Republic of Iraq
Ministry of Higher Education
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College of Science

Lecture 9

Photosunthesis

Dark reactions

Photorespiration (The C_2 oxidative photosynthetic carbon cycle)

Hatch and Slack pathway (C_4 cycle)

Crassulacean Acid Metabolism (CAM Pathway)

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Photorespiration (The C_2 oxidative photosynthetic carbon cycle):

CO_2 is also released in a pathway which is distinct from mitochondrial respiration. The pathway is known as photorespiration or C_2 oxidative photosynthetic carbon cycle or photosynthetic carbon oxidation cycle (PCO). Rubisco possess carboxylase as well as oxygenase activities, since both CO_2 and O_2 compete for same catalytic site of the enzyme. Rubisco reacts with its second substrate, RuBP, to generate an unstable intermediate that splits into 2-phosphoglycolate and 3-phosphoglycerate in the presence of light and O_2. So Rubisco has the capacity to catalyze both the carboxylation and oxygenation of ribulose 1,5-bisphosphate. Carboxylation yields two molecules of 3-phosphoglycerate, while oxygenation produces one molecule each of 3-phosphoglycerate and 2-phosphoglycolate. The oxygenation of ribulose 1,5-bisphosphate catalyzed by rubisco initiates a coordinated network of enzymatic reactions that are compartmentalized in chloroplasts, leaf peroxisomes, and mitochondria. This process, known as photorespiration, causes the partial loss of CO_2 fixed by the Calvin-Benson cycle.

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(a) Carboxylase activity

$$\text{RuBP} + \text{CO2} + \text{H2O} \xrightarrow{\text{Rubisco}} \text{2 Moles of 3 PGA}$$

(b) Oxygenase activity

$$\text{RuBP} + O_2 \xrightarrow{\text{Rubisco}} \text{Phosphoglycolic acid (2C) + 3 PGA (3C)}$$

In the next step phosphoglycolic acid undergoes decarboxylation to form glycolic acid. The reaction is catalyzed by enzyme phosphatase.

Phosphatase

Phosphoglycolic acid + H_2O $\longrightarrow$ Glycolic acid + Phosphoric acid

The glycolic acid which is formed in chloroplast is transported out into the peroxisomes where glycolic acid is converted into glyoxylic acid in presence of enzyme glycolate oxidase.

Glycolic acid + O2 $\longrightarrow$ Glyoxylic acid + H_2O

Here glycolic acid oxidase transfers electrons (present in H atoms) from glycolate to O_2 reducing O_2 to H_2O_2. Then H_2O_2 is broken down to H_2O and O_2 by catalase. In the next step glyoxylic acid is converted into glycine under the influence of enzyme glutamate glyoxylate amino transferase (transamination reaction)

Glyoxylic acid + Glutamic acid $\longrightarrow$ Glycine + α Keto glutaric acid

Glycine which is formed in peroxysomes is transported to mitochondria via cytoplasm. Glyoxylic acid may also form glycine by serine by transfer of amino group to it from serine instead of glutamic acid.

Serine amino transferase

Glyoxylic acid + Serine $\longrightarrow$ Glycine + Hydroxy Pyruvic acid

In the mitochondria two molecules of glycine joins together to form a molecule of serine. CO_2 and NH_3 are also released in this reaction.

2 Glycine + H_2O + NAD $\longrightarrow$ Serine + CO_2 + NH_3 + NADH

It is the stage of formation of serine that light induced CO_2 liberates. Serine is then transported out of mitochondria and into peroxysomes where it is converted into hydroxy pyruvic acid and then to glyceric acid. Finally glyceric acid is transported to chloroplast where it undergoes phosphorylation by ATP to form 3 PGA. The molecules of 3 PGA join the pool in the CO_2 reduction cycle. In C_4 plants the rate of photorespiration is almost nil because CO_2 concentrates in bundle sheath cells. The positive movement of CO_2 from atmosphere towards bundle sheath cells is called CO_2 pump.

