynthesis is central to all life on the planet and has been for many thousands of years. As a result, there are numerous variations in the way it occurs in different cells. The efficient collection of carbon dioxide mentioned earlier is one example of variation in photosynthesis. Other differences occur when the process takes place in bacteria rather than plants.

Antenna Complex

The antenna complex is composed of molecules of chlorophyll and carotenoids mounted on two proteins.These pigment molecules transmit the resonance energy from photons when they become photoexcited. Antenna molecules can absorb all wavelengths of light within the visible spectrum. The number of these pigment molecules varies from organism to organism. For instance, the cyanobacterium *Synechococcus elongatus* (*Thermosynechococcus elongatus*) has about 100 chlorophylls and 20 carotenoids, whereas spinach chloroplasts have around 200 chlorophylls and 50 carotenoids.Located within the antenna complex of PS I are molecules of chlorophyll called P700 reaction centers. The energy passed around by antenna molecules is directed to the reaction center. There may be as many as 120 or as few as 25 chlorophyll molecules per P700.

Antenna pigments

A photosynthetic unit containing chlorophyll-a and other pigments, enzymes and proteins, situated within the thylakoid membrane of chloroplast, helps to absorb the photon molecules of light energy and transfers it to the reaction centre, is known as antenna pigments.

Components

The antenna of one particular photosystem contains two different parts- the peripheral or outer part and the central or inner part.

Pigments of peripheral part collect the photon molecules and transfer it to the central part from where these activated energy further transferred to the reaction centre.

Components of photosystem I and II

PS-I : Central part of the antenna contains 100-200 molecules(approx) of chlorophyll-a, 15 molecules of β-carotene, which together surrounds the P700 reaction centre.

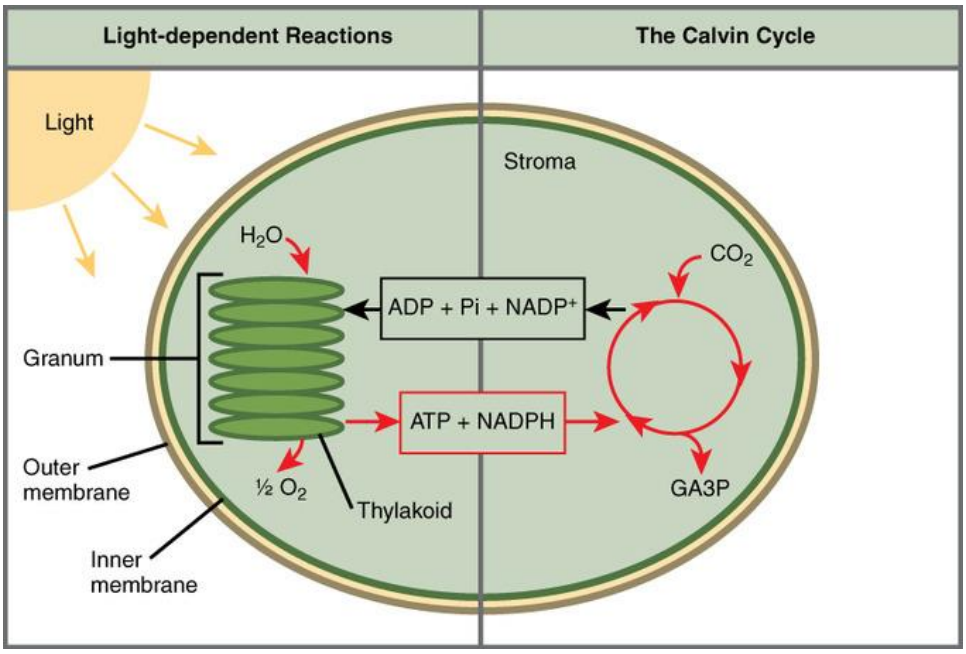
PS-II : Central part of the antenna contains two pigment-protein complex. Each PPC contains 20-25 molecules of chlorophyll-a and some molecules of β-carotene is also present.

Photosynthesis takes place in two sequential stages:

1. The light-dependent reactions;
2. The light-independent reactions, or Calvin Cycle.

Light-Dependent Reactions

Just as the name implies, light-dependent reactions require sunlight. In the light-dependent reactions, energy from sunlight is absorbed by chlorophyll and converted into stored chemical energy, in the form of the electron carrier molecule NADPH (nicotinamide adenine dinucleotide phosphate) and the energy currency molecule ATP (adenosine triphosphate). The light-dependent reactions take place in the thylakoid membranes in the granum (stack of thylakoids), within the chloroplast.



The two stages of photosynthesis

Photosynthesis takes place in two stages: light-dependent reactions and the Calvin cycle (light-independent reactions). Light-dependent reactions, which take place in the thylakoid membrane, use light energy to make ATP and NADPH. The Calvin cycle, which takes place in the stroma, uses energy derived from these compounds to make GA3P from CO2.

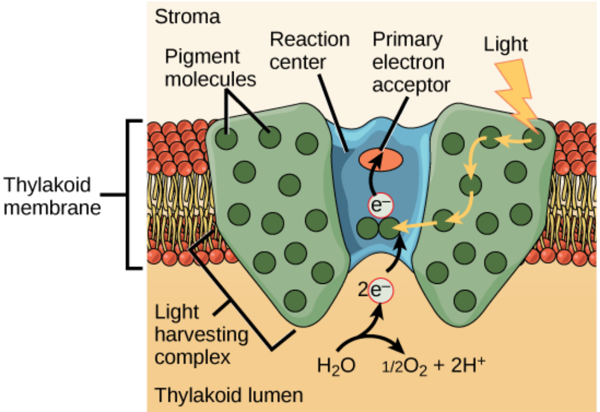
Photosystems

The process that converts light energy into chemical energy takes place in a multi-protein complex called a photosystem. Two types of photosystems are embedded in the thylakoid membrane: photosystem II (PSII) and photosystem I (PSI). Each photosystem plays a key role in capturing the energy from sunlight by exciting electrons. These energized electrons are transported by "energy carrier" molecules, which power the light-independent reactions.

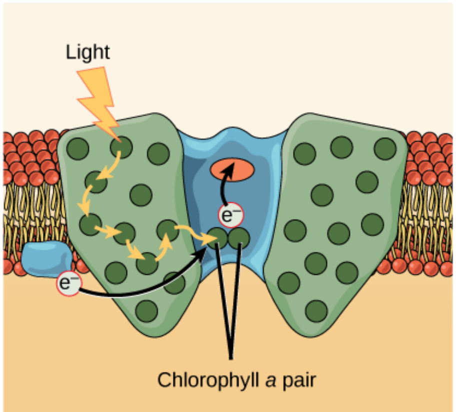
Photosystems consist of a light-harvesting complex and a reaction center. Pigments in the light-harvesting complex pass light energy to two special chlorophyll *a* molecules in the reaction center. The light excites an electron from the chlorophyll *a* pair, which passes to the primary electron acceptor. The excited electron must then be replaced. In photosystem II, the electron comes from the splitting of water, which releases oxygen as a waste product. In photosystem I, the electron comes from the chloroplast electron transport chain.

The two photosystems oxidize different sources of the low-energy electron supply, deliver their energized electrons to different places, and respond to different wavelengths of light.

