CHAPTER 13

PHOTOSYNTHESIS IN HIGHER PLANTS

PHOTOSYNTHESIS

Photosynthesis is a physico-chemical process by which green plants use light energy (solar energy) to synthesise organic compounds.

Photosynthesis is the basis of life on earth.

Ultimately, all living forms depend on sunlight for energy.

Chlorophyll (green pigment of the leaf), light, water and CO_2 are required for the photosynthesis to occur.

IMPORTANCE OF PHOTOSYNTHESIS

01 It is the primary source of all food on earth.

02 It releases oxygen into the atmosphere

EXPERIMENTS RELATED WITH PHOTOSYNTHESIS

1. VARIEGATED LEAF EXPERIMENT

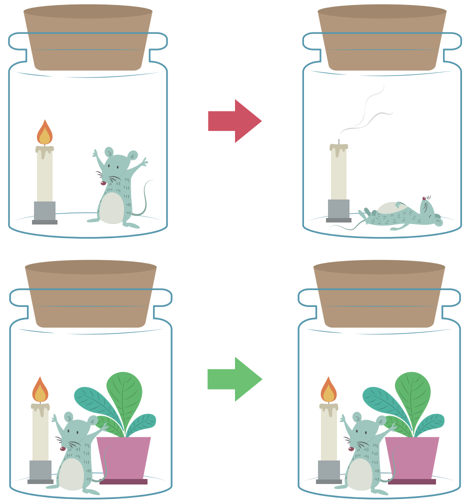
- Take a variegated leaf (or leaf partially covered with black paper) that was exposed to light.
- Test the leaves for starch. It shows that photosynthesis occurs only in green parts of the leaves in presence of light.

2. HALF-LEAF EXPERIMENT

- A part of a leaf is enclosed in a test tube containing KOH soaked cotton (which absorbs CO_2).
- The other half of the leaf is exposed to air.
- Place this setup in light for some time.
- Test the leaf for presence of starch. Exposed part tests positive for starch and portion in the tube tests negative. This proves that CO_2 is required for photosynthesis.

EARLY EXPERIMENTS

1. EXPERIMENTS BY JOSEPH PRIESTLEY (1770)



- In **1770, Priestley** performed experiments to prove the role of air in the growth of green plants.
- He discovered oxygen in 1774 during his experiment on mint plant
- He observed that a candle burning in a closed bell jar gets extinguished. Similarly, a mouse soon suffocated in a closed space. He concluded that a burning candle or a breathing animal damage the air.
- He placed a **mint plant** in the same bell jar. He found that the mouse stayed alive and the candle continued to burn.
- He hypothesised that plants restore to the air whatever breathing animals and burning candles had removed.

2. EXPERIMENTS BY JAN INGENHOUSZ (1730 -1799)

01

- He conducted the same experiment by placing it once in the dark and once in the sunlight.
- He showed that sunlight is essential to the plant for purifying the air fouled by burning candles or animals.

02

- He repeated this experiment with an aquatic plant. It showed that in bright sunlight, small bubbles were formed around green parts while in the dark they did not.
- Later he identified these bubbles to be of oxygen. Thus he showed that only the green parts of plants release O_2.

3. EXPERIMENTS BY JULIUS VON SACHS (1854)

He proved that-

- Glucose is produced when plants grow and it is usually stored as starch.
- Chlorophyll is located in special bodies (chloroplasts).
- Glucose is made in the green parts of plants.

4. EXPERIMENTS BY T.W ENGELMANN (1843 – 1909)

- He split the light using a prism into its spectral components and illuminated a green alga (*Cladophora*) placed in a suspension of aerobic bacteria. **(Odisha NEET 2019)**
- 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. **(NEET 2019)**
- It was the first described action spectrum of photosynthesis. It resembles the absorption spectra of chlorophyll *a* & *b*.
- By the middle of 19th century, it was discovered that plants use light energy to make carbohydrates from CO_2 & H_2O.
- Empirical equation of the process of photosynthesisis

$$CO_2 + H_2O \xrightarrow{\text{Light}} [CH_2O] + O_2$$

- Where, $[CH_2O]$ represents a carbohydrate (e.g., glucose).

