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# PHOTO SYNTHESIS IN HIGHER PLANTS

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# PHOTOSYNTHESIS IN HIGHER PLANTS

## LIGHT REACTIONS, THE ELECTRON TRANSPORT CHAIN, CYCLIC AND NON-CYCLIC PHOTOPHOSPHORYLATOIN, CHEMIOSMOTIC HYOPTHESIS

### Key Takeaways

- Light reactions
  - Electron transport chain (Non-cyclic photophosphorylation)
  - Chemiosmotic theory
  - Cyclic photophosphorylation
  - Cyclic vs non-cyclic photophosphorylation

### Prerequisites

The overall equation of photosynthesis :

$$\underset{\text{Carbon dioxide}}{6CO_2} + \underset{\text{Water}}{12H_2O} \xrightarrow[\text{Sunlight}]{\text{Chlorophyll}} \underset{\text{Glucose}}{C_6H_{12}O_6} + \underset{\text{Water}}{6H_2O} + \underset{\text{Oxygen}}{6O_2}$$

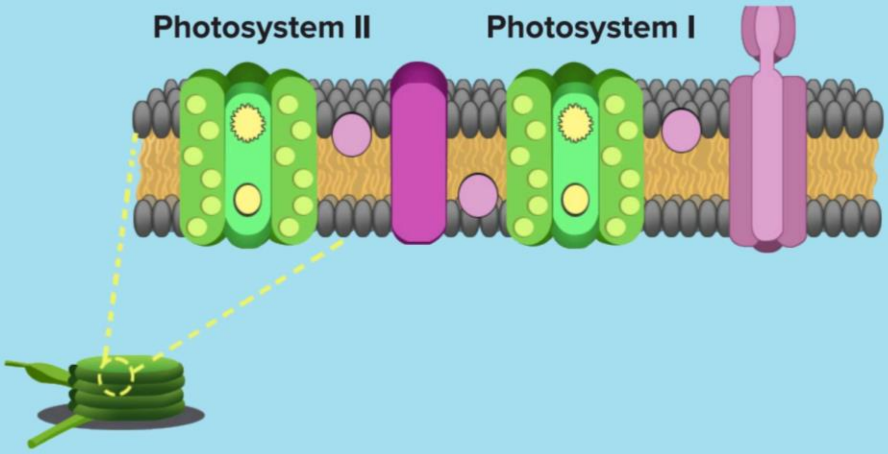
**Photosynthesis Steps**

- **Light Reactions** — Requires light
- **Dark Reactions** — Does not require light

**Photosystems**

**Complex of proteins, photopigments and organic molecules embedded in the thylakoid membrane**

- **Photosystem I**
- **Photosystem II**



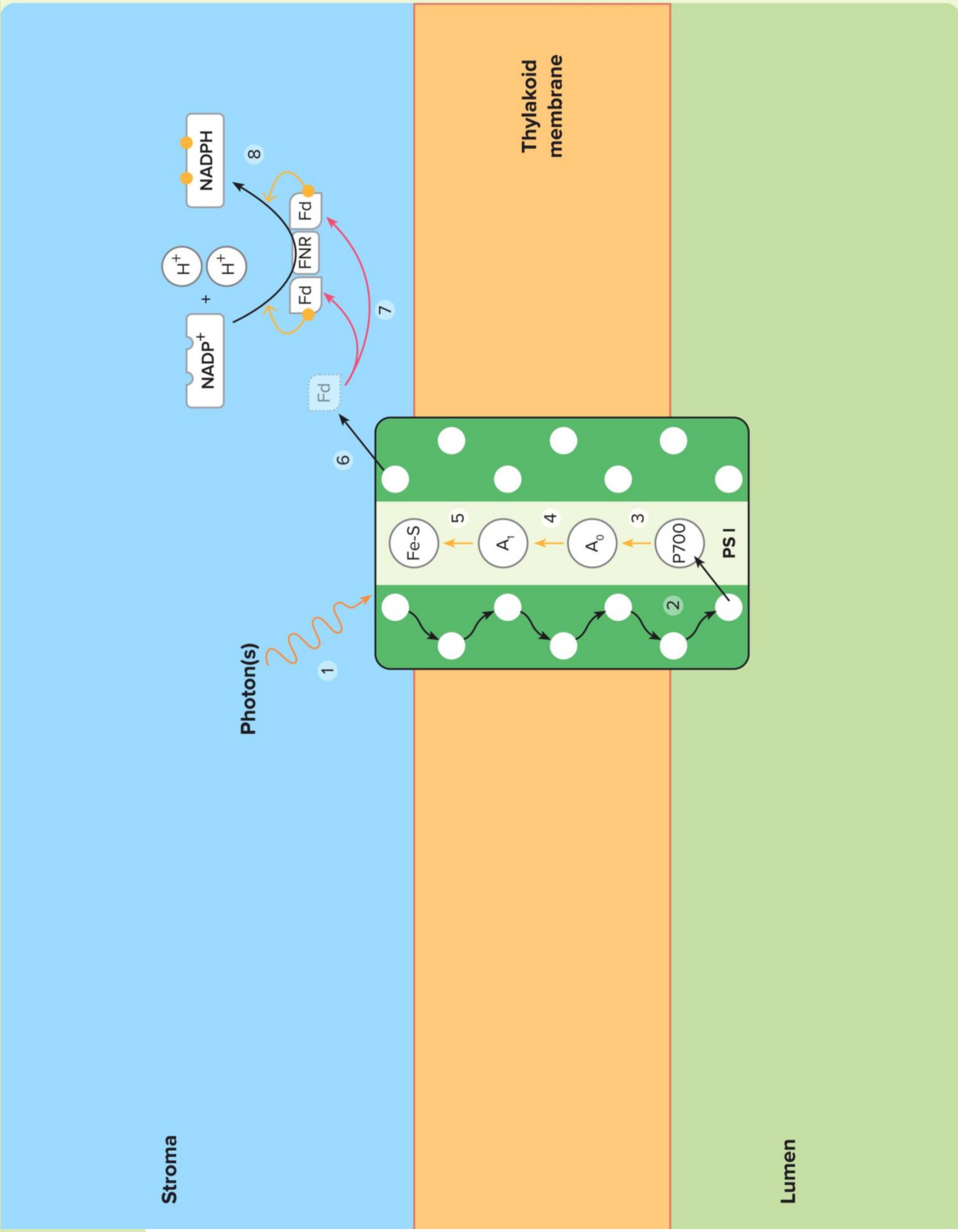

## Light Reactions

- Photosynthesis starts when light hits the leaves.
- Light passes through the cells of the leaves, through the cell membrane, through the chloroplast membrane to finally arrive at the thylakoid membrane.

Light Reactions = **Photochemical** Reactions

**Light** energy ⟶ **Chemical** energy

## Reactions of Photosystem I



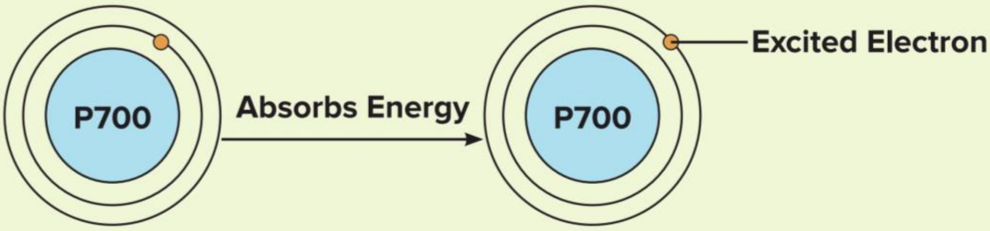
Photosystem (PS) I consists of a P700 (chlorophyll molecule) reaction centre and a bunch of accessory pigments.

### 1. Photon hits photosystem (PS) I

- Photon is the **basic unit that makes up all light**.
- The light reaction of photosynthesis begins when 1 photon falls on the PS I.
- The energy of the photon is transferred to the **accessory pigments** in the PS I.

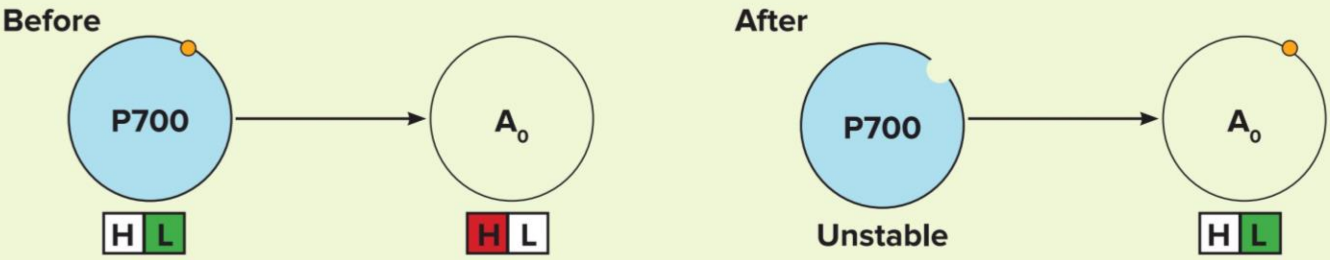
### 2. Accessory pigments → P700

- The accessory pigments absorb the energy of the photon and start vibrating.
- These vibrations are passed on from one accessory pigment molecule to another until the energy in the vibrations is passed on to the P700 **reaction center**.
- **Outermost $e^-$** of P700 absorbs energy and gets excited to a **higher energy level**.



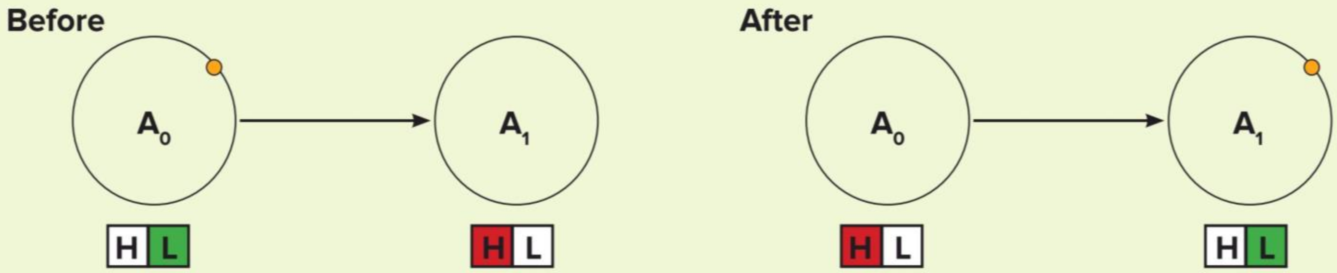

### 3. P700 → Chlorophyll $A_0$

- The electron at the higher energy level of the P700 reaction centre is **volatile**. It has a tendency to leave.
- So the electron jumps out of the higher energy orbital of the P700 reaction centre (RC) and is accepted by another modified **chlorophyll molecule, chlorophyll $A_0$**.
- **Driving force for electron transfer**
  - Electrons always move from a **lower redox potential** to a **higher redox potential**.
  - **Lower** redox potential means they have a tendency to **lose** electrons, while **higher** redox potential means they have a tendency to gain or **have** electrons.
  - In this case, **P700** with the electron in **higher** energy level has a **lower redox potential** and **chlorophyll $A_0$** has a **higher** redox potential.




### 4. Chlorophyll $A_0$ → $A_1$

- **$A_0$** has **lower** redox potential (tendency to **lose its electron**).
- **$A_1$** has **higher** potential (gives off its electron).
- So the electron moves from **$A_0$** to **$A_1$**.




## 5. $A_1$ → Iron Sulphur (Fe-S) Cluster

- Higher and lower redox potentials of components of the thylakoid membrane are **relative** to each other.
- After chlorophyll $A_1$ has gained an electron from chlorophyll $A_0$, chlorophyll $A_1$ has a lower potential compared to the Fe-S and $A_0$. So $A_1$ can potentially lose its electron to either $A_0$ or $A_1$.
- Fe-S has a **higher** redox potential than $A_0$.
- Fe-S is able to attract the electron much **more strongly**.
- After gaining the electron, the redox potential of Fe-S **decreases**.
- **All further** electron transports between the different components of the thylakoid membranes happen in a similar way.


## 6. Iron Sulphur (Fe-S) Cluster → Ferredoxin (Fd)

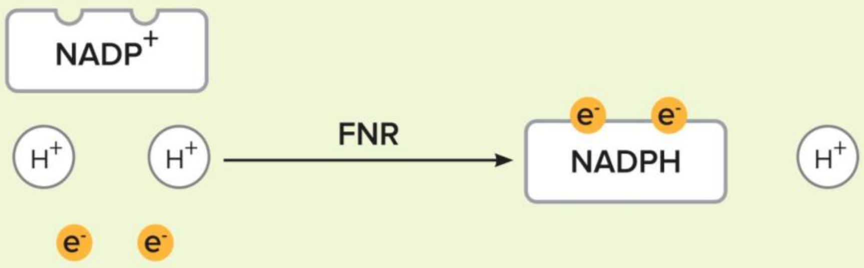
- Fe-S centre has a **lower reduction potential** compared to the next protein **ferredoxin (Fd)**. So Fe-S gives away the electron and Fd takes it.
    - Fd is a small, **water-soluble protein** that is present in the **stroma** but also sometimes in the thylakoid **membrane**.
    - It is a **mobile protein**, as in, it can **move**.

## 7. Ferredoxin movement

- Once Fd has gained the electron, it **moves through the stroma** to arrive at the next stop, **FNR**.
    - **FNR** is an enzyme.

## 8. Ferredoxin → $NADP^+$

FNR **catalyses** the transfer of 2 electrons from 2 Fds to 1 $NADP^+$ (Nicotinamide Adenine Dinucleotide Phosphate). 2 Fds lose 1 electron each and $NADP^+$ gains 2 electrons becoming NADPH.




**If only 1 electron was excited then where does the second electron come from?**

There is not just 1 P700 reaction centre, but there are many such reaction centres. So when a second photon hits the PS I, it leads to the excitation of a second electron of a different P700 RC. Now this electron passes through the same series of steps as the first electron and arrives at the Fe-S.

Just like there are many P700 RCs, there are also many Fds. So the Fe-S donates the second electron to the second Fd, and this Fd carries the electron to the FNR.

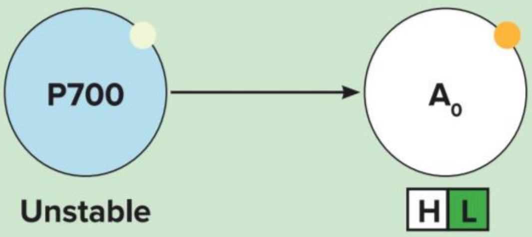
At the FNR, 2 Fd molecules together lose their 2 electrons and the $NADP^+$ gains the 2 electrons becoming NADPH.

NADPH is an electron carrier. It carries 2 electrons, which it can donate later to an electron acceptor.

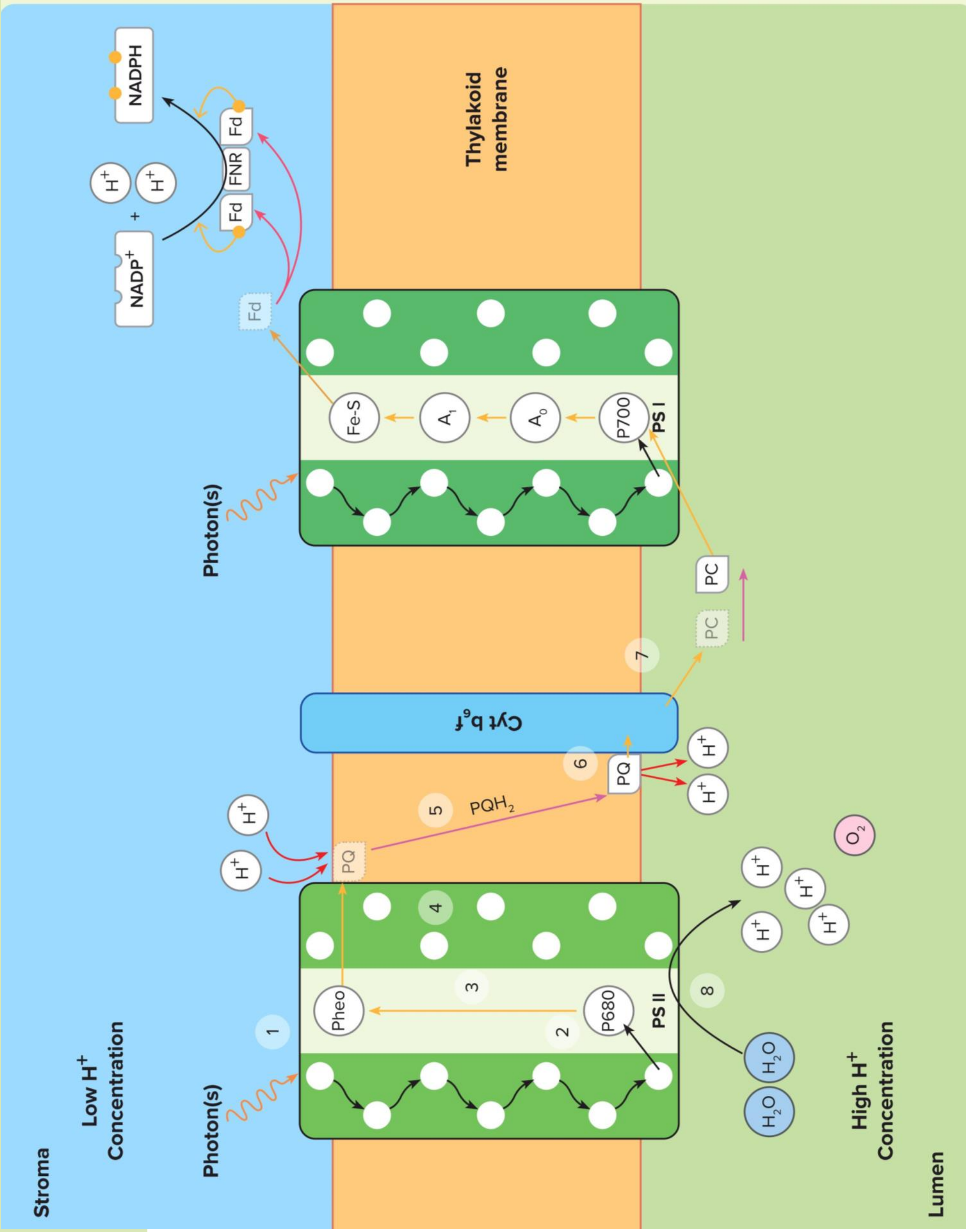

When the 2 photons hit the PS I, their energies were used to excite 2 electrons from the 2 P700 RCs to a higher energy level. And then these 2 electrons were eventually sent all the way to FNR. But the 2 P700 reaction centres which lost 1 electron each are kind of unstable since they **lack** an electron.

They cannot receive energy from photons through the accessory pigments and cannot release more electrons until the originally lost electrons are compensated.

It is to provide these compensating electrons that the **photosystem 2 (PS II)** comes into picture.



## Reactions of Photosystem II

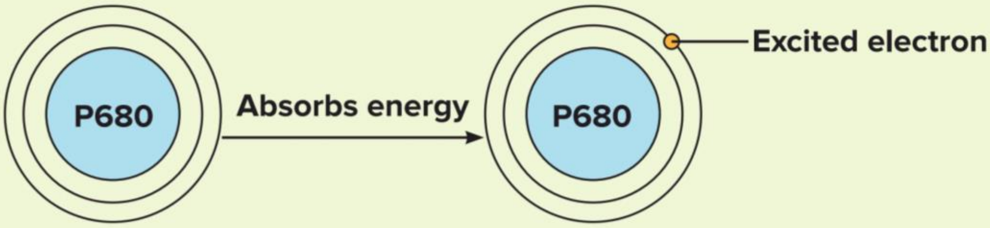


## 1. Photon hits PS II

- When 1 photon falls on the photosystem II, the **accessory pigments absorb it**.

## 2. Photon → P680

- The accessory pigments pass the energy from the photon to the **P680 reaction center**.
- **Outermost electron** of P680 RC absorbs the energy and gets excited to a **higher energy level**.




## 3. P680 → Pheophytin (Pheo)

- P680 with the **excited electron** has a **higher redox potential** compared to the next protein in the **cascade - pheophytin**.
- So the P680 RC loses the electron and **Pheo gains** the electron.

## 4. Pheophytin → Plastoquinone (PQ)

- Next electron acceptor is **plastoquinone** or **PQ**.
  - Present **inside** the **thylakoid** membrane.
  - It is a **mobile** electron carrier.
  - It carries **2 electrons**.

**Where does the second electron come from?**
**Just like the PS I had multiple P700 reaction centres, it is the same with the PS II as well. PS II also has many identical P680 reaction centres, which enable the PS II to accept multiple photons to generate free electrons to be transported.**

**Thus a second photon is used to trigger the release of a second electron from a second P680 RC and this second electron is transported to the PQ protein.**

## 5. Plastoquinone

- PQ takes **two electrons** from the **two pheophytins** and **$2H^+$** from the stroma to **become $PQH_2$**.

