Photosynthesis in Higher Plants

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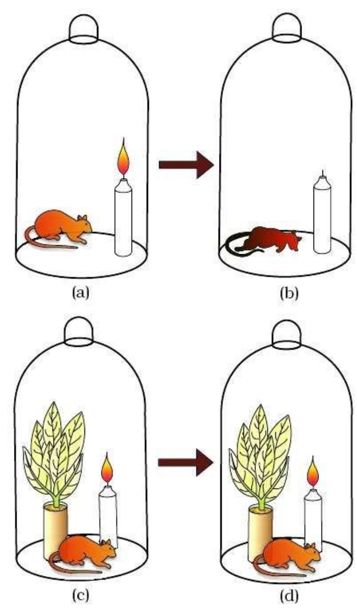
* The synthesis of complex organic substances (carbohydrates) by green parts of the plants in the presence of light with the help of CO_2 and H_2O is called photosynthesis. It can be shown by following equation.

$$6CO_2 + 12\ H_2O \xrightarrow[\text{sunlight}]{\text{chlorophyll}} C_6H_{12}O_6 + 6H_2O + 6O_2$$

* Photosynthesis is **anabolic, endothermic and redox process.**
* Photosynthesis firstly observed in **cyanobacteria.**
* Only 10% of dry matter is produced by land plants while 90% formed by aquatic plants. mostly algae (90% in ocean and 10% in fresh water).
* Radient energy of sun is changed in to chemical energy in the process of photosynthesis. It is also called carbon di-oxide assimilation.
* Photosynthesis is a **Redox process** in which **water** is **oxidized** to form **O_2** while **CO_2** is **reduced** to form **sugars**. Thus it is a oxidation reduction reaction.

HISTORY OF PHOTOSYNTHESIS

* **Aristotle and Theophrastus (320 BC) :–** State that plants absorb all food matter from **soil** (Humus theory).
* **Van Helmont (1648) :–** By weighing the Willow plant, concluded that plant take up their food mostly from soil **water**.
* **J. Woodbard (1699) :–** Besides water, soil also increases the weight of plants.
* **Stephen Hales (1727) :–** Recognised the importance of air (CO_2) and **light** for photosynthesis (nourishment) in plants. He is considered as discoverer of photosynthesis and **"Father of plant physiology"**.
* **J. Priestley (1772) :–** He carried out very interesting **experiment on Bell jar**, Rat, Pudina & Candle. He came to conclude that plants purify air (burning of candles) and gaseous exchange occurs during photosynthesis. (Phlogiston r Bad air from candles)



* **Jan Ingenhousz (1779) :–** He explained the importance of **light and green colour** and also suggested the O_2 releases in the presence of light by green parts.
* **Senebier (1782) :–** Green plants absorb CO_2 from atmosphere and when the concentration of CO_2 increases the rate of O_2 evolution also increases.
* **N. De–Saussure (1804) :–** Clarified that released O_2 is equal to the absorbed CO_2. He realised the **significance of H_2O in this process**. De–Saussure stated that O_2 comes from CO_2 during photosynthesis. (Later on it was disproved by Van Niel)
* **Pallatier & Caventou (1818) :–** They named green pigment as **'Chlorophyll'** and isolated the chlorphyll with the help of alcohol.
* **Englemann (1888) :–** Described **action spectrum** of photosynthesis with the help of **Spirogyra/Cladophora** and **aerobic bacteria** experiment.
* **Mayer (1845) :–** Green plants convert **solar energy into chemical (potential) energy** in the form of organic substance. He gave law of conservation of energy. Formation of organic matter recognised by Mayer.
* **Liebig (1845) :–** Organic matter are derived from CO_2 and H_2O, during the process of photosynthesis.
* **J. V. Sachs (1862) :–** Recognised the relation among photosynthesis, chloroplast and starch. First visible product of photosynthesis is starch. Founder of modern concept of photosynthesis. Some people consider Sachs as father of plant physiology. Three cardinal point concept wal also given by him.
* **Willstater, Stall Fisher :–** Chemistry, structure and properties of Chl–a, and nobel prize winner.
* **F. F. Blackman (1905) :– Dark reaction** associated with **light reaction** in photosynthesis and **law of limiting factors.**
* **Warburg (1920) :– Intermittent** or **flash light experiment** on **Chlorella** and proved that dark reaction exists in photosynthesis.
* **Emerson and Arnold (1932) :–** Concept of **two pigment system** (photosystem) in light reaction. **Red drop & Emerson enhancement effect.**
* **Van Niel :– O_2 releases from water** and O_2 of glucose comes from CO_2.

$$6CO_2 + 12H_2S \xrightarrow{\text{Bacteria}} C_6H_{12}O_6 + 12S + 6H_2O$$

* **Robert Hill & Bendal (1937) :–** Detailed study of light reaction in isolated chloroplast of **Stellaria.**
* **Photolysis of H_2O** is the chief role of chloroplast and evolution of O_2 only in the presence of suitable e^- acceptor, from water in photosynthesis. **(Hill–reaction)**
* **Ruben, Hassid & Kamen (1941) :–** Used **O^{18}** to experimentally show that O_2 in photosynthesis released from water.

$$6CO^{16}_2 + 12H_2O^{18} \xrightarrow[\text{Chlorophyll}]{\text{Light}} C_6H_{12}O^{16}_6 + 6H_2O + 6O_2^{18}$$

* **Arnon :–** ATP formation in presence of light **(photophosphorylation)** and cyclic and non–cyclic electron transport system.
* **M. Calvin and Benson (1954) :–** Biochemical cyclic pathway of dark reaction and recognised **PGA** is I^{st} stable product in dark reaction. (It is formed from unstable 6C Keto Acid)
  • C_3–cycle or Calvin – Benson–cycle discovered.
  • **Chromatography** and **Radioisotopy (C_{14})** techniques used in **Chlorella** and **Scenedesmus** algae. (Nobel Prize 1960).
* **Arnon, Allen & Whitley (1954) :–** CO_2 fixation demonstrated in isolated chloroplast by $C^{14}O_2$ isotope.
* **Hatch & Slack (1967) :–** C_4 pathway dicarboxylic acid cycle (DCA cycle) in sugarcane and maize. I^{st} stable product is oxaloacetic acid (OAA 4C).

* **Moll :–** CO_2 is essential for photosynthesis by **half leaf experiment.**
* **Govindji & Rabinowitch :–** Studied ultrastructure of pigment system in detail.
* **Kok & Clayton :–** Chl–a, P–700 discovered
* **Bussingault** :– **Photosynthetic Quotient (PQ)**

or **Assimillatory coefficient** = $\frac{O_2}{CO_2}$ **= 1**

* **Park & Biggins :–** Photosynthetic units as **Quantasome** in chloroplast.
* **Huber Michel and Dissenhofer :–** Crystalization & X–ray crystallography of reaction center in Rhodobacter. (Nobel–1988)

INTRODUCTION

"Photosynthesis is a photo–biochemical process **(anabolic & endergonic)** in which organic compounds (carbohydrates) are synthesised from the inorganic **raw material (H_2O & CO_2)** in presence of light & pigments. O_2 is evolved as a by product".

* **Light energy is conserved into chemical energy by photosynthesis.**

$$6CO_2 + 12H_2O \xrightarrow[\text{light}]{\text{Pigment}} C_6H_{12}O_6 + 6O_2\uparrow + 6H_2O$$

* 90% of total photosynthesis is carried out by **aquatic plants** (85% algae) & 10% by land plants.
* First true & oxygenic photosynthesis started in **cyanobacteria**. (BGA)
* In the **Cuscuta** & **fungi** photosynthesis is absent. **Euglena** is photosynthetic organism & is link between animal & plants.
* Roots of **Tinospora** & **Trapa** are assimilatory or photosynthetic.
* **Absorption spectrum** of photosynthesis is **blue** & **red** light. (maximum absorbed part of spectrum)
* Action spectrum of photosynthesis is **red** & **blue** light. (most effective in reaction)
* Rate of photosynthesis is higher in red wavelength of light, but **highest in white light** (Full spectrum), than monochromatic light.

IMPORTANT SCIENTIFIC CONTRIBUTION

* According to **Van Niel,** oxygen comes from water in photosynthesis.

$$6CO_2 + 12H_2S \longrightarrow C_6H_{12}O_6 + 12S + 6H_2O$$

* **Ruben, Hassid** and **Kamen (1941) :–** Used $\mathbf{O^{18}}$ to show experimentally that O_2 in photosynthesis comes from water.

$$6CO^{16}_2 + 12H_2O^{18} \xrightarrow[\text{Chlorophyll}]{\text{Light}} C_6H_{12}O^{16}_6 + 6H_2O + 6O_2^{18}$$

Existence of two steps in Photosynthesis –

* **Blackman** discovered dark reaction (By study of Q_{10} value or tempereture coefficient).

Calvin and **Benson** gave cyclic pathway for this, thus dark reaction is called as **Calvin cycle** OR **C_3–cycle**.

* Q_{10} (Tempereture coefficient) for **light reaction is one,** while Q_{10} for **dark reaction is between 2-3**. (By Vont Hoff).
* Q_{10} means the doubling of rate of reaction, which involves chemicals, on 10°C rise in temperature in it's optimum range.
* Experimental evidences for Blackman findings were given by **Warburg** 1920. He carried out **intermittent light experiment on Chlorella.** (by using flash light)
* The product of photosynthesis has been found greater in **intermittent light** (i.e., light given after intervals of dark periods) than in continuous light.
* This is due to the fact that light reactions are faster than the dark reaction.

In continuous light product of light reactions (**ATP** and **NADPH$_2$**) are not consumed at the same rate as in subsequent dark reaction. Thus dark reaction is rate limiting step of photosynthesis.

* Photosynthesis –

(i) Light react^n/Hill react^n

(ii) Dark reaction/Blackman react^n.

* **Hill Reaction** – Experiment on isolated chloroplast (**Stelaria** plant) study of light reaction, which is called as **Hill Reaction**.

O_2 gas liberated from **photolysis of H_2O**, only in the presence of suitable e^- acceptor. (**DCPIP** (Dichlorophenol Indophenol- a dye), **ferricyanide**, **$NADP^+$ – Hill reagents**)

$$\frac{1}{2}O_2 \leftarrow \overset{\text{Light}}{\boxed{H_2O}} \begin{cases} 2H^+ \\ 2e^- \end{cases} + NADP \longrightarrow NADPH_2$$

* **Emerson & Arnold** – worked on **Chlorella** and gave the concept of **two photosystem** or two pigment systems.