Significance of photorespiration:

• It protects the chloroplast against the light destruction. It consumes O_2 thereby helps to prevent build up of O_2 accumulation in chloroplast which may destroy the chloroplast membrane.

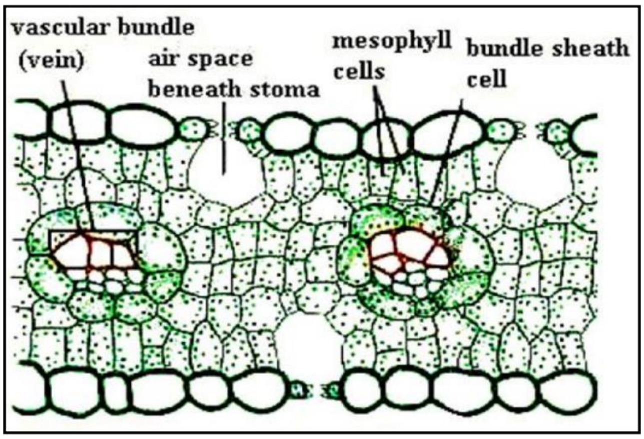
• In this process excess ATP and NADPH are utilized thus prevents solarization.

- Photorespiratory cycle also plays an important role in synthesis of two essential amino acids, glycine and serine. Alternate pathways for synthesis of these amino acids function when photorespiration is suppressed.
- In addition to role of photorespiration in carbon economy, it plays significant role in nitrogen economy. When two molecules of glycine are converted to serine in mitochondria, one nitrogen atom, which is lost as NH_3, is re-assimilated in chloroplasts. During NH_3 assimilation, reducing equivalents are utilized as reduced ferredoxin and NADPH.
- The activity of the cycle recovers some of the carbon found in 2-phosphoglycolate, but some is lost to the atmosphere, Seventy-five percent of carbon lost from Calvin cycle as 2-phosphoglycolate is recovered in the C_2 oxidative photosynthetic carbon cycle. Out of ten carbons of RuBP (two molecules), only one carbon is lost as CO_2, while nine carbons are recycled as 3-PGA.

Hatch and Slack pathway (C_4 cycle)

The photosynthetic carbon metabolism of certain plants in which the initial fixation of CO_2 and its subsequent reduction takes place in different cells, the mesophyll and bundle sheath cells, respectively. The initial carboxylation is catalyzed by phosphorenolpyruvate carboxylase, (not by rubisco as in C_3 plants), producing a four-carbon compound (oxaloacetate), which is immediately converted to malate or aspartate. The first product of this cycle is 4 carbon acid. This cycle occurs mainly in sugarcane, maize, grasses, atriplex etc. C_4 plants possess Kranz anatomy. In this case the mesophyll cells are not differentiated into palisade and spongy parenchyma. Vascular bundles are surrounded by layers of radially arranged parenchymatous cells. The sheath appears like a wreath, hence called Kranz (wreath) anatomy .Phospho enol pyruvate is the initial acceptor of CO_2.

$$\textbf{PEP + CO2 + H2O} \xrightarrow{\textbf{PEP Carboxylase}} \textbf{Oxalo acetic acid}$$