5. EXPERIMENTS BY CORNELIUS VAN NIEL (1897–1985)

- Cornelius van Niel (microbiologist) conducted some studies in purple and green sulphur bacteria.
- He demonstrated that photosynthesis is a light-dependent reaction in which hydrogen from a suitable oxidisable compound reduces CO_2 to carbohydrates.
- This can be expressed by:

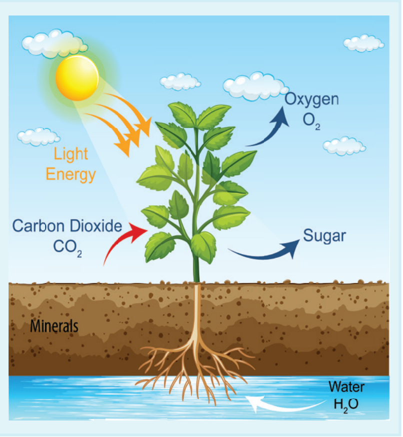
$$2H_2A + CO_2 \xrightarrow{\text{Light}} 2A + CH_2O + H_2O$$

- In green plants, H_2O is the hydrogen donor and is oxidised to O_2.
- Purple and green sulphur bacteria use H_2S as H-donor. So the 'oxidation' product is sulphur or sulphate and no O_2 is produced.
- Thus, he inferred that the O_2 evolved by the green plant comes from H_2O, not from CO_2. This was later proved by using radioisotopic techniques.
- Therefore overall correct equation for photosynthesis is:

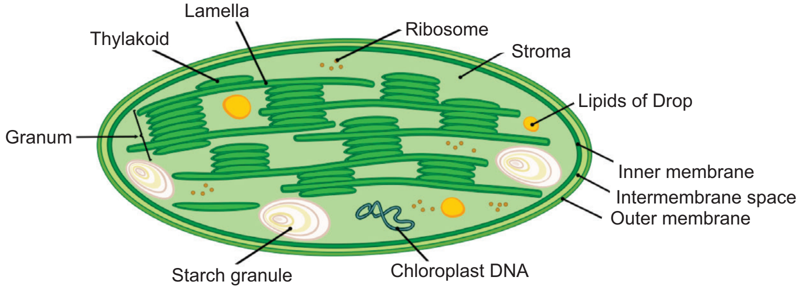
$$6CO_2 + 12H_2O \xrightarrow{\text{Light}} C_6H_{12}O_6 + 6H_2O + 6O_2$$

PHOTOSYNTHESIS: SITE AND PIGMENTS

- Photosynthesis occurs in green leaves & other green parts of the plant.
- Chloroplasts are present in the mesophyll cells of leaves so that they get optimum quantity of incident light.
- Chloroplast contains a membranous system. It consists of **grana**, **stroma lamellae** and fluid **stroma**.

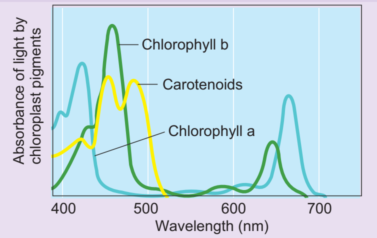


- Each granum is a group of membrane-bound sacs called **thylakoids** (lamellae). They contain leaf pigments.
- The membrane system traps light energy and synthesizes ATP and NADPH. It is called light reaction.
- In stroma, enzymatic reactions incorporate CO_2 into the plant for synthesizing sugar, which in turn forms starch. It is called **dark reaction**. It does not mean that they occur in darkness or that they are not light dependent. **(AIPMT 2009)**

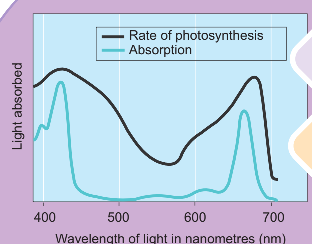


PIGMENTS INVOLVED IN PHOTOSYNTHESIS

- Pigments are substances that have the ability to absorb light, at specific wavelengths.
- Chromatography shows the following leaf pigments:
  - Chlorophyll *a* (bright or blue green in chromatogram)
  - Chlorophyll *b* (yellow green)
  - Xanthophylls (yellow)
  - Carotenoids (yellow to yellow-orange)



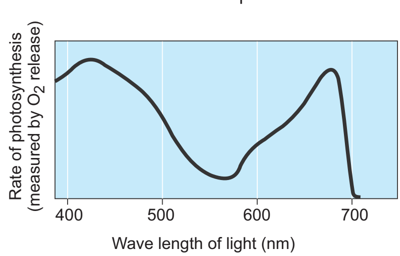
FUNCTIONS OF ACCESSORY PIGMENTS:



1. They absorb light at different wavelength and transfer the energy to chlorophyll .
2. They protect chlorophyll *a* from photo-oxidation.
3. The absorption spectrum & action spectrum coincide closely showing that photosynthesis is maximum in the blue & red regions of the spectrum.
4. The graphs also show that chlorophyll *a* is the chief pigment associated with photosynthesis

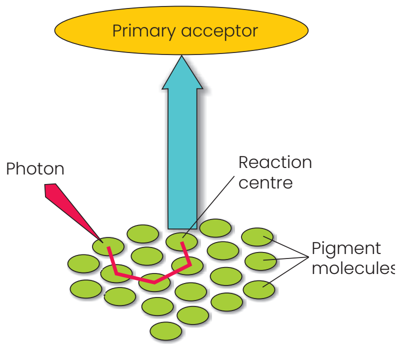
PHOTOSYSTEMS

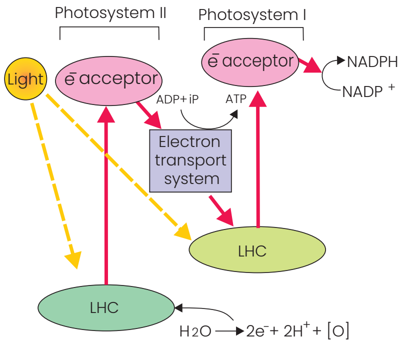
- Pigments are organised into two Photosystems called **Photosystem I (PS I)** & **Photosystem II (PS II)**. These are named in the sequence of their discovery.
- Each photosystem has a chlorophyll *a* molecule and accessory pigments bound to proteins.
- Each photosystem have all pigments (except one molecule of chlorophyll *a*) form a light harvesting complex (LHC or antennae).



- Single chlorophyll *a* acts as reaction centre.
- In PS I, the reaction centre absorbs light at 700 nm, and so called P700.
- In PS II, the reaction centre absorbs light at 680 nm, and so called P680.

LIGHT REACTION (PHOTOCHEMICAL PHASE)





- Light reactions include light absorption, water splitting, oxygen release and formation of ATP & NADPH (high-energy chemical intermediates). **(NEET 2018)**

1. THE ELECTRON TRANSPORT

- When PS II absorbs red light of 680 nm wavelength, electrons are excited and transferred to an electron acceptor.
- The electron acceptor passes them through a chain of electron transport system consisting of cytochromes.
- This movement of electrons is downhill, in terms of redox potential scale.
- Then electrons are transferred to the pigments of PS I.
- Simultaneously, electrons in PS I are also excited when they receive red light of 700 nm and are transferred to another acceptor molecule having a greater redox potential.
- These electrons are moved downhill to a molecule of $NADP^+$. As a result, $NADP^+$ is reduced to NADPH + H^+.
- Transfer of electrons from PS II to PS I and finally downhill to $NADP^+$ is called the **Z scheme**, due to its zigzag shape. This shape is formed when all the carriers are placed in a sequence on a redox potential scale.

2. SPLITTING OF WATER (PHOTOLYSIS)

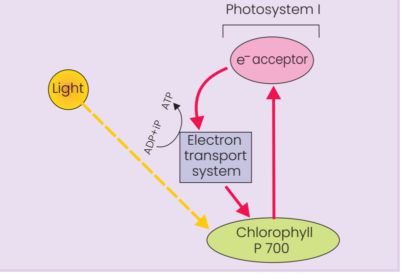
- The water splitting complex in PS II is located on the inner side of the thylakoid membrane.
- Water is split into H^+, [O] and electrons.

$$2H_2O \rightarrow 4H^+ + O \ + 4e^-$$

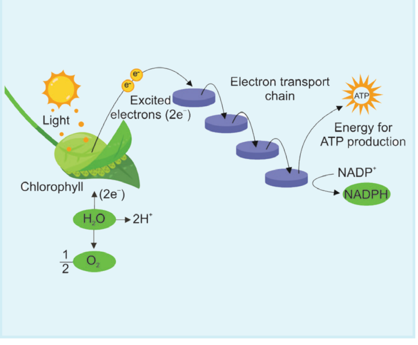
- These electrons are needed to replace the electrons that are moved from PS II
- The protons (H^+) are used to reduce NADP to NADPH.
- Oxygen is liberated as a by-product of photosynthesis.
- PS II provides electrons needed to replace those removed from PS I.

