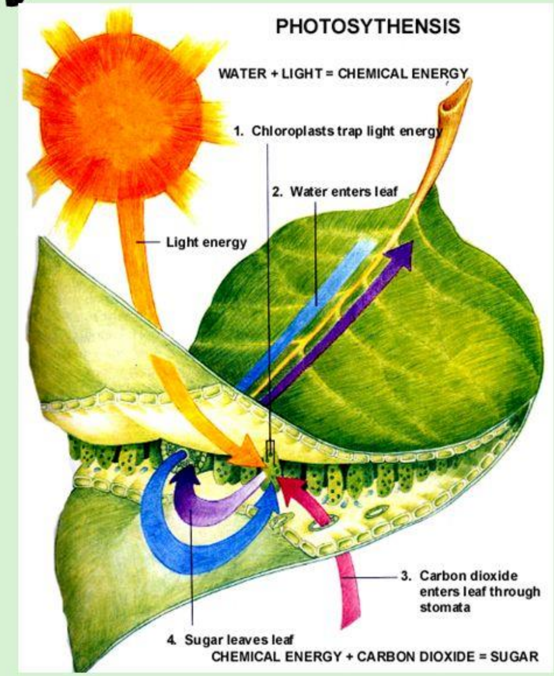
Photosynthesis

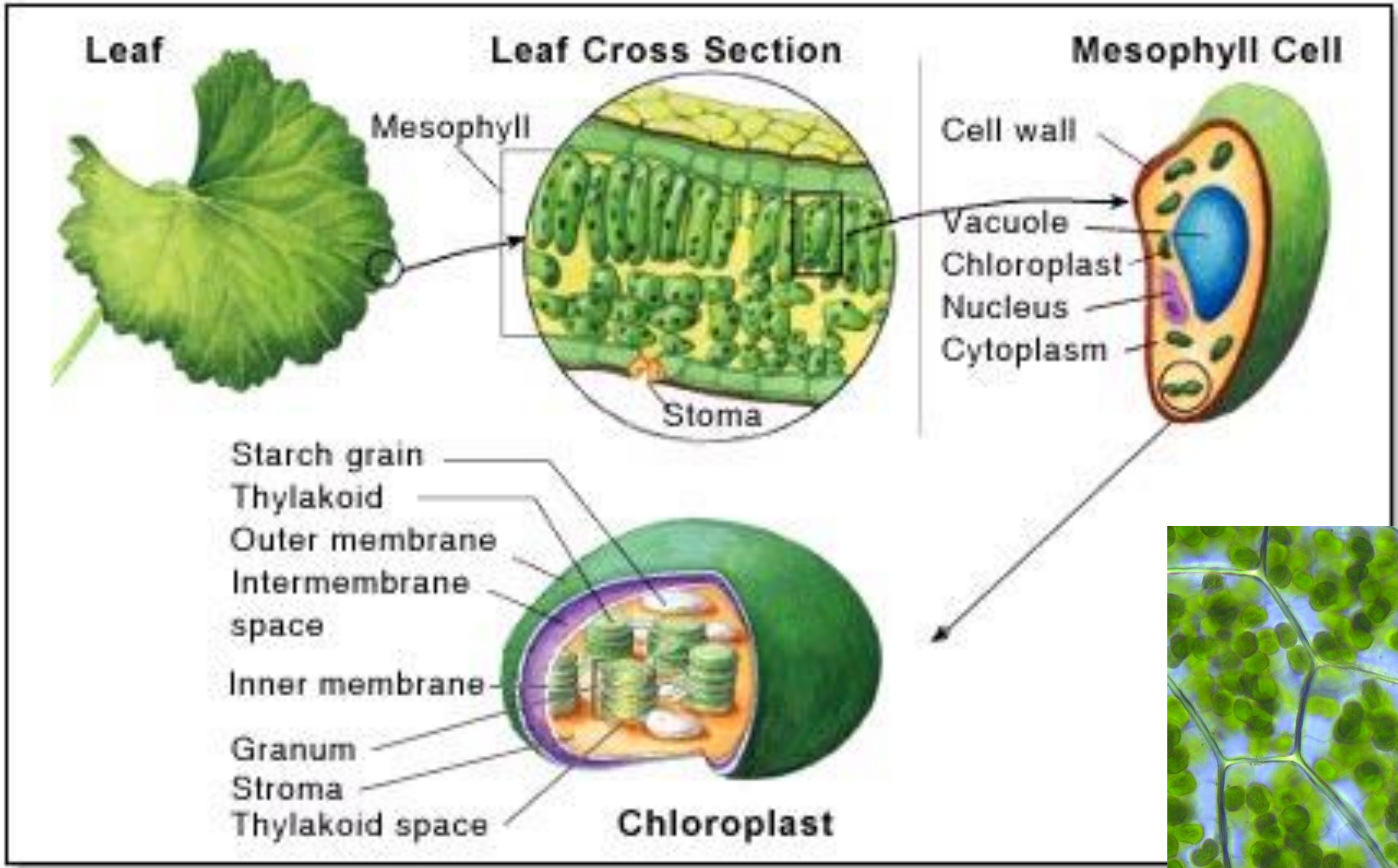
Photosynthesis

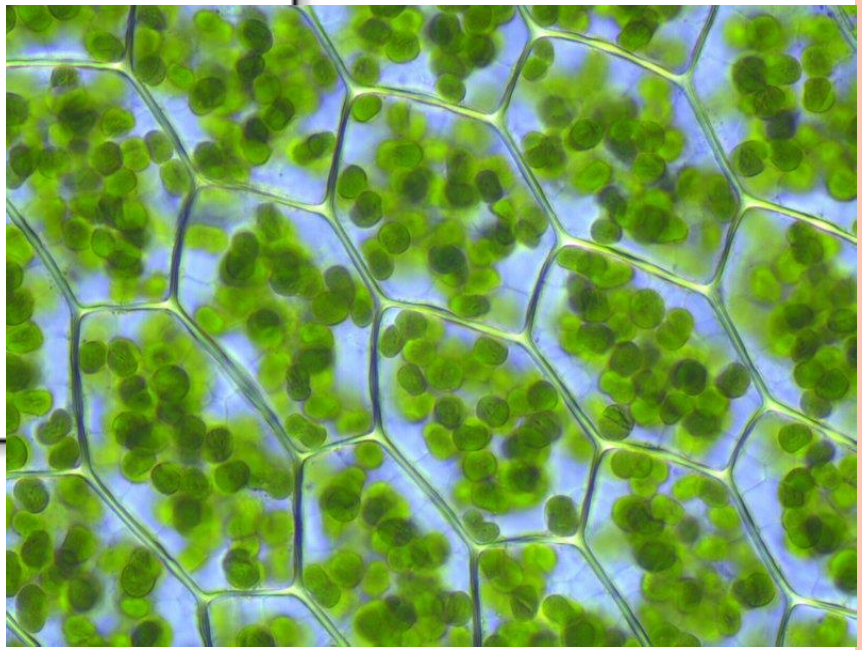
- the process by which plants make sugar from sunlight, water, and carbon dioxide):



- The process that plants, algae and prokaryotes perform by using light energy to synthesize organic compounds is called **photosynthesis**. This is a biological oxidation-reduction (redox) process.

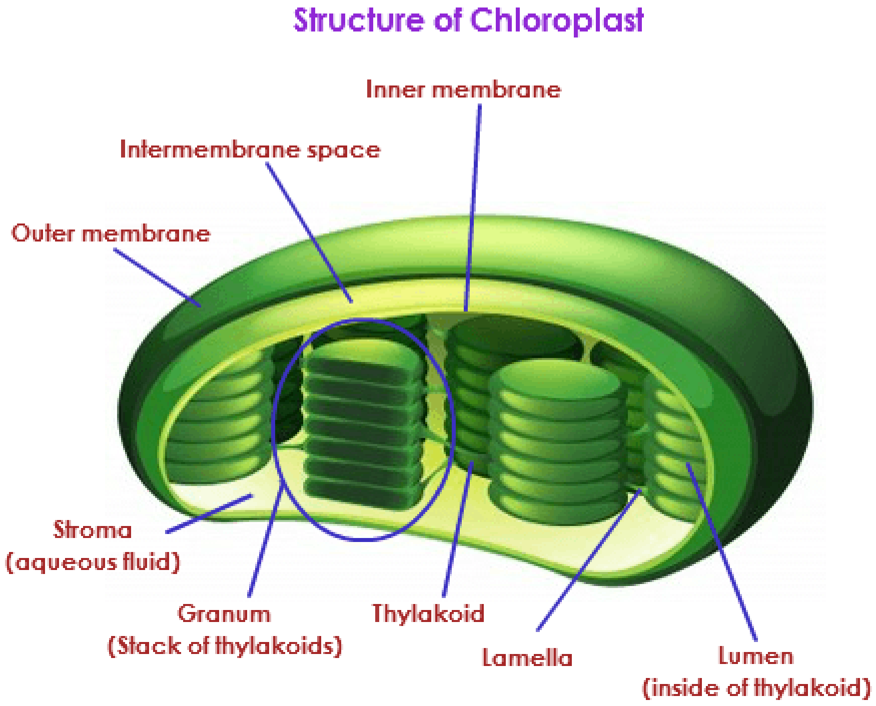
- It compasses a complex series of reactions:
  - light absorption
    - energy conversion
      - electron transfer
        - multistep enzymatic pathway that converts carbon dioxide and water into carbohydrates.


Leaf
Leaf Cross Section
Mesophyll Cell
Mesophyll
Cell wall
Vacuole
Chloroplast
Nucleus
Cytoplasm
Stoma
Starch grain
Thylakoid
Outer membrane
Intermembrane space
Inner membrane
Granum
Stroma
Thylakoid space
Chloroplast



WHAT IS PHOTOSYNTHESIS?

- In eukaryotes, photosynthesis occurs in **chloroplast**, which is a specialized plastid. Chloroplasts from higher plants are surrounded by a double-membrane system that consists of an outer and inner envelope. It also contains an internal membrane system, which is called **thylakoid membrane**. Some thylakoids (**granal thylakoids**) are organized into grana (stacks of apressed membranes) and others (**stromal thylakoids**) are unstacked and therefore exposed to the surrounding fluid membrane (the **chloroplast stroma**).The thylakoid membranes are interconnected and enclose an internal space which is called the **lumen**.



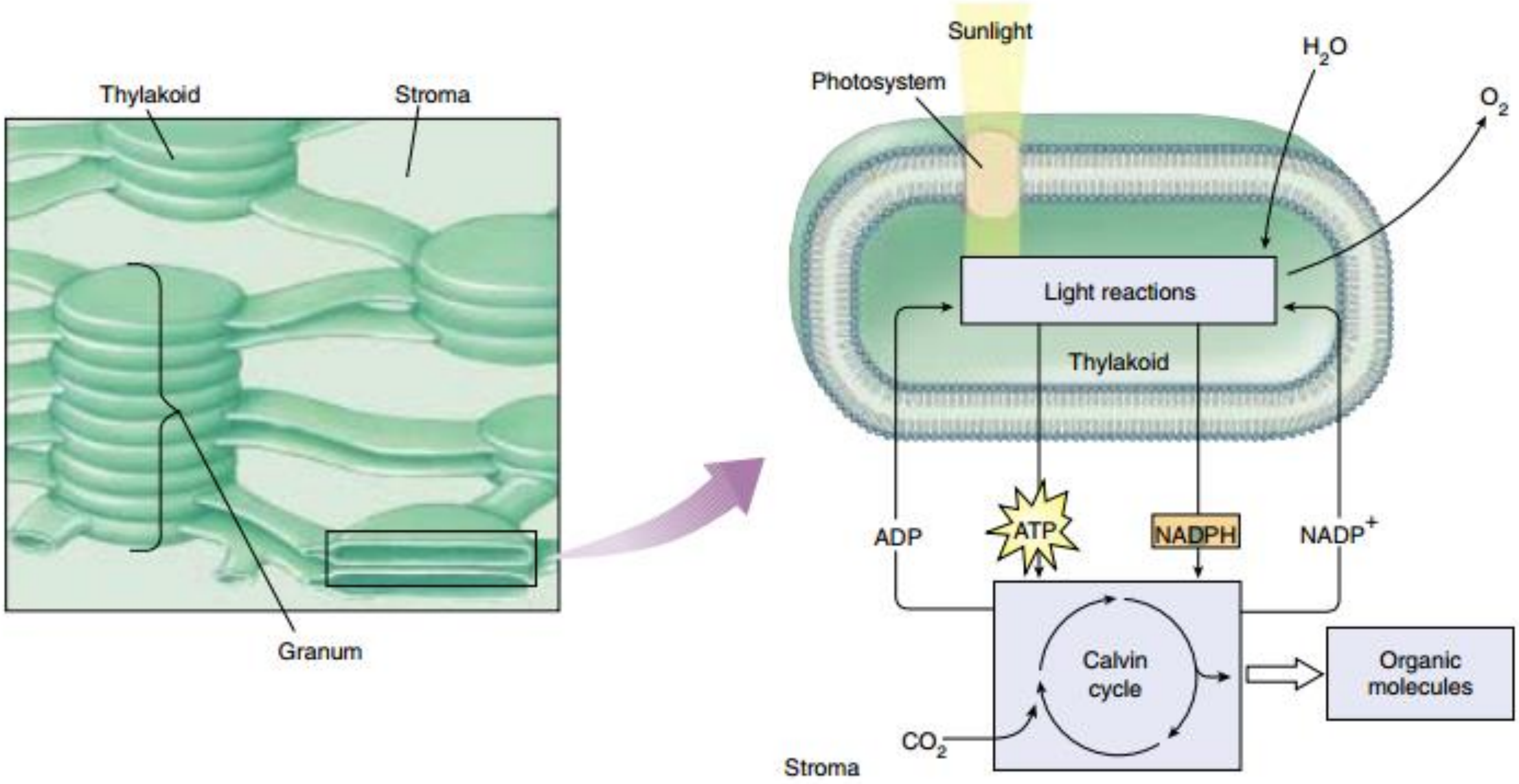


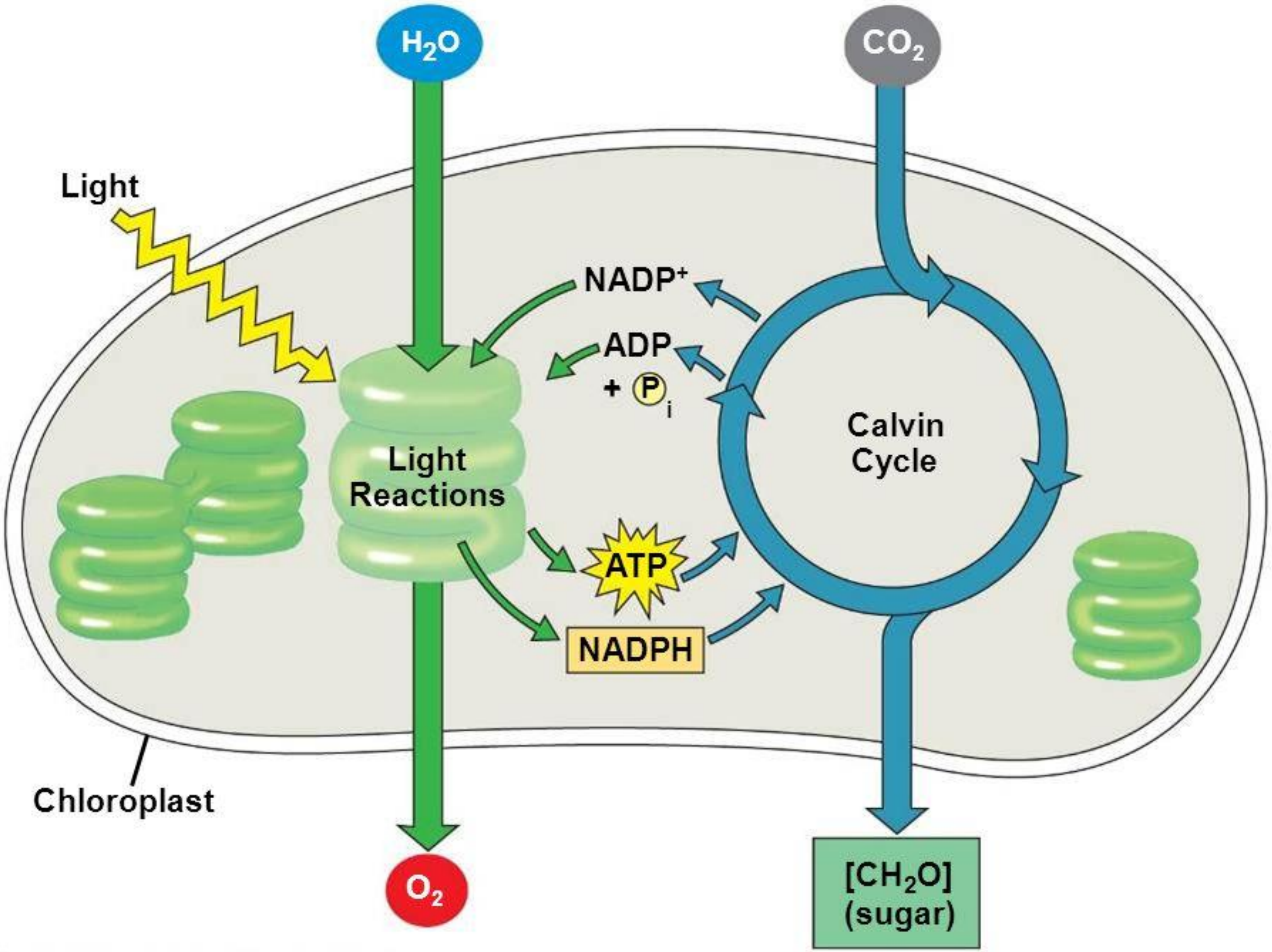
FIGURE 10.2 (continued)
membrane and generate the ATP and NADPH that fuel the Calvin cycle. The fluid interior matrix of a chloroplast, the stroma, contains the enzymes that carry out the Calvin cycle.

The Photosynthetic Process:

Photosynthesis takes place in three stages:

- (1) capturing energy from sunlight;
- (2) using the energy to make ATP (Adenosine triphosphate) and reducing power in the form of a compound called NADPH (Nicotinamide Adenosine Dinucleotide Phosphate); and
- (3) using the ATP and NADPH to power the synthesis of organic molecules from CO_2 in the air (carbon fixation).

In other words, light reactions produce O_2, ATP and NADPH and carbon-linked reactions (Calvin cycle or carbon reduction cycle) reduces CO_2 to carbohydrate and consume the ATP and NADPH produced in the light reactions.



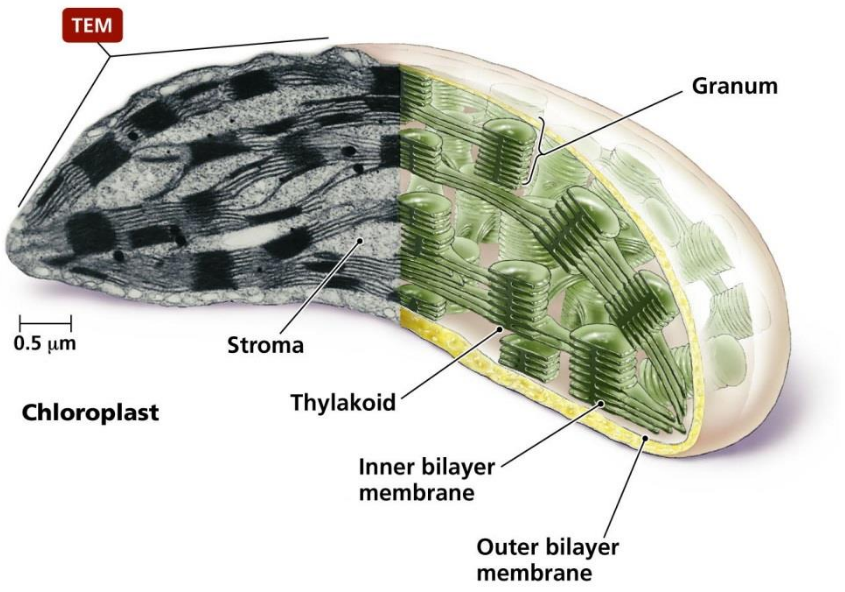
H_2O
CO_2
Light
$NADP^+$
ADP
+ P_i
Light Reactions
Calvin Cycle
ATP
NADPH
Chloroplast
O_2
$[CH_2O]$ (sugar)

- The first two stages take place in the presence of light and are commonly called the light reactions. The third stage, the formation of organic molecules from atmospheric CO_2, is called the Calvin cycle. **As long as ATP and NADPH are available, the Calvin cycle may occur in the absence of light.**

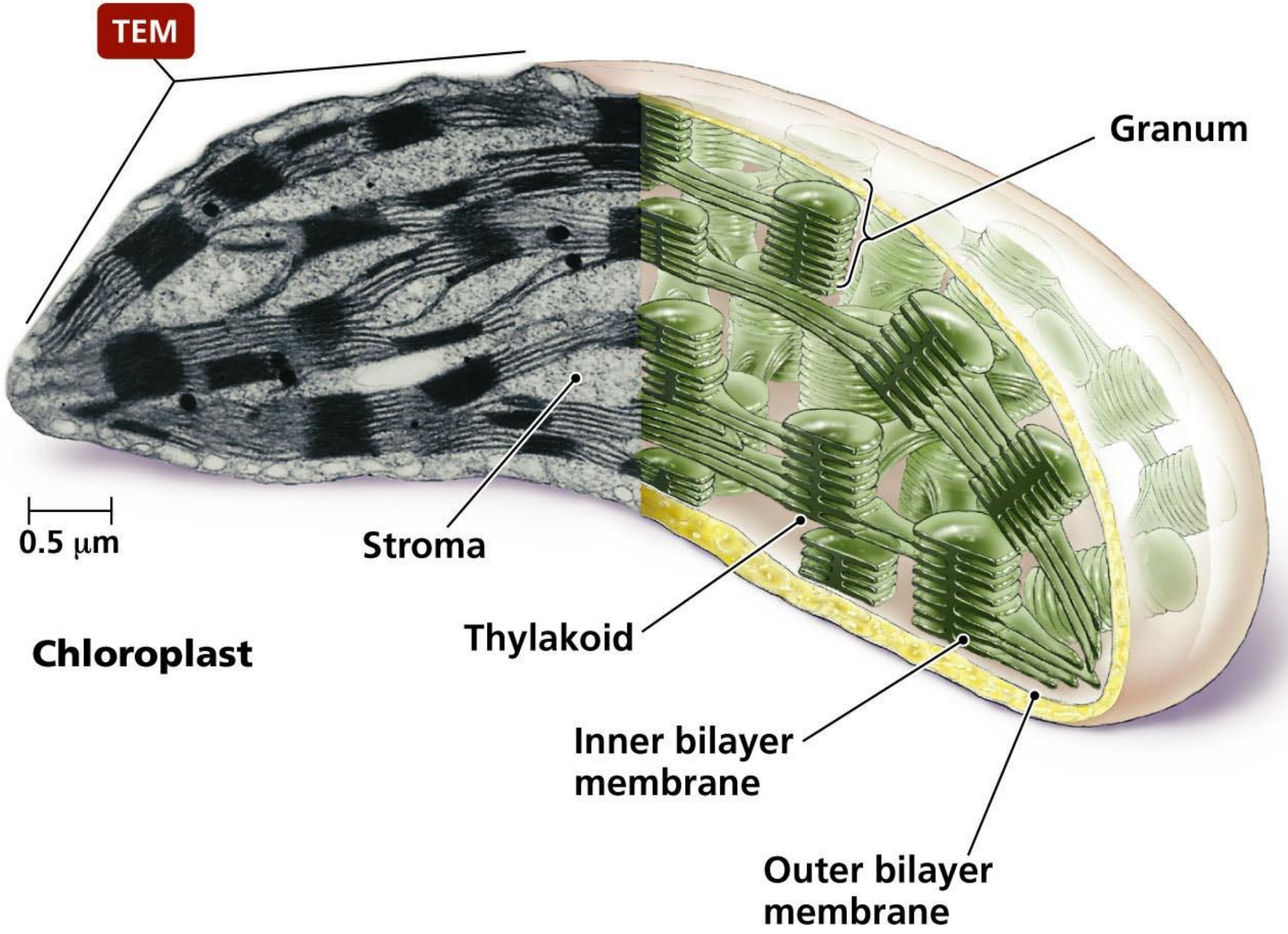
- The following simple equation summarizes the overall process of photosynthesis:

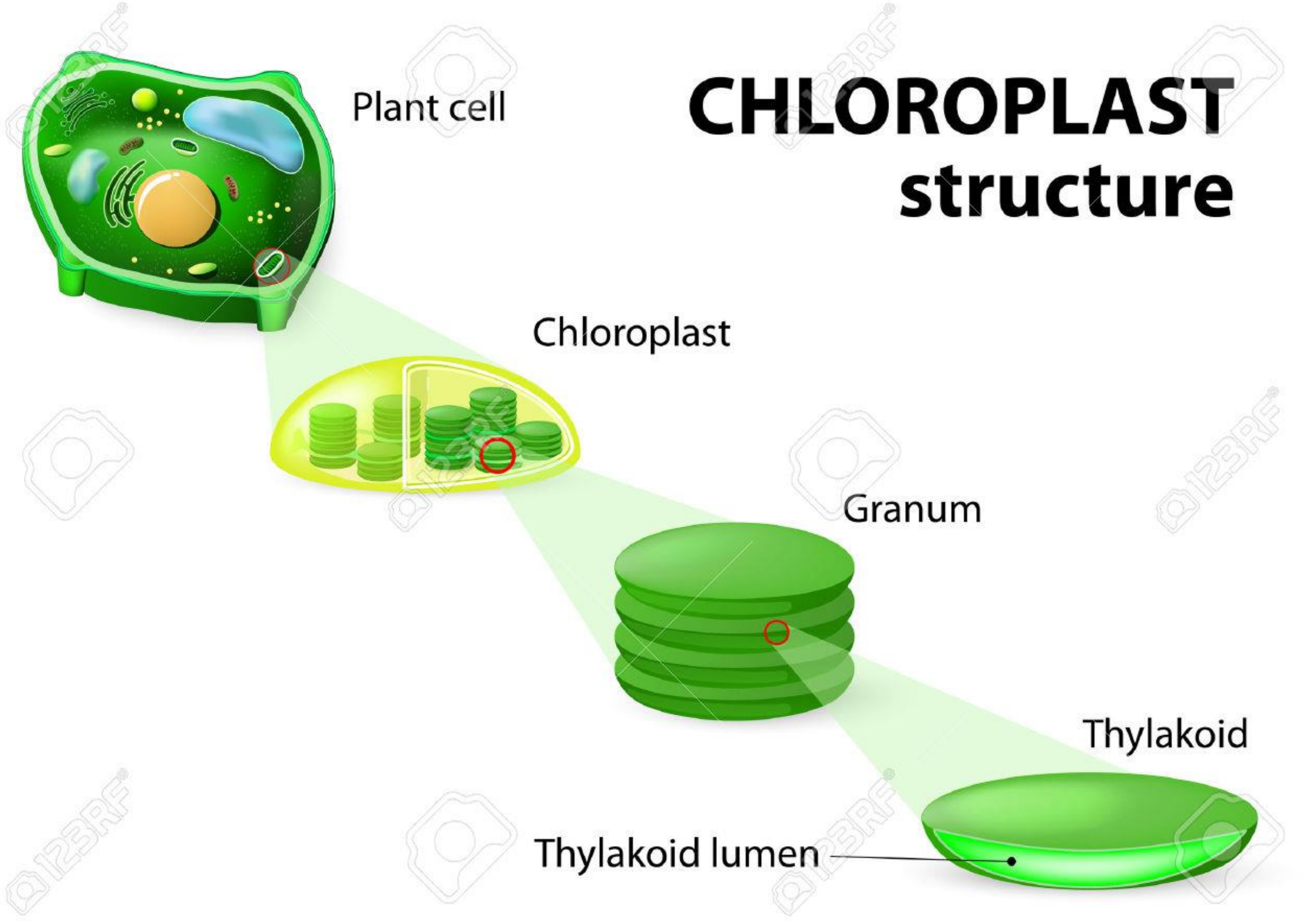
$$\underset{\text{carbon dioxide}}{6\ CO_2} + \underset{\text{water}}{12\ H_2O} + \text{light} \longrightarrow \underset{\text{glucose}}{C_6H_{12}O_6} + \underset{\text{water}}{6\ H_2O} + \underset{\text{oxygen}}{6\ O_2}$$

- Inside the Chloroplast The internal membranes of chloroplasts are organized into sacs called **thylakoids,** and often numerous thylakoids are stacked on one another in columns called **grana**. The thylakoid membranes house the photosynthetic pigments for capturing light energy and the machinery to make ATP.

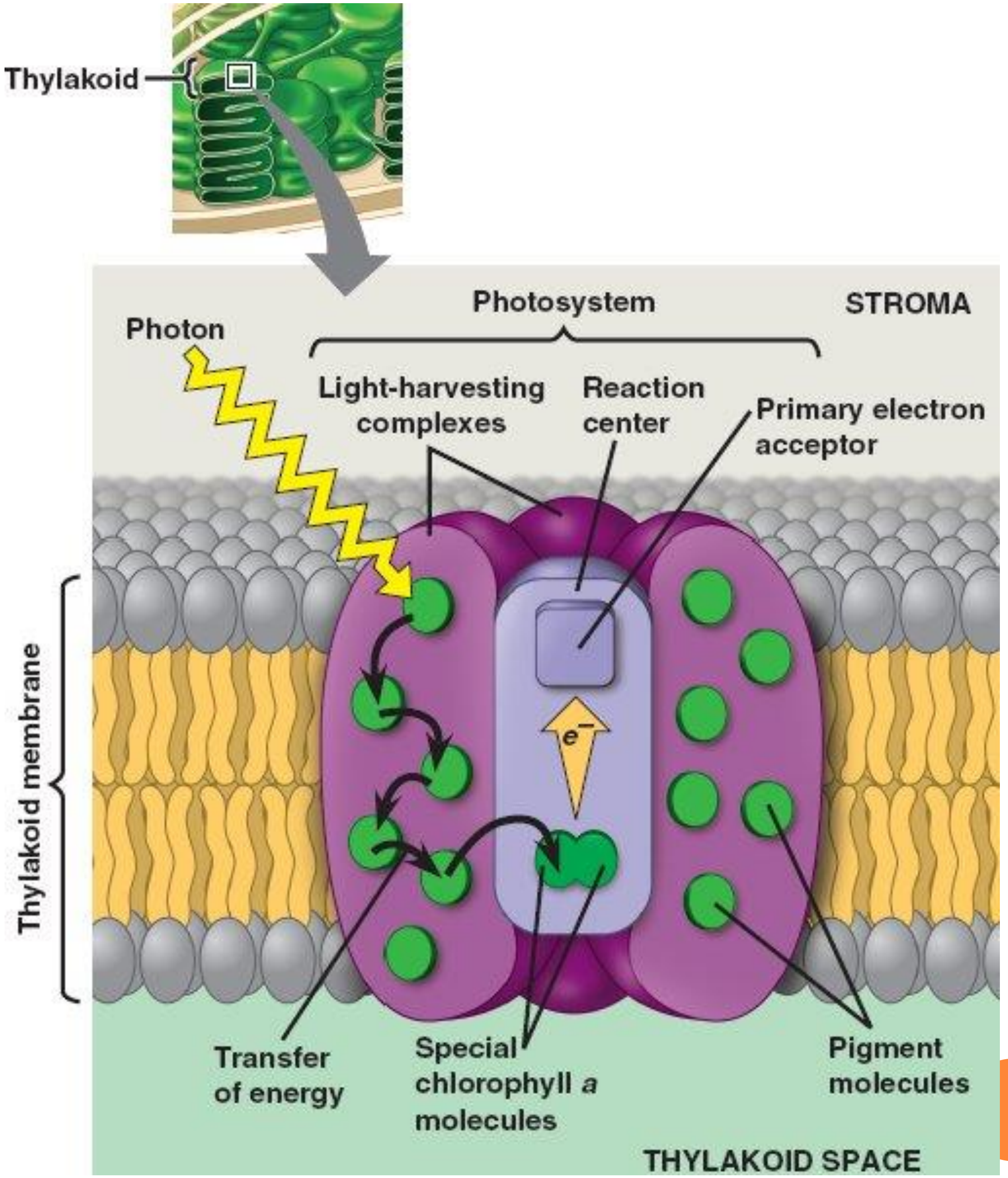


- Surrounding the thylakoid membrane system is a semiliquid substance called **stroma.** The stroma houses the enzymes needed to assemble carbon molecules. In the membranes of thylakoids, photosynthetic pigments are clustered together to form a photosystem.




CHLOROPLAST
structure
Plant cell
Chloroplast
Granum
Thylakoid
Thylakoid lumen

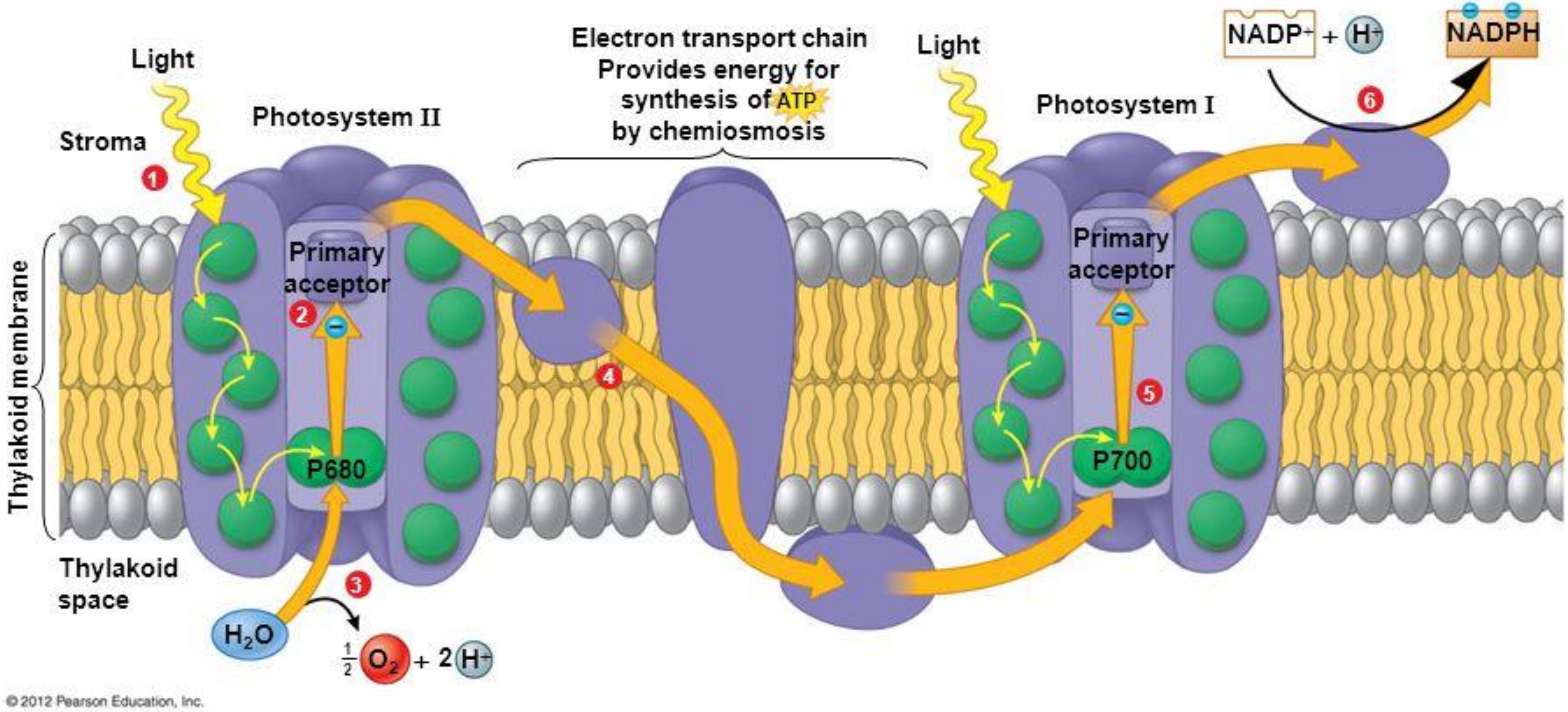
- Each pigment molecule within the photosystem is capable of capturing **photons**, which are packets of energy. A lattice of proteins holds the pigments in close contact with one another. When light of a proper wavelength strikes a pigment molecule in the photosystem, the resulting excitation passes from one chlorophyll molecule to another.
- The excited electron is not transferred physically—it is the energy that passes from one molecule to another.



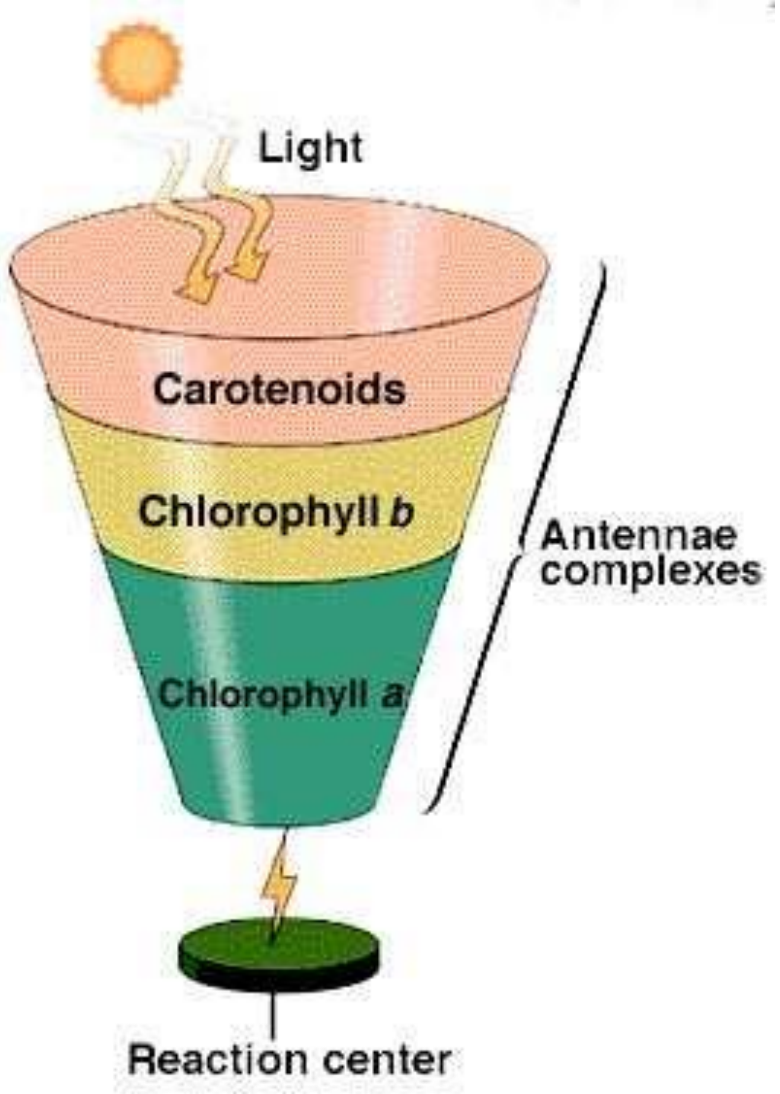
Photosystem I and II

- Thylakoid membranes contain the multiprotein photosynthetic complexes: **photosystem I and II** (PSI and PSII). These include the reaction centers responsible for converting light energy into chemical bond energy. These reaction centers are a part of a photosynthetic electron transfer chain which moves electrons from water in the thylakoid lumen to soluble redox-active compounds in the stroma (e.g. $NADP^+$).

- Photosystem II (P680) - oxidizes H_2O
- Photosystem I (P700) - reduces $NADP^+$

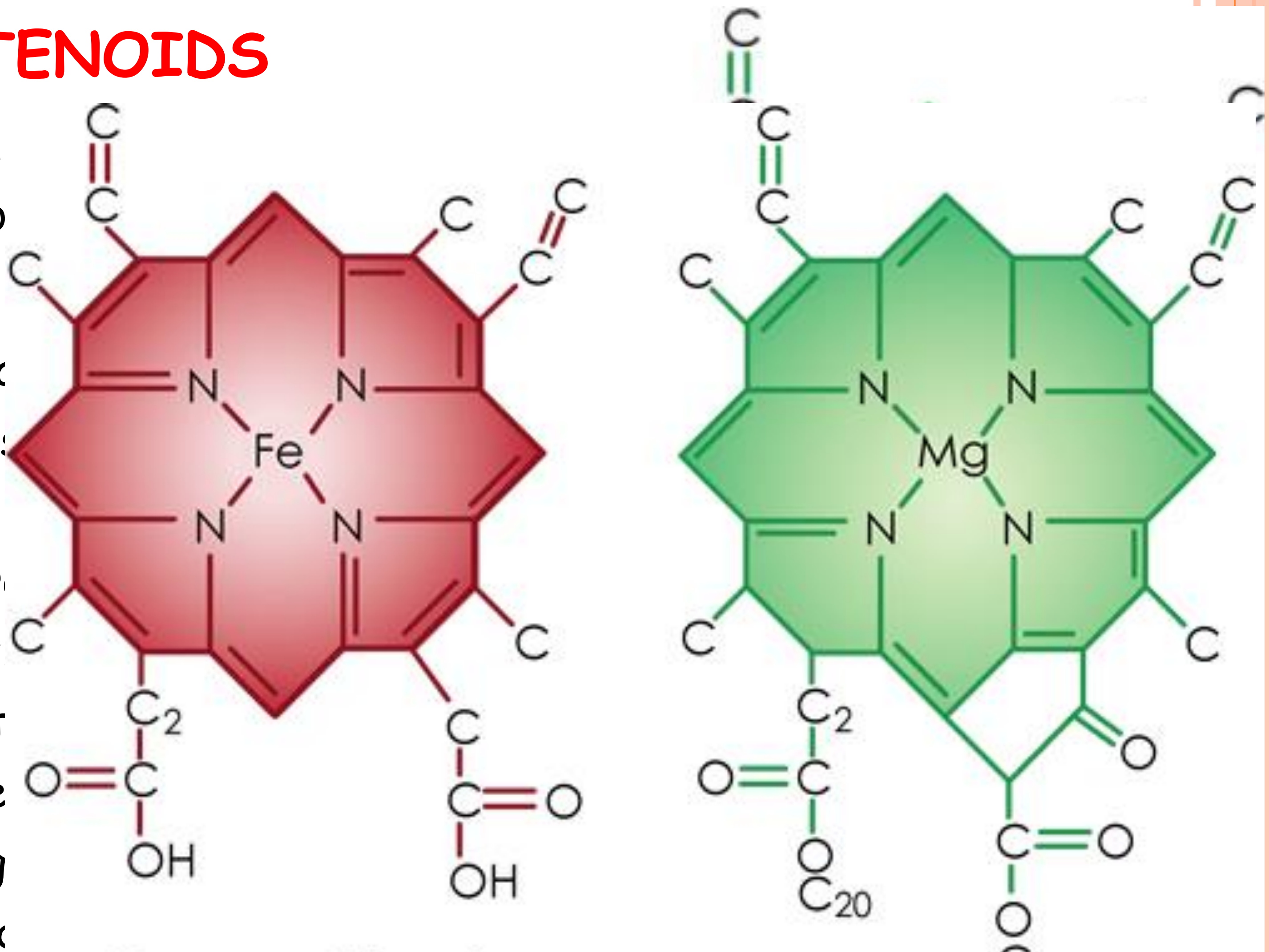


- Eventually the energy arrives at a key chlorophyll molecule that is touching a membrane-bound protein. The energy is transferred as an excited electron to that protein, which passes it on to a series of other membrane proteins that put the energy to work making ATP and NADPH and building organic molecules. The photosystem thus acts as a large antenna, gathering the light harvested by many individual pigment molecules.



Chlorophylls and Carotenoids

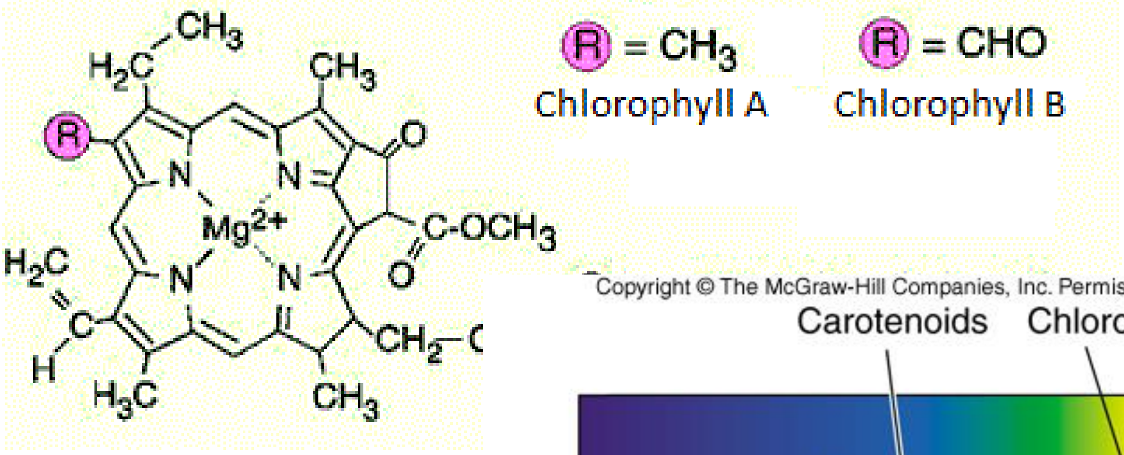
- For light energy to be used by any system be absorbed. And molecules that abso pigments.
- Chlorophylls absorb photons by means of analogous to the photoelectric effect. The complex ring structure, called a porphyrin single and double bonds. At the centr magnesium atom. Photons absorbed by t excite electrons in the ring, which are t through the alternating carbon-bond syste groups attached to the outside of the ring properties of the molecule in different kin
- The precise absorption spectrum is also inf microenvironment created by the associati with specific proteins.