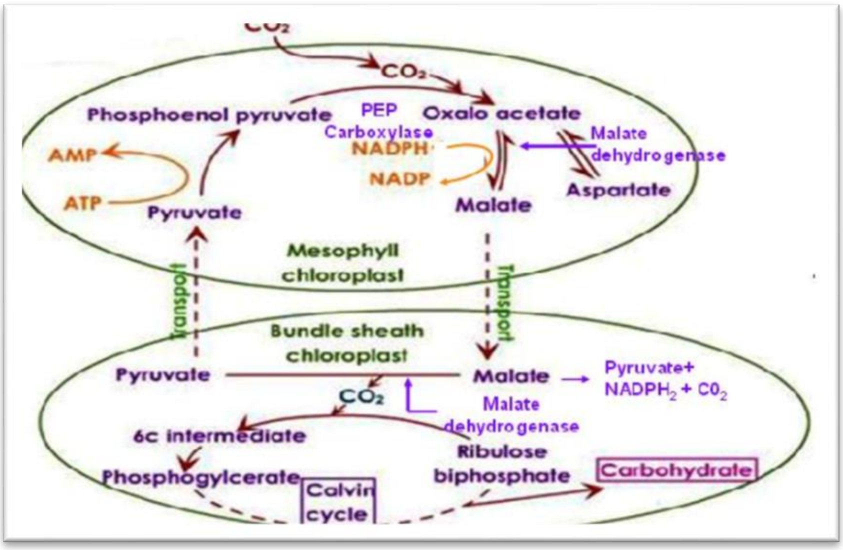
Initially CO_2 is accepted by Phospho enol pyruvate (PEP) under influence of PEP carboxylase enzyme forming aspartate. Malate is produced by activity of malic dehydrogenase in presence of $NADPH_2$. Malate is transferred to chloroplast of bundle sheath. Here malate is decarboxylated under influence of malate dehydrogenase to produce pyruvate, CO_2 and $NADPH_2$. NADPH + H^+ travels back to mesophyll cells to regenerate malate, while pyruvate also travels back to mesophyll cells, where it utilizes the light generated ATP to produce PEP again. CO_2 released by decarboxylation of malate is fixed in the bundle sheath cells by C_3 pathway (accepted by RuBP). In C_4 plants there are two carboxylations, one by atmospheric CO_2 which forms dicarboxylic acids and second by internally generated CO_2 entering the RuBP. In this case C_3 and C_4 both pathways operate. C_3 and C_4 pathways are delimited to bundle sheath cells and mesophyll cells, respectively. Because there is carboxylations at two sites, the pathway is also known as dicarboxylation pathway.

There are three categories of C4 plants.

1. Fixation of CO_2 by PEP which forms oxalo acetate then malate Ex. maize, sugarcane.

2. Oxalo acetate gets converted into aspartate in mesophyll cells and it is transported to bundle sheath. In bundle sheath cells aspartate is reconverted to oxalo acetate which is then converted to pyruvate and CO_2 Ex. *Panicum maximum*, *Chloris guyana*.

3. Aspartate produced in mesophyll cells is transported to bundle sheath cells where it gets transaminated to oxalo acetate first and then gets reduced to malate in mitochondria using NADH. The malate is decarboxylated to produce pyruvate and CO_2 Ex. Atriplex spongiosa.



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Significance of C_4 pathway

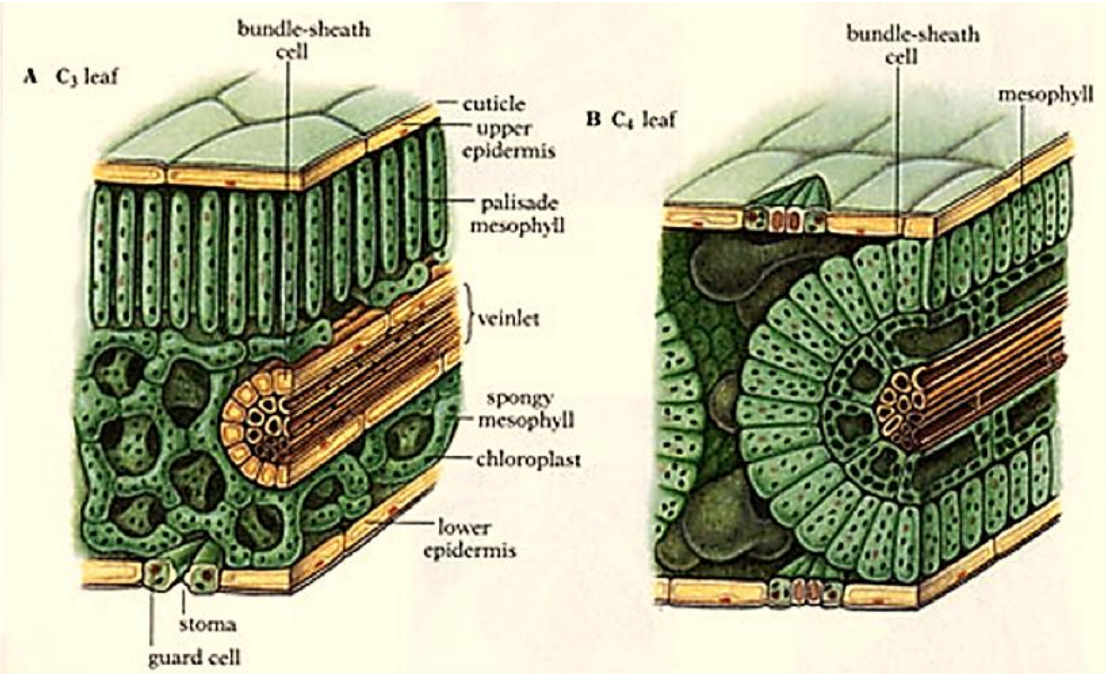
1. They possess higher rates of photosynthesis due to higher affinity of PEP carboxylase to CO_2.