3. PHOTO-PHOSPHORYLATION

- The synthesis of ATP by cells (in mitochondria & chloroplasts) is called phosphorylation.
- Photo-phosphorylation is the synthesis of ATP from ADP in chloroplasts in presence of light.
- It occurs in 2 ways: Non-cyclic and Cyclic.



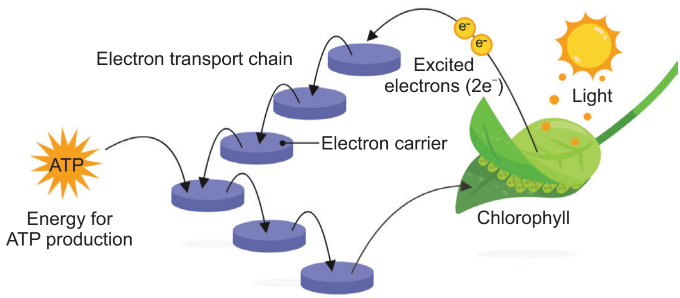
A) NON-CYCLIC PHOTO-PHOSPHORYLATION



- It occurs when the two photosystems work in a series, (first PS II and then PS I) through an electron transport chain as seen in the Z scheme.
- Here, ATP & $NADPH^+ + H^+$ are synthesised.

B) CYCLIC PHOTO - PHOSPHORYLATION

- It occurs in **stroma lamellae** when only PS I is functional.



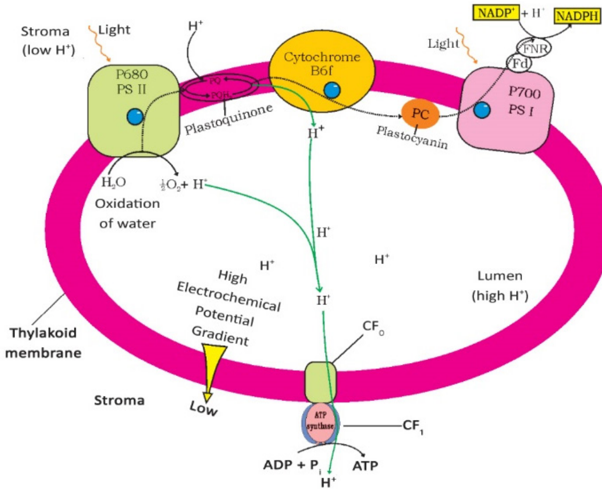
- The electron is circulated within the photosystem and the ATP synthesis occurs due to cyclic flow of electrons.
- The lamellae of grana have PS I & PS II. The stromal lamellae membranes lack PS II and NADP reductase.
- The electron does not pass on to $NADP^+$ but is cycled back to PS I complex through electron transport chain.
- Here, only ATP is synthesised (no $NADPH^+ + H^+$).
- Cyclic photophosphorylation also occurs when only light of wavelength beyond 680 nm are available for excitation.

4. CHEMIOSMOTIC HYPOTHESIS

- It explains mechanism of ATP synthesis in chloroplast and mitochondria.
- ATP synthesis is linked to development of a proton gradient across thylakoid membranes.

- Cause of proton gradients across the membrane:
  (a) Splitting of water occurs on the inner side of the membrane. So the protons accumulate in the lumen of thylakoids.
  (b) As electrons move through the photosystems, protons are transported across the membrane. The primary electron acceptor is located towards the outer side of the membrane and transfers its electron to a H^+ carrier. So this molecule removes a proton from the stroma while transporting an electron. When this molecule passes on its electron to the electron carrier on the inner side of the membrane, proton is released into the lumen of the membrane.
  (c) The NADP reductase enzyme is located on the stroma side of the membrane. Along with electrons coming from PS I, protons are necessary to reduce $NADP^+$. These protons are also removed from the stroma.

Hence, protons in the stroma decrease in number, while in the lumen, protons are accumulated. This creates a proton gradient across the thylakoid membrane and decrease in pH in the lumen. **(NEET 2016)**



- Breakdown of proton gradient leads to release of energy.
- The gradient is broken down due to the movement of protons across the membrane to the stroma through the transmembrane channel of the F0 of the enzyme ATPase.

