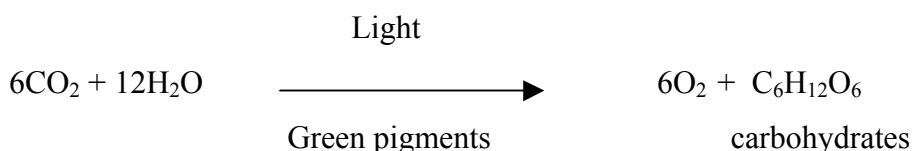


10. PHOTOSYNTHESIS

Photosynthesis is a vital physiological process where in the chloroplast of green plants synthesizes sugars by using water and carbon dioxide in the presence of light.

Photosynthesis literally means *synthesis with the help of light* i.e. plant synthesise organic matter (carbohydrates) in the presence of light.

Photosynthesis is sometimes called as carbon assimilation (assimilation: absorption into the system). This is represented by the following traditional equation.



During the process of photosynthesis, the light energy is converted into chemical energy and is stored in the organic matter, which is usually the carbohydrate. One molecule of glucose for instance, contains about 686 K Calories energy. CO₂ and water constitute the raw material for this process and oxygen and water are formed as the by products during photosynthesis. *Stephen Hales* (1727) first explained the relationship between sunlight and leaves and *Sachs* (1887) established that starch was the visible product of photosynthesis.

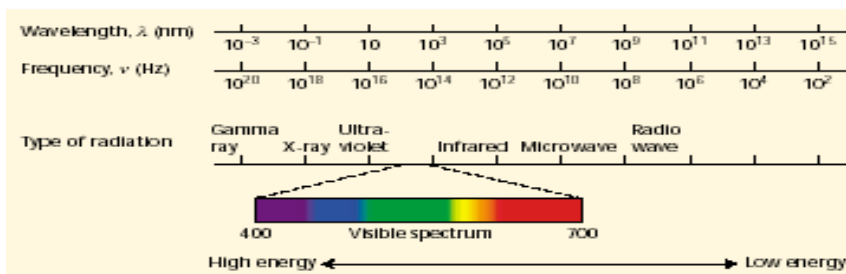


FIGURE 7.2 Electromagnetic spectrum. Wavelength (λ) and frequency (ν) are inversely related. Our eyes are sensitive to only a narrow range of wavelengths of radiation, the visible region, which extends from about 400 nm (violet) to about 700 nm (red). Short-wavelength (high-frequency) light has a high energy content; long-wavelength (low-frequency) light has a low energy content.

Photosynthetic apparatus

The chloroplast in green plants constitutes the photosynthetic apparatus. In higher plants, the chloroplast is discoid in shape, 4-6 μ in length and 1-2 μ thick. The chloroplast is bounded by two unit membranes of approximately 50 Å thickness and consists of lipids and

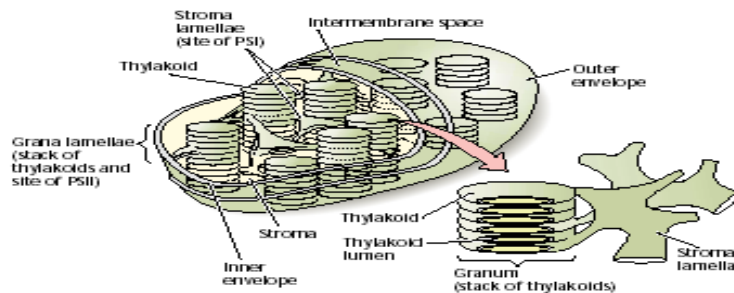
proteins. The thickness of the two membranes including the space enclosed by them is approximately 300°A (1 Angstrom: 0.1 cm).

Internally, the chloroplast is filled with a hydrophilic matrix called as *stroma* embedded with *grana*. Each grana consists of 5-25 disk shaped grana lamellae (thylakoid) placed one above the other like the stack of coins. Each grana lamella of thylakoid encloses a space called *loculus* and the thylakoid membrane consists of alternating layer of lipids and proteins. Some of the grana lamella of thylakoid of grana are connected with thylakoid of other grana by somewhat thinner *stroma lamella or fret membrane*. Chlorophyll and other photosynthetic pigments are confined to grana. The chlorophylls are the site of photochemical reactions.

Photosynthetic pigments

Photosynthetic pigments are of three types; Chlorophylls, Carotenoids and Phycobillins.

- Chlorophylls and Carotenoids are insoluble in water and can be extracted only with organic solvents such as acetone, petroleum ether and alcohol.
- Phycobillins are soluble in water
- Carotenoids include carotenes and xanthophylls. The xanthophylls are also called as *carotenols*.



Chlorophylls (green pigments)

Chlorophylls are magnesium porphyrin compounds. The porphyrin ring consists of four pyrrol rings joined together by CH bridges. Long chain C atoms called as phytol chain is attached to porphyrin ring at pyrrol ring IV.