(a) Photosystem II (P680)



(b) Photosystem I (P700)



PS-I AND PS-II

Light-Independent Reactions

In the light-independent reactions or Calvin cycle, the energized electrons from the light-dependent reactions provide the energy to form carbohydrates from carbon dioxide molecules. The light-independent reactions are sometimes called the Calvin cycle because of the cyclical nature of the process.Although the light-independent reactions do not use light as a reactant (and as a result can take place at day or night), they require the products of the light-dependent reactions to function. The light-independent molecules depend on the energy carrier molecules, ATP and NADPH, to drive the construction of new carbohydrate molecules. After the energy is transferred, the energy carrier molecules return to the light-dependent reactions to obtain more energized electrons. In addition, several enzymes of the light-independent reactions are activated by light.

Difference between light-dependent and light-independent reaction

Light-dependent reaction	**Light-independent reaction**
Occurs : Grana of the chloroplasts.	Occurs : Stroma of the chloroplast.
It is a light dependent process involves two photosystems : PS-I and PS-II	This process does not require light. No photosystem is required.
Photlysis of water takes place and oxygen is liberated.	Photolysis of water does not take place. Carbon-dioxide is absorbed.
ATP and NADPH is produced and they are	Glucose is produced. Reduced NADP is

used to drive the dark reaction.	oxidized.

Reaction Centre

A **photosynthetic reaction centre** is a complex of several proteins, pigments and other co-factors that together execute the primary energy conversion reactions of photosynthesis. Molecular excitations, either originating directly from sunlight or transferred as excitation energy via light- harvesting antenna systems, give rise to electron transfer reactions along the path of a series of protein-bound co-factors. These co-factors are light-absorbing molecules (also named chromophores or pigments) such as chlorophyll and phaeophytin, as well as quinones. The energy of the photon is used to excite an electron of a pigment.

The free energy created is then used to reduce a chain of nearby electron acceptors, which have subsequently higher redox-potentials. These electron transfer steps are the initial phase of a series of energy conversion reactions, ultimately resulting in the conversion of the energy of photons to the storage of that energy by the production of chemical bonds.

Components

1.Photosystem-I : The reaction centre contains two P700 chlorophyll-a and accessory proteins.

2.Photosystem-II : The reaction centre contains two P680 chlorophyll-a and accessory proteins.

Difference between PS-I and PS-II

PHOTOSYSTEM-I	PHOTOSYSTEM-II
1.The system contains 100-200 molecules of chlorophyll-a, 15 molecules of β-carotene and proteins.	1.The system contains 40-50 molecules of chlorophyll-a, some molecules of β-carotene and proteins.
2.Chlorophyll-a absorbs 700nm wavelength light of visible spectrum.	2.Chlorophyll-a absorbs 680nm wavelength light of visible spectrum.
3.Fd works as the peripheral electron receptor for this system.	3.PQworks as the peripheral electron receptor for this system.
4.Takes part in both cyclic and non-cyclic photophosphorylation.	4.Takes part in only non-cyclic photophosphorylation.
5.Light-reduction of water molecules does not takes place.	5.Light-reduction of water molecules takes place.
6.Reduction of NADP takes place.	6.Reduction of NADP does not takes place.
7.Found in higher plants and bacteria.	7.Found only in higher plants.

Electron Transport System

Definition : Transportation of electrons within PS-I and PS-II by the help of different carries is known as Electron Transport System.

Types : Cyclic and Non-cyclic electron transport system

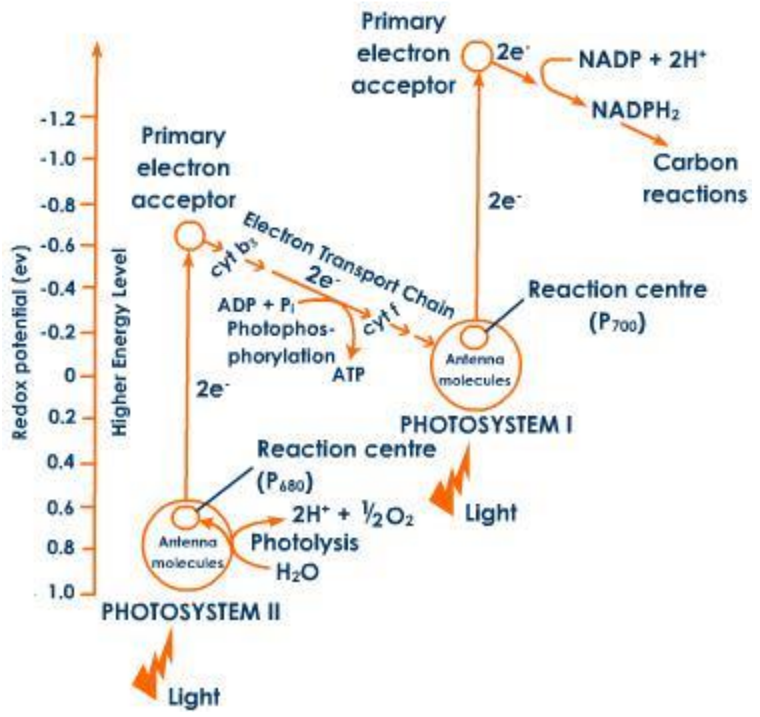
Photophosphorylation (Cyclic and Non-cyclic)

Photosynthetic phosphorylation or photophosphorylation is the process of phosphate group transfer into ADP to synthesize energy rich ATP molecule making use of light as external energy source. According to chemiosmotic hypothesis (Mitchell 1961) the ATP is synthesized on ATPase complexes located on the non appressed portions of thylakoid membranes particularly towards margins.During photosynthetic electron transport, hydrogen protons (H^+) accumulate in the thylakoid space, due to splitting of water and transport between PQH_2 to Cytf.

Increase in the number of hydrogen protons in the thylakoid space results in increase of proton gradient. Down flow of protons from high to low concentration along H^+ conc. gradient through ATPase complex provides the energy that allows an ATP synthase enzyme to produce ATP from ADP + P_i

Non - Cyclic Photophosphorylation

The electrons lost by P_{680} (PS-II) are taken up by P_{700} (PS-I) and do not get back to P_{680} i.e., unidirectional and hence it is called non- cyclic phosphorylation. The electrons pass through the primary acceptor, plastoquinone (PQ), cytochrome complex, plastocyanin (PC) and finally to P_{700}.

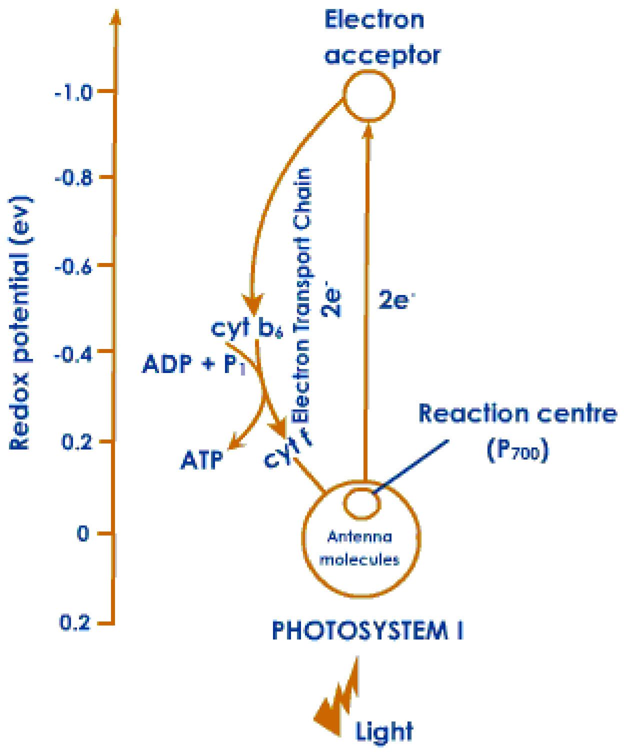


Electron Transport flow and Non-cyclic Photophosphorylation

The electrons given out by P_{700} are taken up by primary acceptor and are ultimately passed on to NADP. The electrons combine with H^+ and reduce NADP to $NADPH_2$. The hydrogen ions also called protons are made available by splitting up of water. Non-cyclic photophosphorylation needs a constant supply of water molecules. The net result of non-cyclic phosphorylation is the formation of oxygen, NADPH and ATP molecules. Oxygen is produced as a waste product of photosynthesis.