When they gave only monochromatic light, longer than 680 nm wavelength, then quantum yield is suddenly dropped down, this event is called as **red drop**.

* When Emerson gave light, shorter and greater than 680 nm (combined light) then photosynthetic, activity increases, this is called as **Emerson effect** or **enhancement effect**.

(i) 680 nm↑ → PS – I (cyclic process) **red drop appears**.

(ii) 680 nm↓ + 680↑ nm (Mixed light) → Both cyclic & non cyclic operates. **(Emerson effect)**

Quantum requirement –

The number of light Quanta or photons required for the evolution of 1 mol. of O_2 in photosynthesis = **8**

Quantum Yield –

The number of oxygen molecule evolved by one quantum of light in photosynthesis is called as **Quantum yield.** Emerson calculated that the quantum requirement is 8. Hence the quantum yield is 0.125 or 12.5%)

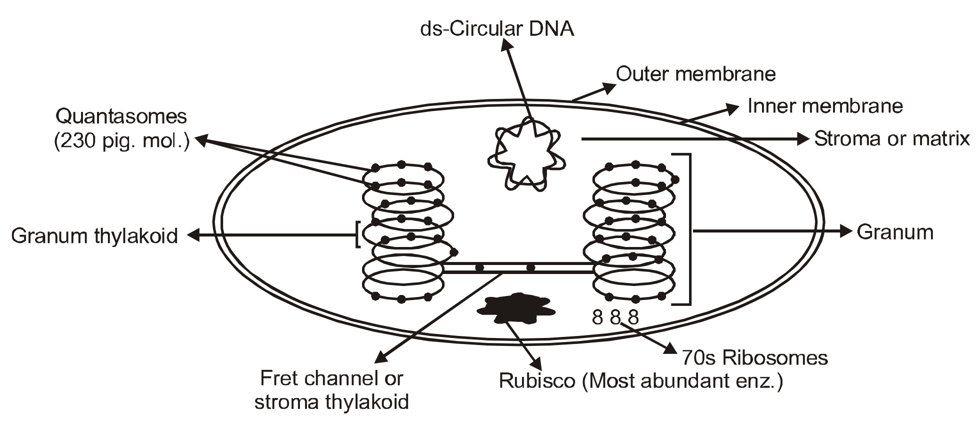
* **Arnon's experiment (Chlorella) –**

Discovered cyclic and non–cyclic photophosphorylation

$$(ADP + iP \xrightarrow[\text{Chl.}]{\text{light}} ATP.).$$

E.T.S. in photosynthesis was proposed by Arnon.

CHLOROPLAST AND PIGMENTS



Chloroplast

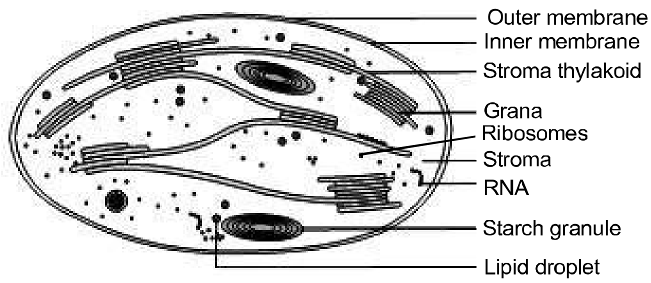


Fig: Diagrammatic representation of an electron micrograph of a section of chloroplast

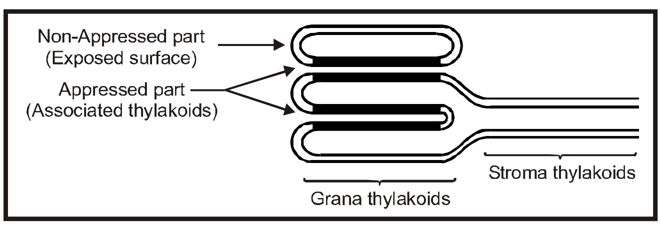
PHOTOSYNTHETIC PIGMENTS

There are three types of pigments in the chloroplasts

(1) Chlorophyll

(2) Carotenoids

(3) Phycobilins



* Many pigment present in photosynthetic cells. **PSU** (Photosynthetic units) presents on thylakoid membranes, are made up of 230-400 molecules of various pigments, called **Quantasomes** by **Park** & **Biggins**.

* The PS II is located in the **appressed region** of granal thylakoids and PS I in **non appressed** region of grana and stroma thylakoids.

* PS I located - on both granum & intergranum (Stroma thylakoid), **(P-700, 680 nm↑, Cyclic ETS).**

* PS II located - on only granum, **(P-680, 680 nm↓, non cyclic ETS)**.

* **Chlorophyll – a** $C_{55}H_{72}O_5N_4Mg$ → CH_3 grp. at IIIrd C of IInd pyrrole ring.

* **Chlorophyll – b** $C_{55}H_{70}O_6N_4Mg$ → CHO group at IIIrd C of IInd pyrrole.

* Chlorophylls are magnesium porphyrin compounds. Porphyrin ring consists of four–pyrrole rings (Tetrapyrrole).

* Chlorophyll molecule has a Mg–porphyrin head and alcoholic phytol tail. Head is hydrophilic and phytol tail is lipophilic (hydrophobic).

* Phytol tail is alcoholic with one double bond. Phytol part embeded in lipid layer.

* **Chl–a** and **carotenes** are universal pigment, which are found in all O_2 liberating cells.

* Chlorophylls are soluble only in organic solvents like ketons, ethers etc.

→ Stroma lamellae/stroma thylakoids lack PS II and enzyme NADP reductase .

→ In paper chromatography/chromatogram –

Chlorophyll 'a' appears bright or blue-green.

Chlorophyll 'b' as — yellow green/grass green.

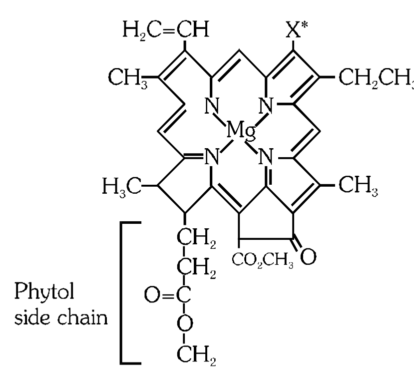
Xanthophyll as — yellow

Carotenoids as — Yellow to yellow - orange

Chlorophyll synthesis :

* Succinyl CoA + Glycine→ Protochlorophyll (Protochlorophyllide) $\xrightarrow[2H]{Light}$ Chlorophyll.

Light for chlorophyll synthesis is required only in angiosperms, (exception **Nelumbium** and **Citrus**)



CHLOROPHYLL STRUCTURE x* –CH_3 in Chlorophyll A, –CHO in Chlorophyll 'b'

DISTRIBUTION & LIGHT ABSORPTION OF PIGMENTS

Pigments	Formula	Distribution	Absorption (m↕)
Chlorophylls →			
Chl. – a	$C_{55}H_{72}O_5N_4Mg$	**All green plants.**	435, 670, 680 (Several forms)
Chl. – b	$C_{55}H_{70}O_6N_4Mg$	All green plants (except BGA Red, brown and diatoms algae)	453, 480, 650
Chl. – c	$C_{35}H_{32}O_5N_4Mg$	**Brown algae** and diatoms	645
Chl. – d	$C_{54}H_{70}O_6N_4Mg$	**Red Algae** (Rhodophyceae)	740
Chl. – e		**Xanthophyta (Tribonema** & **Vaucheria** Zoospores)	
Bacterio Chl. – a	$C_{55}H_{74}O_6N_4Mg$	Purple & green bacteria	800, 850, 890
Bacterio Chl. – b	$C_{55}H_{74}O_6N_4Mg$	**Purple bacteria (Rhodopseudomonas)**	1017
Bacterioviridin (Chlorobium chlorophyll)		Green bacteria **(Chlorobium)**	750, 760
Carotenoids →			
Carotenes →			
a–carotene	$C_{40}H_{56}$	Red, green algae & All green plants	450, 470
b–carotene	$C_{40}H_{56}$	In all green plants	450, 480
g–carotene		Green bacteria	
Xanthophylls/Carotenols→			
Luteole	$C_{40}H_{56}O_2$	Red, green algae, all plants	425, 475
Violaxanthin	$C_{40}H_{56}O_2$	Green leaves	425, 450, 475
Fucoxanthin	$C_{40}H_{56}O_3$	In Brown algae	
Phycobilins →			
Phycocyanin		**BGA** (mainly), red algae	618
Phycoerythrin		**Red algae** (mainly), BGA	490, 576
Allophycocyanin			

400 – 700 nm light is used in photosynthesis also known as **PAR (Photosynthetic active radiation**)

TERMINOLOGY :

(1) Absorption and action spectra :

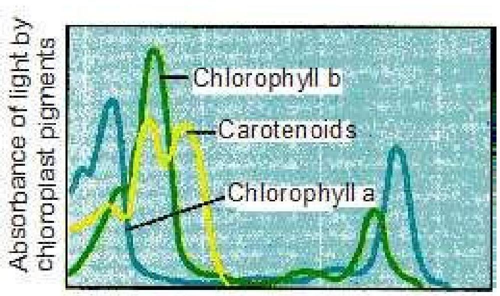
Absorption spectrum :

* Visible light has wavelength range of **3900 Å - 7600 Å.** The particles of visible light are called **photon**.
* Out of seven colours (VIBGYOR) of visible light, green light remain unabsorbed and is reflected back imparting green colour to the leaves.
* Chl a absorbs maximum **blue** followed by **red** region of spectrum. The graph showing the amount of different wavelengths of light absorbed by a substance is called **absorption spectrum**.

Action spectrum :

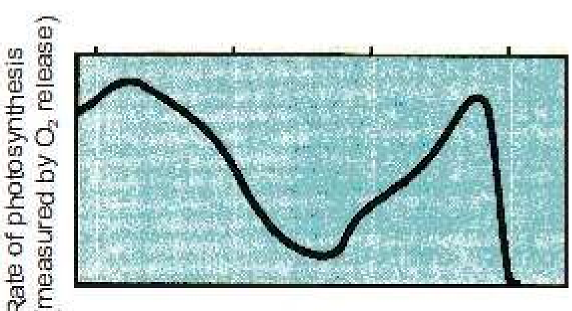
* It is a graph showing actual rate of photosynthesis measured in terms of O_2 production at different wavelength of light. It is maximum in **Red** followed by **blue** and minimum in **green** light.

