PHOTOSYNTHESIS

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The biological world with negligible exceptions runs at the expense of the material and energy capital accumulated as a result of photosynthesis. From the products of photosynthesis, living organisms have been buildup by complex kinds of molecules, which constitutes the cellular structure of plants and animals. Apart from this, the energy expended in the operation of living organisms also derives from this source.

On the oxidation of food, energy released and it can be used in metabolic process. The chemical energy of foods releasable upon oxidation represents the converted energy of sunlight which was originally entrapped within the molecules of organic compounds during photosynthesis.

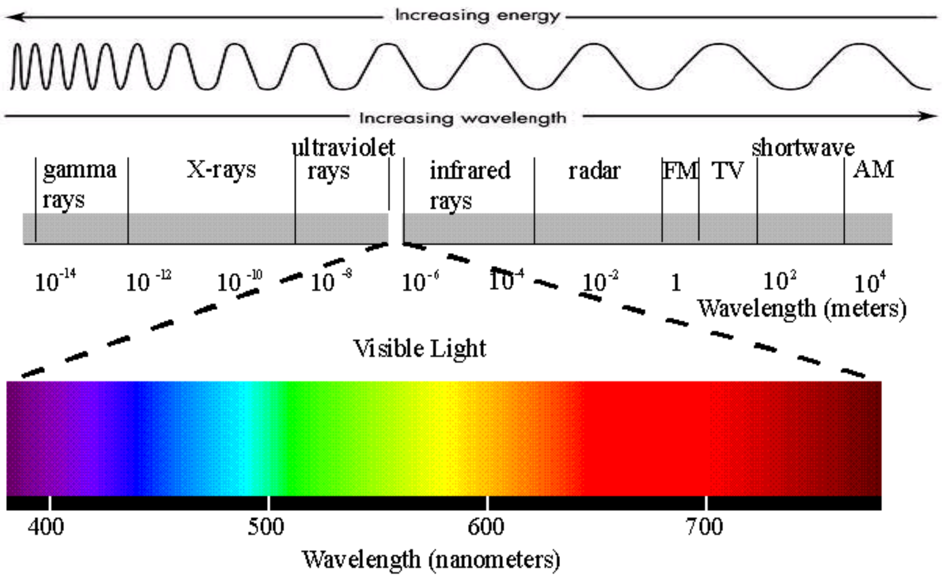
According to biological economists, wealth originates directly or indirectly as a consequence of photosynthesis. This is true of all plant and animal products and also our heritage of coal and natural gas from past geological ages. These latter products are derived from the remains of living organisms and hence also represent photosynthetic capital. The energy released from them upon combustion represents the sunlight of past geological epochs.

Hence photosynthesis is the biggest photochemical reaction and biochemical phenomena acting as a master key for the existence of life on this globe. In turn solar energy (sunlight) is the chief driver of this photochemical reaction.

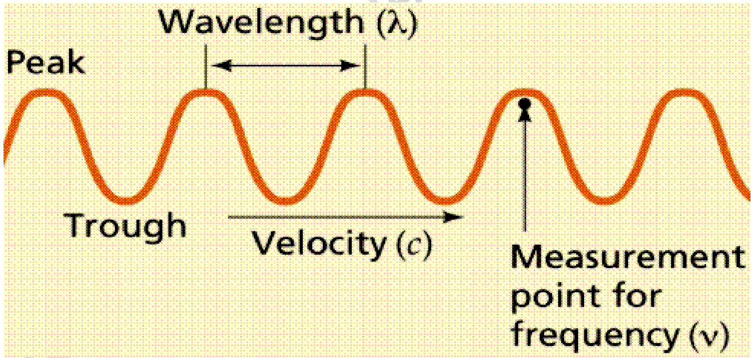
The nature of the light energy

An elementary knowledge of the physical properties of light and other kinds of radiant energy is essential for proper understanding of photosynthesis and many other photobiological reactions.

Light appears to be propagated across the space as an undulatory waves. The energy for photosynthesis is derived from light. Although sunlight appears to be white it is actually a mixture of different colours. The electromagnetic spectrum of light is as follows.



According to wave theory of light, each colour of the spectrum consists of a different wavelength. A wave length is the distance between two successive crests of a wave and it is indicated by the lambda.



The wave lengths which induces the sensation ranges from 390 nm to 760 nm of visible spectrum. Above the visible range all are possessing longer wavelength and have less energy. Below the visible range the waves have smaller wavelengths and they possess high energy.

Based on the role of light in photosynthesis, there is an assumption that light is particulate in nature. According to particulate or quantum theory, the light is composed of a stream of tiny particles. Each of these particles is called a quanta or photon (packets of light energy). When such photon impinges against a suitable substance, their energy may be transferred to the electrons which they strike, thus inducing photochemical reactions. The energy manifestation of a photon or quanta is called a quantum.

When a photon of light strikes a chlorophyll molecule it can transfer its energy to the outer electron. This electron now becomes excited and is raised to a higher energy level. The molecule then becomes unstable. The excited electron is now trapped by various electron acceptors. Chlorophyll thus converts light energy of photon in to chemical energy which is stored in ATP.