The chemical structure of chlorophyll *a* and chlorophyll *b* are well established. The molecular formula for chlorophyll *a*: $C_{55}H_{72}O_5N_4$ Mg and chlorophyll *b*: $C_{55}H_{70}O_6N_4$ Mg. Both of them consist of Mg porphyrin head which is hydrophilic and a phytol tail which is

lipophilic. The two chlorophylls differ because in chlorophyll *b* there is a –CHO group instead of CH₃ group at the 3rd C atom in pyrrol ring II.

Chlorophyll is formed from protochlorophyll in light. The protochlorophyll lacks 2H atoms one each at 7th and 8th C atoms in pyrrol ring IV.

Carotenoids (yellow or orange pigments)

1. Carotenes: Carotenes are hydrocarbons with a molecular formula C₄₀H₅₆

2. Xanthophylls (carotenols)

They are similar to carotenes but differ in having two oxygen atoms in the form of hydroxyl or carboxyl group. The molecular formula is C₄₀H₅₆O₂. The role of Carotenoids is absorption of light energy and transfer the light energy to chlorophyll *a* molecules. They also play a very important role in preventing photodynamic damage within the photosynthetic apparatus. Photodynamic damage is caused by O₂ molecules which is very reactive and is capable of oxidizing whole range of organic compounds such as chlorophylls and there by making them unfit for their normal physiological function.

Phycobillins (red and blue pigments)

These also contain four pyrrol rings but lack Mg and the phytol chain.

Location of photosynthetic pigments in chloroplast

The photosynthetic pigments are located in grana portions of the chloroplast. They are present in the thylakoid membrane or membrane of grana lamella. The membrane of thylakoid is made up of proteins and lipids or the membrane consists of both lipid layer and protein layer. The hydrophilic *heads* of the chlorophyll molecules remain embedded in the protein layer while lipophilic phytol tail in the lipid layer. The other pigments are thought to be present along with chlorophyll molecules.

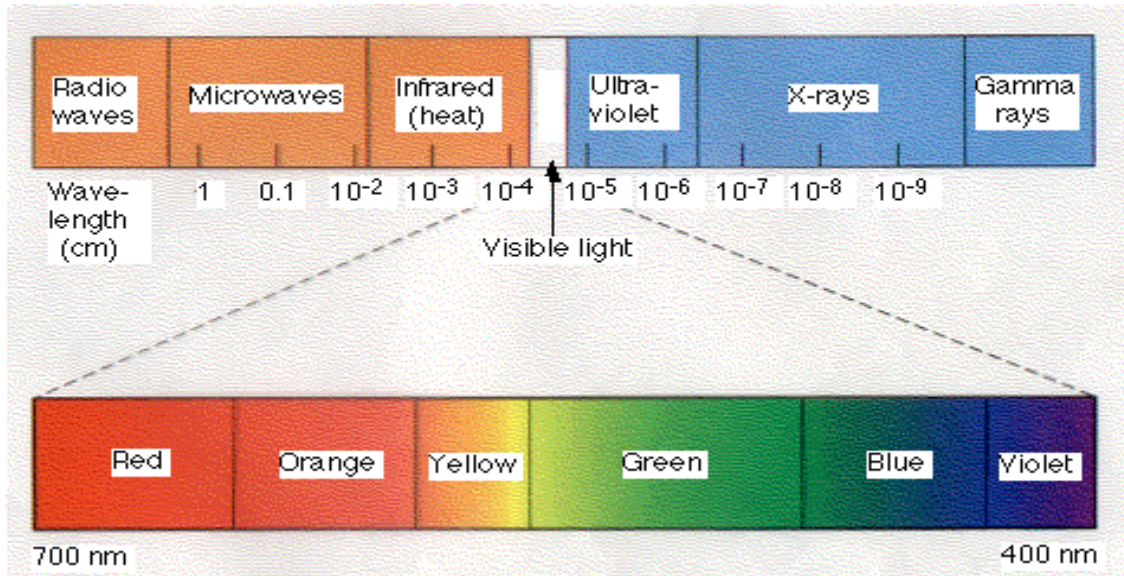
Distribution of photosynthetic pigments in plant kingdom

Pigments	Distribution in plant kingdom
Chlorophylls	

Chlorophyll <i>a</i>	All photosynthesizing plants except bacteria
Chlorophyll <i>b</i>	Higher plants and green algae
Chlorophyll <i>c</i>	Diatoms and brown algae
Chlorophyll <i>d</i>	Red algae
Bacteria chlorophylls <i>a, b, c, d & e</i>	Purple and green bacteria
Carotenoids	
Carotenes (α and β)	Higher plants and algae
Xanthophylls	Higher plants and algae
Lutein	Green leaves and Green and Red algae
Violaxanthin	Green leaves
Fucoxanthin	Brown algae
Phycobillins	
Phycocyanins	Blue green algae and red algae
Phycoerythrins	Blue green algae and Red algae
Allophycocyanin	Blue – green and Red algae

Light

The chief source of light energy for photosynthesis is sun. The solar radiation or solar energy passes through the space and reaches the earth in the form of *electromagnetic radiation* with waves of varying lengths. The various portions of electromagnetic spectrum are gamma rays, ultraviolet rays, visible rays and infrared rays. The wavelength of these rays ranges from 280 nm to 1000 nm.