## 6. Plastoquinone → Cytochrome $b_6f$

- $PQH_2$ **moves** across the thylakoid membrane from the outer side to the inner side, where it meets the next protein complex **Cytochrome $b_6f$ (Cyt $b_6f$)**.
- Cyt $b_6f$ spans throughout the **thylakoid membrane**.
- Once $PQH_2$ arrives at the Cyt $b_6f$
  - 2 $H^+$ are released into the lumen
  - 2 electrons donated to Cyt $b_6f$

## 7. Cytochrome $b_6f$ → Phycocyanin

- The electrons, again **one at a time** now, are transferred to the next protein.
- Cyt $b_6f$ has a higher potential compared to **Phycocyanin (PC)**. Cyt $b_6f$ loses an electron and PC gains an electron.
  - **Mobile** electron carrier (one at a time).
  - Present inside the **lumen**.
  - PC finally gives off its electron to the **unstable P700**.
    - P700 is stable now.
    - Two electrons from the Cyt $b_6f$ are used to satisfy the deficiency of two electrons in the 2 P700s

The electron deficiency of the 2 P700 reactions centres is compensated by the 2 electrons released from the 2 P680 reactions centres as a result of 2 photons.

But the **2 P680** reaction centres are left with an **electron deficiency** now.

The 2 P680 reaction centres get their electrons from the **splitting of water** molecule caused by **light** through a process called **photolysis**.

## 8. Photolysis of water

- **Photo** - Light, **Lysis** - breakdown
- **Photolysis** is the **splitting** of **water** in the presence of **sunlight** to yield
  - 4 $H^+$ ions or protons
  - 4 electrons
  - 1 oxygen molecule

  into the **thylakoid lumen**.

$$2H_2O \longrightarrow 4H^+ + 4e^- + 1O_2$$

- Photolysis is **catalyzed** by the **PS II** present in the **thylakoid membrane**.

The photolysis/splitting of 2 molecules of water results in the release of 4 electrons. 2 of these electrons are used to compensate the loss of 2 electrons by 2 P680 reaction centres. There are 2 extra electrons.

**What happens to the other 2 electrons?**

In the above explanation, we assumed 2 photons falling on PS II and 2 photons on PS I. The 2 electron deficiencies created at the P680 reaction centres of PS II were compensated by the 2 electrons from the photolysis of 2 molecules of water.

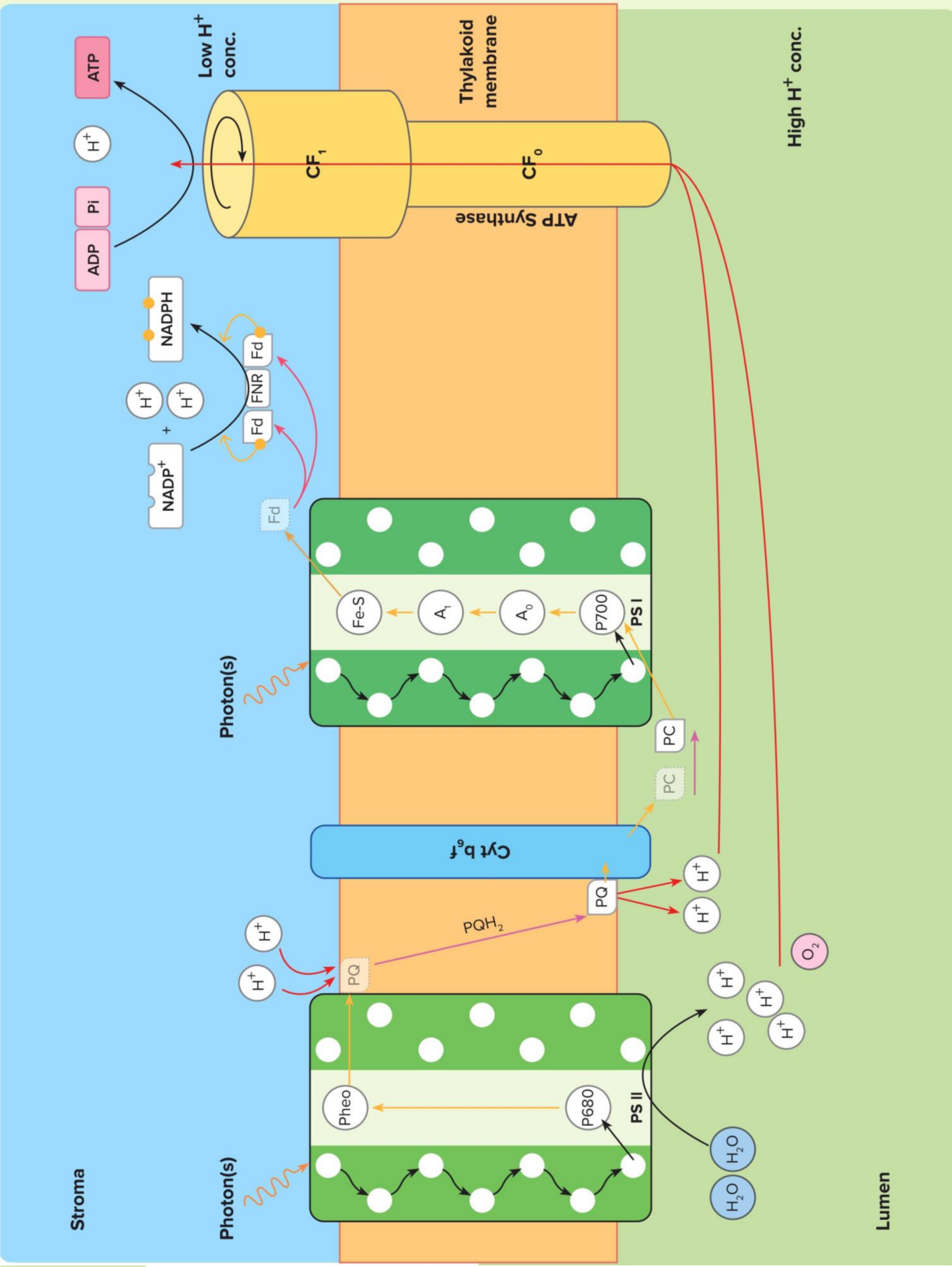
But if we were to double the photons at each photosystem, then you would have 4 photons at PS II, 4 photons at PS I and 4 electron deficiencies at the 4 P680 reaction centres.

At this point, all 4 electrons are utilized to compensate the 4 electron deficiencies at the P680 reaction centres.

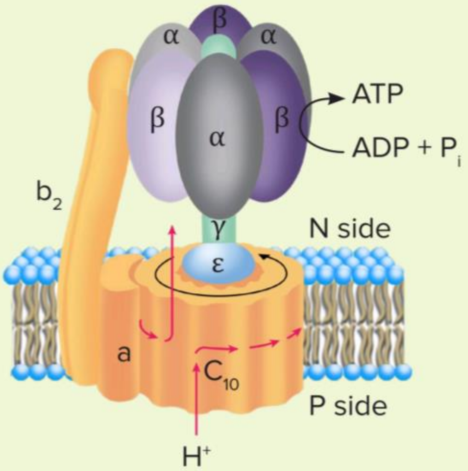
**Did you know?**

Photosystem I, discovered first, was responsible for formation of NADPH. The new photosystem, which was discovered later, was called PS II.

## Chemiosmotic theory



- A **high concentration** of **$H^+$ ions** or **protons** is created in the **thylakoid lumen** due to
  - Influx of $H^+$ ions during the **electron transport** by **PQ**
  - Release of $H^+$ ions due to the **splitting of water** catalyzed by **PS II**
- A higher $H^+$ ion concentration at the thylakoid lumen means that there's a lower $H^+$ ion **concentration** in the **stroma**. This creates a $H^+$ ion gradient or a proton gradient across the **thylakoid membrane**.
- In addition to the photosystems and the cytochrome, the thylakoid membrane has yet another very important protein, the **ATP synthase**.




- It is an enzyme consisting of two parts
  - $CF_0$
    - Embedded in the **thylakoid membrane**
    - Forms a **transmembrane channel** that carries out **facilitated diffusion** of **$H^+$ ions** or **protons** across the membrane
  - $CF_1$
    - **Protrudes** on the outer surface of the thylakoid membrane
    - Faces **stroma**

### Proton Movement

There is a higher concentration of protons in the thylakoid lumen and a lower concentration of protons in the stroma. So protons should be able to diffuse from the lumen to the stroma. But the thylakoid membrane is impermeable to $H^+$ ions or protons.

This is why the protons undergo **facilitated diffusion** instead. This diffusion is facilitated by the **ATP synthase** enzyme. When the protons from the lumen diffuse through the ATP synthase, they cause the enzyme to **churn** and **rotate**.

During this rotation, there is a conformational change of in the $CF_1$, **adenosine diphosphate (ADP)** molecules get hit with **free phosphate** molecules to form **adenosine triphosphate (ATP)**. ATP is the **energy currency** of the cell.

### Chemiosmotic Theory

This theory states that, "**Synthesis of ATP** is linked to the development of a proton gradient across a membrane (thylakoid membrane, in case of photosynthesis). The **facilitated diffusion** of **protons** or $H^+$ ions (due to the **proton gradient**) through the **ATP synthase** across a membrane leads to the **formation of ATP** with the **breakdown** of the **gradient**.

## Photophosphorylation

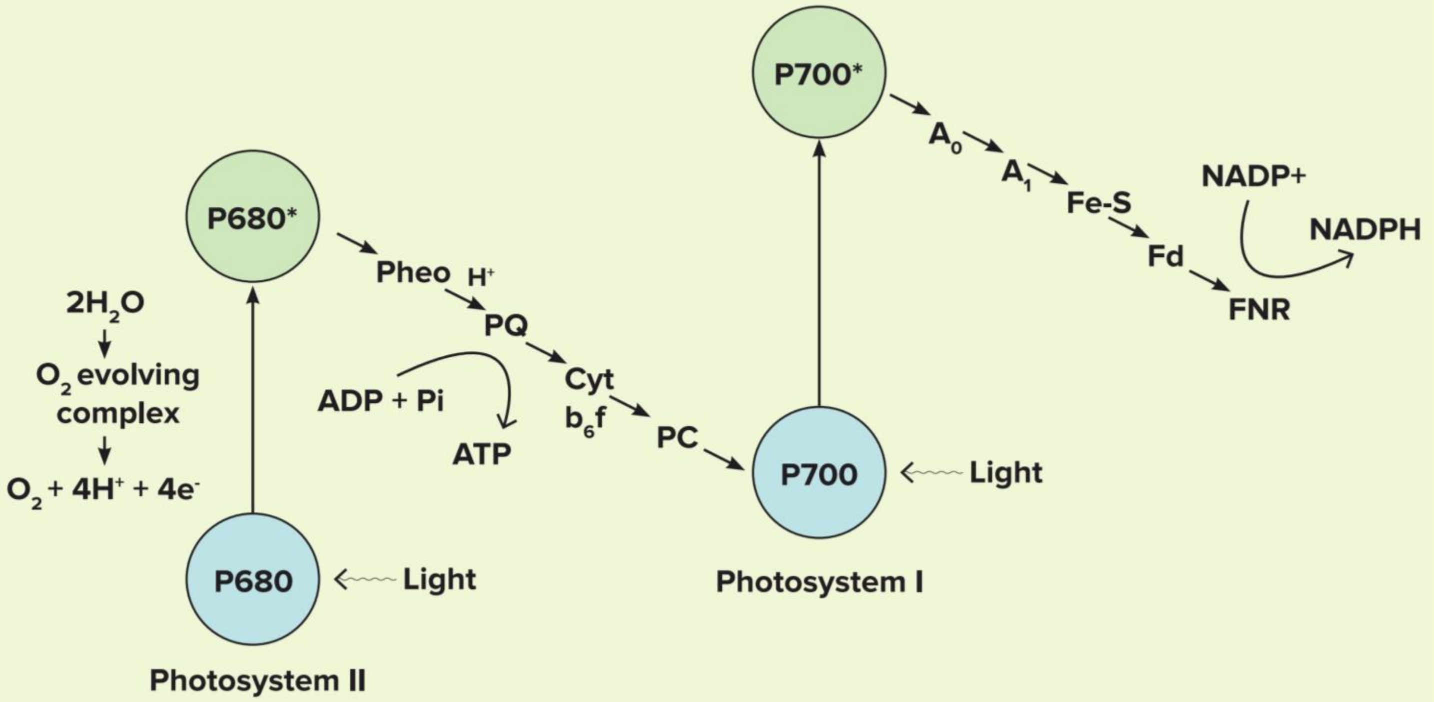
- Since the whole process beginning from the photons hitting the photosystems to the complete electron transport was done with the sole purpose of adding phosphate to **ADP to form ATP**, it is know as **phosphorylation.**
- And since this whole process is powered by light (photolysis of water at PS II) in the form of the **photons**, it is known as **photophosphorylation**.

**Photophosphorylation**

- **Non-cyclic**
- **Cyclic**

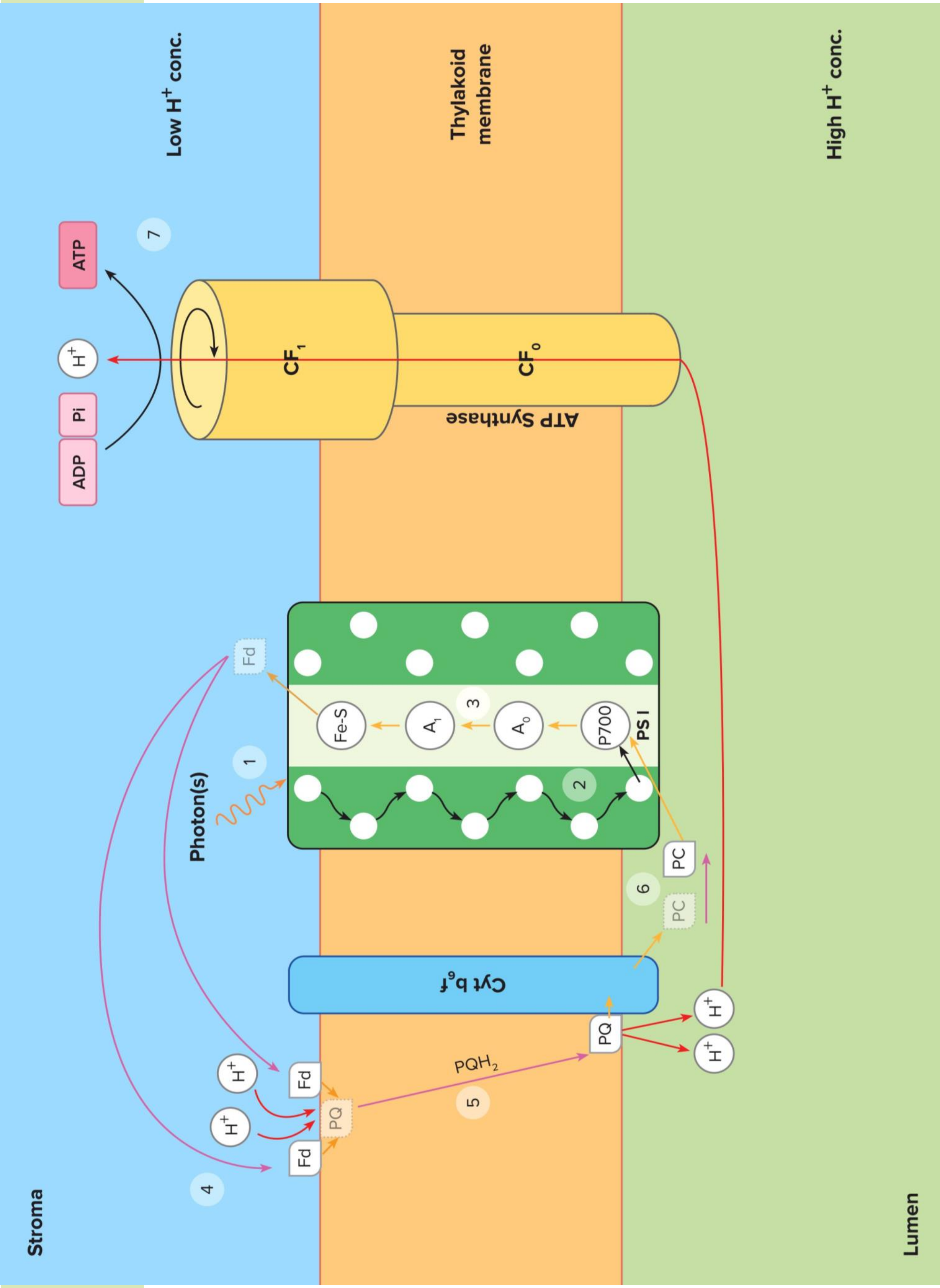
## Non-cyclic photophosphorylation

- This is the only type of photophosphorylation we have seen until now. It involves both **photosystems**.
- Also called **Z scheme**.
- Produces NADPH.




## Cyclic photophosphorylation

- This is the kind of photophosphorylation that takes place when plants need more ATP than **NADPH**.
- **PS II is rested** and photophosphorylation continues **with only PS I**.
- Takes place in the **lamellar region** of the chloroplast.


Stroma
Low H+ conc.
Thylakoid membrane
High H+ conc.
Lumen
ADP
Pi
H+
ATP
7
CF1
CF0
ATP Synthase
Photon(s)
1
2
3
Fd
Fe-S
A1
A0
P700
PS I
PC
6
Cyt b6f
PQ
PQH2
5
4
H+

### 1. Light hits PS I

- A photon of light hits PS I. The energy in it is absorbed by the accessory pigments.

### 2. Accessory Pigments of PS I→ P700 Reaction Centre

- The accessory pigments pass the energy to the **P700 reaction centre**.
- **Outermost electron** of P700 RC absorbs energy and gets excited to a **higher energy level.**
- The P700 RC is left with a deficiency of 1 electron.

### 3. P700 to Ferredoxin

- The electron follows the same path as non-cyclic photophosphorylation from P700 RC to Fd.

**P700** → **$A_0$** → **$A_1$** → **Fe-S** → **Fd**

### 4. Ferredoxin → Plastoquinone

- Fd is a **mobile** electron carrier.
- It moves through the stroma from Fe-S to PQ (instead of Fe-S to FNR in non-cyclic photophosphorylation).

### 5. Plastoquinone → Cyt $b_6f$

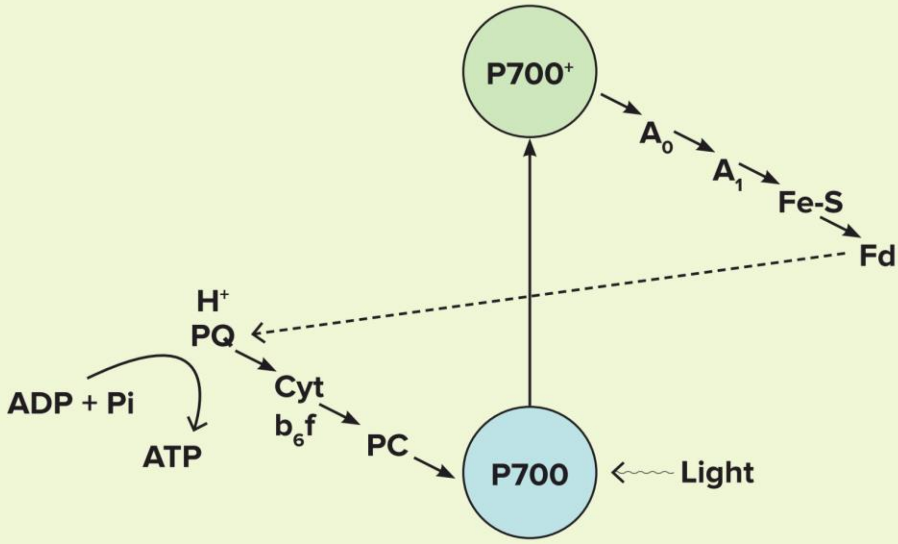
- PQ is a mobile transporter that transports a hydrogen molecule, **$2e^-$** and **$2 H^+$**.
- As seen earlier there are **multiple copies** of these proteins, E.g. P700, Fd.
- So a **2nd photon** hits **PS I**, there are**2 electrons** there are **2 P700 RCs** that finally arrive at PQ with the help of **2 Fds**. This means there are **2 P700 RCs** with a **deficiency** of **1 electron each**.
- **2 $H^+$ ions** are taken up from the **stroma**.
- So with the 2 electrons and 2 $H^+$ ions, **PQ** becomes **$PQH_2$**.
- It moves through the **thylakoid membrane** from the stromal side to the lumen side and reaches **Cyt $b_6f$** complex
- At the lumen side, PQ releases the **2 $H^+$ ions** in the **lumen** and the **2 electrons** to Cyt $b_6f$.

