

CHAPTER-13

PHOTOSYNTHESIS IN HIGHER PLANTS

Introduction

Photosynthesis is a process by which plants create their food by using sunlight. This process was first seen more than 3.4 billion years ago in organisms that were similar to bacteria. Evidence showed that they did not absorb visible light, instead, they used near-infrared and produced sulphur or sulphate compounds. It would be another 470 million years until the first land plants emerged.

“**Photosynthesis** is a process used by plants in which energy from sunlight is used to convert carbon dioxide and water into molecules needed for growth. These molecules include sugars, enzymes, and chlorophyll. Light energy is absorbed by the green chemical chlorophyll.”

All animals and human beings are dependent on plants for food and these plants synthesize the food via a physiochemical process called **Photosynthesis**. This process is important because:

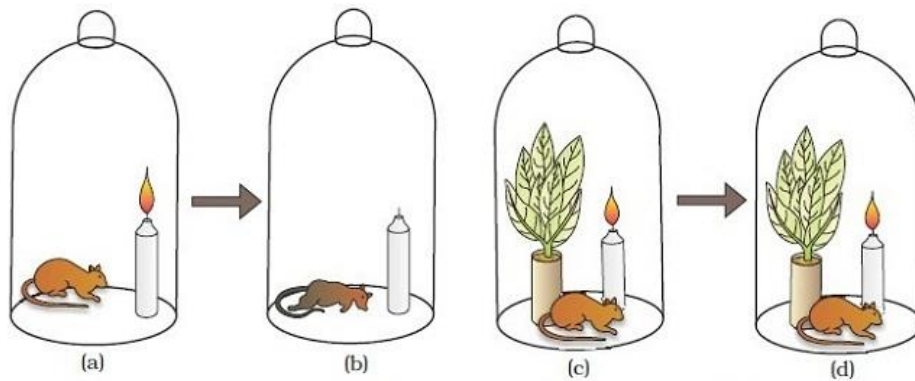
- It is the primary source of food.
- It results in the release of oxygen in the atmosphere.

The experiment to look for starch formation in two leaves – a variegated leaf or a leaf that was partially covered with black paper, and exposed to light. On testing these leaves for the presence of starch it was clear that photosynthesis occurred only in the green parts of the leaves in the presence of light.

Another experiment you may have carried out where a part of a leaf is enclosed in a test tube containing some KOH soaked cotton (which absorbs CO₂), while the other half is exposed to air. The setup is then placed in light for some time. On testing for the presence of starch later in the two parts of the leaf, you must have found that the exposed part of the leaf tested positive for starch while the portion that was in the tube, tested negative. This showed that CO₂ was required for photosynthesis.

Early experiment for Photosynthesis

In the year 1770, **Joseph Priestly** performed several experiments that revealed the role of air in the growth of green plants. The following figure shows the experiment carried out by Priestly:



Priestly observed that the candle burning in closed space, i.e. a bell jar, extinguishes after some time. As shown in **figure (a) and (b)** mouse fainted after some time. This concluded that both candle and mouse require air but somehow damaged it. But when the mint plant was placed in the jar, **(c) and (d)** the candle was burning after some time, and the mouse also stayed alive. After this experiment, Priestly hypothesized that:

“Plants restore to the air whatever breathing animals and burning candles remove.”

Using the similar set up used by **Priestly, Jan Ingenhousz** (1730 – 1799) experimented to show the importance of sunlight to plants, which somehow purifies the air fouled by breathing animals or burning candles. He took aquatic plants into observation and showed that in the presence of bright sunlight, small bubbles were formed around the green parts, while there were no bubbles during the night. Later, he concluded that the bubbles were of oxygen and only the green parts can release oxygen.

In the year 1854, **Julius Von Sachs** provided evidence of the production of glucose during the growth of plants. This glucose is stored as starch and later, he concluded that the green substances are located in special bodies within plant cells. He also concluded that glucose is made in the green part of the plant and is stored as **Starch**.

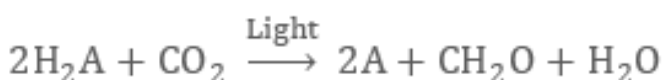
T.W. Engelmann (1843 – 1909) also carried out an interesting experiment. He used prism and split the light into several components and illuminated green algae, called **Cladophora**, placed in the suspension of aerobic bacteria. These bacteria helped in detecting the site of the evolution of oxygen. During the experiment, he observed that the bacteria accumulated mainly in the region of red and blue light of the split spectrum. This was the first time when photosynthesis was described and it resembled the absorption of spectra of chlorophyll.

By the middle **19th century**, the were features about the photosynthesis were known and the following empirical equation was introduced that represented the entire process of photosynthesis:

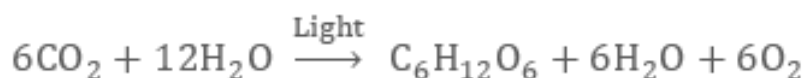
Then, **Cornelius van Niel** (1897 – 1985) added that photosynthesis is a light-dependent reaction in which hydrogen from an oxidizable compound and reduces carbon dioxide to carbohydrates. The entire reaction is represented as follows:



He also concluded that O_2 evolved from green plants comes from H_2O and not from CO_2 . This was later proved via radioisotopic techniques. The equation that represented the entire photosynthesis process is:



Where $\text{C}_6\text{H}_{12}\text{O}_6$ is glucose and O_2 is released from water.

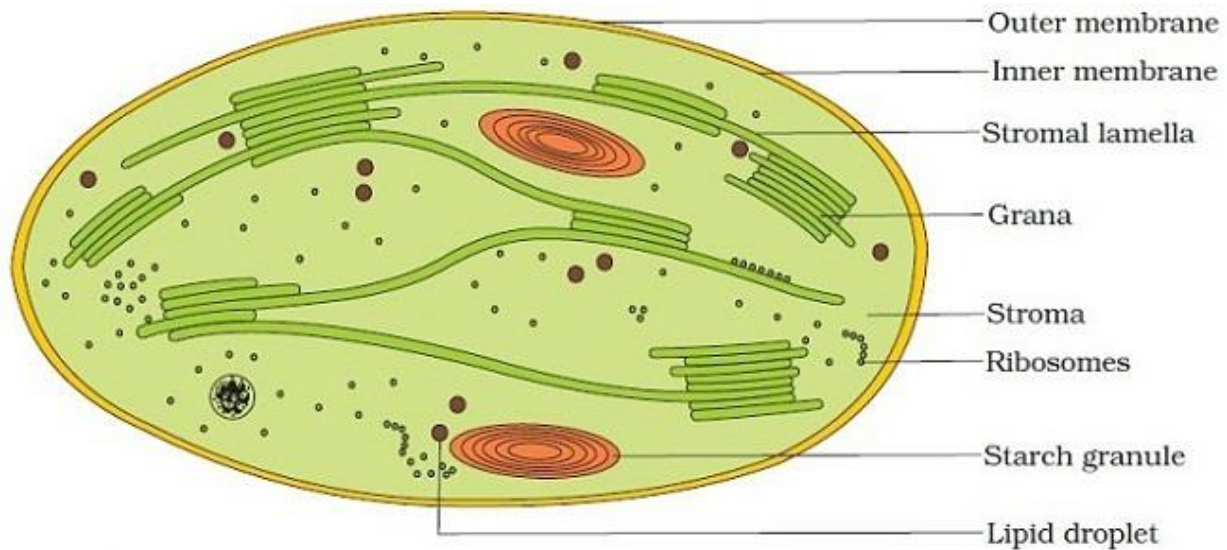


Where Photosynthesis does takes place?

Photosynthesis includes a series of chemical reactions which are carried out in chloroplast, i.e. The specialized structures found on cells of plants. In these series of reactions, water and carbon dioxide are converted into glucose and in this reaction energy from sunlight is used. Because it is an endothermic reaction, the entire process requires an input of energy. Photosynthesis is also classified as an oxidation-reduction reaction as it includes the loss of electrons by water and the gain of electrons by carbon dioxide.