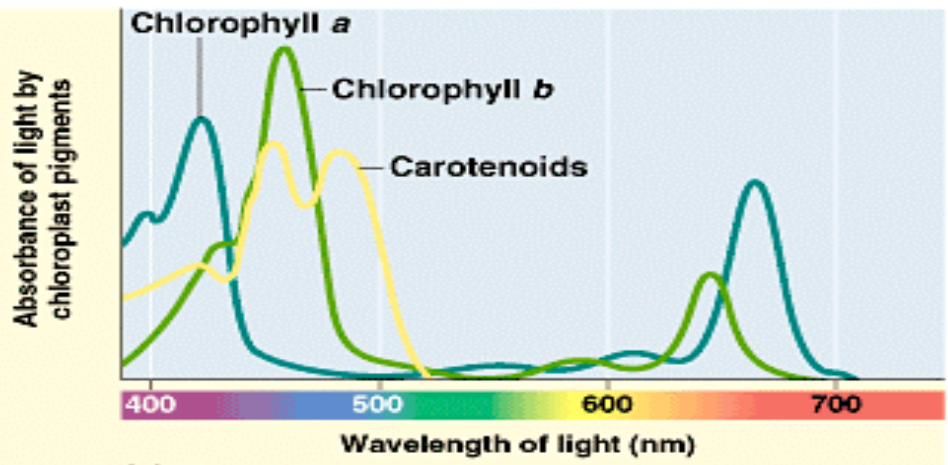


Below 280 nm	-	X rays, Gamma rays and Cosmic rays	
280-390 nm	-	Ultra violet radiation	
400-510 nm	-	Blue light	} Visible light (PAR) (VIBGYOR)
510-610 nm	-	Green light	
610-700 nm	-	Red light	
700-1000 nm	-	Far red light (IR)	

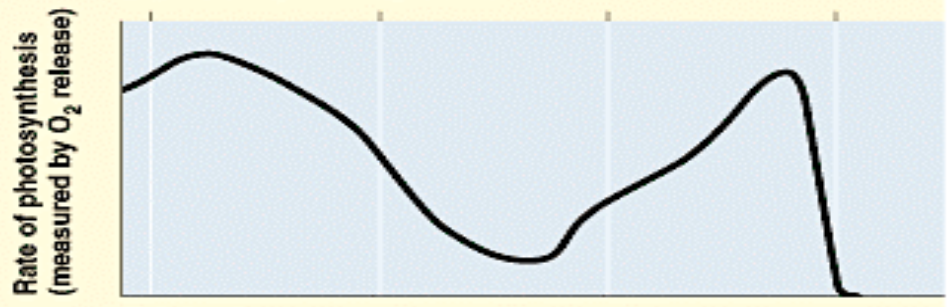
Photosynthetic pigments absorb light energy only in the visible part of the spectrum. The earth receives only about 40% (or about 5×10^{20} K cal) of the total solar energy. The rest is either absorbed by the atmosphere or scattered into the space. Only about 1% of the total solar energy received by the earth is absorbed by the pigments and utilized in photosynthesis.

Absorption spectra of chlorophyll

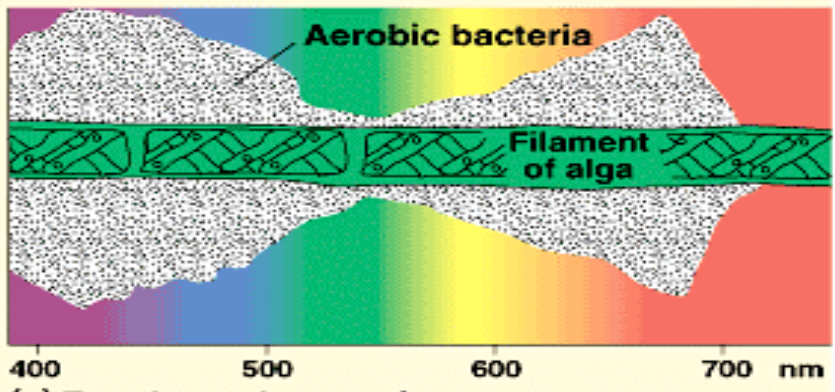
The absorption of different wavelengths of light by a particular pigment is called *absorption spectrum*. Chlorophylls absorb maximum light in the violet blue and red part of the spectrum. The absorption peaks of chlorophyll *a* are 410 and 660; for chlorophyll *b* 452 and 642. Carotenoids absorb light energy in blue and blue green part of the spectrum.