2. They can carry on photosynthesis even under low CO_2 concentrations (10ppm).

3. Even under almost closed conditions of stomata C_4 plants can continue to photosynthesize.

4. There is almost negligible photorespiration. It is not necessary that C_4 pathway is always more efficient than C_3 pathway but most of the time C_4 pathway leads to better utilization of available CO_2 in C_3 fixation . C_4 pathway itself does not produce carbohydrates. It is only contributory pathway for C_4 cycle.

There are differences in leaf anatomy between plants that have a C_4 carbon cycle (called C_4 plants) and those that photosynthesize solely via the Calvin photosynthetic cycle (C_3 plants). A cross section of a typical C_3 leaf reveals one major cell type that has chloroplasts, the mesophyll. In contrast, a typical C_4 leaf has two distinct chloroplast-containing cell types: mesophyll and bundle sheath.

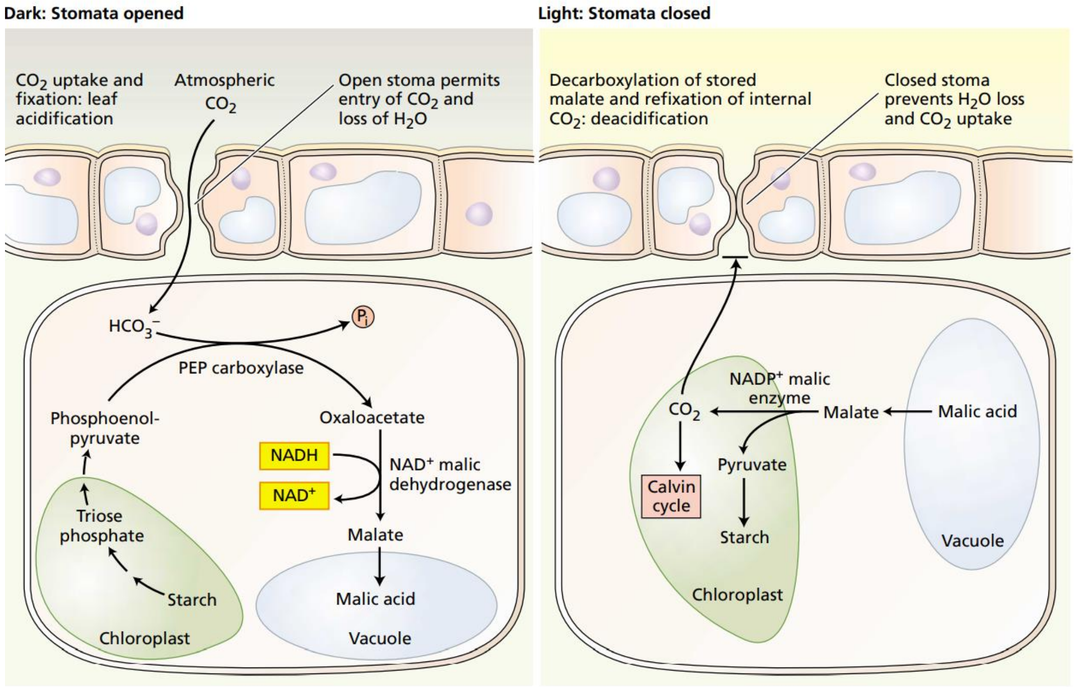


Crassulacean Acid Metabolism (CAM Pathway)

• Stomatal opening in night due to accumulation of malic acid which acts as strong solute and closing during day as a result of disappearance of malic acid from stomatal guard cells.