The process of photosynthesis takes place in **Mesophyll Cells** and the carbon dioxide required by the process enters the process via stomata, i.e. the small holes present on the outer layer of leaves. The water required for the process is transported via roots through the vascular tissues.

The chloroplast contains a membranous system consisting of the stroma lamellae, grana, and the fluid stroma. The membrane system traps light energy and helps in synthesizing **ATP** and **NADPH**. Following diagram shows the electron micrograph of a section of chloroplast:



Diagrammatic representation of an electron micrograph of a section of chloroplast

How many types of pigments are involved in photosynthesis?

The leaf pigments of any green can be separated plant through paper chromatography.

Chromatographic separation of the leaf pigments shows that the colour that we see in leaves is not due to a single pigment but due to four pigments: **Chlorophyll a** (bright or blue-green in the chromatogram), **chlorophyll b** (yellow-green), **xanthophylls** (yellow), and **carotenoids** (yellow to yellow-orange).

The graph showing the ability of chlorophyll *a* pigment to absorb lights of different wavelengths (Figure 13.3 a). Of course, you are familiar with the wavelength of the visible spectrum of light as well as the VIBGYOR.

Can you see that the wavelengths at which there is maximum absorption by chlorophyll *a*, i.e., in the blue and the red regions, also show a higher rate of photosynthesis? Hence, we can conclude that chlorophyll is the chief pigment associated with photosynthesis.

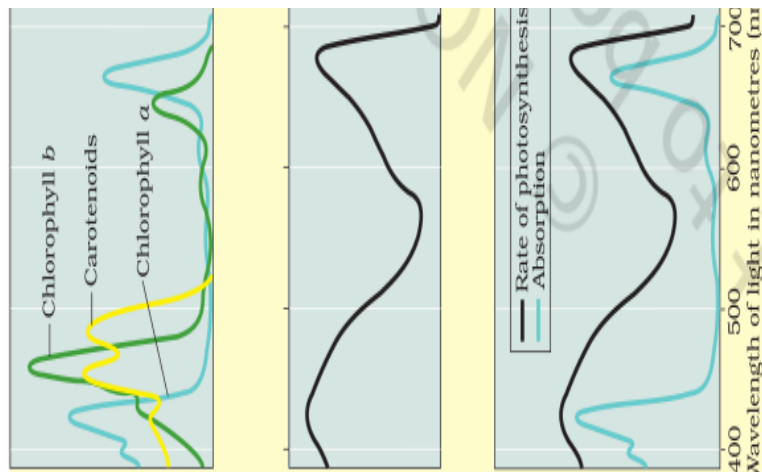


Figure 13.3a Graph showing the absorption spectrum of chlorophyll *a*, *b* and the carotenoids

Figure 13.3b Graph showing action spectrum of photosynthesis

Figure 13.3c Graph showing action spectrum of photosynthesis superimposed on absorption spectrum of chlorophyll *a*

An **absorption spectrum** shows all the colours of light **absorbed** by a plant. An **action spectrum** shows all the colours of light that are used in **photosynthesis**. Chlorophylls are the green pigments that absorb red and blue and participate in **photosynthesis** directly.

Pigments absorb light as a source of energy for **photosynthesis**. The **absorption spectrum** indicates the wavelengths of light **absorbed** by each pigment (e.g. chlorophyll) The action **spectrum** indicates the overall rate of **photosynthesis** at each wavelength of light.

An **action spectrum** is a graph of the rate of biological effectiveness plotted against wavelength.

It is studied with the help of a spectrophotometer.

These graphs, together, show that most of the photosynthesis takes place in the blue and red regions of the spectrum; some photosynthesis does take place at the other wavelengths of the visible spectrum.

Though chlorophyll is the major pigment responsible for trapping light, other thylakoid pigments like chlorophyll *b*, xanthophylls, and carotenoids, which are called accessory pigments, also absorb light and transfer the energy to chlorophyll *a*. Indeed, they not only enable a wider range of wavelengths of incoming light to be utilized for photosynthesis but also protect chlorophyll from photo-oxidation.

Types of Photosynthetic Reactions

Photosynthetic Reactions are of two types, i.e.

- **Light Dependent Reaction** – In these reactions, the energy from sunlight is absorbed by chlorophyll and transformed into chemical energy in the form of **ATP** and **NADPH** (electron carrier molecule).
- **Light Independent Reaction** – This reaction is also referred to as **Calvin Cycle**. In this reaction, the energized electron from light-dependent reactions provides energy to form carbohydrates from **CO₂** molecules.

Light Reaction

Light reactions or the 'photochemical' phase include light absorption, water splitting, oxygen release, and the formation of high-energy chemical intermediates, ATP, and NADPH.

The light reaction is a light-dependent process that includes a series of events such as light absorption, hydrolysis, the release of oxygen, formation of ATP, and NADPH.

The light reaction of photosynthesis initiates only when it is supplied with light energy.

The light reaction occurs in the thylakoids of the chloroplast. When the light hits, chlorophyll *a* gets excited to higher energy state followed by a series of reactions. This energy is converted into energy molecules ATP and NADPH by using PS I and PS II. Also, hydrolysis occurs and releases oxygen.

- The pigments are organized into two discrete photochemical light-harvesting complexes (LHC) within the Photosystem I (PSI) and Photosystem II (PS II).

The photosystem is the arrangement of pigments including chlorophyll within thylakoids.

There are two photosystems in plants:

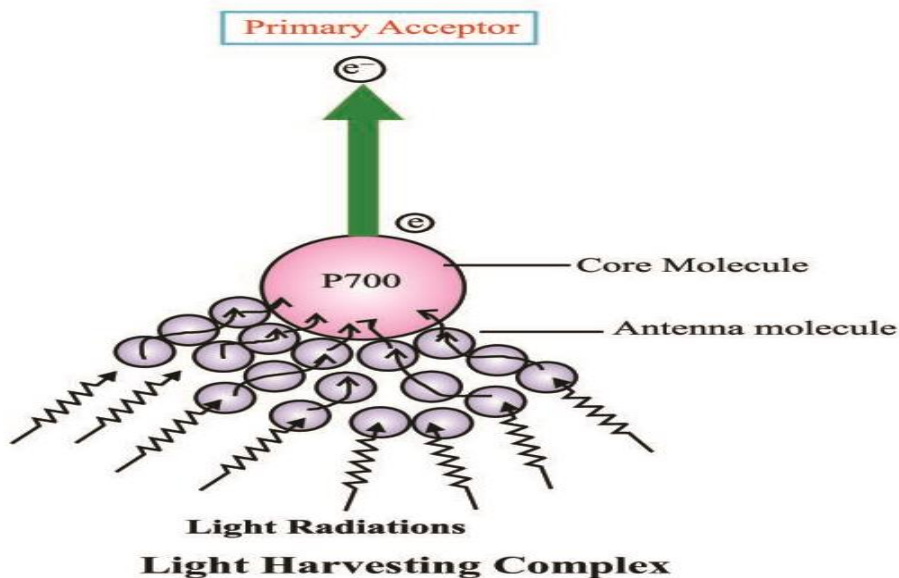
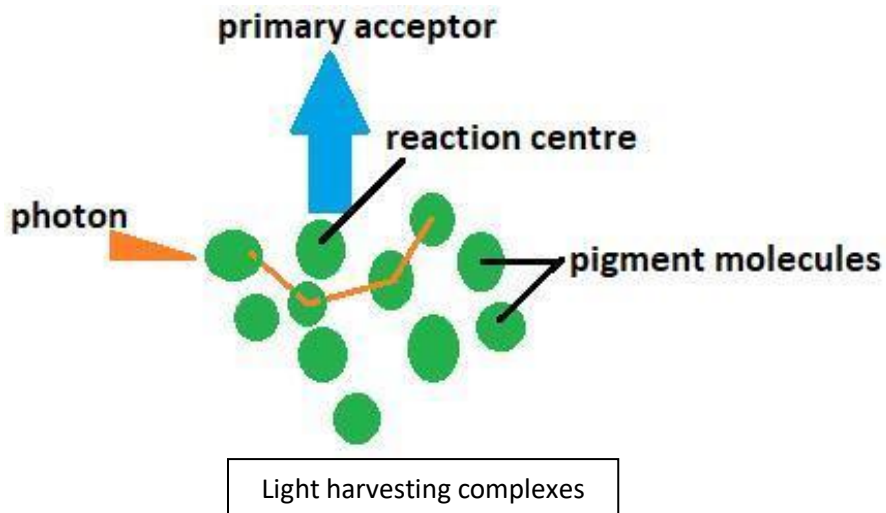
- Photosystem I (PS-I)
- Photosystem II (PS-II)

Photosystem I absorbs light at a wavelength of 700 nm, whereas Photosystem II absorbs light at a wavelength of 680 nm.