(a) Absorption spectra



(b) Action spectrum



(c) Engelmann's experiment

Transfer of light energy absorbed by accessory pigments to chlorophyll *a*

All pigments except chlorophyll *a* are called as *accessory pigments or antenna pigments*. The light energy absorbed by accessory pigments is transferred to chlorophyll *a* molecule. The transfer of light energy from accessory pigments to chlorophyll *a* is called as *resonance or Forster transfer* and takes part in primary photochemical reaction in photosynthesis. Chlorophyll *a* molecules also absorb light energy directly. As a result of absorbing the light energy, the chlorophyll molecule gets *excited*.

Excited states of atoms or molecules (*fluorescence and phosphorescence*)

The normal state of the chlorophyll molecule or atom is called as *ground state or singlet state*. When an electron of a molecule or an atom absorbs a quantum of light, it is raised to a higher energy level which is called as *excited second singlet state*. This state is unstable and has a life time of 10^{-12} seconds.

The electron comes to the next higher energy level by the loss of some of its extra energy in the form of heat. This higher energy level is called as *excited first singlet state* and is also unstable with a half life of 10^{-9} seconds. From the first singlet state, the excited electron may return to the ground state in two ways viz., either losing its remaining extra energy in the form of heat or in the form of radiant energy. The second process is called *fluorescence*. The chlorophyll molecules exit the extra energy in the form of fluorescent light when they are exposed to incident light. Fluorescent light is of longer wavelength than the incident light.

The excited molecule or the atom may also lose its excitation energy by internal conversion and comes to another excited state called as *triplet state* which is meta stable with a half life of 10^{-3} seconds. From the triplet state, the excited molecule or the atom may return to the ground state in three ways.

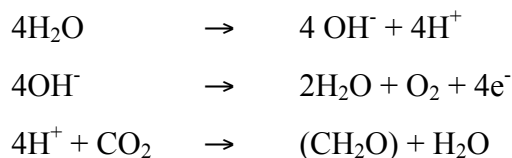
- (i) By losing its remaining extra energy in the form of heat
- (ii) By losing extra energy in the form of radiant energy (*phosphorescence*) and the chlorophyll molecules emit phosphorescent light even after the incident radiant light is cut off. The phosphorescent light is of longer wavelength than incident light and also fluorescent light.

- (iii) Electrons carrying the extra energy may be expelled from the molecule and is consumed in some further photochemical reaction and the fresh normal electron returns to the molecule.

Quantum requirement and quantum yield

Light rays consist of tiny particles called *photons* and the energy carried by a photon is called *quantum*. The number of photons (quantum) required to release one molecule of oxygen in photosynthesis is called *quantum requirement*. On the other hand, the number of oxygen molecules released per photon of light in photosynthesis is called as *quantum yield*. The quantum yield is always in fraction of one.

Warburg found minimum quantum requirement for photosynthesis as four. It is because the reduction of one molecule of CO₂ by two molecules of H₂O requires the transfer of 4H atoms. The transfer of each H atoms from H₂O to CO₂ requires one photon or quantum of light.



(CH₂O) in the above equation represent 1/6 of the carbohydrate molecule such as glucose. One molecule of glucose contains 686 K. cal of energy. Therefore, 1/6 glucose molecule contains 686/6 i.e., approximately 112 K.cal energy. It is also known that the rate of photosynthesis is maximum at red light and each photon of red light contains about 40 K cal. of energy. This would suggest that the efficiency with which the plants can convert light energy into chemical energy is 112 / 40 x 4: 70%, which indeed is very high.

According to Emerson and his coworkers, photosynthesis is a very complicated process and is not so efficient to convert all the light energy into chemical energy. There is a considerable loss of light energy absorbed during photosynthesis and therefore the minimum quantum requirement for photosynthesis as suggested by Emerson and coworkers are 8-10. Considering that the quantum requirement for photosynthesis is 8-10, the quantum yield would accordingly be 1/8 to 1/10 (0.125 to 0.10)

Mechanism of Photosynthesis

Photo systems (Two pigment systems)

The discovery of red drop and the Emerson's enhancement effect led the scientists to suggest that photosynthesis is driven by two photochemical processes. These processes are associated with two groups of photosynthetic pigments called as *pigment system I* and *pigment system II*. Wavelength of light shorter than 680 nm affect both the pigments systems while wavelength longer than 680 nm affect only pigment system I.

In green plants, pigment system I contains chlorophyll *a*, *b* and carotene. In this pigment system, a very small amount of chlorophyll *a* absorbing light at 700 nm, known as P700 however constitutes the reaction centre of *photosystem I*.

The pigment system II contains chlorophyll *b* and some forms of chlorophyll *a* (such as chlorophyll *a* 662, chlorophyll *a* 677 and chlorophyll *a* 679) and xanthophylls. A very small amount of special form of chlorophyll called P680 constitute the reaction centre of pigment system II. Carotenoids are present in both the pigment systems

The two pigment systems I and II are interconnected by a protein complex called cytochrome b_6-f complex. The other intermediate components of electron transport chain *viz.*, plastoquinone (PQ) and plastocyanin (PC) act as mobile electron carriers between the complex and either of the two pigment systems. The light energy absorbed by other pigment is ultimately trapped by P700 and P680 forms of chlorophyll *a* which alone take part in further photochemical reaction.