Photosynthetic pigments

The photosynthetic pigments of higher plants fall into two classes, the Chlorophylls and Carotenoids. These pigments absorb light energy and convert it to chemical energy. They are located on the chloroplast membranes (Thylakoids) and the chloroplasts are usually arranged with in the cells so that the membranes are at right angles to the light source for maximum absorption.

Chlorophylls

There are 6-7 types of chlorophylls known as chlorophyll a, b, c, d, e, bacteriochlorophyll (in bacteria) and chlorobium chlorophyll (in green sulphur bacteria). Chlorophylls absorb mainly red and blue violet light, reflecting green light. Chlorophyll a is the most abundant photosynthetic pigment and other pigments are accessory or light harvesting antenna molecules.

Carotenoids

Carotenoids are of two types. Orange carotene and yellow xanthophylls. The carotenoids are known to perform two distinct roles.

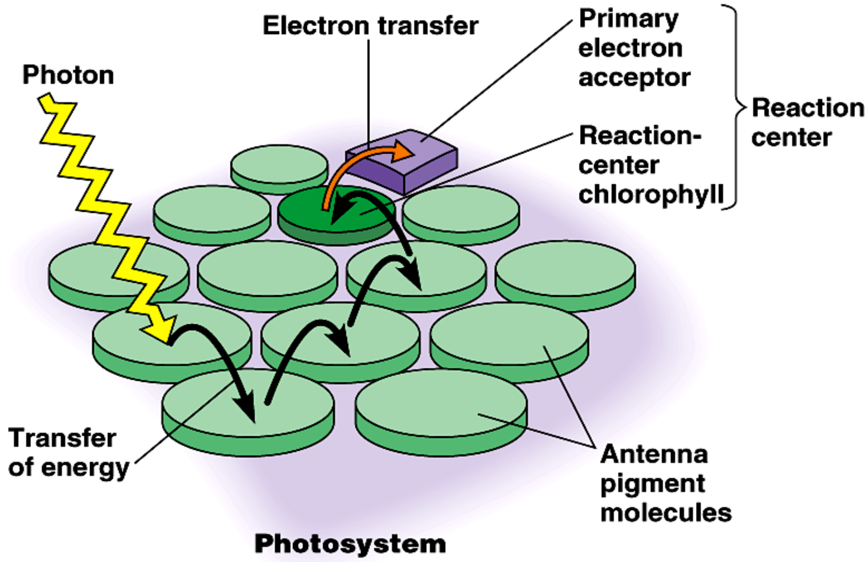
i. Carotenoids prevents the photo-oxidation of chlorophyll by chlorophyllase.
ii. ii. Carotenoids absorb energy from light and transfer it to chlorophyll a with which they are associated.

Photosynthetic Unit:

A photosynthetic unit is the smallest group of molecules which collaborate together to cause a photochemical act *i.e.* the absorption and migration of light quantum to a trapping center where it brings about the release of an electron.

Photochemical reaction centre:

All the pigment molecules in a photosystem can absorb photons but there is only one molecule in each cluster that converts the light energy into chemical energy. This specialized energy converting pigment molecule consists of a chlorophyll molecule combined with a specific protein and is called the photochemical reaction center. This chlorophyll complex is associated with a primary electron donor and acceptor.



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PHOTOSYNTHETIC UNIT

Redox Potential

The tendency for release and acceptance of electrons is called the redox potential. The term redox has been derived from reduction-oxidation. The redox potential is expressed in volts or milivolts.

Outline of photosynthetic reactions

There are two reactions involved in photosynthesis. The first reaction requires light and is called the light or hill reaction. The second reaction does not require light and is called dark or Blackman reaction. The light reaction is a photochemical reaction, while the dark reaction is a thermochemocal reaction. The unit of photosynthesis is believed to consist of two types of centers, Photosystem I and Photosystem II. These are excited at different wavelength of light. The two systems are linked by redox catalysts. The light reaction involves two processes, photophosphorylation and photolysis of water. In photophosphorylation there is a conversion of light energy in to chemical energy. Photophosphorylation is of two types i.e., cyclic photophosphorylation and non cyclic photophosphorylation.

The dark reaction takes place through a series of steps as the Calvin Benson cycle.

The Light Reaction

The light reaction involves two processes i.e., photophosphorylation and photolysis of water.

The essential features of light reaction are

1. Absorption of light energy by chlorophyll

2. The transfer of this energy and utilization of the energy in the electron transfer chain.

Besides the evolution of O_2, the light reaction gives rise to two important products

1. A reducing agent – $NADPH^+$ and

2. An energy rich compound – ATP.

These two products of light reaction are utilized in the dark phase of photosynthesis.

Photosystems

(Electron Transfer Chain or the energy conversion Process)

The photochemical phase of photosynthesis requires the interaction of two kinds of photosystems. Photosystem I is a complex consists of ~200 light harvesting chlorophylls, ~50 Carotenoids, a molecule of P700, one molecule of an unidentified compound (X), one cytochrome f, one plastocyanin, two cytochrome b 563, Ferredoxin reducing substance and one or two membrane bound ferredoxin molecule. It produces a strong reductant which reduces $NADP^+$ to $NADPH_2^+$.