Cyclic Photophosphorylation

The electrons released by P_{700} of PS-I in the presence of light are taken up by the primary acceptor and are then passed on to ferredoxin (Fd), plastoquinone (PQ), cytochrome complex, plastocyanin (PC) and finally back to P_{700} i.e., electrons come back to the same molecule after cyclic movement.



Cyclic Photophosphorylation diagram

The cyclic photophosphorylation also results in the formation of ATP molecules just like in non - cyclic photophosphorylation.

As the electrons move downhill in the electron transport chain, they lose potential energy and ATP molecules are formed in the same way as in mitochondria during respiration.

During cyclic photophosphorylation, electrons from photosystem - I are not passed to NADP from the electron acceptor. Instead the electrons are transferred back to P_{700}. This downhill movement of electrons from an electron acceptor to P_{700} results in the formation of ATP and this is termed as cyclic photophosphorylation. It is very important to note that oxygen and $NADPH_2$ are not formed during cycle photophosphorylation.

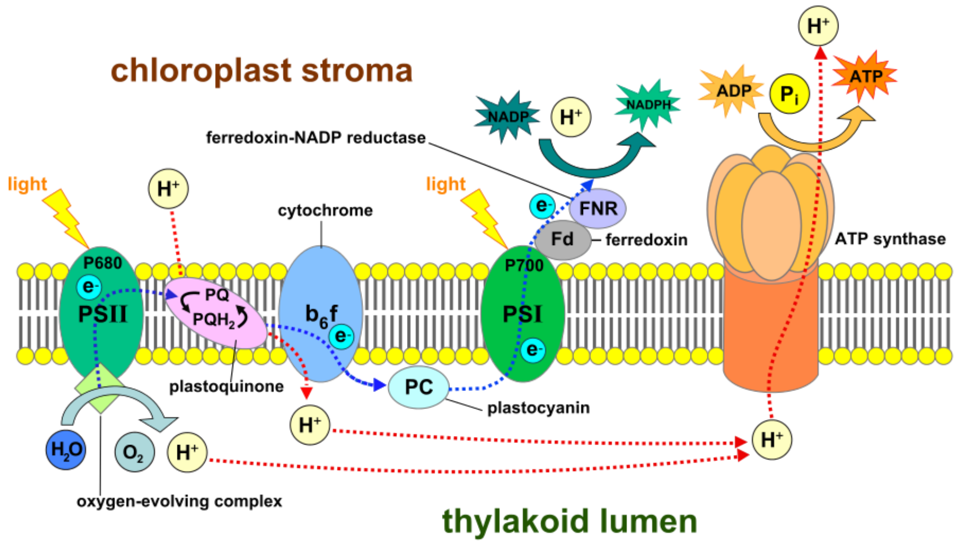
Non-cyclic photophosphorylation	Cyclic photophosphorylation
Electrons do not come back to the same molecule.	Electrons come back to the same molecule
First electron donor is water	First electron donor is P_{700} (PSI)
Involves both PSI & PSII	Involves PSI only
Last electron acceptor is NADP	Last electron acceptor is P_{700} (PSI)
The net products are ATP, NADPH and O_2	The product is ATP only

Hill Reaction

[The process discovered by scientist Robert Hill in 1937.]

Definition : Hill reaction is that portion of the photosynthesis reaction that involves the photolysis of water and the liberation of oxygen and does not include carbon dioxide fixation. It involves the addition of oxidants (quinones or ferricyanide) to chloroplasts; upon illumination, O_2 is evolved and the added oxidant is reduced.

Biochemistry of the Hill reaction



Noncyclic photophosphorylation through light-dependent reactions of photosynthesis at the thylakoid membrane

Natural electron acceptor of photosynthesis

Photosynthesis is the process in which light energy is absorbed and converted to chemical energy. This chemical energy is eventually used in the conversion of carbon dioxide (CO_2) to sugar (CH_2O) in plants. During the process of photosynthesis, a natural electron acceptor, nicotinamide adenine dinucleotide phosphate (NADP), is reduced in chloroplasts to NADPH.

Overall within a chloroplast, the following *equilibrium reaction* takes place.A reduction reaction that stores energy as NADPH: $NADP^+ + 2H^+ + 2e^- \rightarrow NADPH + H^+$ (Reduction)

An oxidation reaction as NADPH's energy is used elsewhere: $NADP^+ + 2H^+ + 2e^- \leftarrow NADPH + H^+$ (Oxidation)

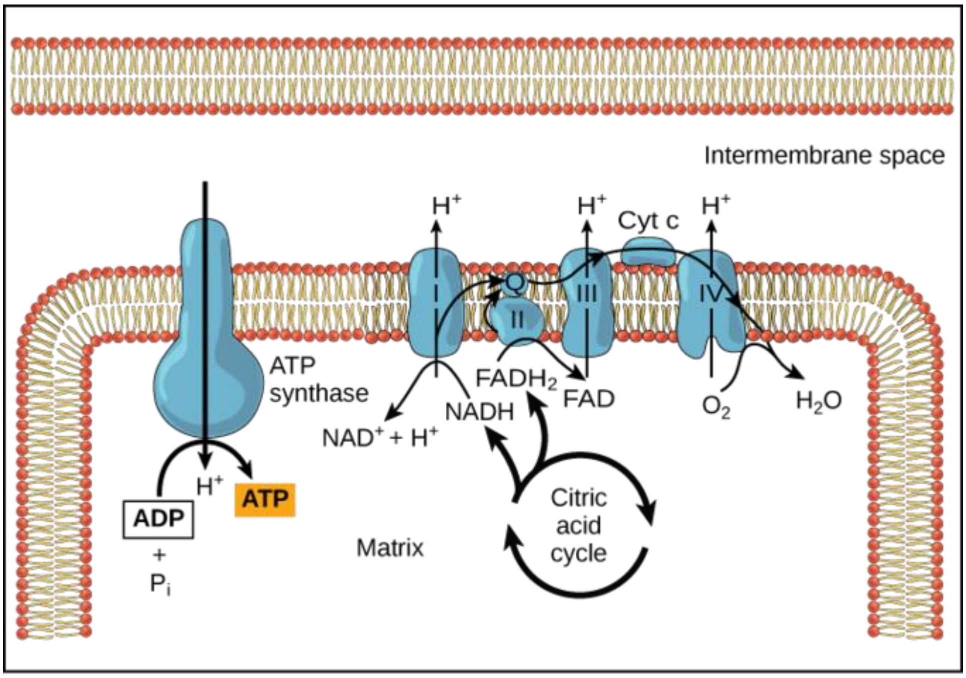
Ferredoxin, also known as a NADH+ reductase, is an enzyme that catalyzes the reduction reaction. It is easy to oxidize NADPH but difficult to reduce $NADP^+$, hence a catalyst is involved. Cytochromes are conjugate proteins that contain a *haem* group The iron atom from this haem group undergoes redox reactions: $Fe^{3+} + e^- \rightarrow Fe^{2+}$ (Reduction) $Fe^{3+} + e^- \leftarrow Fe^{2+}$ (Oxidation)

Relation to phosphorylation

The association of phosphorylation and the reduction of an electron acceptor such as ferricyanide increase similarly with the addition of phosphate, magnesium (Mg), and ADP. The existence of these three components is important for maximal reductive and phosphorylative activity. Similar increases in the rate of ferricyanide reduction can also be stimulated by a *dilution technique*. The dilution technique will not cause a further increase in the rate in which ferricyanide is reduced with the accumulation of ADP, phosphate, and Mg to a treated chloroplast suspension. ATP has been shown to inhibit the rate of ferricyanide reduction. By the studies of light intensities, it is concluded that the effect is largely on the light-independent steps of the Hill reaction. These observations are explained in terms of a proposed method in which phosphate esterfies during electron transport reactions, leading to the reduction of ferricyanide, and the rate of electron transport is limited by the rate of phosphorylation. If there is an increase in the rate of phosphorylation, then there will be an increase in the rate by which electrons are transported in the electron transport system (ETS).