Pigment system I (PSI) complex consists of 200 chlorophylls, 50 Carotenoids and a molecule of chlorophyll *a* absorbing light at 700 nm(P700) and this constitute the reaction centre of photosystem I. Pigment system II (PSII) complex consists of 200 chlorophylls, 50 Carotenoids and a mole of chlorophyll *a* absorbing light at 680 nm, called P 680 at the centre. This constitutes the reaction centre of pigment system II.

Photosynthetic units – The Quantasomes

Emerson and Arnold (1932) showed that about 2500 chlorophyll molecules are require fixing one molecule of CO₂ in photosynthesis. This number of chlorophyll molecules was called the *chlorophyll unit* but the name was subsequently changed to *photosynthetic*

unit. However, since the reduction or fixation of one CO₂ molecule requires about 10 quanta of light, it is assured that 10 flashes of light are required to yield one O₂ molecule or reduction of one molecule of CO₂. Thus each individual unit would contain 1/10th of 2500 i.e., 250 molecules.

Action spectrum

The pigments present in plants or any living organism have the ability to absorb radiant energy to carry out photo physiological reactions. It is difficult to decide which specific pigment is actually associated with the particular photochemical reactions. Hence, a common procedure to identify the pigment involved in a particular photoreaction is to determine the action spectrum i.e. measuring the rate of the particular photoreaction.

Once the action spectrum for a photo physiological reaction is determined, the next step is to compare this action spectrum with absorption spectrum of a pigment.

Two pigments, A and B were isolated from the same plant and their absorption spectra were determined. Pigment A has a peak in absorption at 395 nm and the pigment B at 660 nm. The close correspondence between the absorption spectrum and the action spectrum of pigment B strongly supports that Pigment B is responsible for absorbing radiant energy to drive this photoreaction.

Mechanism of photosynthesis

The biosynthesis of glucose by the chloroplast of green plants using water and CO₂ in the presence of light is called photosynthesis. Photosynthesis is a complex process of synthesis of organic food materials. It is a complicated oxidation- reduction process where water is oxidized and CO₂ is reduced to carbohydrates. The mechanism of photosynthesis consists of two parts.

1. Light reaction / Primary photochemical reaction / Hill's reaction/ Arnon's cycle
2. Dark reaction / Black man's reaction / Path of carbon in photosynthesis.

1. Light reaction or Primary photochemical reaction or Hill's reaction

In light reaction, ATP and NADPH₂ are produced and in the dark reaction, CO₂ is reduced with the help of ATP and NADPH₂ to produce glucose. The light reaction is called primary photochemical reaction as it is induced by light. Light reaction is also called as Hill's

reaction as Hill proved that chloroplast produce O₂ from water in the presence of light. It is also called as Arnon's cycle because Arnon showed that the H⁺ ions released by the break down of water are used to reduce the coenzyme NADP to NADPH. Light reaction includes photophosphorylation as ATP is synthesized in the presence of light. The reaction takes place only in the presence of light in *grana* portion of the chloroplast and it is faster than dark reaction. The chlorophyll absorbs the light energy and hence the chlorophyll is called as *photosystem* or *pigment system*. Chlorophylls are of different types and they absorb different wavelengths of light. Accordingly, chlorophylls exist in two photo systems, Photosystem I (PSI) and Photosystem II (PS II). Both photo systems are affected by light with wavelengths shorter than 680nm, while PS I is affected by light with wavelengths longer than 680nm.

The components of photo systems

Photosystem I	Photosystem II
Chlorophyll <i>a</i> 670	Chlorophyll <i>a</i> 660
Chlorophyll <i>a</i> 680	Chlorophyll <i>a</i> 670
Chlorophyll <i>a</i> 695	Chlorophyll <i>a</i> 680 or P680
Chlorophyll <i>a</i> 700 or P700	Chlorophyll <i>b</i>
Chlorophyll <i>b</i>	Phycobillins
Carotenoids	Xanthophylls
P700 form of Chlorophyll <i>a</i> is the active reaction centre	P680 form of Chlorophyll <i>a</i> is the active reaction centre

The light reaction can be studied under the following headings.

i. Absorption of light energy by chloroplast pigments

Different chloroplast pigments absorb light in different regions of the visible part of the spectrum.