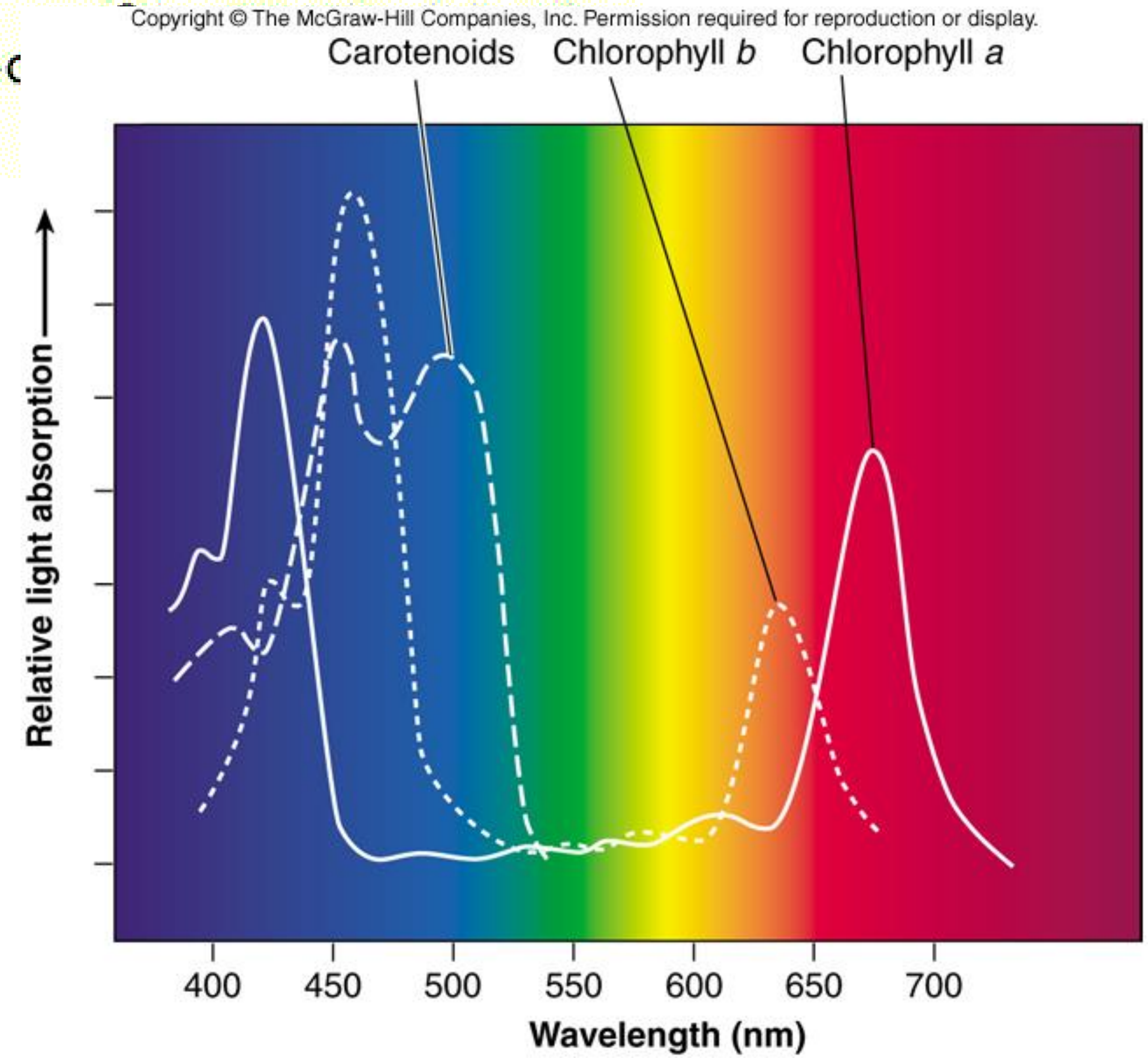


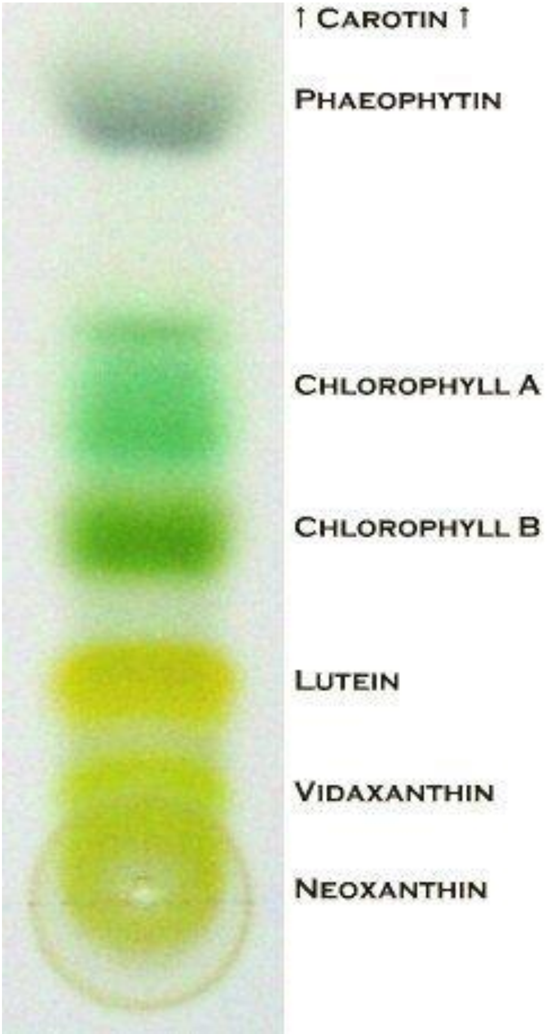
Human Blood Hemoglobin

Plant Chlorophyll

Chlorophyll a is bluish-green colored and chlorophyll b is yellowish-green colored. In nature, chlorophyll a is found **3 times more** than chlorophyll b.

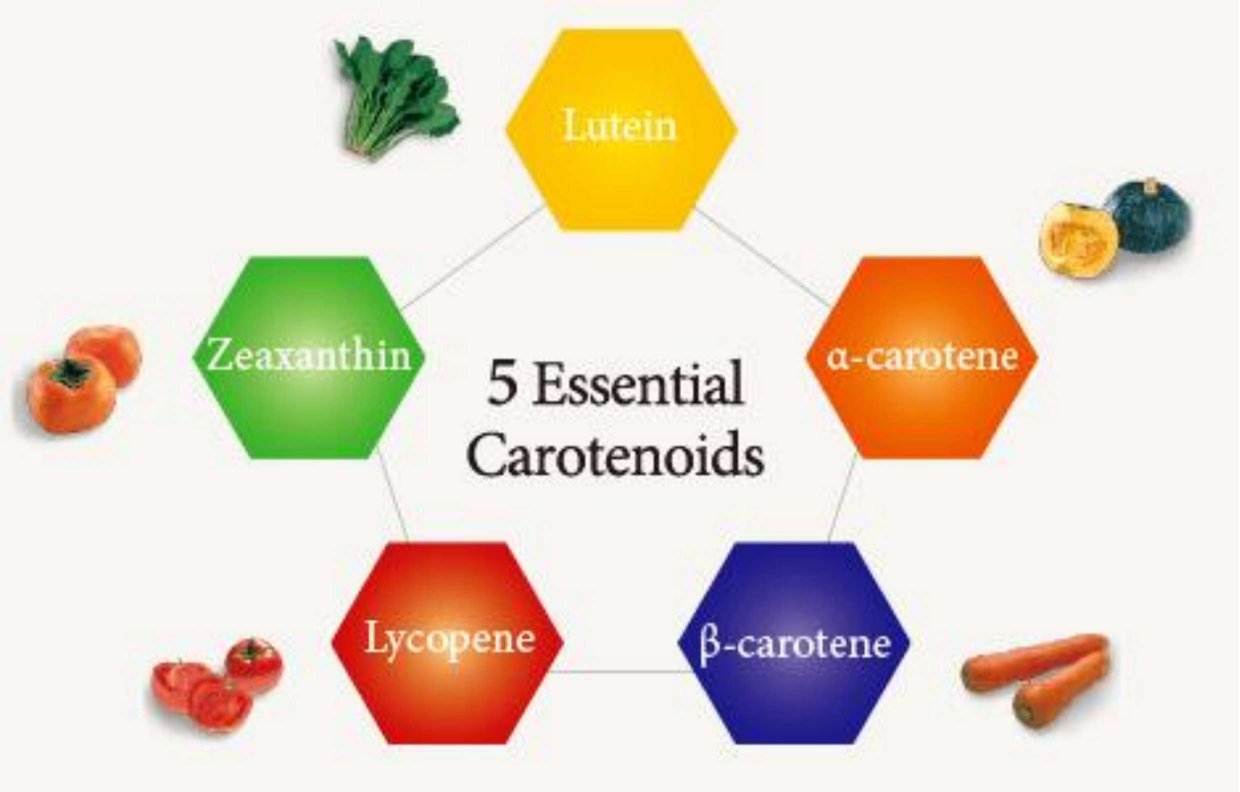


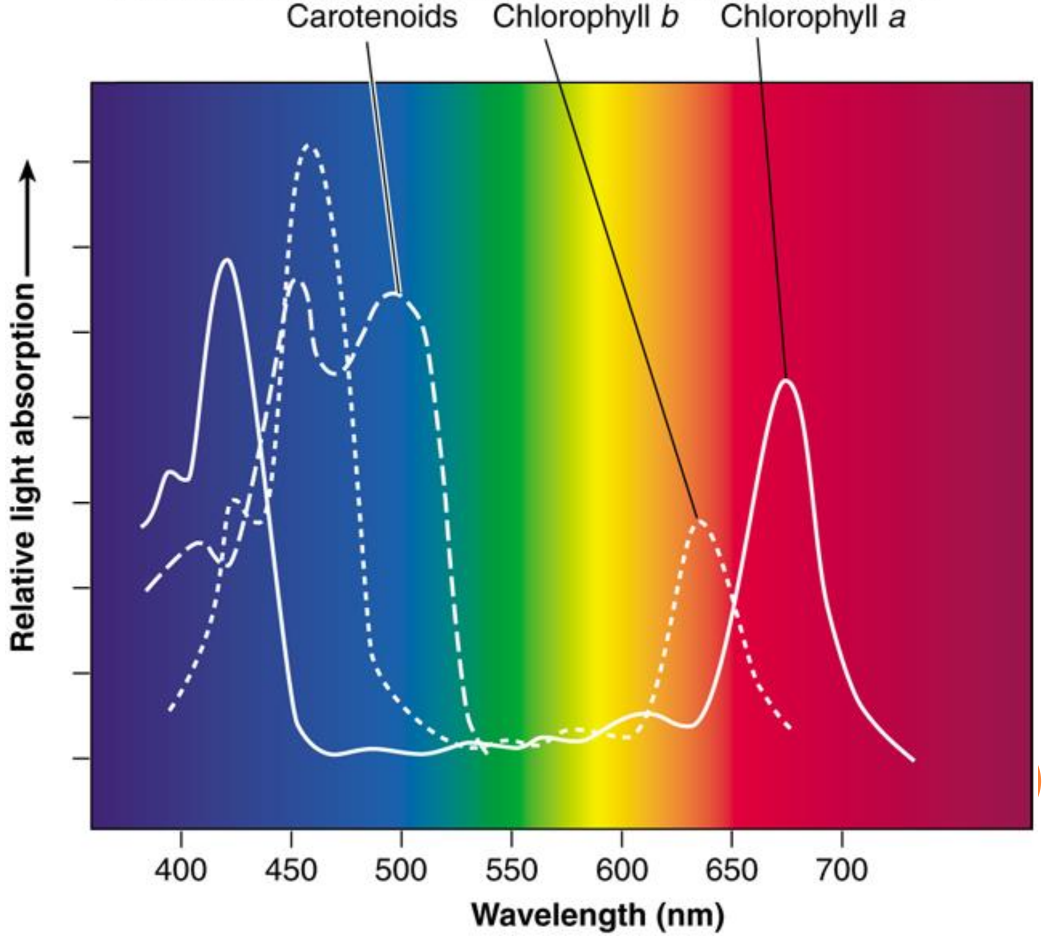




- All plants, algae, and cyanobacteria use chlorophyll a as their primary pigments. It is reasonable to ask why these photosynthetic organisms do not use a pigment like retinal (the pigment in our eyes), which has a broad absorption spectrum that covers the range of 500 to 600 nanometers. The most likely hypothesis involves photoefficiency. Although retinal absorbs a broad range of wavelengths, it does so with relatively low efficiency. Chlorophyll, in contrast, absorbs in only two narrow bands, but does so with high efficiency. Therefore, plants and most other photosynthetic organisms achieve far higher overall photon capture rates with chlorophyll than with other pigments.

- Carotenoids consist of carbon rings linked to chains with alternating single and double bonds. They can absorb photons with a wide range of energies, although they are not always highly efficient in transferring this energy. Carotenoids assist in photosynthesis by capturing energy from light of wavelengths that are not efficiently absorbed by chlorophylls.





Classification of Carotenoids

CAROTENES

- Oxygen free Carotenoids which contains only carbon & Hydrogen.
- Readily soluble in petroleum Ether & hexane.
- Found in carrots, Apricots & gives bright orange colour.
- E.g Lycopene, β Carotene

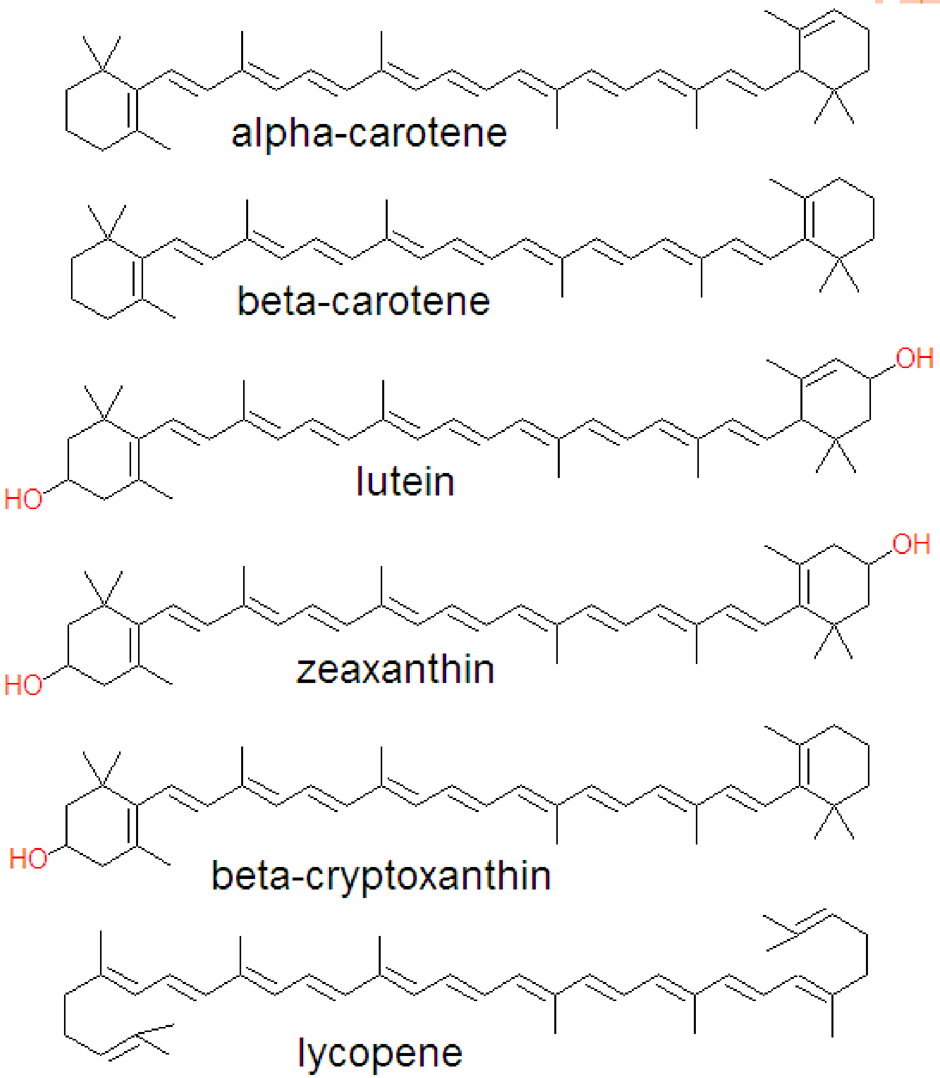
XANTHOPHYLLS

- Contains 1 or more O2 atoms and functions like hydroxy, epoxy, keto, carboxy and methoxy groups.
- Dissolve best in Methanol & Ethanol.
- Generally yellow in colour.
- E.g Lutein, Zeaxanthin

Carotenoids…

- The word carotenoid has its origin in Daucus carota, the Latin name of the carrot from which beta-carotene was first extracted and isolated in 1831
- The carotenoids is a family of more than 750 molecules (Maoka, 2009) without which there could be no life in nature. They are responsible, in particular, for the colouring of fruits, vegetables and flowers.
- Nature produces more than 3 tonnes every second from plants, microorganisms
- Animals get carotenoids from the diets

- A typical carotenoid is β-carotene, whose two carbon rings are connected by a chain of 18 carbon atoms with alternating single and double bonds. Splitting a molecule of β-carotene into equal halves produces two molecules of vitamin A.
- Oxidation of vitamin A produces retinal, the pigment* used in vertebrate vision. This explains why carrots, which are rich in β-carotene, enhance vision. The wavelengths absorbed by a particular pigment depend on the available energy levels to which light-excited electrons can be boosted in the pigment.



*A pigment is a molecule that absorbs light.

How Photosystems Convert Light to Chemical Energy

- Bacteria Use a Single Photosystem Photosynthetic pigment arrays are thought to have evolved more than 3 billion years ago in bacteria similar to the sulphur bacteria studied by van Niel.

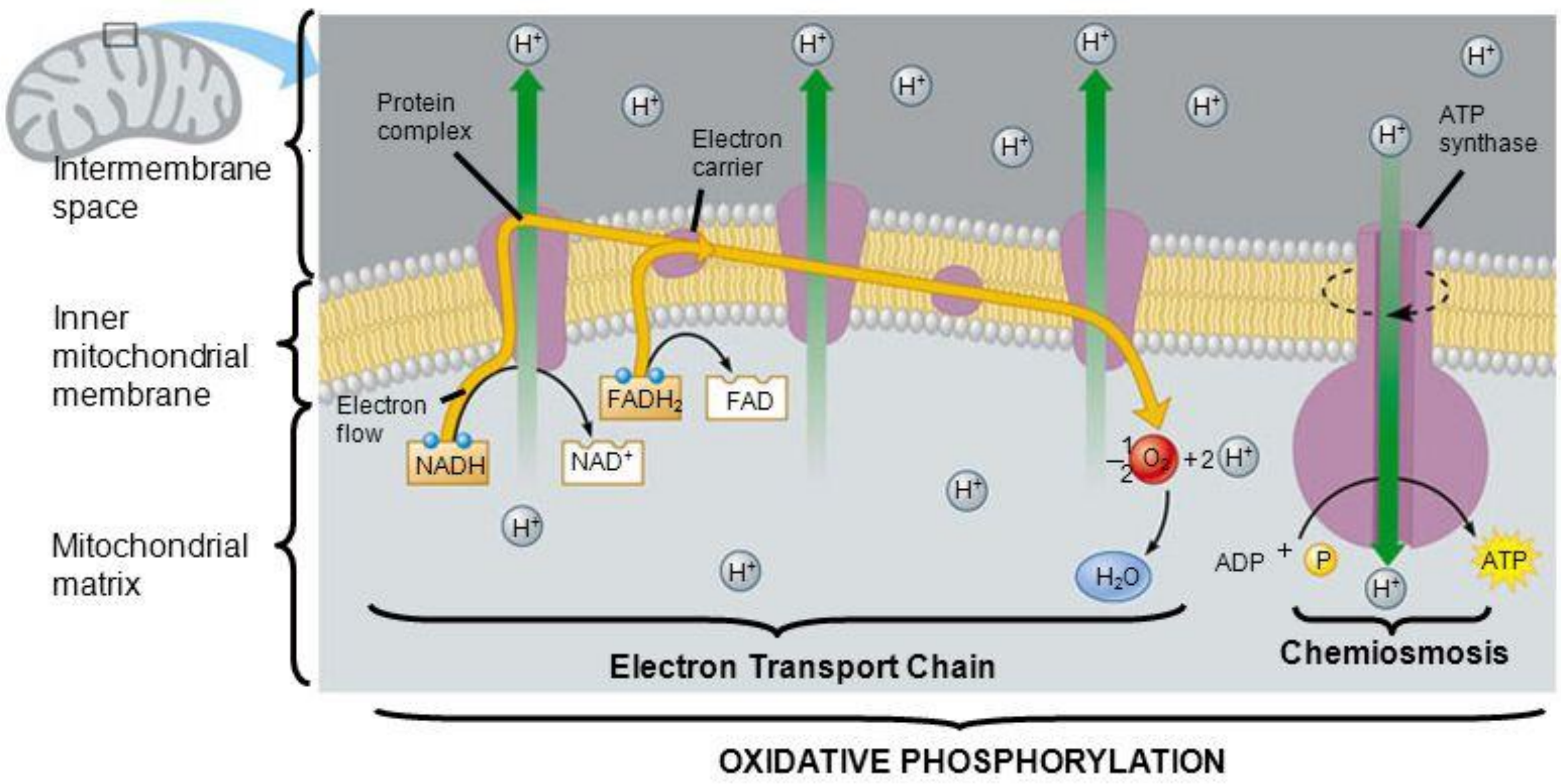
1. Electron is joined with a proton to make hydrogen. In these bacteria, the absorption of a photon of light at a peak absorption of 870 nanometers (near infrared, not visible to the human eye) by the photosystem results in the transmission of an energetic electron along an electron transport chain, eventually combining with a proton to form a hydrogen atom. In the sulphur bacteria, the proton is extracted from hydrogen sulphide, leaving elemental sulphur as a by-product. In bacteria that evolved later, as well as in plants and algae, the proton comes from water, producing oxygen as a by-product.

2. Electron is recycled to chlorophyll

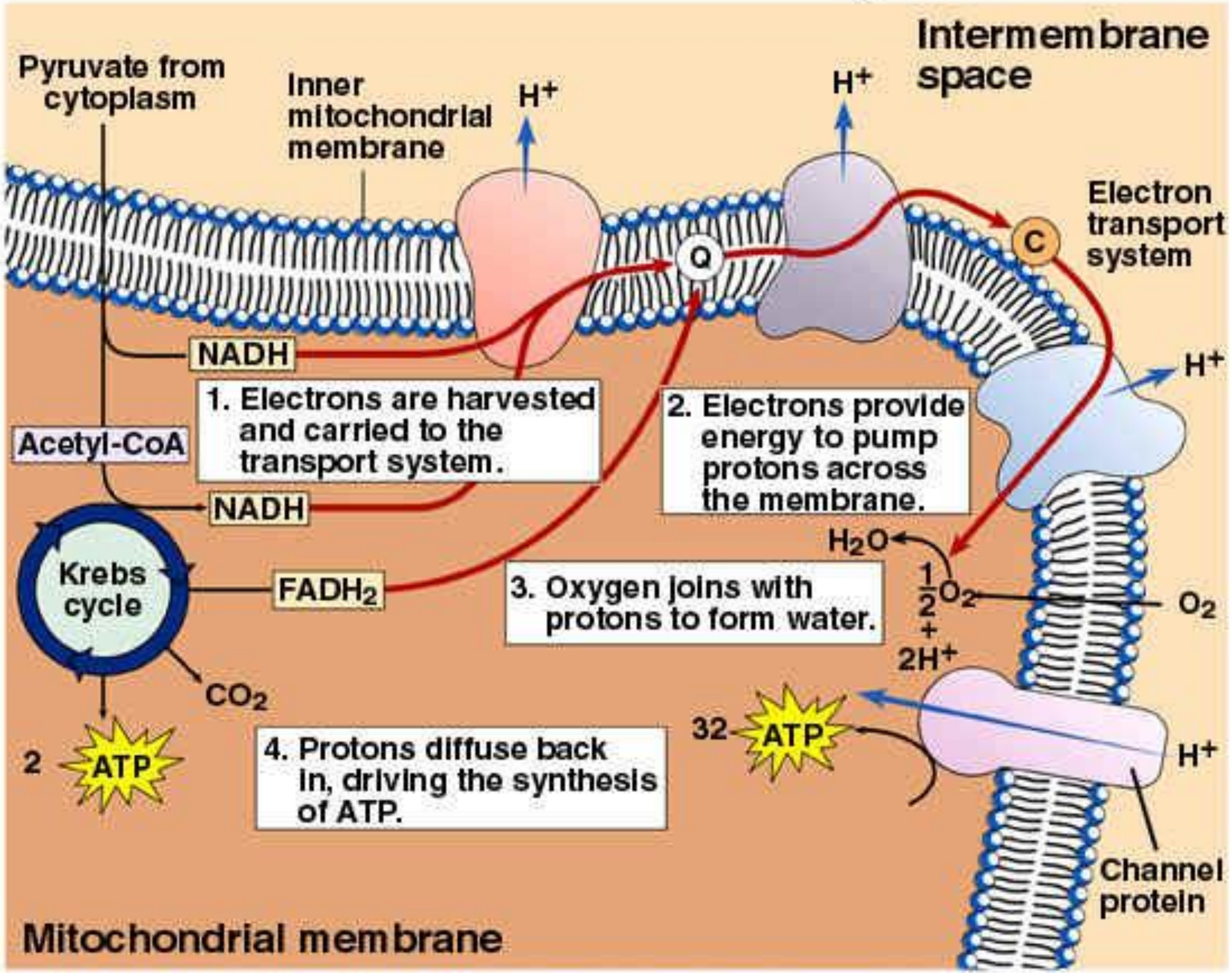
- The ejection of an electron from the bacterial reaction centre leaves it short one electron. Before the photosystem of the sulphur bacteria can function again, an electron must be returned. These bacteria channel the electron back to the pigment through an electron transport; the electron's passage drives a proton pump that promotes the chemiosmotic synthesis of ATP.
- One molecule of ATP is produced for every three electrons that follow this path. Viewed overall, the path of the electron is thus a circle. Chemists therefore call the electron transfer process leading to ATP formation cyclic photophosphorylation.
- Note, however, that the electron that left the P870 reaction centre was a high-energy electron, boosted by the absorption of a photon of light, while the electron that returns has only as much energy as it had before the photon was absorbed.
- The difference in the energy of that electron is the photosynthetic payoff, the energy that drives the proton pump.