THE ATPase (ATP SYNTHASE)

Consists of two parts:

- F_0 : It is embedded in the membrane and forms a transmembrane channel that carries out facilitated diffusion of protons across the membrane.
- F_1: It protrudes on the outer surface of the thylakoid membrane. The energy due to breakdown of gradient causes a conformational change in the F_1 particle. It makes the enzyme to synthesise ATP molecules.

Thus, chemiosmosis requires a membrane, a proton pump, a proton gradient and ATPase.

Energy is used to pump protons across a membrane, to create a gradient or a high concentration of protons within the thylakoid lumen.

ATPase has a channel that allows diffusion of protons back across the membrane. This releases energy to activate ATPase enzyme that catalyses formation of ATP.

DARK REACTION (BIOSYNTHETIC PHASE)/USE OF ATP & NADPH

- Products of light reaction are **ATP, NADPH** and **O_2**.
- In dark reaction ATP and NADPH is used to drive the processes for the synthesis of food (sugars).
- It is the biosynthetic phase of photosynthesis.
- This phase does not directly depend on light but is dependent on the products of light reaction. (i.e. ATP and NADPH besides CO_2 and H_2O)
- It can be verified as follows: Immediately after light becomes unavailable, the biosynthetic process continues for some time, and then stops. If light is available, the synthesis starts again.
- CO_2 combines with H_2O to form $(CH_2O)_n$ or sugars.
- CO_2 assimilation during photosynthesis is of 2 types :
  1. **C_3 pathway:** In this, first stable product of CO_2 fixation is a C_3 acid (PGA). Melvin Calvin studied algal photosynthesis using ^{14}C. He discovered that the first CO_2 fixation product was 3-phosphoglyceric acid (PGA), a 3-carbon organic acid.
  2. **C_4 pathway:** In this, first stable product is oxaloacetic acid (OAA), a 4-carbon (C_4) organic acid.

1. THE CALVIN CYCLE (C_3 PATHWAY)

- It occurs in all photosynthetic plants.
- It has 3 stages: carboxylation, reduction and regeneration.

01

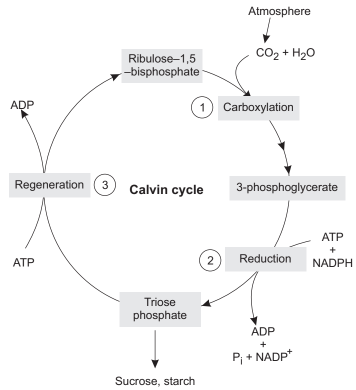
CARBOXYLATION OF RUBP

- RuBP (ribulose bisphosphate - a 5-carbon ketose sugar) is the primary CO_2 acceptor.
- It is the most crucial step. CO_2 is fixed by RuBP to two 3-PGA in presence of the enzyme RuBP carboxylase.
- Since this enzyme also has an oxygenation activity it is called RuBP carboxylase-oxygenase (RuBisCO).

02

REDUCTION

- It is a series of reactions leading to the glucose formation.
- Here, 2 ATP molecules for phosphorylation and two molecules of NADPH for reduction per CO_2 molecule are used. **(AIPMT 2005)**
- Fixation of 6 CO_2 molecules and 6 turns of the cycle are needed for the formation of one glucose molecule from the pathway. **(AIPMT 2005)**



03

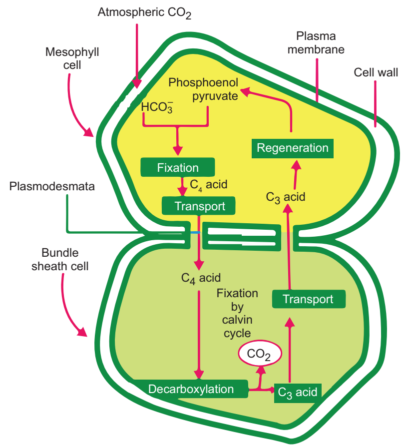
REGENERATION OF RUBP

- It is crucial for continuation of the cycle.
- It requires one ATP for phosphorylation to form RuBP hence, for every CO_2 molecule, 3 ATP molecules and 2 NADPH molecule are required.
- It is probably to meet this difference in number of ATP and NADPH used in the dark reaction that cyclic phosphorylation takes place.
- To make 1 glucose molecule, 6 turns of the cycle are needed

WHAT GOES IN AND COMES OUT OF THE CALVIN CYCLE?