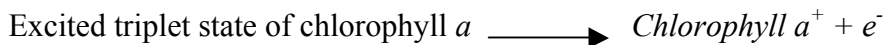
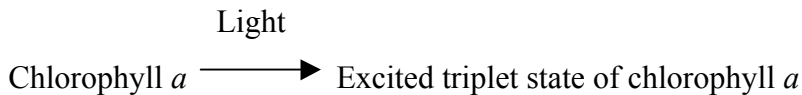
ii. Transfer of light energy from accessory pigments to chlorophyll *a*

All the photosynthetic pigments except chlorophyll *a* are called as accessory or antenna pigments. The light energy absorbed by the accessory pigments is transferred by resonance to chlorophyll *a* which alone can take part in photochemical reaction. Chlorophyll

a molecule can also absorb the light energy directly. In pigment system I, the photoreaction centre is P700 and in pigment system II, it is P680.

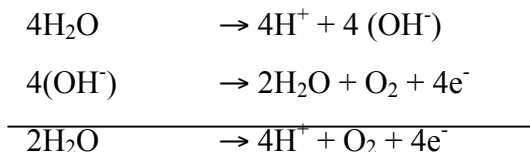
iii. Activation of chlorophyll molecule by photon of light

When P700 or P680 forms of chlorophyll *a* receives a photon (quantum) of light, becomes an excited molecule having more energy than the ground state energy. After passing through the unstable second singlet state and first singlet stage the chlorophyll molecules comes to the meta stable triplet state. This excited state of chlorophyll molecule takes part further in primary photochemical reaction i.e. the electron is expelled from the chlorophyll *a* molecule.



iv. Photolysis of water and O₂ evolution (oxidation of water)

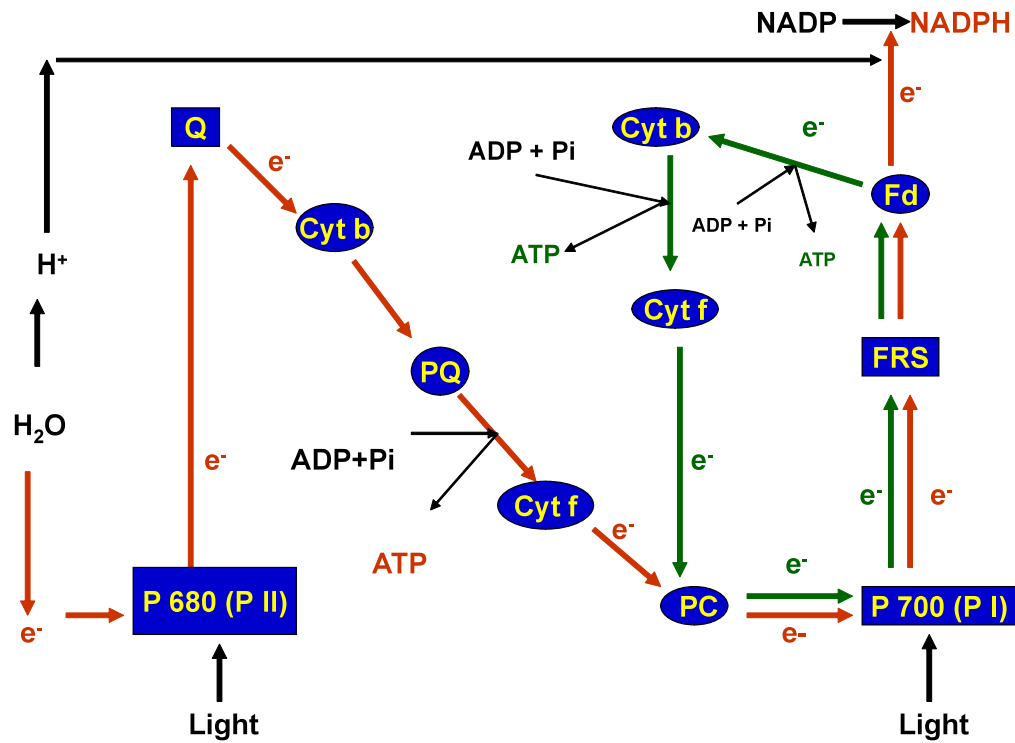
These processes are associated with pigment system II and are catalyzed by Mn⁺⁺ and Cl⁻ ions. When pigment system II is active i.e it receives the light, the water molecules split into OH⁻ and H⁺ ions (*Photolysis of water*). The OH⁻ ions unite to form some water molecules again and release O₂ and electrons.



v. Electron transport and production of assimilatory powers (NADPH₂ and ATP)

It has already been observed that when chlorophyll molecule receives the photon of light, an electron is expelled from the chlorophyll *a* molecule along with extra energy. This electron after traveling through a number of electron carriers is utilized for the production of NADPH₂ from NADP and also utilized for the formation of ATP molecules from ADP and inorganic phosphate (Pi). The transfer of electrons through a series of coenzymes is called *electron transport* and the process of formation of ATP from ADP and Pi using the energy of electron transport is called as *photosynthetic phosphorylation or photophosphorylation*. The types of Phosphorylation include *cyclic and non- cyclic*.