Chemiosmosis

- In chemiosmosis, the H^+ diffuses back through the inner membrane through ATP synthase complexes. Driving the synthesis of ATP



Overview of ATP Synthesis



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- For more than a billion years, cyclic photophosphorylation was the only form of photosynthetic light reaction that organisms used. However, its major limitation is that it is geared only toward energy production, not toward biosynthesis. Most photosynthetic organisms incorporate atmospheric carbon dioxide into carbohydrates. Because the carbohydrate molecules are more reduced (have more hydrogen atoms) than carbon dioxide, a source of reducing power (that is, hydrogens) must be provided. Cyclic photophosphorylation does not do this. The hydrogen atoms extracted from H_2S are used as a source of protons, and are not available to join to carbon. Thus bacteria that are restricted to this process must scavenge hydrogens from other sources, an inefficient undertaking.

Why Plants Use Two Photosystems

- After the appearance of sulphur bacteria, other kinds of bacteria developed an improved version of the photosystem that overcame the limitation of cyclic photophosphorylation in a neat and simple way: a second, more powerful photosystem using another arrangement of chlorophyll a was combined with the original.

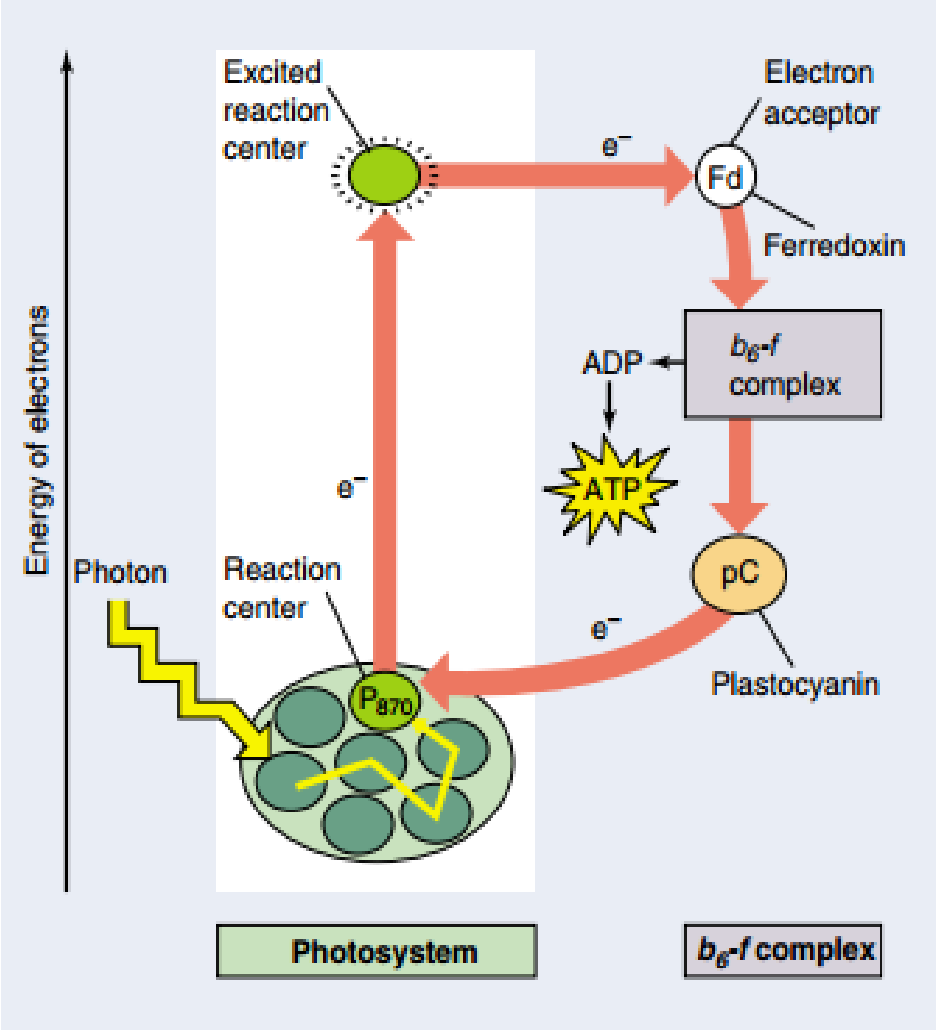
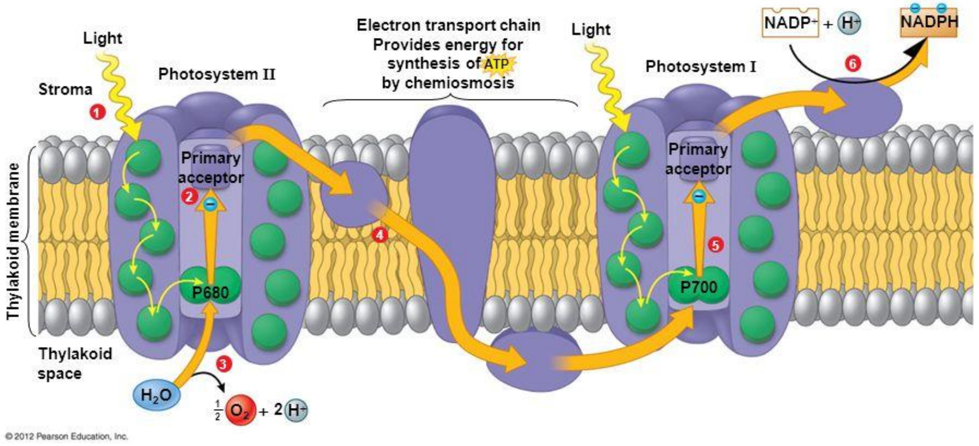


FIGURE 10.12

- In this second photosystem, called photosystem II, molecules of chlorophyll a are arranged with a different geometry, so that more shorter wavelength, higher energy photons are absorbed than in the ancestral photosystem, which is called photosystem I.
- As in the ancestral photosystem, energy is transmitted from one pigment molecule to another within the antenna complex of these photosystems until it reaches the reaction center, a particular pigment molecule positioned near a strong membrane-bound electron acceptor.

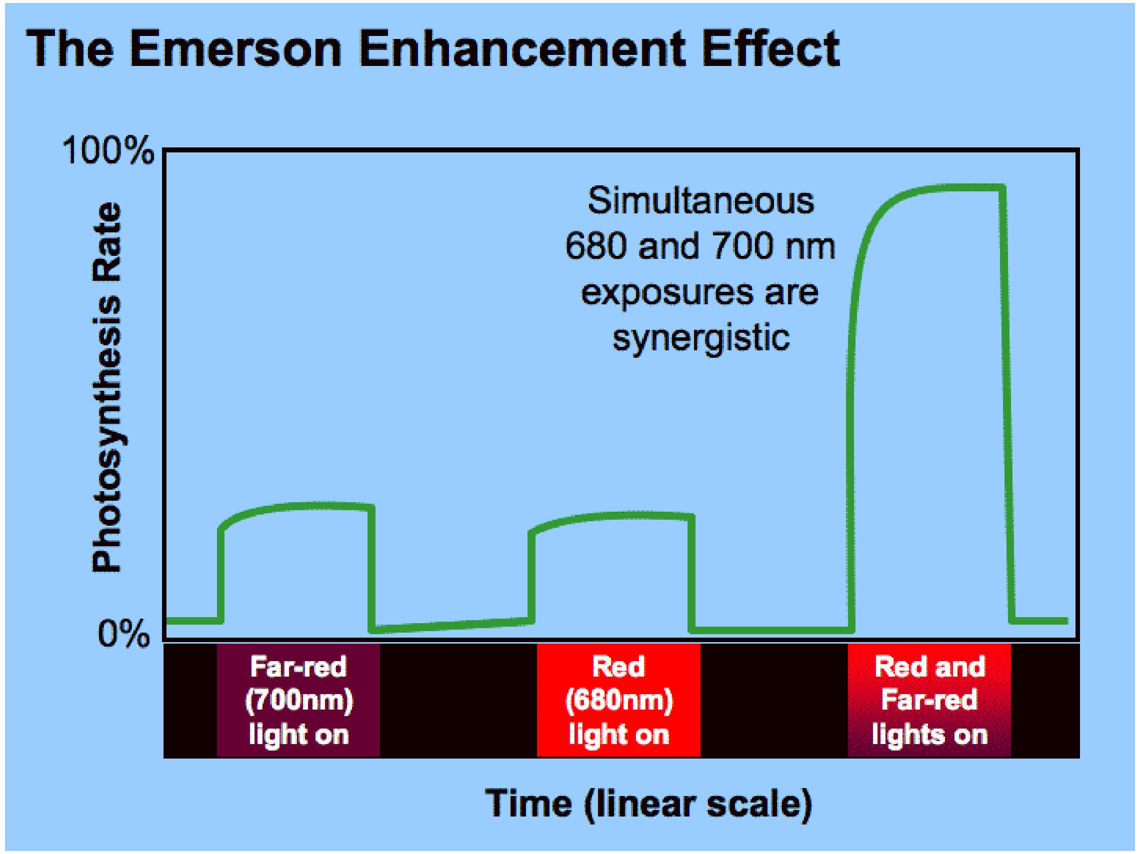
7.7 Two Photosystems Cooperate in the Light Reactions

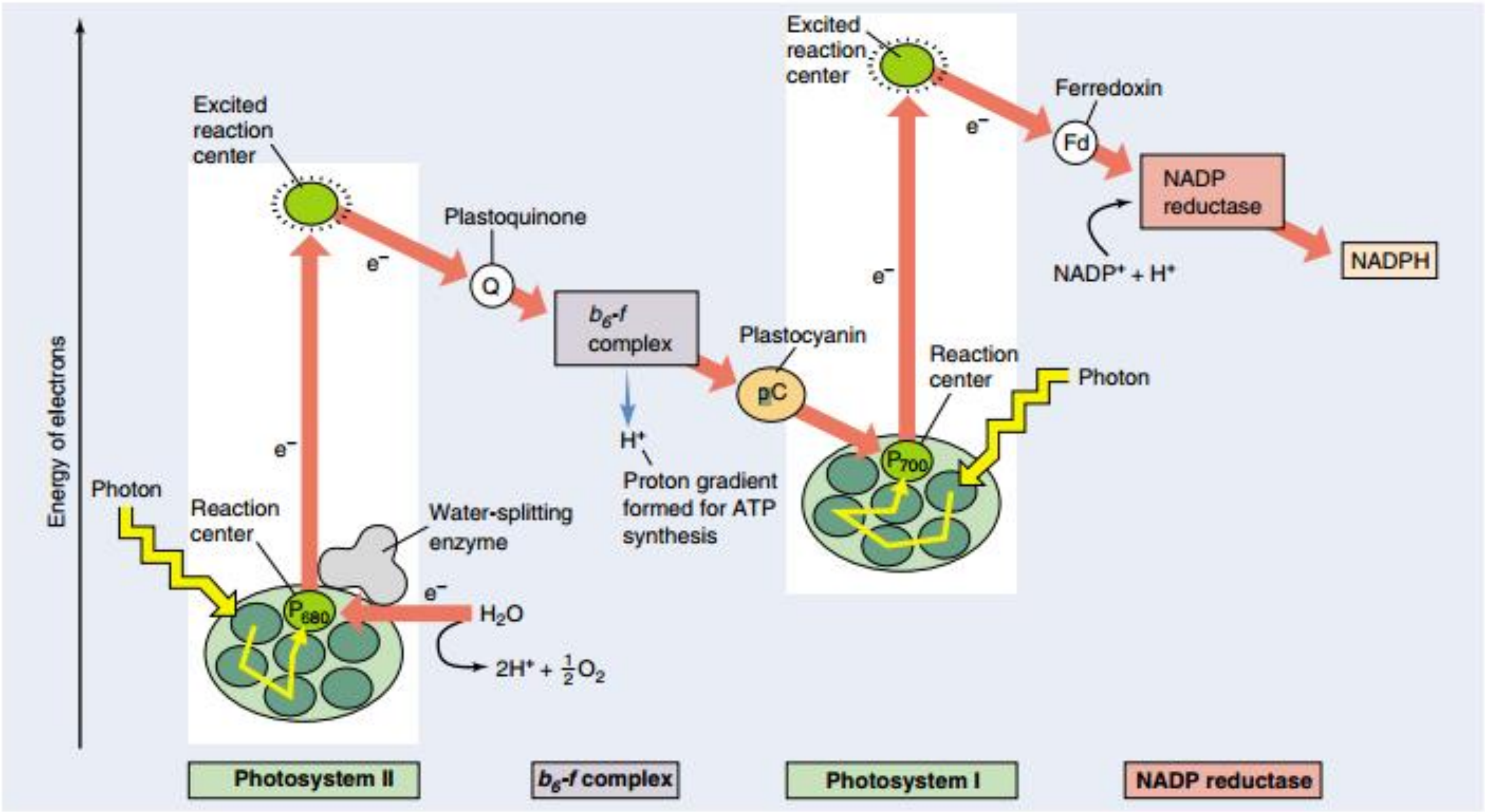
- Photosystem II (P680) - oxidizes H_2O
- Photosystem I (P700) - reduces $NADP^+$



- In photosystem II, the absorption peak (that is, the wavelength of light most strongly absorbed) of the pigments is approximately 680 nanometers; therefore, the reaction center pigment is called P680.
- The absorption peak of photosystem I pigments in plants is 700 nanometers, so its reaction center pigment is called P700. Working together, the two photosystems carry out a noncyclic electron transfer.

- When the rate of photosynthesis is measured using two light beams of different wavelengths (one red and the other far-red), the rate was greater than the sum of the rates using individual beams of red and far-red light. This surprising result, called the enhancement effect, can be explained by a mechanism involving two photosystems acting in series (that is, one after the other), one of which absorbs preferentially in the red, the other in the far-red.

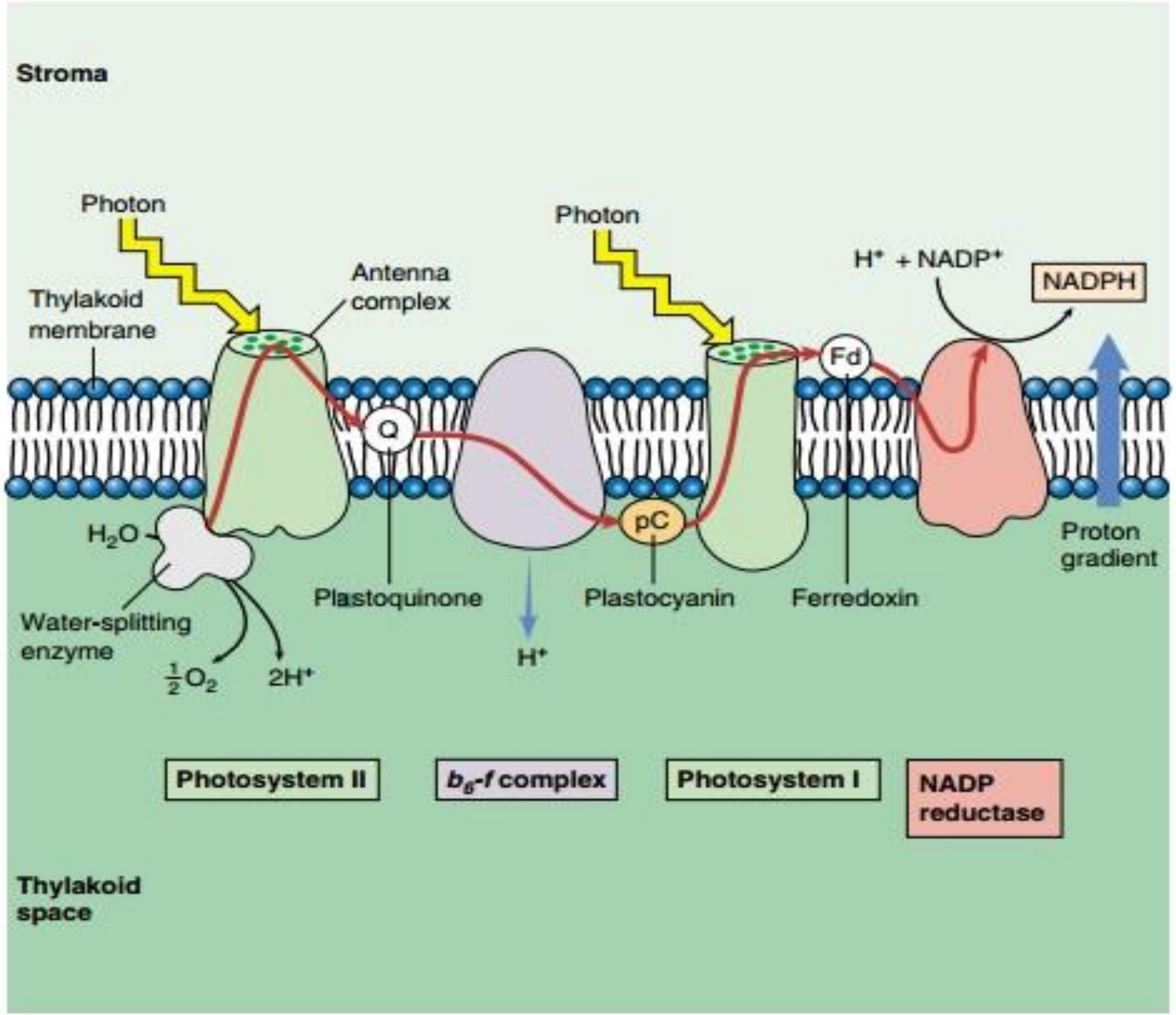




Energy of electrons
Excited reaction center
Plastoquinone
Q
e^-
b_6-f complex
H^+
Proton gradient formed for ATP synthesis
Plastocyanin
pC
Photon
Reaction center
P_{680}
Water-splitting enzyme
H_2O
$2H^+ + \frac{1}{2}O_2$
Excited reaction center
Ferredoxin
Fd
NADP reductase
$NADP^+ + H^+$
NADPH
Reaction center
P_{700}
Photon
Photosystem II
b_6-f complex
Photosystem I
NADP reductase

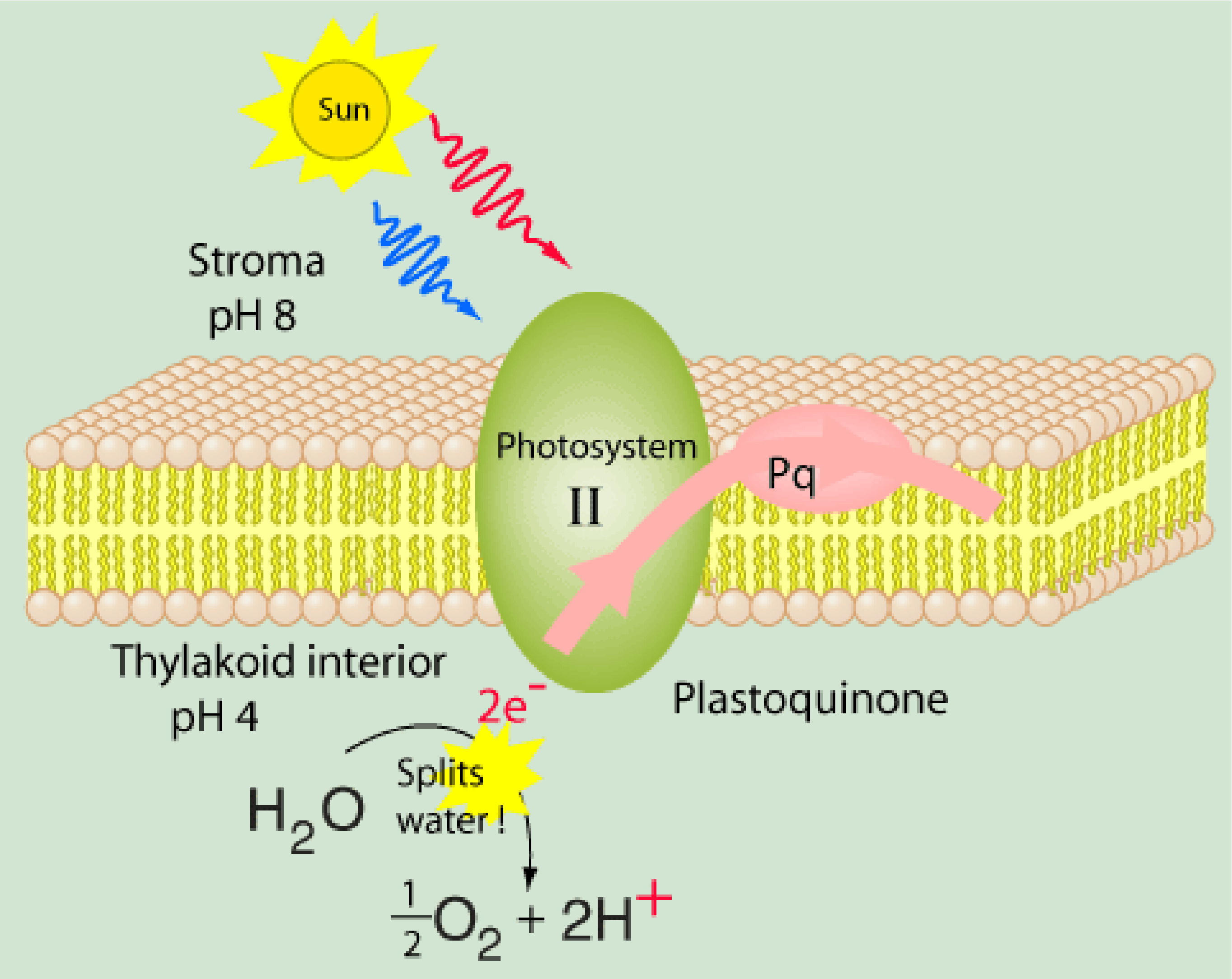
How the Two Photosystems of Plants Work Together

- Plants use the two photosystems discussed earlier in series, first one and then the other, to produce both ATP and NADPH. This two-stage process is called noncyclic photophosphorylation, because the path of the electrons is not a circle—the electrons ejected from the photosystems do not return to it, but rather end up in NADPH. The photosystems are replenished instead with electrons obtained by splitting water. Photosystem II acts first. High-energy electrons generated by photosystem II are used to synthesize ATP and then passed to photosystem I to drive the production of NADPH. For every pair of electrons obtained from water, one molecule of NADPH and slightly more than one molecule of ATP are produced.


Stroma
Photon
Photon
Antenna complex
Thylakoid membrane
$H^+ + NADP^+$
NADPH
Fd
Q
pC
H_2O
Plastoquinone
Plastocyanin
Ferredoxin
Proton gradient
Water-splitting enzyme
$\frac{1}{2}O_2$
$2H^+$
H^+
Photosystem II
b_6-f complex
Photosystem I
NADP reductase
Thylakoid space

Photosystem II

- The reaction centre of photosystem II, called P680, closely resembles the reaction centre of purple bacteria. It consists of more than 10 transmembrane protein subunits. The light-harvesting antenna complex consists of some 250 molecules of chlorophyll a and accessory pigments bound to several protein chains. In photosystem II, the oxygen atoms of two water molecules bind to a cluster of manganese atoms which are embedded within an enzyme and bound to the reaction centre. In a way that is poorly understood, this enzyme splits water, removing electrons one at a time to fill the holes left in the reaction centre by departure of light-energized electrons. As soon as four electrons have been removed from the two water molecules, O_2 is released.