### 6. Cyt $b_6f$ → Phycocyanin → P700

- 2 electrons move to the next mobile carrier protein **phycocyanin**, one at a time.
- Phycocyanin moves through the **lumen** and delivers the electron to P700 RC.
- Since there are **2 electrons** being transported, **2 electrons** are used to compensate the **2 electron deficiencies** in the **2 P700 reaction centres**. Thus, both the P700 RCs are back to **normal**.

### 7. Chemiosmosis

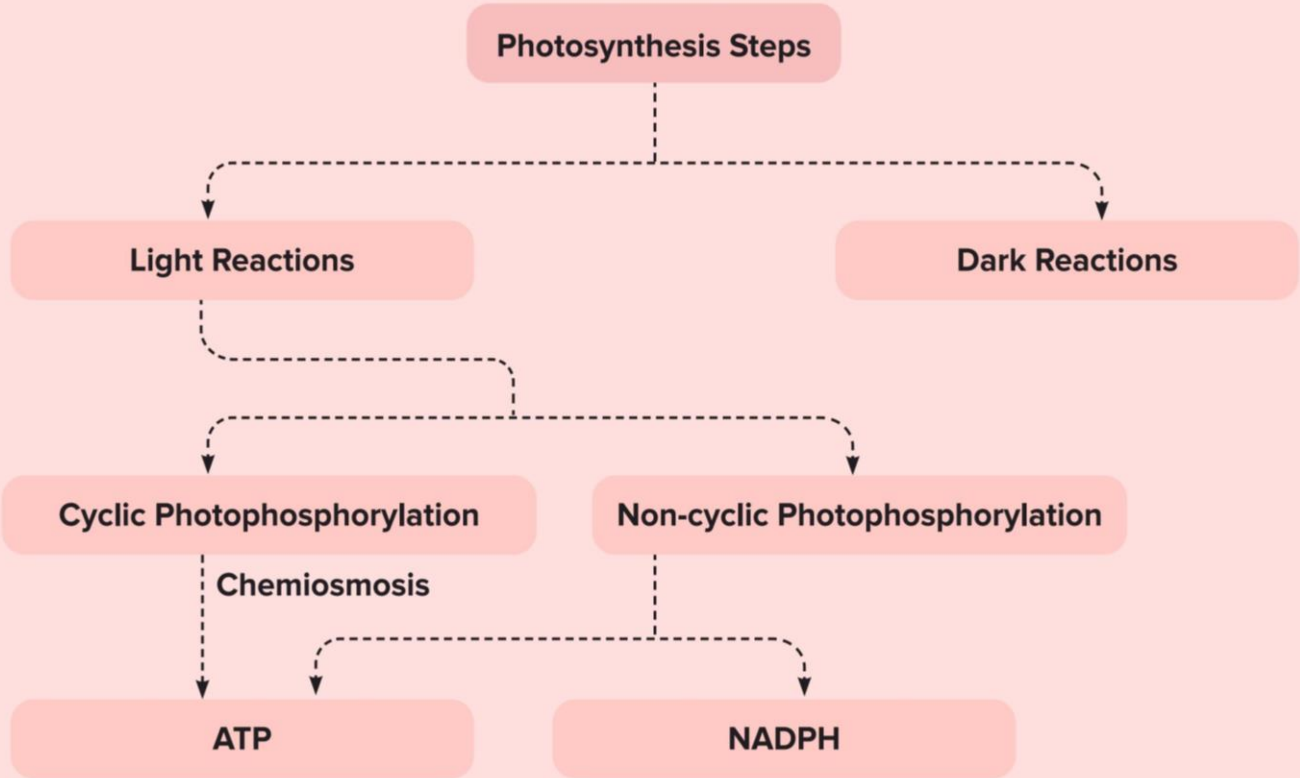
- The influx of $H^+$ ions during the electron transport by PQ results in a **higher $H^+$ ion concentration** in **lumen** and **lower $H^+$ ion concentration** in **stroma**.
- These $H^+$ ions undergo **facilitated diffusion** through the **ATP synthase**.
  - ATP synthase **rotates**
  - **Phosphorylation**; ADP + Pi→ ATP
- Since this photophosphorylation takes place in a **cyclic** manner, it is called **cyclic photophosphorylation**.

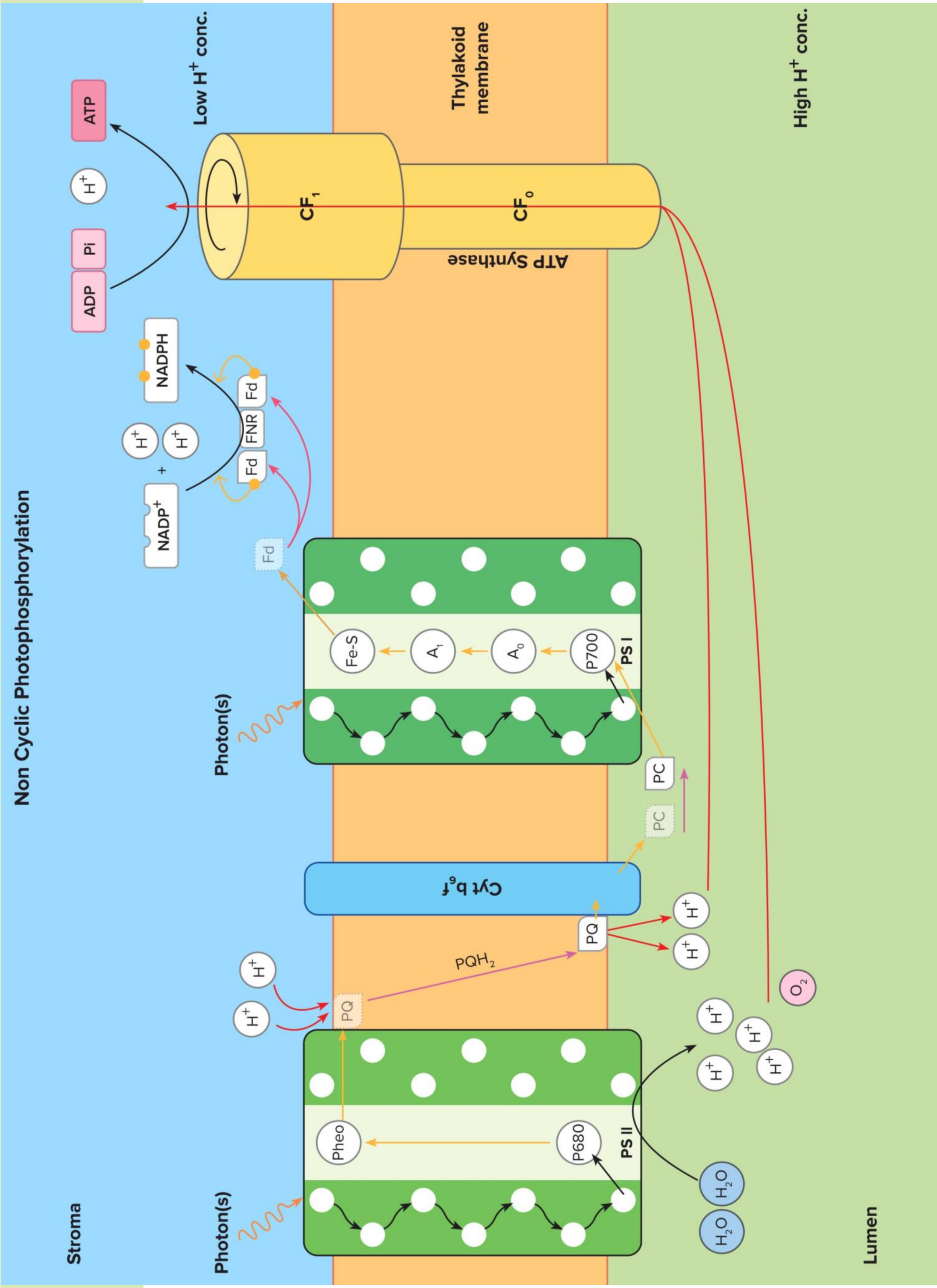



## Cyclic Photophosphorylation vs Non Cyclic Photophosphorylation

| Cyclic photophosphorylation | Non-cyclic photophosphorylation |
|---|---|
| Synthesis of ATP takes place by a cyclic passage of electrons to and from P700 | Synthesis of ATP takes place by a non-cyclic passage of electrons to electron donor and oxygen is produced as byproduct |
| Occurs in isolated chloroplasts and photosynthetic bacteria | Occurs in higher plants, algae and cyanobacteria |
| Occurs in anoxygenic photosynthesis (No oxygen evolved) | Occurs in oxygenic photosynthesis (Oxygen evolved) |
| Electrons move in a cyclic pattern | Electrons in a linear pattern |
| Only PS I is involved | Both PS I and PS II are involved |
| Electrons are first expelled from the reaction centre of PS I | Electrons are first expelled from the reaction centre of PS II |
| Electrons return to the P700 after passing through ETS | Electrons return to the P680 (after photolysis of water) and are accepted by $NADP^+$ |
| Final electron acceptor is P700 | Final electron acceptor is $NADP^+$ |
| Photolysis does not occur | Photolysis occurs |

## Summary Sheet




Non Cyclic Photophosphorylation
Stroma
Low H+ conc.
Thylakoid membrane
High H+ conc.
Lumen
Photon(s)
Photon(s)
PS II
P680
Pheo
PQ
PQH2
PQ
Cyt b6f
PC
PC
PS I
P700
A0
A1
Fe-S
Fd
Fd
FNR
Fd
NADP+
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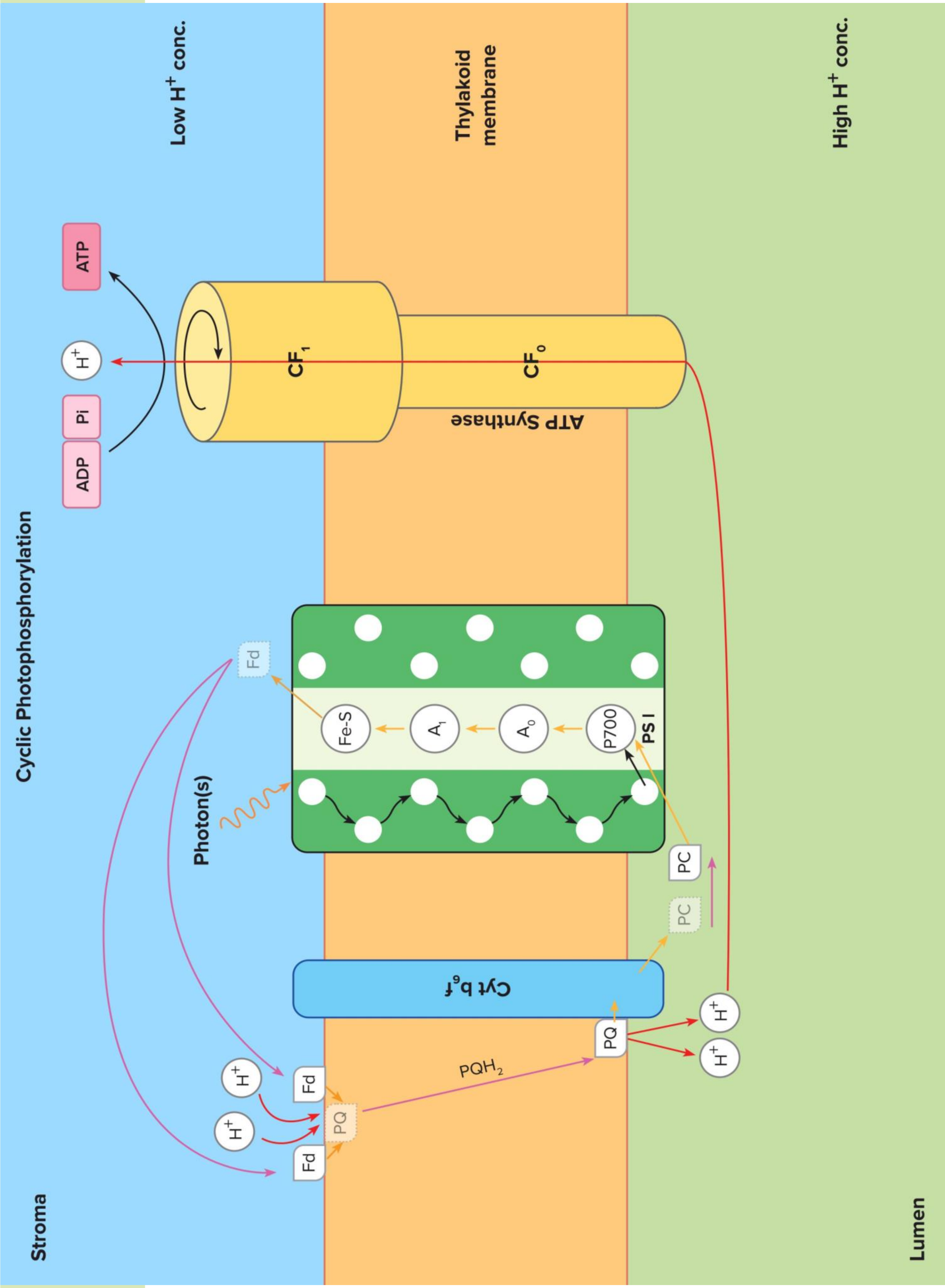
NADPH
ADP
Pi
H+
ATP
CF1
CF0
ATP Synthase
H2O
H2O
O2


Cyclic Photophosphorylation
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CF0
ATP Synthase
Photon(s)
Fd
Fe-S
A1
A0
P700
PS I
PC
Cyt b6f
PQ
PQH2

# PHOTOSYNTHESIS IN HIGHER PLANTS

## DARK REACTION, ENERGY OUTPUT, PHOTORESPIRATION

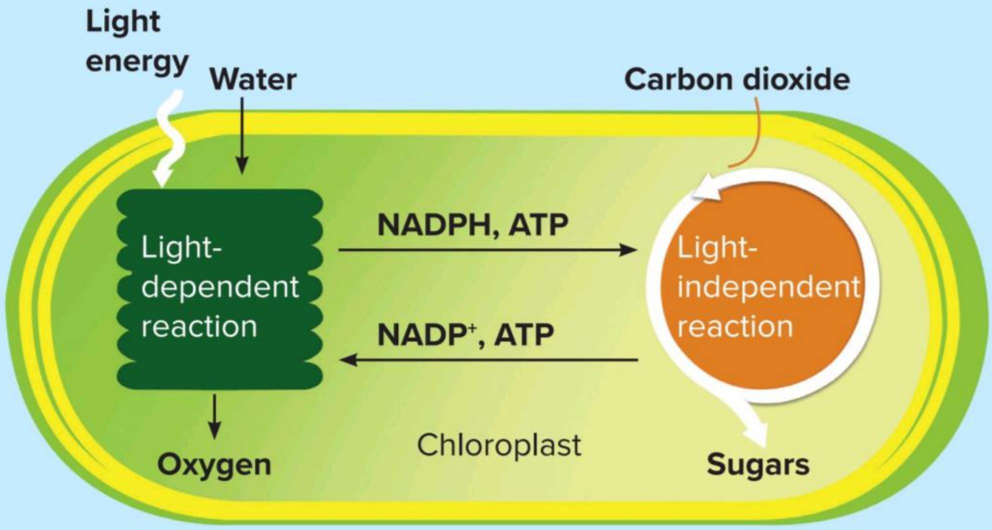
### Key Takeaways

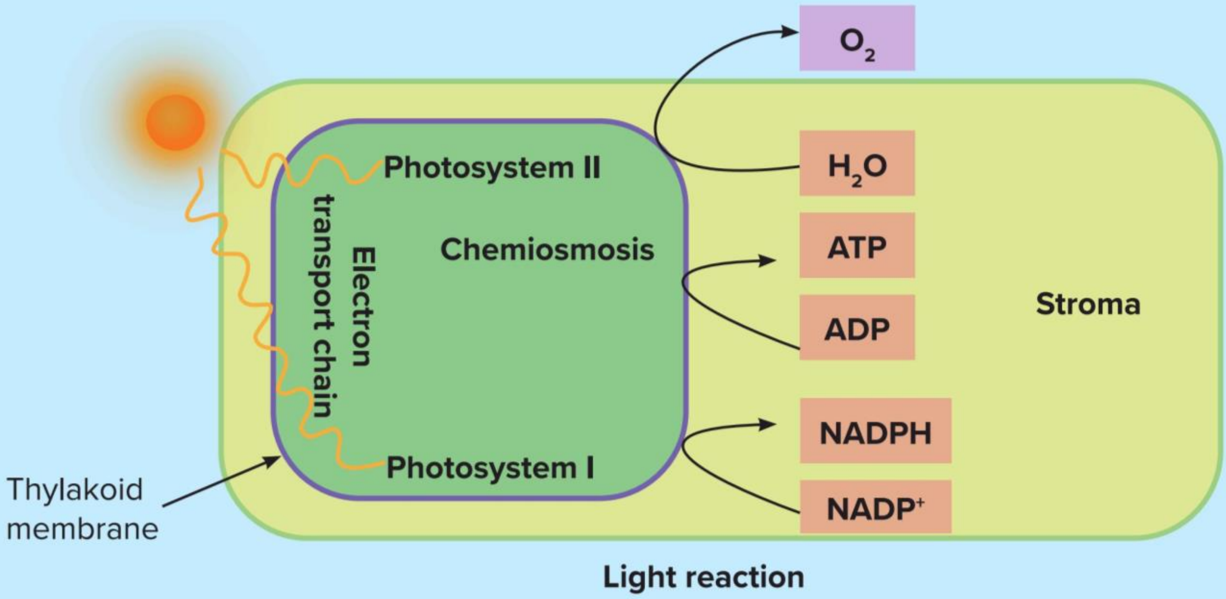
- Dark reaction or Calvin cycle
- Energy required in Calvin cycle
- Photorespiration or $C_2$ cycle
- Steps of Calvin cycle
- Factors affecting RuBisCo binding

### Prerequisites

**Mechanism of photosynthesis**

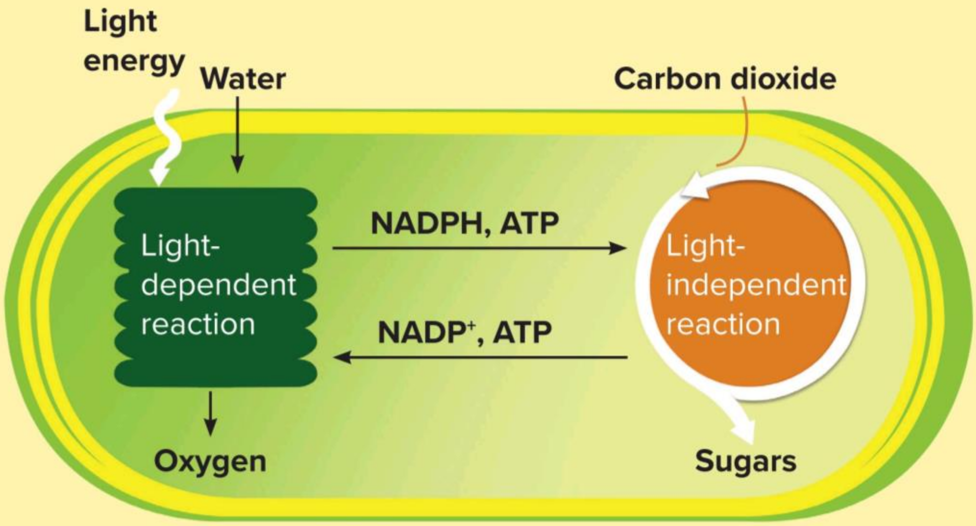
- **Light reaction/Photochemical phase** — Light dependent reaction
- **Dark reaction** — Light independent reaction






## Dark Reaction

- **Light** is **not required** in this reaction.
- It requires the products of light reaction: **NADPH and ATP**.
- Dark reaction does not mean that it **occurs only at night**.
- Though light is not required, this reaction can take place in either **light or darkness**.




- **NADPH** is required for the production of **sugars** in the dark reaction, which is a product of the light reaction.
- **NADPH** is very **short-lived** and is used immediately.
- If there are no light reaction products, the dark reaction cannot occur.
- Hence, the dark reaction stops after some time if the light reaction stops.

## Experimental proof for the dark reaction

### Lollipop experiment

- During photosynthesis, carbon dioxide and water do not spontaneously combine to form glucose.
- An experiment was performed by **Melvin Calvin**, where he mapped the complete conversion of carbon within a plant during the process of photosynthesis.
- From this experiment, Calvin proposed a sequence of events known as the **Calvin cycle** (light-independent reaction or dark reaction).

## Experiment time

### Lollipop experiment

Radioactive carbon-14 was added to a 'lollipop' apparatus containing green algae *(Chlorella)*.