Engelmann using a prism he split light into its spectral components and then illuminated a green alga, Cladophora, placed in a suspension of aerobic bacteria. The bacteria were used to detect the sites of O_2 evolution. He observed that the bacteria accumulated mainly in the region of blue and red light of the split spectrum. A first action spectrum of photosynthesis was thus described. It resembles roughly the absorption spectra of chlorophyll a and b.



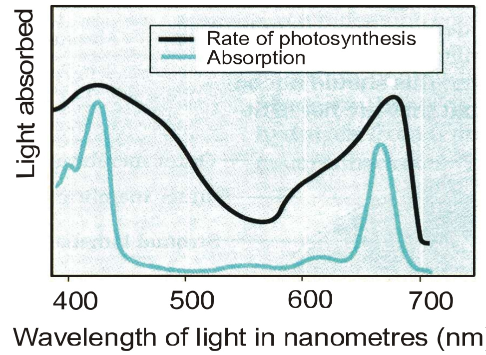
(a)

Fig: (a) Graph showing the absorption of cholophyll a, b and the carotenoids



(b)

Fig: (b) Graph showing action sepectrum of photosythesis



(c)

Fig: (c) Graphy showing action spectrum of photosynthesis superimpoon absorption spectrum of cholorophyll a

(2) Two pigment system :

(1) Pigment system-I (2) Pigment system-II

(1) PS-I or pigment system-I (LHC-I or light harvesting complex-I) :

* It is situated in both non appressed part of grana thylakoids as well as stroma thylakoids.
* It consists of pigments absorbing longer wavelength of light. It contain chla-683, chl a 690, **chl a P-700 (Reaction centre),** chl b, carotenoids cytochrome complex, plastocyanin and ferredoxin.

(2) Pigment system-II or PS-II (LHC-II or light harvesting complex-II) :

* It is located in appressed part of grana thylakoids.
* It consists of pigment absorbing shorter wavelength of light. It contains chl a - 660, chl a - 670 and **chl a-680 (Reaction centre)**, carotenoids, plastoquinons, maganese and chloride, Quencher molecule Q, cytochrome complex and plastocyanin.

Differences between PS-I & PS-II

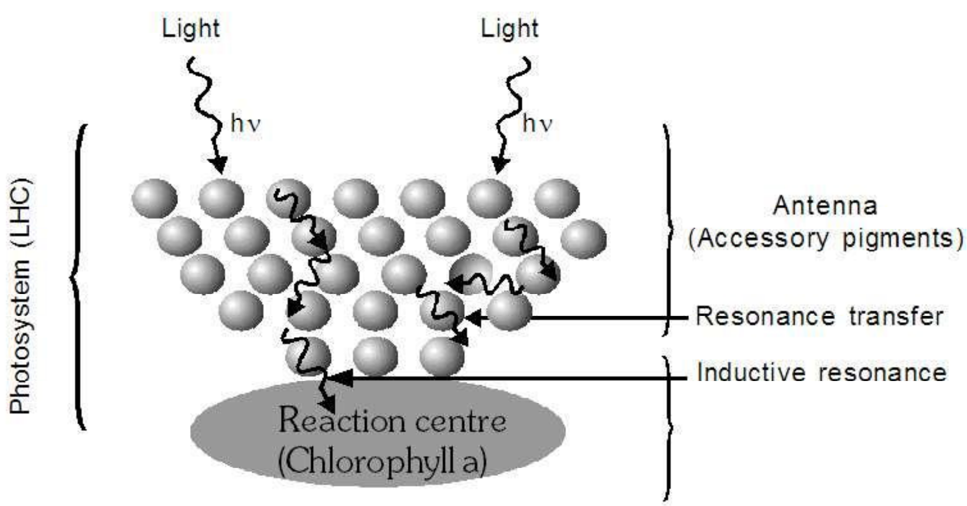
S. No	PS-I	PS-II
1	It is located on the non appressed part of grana and stroma thylakoids	It is located in the appressed part of grana thylakoids
2	P700 is a reaction centre in PS-I	P680 is reaction centre in PS-II
3	It is involved in both cyclic and non cyclic photophosphorylation.	It is involved only in non–cyclic photophosphorylation.
4	During non cyclic photophosphorylation. It obtains electron from PS-II	It obtains electron through photolysis of water
5	Molecular oxygen is not evolved in this system.	Molecular oxygen is evolved due to photolysis of water.

MECHANISM OF PHOTOSYNTHESIS

[A] Light reaction/Hill reaction/Photochemical reaction/Generation of assimilatory powers ($NADPH_2$ + ATPs)/Photophase.

* Antenna or accessory pigments receive radient energy and transfer it among themselves. This transfer of energy is known as **resonance transfer**. Then antenna molecules excited and transfer their energy to the chlorophyll 'a' molecules of **reaction centre**.

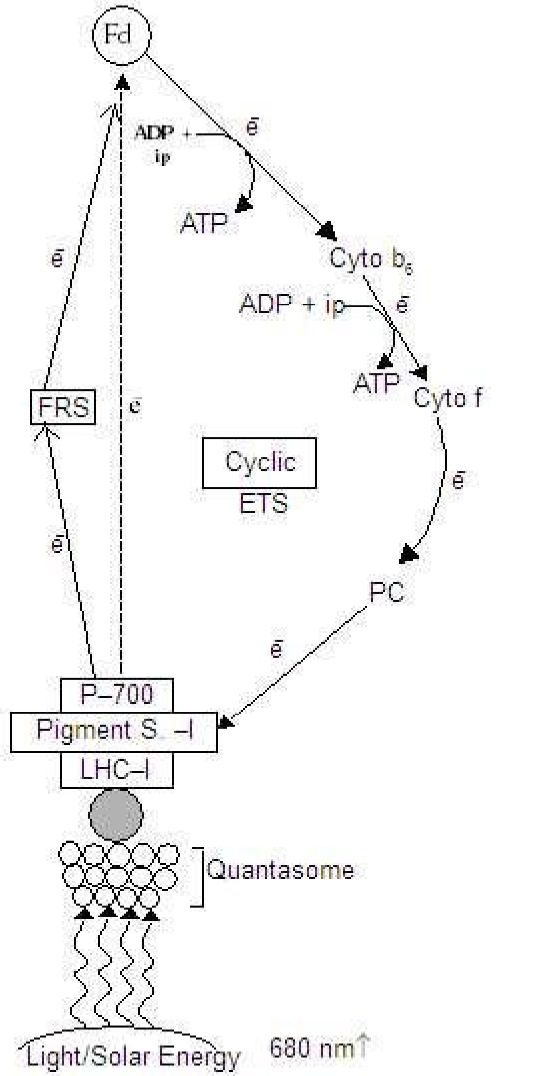
It is known as **inductive resonance.** Finally chl. 'a' of leaf center molecules converts the **light energy into electrical energy** by bringing about **electric charge separation.**



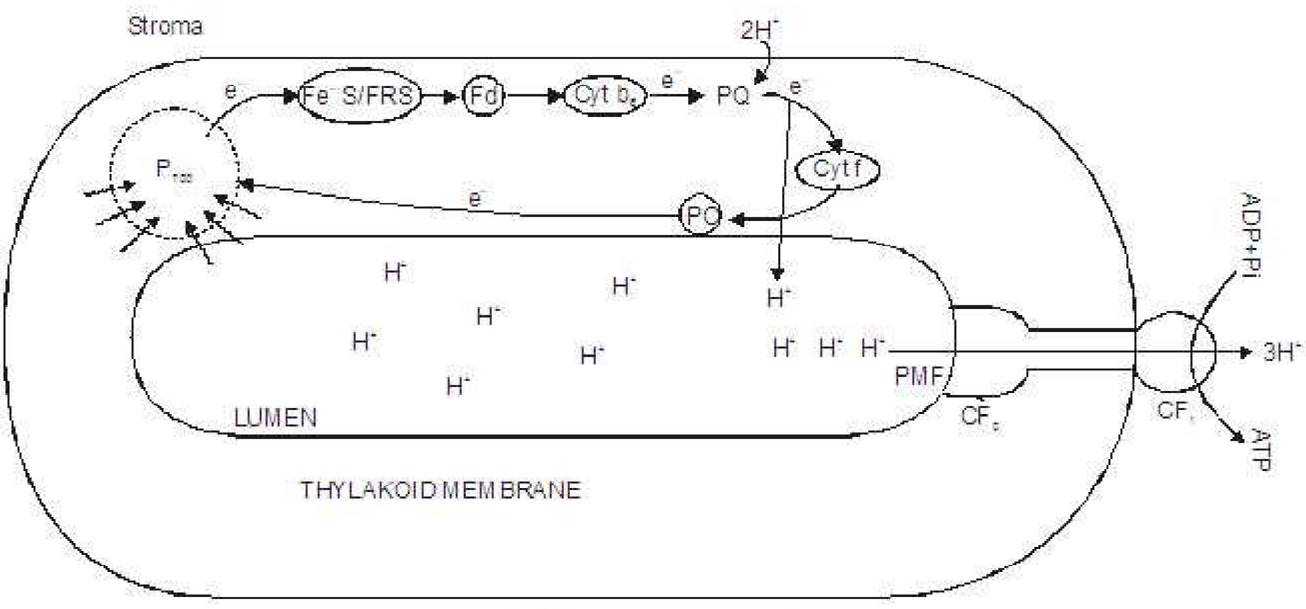
Conversion of light into electrical energy. Accessory pigment molecules absorb light and **funnel** it to the reaction centre for conversion to electrical energy and charge separation.

(I) Cyclic ETS and Photophosphorylation

* In cyclic ETS, only PS–I (LHC–I) works, which consists of Chl–'a' 670, Chl–a–683, Chl–'a'–695, carotenoids, some molecules of chl–'b' & reaction centre–Chl–'a'–700/P–700.
* Cyclic ETS OR PS–I is activated by wavelength of light greater than 680 nm.
* It occurs at grana thylakoids and stroma thylakoids.
* During Cyclic ETS the electron ejected from reaction centre of PS-I, returns back to its reaction centre.
* In cyclic ETS, **no oxygen evolution** occurs, because photolysis of water is absent.
* $NADPH_2$ (reducing power) is not formed in cyclic process.
* Plastocyanin (PC) is **Cu–containing** blue coloured protein in cyclic ETS.
* According to modern researches, first e^- acceptor is FRS (Ferredoxin Reducing Substance), which is a Fe-S containing Protein. Earlier fd (Ferredoxin) was considerd as first e^- acceptor.
* Phosphorylation takes place at two places, thus two ATP generates in each cyclic ETS.