The light reaction occurs in the thylakoids of the chloroplast. When the light hits, chlorophyll *a* gets excited to higher energy state followed by a series of reactions. This energy is converted into energy molecules ATP and NADPH by using PS I and PS II. Also, hydrolysis occurs and releases oxygen.

- The LHC is made up of hundreds of pigment molecules bound to proteins.

- Each photosystem has all the pigments (except one molecule of chlorophyll a) forming a light-harvesting system also called **antennae**.
- The single chlorophyll a molecule forms the reaction centre.
- In PS I, the reaction centre chlorophyll a has an absorption peak at 700 nm, hence is called P₇₀₀, while in PS II it has absorption maxima at 680 nm, and is called P₆₈₀.



Dark Reaction

Dark reaction is also called a carbon-fixing reaction. It is a light-independent process in which sugar molecules are formed from the carbon dioxide and water molecules.

The dark reaction occurs in the stroma of the chloroplast where they utilize the products of the light reaction.

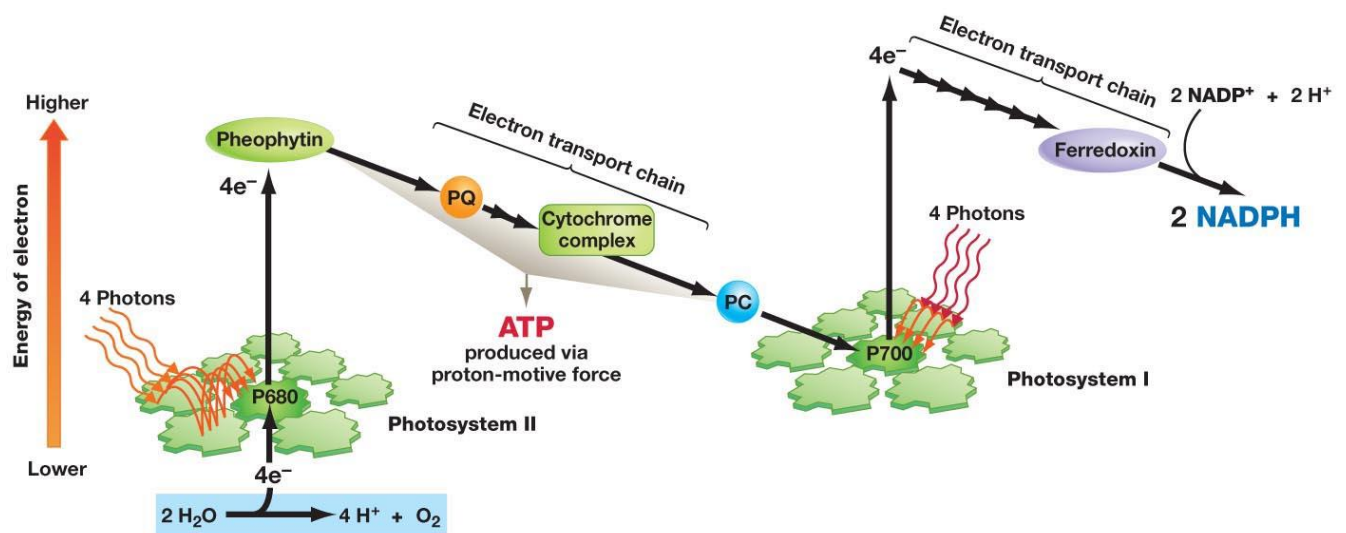
Plants capture the carbon dioxide from the atmosphere through stomata and proceed to the Calvin cycle.

In the Calvin cycle, the ATP and NADPH formed during light reaction drives the reaction and convert 6 molecules of carbon dioxide into one sugar molecule i.e. glucose.

Light reaction	Dark reaction
1. Also called as Hillman reaction	1 Also called as Blackman reaction
2. Occurs in presence of light	2 Occurs in absence of light
3. It takes place in grana	3 It takes place in stroma
4. Photolysis of water takes place and energy rich compound generated ATP & NADPH ₂	4 CO ₂ is reduced to form hexose sugar with utilization of energy produced during light reaction
5. Photo-chemical reaction	5 Bio-chemical reaction

The electron transport

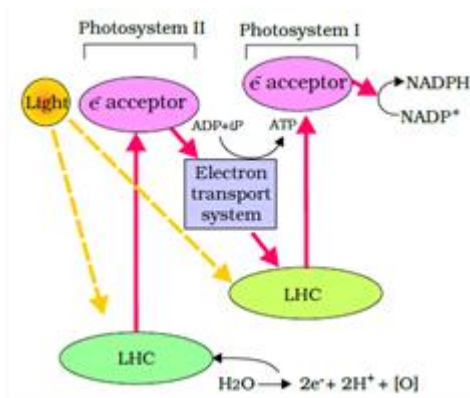
- In photosystem II, the reaction centre chlorophyll a absorbs 680 nm wavelength of red light causing electrons to become excited and jump, which are picked up by an electron acceptor which passes them to an electrons transport system consisting of cytochromes.
- The electrons are passed on to the pigments of photosystem PS I, and the movement of electrons is downhill.
- Electrons in the reaction centre of PS I are also excited when they receive red light of wavelength 700 nm and are transferred to another acceptor molecule that has a greater redox potential.
- The electrons then are moved downhill to a molecule of energy-rich NADP^+ and the addition of these electrons reduces NADP^+ to $\text{NADPH} + \text{H}^+$.
- The whole scheme of transfer of electrons is called the **z-scheme**, due to its characteristic shape



Z-scheme of light reaction

The Electron Transport System

The reaction centre of photosystem II absorbs light of 680 nm in the red region and causing an electron to become excited. These electrons are picked by an electron acceptor which passes to an electron transport system consisting of **cytochromes**.

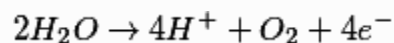


Electrons are passed down the electron transport chain and then to the pigment of PS I.

Electron in the PSI also get excited due to light of wavelength 700nm and are transferred to another acceptor molecule having a greater redox potential.

When an electron passes in the downhill direction, energy is released. This is used to reduce the ADP to ATP and NADP+ to NADPH. The whole scheme of transfer of electron is called **Z-scheme** due to its shape.

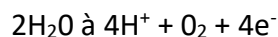
Photolysis of water release electrons that provide electron to PS II. Oxygen is also released during this process.