↓

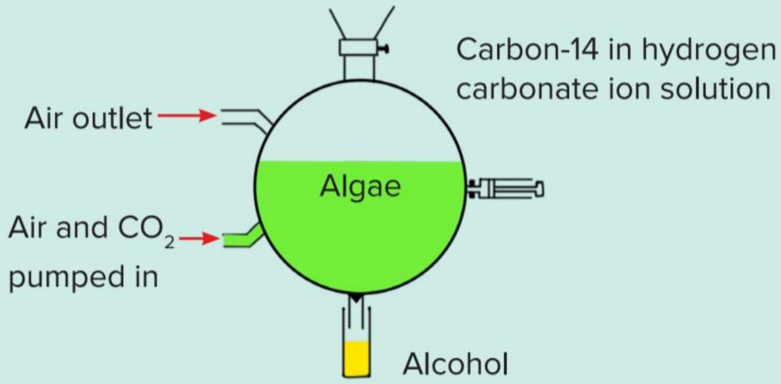
Light was shown on the apparatus to induce photosynthesis.

↓

After some time, the algae was killed by running it into a solution of heated alcohol (stops cell metabolism).

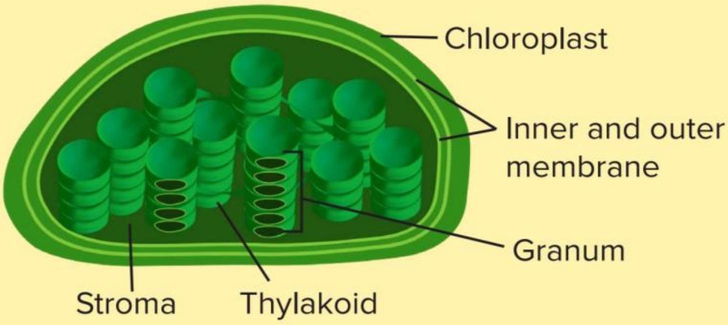
↓

He extracted the intermediates and discovered the compounds that were formed during carbon fixation.



## Dark reaction/Calvin cycle

**Site - Stoma**
(Aqueous fluid surrounding thylakoid)




How does $CO_2$ enter the chloroplast?

$CO_2$ enters the cell through **the stomata** present on the surface of the leaf.

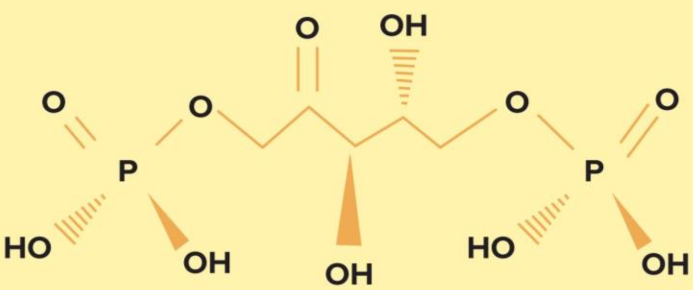
**Raw materials**

- **ATP**
- **NADPH**
- **$CO_2$**

## RuBP and RuBisCo

### RuBP

- It is **ribulose 1,5-bisphosphate**, a five-carbon ketose sugar.
- It is the **primary acceptor of $CO_2$**.
- The RuBP that is being used for carbon fixation has to be replenished by the end of this cycle for the RuBP to accept more $CO_2$.
- RuBP accepts $CO_2$ in the presence of an enzyme known as **RuBisCO**.




**RuBP**


**RuBP**

## RuBisCo

**RuBisCo**
RuBP carboxylase-oxygenase

- Most abundant enzyme
- **Active site** for both **$CO_2$** and **$O_2$**
- Has **greater affinity for $CO_2$** when $CO_2$ and $O_2$ are nearly equal: Binding is competitive

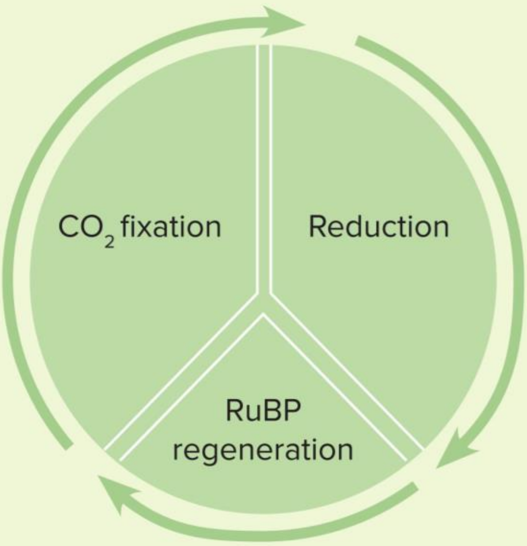
**Dual nature** of RuBisCO

- RuBisCO has both **carboxylation** and **oxygenation** activity
- Since the enzyme has **more affinity for $CO_2$**

## Steps of Calvin Cycle

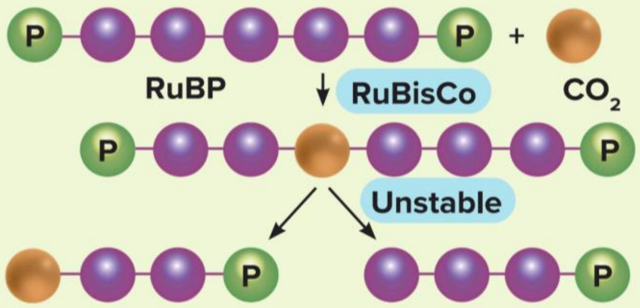
**Calvin cycle**

| Carboxylation | Reduction | Regeneration |
|---|---|---|
| $CO_2$ is fixed. | 3-PGA is reduced; ATP and NADPH are used. | RuBP is regenerated and ATP is used. |



## Carboxylation: Carbon fixation

- The most crucial step in the Calvin cycle is referred to as $CO_2$ fixation or carboxylation of RuBP.
- The fixation of $CO_2$ into RuBP produces an **unstable molecule**.
- The reaction is catalysed by the enzyme **RuBisCO** that can also be called RuBP carboxylase-oxygenase.
- This results in the formation of two molecules of **3-PGA (phosphoglyceric acid)**.




**3-phosphoglycerate (3-PGA)**

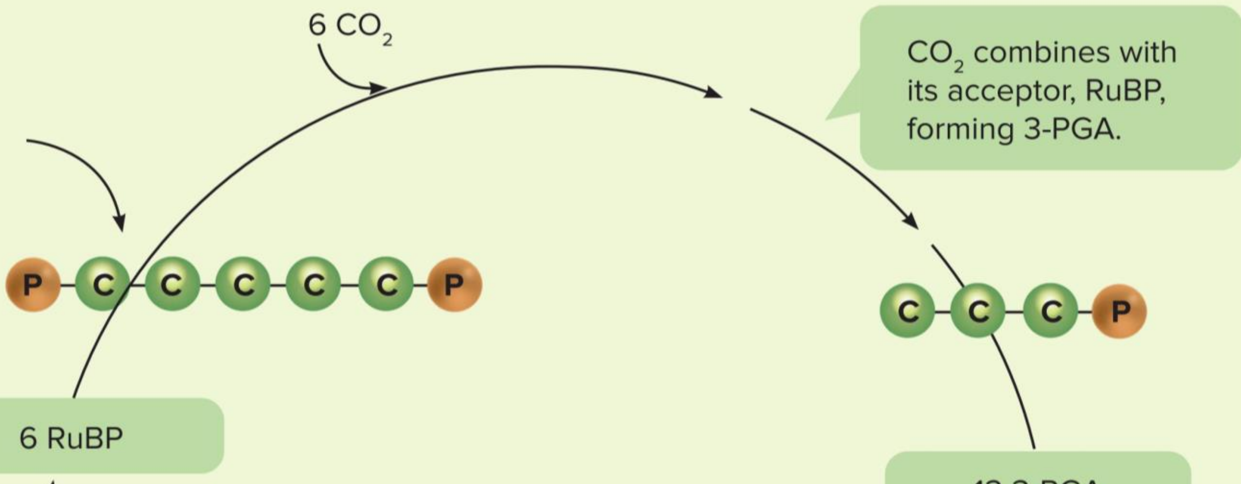
- One molecule of RuBP and one molecule of $CO_2$ give two 3-PGA molecules.

**Six carbon atoms** need to be fixed for one glucose molecule. → It takes **six turns** of the **Calvin cycle**

**Six molecules of $CO_2$** are needed to make one glucose molecule (one for each carbon dioxide molecule fixed).

How many molecules of RuBP will be required to accept six molecules of $CO_2$?

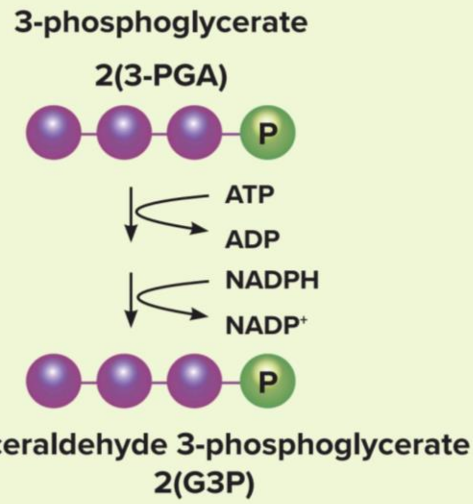
- Six molecules of RuBP will be required to accept six molecules of $CO_2$ to give twelve 3-PGA molecules.




**Carbon Fixation**

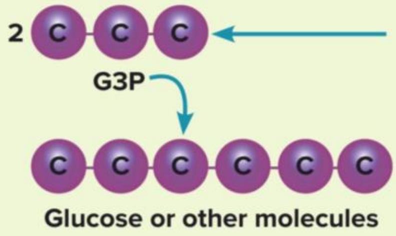
## Reduction of PGA

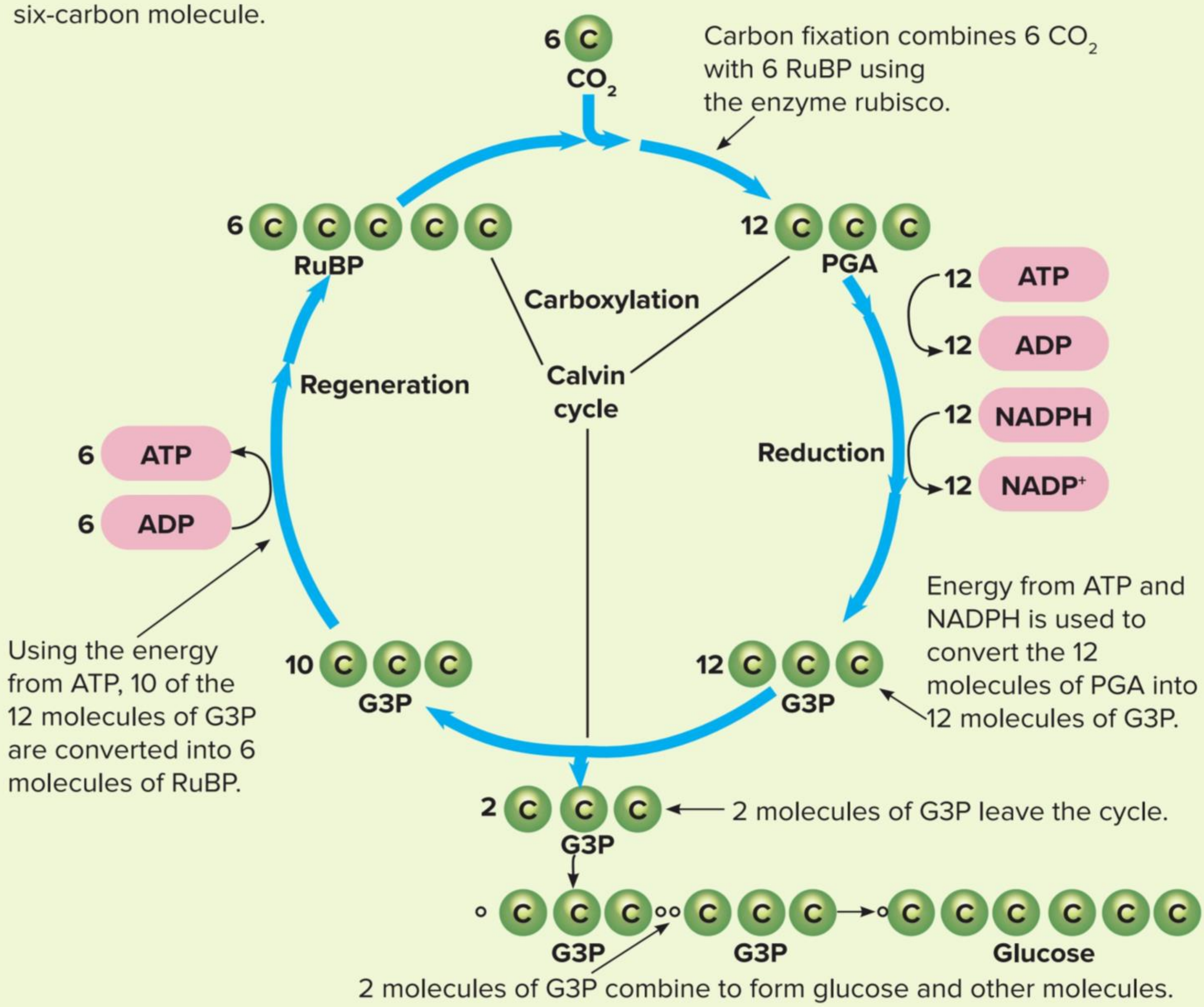
- **Two** molecules of **3-PGA** are converted into two molecules of **glyceraldehyde-3-phosphate (G3P)**.
- **NADPH** donates electrons or reduces **3-PGA** to make **G3P**.
- **ATP** is also used.




### Fate of G3P molecule

- **Two G3P molecules** can be easily converted into a **glucose molecule**.
- **Twelve 3-PGA** molecules use **twelve ATP** and **twelve NADPH** molecules to form **twelve molecules of G3P**.
- Two of the twelve G3P molecules are used to form a molecule of glucose, which is a six-carbon molecule.



## Regeneration of RuBP

- The remaining ten G3P molecules are reused in the next phase of the Calvin cycle, which is known as **regeneration**.
- **Ten** of the twelve molecules of G3P are converted into **six molecules of RuBP**.
- As one RuBP molecule consists of five carbon atoms and 30 divided by 5 is equal to 6, it means that six RuBPs can be formed.
- So, all the borrowed RuBPs are given back to the plant cell.
- The regeneration steps require one **ATP per cycle for phosphorylation to form RuBP**.

## Other Names of Calvin Cycle

**Calvin cycle/Dark reaction**

**Photosynthetic carbon reduction (PCR) Cycle of photosynthesis**

- The carbon from the atmosphere is fixed into a sugar molecule.
- The sugar is further reduced to form carbohydrates.

**Reduction**

$$6CO_2 + 6H_2O \longrightarrow C_6H_{12}O_6 + 6O_2$$

**Biosynthetic phase**

- The carbon dioxide in the atmosphere is fixed into a sugar molecule: carbon fixation.
- ATP and NADPH are used for synthesising carbohydrates.

## Energy Required to Fix Six Carbon Dioxide Molecules

- One molecule of $CO_2$ entering the Calvin cycle:

| In | Out |
|---|---|
| 1 $CO_2$ | 1 carbon is fixed in $C_6$ |
| 3 ATP | 3 ADP |
| 2 NADPH | 2 $NADP^+$ |

- Six $CO_2$ molecules entering the Calvin cycle:

| In | Out |
|---|---|
| 6 $CO_2$ | 1 glucose |
| 18 ATP | 18 ADP |
| 12 NADPH | 12 $NADP^+$ |

- In the Calvin cycle, twelve ATP are used in the conversion of twelve PGA to twelve G3P molecules.
- Another six ATP are used to convert ten G3P molecules to form six RuBP molecules.
- Twelve NADPH are also used.

**Did you know?**

- The first stable product of $CO_2$ fixation in the Calvin cycle is a three-carbon organic acid (**3-PGA**). Hence, the Calvin cycle is also known as **$C_3$ cycle** and such plants are known as $C_3$ plants.
- Examples: Wheat, soyabean, oats

## Factors Affecting RuBisCO Binding

- Low temperature
- High $CO_2 : O_2$ ratio

→ RuBisCO facilitates binding of RuBP and $CO_2$ → **Calvin cycle**

- High temperature
- Low $CO_2 : O_2$ ratio

→ RuBisCO facilitates binding of RuBP and $O_2$ → **Photorespiration**

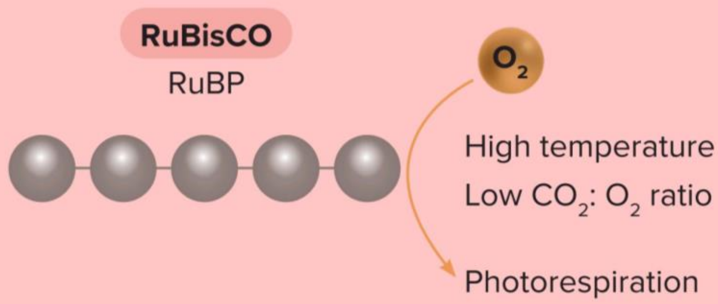
## Photorespiration or $C_2$ Cycle

Respiration → **$O_2$ is used** for burning of food and energy and **$CO_2$ is released.** →

Respiration
$O_2$ → $CO_2$
Organic carbon
Energy

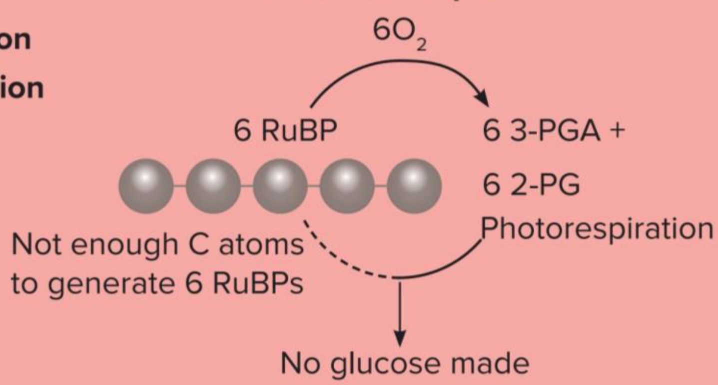
Photorespiration → $O_2$ is consumed and $CO_2$ is released but in the presence of sunlight. → $O_2 \xrightarrow{\text{Sunlight}} CO_2$ Organic carbon

- $O_2$ is consumed and $CO_2$ is released but in the presence of sunlight.
- It refers to a process where the enzyme **RuBisCO oxygenates RuBP**.
- The first main product formed is 2-phosphoglycolate (two carbon molecule); hence, it is known as $C_2$ cycle.
- 10% of carbon is lost in this process.




**It is a wasteful process**

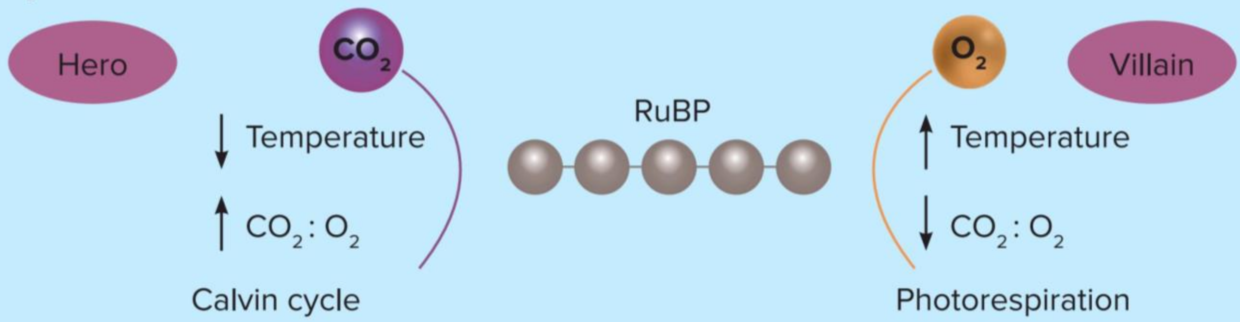
- **No carbon fixation**
- **No RuBP formation**



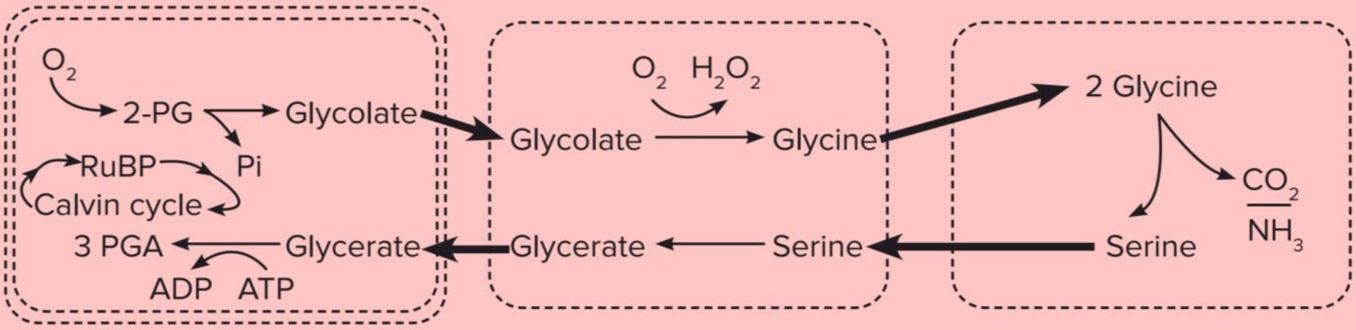

**Did you know?**

**Loss and Gain: RuBisCO**

- When **$CO_2$** is in the surroundings, RuBisCO helps in carbon fixation: **biomass is produced**.
- When **$O_2$** is in the surroundings, RuBisCO loses its sense and there is a **loss of carbons in the cycle**.