Production of ATP by chemiosmosis in photosynthesis

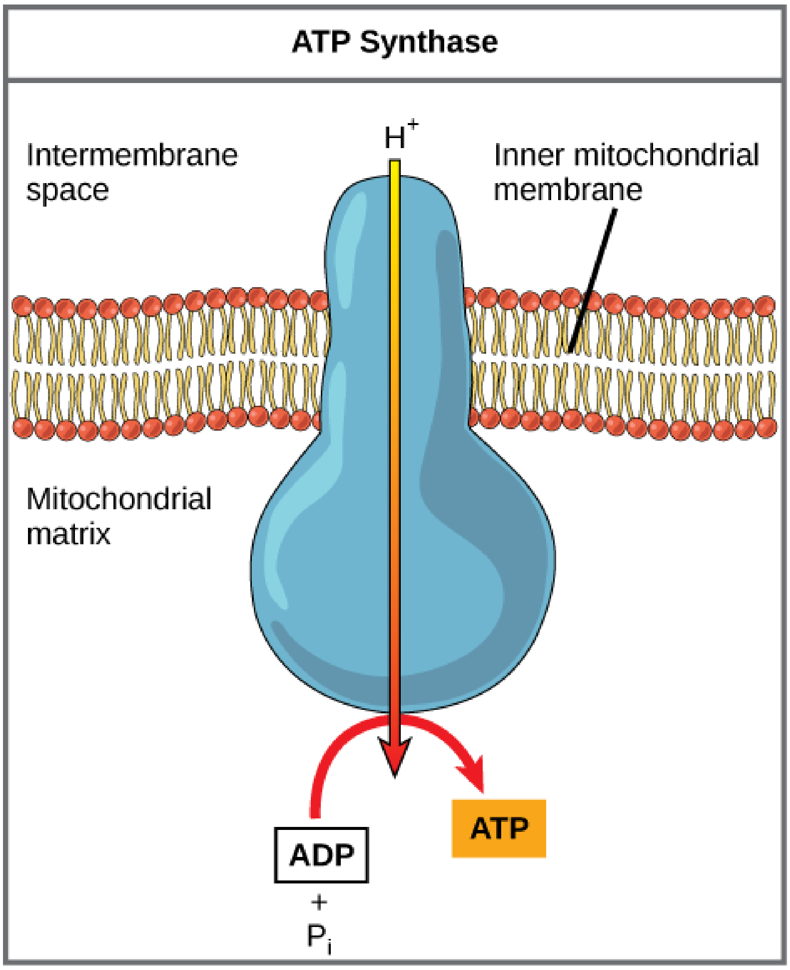
During chemiosmosis, electron carriers like NADH and FADH donate electrons to the electron transport chain. The electrons cause conformation changes in the shapes of the proteins to pump H+ across a selectively permeable cell membrane. The uneven distribution of H^+ ions across the membrane establishes both concentration and electrical gradients (thus, an electrochemical gradient) owing to the hydrogen ions' positive charge and their aggregation on one side of the membrane.



Chemiosmosis

In oxidative phosphorylation, the hydrogen ion gradient formed by the electron transport chain is used by ATP synthase to form ATP.

If the membrane were open to diffusion by the hydrogen ions, the ions would tend to spontaneously diffuse back across into the matrix, driven by their electrochemical gradient. However, many ions cannot diffuse through the nonpolar regions of phospholipid membranes without the aid of ion channels. Similarly, hydrogen ions in the matrix space can only pass through the inner mitochondrial membrane through a membrane protein called ATP synthase. This protein acts as a tiny generator turned by the force of the hydrogen ions diffusing through it, down their electrochemical gradient. The turning of this molecular machine harnesses the potential energy stored in the hydrogen ion gradient to add a phosphate to ADP, forming ATP.



ATP Synthase

ATP synthase is a complex, molecular machine that uses a proton (H+) gradient to form ATP from ADP and inorganic phosphate (Pi).

Chemiosmosis is used to generate 90 percent of the ATP made during aerobic glucose catabolism. The production of ATP using the process of chemiosmosis in mitochondria is called oxidative phosphorylation. It is also the method used in the light reactions of photosynthesis to harness the energy of sunlight in the process of photophosphorylation. The overall result of these reactions is the production of ATP from the energy of the electrons removed from hydrogen atoms. These atoms were originally part of a glucose molecule. At the end of the pathway, the electrons are used to reduce an oxygen molecule to oxygen ions. The extra electrons on the oxygen attract hydrogen ions (protons) from the surrounding medium and water is formed.

Definition of Bacterial Photosynthesis

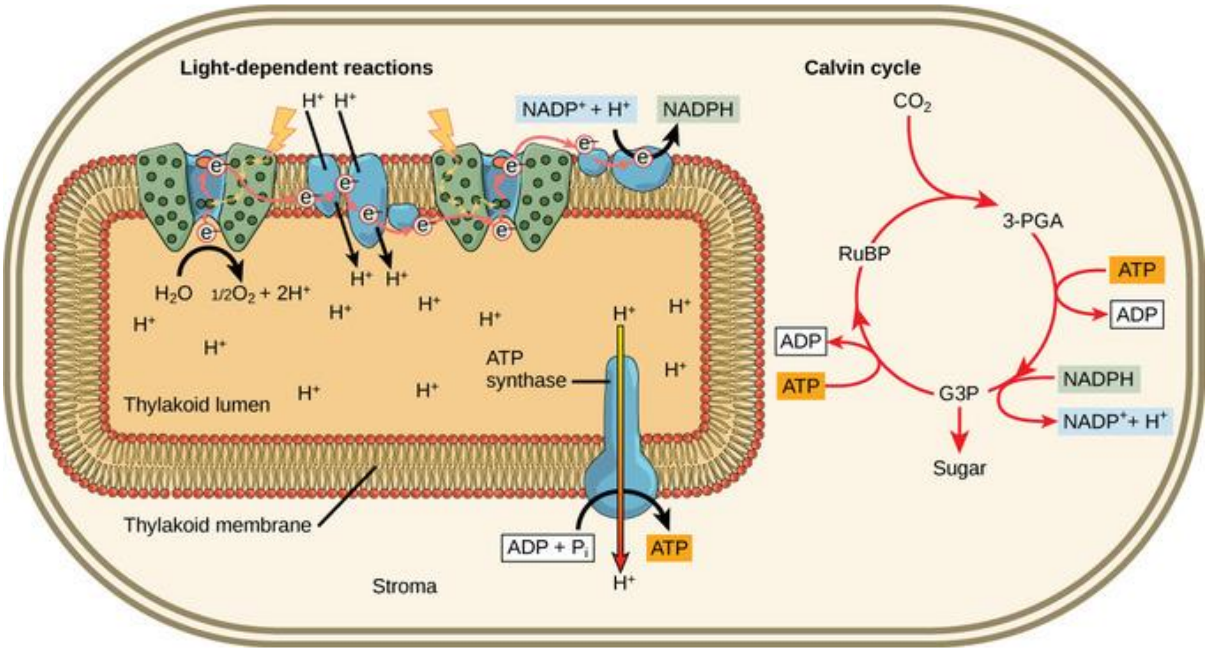
a primitive form of photosynthesis observed in some bacteria using only one photosystem and some reducing agent other than water.