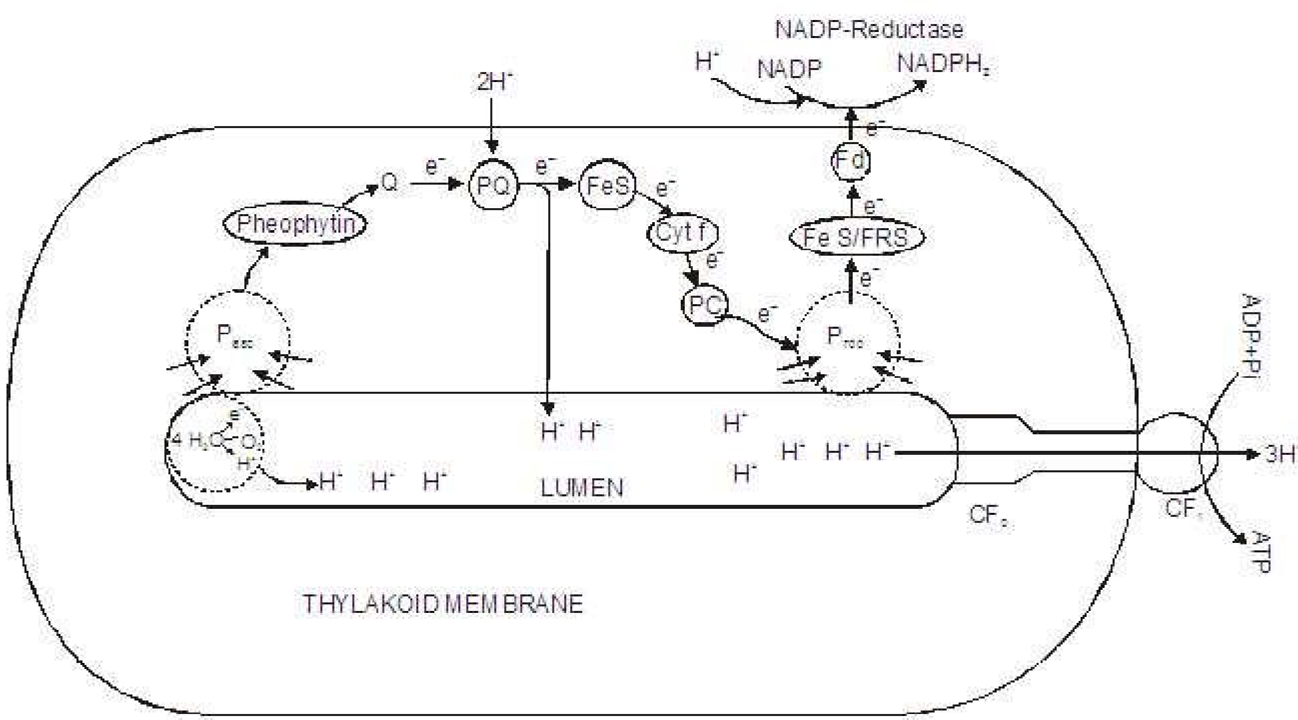
CYCLIC PHOTOPHOSPHORYLATION



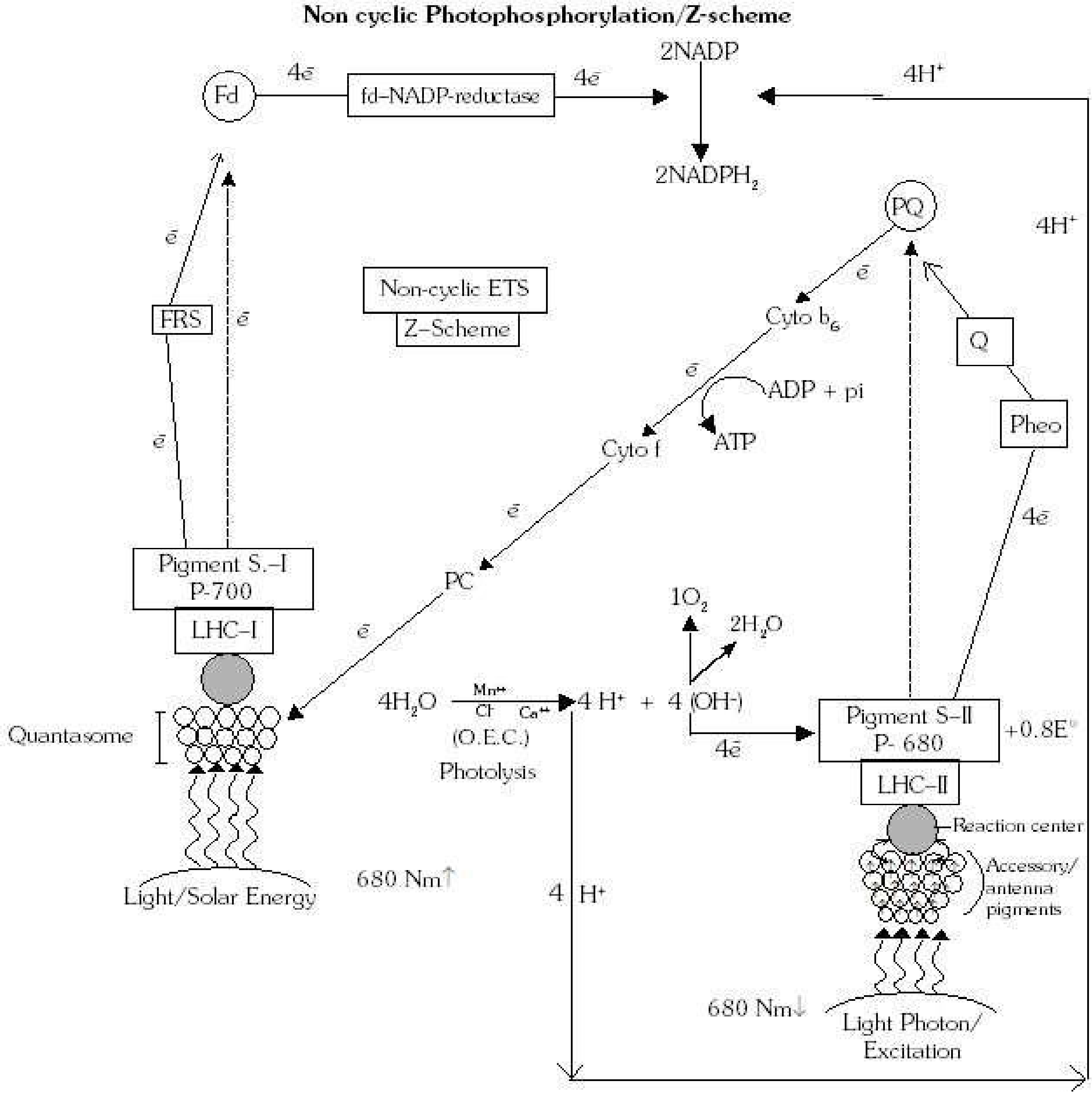
CYCLIC - PHOTOPHOSPHORYLATION

(II) Z-Scheme/Non-cyclic ETS and Photophosphorylation-

* Both PS–I and PS–II involved in non cyclic ETS.
* PS–II (P–680) consists of Chl–a–660, Chl–a–673, Chl–a–680, Chl–a–690, Chl–b, or Chl–c or Chl–d, carotenoids & phycobilins. Phycobilins present only in PS II
* It occurs at grana thylakoids only.
* The e^- ejected from PS–II **never back** to **chl–a–680** (reaction centre) & finally gained by NADP. Thus gap of e^- in PS–II is filled by photolysis of water as a result, **oxygen evolution occurs in Z–scheme.**
* Each turn of non cyclic ETS produces **1 ATP** and **2NADPH$_2$** (4 mol. of water is photolysed and 1 O_2 released)
* **12 NADPH$_2$ + 18 ATP** are required **as assimilatory power** to produce one molecule of Glucose in **dark reaction**, thus **6 turns of Z–scheme** are necessary for the production of one glucose molecule by calvin cycle.
* Additional 12 ATP come from **6 turn of cyclic ETS**. (over all 54 ATP equivalents)
* Primary e^- acceptor in non–cyclic reaction is PQ or plastoquinone. Recently **pheophytin** (structure like chl. a without Mg) is considered as **Ist e^- acceptor** in Z–scheme.
* **Plastocyanin** (PC) is link between PS–I and PS–II in non cyclic ETS. (Some scientists–cyto-f)
* Final e^- acceptor in Z–scheme is **NADP$^+$** (Hill reagent)
* During Non-Cyclic ETS energy flow takes place from PS II to PS I.



NON-CYCLIC - PHOTOPHOSPHORYLATION



Photophosphorylation :

Chemiosmotic theory : Proposed by **Peter Mitchell**. During ETC of photosynthesis concentration of H^+ gradually increases in thylakoid lumen. During cyclic photphosphrylation PQ leads to shifting of H^+ from stroma to thylakoid lumen. On the other hand during non cyclic photophoshorylation threre are three causes of differential H^+ ion concentration.

(i) Photolysis of H_2O produces H^+

(ii) PQ shifting of H^+ ion from stroma to lumen.

(iii) NADP redutase mediated utilisation of H^+ from stroma.

* This differential H^+ ion concentration leads to development of proton gradient and electrical potential across thylakoid memberane. Both proton gradient and electrical potential collectively called proton motive force (PMF)

* PMF do not allow stay of H^+ ions in lumen so H^+ start to move towards stroma through CF_0 particle selectively. The passage of $3H^+$ ions leads to activation of ATP synthase and forms ATP from ADP and Pi.

* Some physiologist beleive that synthesis of one ATP is required passage of $2H^+$ ions.