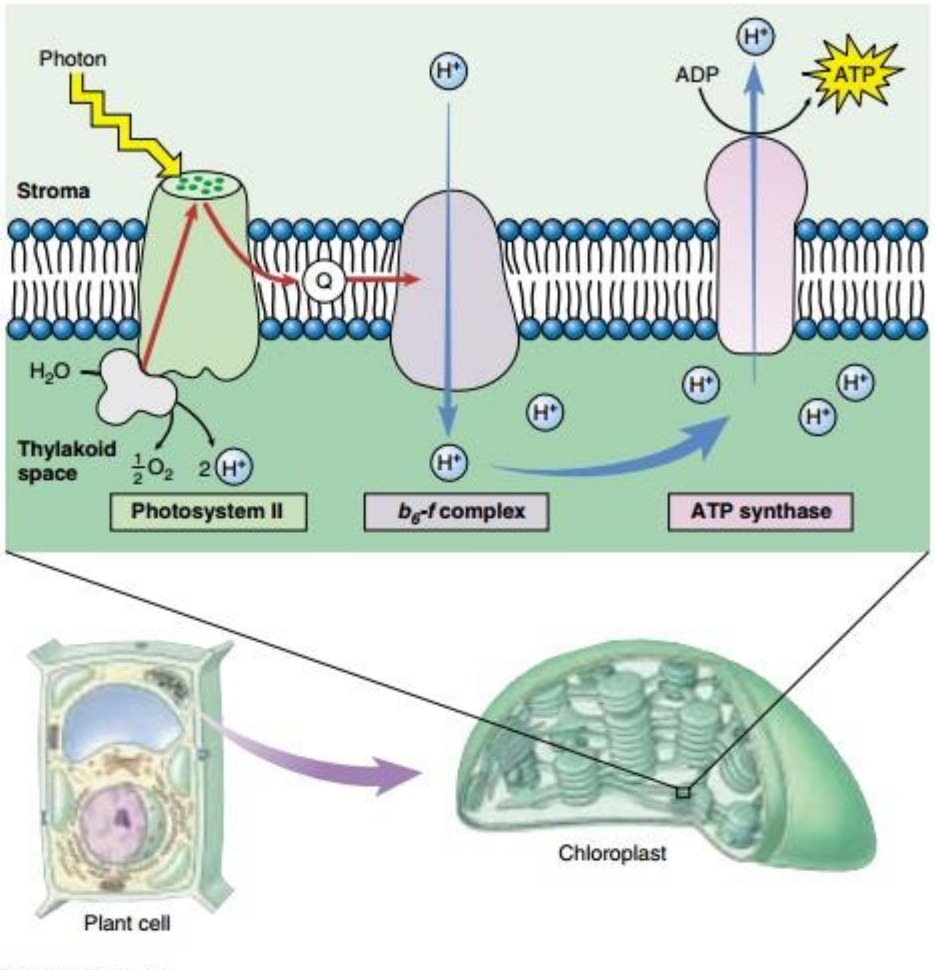

Sun
Stroma
pH 8
Photosystem
II
Pq
Thylakoid interior
pH 4
2e⁻
Plastoquinone
Splits
water !
H_2O
$\frac{1}{2}O_2 + 2H^+$

The Path to Photosystem I

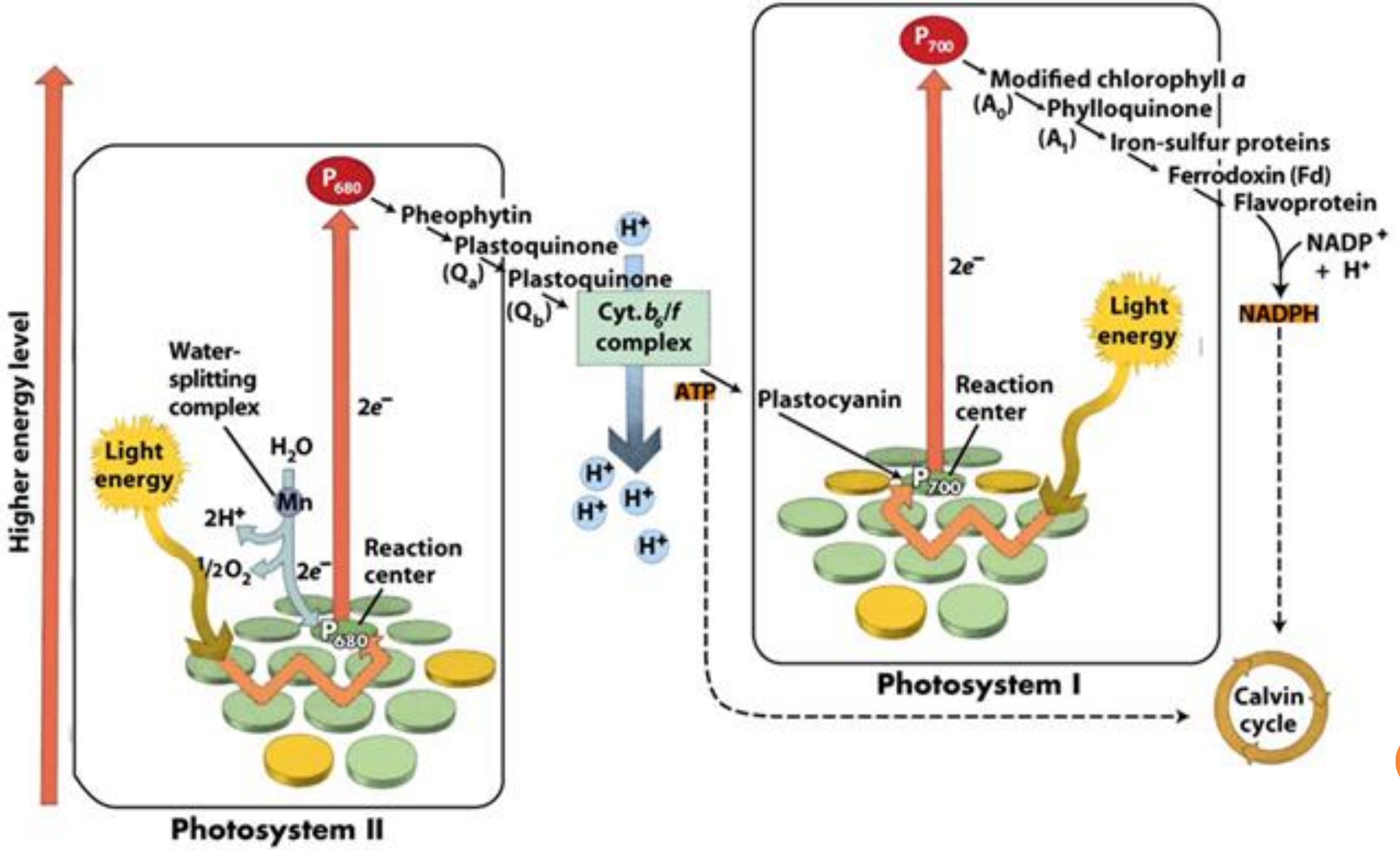
- The primary electron acceptor for the light-energized electrons leaving photosystem II is a quinone molecule, as it was in the bacterial photosystem described earlier. The reduced quinone which results (plastoquinone, symbolized as Q) is a strong electron donor; it passes the excited electron to a proton pump called the b6-f complex embedded within the thylakoid membrane (figure 10.15). This complex closely resembles the bc1 complex in the respiratory electron transport chain of mitochondria discussed in chapter 9. Arrival of the energetic electron causes the b6-f complex to pump a proton into the thylakoid space. A small copper-containing protein called plastocyanin (symbolized pC) then carries the electron to photosystem I.

Making ATP: Chemiosmosis

- Each thylakoid is a closed compartment into which protons are pumped from the stroma by the b6-f complex. The splitting of water also produces added protons that contribute to the gradient.
- The thylakoid membrane is impermeable to protons, so protons cross back out almost exclusively via the channels provided by ATP synthases. These channels protrude like knobs on the external surface of the thylakoid membrane.



- When a photon of light strikes a pigment molecule in photosystem II, it excites an electron. This electron is coupled to a proton stripped from water by an enzyme and is passed along a chain of membrane-bound cytochrome electron carriers. When water is split, oxygen is released from the cell, and the hydrogen ions remain in the thylakoid space. At the proton pump (b6-f complex), the energy supplied by the photon is used to transport a proton across the membrane into the thylakoid.
- The concentration of hydrogen ions within the thylakoid thus increases further. When photosystem I absorbs another photon of light, its pigment passes a second high-energy electron to a reduction complex, which generates NADPH. the thylakoid through the ATP synthase channel, ADP is phosphorylated to ATP and released into the stroma, the fluid matrix inside the chloroplast.The stroma contains the enzymes that catalyze the reactions of carbon fixation.


Higher energy level
P_{680}
Pheophytin
Plastoquinone (Q_a)
Plastoquinone (Q_b)
Cyt. b_6/f complex
H^+
Water-splitting complex
H_2O
Mn
$2H^+$
$1/2 O_2$
$2e^-$
Light energy
Reaction center
P_{680}
Photosystem II
ATP
Plastocyanin
P_{700}
Modified chlorophyll a (A_0)
Phylloquinone (A_1)
Iron-sulfur proteins
Ferrodoxin (Fd)
Flavoprotein
$NADP^+$ + H^+
NADPH
Reaction center
P_{700}
Photosystem I
Calvin cycle

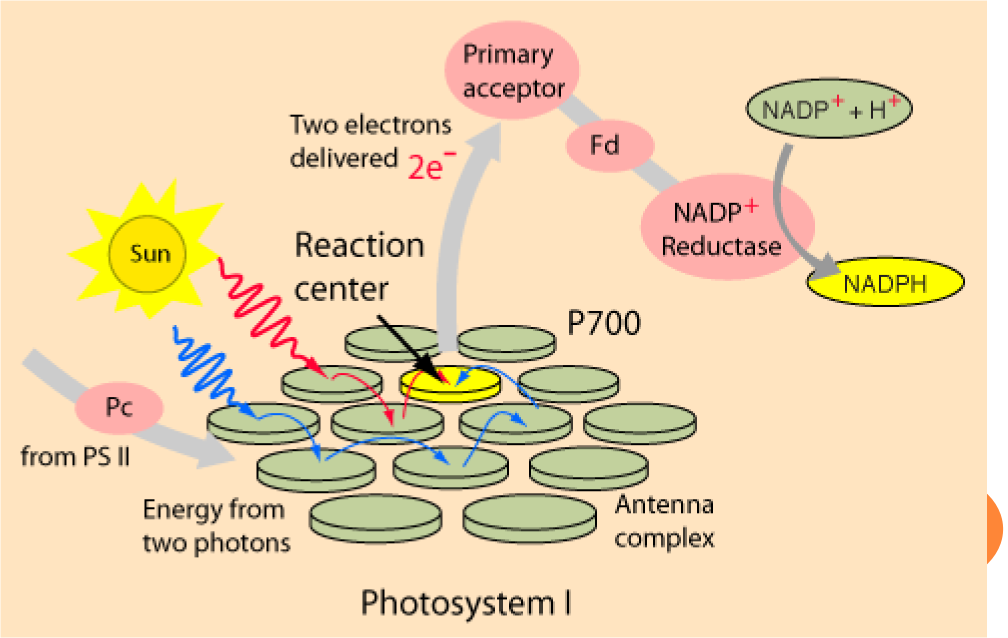
Photosystem I

- The reaction centre of photosystem I, called P700, is a transmembrane complex consisting of at least 13 protein subunits. Energy is fed to it by an antenna complex consisting of 130 chlorophyll a and accessory pigment molecules. Photosystem I accepts an electron from plastocyanin into the hole created by the exit of a light-energized electron.

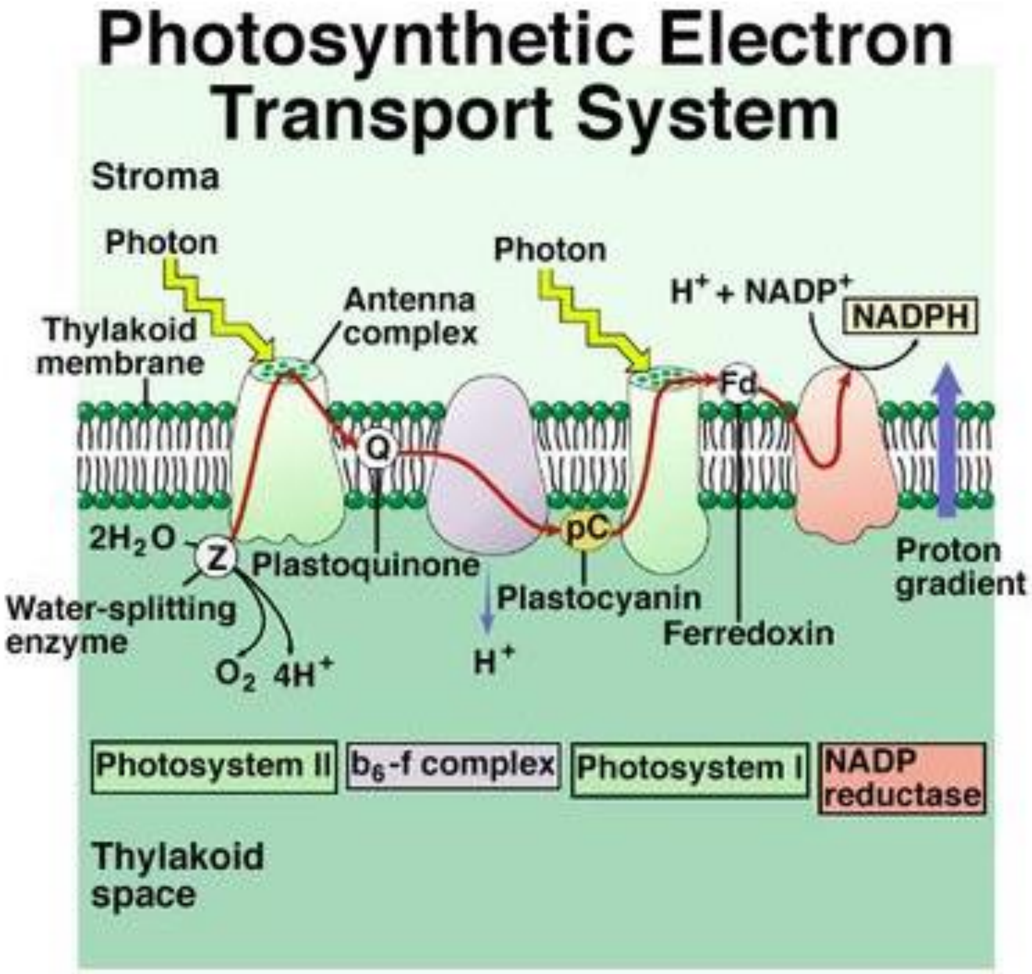
- This arriving electron has by no means lost all of its light-excited energy; almost half remains. Thus, the absorption of a photon of light energy by photosystem I boosts the electron leaving the reaction center to a very high energy level. Unlike photosystem II and the bacterial photosystem, photosystem I does not rely on quinones as electron acceptors. Instead, it passes electrons to an iron-sulphur protein called ferredoxin (Fd).

Making NADPH

- Photosystem I passes electrons to ferredoxin on the stromal side of the membrane (outside the thylakoid). The reduced ferredoxin carries a very-high potential electron.
- Two of them, from two molecules of reduced ferredoxin, are then donated to a molecule of NADP+ to form NADPH. The reaction is catalyzed by the membrane-bound enzyme NADP reductase.

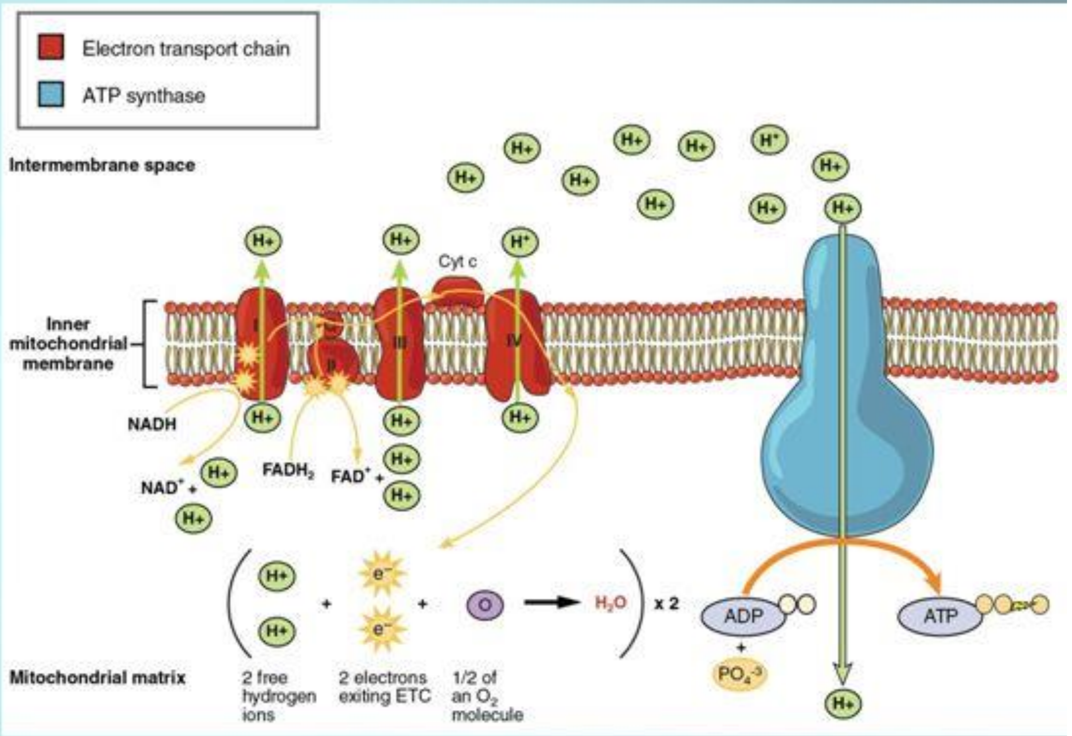


- Since the reaction occurs on the stromal side of the membrane and involves the uptake of a proton in forming NADPH, it contributes further to the proton gradient established during photosynthetic electron transport.



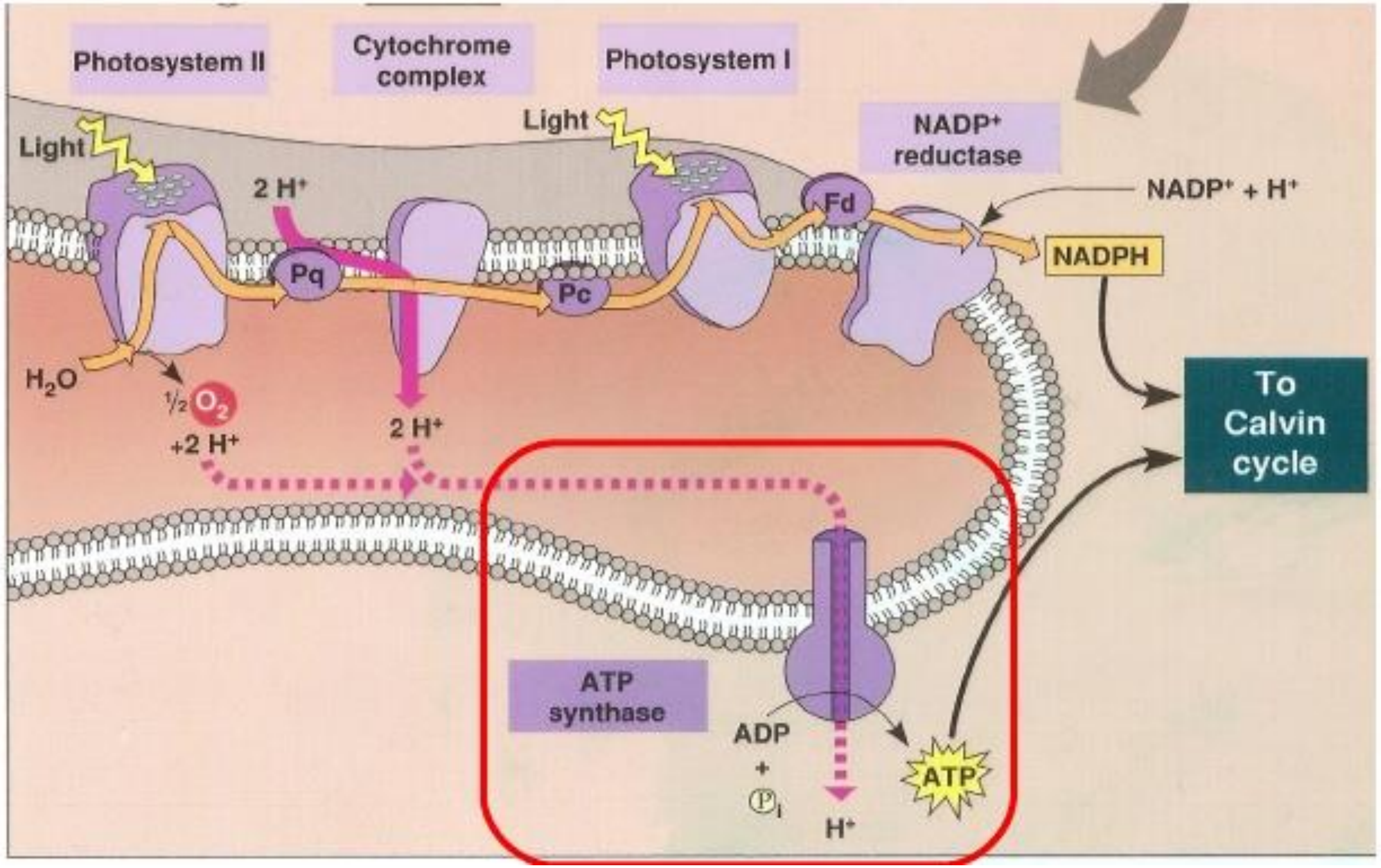
Proton Gradient

- Electron Transport from NADH or $FADH_2$ to O_2 does not produce any ATP!!
- What does?
- Proton Gradient
  - Transport of H^+ ions across the inner mitochondrial membrane from the matrix into the inter-membrane space
- Creates
- Proton-Motive Force
  - Chemical gradient (difference in concentrations)
  - Electro potential gradient is created (because of the positive charge on Hydrogen atom)



Photophosphorylation

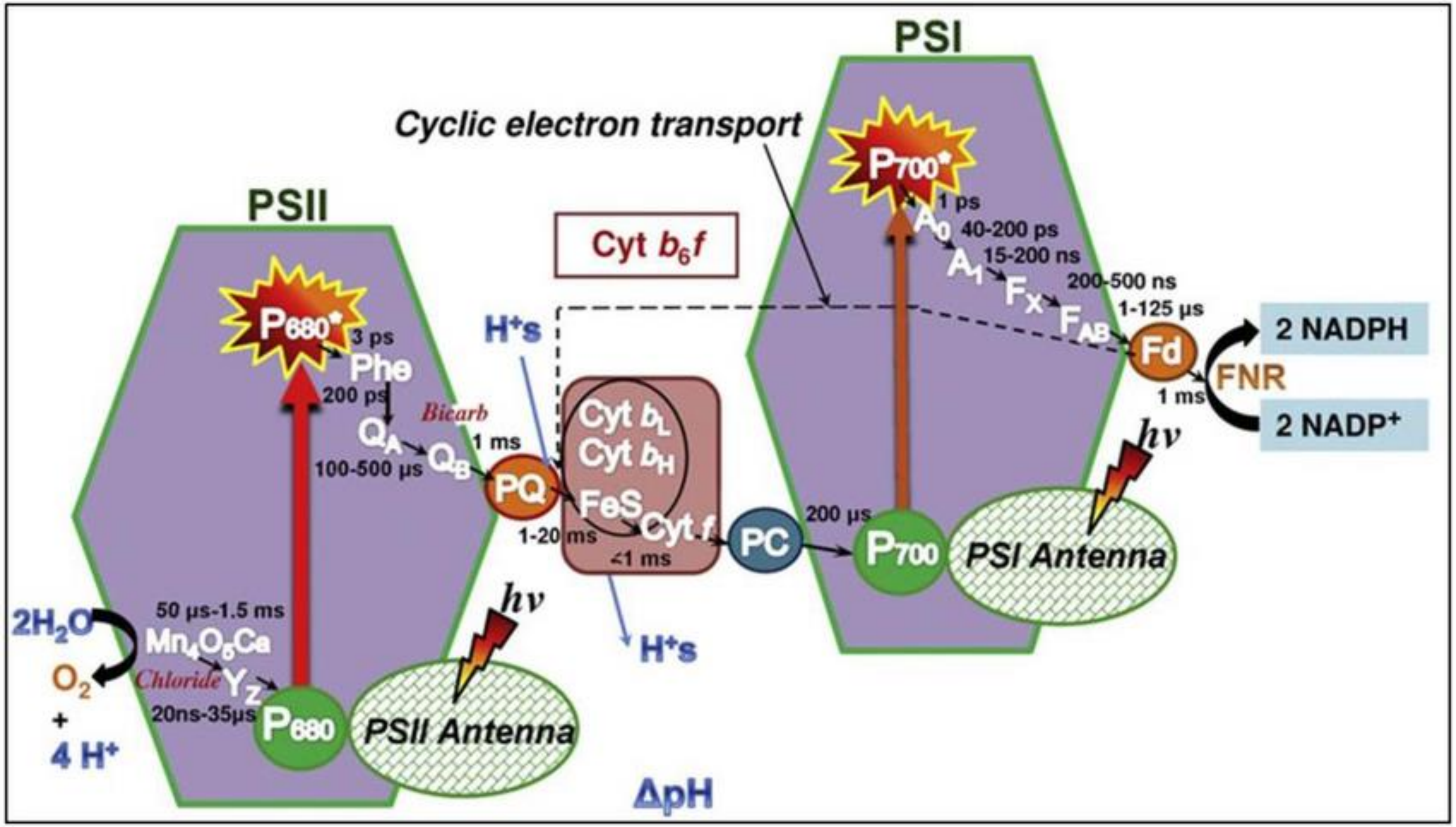
- Electrochemical proton gradient provides proton motive force needed to synthesize ATP



Making More ATP

- The passage of an electron from water to NADPH in the noncyclic photophosphorylation described previously generates one molecule of NADPH and slightly more than one molecule of ATP. However, building organic molecules takes more energy than that—it takes one-and-a-half ATP molecules per NADPH molecule to fix carbon. To produce the extra ATP, many plant species are capable of short-circuiting photosystem I, switching photosynthesis into a cyclic photophosphorylation mode, so that the light-excited electron leaving photosystem I is used to make ATP instead of NADPH.