Photosystem II is a structure bound complex and consists of ~200 light harvesting chlorophylls, ~50 Carotenoids, a trapping chlorophyll molecule of P680, one molecule of an unidentified compound (Z), a plastoquinone, ~4 plastoquinone equivalents, 3 mn molecules, two cytochrome b 559 and chloride. The system is concerned with the release of O_2.

Mechanism of Light Phase

The photophosphorylation is of two kinds; cyclic and non cyclic depending upon whether the electron lost by PSI is not returned to it or is cycled back to it. In the former process both the photosystems participated where as in the latter only the photosystem I operates.

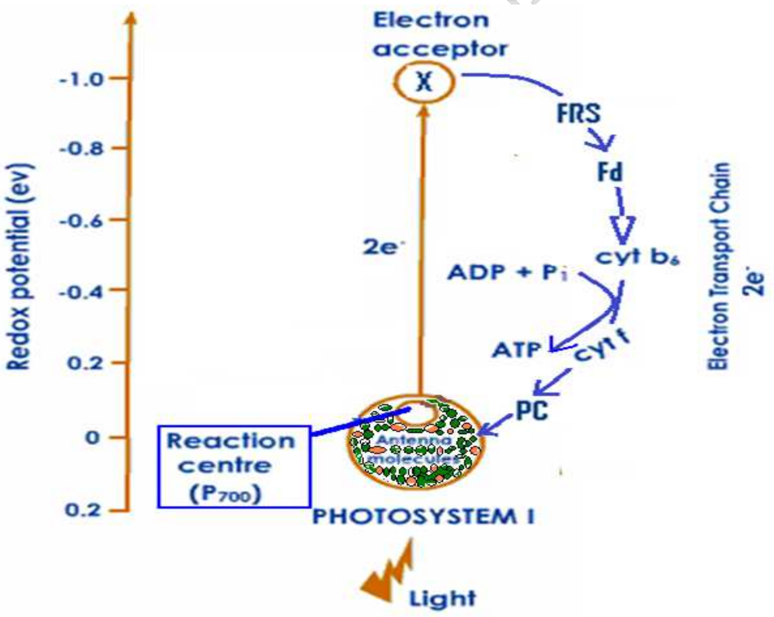
Cyclic Photophosphorylation

Cyclic electron flow involves only photosystem I. It is called cyclic because the electron boosted to the electron accepter P430 by illumination of photosystem I.

Instead of passing to NADP+, flows back in to the electron hole of Photosystem I by a shunt or bypass pathway. This shunt involves some of the electron carriers of the chain between photosystem I and II including the segment that contains the photophosphorylation step. Thus illumination of photosystem I can cause electrons to cycle continuously out of the reaction center of photosystem I and back to it, each electron being propelled round the cycle by the energy yielded by absorption on one light quantum. During cyclic electron flow there is no net formation of NADPH nor is there any O_2 evolution. However, cyclic electron flow is accompanied by the phosphorylation of ADP to yield ATP, referred to as cyclic photophosphorylation. The overall equation for cyclic electron flow and phosphorylation is simply

$$Pi + ADP + \text{Light energy} \rightarrow ATP + H_2O$$

Cyclic electron flow and phosphorylation are believed to occur when the plant cell is already amply supplied with reducing agent in the form of NADPH but requires additional ATP for other metabolic needs. Little is known about the regulation of cyclic pathway.