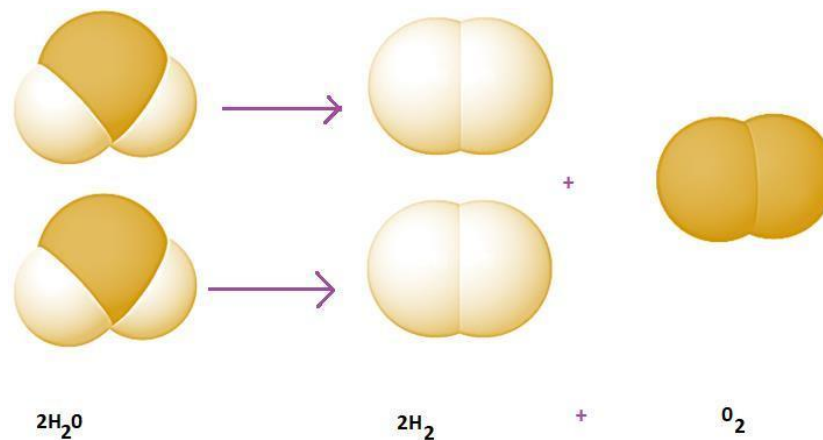
Water Splitting

The light-dependent splitting of water is called photolysis. This process is associated with PS-II in which manganese and chlorine play an important role. The electrons lost from P680 are replaced by the electrons formed in this process. A molecule of water splits to releases oxygen on the absorption of light by P680.

- The process in which water is split into H^+ , $[O]$, and electrons is called the splitting of water.
- Splitting of water creates oxygen, one of the net products of photosynthesis.



- The water-splitting complex is associated with PS II, which itself is physically located on the inner side of the membrane of the thylakoid.

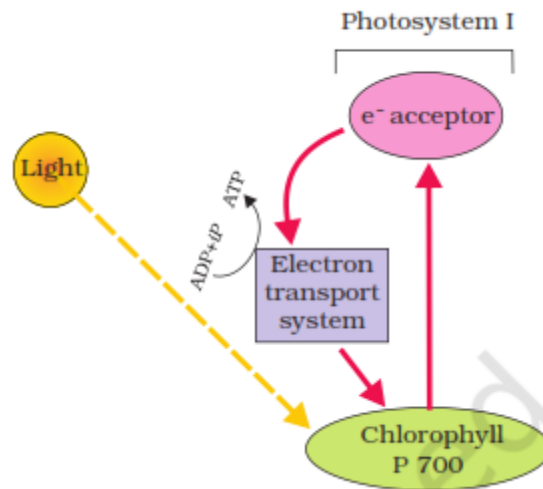


Photophosphorylation is the process of utilizing light energy from photosynthesis to convert ADP to ATP. It is the process of synthesizing energy-rich ATP molecules by transferring the phosphate group into the ADP molecule in the presence of light. **Photophosphorylation** is of two types: Cyclic **Photophosphorylation**.

Cyclic and Non – Cyclic Photo – Phosphorylation

In bacterial photosynthesis, a single PS (**Photo System**) is involved. When an electron is energized by absorption of light, it is ejected from the **PS** reaction centre. This electron then passes through an electron transport system and finally back to the reaction centre. *“The energy released during the electron transport is used to produce **ATP**. Since the excited electron returns to the reaction centre, this mechanism of making **ATP** is called **Cyclic Photophosphorylation**.”*

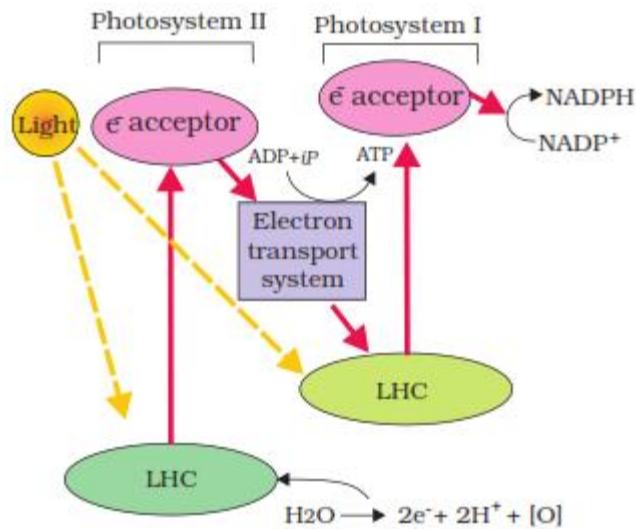
The following diagram shows the above-explained process of cyclic photophosphorylation. No reducing power, required for biosynthesis is generated in this process. In this process, the energy released during the electron transport is used to produce **ATP**, and the excited electron returns to the reaction centre:



Cyanobacteria and **Plants** use two **PS** which simultaneously work to produce energy and reduce power. Primarily, a photon of light ejects a high energy electron from **PS II**. This electron travels from the excited reaction centre of **PS II** down the chain and enters in **PS I**. *“This electron transport system generates a proton motive force that is used to produce **ATP**. Since the excited electron does not return to **PS II**, this mechanism for making **ATP** is called **Non – Cyclic Photophosphorylation**.”*

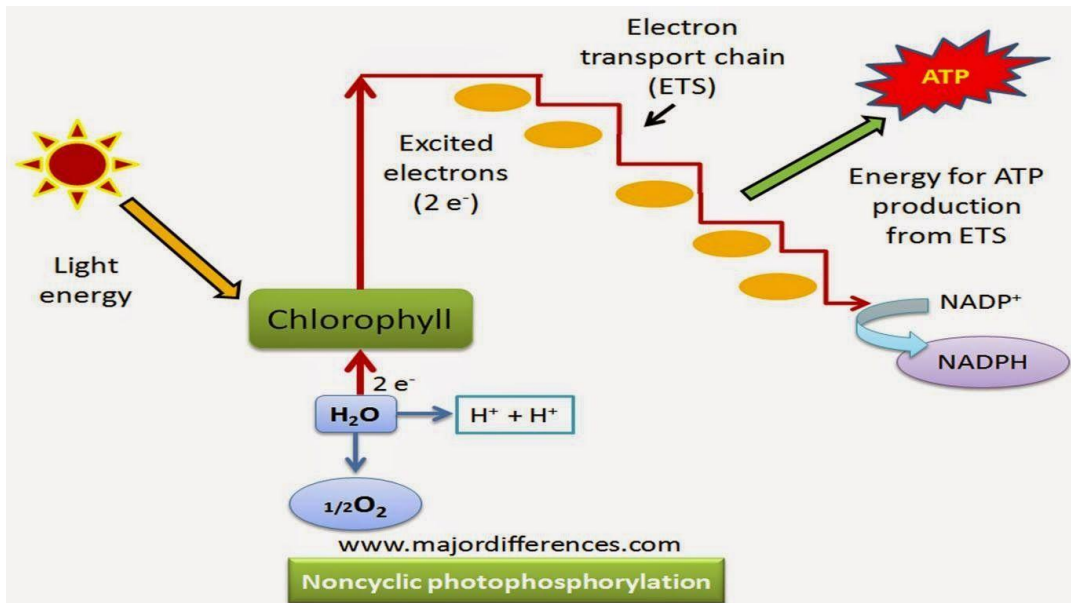
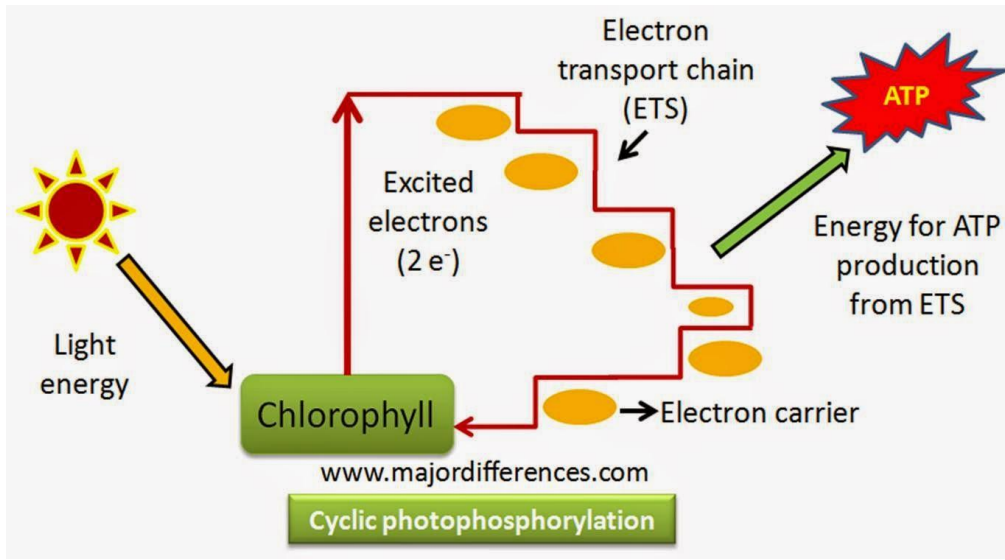
When **PS I** absorb a photon of light, it releases another high energy electron that is used to drive the formation of reducing power in the form of **NADPH**. This ejected electron is replaced by an electron of **PS II**.