In	Out
6 CO_2	1 glucose
18 ATP	18 ADP
12 NADPH	12 NADP

2. C_4 PATHWAY (HATCH & SLACK PATHWAY)



- It is present in plants that are adapted to dry tropical regions.
- They also use C_3 pathway as main biosynthetic pathway. The large cells around the vascular bundles of the C_4 plants are called bundle sheath cells. Such anatomy is called **'Kranz' anatomy** ('Kranz' = 'wreath').
- The bundle sheath cells may form several layers around the vascular bundles.
- They have large number of chloroplasts, thick walls impervious to gas exchange and no intercellular spaces.

STEPS OF HATCH AND SLACK PATHWAY

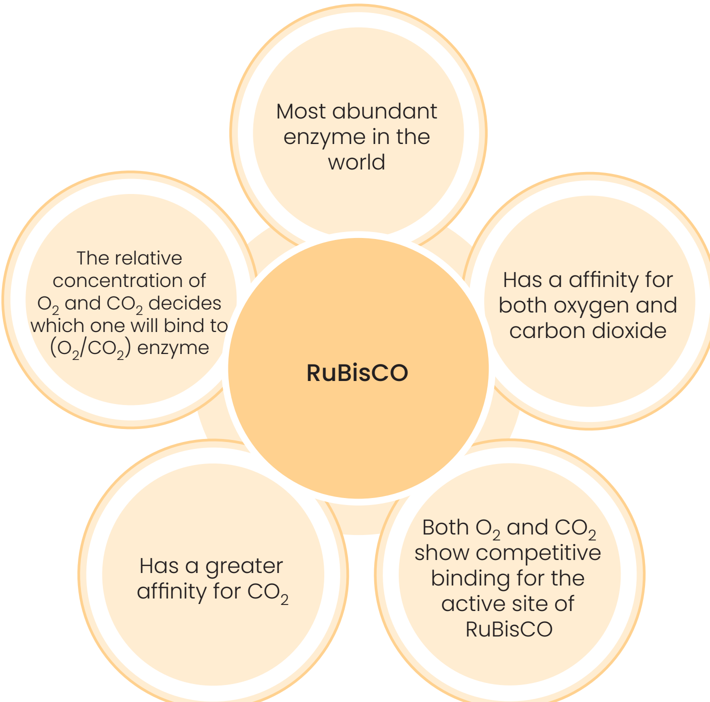
- Primary CO_2 acceptor is phosphoenol pyruvate (PEP), a 3-carbon molecule seen in mesophyll cells. The enzyme for this fixation is PEP carboxylase (PEPcase). **(NEET 2017)**
- The mesophyll cells lack RuBisCO enzyme.
- The C_4 acid OAA is formed in the mesophyll cells.
- OAA then forms other 4-carbon acids like malic acid or aspartic acid. They are transported to bundle sheath cells. **(AIPMT 2008)**
- In the bundle sheath cells, C_4 acids are broken down to release CO_2 and a C_3 molecule.
- The C_3 molecule is transported back to mesophyll where it is converted to PEP again.
- The released CO_2 enters the C_3 pathway.
- Bundle sheath cells are rich in RuBisCO, but lack PEPcase. **(Karnataka NEET 2013)**

Thus, C_3 pathway is common to C_3 & C_4 plants. C_4 plants are special because:

- They have a special type of leaf anatomy (Kranz). **(AIPMT 2010)**
- They tolerate higher temperatures.
- They show a response to high light intensities.
- They lack photorespiration.
- They have greater productivity of biomass.

3. PHOTORESPIRATION

- Photorespiration creates an important difference between C_3 and C_4 plants.