- The energetic electron is simply passed back to the b6-f complex rather than passing on to NADP+. The b6-f complex pumps out a proton, adding to the proton gradient driving the chemiosmotic synthesis of ATP.



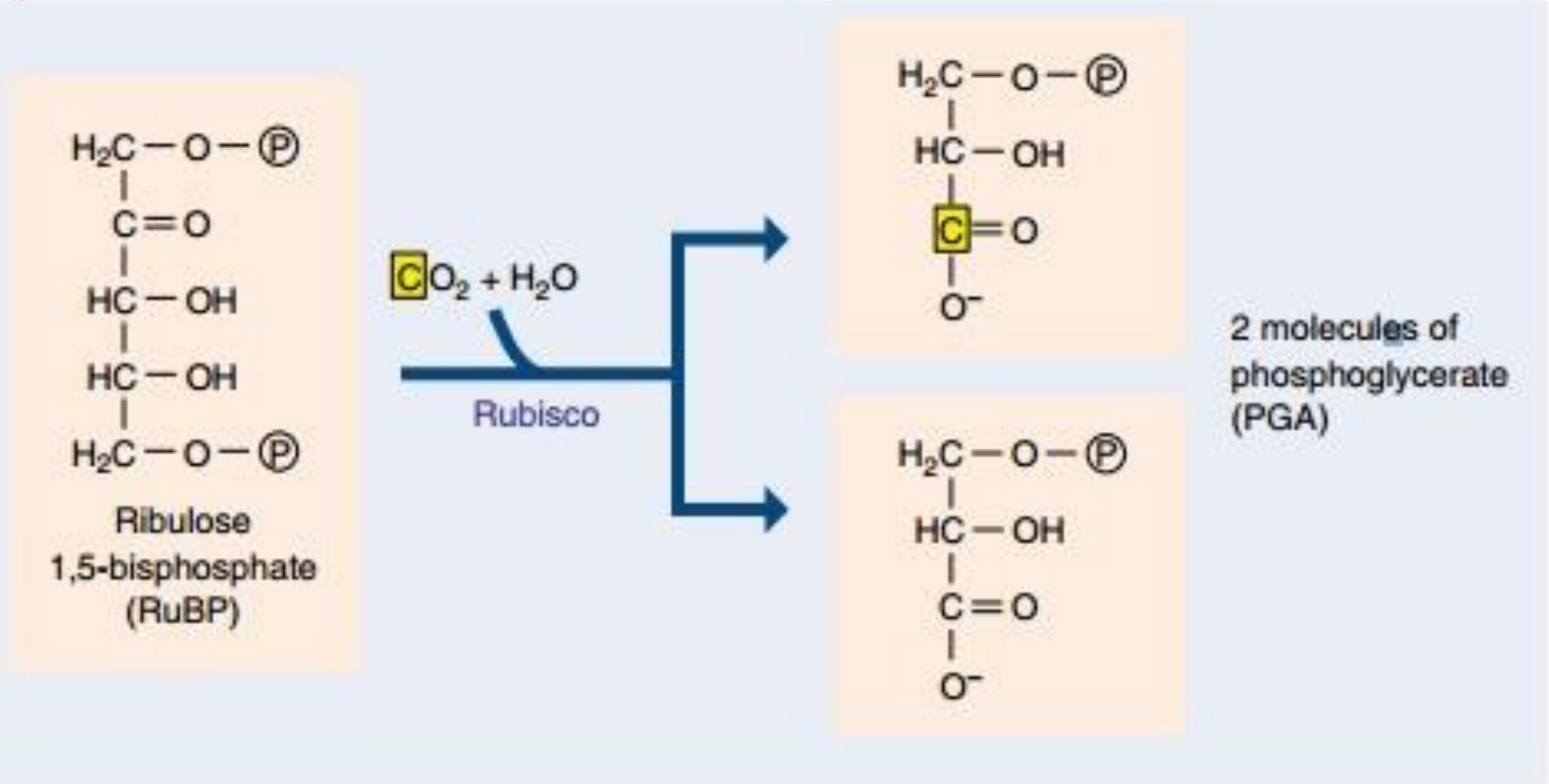
- The relative proportions of cyclic and noncyclic photophosphorylation in these plants determines the relative amounts of ATP and NADPH available for building organic molecules.
- The electrons that photosynthesis strips from water molecules provide the energy to form ATP and NADPH. The residual oxygen atoms of the water molecules combine to form oxygen gas.

The Calvin Cycle

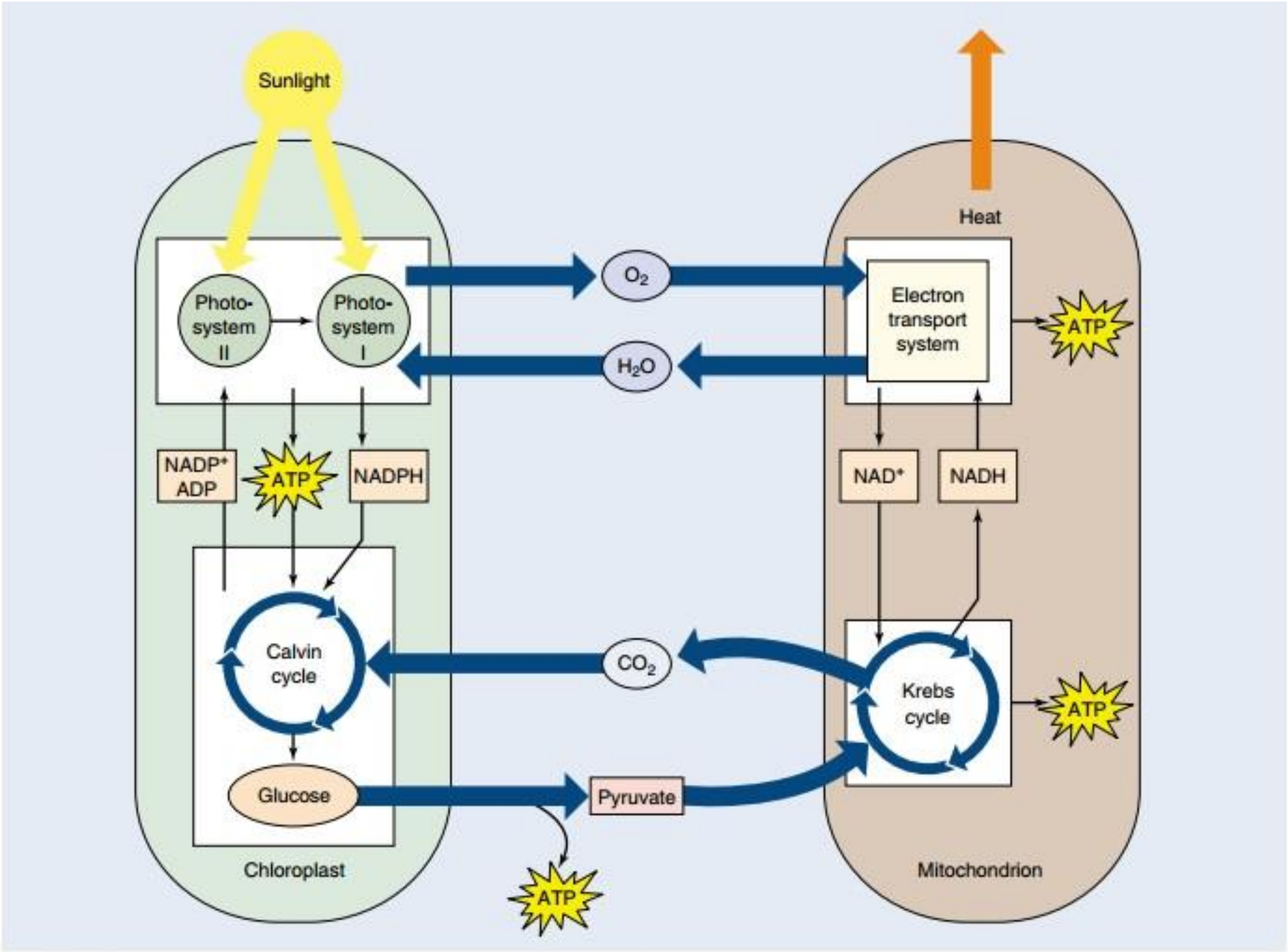
- Photosynthesis is a way of making organic molecules from carbon dioxide (CO_2). These organic molecules contain many C—H bonds and are highly reduced compared with CO_2. To build organic molecules, cells use raw materials provided by the light reactions:
- **1. Energy.** ATP (provided by cyclic and noncyclic photophosphorylation) drives the endergonic* reactions
- **2. Reducing power.** NADPH (provided by photosystem I) provides a source of hydrogens and the energetic electrons needed to bind them to carbon atoms. Much of the light energy captured in photosynthesis ends up invested in the energy-rich C—H bonds of sugars.

(*in an endergonic reaction, the energy released due to cellular respiration is used forthe reactions within the cell).

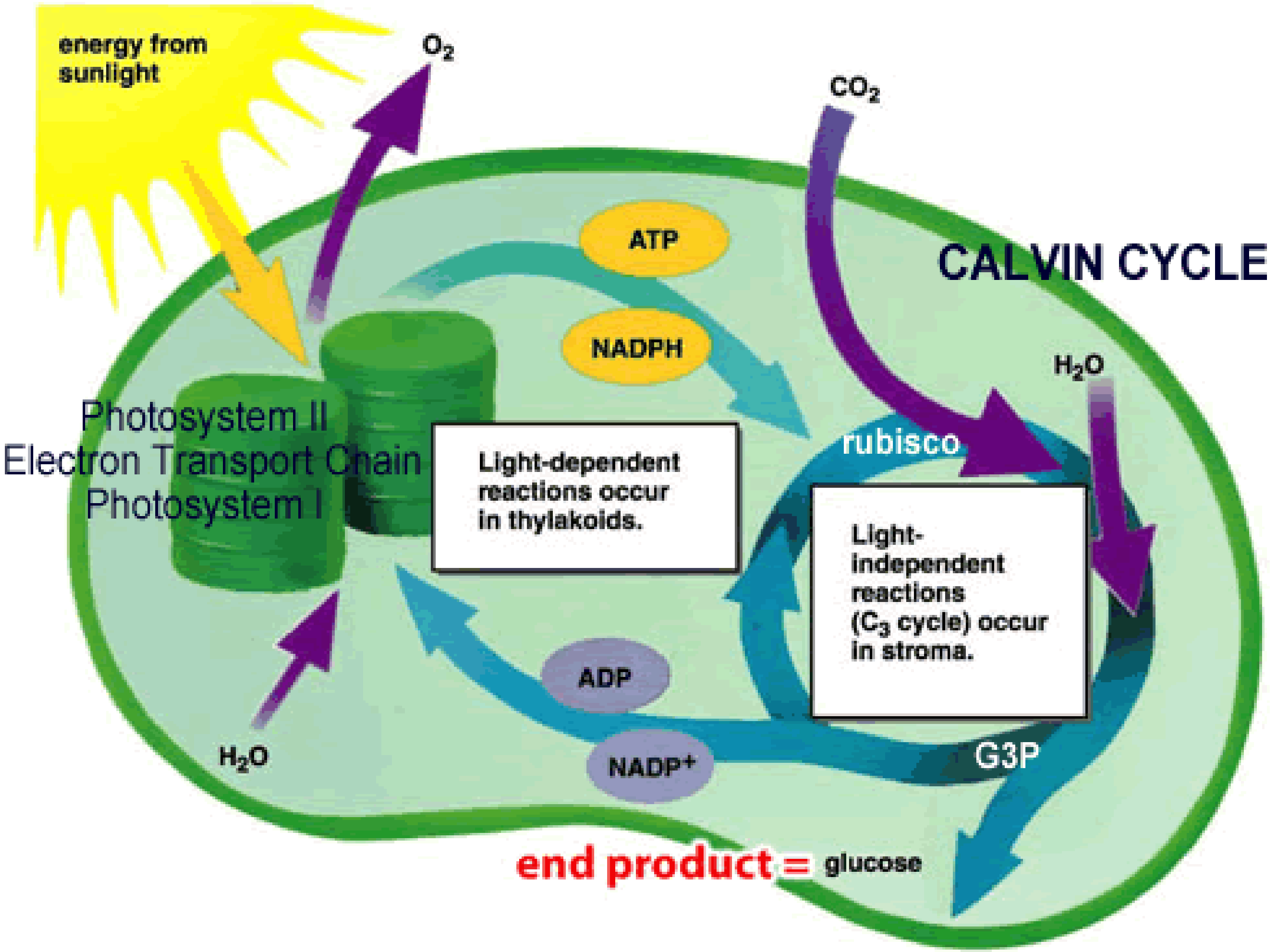
The Calvin Cycle



The key step in the Calvin cycle. Melvin Calvin and his coworkers at the University of California worked out the first step of what later became known as the Calvin cycle. They exposed photosynthesizing algae to radioactive carbon dioxide ($^{14}CO_2$). By following the fate of a radioactive carbon atom, they found that it first binds to a molecule of ribulose 1,5-bisphosphate (RuBP), then immediately splits, forming two molecules of phosphoglycerate (PGA). One of these PGAs contains the radioactive carbon atom. In 1948, workers isolated the enzyme responsible for this remarkable carbon-fixing reaction: rubisco.

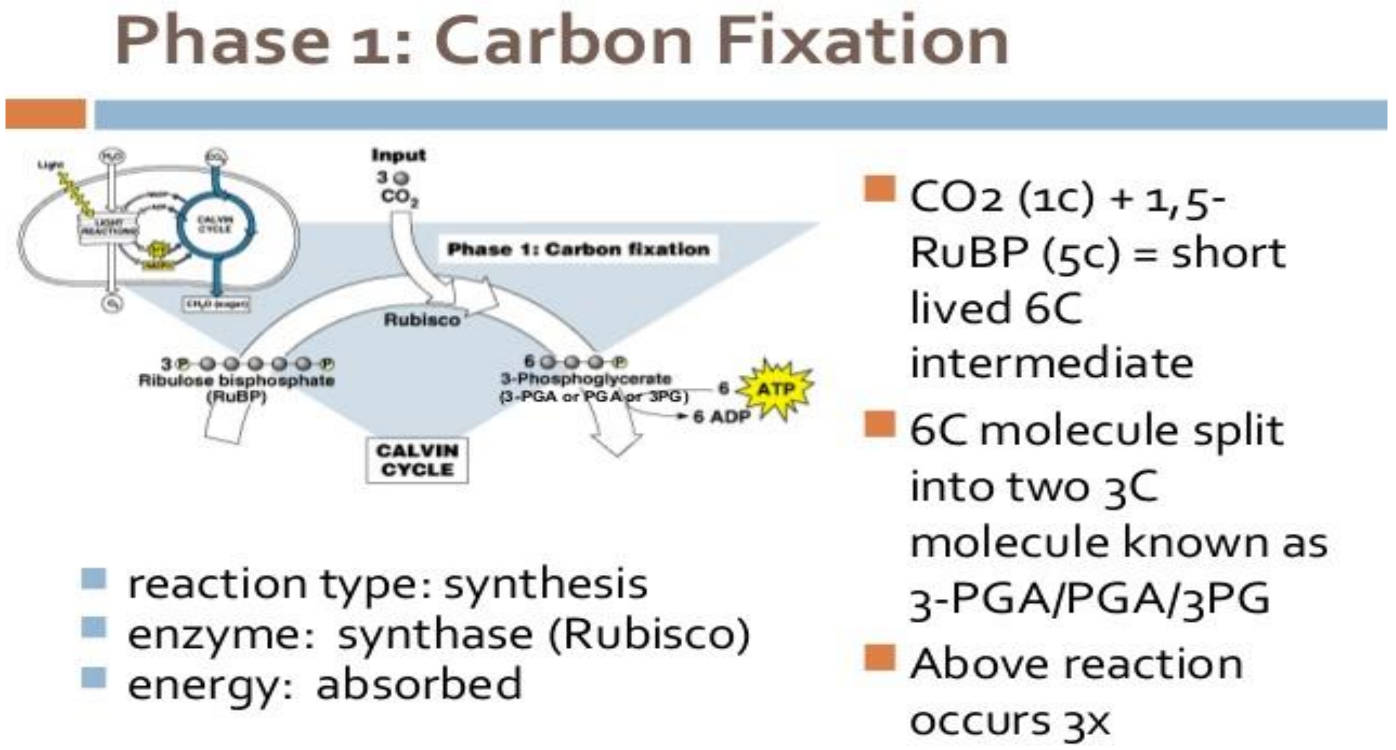


Sunlight
Heat
Photo-system II
Photo-system I
O_2
H_2O
Electron transport system
ATP
NADP+ ADP
ATP
NADPH
NAD+
NADH
Calvin cycle
CO_2
Krebs cycle
ATP
Glucose
Pyruvate
ATP
Chloroplast
Mitochondrion

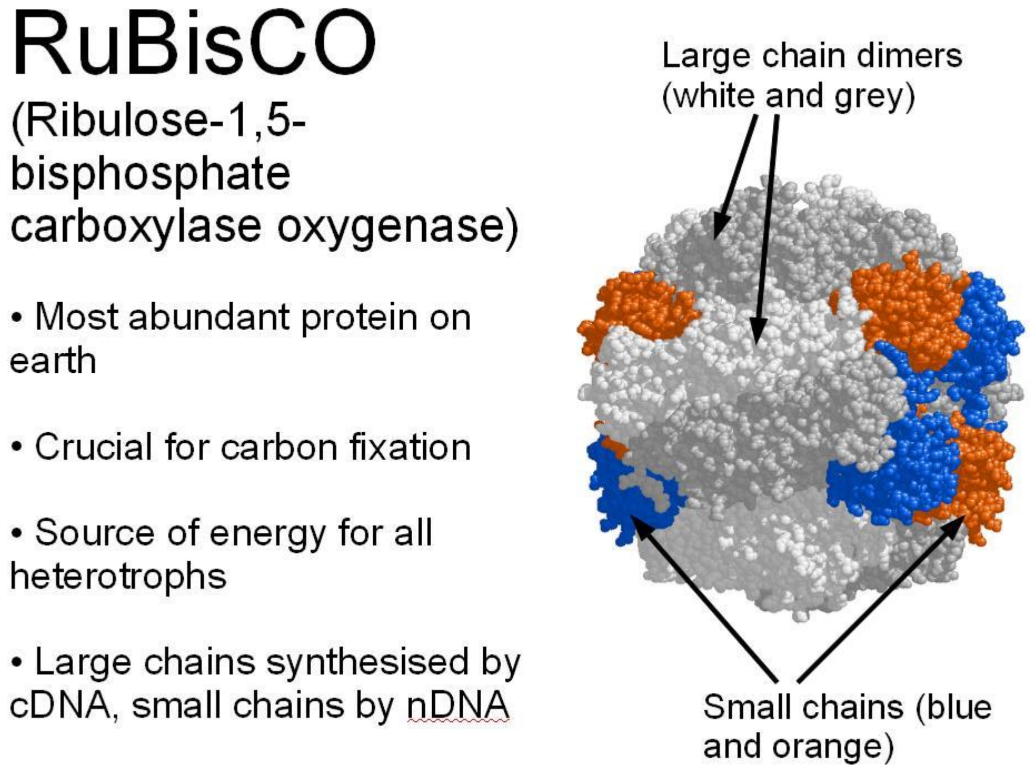

energy from sunlight
O2
CO2
CALVIN CYCLE
ATP
NADPH
H2O
Photosystem II
Electron Transport Chain
Photosystem I
Light-dependent reactions occur in thylakoids.
rubisco
Light-independent reactions (C3 cycle) occur in stroma.
ADP
H2O
NADP+
G3P
end product = glucose

Carbon Fixation

- The key step in the Calvin cycle—the event that makes the reduction of CO_2 possible—is the attachment of CO_2 to a very special organic molecule. Photosynthetic cells produce this molecule by reassembling the bonds of two intermediates in glycolysis, fructose 6-phosphate and glyceraldehyde 3-phosphate, to form the energy-rich five-carbon sugar, ribulose 1,5-bisphosphate (RuBP), and a four-carbon sugar. CO_2 binds to RuBP in the key process called **carbon fixation**, forming two three-carbon molecules of phosphoglycerate (PGA)



- The enzyme that carries out this reaction, ribulose bisphosphate carboxylase/oxygenase (usually abbreviated as rubisco) is a very large four-subunit enzyme present in the chloroplast stroma. This enzyme works very slowly, processing only about three molecules of RuBP per second (a typical enzyme processes about 1000 substrate molecules per second). Because it works so slowly, many molecules of rubisco are needed. In a typical leaf, over 50% of all the protein is rubisco. It is thought to be the most abundant protein on earth.

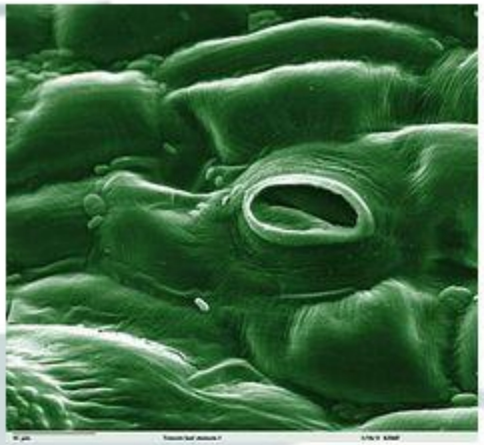


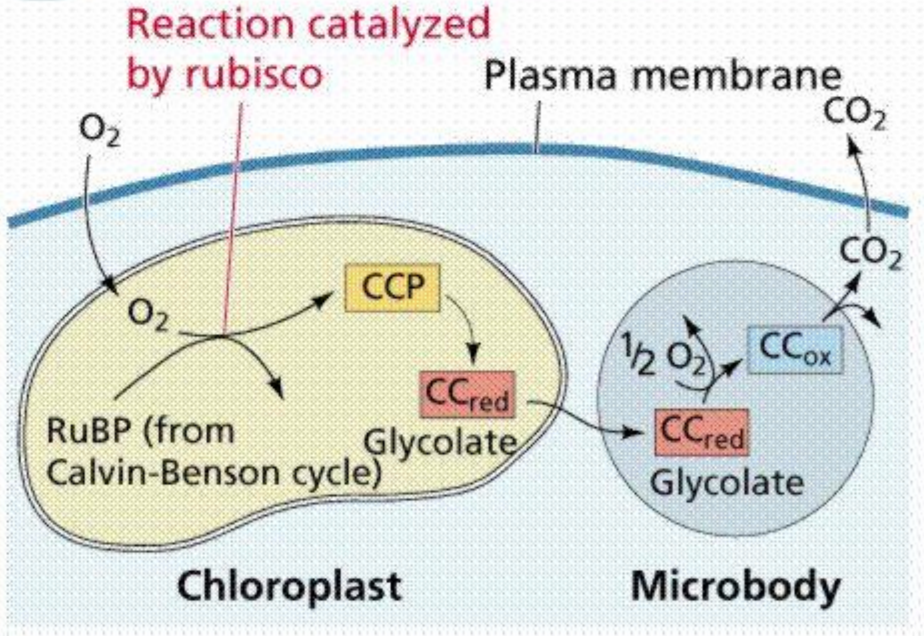
Discovering the Calvin Cycle

- Nearly 100 years ago, Blackman concluded that, because of its temperature dependence, photosynthesis might involve enzyme-catalyzed reactions. These reactions form a cycle of enzyme-catalyzed steps similar to the Krebs cycle.
- This cycle of reactions is called the Calvin cycle, after its discoverer, Melvin Calvin of the University of California, Berkeley. Because the cycle begins when CO_2 binds RuBP to form PGA, and PGA contains three carbon atoms, this process is also called C3 photosynthesis.