Bacterial photosynthesis	Plant photosynthesis
Bacteira lack definite chloroplast.	Plants contain definite chloroplasts.
Name of pigments : bacterio-chlorophyll, bacterioviridin, and open chain aliphatic	Name of pigments : Chlorophylls, carotenoids, and phycobilins.

carotenoids.	
It takes place at wavelengths above 700mμ	It takes place at wavelengths between 400-700mμ.
Organelle : Chromatophore(within which the pigments are situated).	Organelle : Chloroplast(within which chlorophyll is situated).
The reaction centre is only P890.	The reaction centre of PS-I is P700 and of PS-II is P673 or P680.
Two photosystems are involved.	Only one photosystem is involved.
Oxygen is evolved.	Oxygen is not evolved.
Cyclic photophosphorylation is dominant.	Non-cyclic photophosphorylation is dominant.

The Calvin Cycle

In plants, carbon dioxide (CO_2) enters the leaves through stomata, where it diffuses over short distances through intercellular spaces until it reaches the mesophyll cells. Once in the mesophyll cells, CO_2 diffuses into the stroma of the chloroplast, the site of light-independent reactions of photosynthesis. These reactions actually have several names associated with them. Other names for light-independent reactions include the Calvin cycle, the Calvin-Benson cycle, and dark reactions. The most outdated name is dark reactions, which can be misleading because it implies incorrectly that the reaction only occurs at night or is independent of light, which is why most scientists and instructors no longer use it.



Light Reactions

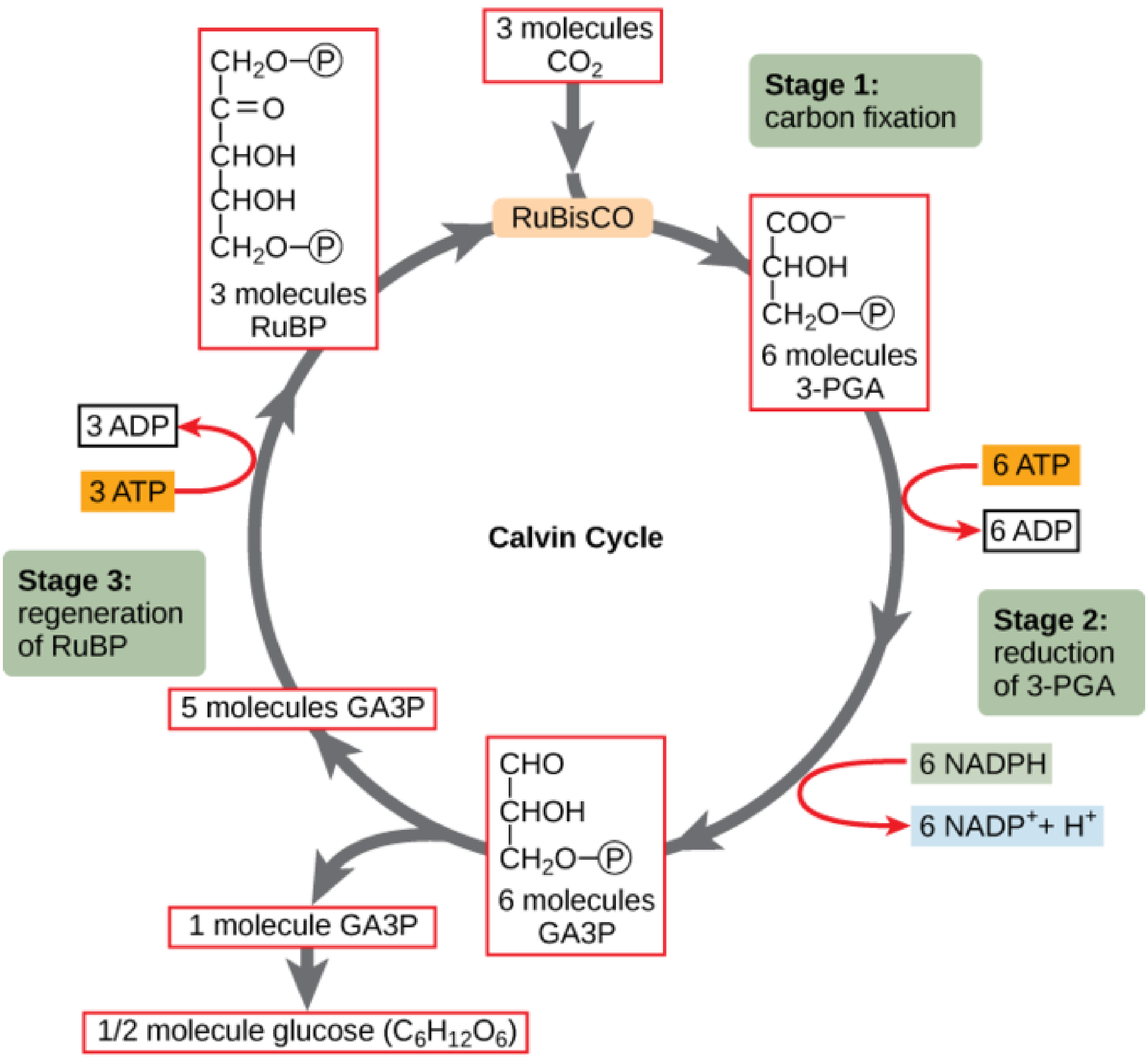


Fig : The Calvin Cycle

The Calvin cycle has three stages. In stage 1, the enzyme RuBisCO incorporates carbon dioxide into an organic molecule, 3-PGA. In stage 2, the organic molecule is reduced using electrons supplied by NADPH. In stage 3, RuBP, the molecule that starts the cycle, is regenerated so that the cycle can continue. Only one carbon dioxide molecule is incorporated at a time, so the cycle must be completed three times to produce a single three-carbon GA3P molecule, and six times to produce a six-carbon glucose molecule.

Stage 1: Fixation

In the stroma, in addition to CO_2, two other components are present to initiate the light-independent reactions: an enzyme called ribulose bisphosphate carboxylase (RuBisCO) and three molecules of ribulose bisphosphate (RuBP).

RuBP has five atoms of carbon, flanked by two phosphates. RuBisCO catalyzes a reaction between CO_2 and RuBP. For each CO_2 molecule that reacts with one RuBP, two molecules of 3-phosphoglyceric acid (3-PGA) form. 3-PGA has three carbons and one phosphate. Each turn of the cycle involves only one RuBP and one carbon dioxide and forms two molecules of 3-PGA. The number of carbon atoms remains the same, as the atoms move to form new bonds during the reactions (3 atoms from $3CO_2$ + 15 atoms from 3RuBP = 18 atoms in 3 atoms of 3-PGA). This process is called carbon fixation because CO_2 is "fixed" from an inorganic form into organic molecules.