The following diagram shows the entire process of noncyclic photophosphorylation as discussed above. In this process, the excited electron does not return to **PS II** and therefore, this entire mechanism for making **ATP** is referred to as **Non – Cyclic Photophosphorylation**:



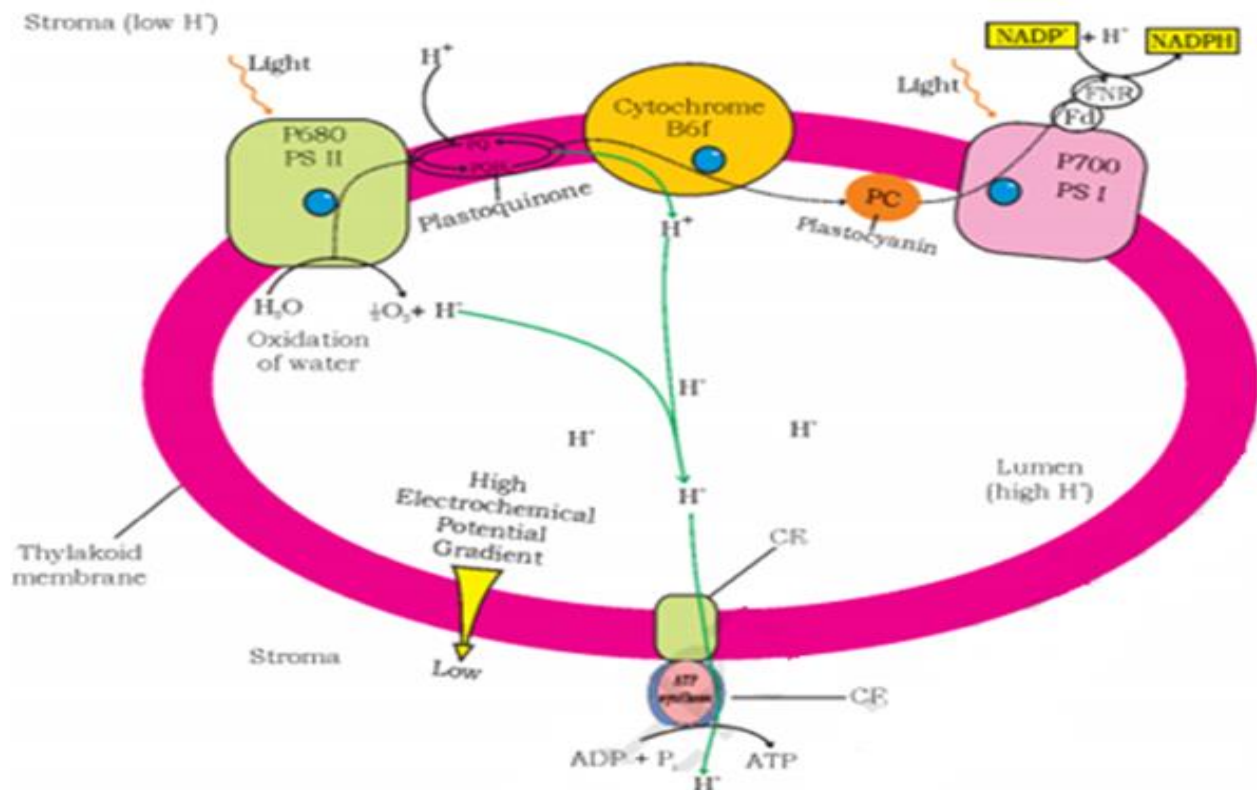
Difference between cyclic and non-cyclic photophosphorylation

Cyclic photophosphorylation	Non-cyclic photophosphorylation
Only PS I is involved	PS I and PS II are involved
No photolysis of water takes place	Photolysis of water takes place
Oxygen not evolved	Oxygen evolved
$NADPH+H^+$ is not synthesized	$NADPH+H^+$ is synthesized
Electron is cycled back to reaction centre	Electron does not return to reaction centre



Chemiosmotic hypothesis

- The theory which explains how ATP is synthesized in the chloroplast is the chemiosmotic hypothesis.
- Like in respiration, in photosynthesis too, ATP synthesis is linked to the development of a proton gradient across the membranes of the thylakoid.
- In photosynthesis, proton accumulation is towards the lumen, whereas in respiration, protons accumulate in the intermembrane space of the mitochondria when electrons move through the ETS.
- The processes that take place during the activation of electrons and their transport to determine the steps that cause a proton gradient to develop are the following:
- Since the splitting of the water molecule takes place on the inner side of the membrane, the hydrogen ions that are produced accumulate within the lumen of the thylakoids.
- As electrons move through the photosystems, protons are transported across the membrane because the primary acceptor of electron transfers its electron to an H carrier; hence, this molecule removes a proton from the stroma while transporting an electron.
- Protons are necessary for the reduction of NADP^+ to $\text{NADPH} + \text{H}^+$, these protons are also removed from the stroma.
- Within the chloroplast, protons in the stroma decrease in number, whereas in the lumen there is an accumulation of protons, which creates a proton gradient across the thylakoid membrane as well as a decrease in pH in the lumen.
- The gradient is broken down due to the movement of protons across the membrane to the stroma through the transmembrane channel of the F_0 of the ATPase.
- The ATPase enzyme consists of two parts
- one is F_0 embedded in the membrane and forms a transmembrane channel that carries out facilitated diffusion of protons across the membrane
- Another portion is called F_1 and protrudes on the outer surface of the thylakoid membrane on the side that faces the stroma.
- The break down of the gradient provides enough energy to cause a conformational change in the F_1 particle of the ATPase, which makes the enzyme synthesize several molecules of energy-packed ATP.
- Chemiosmosis requires a membrane, a proton pump, a proton gradient, and ATPase.



Use of ATP and NADPH

- The phase in which O_2 diffuses out of the chloroplast while ATP and NADPH are used to drive the processes leading to the synthesis of sugar is called the biosynthetic phase of photosynthesis.
- Biosynthetic phase does not directly depend on the presence of light but is dependent on the products of the light reaction, i.e., ATP and NADPH, besides CO_2 and H_2
- CO_2 is combined with H_2O to produce sugars.
- The use of radioactive ^{14}C by Melvin Calvin in algal photosynthesis studies led to the discovery that the first CO_2 fixation product was a 3-carbon organic acid.
- Calvin worked out the complete biosynthetic pathway; hence, it was called the Calvin cycle.
- The first product identified was 3-phosphoglyceric acid (PGA).
- Another experiment on another plant discovered oxaloacetic acid or OAA as the first stable product of photosynthesis.
- CO_2 assimilation during photosynthesis was said to be of two main types:
 - those plants in which the first product of CO_2 fixation is a C_3 acid (PGA), i.e., the C_3 pathway,
 - the plants in which the first product was a C_4 acid (OAA), i.e., the C_4

The Primary Acceptor of CO₂

The acceptor molecule was a 5-carbon ketose sugar – ribulose biphosphate (RuBP). The scientists also took a long time and conducted many experiments to reach this conclusion.