• Plants that fix CO_2 during the night into a four-carbon compound (malate) that, after storage in the vacuole, is transported out of the vacuole and decarboxylated during the day. The CO_2 released is assimilated in the Calvin cycle in the chloroplast stroma.

Many plants belonging to families like Crassulaceae, Orchidaceae, Bromeliaceae, Liliaceae, Asclepiadaceae, Vitaceae etc. Examples Agave, Kalanchoe, Sedum found in arid regions. In such plants stomata open during night and close during day which reduces the rate of transpiration thereby helps in water conservation. In night CO_2 is fixed by phosphoenol pyruvic acid under the influence of PEP carboxylase enzyme. This leads to the formation of oxalo acetic acid which is then reduced to $NADPH_2$ under influence of malic dehydrogenase enzyme. Due to accumulation of malic acid in guard cells the osmotic concentration of guard cells of stomata becomes higher resulting in withdrawal of water from the surrounding cells increasing the turgor pressure of guard cells which results in opening of stomata, whereas, in day malic acid gets converted to CO_2 and pyruvic acid. CO_2 is accepted by RuBP in Calvin cycle and pyruvic acid is utilized in the formation of carbohydrates. Due to disappearance of malic acid in day stomata remain closed. Due to formation of malic acid in dark the pH should become low and stomata should remain closed but malic acid being a strong solute increases the osmotic pressure of guard cells. In such plants starch sugar mechanisms do not operate. Although CO_2 fixation can take place in darkness, the amount of CO_2 fixed is greater in the light because of availability of ATP and NADPH from the light reactions and because the stomata are open and facilitate gas exchange.



Difference between C_3 & C_4

S.N.	Character	C_3 Plants	C_4 Plants
1.	CO_2 Acceptor	RuBP (Ribulose bi or bis phosphate)	PEP (Phospho -enol pyruvate)
2.	First stable product	PGA(Phospho glyceric acid)	Oxaloacetate
3.	Type of chloroplast	One	Dimorphic, bundle sheath chloroplasts lack grana, mesophyll cells have normal chloroplast
4.	Leaf anatomy	Normal	Kranz (German)
5.	Pigment system	All chloroplasts have PS I and PS II	Bundle sheath chloroplasts lack PS II, hence depends on mesophyll cell chloroplasts for supply of NADH
6.	Enzymes of C_3 Pathway	Found in mesophyll cells	Found in bundle sheath cells

7.	CO_2 compensation point	150- 500ppm	0-10 ppm
8.	Photorespiration	Present	Almost absent
9.	Net rate of PS in full sunlight	15-35 mg CO_2 /dm ^{2} of leaf	40-80 mg CO_2 /dm ^{2} of leaf
10.	Saturation intensity	1000-4000 ftc.	Difficult to reach saturation
11.	Bundle sheath cells	Not prominent	Very prominent
12.	CO_2 fixation	C_3 Pathway	Both C_3 and C_4 pathways
13.	Higher O_2 rate	Inhibits PS	No effect on PS
14.	Temperature optimum	10-25 ^{0}C	30-45 ^{0}C
15.	ATP molecules required to synthesize one molecule of glucose	18	30

Factors Affecting Photosynthesis:

a. External Factors

1. CO_2 Concentraton
2. Temperature
3. Light
4. Water and Nutrient Elements
5. Oxygen
6. Pollutants

b. Internal Factor

1. Chlorophyll
2. Accumulation of the Products of Photosynthesis

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