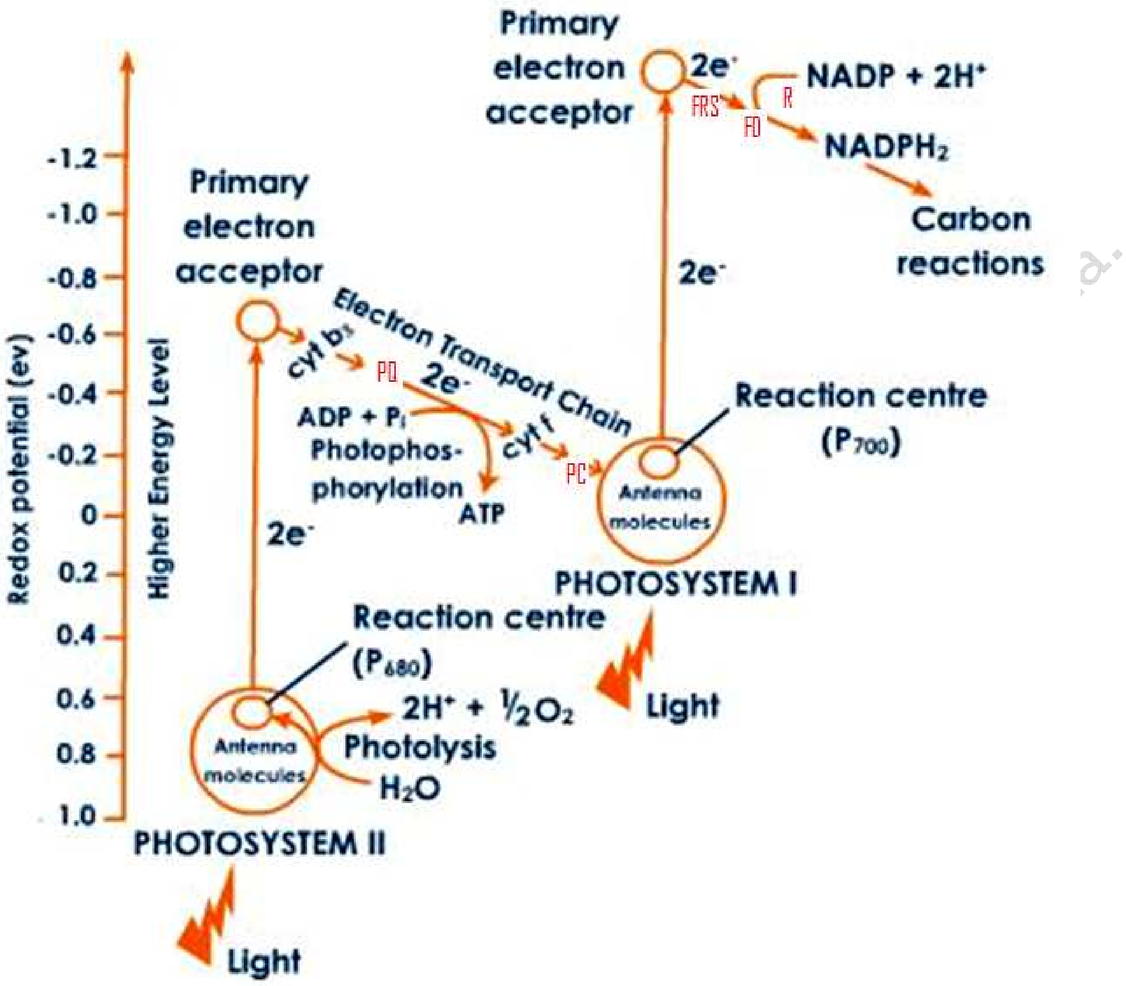


Non Cyclic Photophosphorylation

In contrast to cyclic photophosphorylation, both pigment system (Photosystem I & II) are involved in the flow of electrons. When a quantum of red light of wave length 683 nm or above is absorbed by PS I, a molecule of chlorophyll a 683 absorbs a photon and the energy is transferred to a chain of other chlorophyll a 683 molecule by inductive response, until finally it is transferred to a molecule of P700, which loses an electron. The electron is transferred to a compound labeled X and then FRS (ferredoxin reducing substance – possibly a pteridine-protein complex). Ferredoxin reducing substance being more electronegative reduces an iron containing protein called ferredoxin then reduces NADP to NADPH. The reaction is catalyzed by ferredoxin NADP reductase.

Mean while when a quantum of light of lower wave length is received by PS II, the reaction center P680 loses an electron to a substance which is probably a quinine. The electrons then travels downhill and fall back to PSI through series of electron carriers. The carriers are cytochrome b 559, plastoquinone, cytochrome f and plastocyanin. The energy released in the transfer of electron transfer of electrons from PQ to cytochrome is utilized to convert ADP and pyrophosphate to ATP. Thus PSII makes up the loss of electrons of PSI. At this stage water disassociates into hydrogen and hydroxyl ions and hydroxyl ions lose electrons to Z and becomes hydroxide radicals. The electrons are then transferred to PSII. The hydroxide radicals give rise to hydrogen peroxide which breaks up into water and oxygen. The hydrogen ions are taken up by $NADP^+$, which gets reduced to NADPH, the reducing agent. The photolysis of water is due to the formation of very strong oxidant.

$$\mathbf{4H_2O \text{--->} 4H^+ + 4OH^- \qquad 4OH^- \rightarrow 2H_2O_2 \rightarrow 2H_2O + O_2}$$



C-3 Cycle or Dark Reaction

Melvin Calvin and his colleagues studied photosynthesis using radioactive carbon C^{14} (CO_2) along with paper chromatography and elucidated the reaction of converting CO_2 to carbohydrate. In this reaction first formed stable compound is a three carbon compound. PGA (phosphoglyceric acid) and it participates in all reactions. Hence it is called as C-3 cycle. This reaction cycle can be studies in 4 steps.

1. CO_2 fixation
2. Carbon reduction
3. Carbohydrate synthesis and
4. Regeneration

Carbon dioxide (for our convenience let us say six molecules of CO_2), which is present in the atmosphere is enters into the mesophyll through stomata. Six molecules of 5-carbon compound (Ribulose 1, 5 bisphosphate) accept CO_2 and becomes 6-carbon compound. Which is intermediate, unstable and splits into 2 molecules of 3 carbon compounds *i.e*., 3 phosphoglyceric acid.