They also believed that since the first product was a C acid, the primary acceptor would be a 2-carbon compound; they spent many years trying to identify a 2-carbon compound before they discovered the 5-carbon RuBP.

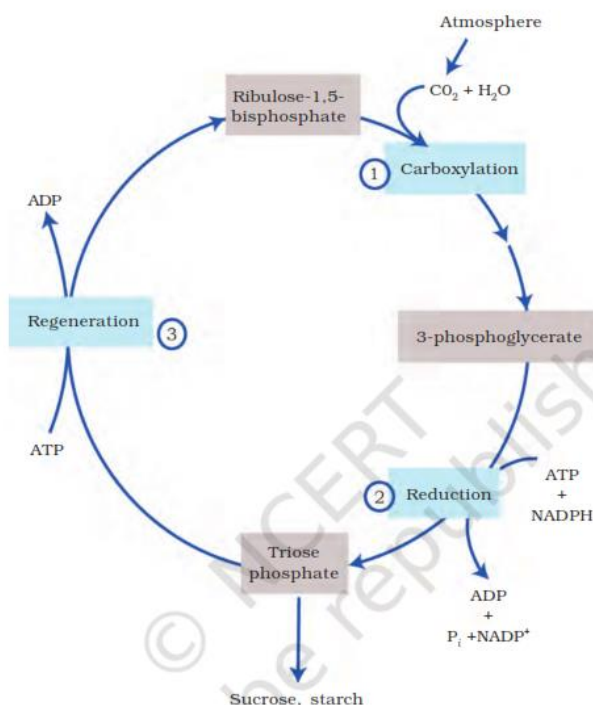
The Calvin Cycle

In **Calvin Cycle**, Carbon atoms from **CO₂** are fixed and are used to form three – **Carbon Sugar**. This process is dependent on **ATP** and **NADPH** formed from light reactions. The light reaction is carried out in the thylakoid membrane while the Calvin Cycle takes place in the stroma. The Calvin cycle can be described in three stages:

- **Carboxylation** – It is the fixation of **CO₂** in stable organic intermediate. It is an important stage in the Calvin Cycle where **CO₂** is utilized for carboxylation of **RuBP** in the presence of enzyme **RuBP** carboxylase. It results in the formation of 2 molecules of **3-PGA**. **RuBP** carboxylase also helps in oxygenation activity and is therefore also referred to as RuBP carboxylase – oxygenase (RuBisCO).
- **Reduction** – This stage includes a series of reactions that result in the formation of glucose. This step utilizes 2 molecules of ATP (for phosphorylation) and two molecules of **NADPH** (for reduction per **CO₂** molecule). The fixation of 6 molecules of **CO₂** and 6 turns of cycle results in the removal of 1 molecule of glucose from the pathway.
- **Regeneration** – This stage includes regeneration of the **CO₂** acceptor molecule and requires 1 **ATP** for phosphorylation to form RuBP.

The cycle starts with carboxylation, followed by reduction and then, finally regeneration. The last stage includes regeneration of **CO₂** acceptor molecule and requires 1 **ATP** for phosphorylation to

form RuBP:



The Calvin cycle proceeds in three stages : (1) carboxylation, during which CO_2 combines with ribulose-1,5-bisphosphate; (2) reduction, during which carbohydrate is formed at the expense of the photochemically made ATP and NADPH; and (3) regeneration during which the CO_2 acceptor ribulose-1,5-bisphosphate is formed again so that the cycle continues

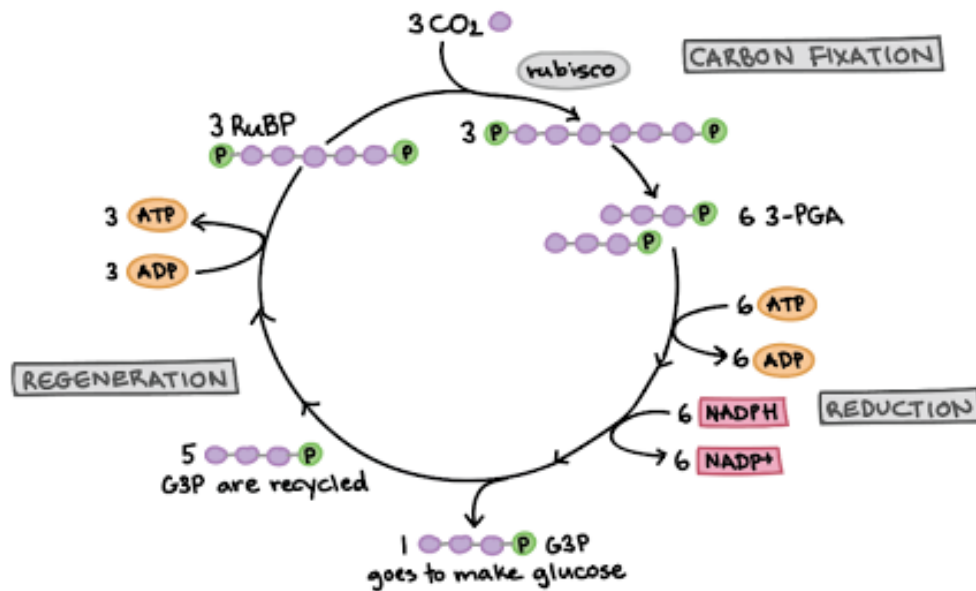
In	Out
Six CO_2	One glucose
18 ATP	18 ADP
12 NADPH	12 NADP

Reactions in Calvin Cycle

Concerning the above diagram, the reactions are divided into three different stages:

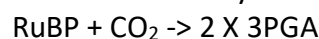
- **Carbon Fixation** – A CO_2 molecule combines with 5 C acceptor molecule and RuBP. This step makes 6 Carbon compound that splits into 2 molecules of 3 Carbon compound and 3PGA. The reaction is catalyzed by RuBP carboxylase or oxygenase.
- **Reduction** – At the second stage, ATP and NADPH are converted to 3 PGA molecules into molecules of three-carbon sugar and G3P (**glyceraldehyde-3-phosphate**).
- **Regeneration** – At the final stage, 3GP molecules go to make glucose while others may be recycled to regenerate RuBP acceptor. The process of regeneration requires ATP along with a complex network of reactions.

For the exiting cycle, three CO_2 molecules enter the cycle for exiting the 3GP molecule. This provides three new atoms of fixed carbon. Entering of 3CO_2 molecules results in the regeneration of 3 molecules of RuBP acceptors.



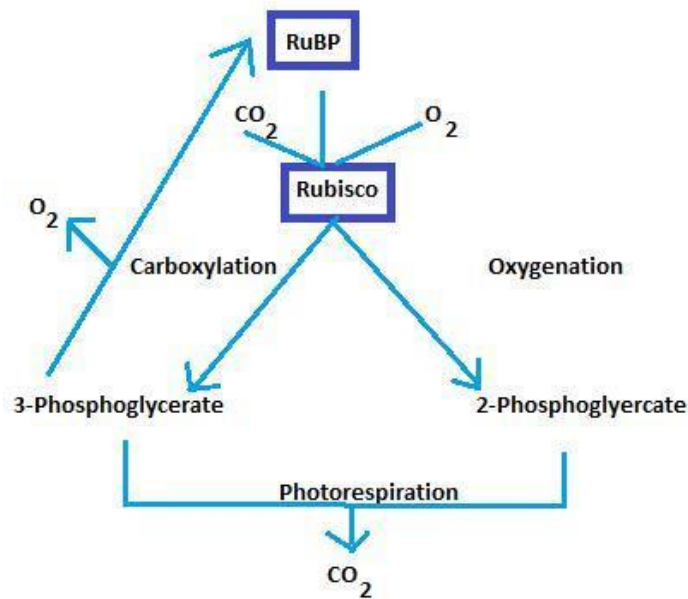
PHOTORESPIRATION

- The first step of the Calvin pathway is the first CO_2 fixation step.
- Respiration is the reaction where RuBP combines with CO_2 to form 2 molecules of 3PGA, which is catalyzed by RuBisCO .