Stage 2: Reduction

ATP and NADPH are used to convert the six molecules of 3-PGA into six molecules of a chemical called glyceraldehyde 3-phosphate (G3P). This is a reduction reaction because it involves the gain of electrons by 3-PGA. Recall that a reduction is the gain of an electron by an atom or molecule. Six molecules of both ATP and NADPH are used. For ATP, energy is released with the loss of the terminal phosphate atom, converting it to ADP; for NADPH, both energy and a hydrogen atom are lost, converting it into $NADP^+$. Both of these molecules return to the nearby light-dependent reactions to be reused and re-energized.

Stage 3: Regeneration

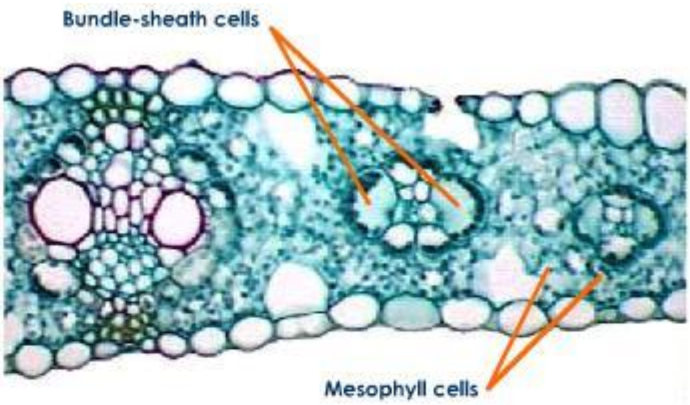
At this point, only one of the G3P molecules leaves the Calvin cycle and is sent to the cytoplasm to contribute to the formation of other compounds needed by the plant. Because the G3P exported from the chloroplast has three carbon atoms, it takes three "turns" of the Calvin cycle to fix enough net carbon to export one G3P. But each turn makes two G3Ps, thus three turns make six G3Ps. One is exported while the remaining five G3P molecules remain in the cycle and are used to regenerate RuBP, which enables the system to prepare for more CO_2 to be fixed. Three more molecules of ATP are used in these regeneration reactions.

The Four - Carbon Pathway

C_4 plants like maize, sugarcane; pearl millet, etc. have evolved a wonderful mechanism to avoid photorespiration, which is considered a wasteful process.

In these plants three or 2 types of photosynthetic cells namely mesophyll cells and bundle sheath cells. The bundle sheath cells are arranged in a wreath like manner, thus calling them as kranz anatomy (kranz : wreath).

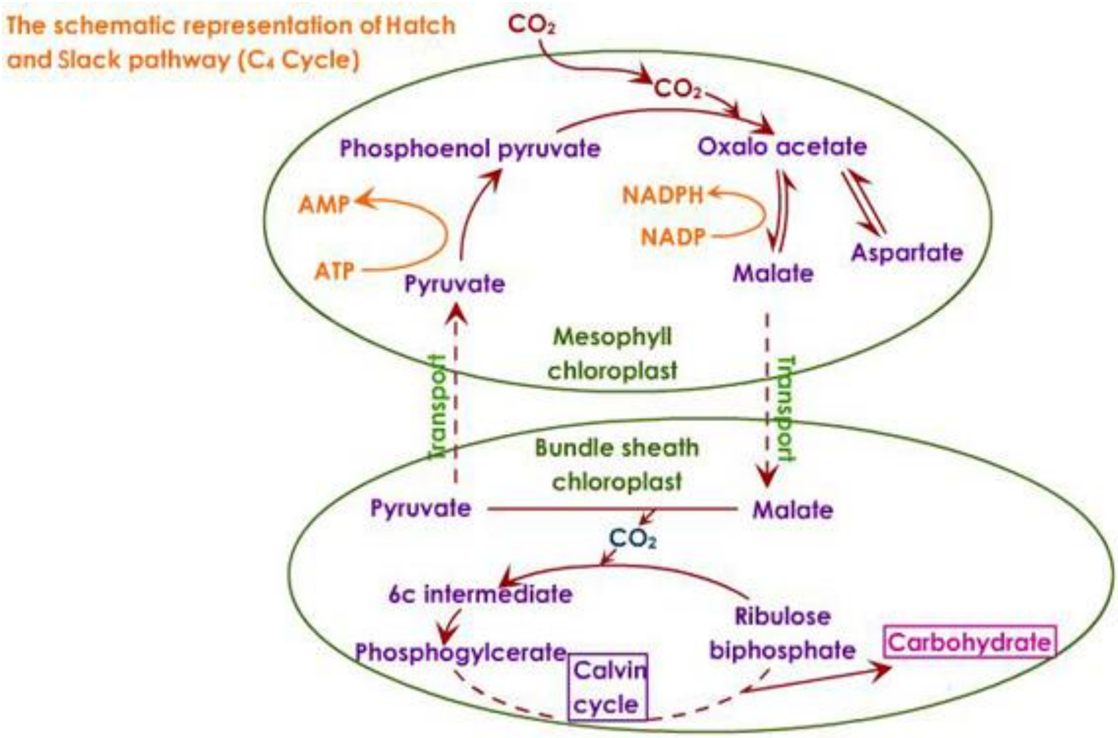
One more speciality of C_4 plants is that they contain dimorphic chloroplasts, that is chloroplasts in bundle sheath cells are agranal. The presence of two types of cells allows the occurrence of light reactions and carbon reactions separately.In C_4 plants, light reactions occur in the mesophyll cells, whereas CO_2 assimilation occurs in the bundle sheath cells. This type of separation does not allow O_2 released in mesophyll cells to escape into the bundle sheath cells. This prevents the oxygenation of RuBP, which is present in the bundle sheath cells.



Transverse section of maize leaf showing the arrangement of mesophyll and bundle-sheath cells. The C_4 pathway takes place in the mesophyll cells, and the C_3 pathway (Calvin cycle) operates in the bundle-sheath cells. Both types of cells contain chloroplasts.

To further avoid photorespiration, C_4 plants have evolved a CO_2 concentrating mechanism called the C_4 pathway. The main objective of C_4 pathway is to build up a high concentration of CO_2 in the vicinity of Rubisco, thus favoring carboxytition and suppressing photorespiration.

Many plants like maize and sugar cane, are far more efficient at taking up CO_2 than C_3 plants. The CO_2 acceptor in C_4 plants is phosphoenolpyruvate (PEP). PEP reacts with CO_2 to form oxaloacetic acid which is reduced by NADPH to form malic acid. The malic acid then reacts with RUBP to form pyruvic acid and PGA. The pyruvic acid is then phosphorylated by ATP to regenerate PEP while PGA is converted to triose phosphate as far as C_3 plants. These reactions are called the Hatch - Slack pathway.



These plants, however first fix carbon dioxide in the four - carbon compound oxaloacetic acid. C_4 plants have two rings of cells surrounding the vascular bundles. The outer mesophyll cells fix CO_2 using PEP and pass malic acid to the inner bundle sheath cells. Here CO_2 is released for acceptance by RUBP and the eventual formation of triose phosphate. The photosynthetic efficiency of C_4 plants is due to their ability to fix CO_2 in environmental conditions where CO_2 is the limiting factor. The C_4 photosynthetic pathway is more efficient than the C_3 pathway due to the absence of photorespiration in C_4 plants.

Difference between C3 and C4 cycle

C3 pathway involves set of carbon reactions which are catalyzed by the enzyme Rubisco to synthesize 3 carbon compound, 3-phosphoglycerate from 5-carbon compound, Ribulose bisphosphate.