C3 Plants

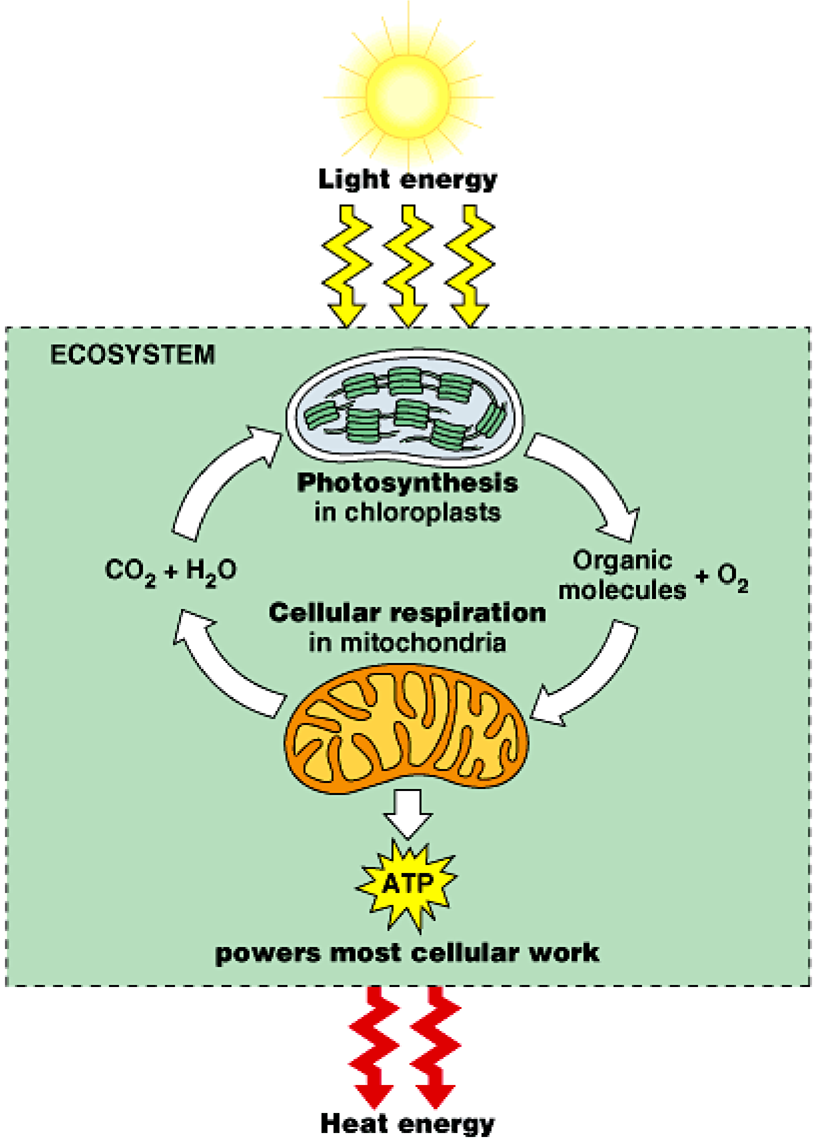
- use CO_2 directly from air
- first organic compound produced is a 3 carbon compound 3-PGA
- reduce rate of photosynthesis in dry weather
- CO_2 enters plants through pores in leaves
- on hot days stomata in leaves close partially to prevent escape of water
- with pores slightly open, adequate amounts of CO_2 cannot enter leaf
- Calvin cycle comes to a halt
- no sugar is made
- in this situation rubisco adds O_2 to RuBP
- 2-carbon product of this reaction is broken down by plant cells to CO_2 + H_2O
- ***Photorespiration***
- provides neither sugar nor ATP





The Energy Cycle

- The energy-capturing metabolisms of the chloroplasts and the mitochondria are intimately related. Photosynthesis uses the products of respiration as starting substrates, and respiration uses the products of photosynthesis as its starting substrates. The Calvin cycle even uses part of the ancient glycolytic pathway, run in reverse, to produce glucose. And, the principal proteins involved in electron transport in plants are related to those in mitochondria, and in many cases are actually the same.



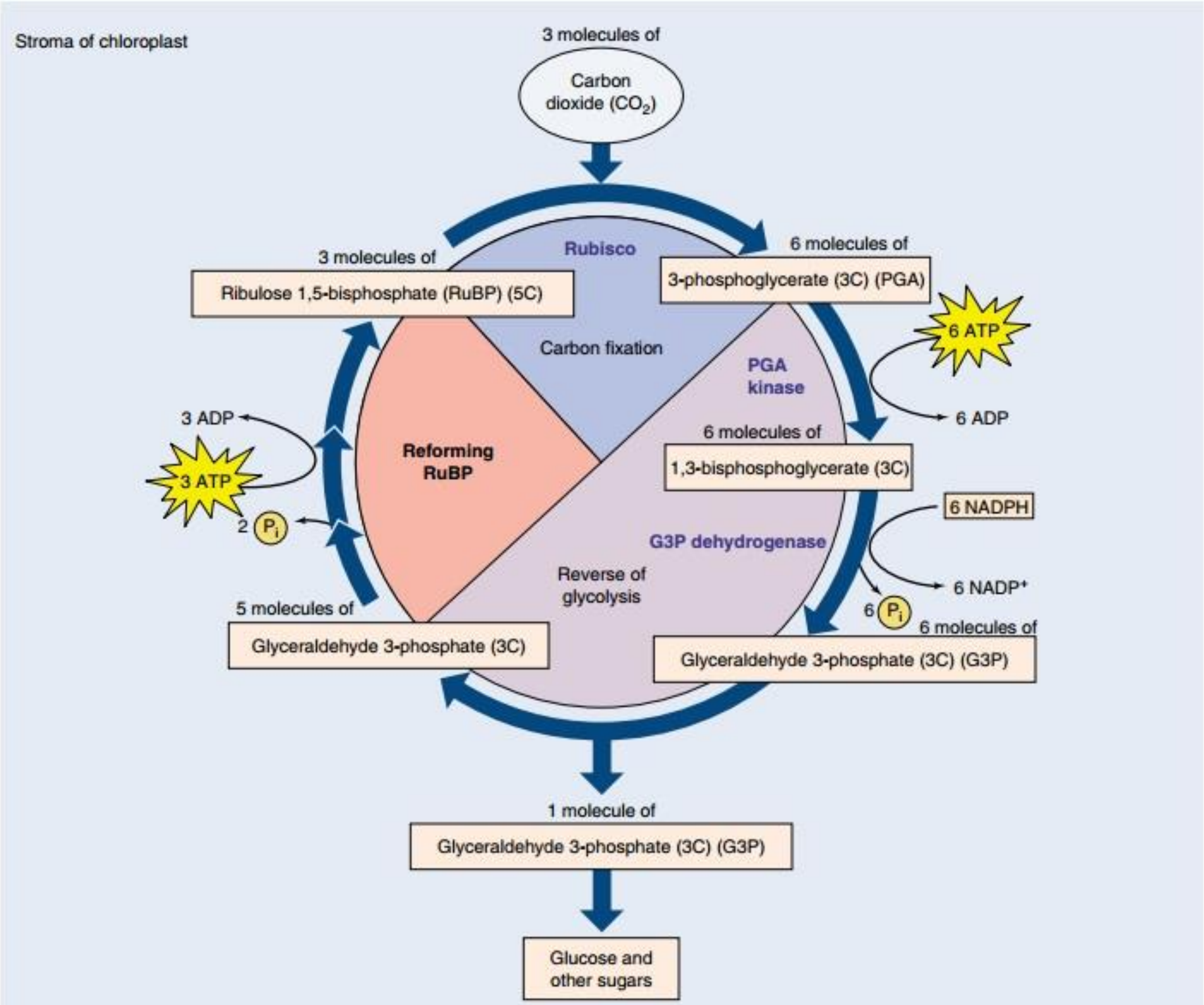
- Chloroplasts put ATP and NADPH to work building carbon-based molecules, a process that essentially reverses the breakdown of such molecules that occurs in mitochondria. Taken together, chloroplasts and mitochondria carry out a cycle in which energy enters from the sun and leaves as heat and work.

Reactions of the Calvin Cycle

- In a series of reactions three molecules of CO_2 are fixed by rubisco to produce six molecules of PGA (containing 6 × 3 = 18 carbon atoms in all, three from CO_2 and 15 from RuBP). The 18 carbon atoms then undergo a cycle of reactions that regenerates the three molecules of RuBP used in the initial step (containing 3 × 5 = 15 carbon atoms). This leaves one molecule of glyceraldehyde 3-phosphate (three carbon atoms) as the net gain.

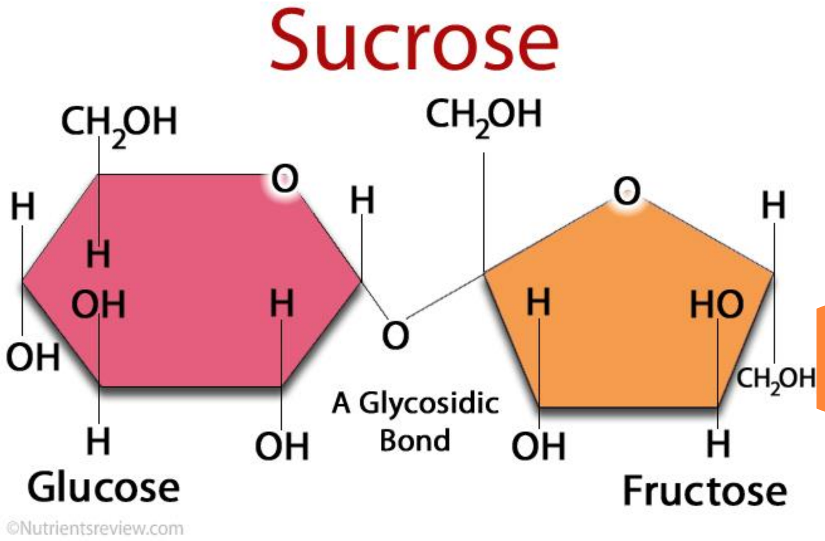
- The net equation of the Calvin cycle is:

3 CO_2 + 9 ATP + 6 NADPH + water → glyceraldehyde 3-phosphate + 8 Pi + 9 ADP + 6 $NADP^+$


Stroma of chloroplast
3 molecules of
Carbon dioxide (CO_2)
Rubisco
6 molecules of
3-phosphoglycerate (3C) (PGA)
3 molecules of
Ribulose 1,5-bisphosphate (RuBP) (5C)
Carbon fixation
6 ATP
PGA kinase
6 ADP
3 ADP
6 molecules of
1,3-bisphosphoglycerate (3C)
Reforming RuBP
3 ATP
6 NADPH
2 P_i
G3P dehydrogenase
Reverse of glycolysis
6 NADP+
6 P_i
5 molecules of
Glyceraldehyde 3-phosphate (3C)
6 molecules of
Glyceraldehyde 3-phosphate (3C) (G3P)
1 molecule of
Glyceraldehyde 3-phosphate (3C) (G3P)
Glucose and other sugars

- With three full turns of the cycle, three molecules of carbon dioxide enter, a molecule of glyceraldehyde 3-phosphate (G3P) is produced, and three molecules of RuBP are regenerated. We now know that light is required indirectly for different segments of the CO_2 reduction reactions.
- Five of the Calvin cycle enzymes—including rubisco—are light activated; that is, they become functional or operate more efficiently in the presence of light. Light also promotes transport of three-carbon intermediates across chloroplast membranes that are required for Calvin cycle reactions. And finally, light promotes the influx of Mg^{++} into the chloroplast stroma, which further activates the enzyme rubisco.

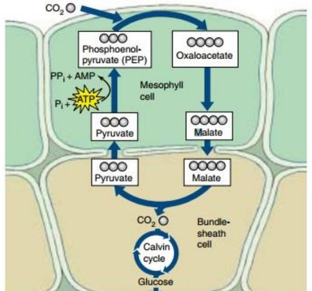
- Output of the Calvin Cycle The glyceraldehyde 3-phosphate that is the product of the Calvin cycle is a three-carbon sugar that is a key intermediate in glycolysis.
- Much of it is exported from the chloroplast to the cytoplasm of the cell, where the reversal of several reactions in glycolysis allows it to be converted to fructose 6-phosphate and glucose 1-phosphate, and from that to sucrose, a major transport sugar in plants (sucrose, common table sugar, is a disaccharide made of fructose and glucose).

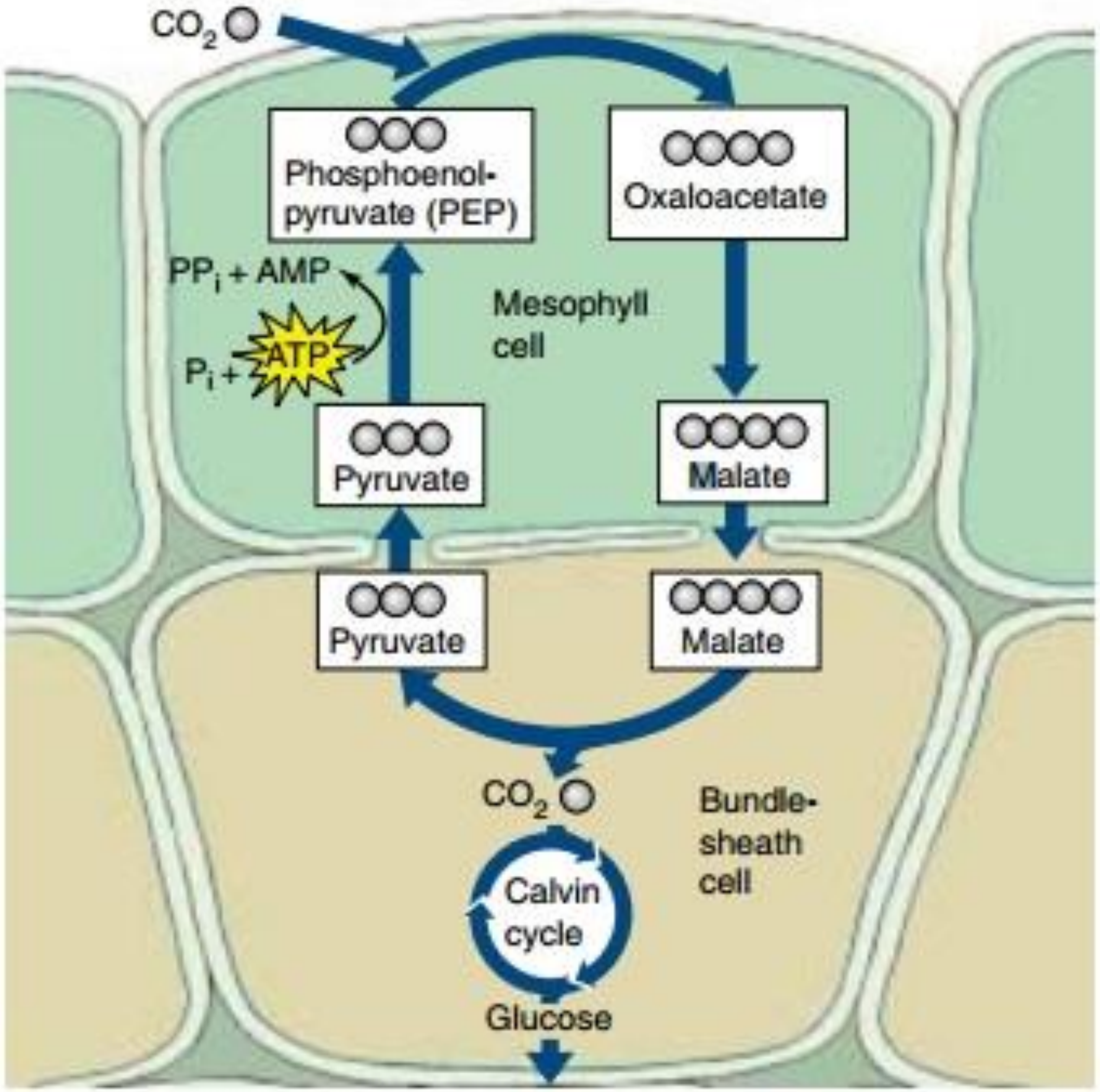


- In times of intensive photosynthesis, glyceraldehyde 3-phosphate levels in the stroma of the chloroplast rise.
- As a consequence, some glyceraldehyde 3-phosphate in the chloroplast is converted to glucose 1-phosphate, in an analogous set of reactions to those done in the cytoplasm, by reversing several reactions similar to those of glycolysis.
- The glucose 1-phosphate is then combined into an insoluble polymer, forming long chains of starch stored as bulky starch grains in chloroplasts.

Photorespiration

- Evolution does not necessarily result in optimum solutions. Rather, it favours workable solutions that can be derived from others that already exist. Photosynthesis is no exception. Rubisco, the enzyme that catalyses the key carbon-fixing reaction of photosynthesis, provides a decidedly suboptimal solution. This enzyme has a second enzyme activity that interferes with the Calvin cycle, oxidizing ribulose 1,5- bisphosphate. In this process, called photorespiration, O_2 is incorporated into ribulose 1,5-bisphosphate, which undergoes additional reactions that actually release CO_2. Hence, photorespiration releases CO_2—essentially undoing the Calvin cycle which reduces CO_2 to carbohydrate.





CO2
Phosphoenol-
pyruvate (PEP)
Oxaloacetate
PPi + AMP
ATP
Pi +
Mesophyll
cell
Pyruvate
Malate
Pyruvate
Malate
CO2
Bundle-
sheath
cell
Calvin
cycle
Glucose

OVERVIEW OF CALVIN CYCLE

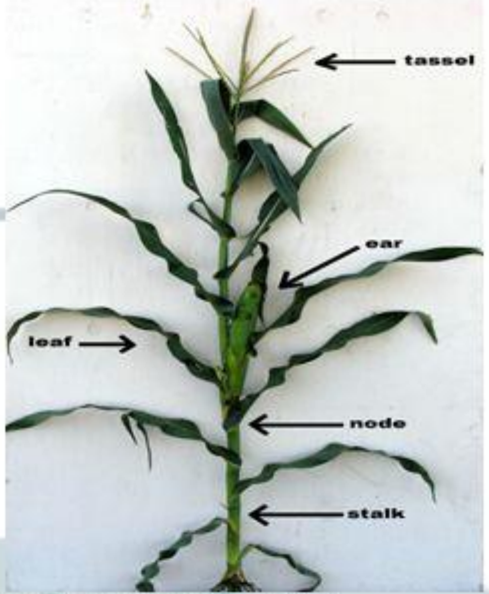
- Calvin cycle, a part of photosynthesis, occurs in 2 stages.
- 1st stage –light dependent chemical reactions capture the energy of light and use it to make the energy-storage and transport molecules ATP and NADPH.
- 2nd stage – light independent Calvin cycle uses the energy from short-lived electronically excited carriers to convert CO_2 and H_2O into organic molecules (glucose).
- This set of reactions is also called carbon fixation.
- The key enzyme of the cycle is called RuBisCO.
- Although called "dark reactions", these reactions don't occur in dark or night time.
- Reactions require reduced NADP(from light dependent reaction).

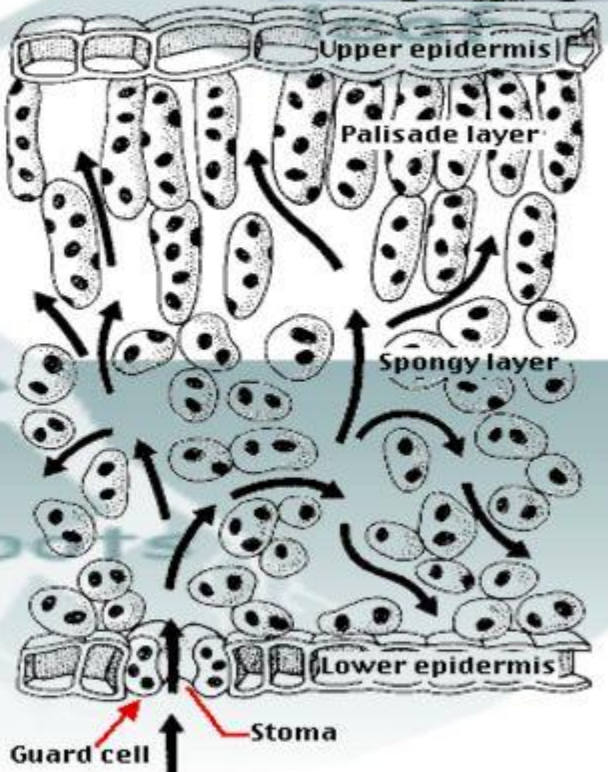
The C4 Pathway

- Plants that adapted to these warmer environments have evolved two principal ways that use the C4 pathway to deal with this problem. In one approach, plants conduct C4 photosynthesis in the mesophyll cells and the Calvin cycle in the bundle sheath cells. This creates high local levels of CO_2 to favour the carboxylation reaction of rubisco. These plants are called C4 plants and include corn sugarcane, sorghum, and a number of other grasses.