[B] Dark Reaction/Blackman Reaction/Calvin cycle/C_3–Cycle/Biochemical phase/ Carbon assimilation/photosynthetic carbon reduction cycle (PCR-Cycle)/Reductive pentose phosphates pathway –

* Blackman reaction is called as **dark reaction,** because no direct light is required for this. Calvin presented these reactions in cyclic manner & thus called as **Calvin cycle.**
* I[st] stable compound of Calvin cycle is **3C–PGA** (Phosphoglyceric acid) thus Calvin cycle is called as **C_3–cycle**. (First compound is unstable, 6C keto acid)
* Study by Calvin was on **Chlorella** & **Scenedesmus.** During his experiment he used **chromatography & radioisotopy (C^{14})** techniques for detecting reactions of C_3–cycle.
* **Rubisco** (Ribulose bis-phosphate carboxylase-oxygenase) is main enzyme in C_3–cycle, which is present in stroma & it makes 16% protein of chloroplast. Rubisco is most abundant enzyme.
* CO_2–acceptor in Calvin cycle is **RuBp**. This carboxylation reaction is catalysed by Rubisco.
* C_3, C_4, C_5, C_6 and C_7 monosaccharides are intermediates of calvin Cycle.
* C_3=Phosphoglyceraldehyde and DHAP, C_4=Erythrose, C_5=Xylulose, Ribose, C_7 = Sedoheptulose.
* The largest monosaccharide in livings are 7C–**Sedoheptulose–P (Ketose)**
* **Warburg effect –** Inhibitory effect of high conc. of O_2 on photosynthesis is called as Warburg effect (It is due to Photorespiration).
* **6 turns** of Calvin cycle are required for the formation of one glucose.

Biochemical reactions of Calvin cycle are as follows –

* **Carboxylation →**

(1) 6, RuBp (RuDp) + 6,CO_2 (HCO_3^-) $\xrightarrow[\text{(Carboxydismutase)}]{\text{Rubisco}}$ 6C unstable comp. $\longrightarrow$ 12,3–PGA (3C)

* **Glycolytic reversal →**

(2) 12 Mol. $\underset{\text{(3C)}}{\boxed{3-\text{PGA}}}$ + 12ATP $\xrightarrow{\text{Triokinase}}$ 12, 1,3–BiPGA

(3) 12, 1,3–BiPGA $\xrightarrow[\text{12NADPH}_2 \to \text{12NADP}^-]{\text{Dehydrogenase}}$ 12, 3–PGAL (Triose phosphate) + 12H_3PO_4

(4) 5 Molecules of PGAL isomerise in to DHAP (Dihydroxy acetone phosphate).

3, PGAL + 3 mol. DHAP $\xrightarrow{\text{Aldolase}}$ 3, Fructose-1,6-Biphosphate

9C (3C × 3) (9C) (3C × 3) (18C) (6C × 3)

[1 mol. fructose $\xrightarrow{\text{Isomerase}}$ $\boxed{C_6H_{12}O_6}$ Glucose $\longrightarrow$ Sucrose/Starch]

* **Regeneration of ribulose 1,5 biphosphate →**

(5) 2, fructose–P + 2, PGAL $\xrightarrow{\text{Transketolase}}$ 2 Mol, Erythrose–P + 2 Mol. Xylulose–P

(12C) (6C) (8C) (10C)

(6) 2, Erythrose–P + 2, DHAP $\xrightarrow{\text{Aldolase}}$ 2, Sedoheptulose-1,7-BiP

(8C) (6C) (14C)

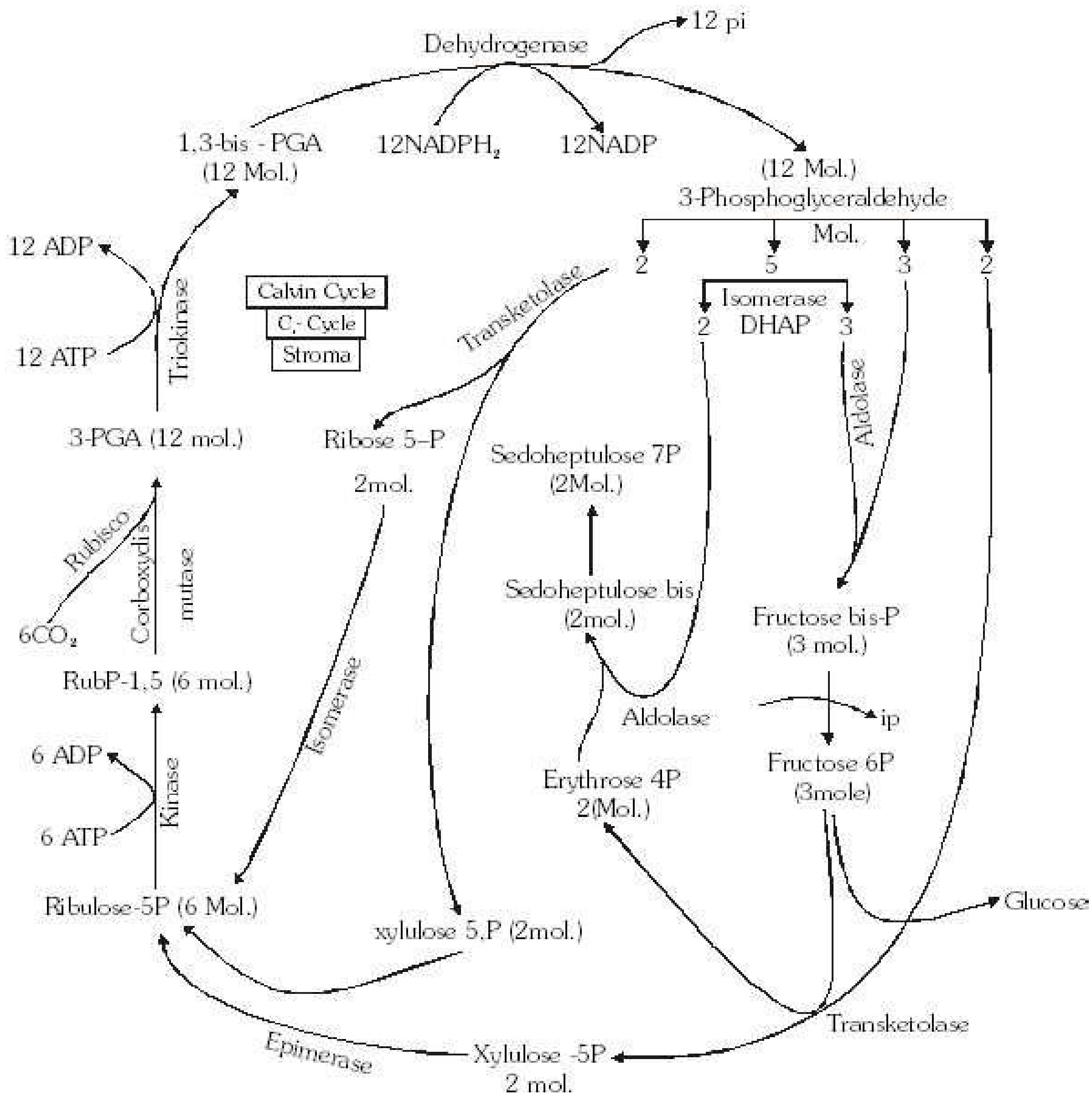
(7) 2, Sedoheptulose–P + 2 PGAL $\xrightarrow{\text{Trans Ketolase}}$ 2, Xylulose–P + 2, Ribose–P
(14C) (6C) (10C) (10C)

(8) 2 + 2, Xylulose–P $\xrightarrow{\text{Epimerase}}$ 4, Ribulose–5P
(20C)

(9) 2 , Ribose–5P $\xrightarrow{\text{Isomerase}}$ 2 Ribulose–5P
(10C)

***(10)** 6, Ribulose–5P + 6ATP $\xrightarrow{\text{Kinase}}$ 6, Ribulose-1, 5-BiP (CO_2 acceptor) + 6 ADP

Calvin Cycle/C_3–Cycle /Reductive Pentose Phosphate Pathway, in chloroplast stroma



DIVERSITY IN DARK REACTIONS

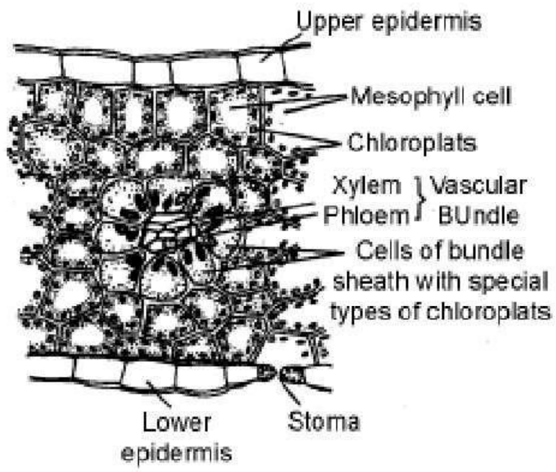
CO_2 concentrating mechanism/Co-operative photosynthesis/Dicarboxylic acid cycle (DCA cycle) /C_4 cycle/Hatch & Slack Pathway

* **Kortschak and Hartt** first observed that 4C, OAA (Oxaloacetic Acid) is formed during dark reaction in sugarcane leaves.
* **Hatch** & **Slack** Australia (1967). Studied in detail and proposed pathway for dark reactions in **sugarcane** & **maize leaves**.
* First stable product of this reaction is OAA. Which is 4C, DCA (Dicarboxylic Acid), thus Hatch & Slack pathway is called as **C_4 cycle** or **DCA cycle**.
* C_4–cycle occurs in 1500 sps. of 19 families of angiosperm, but most of the plants are monocots, which belong to **Graminae** & **Cyperaceae (Sugarcane, Maize, Sorghum, Oat, Chloris, Sedges, Bajra, Panicum, Alloteropsis etc.) Rice sps.**
* **Atriplex hastata** & **A. patula** are temperate sps,. which are C_3–plants.
* Dicots with C_4–cycle are **Euphorbia sps., Amaranthus, Chenopodium**, **Boerhavia, Atriplex rosea, Portulaca, Tribulus.**
* Wheat and barley (monocot) are C_3 species. rice sp. devlopes as C_4 plants by plant breeding scientists.
* **Kranz (Wreath) anatomy** – Present in leaves of C_4 plants.

(i) Green bundle sheath cells (BS cells) present around the vascular bundles.