## Steps in $C_2$ cycle




**Chloroplast**

**Forward:**

- The first product of the $C_2$ cycle is formed in the chloroplast.
- The first main product formed is 2-phosphoglycolate (2-PG), a two carbon molecule.
- Phosphoglycolate loses a phosphate group to form glycolate.
- Glycolate is transported to peroxisome.

**Backward:**

- Glycerate from peroxisome forms 3-phosphoglycerate or 3-PGA with the help of ATP.
- 3-PGA then enters the Calvin cycle.

**Peroxisome**

**Forward:**

- Glycolate is converted into glyoxylate using $O_2$ and releasing hydrogen peroxide.
- Glyoxylate is further converted into glycine.

**Backward:**

- Serine from mitochondria moves to peroxisome and forms glycerate.
- Glycerate moves to chloroplast.

**Mitochondria**

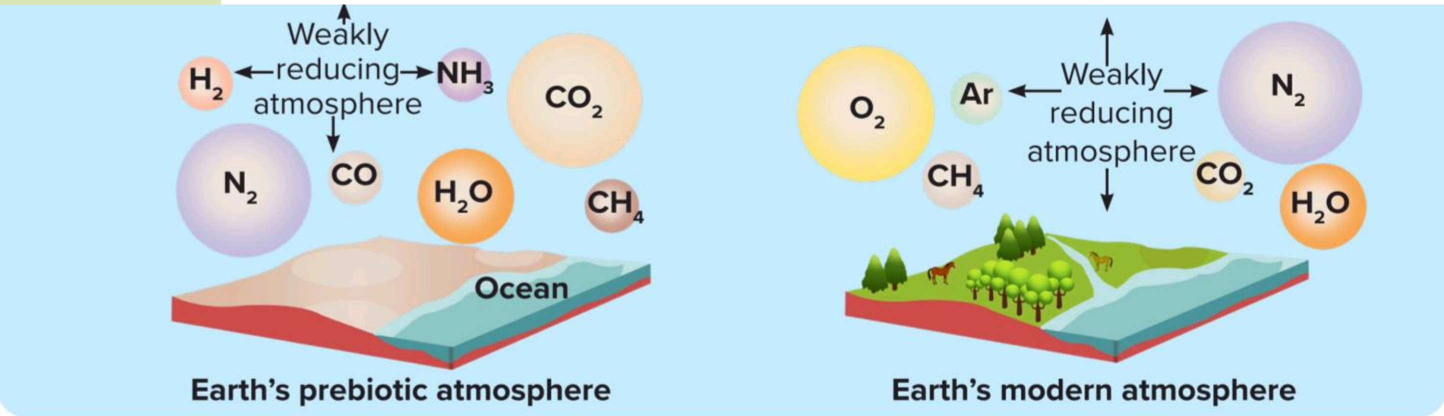
- Glycine moves to mitochondria.
- Another glycine from the repetition of the cycle reaches mitochondria.
- Two glycine molecules form serine.
- $CO_2$ and ammonia are released
- Serine moves to peroxisome.

## Benefits of photorespiration

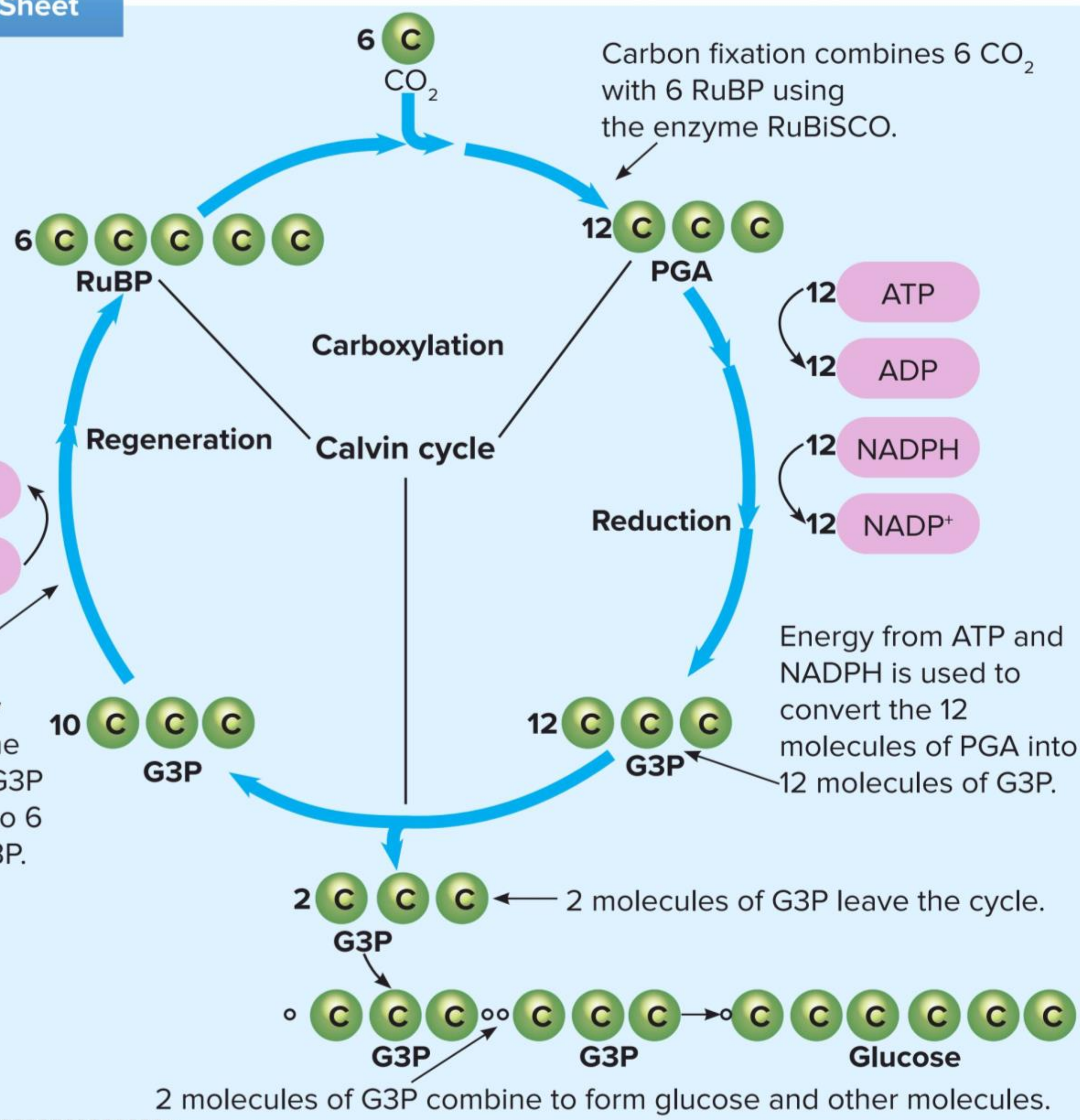
- It removes toxic metabolic intermediates.
- It even protects plants from the damage caused due to excessive light.

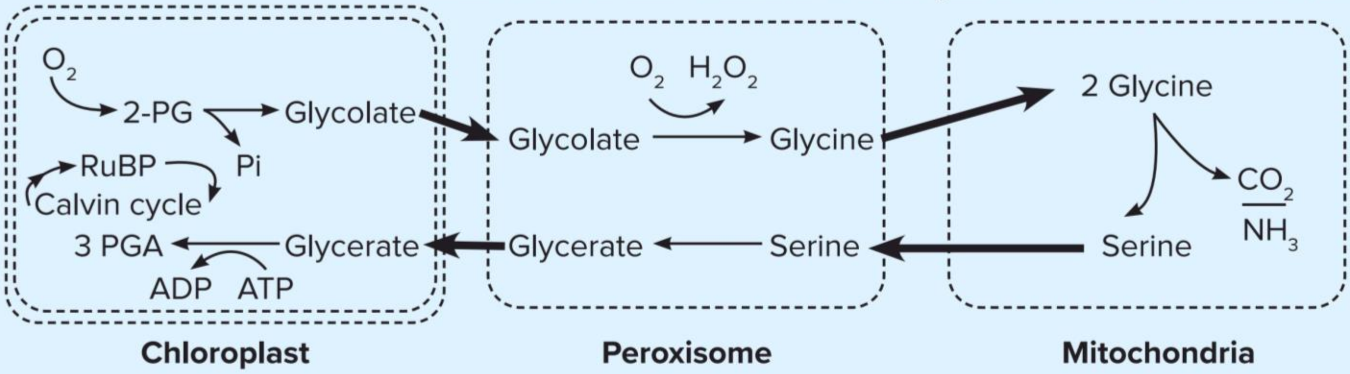
## Did you know?

On the primitive Earth, there was no oxygen. So, **no photorespiration or glycolate pathway** was present.




## Summary Sheet



# PHOTOSYNTHESIS IN HIGHER PLANTS

## KRANZ ANATOMY, $C_4$ CYCLE, COMPARISON OF $C_3$ AND $C_4$ PLANTS, CAM PATHWAY

### Key Takeaways

- $C_4$ pathway
- Comparison of $C_3$ and $C_4$ pathways
- CAM pathways

### Prerequisites

- **Calvin cycle ($C_3$ cycle)**
  - → The Calvin cycle is also known as the **dark reaction.**

**Photosynthesis**

- **Light reactions** — Light is needed to produce organic energy molecules, ATP and NADPH.
- **Dark reactions** — No light is needed. It uses the ATP and NADPH to produce glucose.

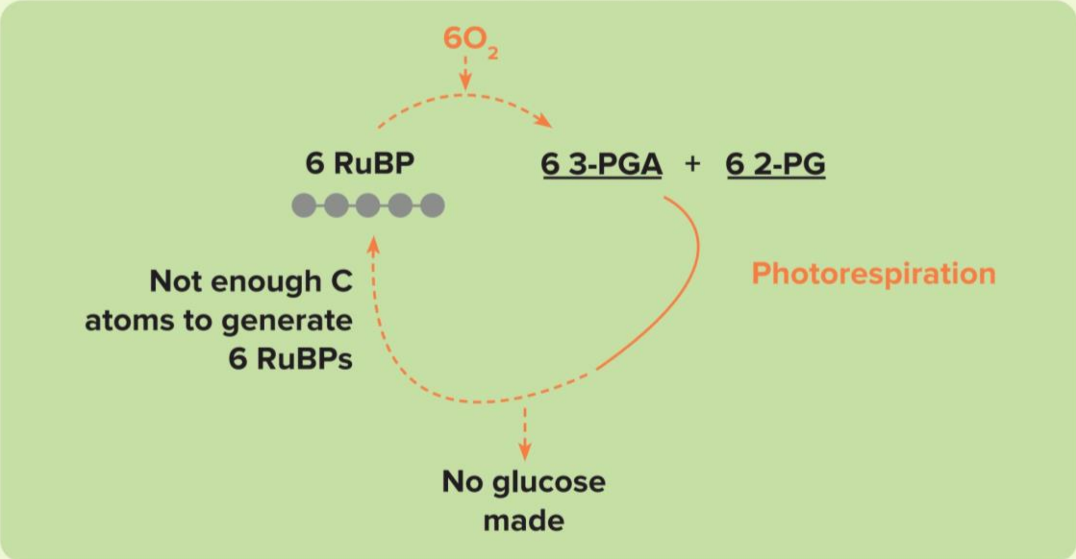
**Calvin cycle**

- **Carboxylation** ($CO_2$ is fixed)
- **Reduction** (NADPH and ATP is used)
- **Regeneration** (RuBP is regenerated and ATP is used)

- Energetics of the Calvin cycle (when 6 $CO_2$ molecules enter the cycle)

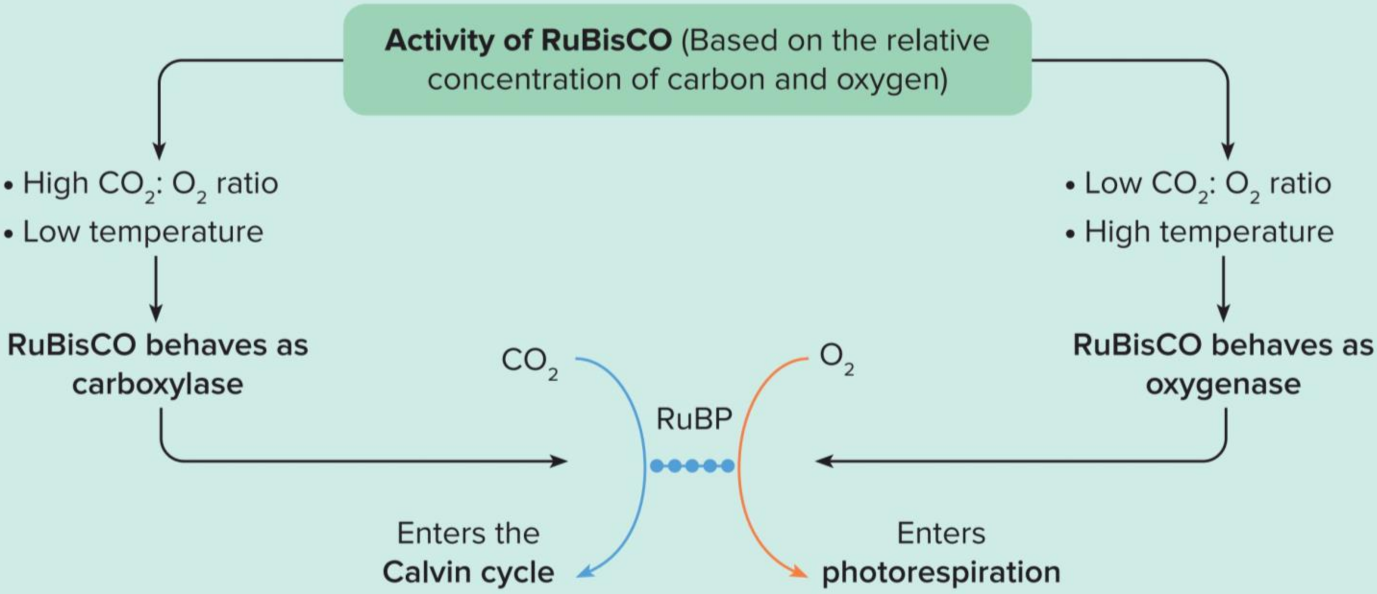
| In | Out |
|---|---|
| 6 $CO_2$ | One glucose molecule |
| 18 ATP | 18 ADP |
| 12 NADPH | 12 $NADP^+$ |

- **Photorespiration:** A wasteful process




## Dual Nature of RuBisCO

- RuBisCO (RuBP carboxylase-oxygenase) plays a key role in photosynthesis.
- RuBisCO has both carboxylase and oxygenase activities.



## Disadvantages of oxygenation reaction of RuBisCO

(a) A compound known as **phosphoglycolate** is formed, which inhibits the steps of the Calvin cycle.

$$\text{Oxygen} + \text{Ribulose bisphosphate} \xrightarrow{\text{RuBisCO}} \text{3-Phosphoglycerate} + \text{2-Phosphoglycolate}$$

(b) ATP is used.

(c) Fixed $CO_2$ is lost.

- **$C_4$ plants exhibit several characteristics that help prevent the oxygenation reaction of RuBisCO.**

## $C_4$ Plants

- They are plants that are adapted to dry, tropical regions.


**Maize**

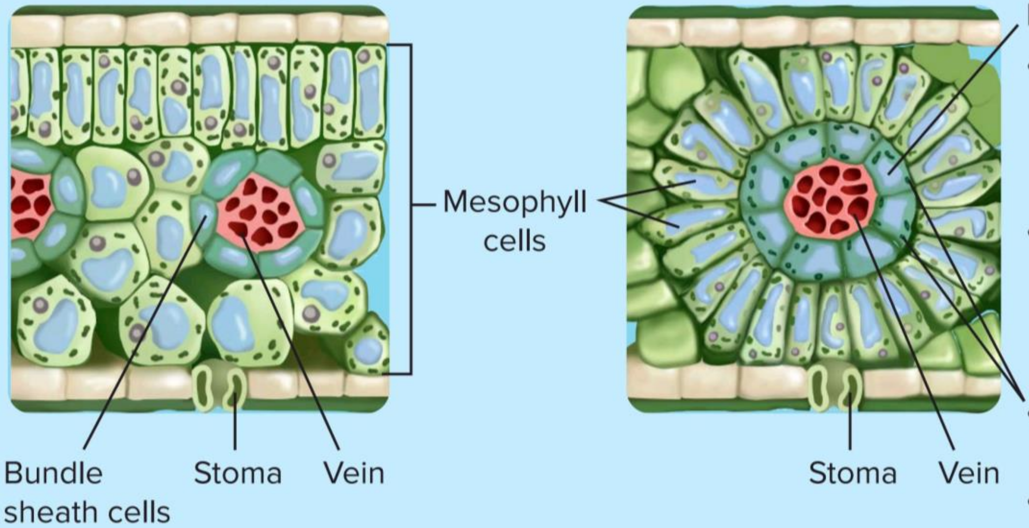

**Sugarcane**


***Sorghum***


***Amaranthus***

- They have a different leaf anatomy when compared to that of $C_3$ plants.

**Leaf anatomy of $C_3$ plants** | **Leaf anatomy of $C_4$ plants**




**Bundle sheath cells**

- Cells are arranged in many layers around the vascular bundles in a wreath-like fashion.
- Such leaves are said to have **Kranz anatomy** (Kranz = Wreath in German).
- The cells have several chloroplasts.
- The walls of the cells are thick to prevent gaseous exchange.
- Intercellular spaces are also absent.

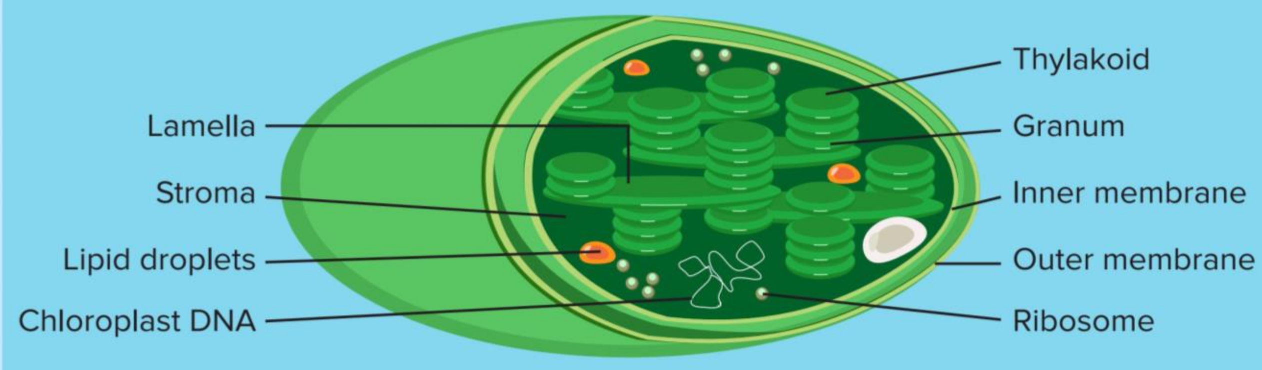
## Strategies to prevent the oxygenation reaction of RuBisCO

(a) RuBisCO-containing bundle-sheath cells are present interiorly. This facilitates the lowering of temperature so that RuBisCO behaves as carboxylase.

(b) $C_4$ Plants exhibit the **dimorphic chloroplast.** This separates the site of evolution of oxygen from the site of $CO_2$ fixation.

→ **In mesophyll cells**

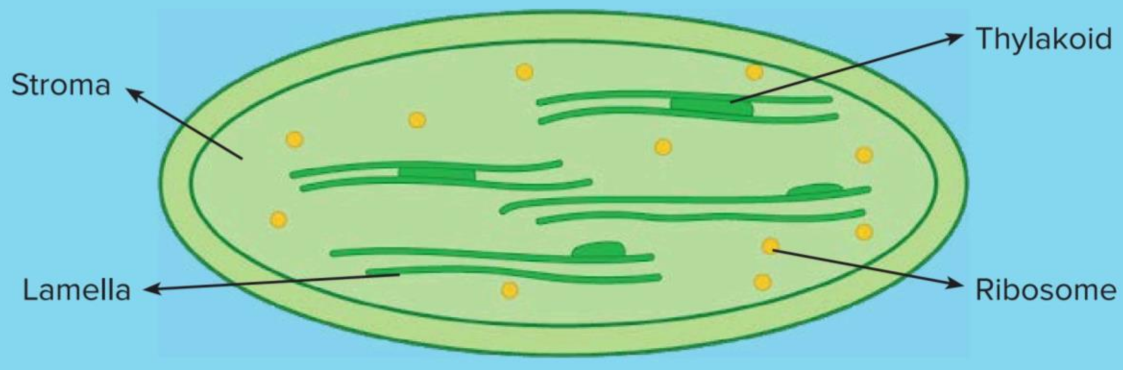
- Granal chloroplast is present.
- Specialised to perform light reaction.
- Oxygen is released through non-cyclic photophosphorylation.