Twelve molecules of 3 phosphoglyceric acid react with 12 molecules of ATP molecules formed in light reaction to produce 12 molecules of 1, 3 bisphosphoglyceric acid. Then 12 molecules of 1, 3 bisphosphoglyceric acid are reduced to 12 molecules of 3-phosphoglyceraldehyde (triose sugar) by 12 molecules of $NADPH^+$. In other words, the bisphosphoglyceric acid undergoes dephosphorylation and reduction process.

12 molecules of phosphoglyceraldehyde participates in 4 kinds of reactions. Firstly 5 molecules of the compound are converted in to an isomer, Dihydroxyacetone phosphate by triose phosphate isomerase.

Three molecules of DHAP condenses with 3 molecules of phosphoglyceraldehyde to yield 3 molecules of fructose 1, 6 bisphosphate. The fructose 1, 6 bisphosphate molecules are then dephosphorylated by a phosphatase enzyme to form fructose 6 phosphate. One of the three molecules of fructose 6 phosphate is released as final product of photosynthesis as glucose 6 phosphate *i.e*., isomerised. Which later dephosphorylated as glucose.

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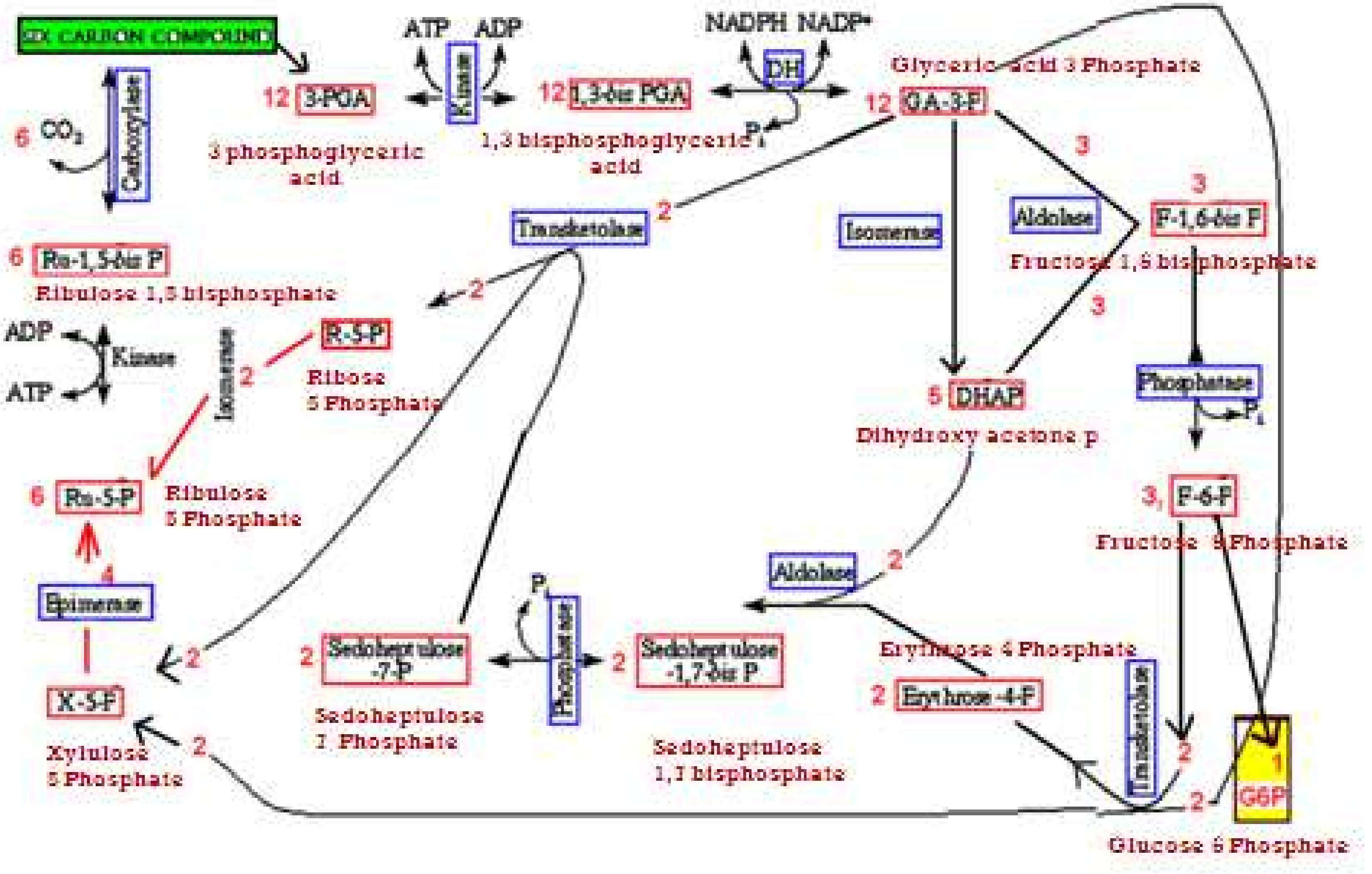