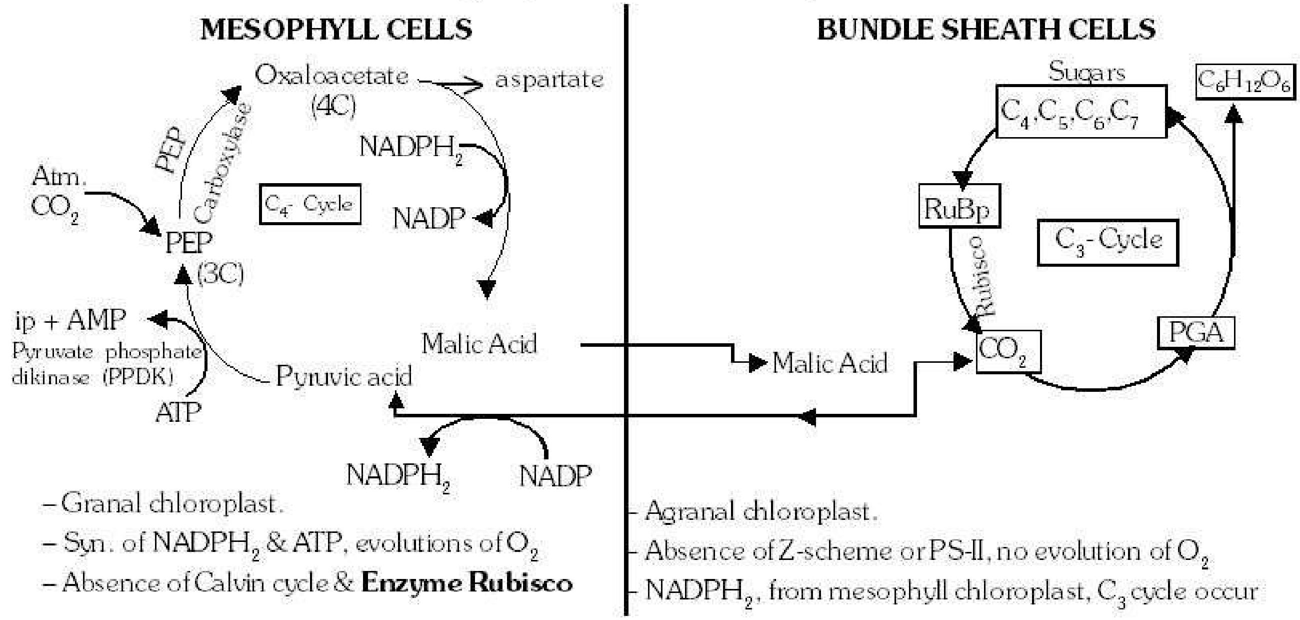
(ii) **Dimorphic chloroplasts** present in leaf cells. Chloroplast of B.S. cells or **Kranz cells** are larger and without grana. Mesophyll chloroplast are small and with grana.

* Rubisco present in BS cells, while PEPCase in mesophyll cells.
* In the C_4–Plant, C_3–cycle occurs in bundle sheath cells, while C_4–cycle occurs in mesophylls.
* Thus operation of **Hatch and Slack pathway** require cooperation of both photosynthetic cell i.e. mesophyll cells and BS cells.



* Photosynthetically C_4 plants are more efficient as there is no Warburg effect or photorespiration, Because at the site of Rubisco (BS cells) no O_2 is release & (mesophyll cells pumps more CO_2 for C_3 cycle).
* C_4–plants found in tropical habitats and adapted themselves, with high temperature, low water availability and intense light.
* If concentration of O_2 increases artificially, then photorespiration may be started in C_4 plants.
* First carboxylation in C_4–cycle occurs by **PEPCase** in mesophyll cytoplsam, while second carboxylation or final CO_2 fixation by C_3 cycle occurs in bundle sheath cells.
* Primary CO_2 acceptor in C_4 mesophyll is **PEP (Phosphoenol Pyruvate)**. (3C–compound), while RuBp in bundle sheath cells.
* 12 $NADPH_2$ & 30 ATP needed for production of 1 Hexose (Glucose) in C_4–plants.
* **Pyruvate phosphate dikinase (PPDK)** (ATP $\rightarrow$ AMP) is a temperature sensitive enzyme of C_4 and CAM plants due to this C_4 plants better photosynthesizes at high temperature.
* C_4 plant evolve by Anatomical, physiological & genetical modified.

C_4 – Cycle/ Hatch & Slack Cycle



Special features of C_4 plants :-

(1) *C_4 plants are more efficient plants at present CO_2 concentration.*

(2) *Present level of atmospheric CO_2 is generally not limiting factor for C_4 plants.*

(3) *C_4 plants posses low CO_2 compensation points. (8-10 ppm)*

(4) *The productivity (fertility) in C_4 plants, does not increase when CO_2 concentration is increases. because :*

(a) Mesophyll cells pump more CO_2 for Calvin cycle.

(b) Thus concentration of CO_2 is high around the **site of Rubisco** in C_4 plants, thus little or no chance of photorespiration.

CAM–Plants / Crassulacean acid metabolism / Dark CO_2 fixation / Dark Acidification

* **Oleary** and **Rouhani** discovered CAM–process in members of **Crassulaceae** family. Succulent xerophytie plants.

Eg. are .– **Kalanchoe, Bryophyllum, Sedum, Kleinia, Opuntia, Crassula, Agave, Aloe, Euphorbiasps, Pineapple, Welwitschia** (Gymnosperm) etc.

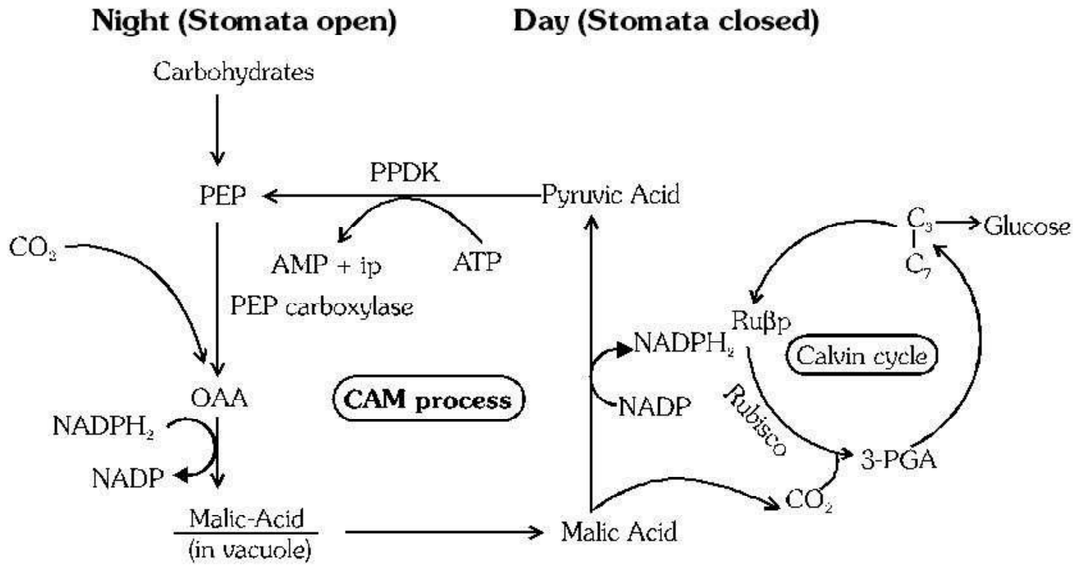
* Primary acceptor of CO_2 is **PEP** (Phosphoenol pyruvate) and oxaloacetic acid is the first product of carboxylation reaction.

* In CAM plants stomata are of **scotoactive type,** so initial CO_2 fixation is found in night but light reactions operates at day time. Final CO_2 fixation (C_3 cycle) occurs in day time. PEPcase induces carboxylation reaction in night.

* **PEP carboxylase** & **Rubisco** present in mesophyll cells. **(No Kranz–anatomy)**

* In CAM plants 30 ATP and 12 $NADPH_2$ are required as assimilatory power for 1 glucose synthesis.

* CAM plants exhibits ecophysiological adaptation with xeric habits.



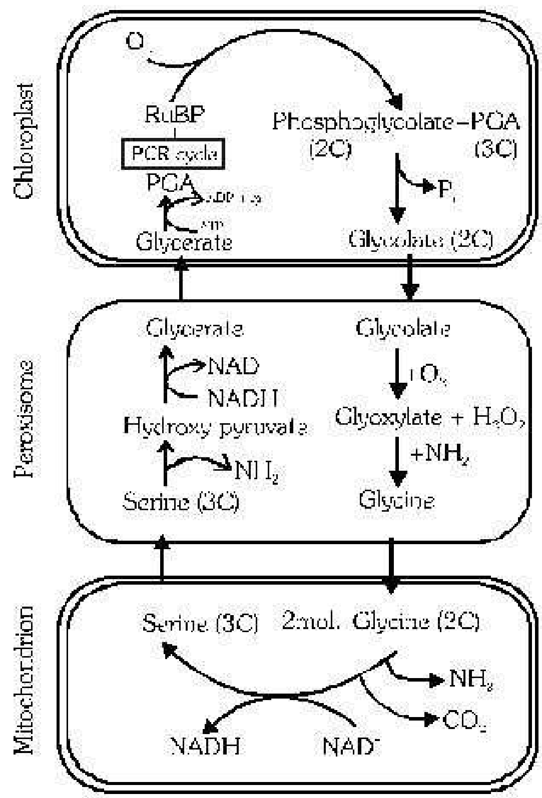
Photosynthetic carbon oxidation cycle/C_2 Cycle/ Photorespiration/Glycolate–Metabolism

* Term was given by **'Krotkov'**
* First of all **Krotkov** et. al indicated that more CO_2 evolves during day time in C_3 plants.
* **Decker** & **Tio** discovered photorespiration and clarified that **C_2–cycle** or **glycolate pathway** operates during day time in C_3–plants & **Rubisco acts as oxygenase** at **higher concentration of O_2** and **low CO_2 concentration** in the C_3 – green cells.
* The light dependent uptake of O_2 & release of CO_2 in C_3 photosynthetic cell is called **photo–respiration**.
* Photorespiration is not linked with ATP generation (in place ATP are consumed) as ordinary **dark respiration**, thus it is harmful or wasteful process linked with C_3 cycle.
* It occurs in **chloroplast**, **peroxisomes** & **mitochondria (three cell organalle reaction)**.

$$RuBP + CO_2 \xrightarrow{\text{Rubisco}} 2PGA$$

$$RuBP + O_2 \xrightarrow[\text{Low } CO_2, \text{ High } O_2 \text{ con}^n\text{, High temp.}]{\text{RuBP – Oxygenase}}$$

1 PGA + 1 Phosphoglycolate.
(3C) (2C)



Photorespiration/Photosynthetic carbon oxidation cycle.