**Granal chloroplast**

→ **In bundle-sheath cells**

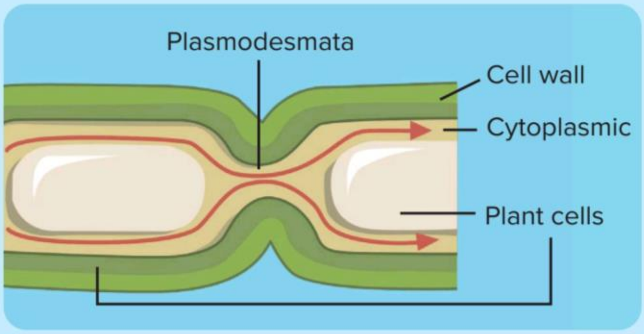
- Agranal chloroplast is present. Here, the grana are rudimentary.
- The $C_3$ cycle or the dark reaction takes place.
- The bundle-sheath cells have thick walls that are impervious to gaseous exchange to prevent the entry of oxygen.




**Agranal chloroplasts**

(c) The transport of $CO_2$ away from the mesophyll cells and into the bundle-sheath cells.

- The transport of $CO_2$ occurs between the mesophyll to the bundle-sheath cells via specialised channels known as **plasmodesmata.**
- **Plasmodesmata** are cytoplasmic channels connecting two plant cells.



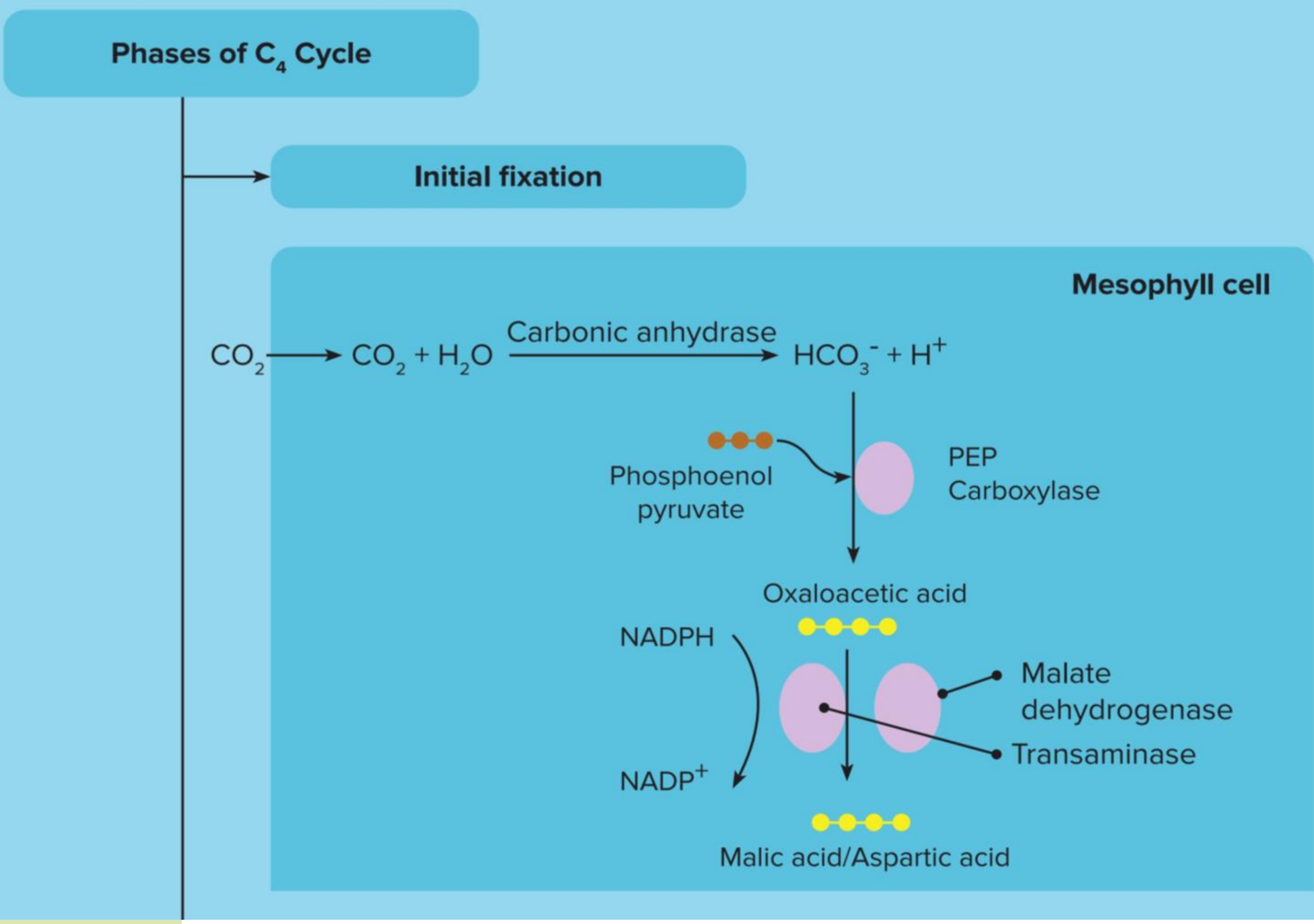
## $C_4$ Pathway

- It is a modified $CO_2$ fixation pathway.
- The name '$C_4$ pathway' is derived from the fact that the first stable product is a **4-carbon compound (oxaloacetic acid)**.
- It was discovered by two Australian scientists, **Marshall Davidson Hatch** and **Charles Roger Slack**, in 1966.
- Hence, it is also known as the **Hatch-Slack pathway**.

Hatch Slack

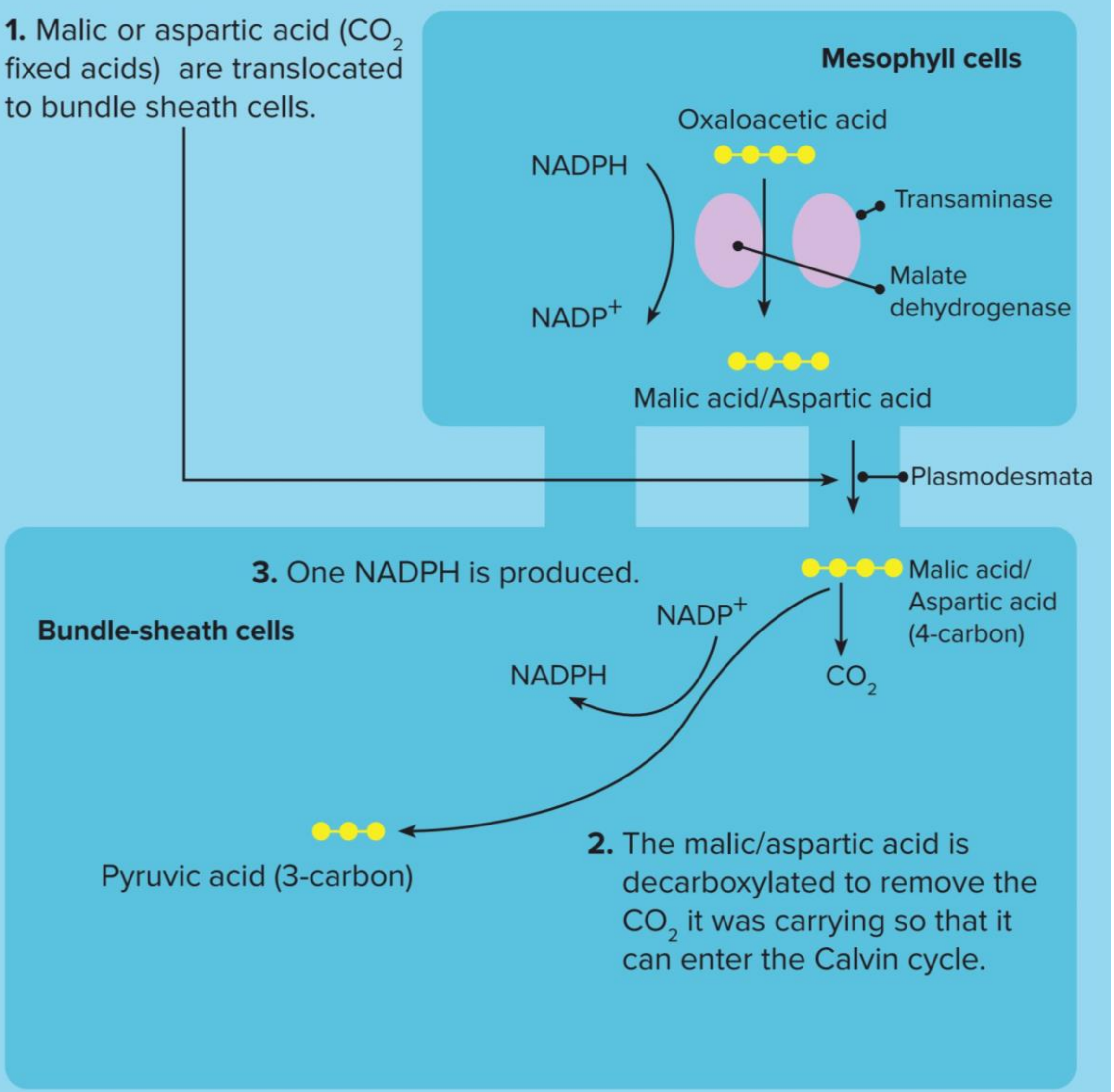
- The $C_4$ pathway takes place in both **mesophyll** and **bundle-sheath cells**.

## Hatch-Slack Cycle ($C_4$ Cycle)

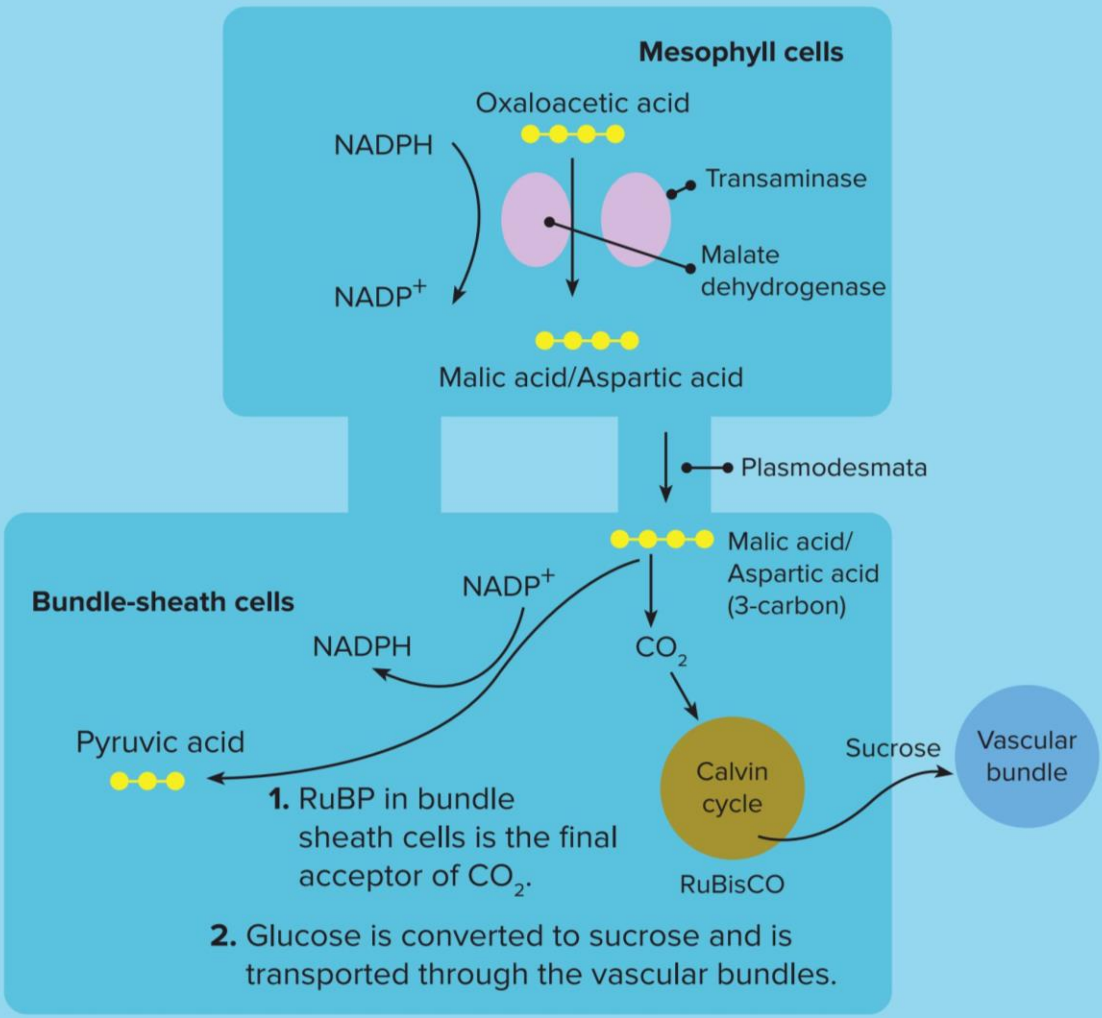


- $CO_2$ enters from the stomata to the mesophyll cells.
- Mesophyll cells lack RuBisCO enzyme.
- The primary $CO_2$ acceptor is a 3-carbon molecule known as phosphoenolpyruvate (PEP).
- The enzyme responsible for this carbon fixation is PEP carboxylase or PEPcase, and it requires $Mg^{2+}$ ions for its proper functioning.
- Oxaloacetic acid is formed in the cytosol and enters the chloroplast.
- Oxaloacetic acid can either change to **malic acid** or undergo **deamination to form aspartic acid** (depending upon the species).
- NADPH is used.

**Transport**

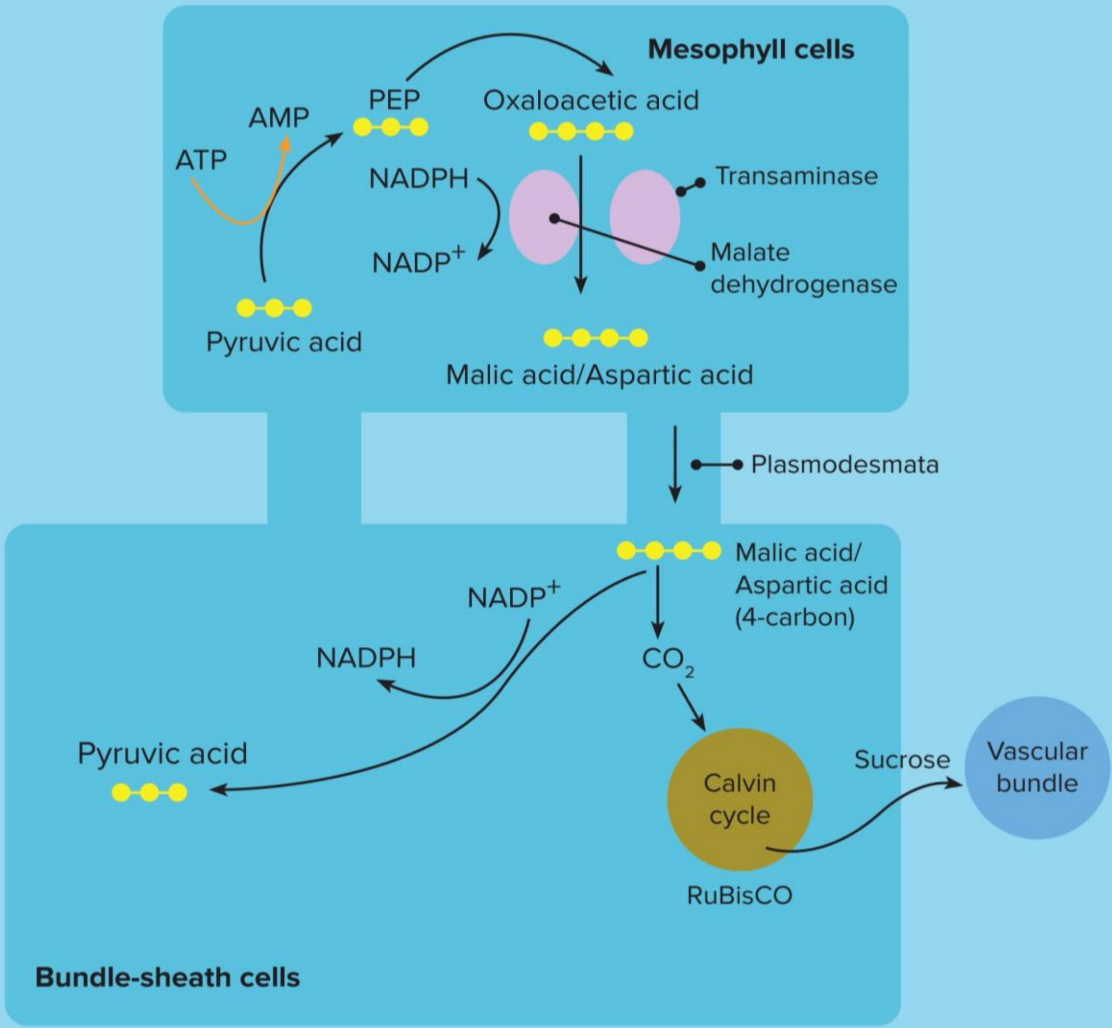


**Final fixation**




**Regeneration of PEP**

1. Pyruvic acid is transported back into the mesophyll cells.
2. Pyruvic acid changes to PEP with the help of the enzyme phosphopyruvate dikinase.
3. This process requires energy equivalent to 2 ATP (two bonds are broken).




## Output of the $C_4$ cycle

- One glucose molecule contains six carbon atoms. One round of the $C_4$ cycle fixes one C atom of $CO_2$ by using 2 ATP.
- Therefore, six turns of the Calvin cycle are needed until 6 C are fixed to produce one molecule of glucose.

## ATP consumption

| | $C_3$ cycle | $C_4$ cycle | Total |
|---|---|---|---|
| **ATP** | Per C atom fixed = **3 ATP** used | Per C atom fixed = **2 ATP** used | Per C atom fixed = 3 + 2 = **5 ATP** |
| | For 1 molecule of glucose (6 C-atoms) = 3 x 6 = **18 ATP** used | For 1 molecule of glucose (6 C-atoms) = 2 x 6 = **12 ATP** used | For 1 molecule of glucose (6 C-atoms) = 18 + 12 = **30 ATP** used |
| **NADPH** | **12 NADPH** per glucose molecule used | **No net gain/loss** of NADPH | **12 NADPH** per molecule of glucose used |

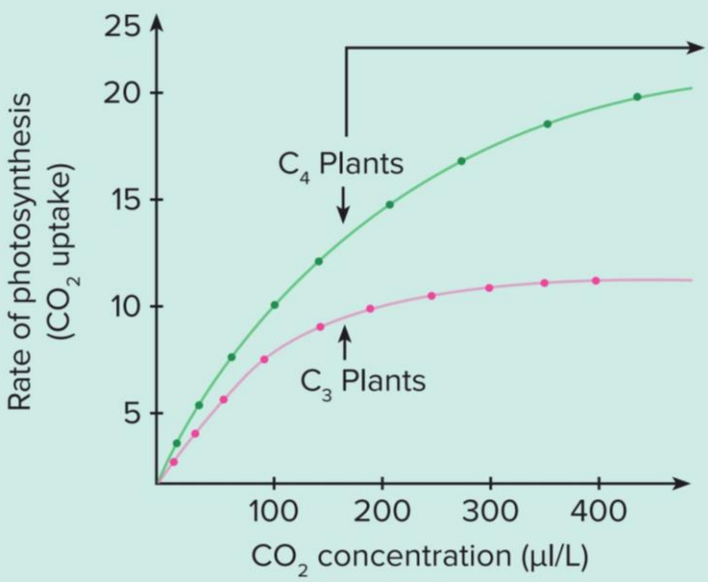
## Differences between mesophyll cells and bundle-sheath cells

| Mesophyll cell | Bundle-sheath cells |
|---|---|
| Carry out light-dependent and independent reactions and evolution of oxygen | Majorly carry out light-independent reactions |
| Thin cell walls | Thick cell walls |
| Absence of starch granules | Presence of starch granules |
| $CO_2$ acceptor: PEP | $CO_2$ acceptor: RuBP |

## $C_3$ vs $C_4$ Cycle

| Characteristics | $C_3$ cycle | $C_4$ cycle |
|---|---|---|
| **Primary carbon acceptor** | RuBP (5-carbon compound) | PEP (3-carbon compound) |
| **Photorespiration** | A higher concentration of oxygen leads to photorespiration that uses the products of photosynthesis, thereby decreasing the effective photosynthetic rate. | No photorespiration occurs. |
| **Site of Calvin cycle** | Mesophyll cells | Bundle-sheath cells |
| **Site of initial carboxylation** | Mesophyll cells | Mesophyll cells |
| **Location of RuBisCO** | Mesophyll cells | Bundle-sheath cells |
| **First stable photosynthetic product** | 3-Phosphoglyceric acid (3C) | Oxaloacetic acid (4C) |

## Rate of carbon assimilation




- $CO_2$ uptake continues even in low $CO_2$ concentrations.
- PEP has a higher efficiency to take up $CO_2$ than RuBisCO.
- It produces more biomass when compared to $C_3$ plants at the same concentration of $CO_2$.