SIX CARBON COMPOUND
6 CO2
Carboxylase
12 3-PGA
3 phosphoglyceric acid
ATP
ADP
Kinase
12 1,3-bis PGA
1,3 bisphosphoglyceric acid
NADPH
NADP+
DH
Pi
Glyceric acid 3 Phosphate
12 GA-3-P
3
3
F-1,6-bis P
Aldolase
Isomerase
Fructose 1,6 bisphosphate
3
Transketolase
2
6 Ru-1,5-bis P
Ribulose 1,5 bisphosphate
2
ADP
Kinase
ATP
Isomerase
2
R-5-P
Ribose 5 Phosphate
5 DHAP
Dihydroxy acetone p
Phosphatase
Pi
6 Ru-5-P
Ribulose 5 Phosphate
3, F-6-P
Fructose 6 Phosphate
4
Epimerase
Aldolase
2
Pi
2 Sedoheptulose -7-P
Phosphatase
2 Sedoheptulose -1,7-bis P
Erythrose 4 Phosphate
2 Erythrose -4-P
Transketolase
2
X-5-F
Xylulose 5 Phosphate
2
Sedoheptulose 7 Phosphate
Sedoheptulose 1,7 bisphosphate
2
2
1
G6P
Glucose 6 Phosphate

Two molecules of fructose 6 phosphate combines with 2 molecules of the 3 phosphoglyceraldehyde *i.e*., undergoes fusion and cleavage reactions to produce 2 molecules of 4 carbon compound erythrose 4 phosphate and 2 molecules of 5 carbon compounds xylulose 5 phosphate. The reaction is catalyzed by transketolase. The enzyme requires thiamine pyrophosphate and Mg^{++} as cofactors.

Two molecules of dihydroxyacetone phosphate react with 2 molecules of erythrose 4 phosphate in the presence of aldolase to produce 2 molecules of sedoheptulose 1, 7 bisphosphate

Sedoheptulose 1, 7 bisphosphate loses one phosphate to become sedoheptulose 7 phosphate, two molecules of which react with the remaining 2 molecules of 3 phosphoglyceraldehyde to produce 2 molecules each of xylulose 5 phosphate and ribose 5 phosphate under the influence of enzyme transketolase.

Both the molecules of riose 5 phosphate are isomerized to ribulose 5 phosphate. All the 4 molecules of xylulose 5 phosphate are also epimerized to ribulose 5 phosphate. Now all the six molecules of ribulose 5 phosphate react with ATP to regenerate the 6 molecules of CO_2 acceptor ribulose 1, 5 bisphosphate. The ultimate reaction in photosynthesis is as follows.