C4 pathway also involves carbon fixation to synthesize 4 carbon compound Oxaloacetic acid. C4 pathway occurs only in some plants to prevent loss of energy by photorespiration.

C3 Pathway	C4 Cycle Pathway
C3 cycle operates in all plants.	C4 cycle operates only in C4 plants.
Ribulose bisphosphate is the primary acceptor of CO2.	Phosphoenol pyruvate is the primary acceptor of CO2.
Chloroplasts present are only of one type(Granal).	Chloroplasts of two different types(Granal and Agranal-bundle sheath chloroplast) are present in bundle sheath cells and mesophyll cells
Anatomy of leaves does not resemble Kranz anatomy	Leaves exhibited Kranz anatomy.
First stable product is a 3-carbon compound, phosphoglyceric acid(PGA).	First stable product is a 4-carbon compound, oxaloacetic acid(OAA).
Single CO2 fixation.	Two CO2 fixation.
Sunlight reaches saturation point.	Sunlight does not become saturates.

Fixation of 1 molecule of CO2 requires 3 ATP and 2 NADH.	Fixation of 1 molecule of CO2 requires 5 ATP and 3 NADH.
The carboxylase enzyme is RuBisCO.	The carboxylase enzyme is PEP carboxylase and RuBisCO.
Cannot operate under very low CO2 concentration.	Can operate under very low CO2 concentration.
CO2 fixation is slow and less efficient.	CO2 fixation is fast and more efficient.
Mesophyll cells exhibit Calvin cycle.	Bundle sheath cells exhibit Calvin cycle.
Photorespiration is observed.	Negligible amount of photorespiration.
Optimum temperature required for photosynthesis is between 20 degrees Celsius to 25 degrees Celsius.	Optimum temperature required for photosynthesis is between 30 degrees Celsius to 45 degrees Celsius.
This cycle is less efficient in utilizing CO2.	Highly efficient in utilizing CO2.
Occurs in plants like Mango, Apple etc.	Occurs in plants like Maize, Sorghum etc.

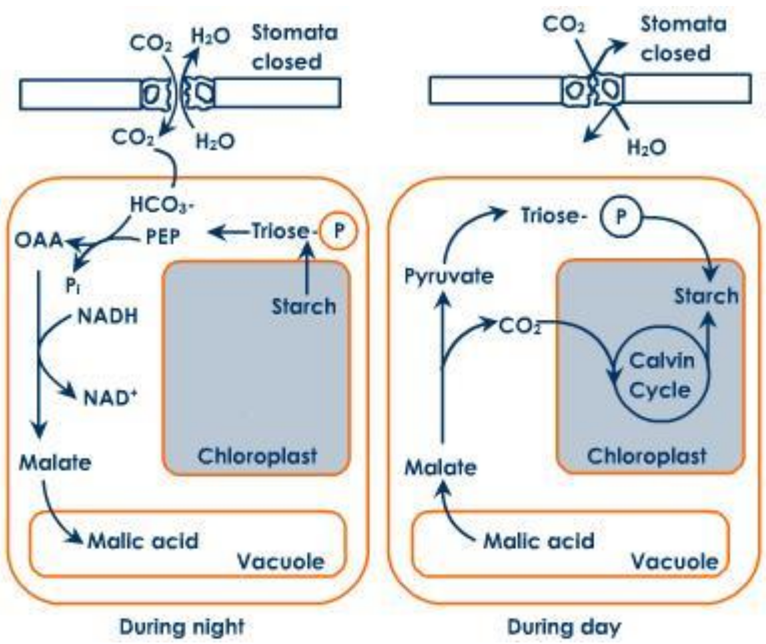
Crassulacean acid metabolism (CAM)

CAM refers to a mechanism of photosynthesis that occurs only in succulents and other plants that grow in dry conditions.

a) In CAM plants, CO_2 is taken up by the leaves, which are present on green stems through the stomata. But the stomata remain open only during the night. During the day it remains closed to conserve moisture.

b) The CO_2 taken is fixed in the same way as in C_4 plants, to from malic acid which is stored in the vacuole.

c) This malic acid formed during the night is used as a source of CO_2 during the day for photosynthesis to proceed via the C_3 pathway. Thus CAM is a kind of adaptation in certain plants (grown in dry conditions) to carry out photosynthesis without much loss of water, which is otherwise unavoidable in C_3 and C_4 photosynthetic mechanisms.



CAM pathway showing carbon dioxide uptake through open stomata during night and its utilization for the formation of malic acid which is stored in the vacuole. During day, the malic acid is decarboxylated to release carbon dioxide which is re-fixed to produce starch inside chloroplast via C_3 calvin cycle.

C3 PLANTS	C4 PLANTS	CAM PLANTS
Found in all photosynthetic plants.	Only in tropical plants.	Specially in succulents growing under semi-arid condition.
Plants that use the cycle can be hydrophytic, mesophytic or xerophytic.	Plants that use the cycle can be mesophytic.	Plants that use the cycle can be xerophytic.
Photoactive stomata.	Photoactive stomata.	Scotoactive cycle.
High rate of photorespiration.	Photorespiration : less or negligible.	Photorespiration : least or negligible.
Normal leaf anatomy.	Laf : Kranz anatomy.	Xeromorphic.
For the synthesis of glucose molecule or 6CO2 fixation : 12 NADPH and 18 ATPs are required.	12 NADPH and 30 ATPs are required.	12 NAPDH and 39ATPS are required.
Single CO2 fixation occurs.	Double carbon dioxide fixation.	Double carbon dioxide fixation.
Primary CO2 atmospheric acceptor RuBP.	Atmosphere CO2 acceptor : PEP(in mesophyll cell) and metabolic CO2 acceptor : RuBP(in bundle sheath cell)	Atmosphere CO2 acceptor : PEP(during night) and metabolic acceptor : RuBP(during day time).
First stable product is 3PGA.	First stable product is oxaloacetic acid(OAA).	First stable product is oxaloacetic acid(OAA).
First enzyme involved RuBisCO.	First enzyme involved PEP carboxylase.	First enzyme involved PEP carboxylase.

FACTORS AFFECTING PHOTOSYNTHESIS

Many external and internal factors affect the rate of photosynthesis. The external or environmental factors at: A light intensity, carbon dioxide concentration and temperature. The internal factor influencing the photosynthesis is chlorophyll content of the leaves and protoplasmic factors.

1.Light

Light is essential for photosynthesis. Photosynthesis does not take place in dark. The sun is the main source of light energy. Both quality and intensity of light are important for photosynthesis.

(a)Light Quality: The light consists of rays of different wavelengths.

Only red and blue light are effective for photosynthesis. Green light is reflected or transmitted. Therefore, it does not play role in photosynthesis. Light of wavelength longer than 700 run is not effective for photosynthesis for green plants. Experiments of **Engelmann** proved that maximum photosynthesis occurs in the red and blue part of the spectrum.

(b)Light Intensity: Photosynthesis begins at very low intensity. It becomes maximum at bright daylight. But it decreases in strong light. Different plants require different intensity of light. Most of light reaching green leaves is reflected or transmitted. Thus only a small part of light is absorbed. Thus only about 0.5 to 1.5% of light energy is in photosynthesis. Thus light is not a limiting factor at high intensity.