- RuBisCO has a much greater affinity for CO_2 than for O_2 .
- In C_3 plants, some O_2 do bind to RuBisCO , and hence CO_2 fixation is decreased.
- The RuBP instead of being converted to 2 molecules of PGA binds with O_2 to form one molecule and phosphoglycolate in a pathway called photorespiration.
- In the photorespiratory pathway, there is neither synthesis of sugars, nor ATP .
- In C_3 plants, some O_2 do bind to RuBisCO , and hence CO_2 fixation is decreased.
- In the photorespiratory pathway, there is no synthesis of ATP or NADPH ; therefore, photorespiration is a wasteful process.
- In C_4 plants, photorespiration does not occur because they have a mechanism that increases the concentration of CO_2 at the enzyme site.

- This takes place when the C₄ acid from the mesophyll is broken down in the bundle cells to release CO₂, which results in increasing the intracellular concentration of CO₂.



Factors affecting Photorespiration

The rate of photorespiration increases at any time when the level of carbon dioxide is low and oxygen is high. Such a condition occurs when stomata remain partially closed or completely closed and photosynthesis is underway.

The majority of the time, the stomata of plants are open, resulting in lowering down the rate of photorespiration. But when plants become water-stressed, they close stomata to prevent loss of water via transpiration. Thus, on the other hand, restricts the normal exchange of gases. The level of CO₂ gradually rises as water splits during light reaction.

In the desert and dry tropical areas, photorespiration is reduced due to water stress and this, on the other hand, results in lowering down the potential of plant growth. Some plants have adapted to this problem by modifying the way they carry out photosynthesis. One of the common adaptations is called **C₂ Metabolism** in which plants develop different leaf anatomy called **Kranz Anatomy**

C₄ pathway/Hatch Slack Pathway

This pathway was worked out by Hatch and Slack (1965, 1967), mainly operational in plants growing in the dry tropical region like Maize, Sugarcane, Sorghum, etc.

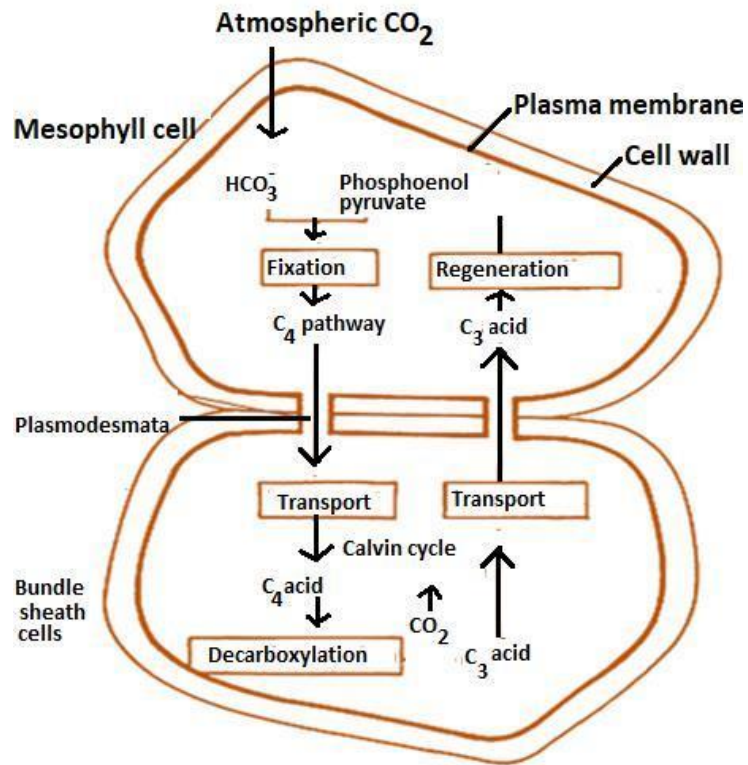
In this pathway first, the stable product is a 4-carbon compound **Oxaloacetic acid** (AAO) so-called as C_4 pathway. C_4 plants have Kranz Anatomy (vascular bundles are surrounded by bundle sheath cells arranged in a wreath-like manner), characterized by a large no of the chloroplast, thick wall impervious to gases, and absence of intercellular spaces.

The primary/acceptor is a 3-carbon molecule **Phosphoenol Pyruvate** present in mesophyll cells and the enzyme involved is PEP carboxylase.

OAA formed in mesophyll cell forms a 4-carbon compound like malic acid or aspartic acid which is transported to bundle sheath cells.

In bundle sheath cell, it is broken into CO_2 and a 3-carbon molecule. The 3-carbon molecule is returned to mesophyll cells to form PEP.

The CO_2 molecules released in bundle sheath cells enter the Calvin cycle, where enzyme RuBisCO is present that forms sugar.



Characteristics	C ₃ Plants	C ₄ Plants	Choose from
Cell type in which the Calvin cycle takes place			Mesophyll/Bundle sheath/both
Cell type in which the initial carboxylation reaction occurs			Mesophyll/Bundle sheath /both
How many cell types does the leaf have that fix CO ₂ .			Two: Bundle sheath and mesophyll One: Mesophyll Three: Bundle sheath, palisade, spongy mesophyll
Which is the primary CO ₂ acceptor			RuBP/PEP/PGA
Number of carbons in the primary CO ₂ acceptor			5 / 4 / 3
Which is the primary CO ₂ fixation product			PGA/OAA/RuBP/PEP
No. of carbons in the primary CO ₂ fixation product			3 / 4 / 5
Does the plant have RuBisCO?			Yes/No/Not always
Does the plant have PEP Case?			Yes/No/Not always
Which cells in the plant have Rubisco?			Mesophyll/Bundle sheath/none
CO ₂ fixation rate under high light conditions			Low/ high/ medium
Whether photorespiration is present at low light intensities			High/negligible/sometimes
Whether photorespiration is present at high light intensities			High/negligible/sometimes
Whether photorespiration would be present at low CO ₂ concentrations			High/negligible/sometimes
Whether photorespiration would be present at high CO ₂ concentrations			High/negligible/sometimes
Temperature optimum			30-40 C/20-25C/above 40 C
Examples			Cut vertical sections of leaves of different plants and observe under the microscope for Kranz anatomy and list them in the appropriate columns.

	C ₃ plants	C ₄ plants
1.	Photosynthesis occurs in mesophyll tissues.	Photosynthesis occurs both in mesophyll and bundle sheath cells.
2.	The carbon dioxide acceptor is RuBisco.	The carbon dioxide acceptor is PEP carboxylase.
3.	Krantz anatomy is absent.	Krantz anatomy is present
4.	The 1 st stable compound formed is 3C compound called 3-Phospho Glyceric Acid (PGA).	The 1 st stable compound is 4-carbon Oxaloacetic acid (OAA).
5.	The optimum temperature is 20-25oC	The optimum temp is 35 – 44oC.
6.	Photorespiratory loss is high.	Photorespiration does not take place.

Factors affecting photosynthesis

Photosynthesis is under the influence of several factors, both internal and external.

The plant factors include the number, size, age, and orientation of leaves, mesophyll cells and chloroplasts, internal CO₂ concentration, and the amount of chlorophyll.

The external factors would include the availability of sunlight, temperature, CO₂ concentration, and water.

When several factors affect any biochemical process, Blackman's law of limiting factors comes into effect, which states that "If a chemical process is affected by more than one factor, then its rate will be determined by the factor which is nearest to its minimal value: it is the factor which directly affects the process if its quantity is changed."