- In C_3 plants, some O_2 binds to RuBisCO. Hence CO_2 fixation is decreased. Here RuBP binds with O_2 to form one molecule of phosphoglycerate and phosphoglycolate. This pathway is called photorespiration. **(NEET 2020)**
- In this pathway, there is neither synthesis of sugars, nor of ATP and NADPH. Hence photorespiration is a wasteful process. Rather it causes the release of CO_2 by using ATP.
- In C_4 plants, photorespiration does not occur because they can increase CO_2 concentration at the enzyme site. **(NEET 2016)** This takes place when C_4 acid from the mesophyll is broken down in the bundle cells to release CO_2. This minimises the oxygenase activity of RuBisCO.
- Due to the lack of photorespiration, productivity and yields are better in C_4 plants. In addition, these plants show tolerance to higher temperatures

4. DIFFERENCES BETWEEN C_3 AND C_4 PLANTS

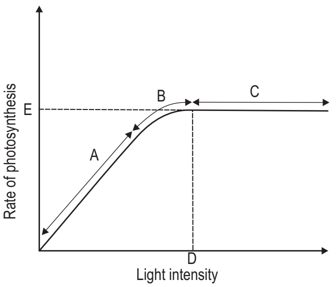
C_3 Plants	C_4 Plants
Photosynthesis occurs in mesophyll cells	In mesophyll and bundle sheath cells
Kranz anatomy absent	Present
RuBP is the primary CO_2 acceptor	PEP is the primary CO_2 acceptor
3-PGA, a 3-C compound in the first stable product	OOA, a 4-C compound is the first stable product
Chloroplast are of only one type (granal)	Dimorphic (granal in mesophyll and agranal in bundle sheath)
Photo respiratory loss is high	Photo respiration is absent or negligible
Optimum temperature for photosynthesis is about 25°C	About 35°C-45°C
Photosynthetically less efficient and productivity low	Photosynthetically more efficent and productivity high
E.g. Rice, wheat, bean, potato, etc.	E.g. Maize, sugarcane, amaranth, *Sorghum*, etc.

FACTORS AFFECTING PHOTOSYNTHESIS

- **Internal (plant) factors:** The number, size, age and orientation of leaves, mesophyll cells and chloroplasts, internal CO_2 concentration and amount of chlorophyll.
- **External factors:** Sunlight, temperature, CO_2 concentration and water.
- **Blackman's Law of Limiting Factors (1905):** "If a biochemical process is affected by more than one factor, its rate is determined by the factor nearest to its minimal value: it is the factor which directly affects the process if its quantity is changed."
- E.g. a plant with green leaf, optimal light & CO_2 conditions may not photosynthesize if the temperature is very low. If optimal temperature is given, it will start photosynthesis.

01 LIGHT

- Light quality, light intensity and duration of exposure to light influences photosynthesis.
- There is a linear relationship between incident light and CO_2 fixation rates at low light intensities.
- At higher light intensities, the rate does not further show increase because other factors become limiting.

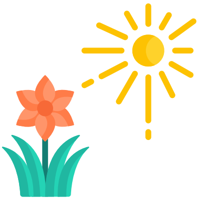


- Light saturation occurs at 10% of the full sunlight. Hence, except for plants in shade or in dense forests, light is rarely a limiting factor in nature.
- High increase in incident light breaks down chlorophyll which results in decrease in the process of photosynthesis.

02 CARBON DIOXIDE CONCENTRATION

- CO_2 is the major limiting factor for photosynthesis.
- CO_2 concentration is very low in the atmosphere (0.03 - 0.04%). Increase in concentration up to 0.05% cause increase in CO_2 fixation rates. Beyond this the levels can become damaging over longer periods.

- At low light, C_3 and C_4 plants do not respond to high CO_2. At high light, they show increased rate of photosynthesis.
- C_4 plants show saturation at about 360 $\mu L L^{-1}$
- C_3 plants respond to increased CO_2 concentration and saturation is seen only beyond 450 $\mu L L^{-1}$. Thus, current availability of CO_2 levels is limiting to the C_3 plants.
- Due to response to higher CO_2 concentration, C_3 plants show increased photosynthesis and higher productivity. This fact is used for some green house crops (tomatoes, bell pepper etc). They are grown in CO_2 enriched atmosphere.



03

TEMPERATURE

- Dark reactions, being enzymatic, are temperature controlled. Influence of temperature on Light reactions is very less.
- The C_4 plants respond to higher temperatures and show higher rate of photosynthesis.
- C_3 plants have a much lower temperature optimum.
- The temperature optimum of plants also depends on their habitat. Tropical plants have a higher temperature optimum than the plants adapted to temperate climates.

04

WATER

- Water stress closes the stomata hence reduce the CO_2 availability.
- Water stress also wilts leaves, thus reduce the surface area of the leaves and their metabolic activity.

Notes