## Crassulacean Acid Metabolism (CAM)

- The CAM pathway was first observed in the Crassulaceae family, which includes plants like *Bryophyllum* and succulent xerophytes.
- In these plants, the opening of stomata in hot and dry conditions leads to the loss of great amounts of water.


*Agave*


*Kalanchoe*


Pineapple


*Opuntia*

### The strategy of CAM plants

- Stomata in CAM plants open during the night and not during the day.
- The low temperature in the night helps to take in $CO_2$ for fixation without losing much water.
- Stomata that open during the night are known as **scotoactive stomata**.
- They also exhibit **sunken stomata**.

### The CAM pathway

**During night**

**$CO_2$ enters through the stomata and diffuses into mesophyll cells.**

- $CO_2$ reacts with water molecules to form carbonic acid.
- Carbonic acid dissociates into bicarbonate ions ($HCO_3^-$) and $H^+$ in the presence of enzyme carbonic anhydrase.

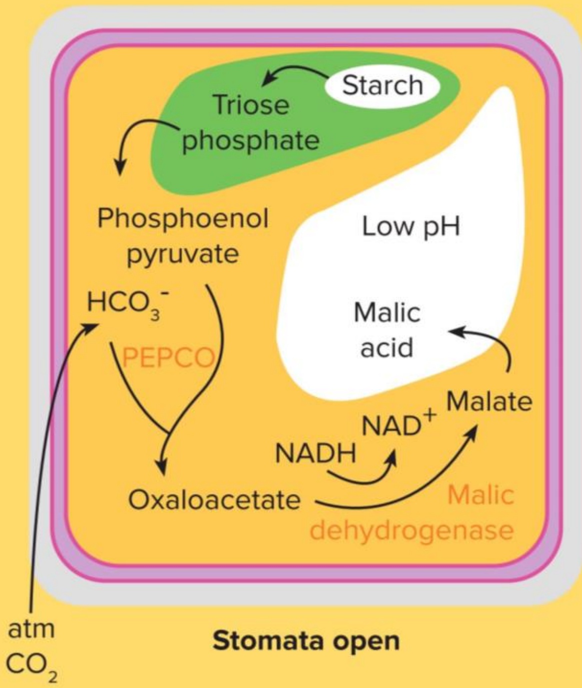
↓

**$CO_2$ is fixed into oxaloacetate and then into malate.**

- PEP accepts $HCO_3^-$ in the presence of PEPCO and OAA is formed.
- OAA is converted into malate.

↓

**Malate enters the vacuole and gets converted to malic acid.**



Stomata open

**During day**

**Malic acid dissociates into $H^+$ and malate ions.**

↓

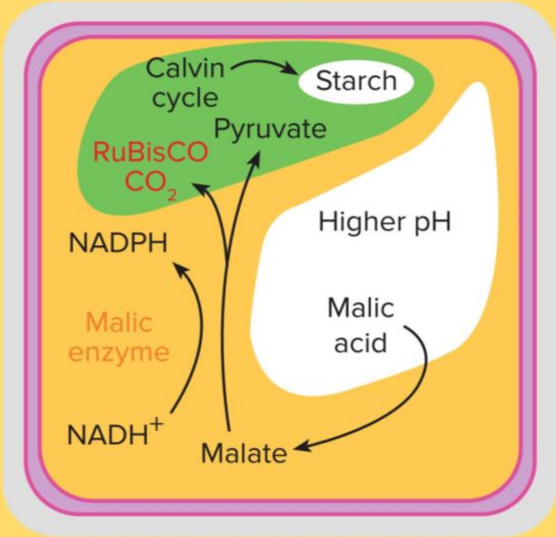
**Malate ions move out of vacuole and enter the chloroplast.**

↓

**Malate ions are converted into pyruvate and $CO_2$.**

↓

**$CO_2$ is introduced into the Calvin cycle and, glucose is synthesized.**




## Summary Sheet

### Phases of $C_4$ Cycle

**Initial fixation**
- $CO_2$ acceptor is a 3-carbon molecule PEP.
- The enzyme responsible for this carbon fixation is PEPcase.
- Oxaloacetic acid is formed in the cytosol.
- Oxaloacetic acid is converted to malic acid or aspartic acid.
- NADPH is used.

**Transport**
- Malic or aspartic acid are translocated to bundle-sheath cells.
- $CO_2$ is removed from malic acid or aspartic acid to enter the Calvin cycle.

**Final fixation**
- $CO_2$ released is fixed in bundle-sheath cells through **Calvin cycle**.
- **RuBP** is the secondary or **final acceptor** of $CO_2$ in $C_4$ plants.

**Regeneration of PEP**
- Pyruvic acid changed to **PEP** with the enzymes **phospho-pyruvate dikinase** (ATP ---> AMP + $PP_i$). This process requires energy equivalent to 2 ATP (two bonds are broken) in addition to what is required for Calvin cycle.

| Characteristics | $C_3$ cycle | $C_4$ cycle |
|---|---|---|
| **Primary carbon acceptor** | RuBP (5-carbon compound) | PEP (3-carbon compound) |
| **Photorespiration** | A higher concentration of oxygen leads to photorespiration that uses the products of photosynthesis, thereby decreasing the effective photosynthetic rate. | No photorespiration occurs. |
| **Site of Calvin cycle** | Mesophyll cells | Bundle-sheath cells |
| **Site of initial carboxylation** | Mesophyll cells | Mesophyll cells |
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| **First stable photosynthetic product** | 3-phosphoglyceric acid (3C) | Oxaloacetic acid (4C) |

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**$CO_2$ is fixed into oxaloacetate and then into malate.**

- PEP accepts $HCO_3^-$ in the presence of PEPCO and OAA is formed.
- OAA is converted into malate.

↓

**Malate enters the vacuole and gets converted to malic acid**

**During day**

**Malic acid dissociates into $H^+$ and malate ions.**

↓

**Malate ions move out of vacuole and enter the chloroplast.**

↓

**Malate ions are converted into pyruvate and $CO_2$.**

↓

**$CO_2$ is introduced into the Calvin cycle and, glucose is synthesized.**

# PHOTOSYNTHESIS IN HIGHER PLANTS

## FACTORS AFFECTING PHOTOSYNTHESIS, SIGNIFICANCE OF PHOTOSYNTHESIS

### Key Takeaways

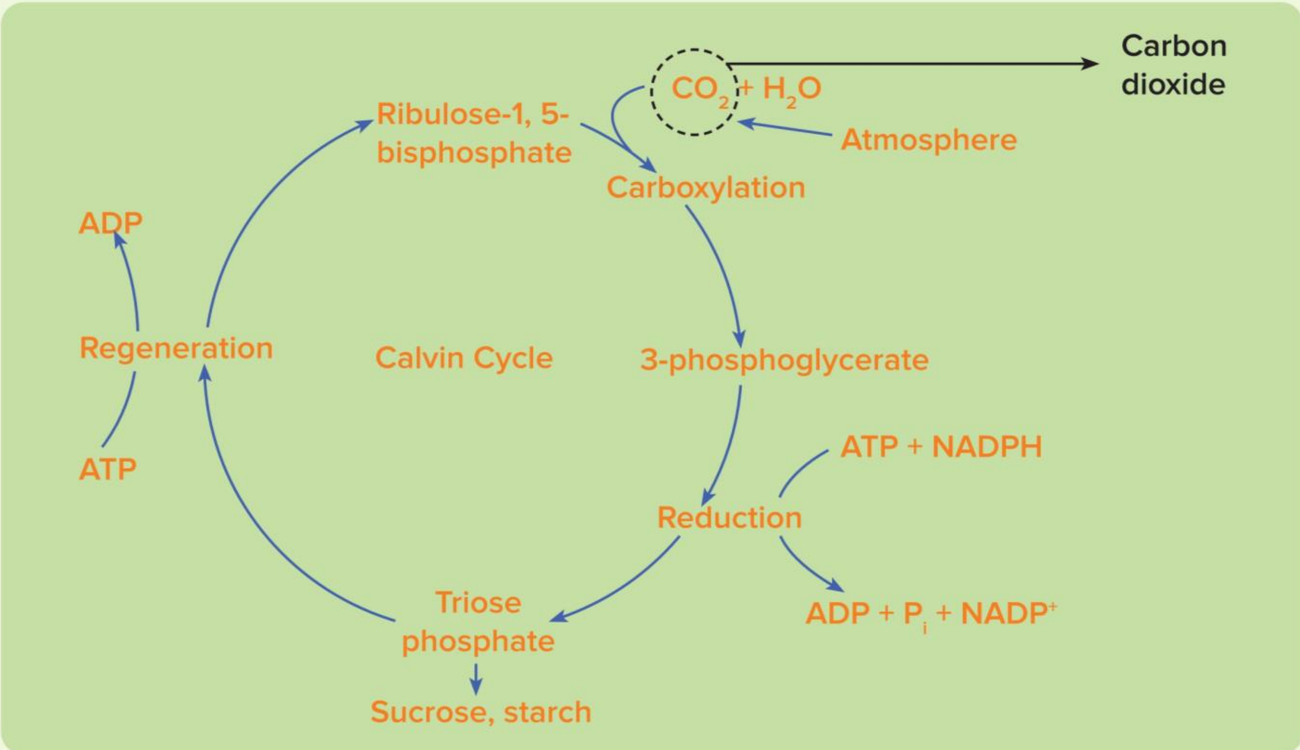
- Factors affecting photosynthesis
  - → External factors
  - → Internal factors
- Law of limiting factors
- Significance of photosynthesis

### Prerequisites

- **Photosynthesis reaction**

$$\text{Carbon dioxide} + \text{Water} \xrightarrow[\text{Chlorophyll}]{\text{Sunlight}} \text{Glucose} + \text{Oxygen}$$

- **Dark reaction of photosynthesis**

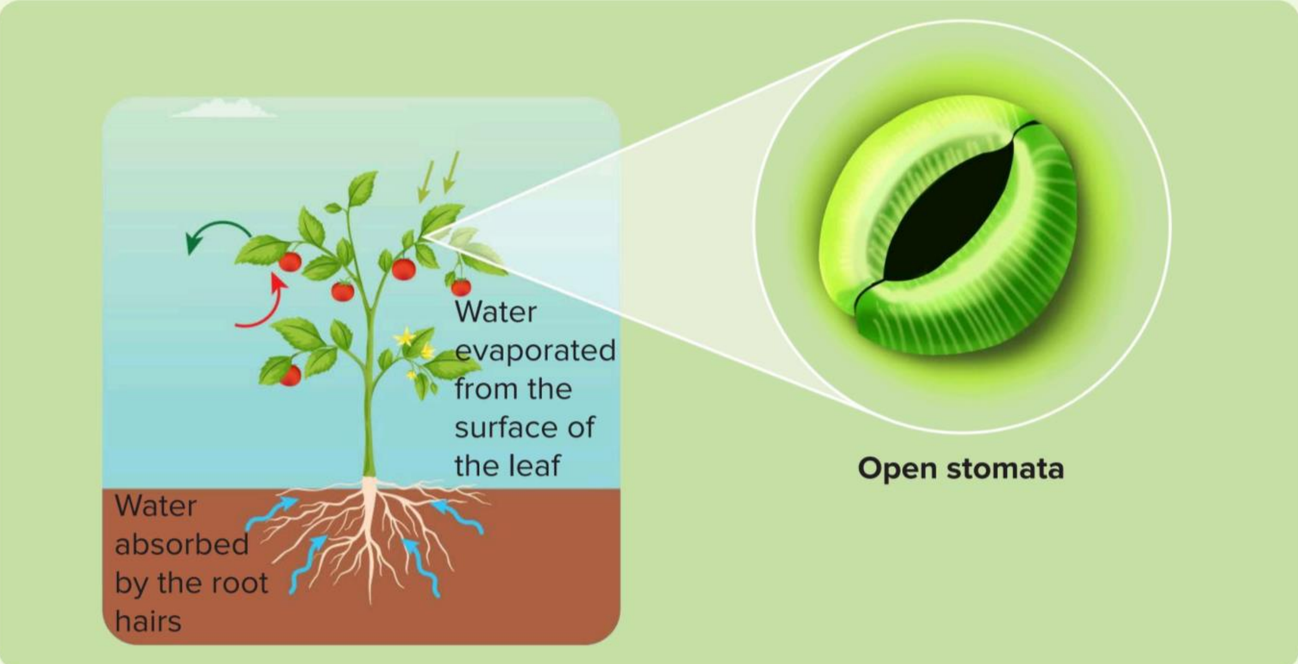


- **$C_3$ and $C_4$ plants**

| $C_3$ Pathway | $C_4$ pathway |
|---|---|
| Photosynthesis occurs in mesophyll cells. | Photosynthesis occurs in mesophyll and bundle sheath cells. |
| The $CO_2$ molecule acceptor is **RuBP**. | The $CO_2$ acceptor molecule is **phosphoenolpyruvate**. |
| The first stable product is a 3C compound known as 3-PGA. | The first stable product is a 4C compound known as OAA. |
| The rate of photorespiration is high and leads to the loss of fixed $CO_2$. It **decreases the rate of fixation**. | The rate of photorespiration is negligible. Hence, it **increases the rate of fixation of $CO_2$**. |
| Examples of $C_3$ plants are rice, wheat, and potato. | Examples of $C_4$ plants are maize, sugarcane, *Tribulus*, and *Amaranthus*. |

- **Transpiration**

It is the evaporative loss of water by plants through the stomata.




## Factors Affecting Photosynthesis

- Photosynthesis is the process by which the plants transform light energy into chemical energy.
- It is under the influence of several factors, both **external** and **internal**.
- **Blackman's law of limiting factors** is observed when several factors affect any biochemical reaction.

## Blackman's law of limiting factors

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

## External factors

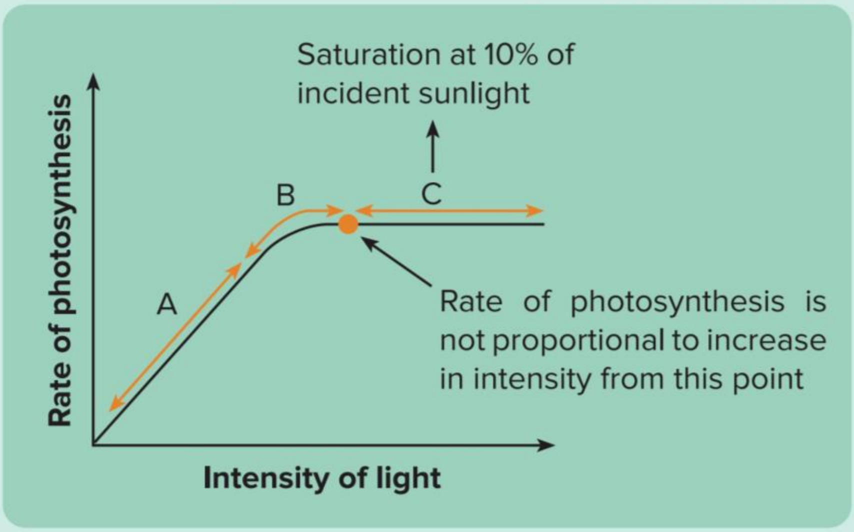
### Light

- Plants trap light energy from the Sun to carry out photosynthesis.

#### Characteristics of light

##### Intensity of light

- As the intensity of light increases, the **rate of photosynthesis** also increases in a gradual manner (represented by A).
- After a certain point, an increase in the intensity of light does not cause a proportional increase in the rate of photosynthesis.
- This is because, at this stage, though sunlight is available, the plant does not have enough of other resources to perform photosynthesis (represented by B).
- Further increase in the intensity of light does not increase the rate of photosynthesis. This **saturation** occurs at 10% of the total incident **sunlight** (represented by C).
- Plants cannot use more than 10% of the sunlight falling on them. Hence, except for plants in shade or in dense forests, light is rarely a **limiting factor** in nature.



### Quality of light

- The rate of photosynthesis is affected by the wavelength of the incident light.
- The experiments conducted by Engelmann prove that **blue and red wavelengths of light** are ideal for photosynthesis.

### Duration of exposure

- The longer the plant is exposed to light, the longer will be the process of photosynthesis.

## Carbon dioxide

- An increase in the concentration of carbon dioxide (up to 0.05%), increases the rate of carbon dioxide fixation in plants.

- The increase in the levels of $CO_2$ beyond **0.05%** can become damaging to the plants over longer periods.

- Under low-light conditions, an increase in $CO_2$ levels does not lead to an increase in the rate of photosynthesis.
- However, under higher conditions of light, an increase in $CO_2$ levels leads to an increase in the rate of photosynthesis.

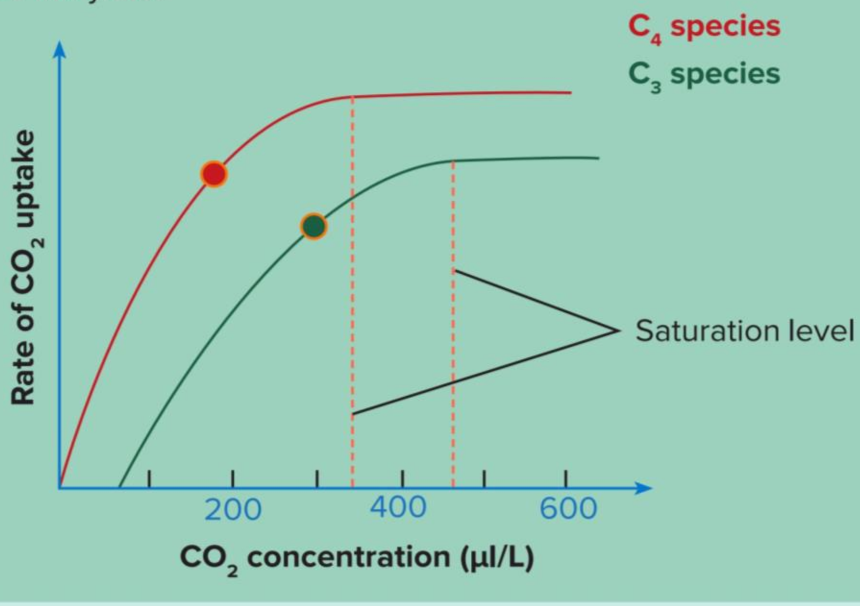
**Responses of $C_3$ and $C_4$ plants to increasing $CO_2$ concentrations**

- An increase in the levels of $CO_2$, increases the rate of uptake in both $C_3$ and $C_4$ plants.
- Beyond a certain level, increasing $CO_2$ concentration does not increase the rate of assimilation or uptake of $CO_2$. This concentration of atmospheric $CO_2$ is said to be the **saturation level**.

**Saturation level**

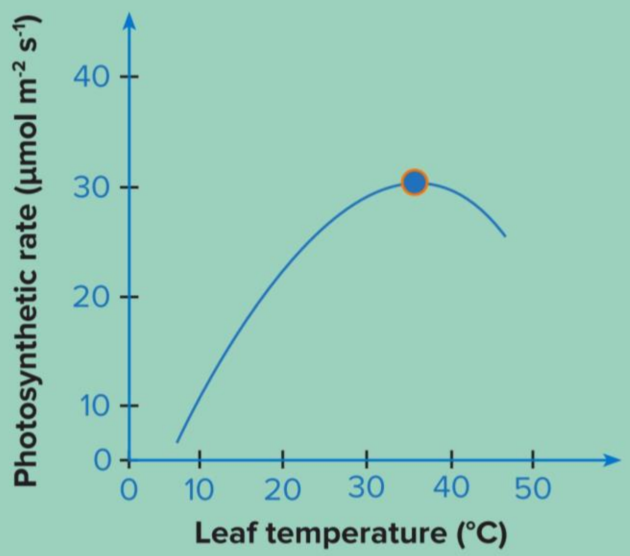
It is the concentration of carbon dioxide beyond which an increase in the concentration would not lead to an increase in the rate of photosynthesis.

- The saturation levels of $CO_2$ for $C_4$ plants is approximately **360 µl/L**.
- The saturation levels of $C_3$ plants is approximately **450 µl/L**.
- $C_3$ plants respond to higher $CO_2$ concentrations by showing increased rates of photosynthesis, leading to higher productivity.
  - ➜ Due to this, $C_3$ plants like tomatoes and bell peppers are grown in greenhouses having a carbon dioxide-enriched atmosphere to increase the yield.