* During photorespiration, 75 percent of the carbon lost by the oxygenation of RUBP is recovered. Because two molecules of glycine (2C + 2C = 4C) form one molecule of serine (3C). During this one carbon releases in form of CO_2 in mitochondria thus 25 percent carbon is lost.

* This serine molecule changes into PGA via different reactions of C_2 cycle.
* H_2O_2 (Peroxisome) and NH_3 (Mitochondria) produced in photorespiration.
* Glycine (Peroxisome) and serine (mitochondria) are also formed in photorespiration.
* Scientists are trying to change C_3 spe. into C_4 sps.
* It is assumed that in C_3 plants, if photorespiration does not occur, then increases O_2 conc. which may oxidise (Photooxidation or Solarization) the different protoplasmic parts of photosynthetic cell at high light intensity.

FACTOR AFFECTING PHOTOSYNTHESIS

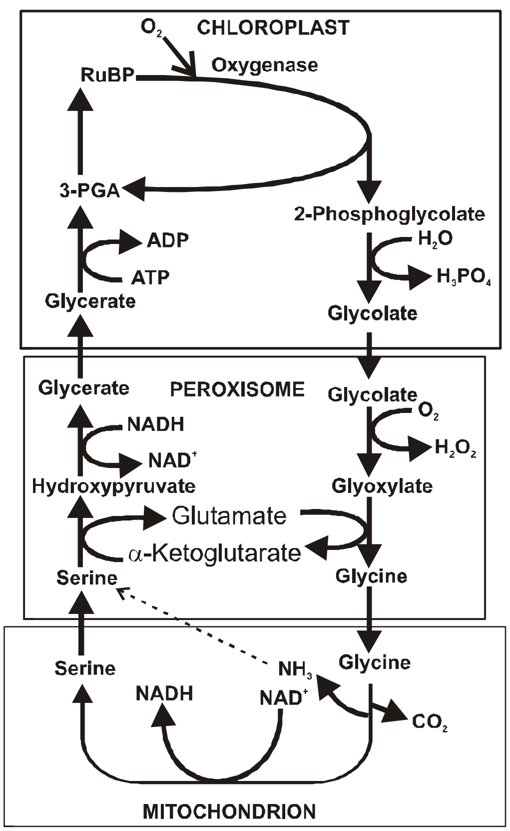


Fig:- C_2cycle

* **Sachs (1860)** proposed concept of cardinal point. According to this, factor affecting any physiological reaction has 3-main values-

(a) **Minimum :** Physiological reaction does not occur if the value is below minimum.

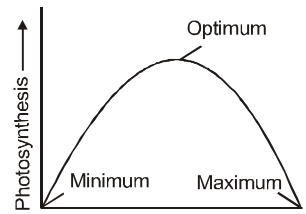
(b) **Optimum :** At optimum value, the reaction can occur at the maximum speed for an indefinite period.

(c) **Maximum :** The value beyond maximum the activity stops.

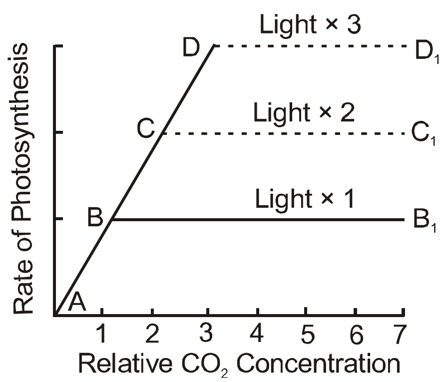
Blackman's law of limiting factor :

* According to this law when a process is affected by many factors, the rate of the process is limited by the factor

that is available in minimum quantity.



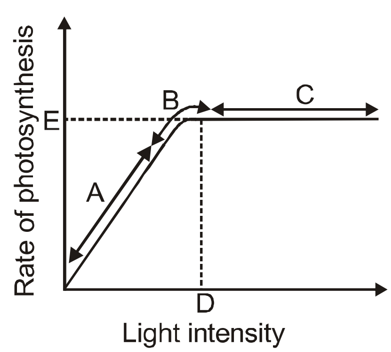
Concept of three Cardinal points



Representation of Blackman's Law of Limiting factor

EXTERNAL FACTORS

(1) **Light :**



(A) Light intensity : The rate of photosynthesis is more in intense light than diffused light. Rate of photosynthesis increases with increase in light intensity but in the presence of high light intensity photo-oxidation of chlorophyll occurs this phenomenon is called **'Solarization'** and the rate of photosynthesis declined.

* Usually the rate of photosynthesis is 10 times more than respiration during daytime but in the evening at the one point the rate of photosynthesis & respiration is equal it is called **light compensation point**. The latter is not good for plants.

(B) Light quality : The rate of photosynthesis is higher in **Red light** followed by **blue ligh**t & It is **minimum** in **green light** It is **maximum** in **polychromatic light (white light).**

(2) CO_2 : The normal concentration of CO_2 is **0.36% (360 ppm)** in atmosphere. If the CO_2 concentration increases the rate of photosynthesis also increases but in the presence of higher concentration of CO_2 it is diclined.

* **CO_2 compensation point :** It is a point on which amount of CO_2 consumption in photosynthesis is equal to the amount of CO_2 liberation in Respiration. It is **25–100ppm for C_3-plants and 0-10ppm for C_4 plants**.

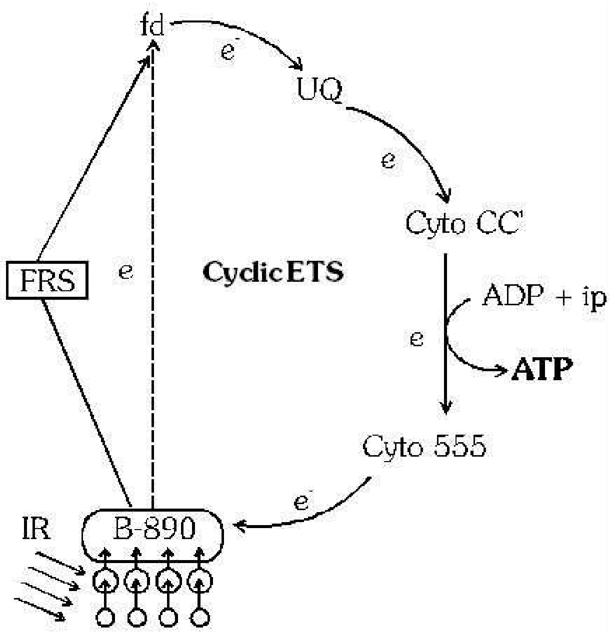
(3) Temperature : The optimum temperature for photosynthesis is **20º– 35ºC**. But above the 40ºC the rate of photsynthesis is declined due to denaturation of enzymes. Photosynthesis is inhibited at 0ºC but exceptionally lichens & conifers show phtosynthesis even at –20º to–35ºC. Also there are some BGA like **Oscillitoria brevis** which show photosynthesis at high temperature at 70^{0}C.

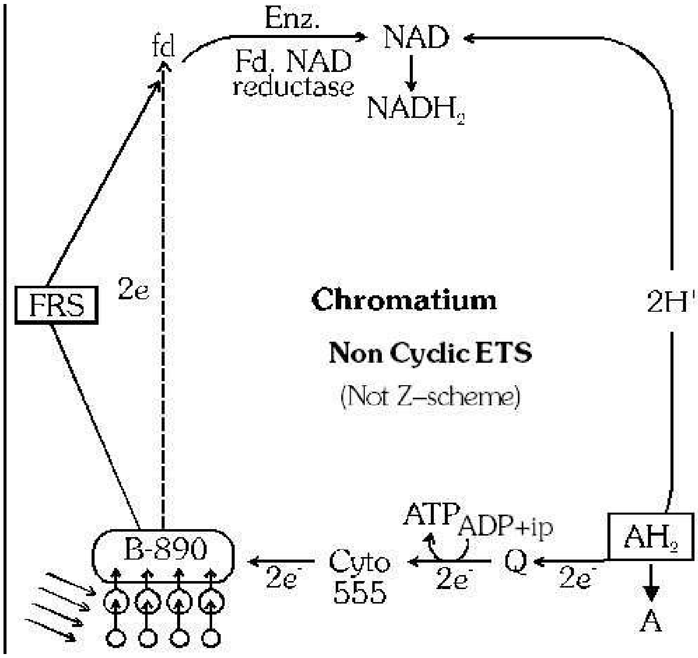
(4) O_2 : The rate of photosynthesis is declined in the presence of higher concentration of O_2 in C_3 plants due to photorespiration. It is called **warburg effect.**

(5) Water : 1% absorbed water is utilized in photosynthesis. Deficiency of water causes closing of stomata & the rate of photosynthesis is declined.

BACTERIAL PHOTOSYNTHESIS

* Certain bacteria are capable for photosynthesis Eg:- **Chlorobium** (Green Sulphur), **Chromatium** (Purple Sulphur), **Rhodospirillum, Rhodopseudomonas** (Purple non sulphur).
* Cyclic photophosphorylation is an important method in bacterial photosynthesis.
* Absorption of Infra red spectrum takes place during bacterial photosynthesis thus **no red drop**.
* Pigment system of bacteria denoted by – B–890 or 870
* Evolution of **O_2 is not related to** bacterial photosynthesis, because water is not e^- donor and PS II is absent.
* Only one ATP is produced in each turn of cyclic photophosphorylation, in bacteria.
* **Olson** 1970 gave a non cyclic scheme in bacterial photosynthesis.
* $6CO_2 + 12\ H_2S \xrightarrow[\text{Pigments in chromotophores}]{\text{IR light}} C_6H_{12}O_6 + 6H_2O + 12S.$
* Bacteria has only one pigment system, PS I.





HETEROTROPHIC PLANTS NUTRITION

* **Heterotrophs** – Heterorophic plants are of following types –

[A] Parasites –

(1) **Total stem parasites** – Cuscuta or dodar (totally depend)

(2) **Partial stem parasites** – Loranthus, Viscum (depend on host for H_2O & minerals)

(3) **Total root parasites** – Members of Rafflesiaceae, Balanophoraceae & Orobanchaceae (totally depends on host)

(4) **Partial root parasites – Santalum album** & **Striga**.