Cyclic electron transport and cyclic photophosphorylation



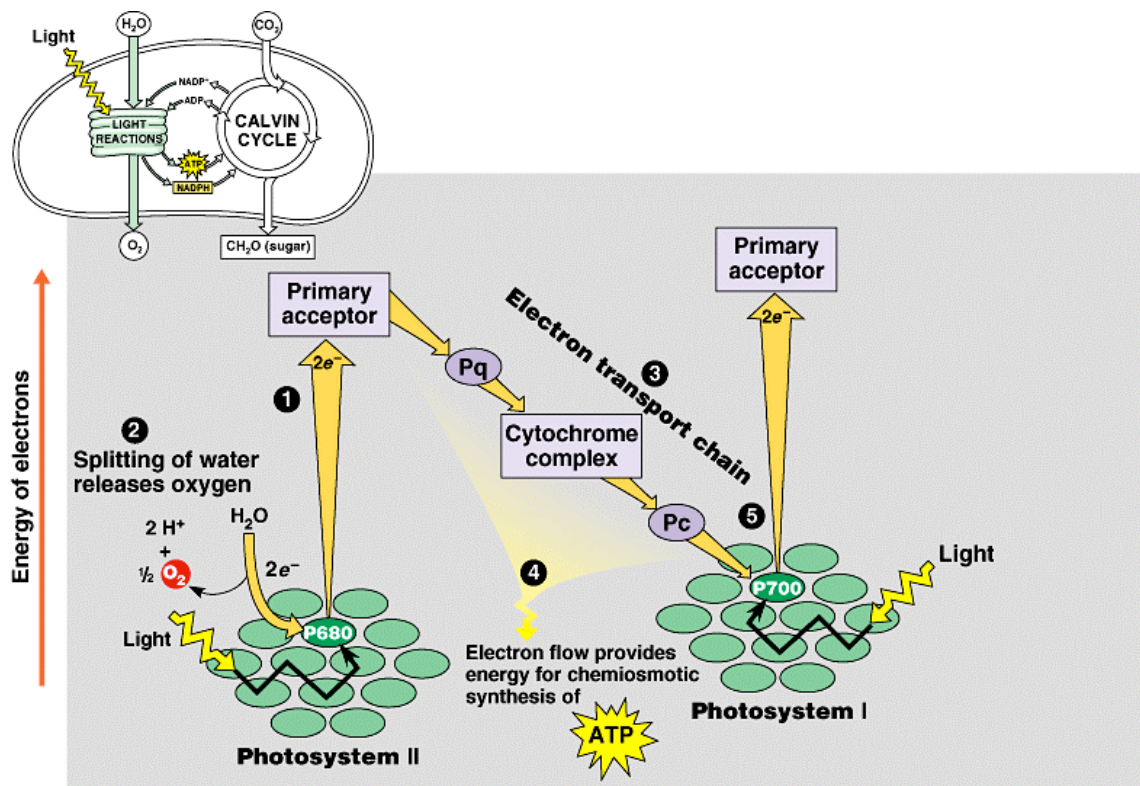
The electrons released from photosystem I goes through a series of coenzymes and returns back to the same photosystem I. This electron transport is called *cyclic electron transport*. The synthesis of ATP occurring in cyclic electron transport is called *cyclic photophosphorylation*. The cyclic electron transport involves only pigment system I. This situation is created when the activity of pigment system II is blocked. Under this condition,

1. Only pigment system I remain active
2. Photolysis of water does not take place
3. Blockage of noncyclic ATP formation and this causes a drop in CO₂ assimilation in dark reaction
4. There is a consequent shortage of oxidized NADP

Thus, when P700 molecule is excited in pigment system I by absorbing a photon (quantum) of light, the ejected electron is captured by ferredoxin *via* FRS. From ferredoxin, the electrons are not used up for reducing NADP to NADPH + H⁺ but ultimately it falls back

to the P700 molecule via number of other intermediate electron carriers. The electron carriers are probably cytochrome b_6 , cytochrome f and plastocyanin.

During this electron transport, phosphorylation of ADP molecule to form ATP molecule take place at two places i.e., between ferredoxin and cytochrome b_6 and between cytochrome b_6 and cytochrome f . Thus, two ATP molecules are produced in this cycle. Since the electron ejected from P700 molecule is cycled back, the process has been called as *cyclic electron transport* and the accompanying phosphorylation as the *cyclic photophosphorylation*.



Significance of cyclic photophosphorylation

1. During cyclic electron transport and phosphorylation, photolysis of water, O₂ evolution and reduction of NADP do not take place.
2. The electron returns or cycles back to original position in the P700 form of chlorophyll *a*. Here, chlorophyll molecule serves both as donor and acceptor of the electron.
3. It generates energy rich ATP molecules at two sites and as such cannot drive dark reactions of photosynthesis

On the other hand, non- cyclic photophosphorylation does not produce sufficient ATP in relation to NADPH to operate the dark phase of photosynthesis. Therefore, the deficiency of ATP molecule in non-cyclic photophosphorylation is made up by the operations of cyclic photophosphorylation.