$$\mathbf{6\ CO_2 + 18\ ATP + 12\ H_2O + 12\ NADPH^+ / 2\ H^+}$$

$$\longrightarrow$$

$$\mathbf{C_6H_{12}O_6 + 18\ Pi + 18\ ADP + 12\ NADP^+ + CO_2}$$

C-4 Pathway

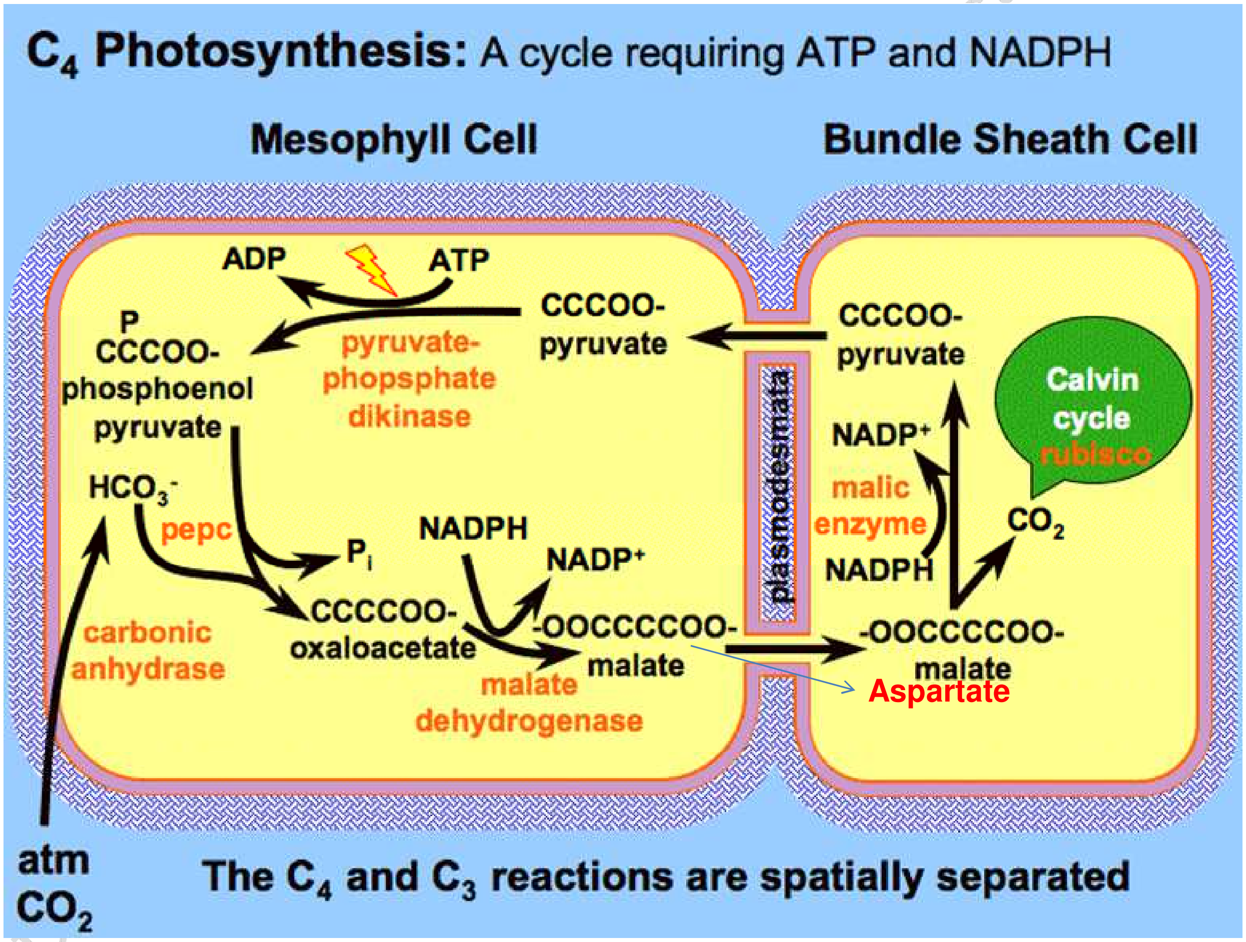
In C-3 cycle, the first stable compound formed is phosphoglyceric acid (PGA), which has three carbon atoms. Plants in which PGA is the first formed substance are therefore called C-3 plants. However, in some other plants four carbon compounds like oxaloacetate, malate and aspartate are formed. The pathway in which these compounds are formed has been called the Hatch-Slack-Kortschak (HSK) pathway.

Plants in which the cycle takes place are called C-4 plants. The C-3 plants have been called non efficient plants by some authors because they cannot grow fast at high temperature and light intensities and they carryout carbon fixation through Calvin Benson cycle 3 carbon pathway. The C-4 plants are called efficient plants because they grow fast at high temperature and light intensities. The predominant pathway for carbon fixation in C-4 plants is the HSK pathway although the Calvin Benson cycle also functions alongside. C-4 plants include monocots like maize, rice, wheat, corn, sorghum and sugar cane. Some dicots are also falls under this category. eg, members of the family *Amaranthaceae* and C*henopodiaceae*.

Plants that utilize the C-4 plant pathway also possess a common features of the leaf anatomy in which the vascular tissues(phloem and Xylem) are surrounded by a row of bundle sheath cells and then in turn by one or more layers of mesophyll cells.

This characteristic anatomy is called as Kranz anatomy. It has been found that bundle sheath cells apparently use the 3-Carbon pathway, while the mesophyll cells predominantly use the hatch-Slack pathway.

Reactions of C4 pathway



CO_2 entering the leaf of a C_4 plant during stomatal opening will diffuse in to mesophyll, where it is converted into bicarbonate ion (HCO_3^-) by carbonic anhydrase.

The 3-carbon compound phosphoenol pyruvate (PEP) is carboxylated to form oxaloacetate, a 4-C compound. The reaction is catalysed by PEP carboxylase , which is present in large amounts in mesophyll cells.

Oxaloacetate is very unstable and is converted in to either malate or aspartate. Oxaloacetate is reduced to malate by light generated $NADPH_2$, the reaction is catalyzed by malic dehydrogenase. Oxaloacetate is converted to aspartate by an aspartic transaminase. These reactions take place in the cytosol of mesophyll cells. Malate and aspartate are then transported to bundle sheath cells.

In bundle sheath cells malate undergoes oxidative decarboxylation to pyruvate. The reaction is catalyzed by malic enzyme.

In some C4 species, the aspartate undergoes transamination to oxaloacetate which is then presumably decarboxylated to pyruvate. The transamination is catalyzed by aspartate transaminase.

The pyruvic acid produced in the bundle sheath cells is transported back to the mesophyll cells. Here the enzyme pyruvate phosphate dikinase phosphorylates pyruvic acid to phosphoenol pyruvate (PEP). This enzyme is unusual in that it splits ATP into AMP and ppi. This ppi is then degraded to pi.

The CO_2 and NADPH generated in the chloroplasts of bundle sheath cells are utilized in the Calvin Benson Cycle or carboxylation of ribulose 1, 5 bisphosphate to synthesis of 3-phosphoglyceric acid (PGA). There is a now evidence that 85% of the CO_2 used in bundle sheath cells comes from C-4 cycle and only 15% is diffused atmospheric CO_2.