[B] Insectivorous plants –

These are green plants but of insectivorous habits which develop, due to deficiency of nitrogen, because they grow on N_2–deficient places (Swampy places).

(1) **Nepenthes** or pitcher plant – Found in north eastern parts of India (Endangerd).

(2) **Utricularia** or bladderwort – hydrophyte and pollution Indicator.

(3) **Drosera** or Sundew

(4) **Pinguicula** or butterwort.

(5) **Dionaea** or venus fly trap.

(6) **Saracenia** or pitcher plant with symbiotic bacteria.

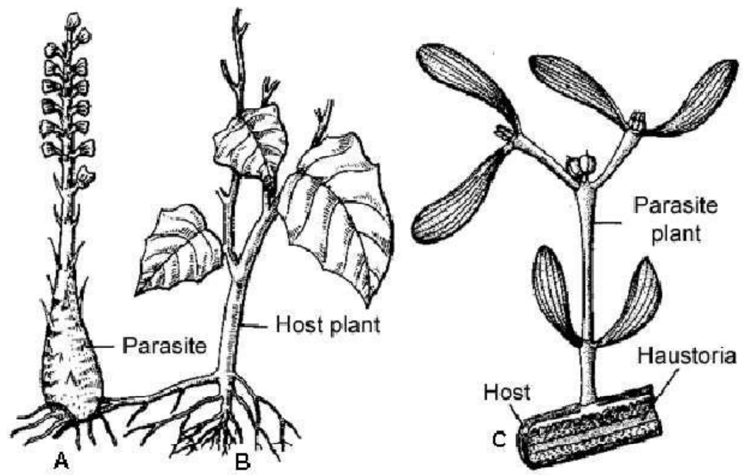
(7) **Aldrovanda** (Water flea trap)

(8) **Genlisea** (Lobster pot trap)

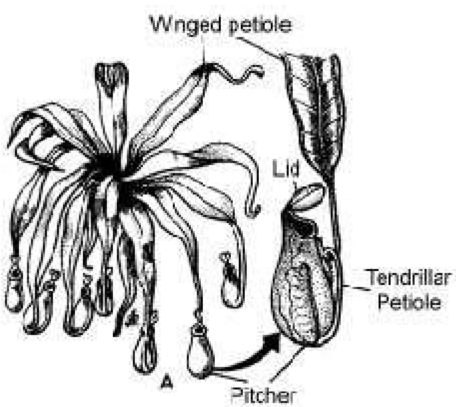
[C] Saprophytes –

Non green plants, which depend on dead organic matter – **Monotrapa** (Indian Pipe) **Neottia** (Birds eye nest)

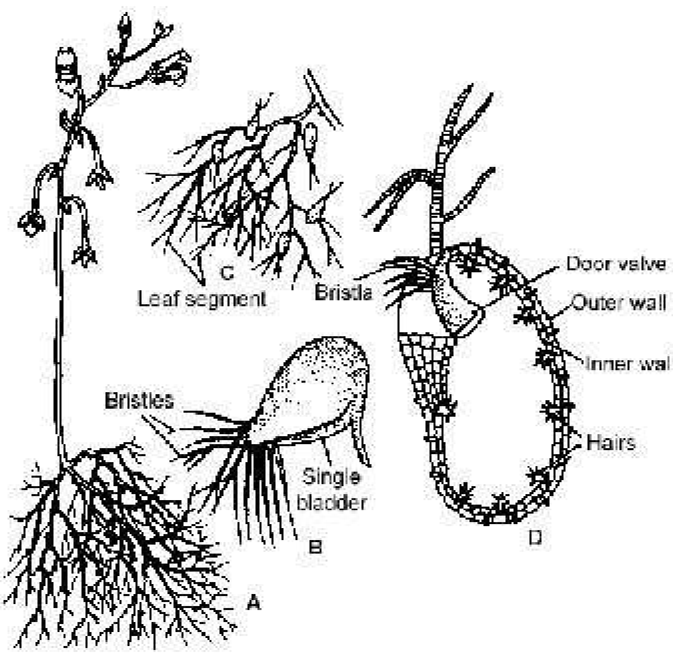
(**Dischidia** is a pitcher plant but not insectivorous).



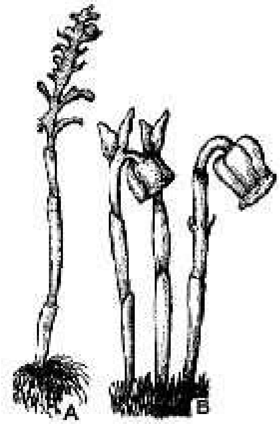
Parasitic plants-*Orobanche*
(A) A flowering plant growing on the root of *bringal*
(B) *Viscum*-Plant attached to the host stem
(C) Part of host stem is cut open to show the haustorium



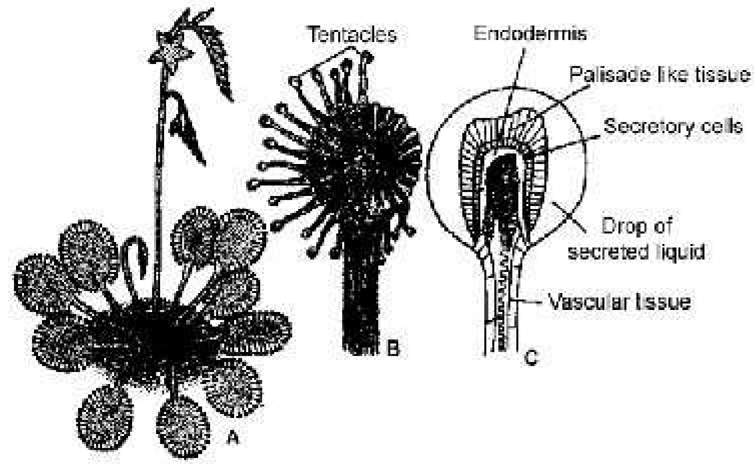
Insectivorous plant - *Nepenthes*
(Pitcher plant)
(A) A pitcher plant with pitcher.



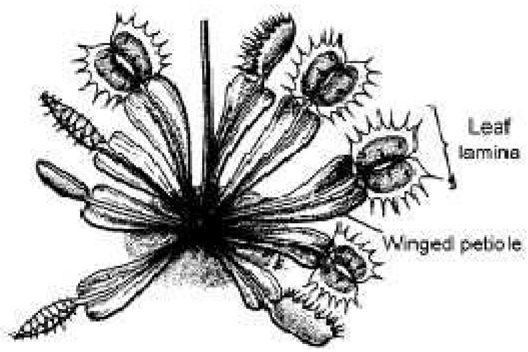
Insectivorous plant - *Utricularia* - (Bladderwort) (A) Complete plant
(B) One bladder (C) Part of leaf with several bladders
(D) Internal structure of bladder



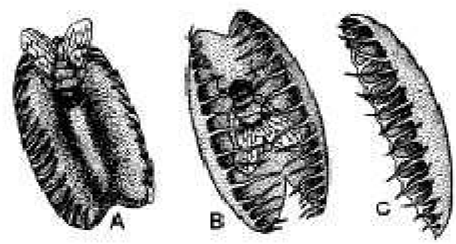
Saprophytic Plants (A) *Neottia* (Birds nest plant) (C) *Monotrapa* (Indian pipe)



Insectivorous plant - *Drosera* (A) Complete plant (b) One leaf (C) One glandular tentacle



Insectivorous plant - *Dionaea* (Venus fly trap)



Insectivorous plant *Dionaea* : Different stages in the capture of the insect

DIFFERENCES

	Photorespiration		**Dark Respiration**
(i)	Occurs in **chloroplast**, **peroxisome** and **mitochondria**.	(i)	Occurs in **cytoplasm**, **mitochondria**.
(ii)	Wasteful process.	(ii)	Useful process.
(iii)	NH_3 & CO_2, H_2O_2 are produced	(iii)	CO_2, H_2O & ATP generated.
(iv)	In green cells of C_3–plants.	(iv)	In all living cells.
(v)	Occurs during day time only.	(v)	All time

	Cyclic photophosphorylation		Non–cyclic photophosphorylation
(1)	Only PS–I involved in cyclic process.	(1)	Both PS–II & PS–I works in non–cyclic process.
(2)	The e^- expelled from chl–700 is cycled back.	(2)	The e^- expelled from reaction center is not cycled back. Its loss is compensated by e^- from H_2O.
(3)	Phosphorylation at two place.	(3)	Phosphorylation at one site.
(4)	Photolysis of water and evolution of O_2 does not take place.	(4)	Photolysis of water and evolution of O_2 takes place.
(5)	$NADP^+$ is not reduced.	(5)	$NADP^+$ is reduced to NADPH.
(6)	Activated by 680 NM↑ light.	(6)	Activated by 680 NM ↓

	C_3–pathway		C_4–pathway		CAM- pathway
(1)	I[st] stable compound is 3–C PGA	(1)	I[st] stable compound is 4C O.A.A.	(1)	First formed compound is O.A.A.
(2)	18 ATP & 12 $NADPH_2$ used for 1 glucose formation	(2)	30 ATP & 12 $NADPH_2$ used for 1 glucose formation	(2)	30 ATP and 12 $NADPH_2$ used for Production of 1 glucose
(3)	Kranz anatomy absent	(3)	Kranz anatomy present	(3)	Kranz anatomy absent
(4)	Presence of photorespiration	(4)	Absence of photorespiration	(4)	photorespiration may present
(5)	One type of carboxylase enzyme, **Rubisco** only	(5)	Two type of carboxylase enzyme **Rubisco & PEPcase**	(5)	Two type of carboxylase enzyme **Rubisco & PEPcase**
(6)	CO_2 acceptor - RUBP	(6)	Primary CO_2 acceptor - PEP & RUBP is secondary acceptor	(6)	Primary CO_2 acceptor - is PEP & RUBP is secondary acceptor
(7)	Exhibits high CO_2 compensation point (40–100 PPM)		Low CO_2 compensation point (8-10 PPM)	(7)	High CO_2 compensation point (40–100 PPM)
(8)	Transpiration ratio (TR)	(8)	TR - 200-300	(8)	TR - 50-100