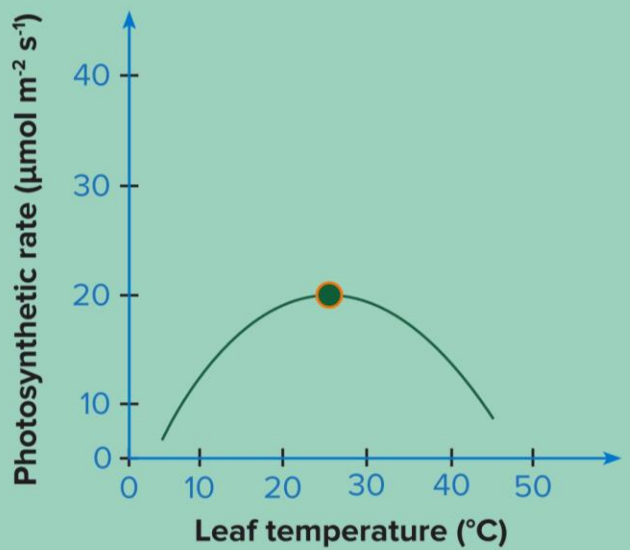



**Temperature**

- Photosynthesis is an **enzyme-controlled reaction**. Hence, the rate of photosynthesis is affected by the temperature.
- The rate of photosynthesis increases with an increase in temperature.
- However, after a certain temperature maximum is reached, the rate of photosynthesis declines as the enzymes begin to denature.
- $C_4$ plants have a higher temperature maximum. This is because these plants are **adapted to the dry and high-temperature conditions** with the help of the $C_4$ pathway.




- C3 plants have a much lower temperature optimum.




- Optimum temperature depends on the habitat too.
- Temperature optimum depends on the habitat too. Tropical plants (Example: Orchid), which are adapted to higher temperatures, have a higher temperature optimum compared to the temperate plants (Example: Maple).

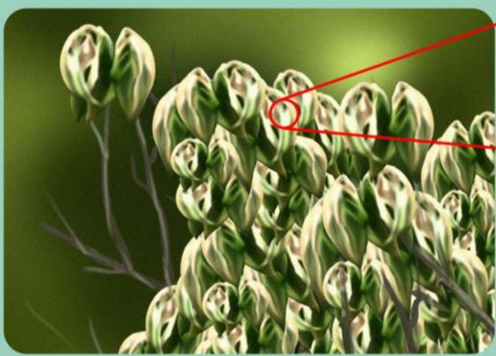
Orchid (Tropical plant)

Maple (Temperate plant)

**Water** : The effect of water is usually through its effect on the plant, rather than directly on photosynthesis.

- The loss of water from the plant as a result of **transpiration** causes the stomata to close, thereby reducing the availability of $CO_2$.

- The loss of water also causes leaves to wilt, thereby reducing the surface area of the leaves. This reduces the metabolic activities of the plant.



Drying of leaves

**Closed stomata**

↓

Prevents exchange of gases like $CO_2$

↓

↓↓ **Rate of photosynthesis**

**Oxygen**

- Under the conditions involving high concentrations of oxygen, RuBisCO* (Ribulose-1, 5-bisphosphate carboxylase-oxygenase) competitively binds to oxygen and acts as an oxygenase. This is known as the **Warburg effect**.

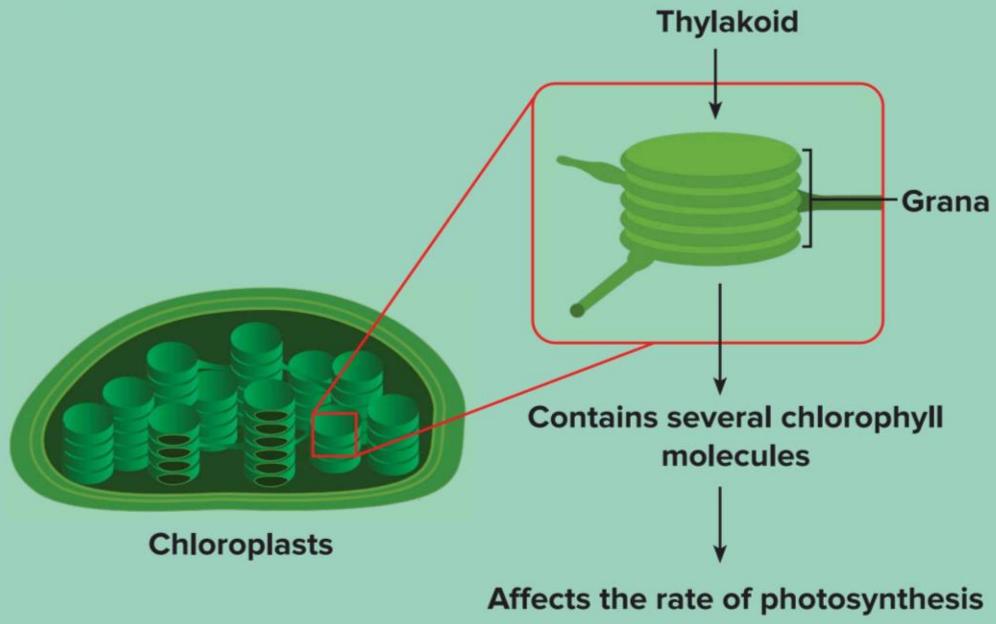
- This prevents RuBisCO from binding to $CO_2$, catalyses the $CO_2$ fixation, and thus, **reduces** the **rate of photosynthesis**.

*RuBisCO is an enzyme involved in the first major step of photosynthesis.

## Internal factors

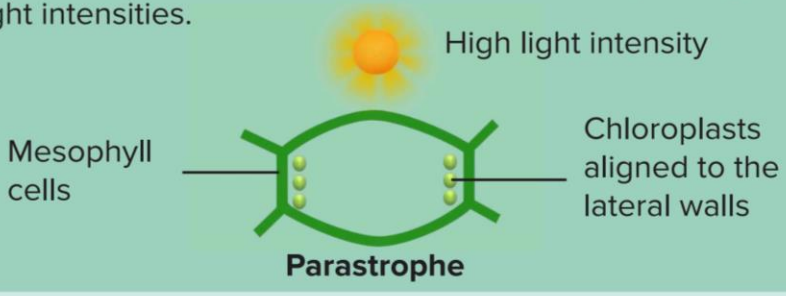
### Amount of chlorophyll

- Chlorophyll is a **green pigment** located within the **thylakoid membrane** of the chloroplast in plants.

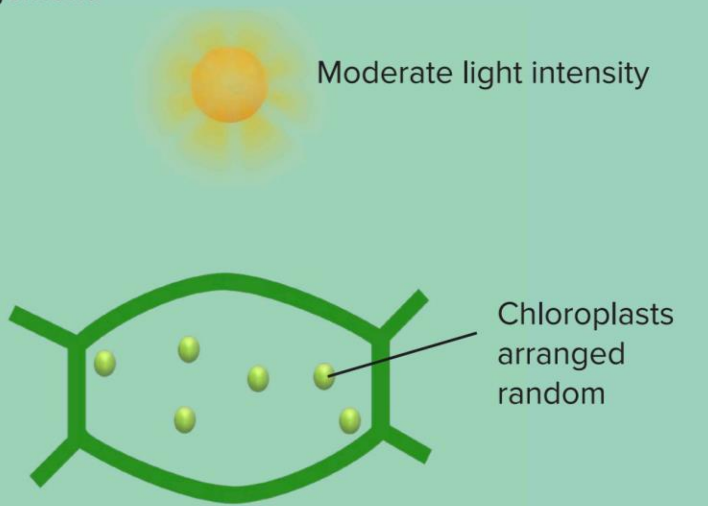



The **number of chlorophyll molecules** in the cell directly affects the rate of photosynthesis.

- Chloroplasts align themselves within the mesophyll cells usually in three distinct ways so as to get the optimum quantity of incident light.
- The arrangement of the chloroplasts with respect to the incident light intensities also affects the rate of photosynthesis.
  - Under high-light conditions, the chloroplasts align on the lateral walls of the mesophyll cells in a parallel fashion to the direction of the incident light. This condition is known as **parastrophe**.
  - This alignment **protects the chloroplasts** from being damaged by the high light intensities.

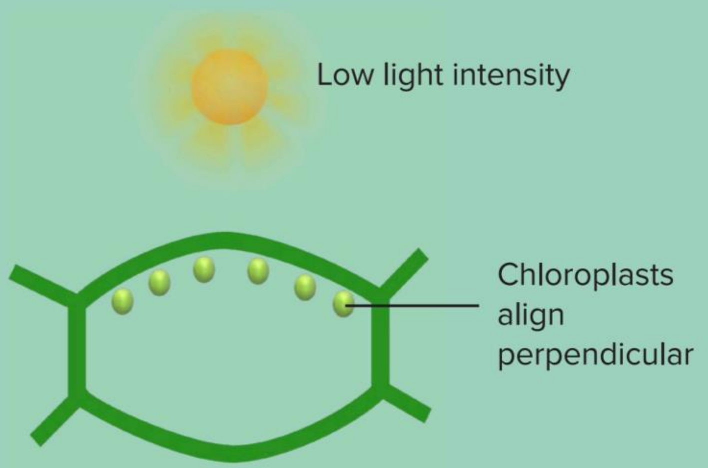


- Under moderate light intensities, the chloroplasts are arranged in a random pattern in the mesophyll cells. This alignment is known as **apostrophe** arrangement.




**Apostrophe**

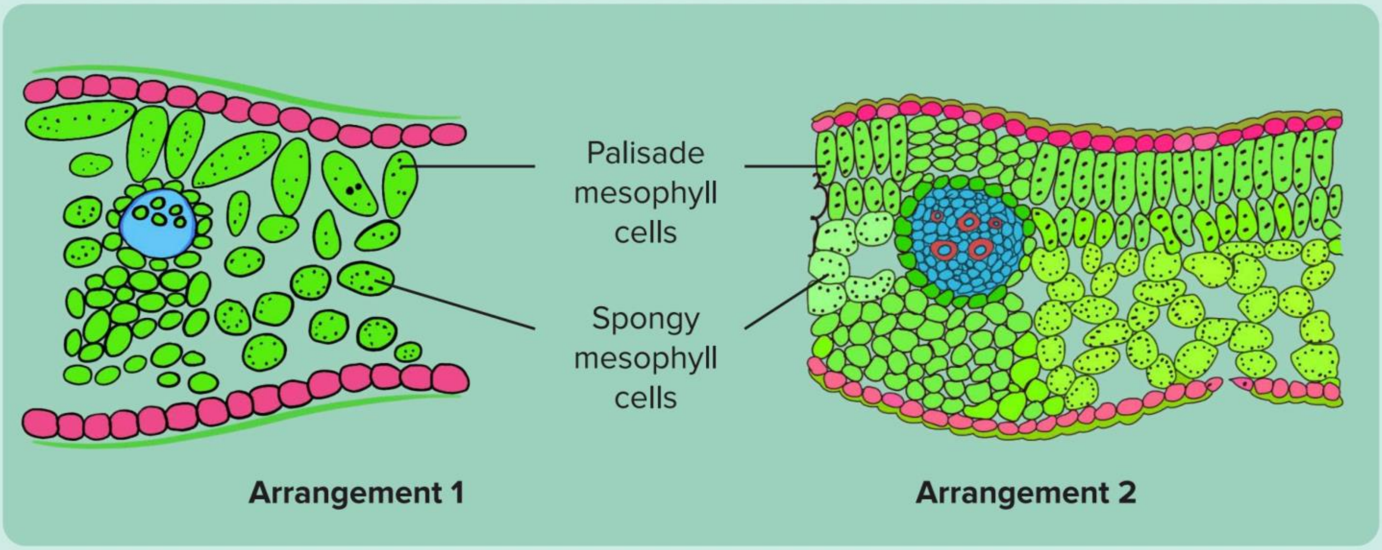
- Under low light intensities, the chloroplasts align themselves perpendicular to the incident light. This alignment is known as **epistrophe**.
- It allows the chloroplasts to **capture the maximum amount of incident sunlight.**




**Epistrophe**

## Characteristics of a leaf

- **Number of mesophyll cells**
  - Mesophyll cells contain chlorophyll that helps in photosynthesis. **Higher the number of mesophyll cells, the greater will be the rate of photosynthesis**.
  - In the following figure, the second arrangement of mesophyll cells will result in the higher rate of photosynthesis.




- **Orientation of leaves**
  - Turgid and upright leaves have **more surface area to capture the maximum amount of light**, as compared to dry and drooping leaves, increasing the rate of photosynthesis in the upright leaves.

Upright leaf

Dry leaf

- **Age of leaves**
  - The rate of photosynthesis of either **too young or too old leaves is lower** than that of the mature leaves.


Young leaves


Mature leaves


Old leaves

- **Size of leaves**
  - Photosynthesis is **higher in bigger leaves** due to more surface area.


Big leaves


Small leaves

- **Number of leaves**
  - Plants with more leaves would have **more chlorophyll**. Hence, they will be able to sustain a much **higher rate of photosynthesis**.


Many leaves


Few leaves

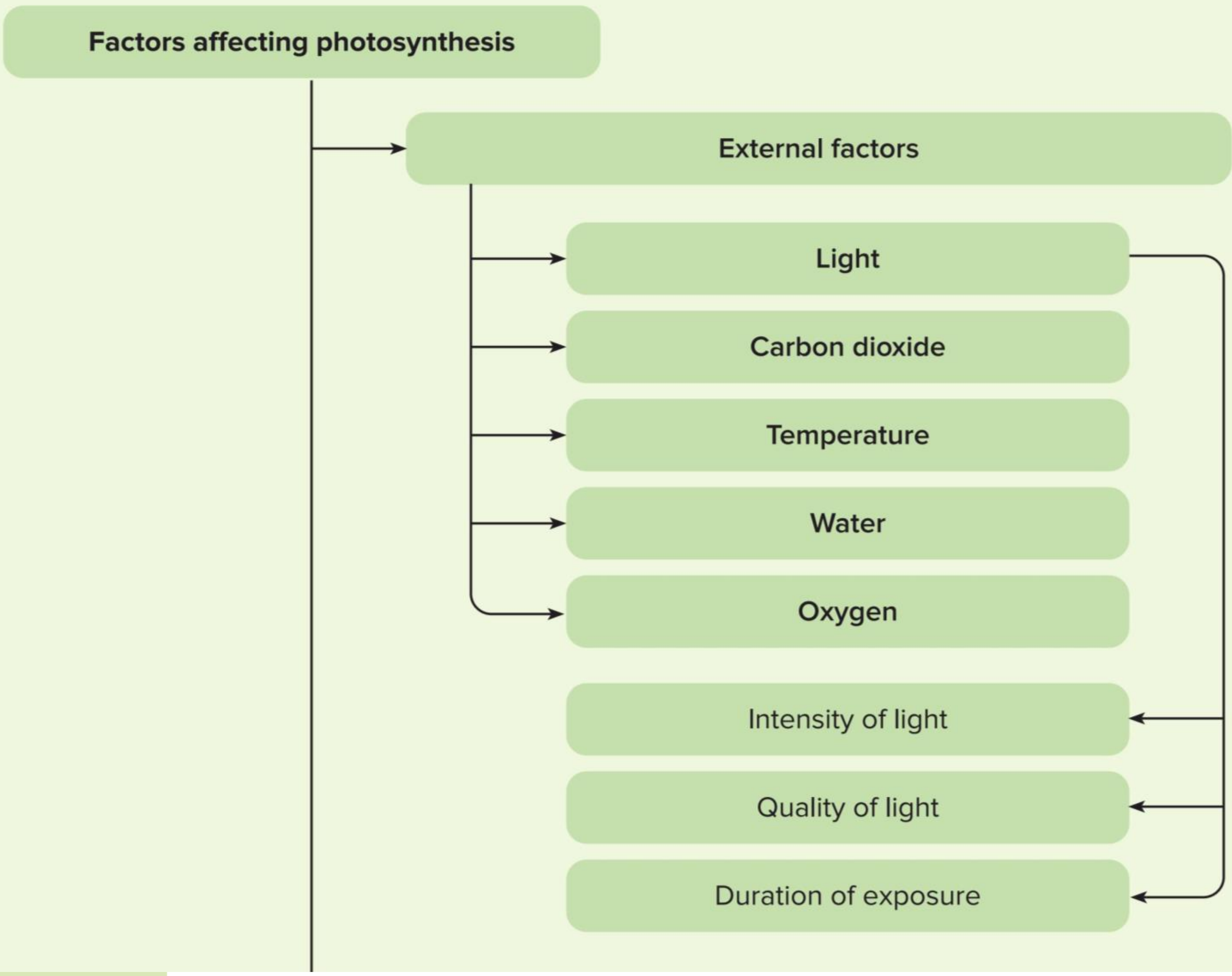
## Accumulation of carbohydrate

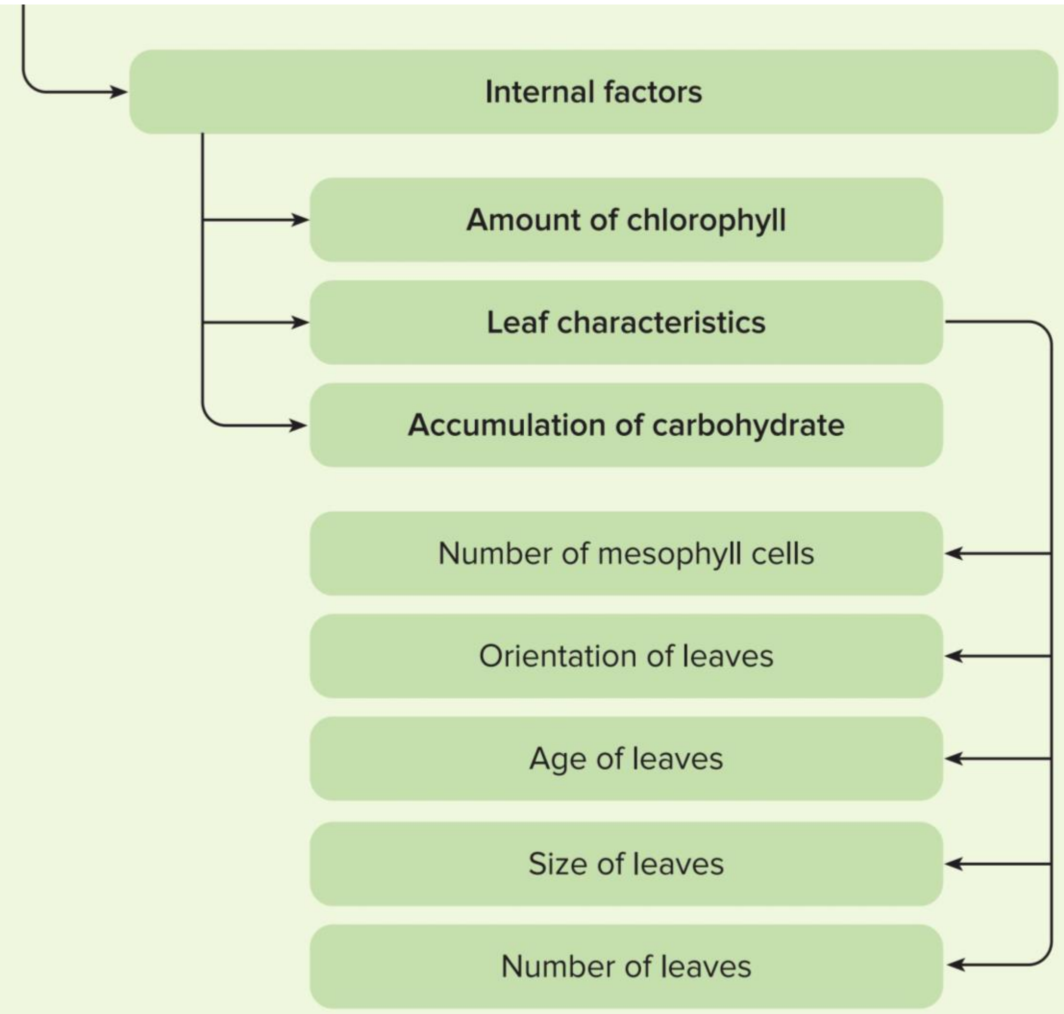
- In the leaves, an **increased accumulation of carbohydrates** tends to saturate and **reduce the rate of photosynthesis**.
- This happens because of the **feedback inhibition**. The accumulation of the products of photosynthesis prevents further photosynthesis reactions from happening.

## Significance of Photosynthesis

- Photosynthesis is essential for the existence of all life on Earth. It serves a **crucial role in the food chain**. The plants create their food using this process, thereby, forming the primary producers.
- Photosynthesis is also responsible for the **production of oxygen**, which is needed by most organisms for their survival.

## Summary Sheet




Internal factors
Amount of chlorophyll
Leaf characteristics
Accumulation of carbohydrate
Number of mesophyll cells
Orientation of leaves
Age of leaves
Size of leaves
Number of leaves