Light is a limiting factor at low intensity. Thus the rate of photosynthesis increases with an increase in light intensity. High light intensities affect the rate of photosynthesis. It increases the temperature of the leaves. Therefore, rate of transpiration increases. The stomata are closed. It stops the.Entry of CO_2. Thus photosynthesis is stopped. Light also cause photorespiration. Photorespiration reduces the yield.

2.Carbon dioxide

The atmosphere is the chief source of carbon dioxide. It contains only 0.03 % of the gas by volume. It is very small amount. Therefore, CO, remain a limiting factor. The increase in the amount of carbon dioxide increases the photosynthesis. This increase is more rapid up to I % of carbon dioxide concentration. But it slows down beyond this point. Higher concentrations have an inhibitory effect on photosynthesis. It is clear that increase in concentration of CO, increases the yield of plant

3.Temperature

A suitable temperature is necessary for photosynthesis. There are three cardinals of temperature for photosynthesis.

(a) Minimum: It is minimum temperature at which the photosynthesis starts. The plants of cold and temperate regions have lower values of these cardinals. But tropical plants have higher sable of these cardinals. Minimum temperature for many lichens is – 20°C. It is – 35^0 C for some conifers. Photosynthesis hardly starts at about 5°C in tropical plants. Desert plants like cactus can carry on photosynthesis even at 55°C

(b)Optimum: Maximum photosynthesis occurs at that point The optimum temperature also varies greatly. Photosynthesis increases with rise in temperature up to 25°C. This increase follows **Vant Hoffs law.** According to this law the rate of chemical reaction doubles for every rise of 10°C. This is true only if light or carbon dioxide is not the limiting factors.

(c) Maximum: It is the highest temperature at which photosynthesis can take place. There is an initial increase in the rate of photosynthesis at this temperature. But this is soon followed by a decline. Higher the temperature the more rapid is the decline. The decline may be due to one or more of the following causes:

(i) Accumulation of the end products of photosynthesis.

(ii) Inhibitory effect of high temperature on the activity of enzymes.

(iii)Failure of carbon dioxide to diffuse rapidly.

(iv) Increased consumption of the photosynthate in photorespiration

(v) Destructive effect of high temperatures on chlorophyll.

4. WATER

Water is one of the raw materials of photosynthesis. The amount of water actually used in photosynthesis is very small. Less than 1 percent water is absorbed by the plant. Therefore, it cannot be a limiting factor directly. But the water content of the leaf often acts as a limiting factor indirectly. The limiting effect of water is indirect. It maintains the turgor of the assimilatory cells. The rate of photosynthesis decreases in the cells which have lost their turgor, The loss of turgor of guard cells closed the stomata. It reduces the rate of photosynthesis.

5. OXYGEN

Photosynthesis does not take place in cells which lack oxygen. There are two reasons of this. First, the energy produced in oxygen respiration is necessary for photosynthesis. Second. oxygen is required for the production and maintenance of some substance. This substance is essential for photosynthesis. High concentrations of oxygen inhibit the rate of photosynthesis. It promotes photorespiration.

6. LEAF ANATOMY

Many factors of leaf anatomy affect the rate of photosynthesis. These factors influences the diffusion of carbon dioxide through the stomata. They also effect on the amount of light reaching the chlorenchyma. These factors are:

(i)Different leaves have different thickness of the cuticle and epidermis.

(ii)They develop palisade. They have different sizes and distributions of the intercellular spaces.

(iii)They have difference sizes, positions and distributions of the stomata.

(iv)They develop different types of chlorenchyma and the vascular tissues.

7. CHLOROPHYLL CONTENT

Chlorophyll is essential for photosynthesis. **Etiolated** plants and non-green tissues do not show photosynthesis. The green cells produce starch in variegated leaves. There are two views about the affect of chlorophyll on photosynthesis:

(i)Willstatter and Stoll: They believe that the rate of photosynthesis is not proportional to the amount of chlorophyll content. The rate of photosynthesis depends on the concentration of enzymes and chlorophyll.

(ii)Emerson (1927): He found a direct relationship between the amount of food formed and the chlorophyll content.

8. PROTOPLASMIC FACTOR

Photosynthesis does not start immediately after the appearance of chlorophyll in very young leaves. It starts after some time. Same thing happens when plants are transferred from dark to light. Thus some internal factor is present in the protoplasm of the cells. This is called **"the unknown factor" or the "protoplasmic factor"** It is enzymatic in nature. **Arnon** (1954) has demonstrated that cell free chloroplasts are capable of carrying out photosynthesis. This indicates that protoplasm is not necessary for photosynthesis. Thus the chloroplasts are the complete photosynthetic units. They contain all the necessary enzymes.

Importance of photosynthesis

Photosynthesis involves the production of organic compounds inside the chlorophyll containing cells from carbon dioxide and water in the presence of sunlight.

1. The process of photosynthesis results in synthesis of food from inorganic raw materials.
2. Green plants provides organic food to all the animals and heterotrophic plants.
3. Coal, petroleum and natural gas originated on degradation of the past plant and animal parts (formed by photosynthesis).
4. Plant products like timber ,rubber, resin, drugs, oils are derived from photosynthesis.
5. Photosynthesis helps in the addition of oxygen in the atmosphere required by all organisms.
6. Photosynthesis decreases the concentration of carbon dioxide increase due to respiration of organisms.

Photorespiration

Definition : The process by which in the presence of light plant consumes oxygen and releases carbon dioxide (instead of fixing carbon dioxide) during photosynthesis, resulting in a decrease in photosynthetic output since no ATP is produced and carbon (as well as nitrogen in the form of ammonia) is lost inevitably.

Supplement : Plants, especially C3 plants, face the problem of **photorespiration**. In hot dry days, these plants tend to close their stomata to prevent excessive loss of water (from transpiration). Inevitably, the carbon dioxide cannot enter the leaves (via the stomata) resulting in the levels of carbon dioxide within the leaves to become low. Since there are few carbon dioxide molecules to fix, the oxygen molecules are used as a substitute to produce G3P. Because of **photorespiration**, instead of about 2 molecules of G3P, only one G3P is produced and a toxic phosphoglycolate (which the plant must get rid of) is also formed. Some plants such as CAM plants and C4 plants have evolved mechanisms to avoid **photorespiration**.

Process : Photorespiration is a biochemical process in plants in which, especially under conditions of water stress, oxygen inhibits the Calvin cycle, the carbon fixation portion of photosynthesis.

Photorespiration results in the light-dependent uptake of oxygen and release of carbon dioxide and is associated with the synthesis and metabolism of a small molecule called glycolate.

Photorespiration takes place in green plants at the same time that photosynthesis does. Because in photosynthesis carbon dioxide is taken in, and in photorespiration carbon dioxide is given off, these two processes work against each other.

The end result is that photorespiration decreases the net amount of carbon dioxide which is converted into sugars by a photosynthesizing plant. By interfering with photosynthesis in this way, photorespiration may significantly limit the growth rate of some plants.Plants of photorespiration : *Nicotiana*; *Psium*; *Grossypium*; *Nitella*; *Oryza etc.*

Importance of photorespiration

Photorespiration takes place in the presence of light under high temperature and oxygen concentration. As a result of photorespiration excess amount of carbon dioxide is evolved. Photorespiration always competes with the carbon fixing process. It causes heavy loss of fixed carbon. It does not produce any energy rich compounds. It protects the plants from the photo oxidative damage. When the amount of carbon dioxide is low so as to utilize the light energy, the excess light energy is then used for photorespiration. The increased amount of carbon dioxide favors photosynthesis whereas the increased amount of oxygen and light energy initiates the photorespiration. The photorespiration is negligible or absent in the C_4 plants.