Photorespiration

Photorespiration is a light driven efflux of CO_2 and O_2 consumption; it has the effect of decreasing photosynthesis and therefore decreasing plant growth and crop yield. For this reason the phenomenon has been studied.

Photorespiration may attain 50% of the net rate of photosynthesis. It is a wasteful process which prevents plants from achieving a maximum yield in photosynthesis. In crop species the yield would be greater if photorespiration did not occur.

Photorespiration is exhibited by crop plants like wheat, rice, other cereals, many legumes and sugar beets while crops like corn, sorghum and sugar cane do not have photorespiration. The rate of photorespiration is more in C-3 plants when compared to C-4 plants. CO_2 generated in C-4 plants during photorespiration is trapped and recycled internally by cytoplasmic carboxylase of mesophyll cells. Thus CO_2 efflux is prevented.

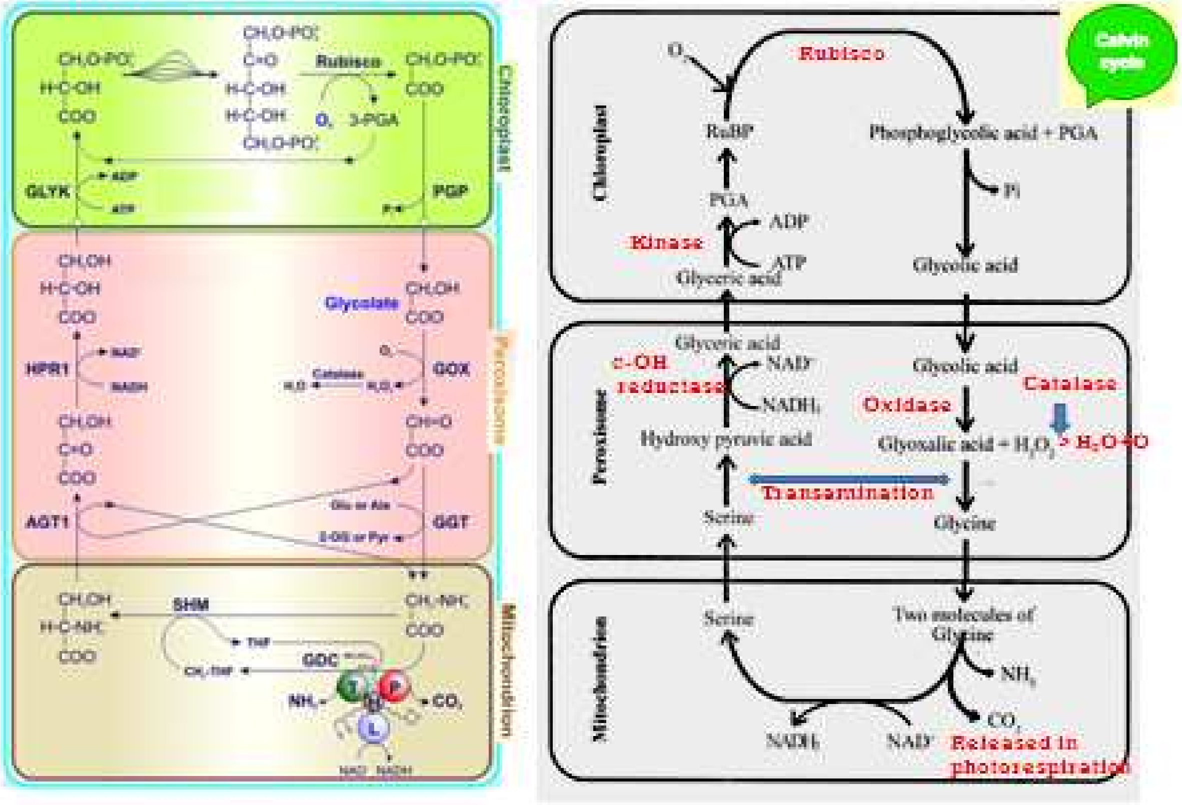
Glycolic acid is the substrate in photorespiration. The first reaction in this process is the formation of glycolic acid, the enzyme involved is ribulose 1, 5 bisphosphate carboxylase, the carboxylation enzyme of the Calvin cycle. When this enzyme is exposed to high concentration of O_2 (20% and up) and no CO_2, ribulose 1,5 bisphosphate is cleaved as 3 phosphoglyceric acid and phosphoglycolic acid. The phosphoglycolic acid so produced then enters a series of reactions that results in the release of 25% of the carbon in the glycolic acid as CO_2 and the regeneration of the 3 phosphoglyceric acid. The latter enters the Calvin cycle again to continue the process.

Glycollate is rapidly metabolized in the peroxisomes. A flavoprotein oxidase converts glycollate in to glyoxallate with the formation of H_2O_2. H_2O_2 is probably destroyed by peroxidases or catalses. Glyoxallate undergoes transamination as glycine.

In mitochondria, glycine decarboxylated and converted to serine. Later in peroxisomes, serine undergoes oxidative deamination to form hydroxypyruvate and glycerate.

In chloroplasts, glyceric acid can be synthesized in to glucose.

Photorespiration Pathway



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