When several factors affect any [bio] chemical process, Blackman's (1905) **Law of Limiting Factors** comes into effect. This states the following:

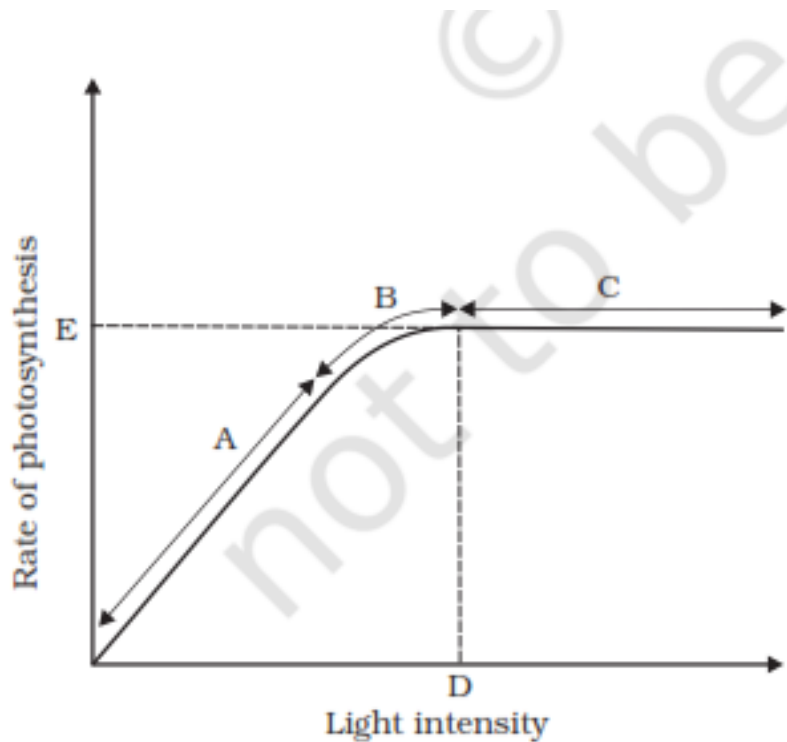
If a chemical process is affected by more than one factor, then its rate will be determined by the factor which is nearest to its minimal value: it is the factor that directly affects the process if its quantity is changed. BCD Light intensity.

Several factors affect the rate of photosynthesis. These factors are both internal and external:

Temperature – When carbon dioxide, light, and other factors are not limiting, the photosynthesis rate increases with the rise in temperature. The most preferred range of temperature is **6° C – 37° C**. High-temperature results in the inactivation of enzymes and thereby affects enzymatically controlled dark reactions.

Carbon Dioxide Concentration – It is the major limiting factor and its concentration is very low in the atmosphere, i.e. 0.03 – 0.04%. An increase in concentration to 0.05% causes an increase in the fixation rate of **CO₂**. Added to this, the C₃ and C₄ plants differently respond to the concentration of carbon dioxide. “The fact that C₃ plants respond to higher **CO₂** concentration by showing an increased rate of photosynthesis leading to higher productivity has been used for some greenhouse crops like bell pepper and tomatoes.” Such plants are allowed to grow in a **CO₂** enriched environment that leads to higher yields.

Light – The light varies as per quality, duration, per cent, and intensity and has a significant impact on the rate of photosynthesis. For instance, there is a linear relationship between the incident light and **CO₂** fixation at low light intensities. Added to this, an increase in the incident light beyond point causes the breakdown of chlorophyll and a decrease in photosynthesis.



Graph of light intensity on the rate of photosynthesis

Oxygen – Oxygen inhibits photosynthesis in C_3 plants but C_4 plants show little effect. This is so because C_4 plants carry out photorespiration and high oxygen stimulates it. The rate of photosynthesis increases with the reduction of the concentration of oxygen.

Water – It is an essential raw material for the assimilation of carbon. Less than one per cent of absorbed water is utilized in photosynthesis. The decrease in water content in soil decreases the rate of photosynthesis as well. This is so because it results in dehydration of protoplasm and also results in stomatal closure. Added to this, it impairs enzymatic efficiency, affects its colloidal state, inhibits respiration, etc.

Mineral elements – These are also essential for the growth of plants and it includes **Cu, Cl, Mg, Fe, P** and these are closely related to the process of photosynthesis.

Air pollutants – Metallic and gaseous pollutants reduce photosynthesis. The pollutants include **SO₂**, oxidants, ozone, and hydrogen fluorides.

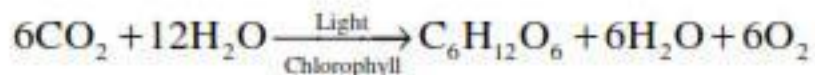
Chemical compounds – Although, chemical compounds are present in very less quantity even the small quantity depresses the rate of photosynthesis. On the contrary, an increase in the presence of chemical compounds results in the death of cells.

Thus, several factors affect the rate of photosynthesis. Other factors include the content of chlorophyll, protoplasmic factor, accumulation of carbohydrates, etc.

Important terms

Photosynthesis :

Photosynthesis is an enzyme regulated anabolic process of manufacture of organic compounds inside the chlorophyll-containing cells from carbon dioxide and water with the help of sunlight as a source of energy.



Chlorophyll a : (Bright or blue-green in chromatograph). Major pigment, act as a reaction centre, involved in trapping and converting light into chemical energy.

Chlorophyll b : (Yellow-green)

Xanthophyll : (Yellow)

Carotenoids : (Yellow to yellow-orange) In the blue and red regions of the spectrum shows a higher rate of photosynthesis.

Light Harvesting Complexes (LHC): The light-harvesting complexes are made up of hundreds of pigment molecules bound to protein within the photosystem I (PSI) and photosystem II (PSII). Each photosystem has all the pigments except one molecule of chlorophyll 'a' forming a light-harvesting system (antennae). The reaction centre (chlorophyll a) is different in both the photosystems.

Photosystem I (PSI): Chlorophyll 'a' has an absorption peak at 700 nm (P700). **Photosystem II (PSII)**: Chlorophyll 'a' has an absorption peak at 680 nm (P680).

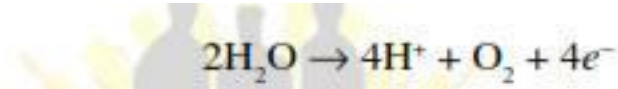
Photophosphorylation: The process of formation of high-energy chemicals (ATP and NADPH).

Cyclic photophosphorylation: Two photosystems work in series – First PSII and then PSI. These two photosystems are connected through an electron transport chain (Z. Scheme). Both ATP and NADPH + H are synthesized by this process. PSI and PSII are found in lamellae of grana, hence this process is carried here.

Non-cyclic photophosphorylation: Only PSI works, the electron circulates within the photosystem. It happens in the stroma lamellae (possible location) because in this region PSII and NADP reductase enzymes are absent. Hence only ATP molecules are synthesized.

The electron transport (Z-Scheme): In PS II, the reaction centre (Chlo. a) absorbs 680 nm wavelength of red light which makes the electrons excited. These electrons are taken up by the electron acceptor that passes them to an electron transport system (ETS) consisting of cytochromes. The movement of the electron is downhill. Then, the electron passes to PSI and move downhill further.

The splitting of water: It is linked to PS II. Water splits into H, O, and electrons.



Chemiosmotic Hypothesis: Chemiosmotic hypothesis explain the mechanism of ATP synthesis in the chloroplast. In photosynthesis, ATP synthesis is linked to the development of a proton gradient across a membrane. The electrons are accumulated inside of membrane of thylakoids (in lumen). ATPase has a channel that allows diffusion of protons back across the membrane. This releases energy to activate the ATPase enzyme that catalyzes the formation of ATP.

Photorespiration: The light-induced respiration in green plants is called photorespiration. In C 3 plants some O₂ binds with RuBisCo and hence CO fixation is decreased. In this process RuBP instead of being converted to 2 molecules of PGA binds with O to form one molecule of PGA and phosphoglycolate.

Law of Limiting Factors: If a chemical process is affected by more than one factor, then its rate will be determined by the factor which is nearest to its minimal value. It is the factor that directly affects the process if its quantity is changed.