Secondly, the cyclic photophosphorylation may be an important process in providing ATP for photosynthesis and other processes such as synthesis of starch, proteins, lipids, nucleic acids and pigments within the chloroplast.

Non cyclic photophosphorylation

The electron released from photosystem II goes through a series of enzymes and Co-enzymes to photosystem I. This is called non cyclic electron transport and the Synthesis of ATP in non cyclic electron transport is called non- cyclic photo phosphorylation. The main function of non cyclic electron transport is to produce the assimilatory powers such as NADPH₂ and ATP and the process occurs in photosystem I and II.

This process of electron transport is initiated by the absorption of a photon (quantum) of light by P680 form of chlorophyll *a* molecule in the pigment system II, which gets excited and an electron is ejected from it so that an electron deficiency or a hole is left behind in the P680 molecule.

The ejected electron is trapped by an unknown compound known as Q. From Q, the electron passes downhill along a series of compounds or intermediated electron carriers such as cytochrome *b*₆, plastoquinone, cytochrome *f* and a copper containing plastocyanin and ultimately received by pigment system I. At one place during electron transport i.e.

between plastoquinone and cytochrome *f*, one molecule of ATP is formed from ADP and inorganic phosphate.

Now, when a photon of light is absorbed by P700 form of chlorophyll molecule in the pigment system I, this gets excited and an electron is ejected from it. This ejected electron is trapped by FRS (Ferredoxin Reducing Substance) and it is then transferred to a non-heme iron protein called ferredoxin. From ferredoxin, electron is transferred to NADP so that NADP is reduced to NADPH + H⁺

The hole in pigment system I has been filled by electron coming from pigment system II. But, the hole or an electron deficiency in pigment system II is filled up by the electron coming from photolysis of water where, water acts as electron donor.

In this scheme of electron transport, the electron ejected from pigment system II did not return to its place of origin, instead it is taken up by pigment system I. Similarly, the electron ejected from pigment system I did not cycle back and was consumed in reducing NADP. Therefore, this electron transport has been called as *non-cyclic electron transport* and accompanying phosphorylation as *non-cyclic photophosphorylation*.

The non cyclic electron transport (photophosphorylation) takes the shape of Z and hence it is called by the name Z-scheme. Non cyclic photophosphorylation and O₂ evolution are inhibited by CMU (3-(4'-Chlorophyl) – 1-dimethyl urea and 3-(3-4-dichlorophenyl)-1, 1-dimethyl urea (DCMU).

Significance of non cyclic electron transport

1. It involves PS I and PSII
2. The electron expelled from P680 of PSII is transferred to PS I and hence it is a non cyclic electron transport.
3. In non cyclic electron transport, photolysis of water (Hill's reaction and evolution of O₂) takes place.
4. Phosphorylation (synthesis of ATP molecules) takes place at only one place.
5. The electron released during photolysis of water is transferred to PS II.
6. The hydrogen ions (H⁺) released from water are accepted by NADP and it becomes NADPH₂

7. At the end of non cyclic electron transport, energy rich ATP, assimilatory power NADPH_2 and oxygen from photolysis of water are observed.
8. The ATP and NADPH_2 are essential for the dark reaction wherein, reduction of CO_2 to carbohydrate takes place.

Comparison of cyclic and non cyclic electron transport and photophosphorylation in chloroplasts

	Cyclic electron transport and photo phosphorylation	Non cyclic electron transport and photo phosphorylation
1	Associated with pigment system I	Associated with pigment system I and II
2	The electron expelled from chlorophyll molecule is cycled back	The electron expelled from chlorophyll molecule is not cycled back. But, its loss is compensated by electron coming from photolysis of water
3	Photolysis of water and evolution of O_2 do not take place	Photolysis of water and evolution of O_2 take place
4	Phosphorylation takes place at two places	Phosphorylation takes place at only one place
5	NADP^+ is not reduced	NADP^+ is reduced to $\text{NADPH}^+ + \text{H}^+$

Significance of light reaction

1. Light reaction takes place in chlorophyll in the presence of light.
2. During light reaction, the assimilatory powers ATP and NADPH_2 are synthesized.
3. The assimilatory powers are used in dark reaction for the conversion of CO_2 into sugars.
4. Photolysis of water occurs in light reaction. The H^+ ions released from water are used for the synthesis of NADPH_2
5. Plants release O_2 during light reaction

Red drop and Emerson's enhancement effect

Robert Emerson noticed a sharp decrease in quantum yield at wavelength greater than 680 nm, while determining the quantum yield of photosynthesis in *chlorella* using

monochromatic light of different wavelengths. Since this decrease in quantum yield took place in the red part of the spectrum, the phenomenon was called as *red drop*.

Later, they found that the inefficient far-red light beyond 680 nm could be made fully efficient if supplemented with light of shorter wavelength (blue light). The quantum yield from the two combined beams of light was found to be greater than the sum effects of both beams used separately. This enhancement of photosynthesis is called as *Emerson's Enhancement*.