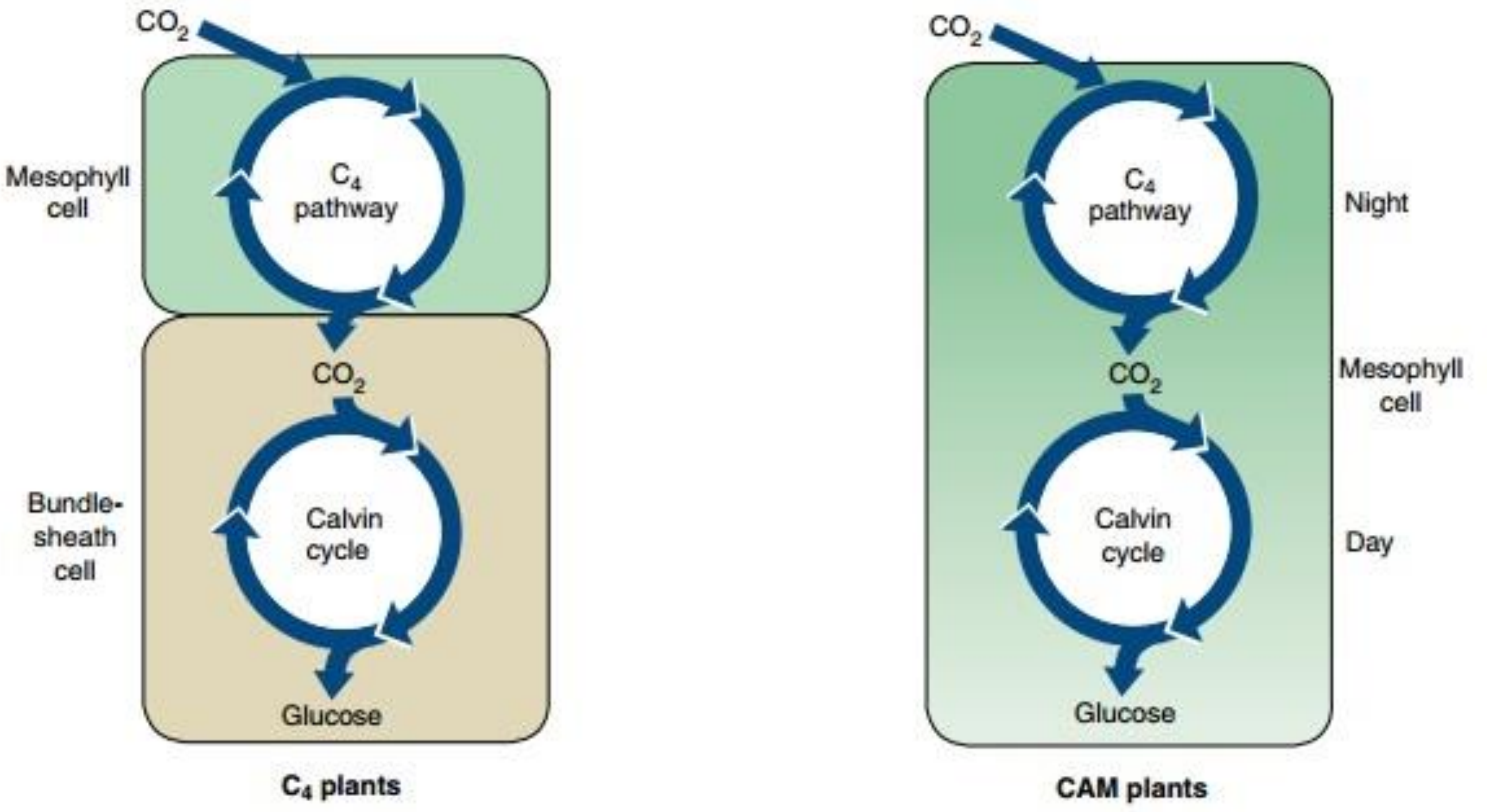
C4 Plants

- have special adaptations allowing them to save water without shutting down photosynthesis
- corn, sugar cane & crabgrass
- evolved in hot, dry environments
- when hot & dry→ stomata are closed
- saves water
- sugar is made via another route
- developed way to keep CO_2 flowing without capturing it directly from air





The C4 Pathway



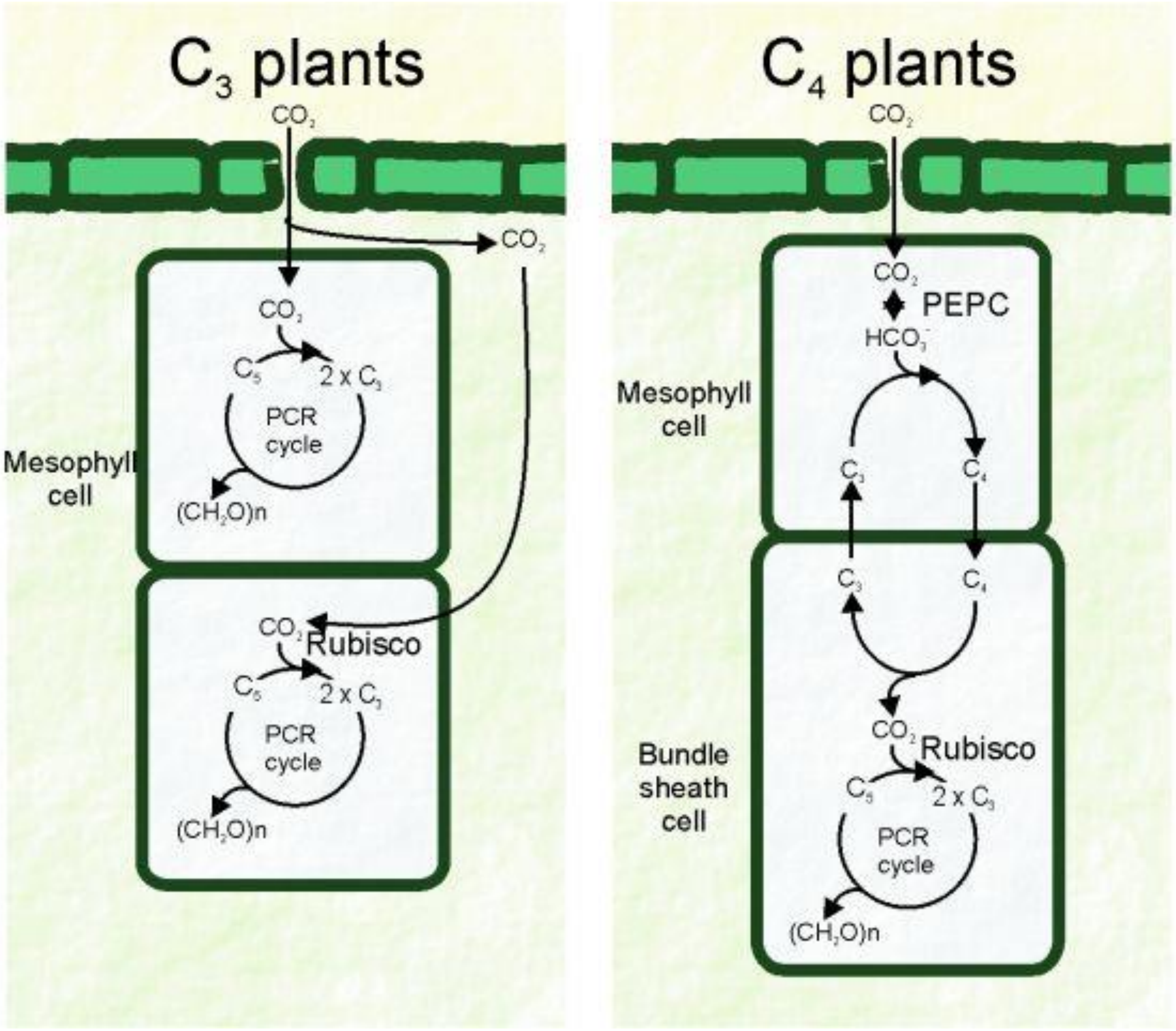
- In the C4 pathway, the three-carbon metabolite phosphoenolpyruvate is carboxylated to form the four-carbon molecule oxaloacetate, which is the first product of CO_2 fixation. In C4 plants, oxaloacetate is in turn converted into the intermediate malate, which is transported to an adjacent bundle-sheath cell. Inside the bundlesheath cell, malate is decarboxylated to produce pyruvate, releasing CO_2. Because bundle-sheath cells are impermeable to CO_2, the $CO_2$is retained within them in high concentrations. Pyruvate returns to the mesophyll cell, where two of the high-energy bonds in an ATP molecule are split to convert the pyruvate back into phosphoenolpyruvate, thus completing the cycle.

The enzymes that carry out the Calvin cycle in a C4 plant are located within the bundle-sheath cells, where the increased CO_2 concentration decreases photorespiration.

Because each CO_2 molecule is transported into the bundlesheath cells at a cost of two high-energy ATP bonds, and since six carbons must be fixed to form a molecule of glucose, 12 additional molecules of ATP are required to form a molecule of glucose. In C4 photosynthesis, the energetic cost of forming glucose is almost twice that of C3 photosynthesis:

30 molecules of ATP versus 18.

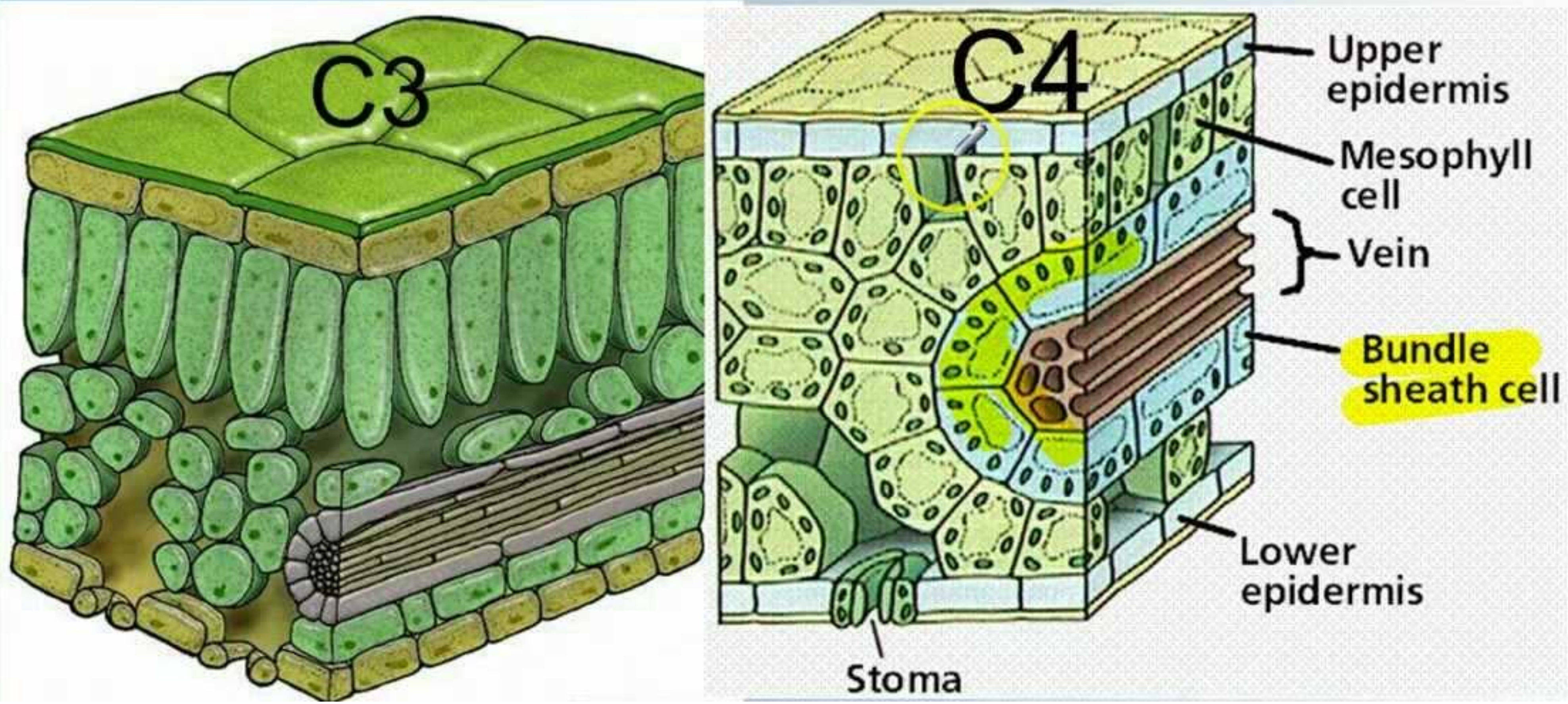
Nevertheless, C4 photosynthesis is **advantageous in a hot climate**: photorespiration would otherwise remove more than half of the carbon fixed.

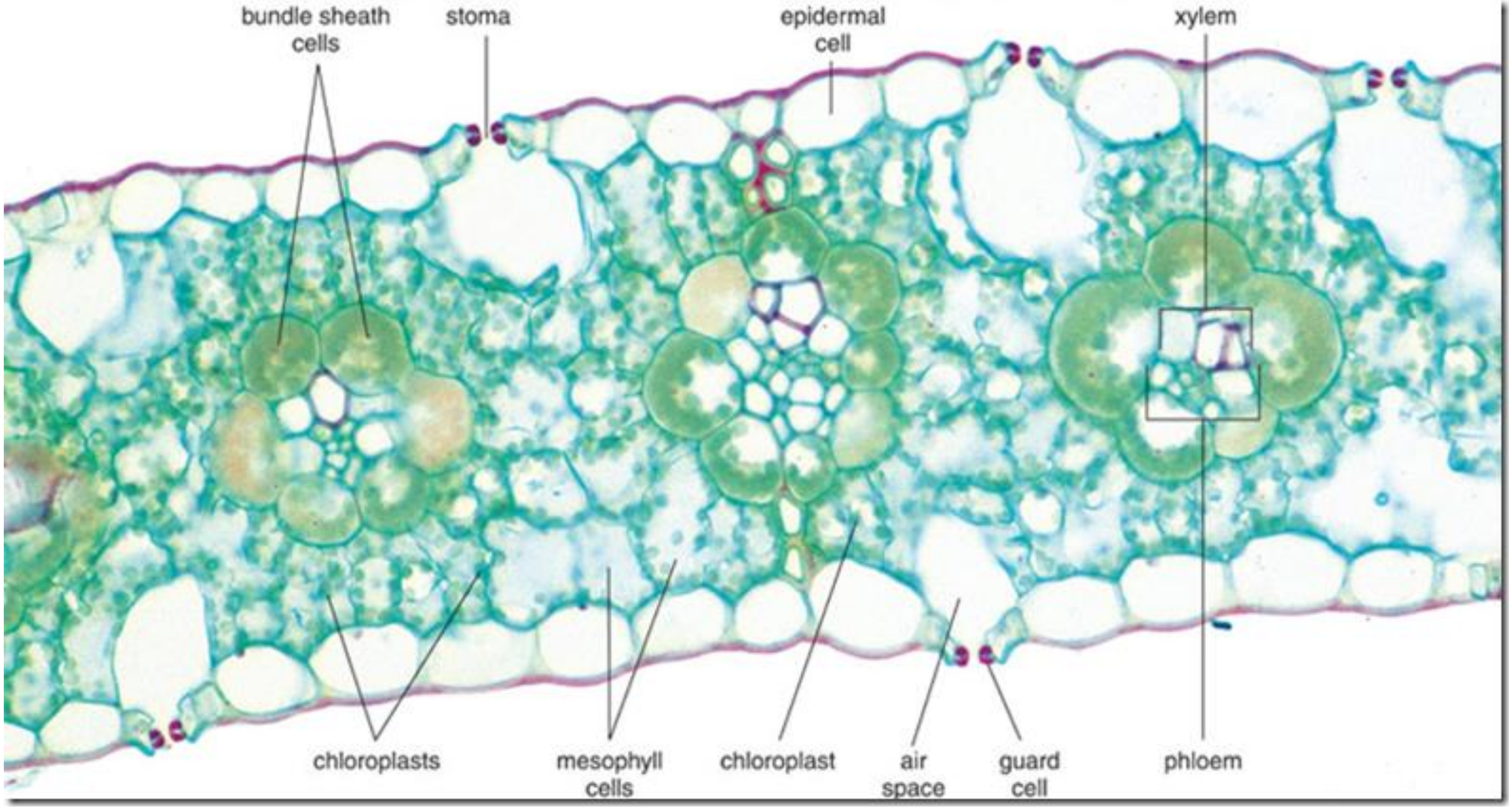


C3 plants
CO2
CO2
CO2
C5
2 x C3
PCR cycle
(CH2O)n
Mesophyll cell
CO2
Rubisco
C5
2 x C3
PCR cycle
(CH2O)n
C4 plants
CO2
CO2
PEPC
HCO3-
Mesophyll cell
C3
C4
C3
C4
CO2
Rubisco
Bundle sheath cell
C5
2 x C3
PCR cycle
(CH2O)n

C-4 Pathway

C4 Pathway - uses a unique anatomical difference to ensure optimal Carbon fixation.



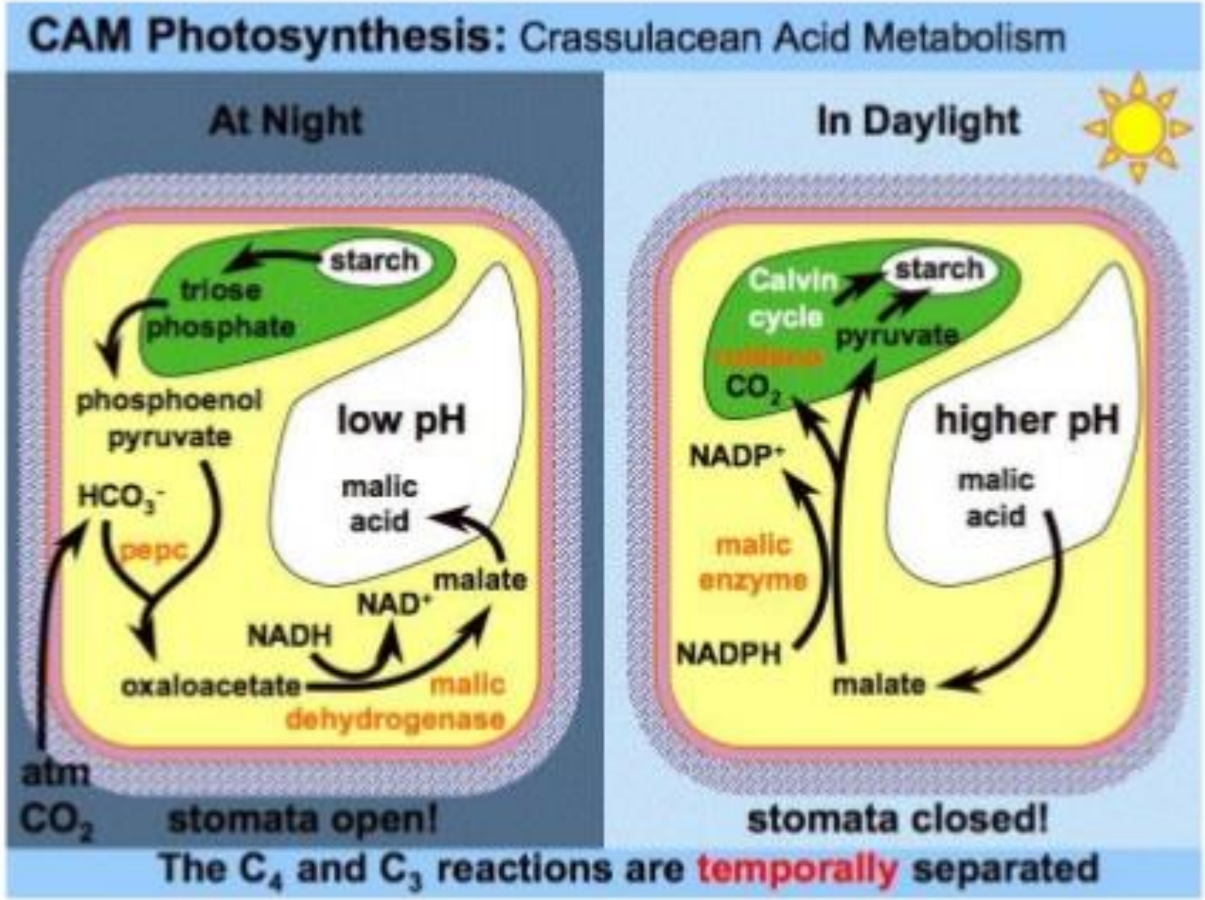

bundle sheath cells
stoma
epidermal cell
xylem
chloroplasts
mesophyll cells
chloroplast
air space
guard cell
phloem

The Crassulacean Acid Pathway

A second strategy to decrease photorespiration in hot regions has been adopted by many succulent (water-storing) plants such as cacti, pineapples, and some members of about two dozen other plant groups. This mode of initial carbon fixation is called crassulacean acid metabolism (CAM), after the plant family Crassulaceae (e.g. the stonecrops (*Sedum* sp.)), in which it was first discovered. In these plants, the stomata (singular, stoma), specialized openings in the leaves of all plants through which CO_2 enters and water vapor is lost, open during the night and close during the day. This pattern of stomatal opening and closing is the reverse of that in most plants. CAM plants open stomata at night and initially fix CO_2 into organic compounds using the C4 pathway.

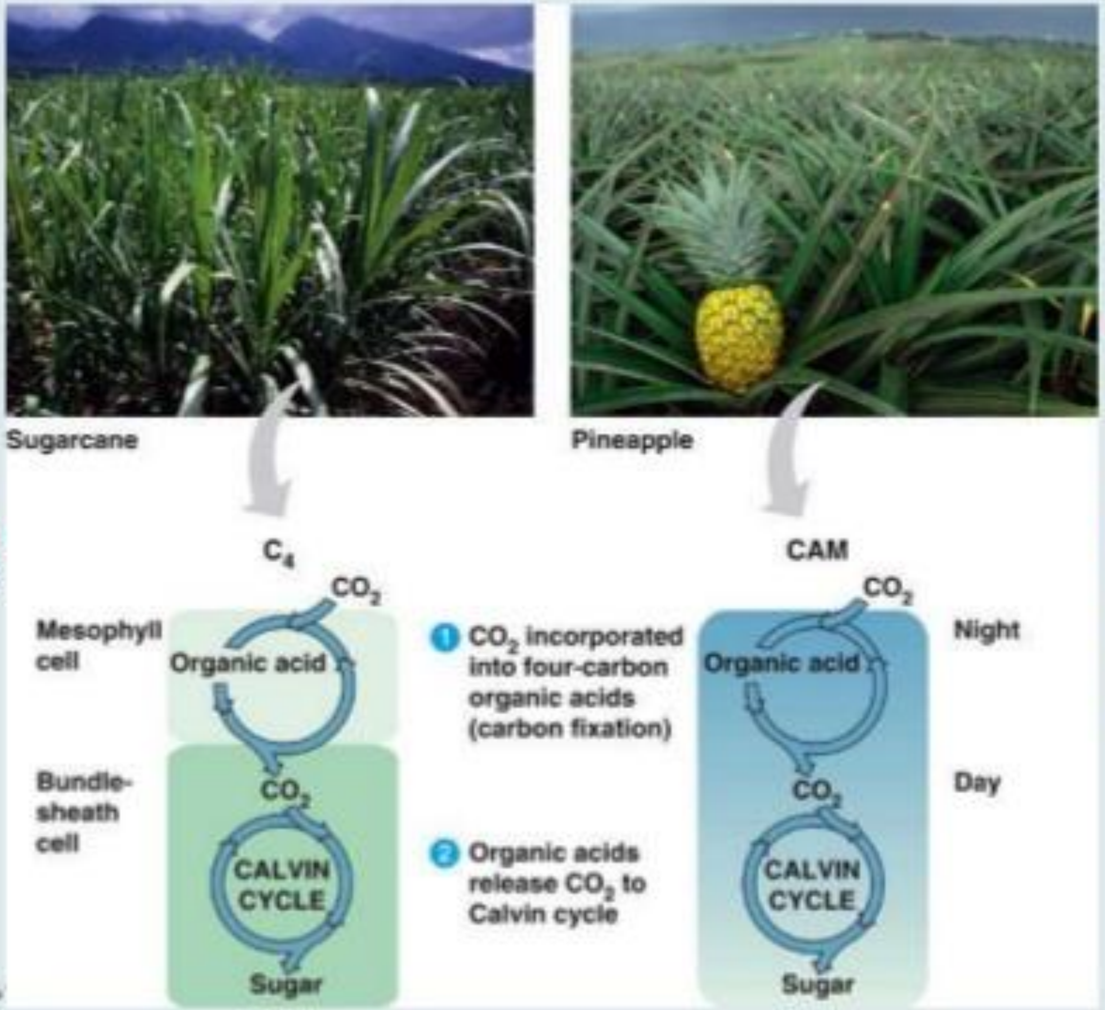
Sedum sp

PROCESS OF CAM



C4 vs CAM Summary

<u>C4 plants</u>
separate 2 steps of C fixation **<u>anatomically</u>** in 2 different cells



<u>CAM plants</u>
separate 2 steps of C fixation **<u>temporally</u>** at 2 different times

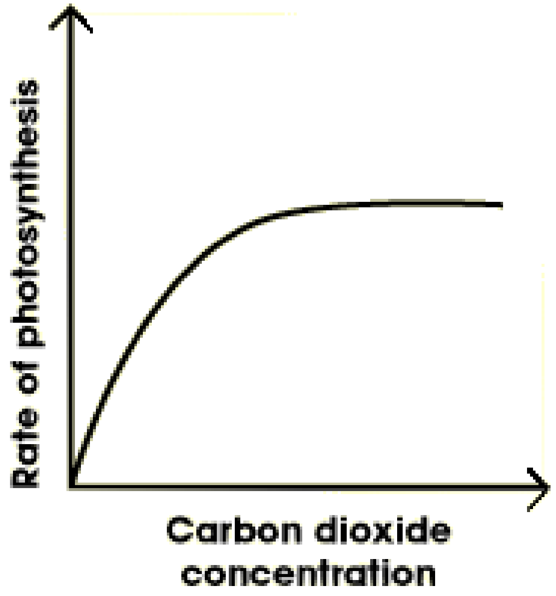
- These organic compounds accumulate throughout the night and are decarboxylated during the day to yield high levels of CO_2.
- In the day, these high levels of CO_2 drive the Calvin cycle and minimize photorespiration. Like C4 plants, CAM plants use both C4 and C3 pathways.
- They differ from C4 plants in that they use the C4 pathway at night and the C3 pathway during the day within the same cells. In C4 plants, the two pathways take place in different cells.
- Photorespiration results in decreased yields of photosynthesis. C4 and CAM plants circumvent this problem through modifications of leaf architecture and photosynthetic chemistry that locally increase CO_2 concentrations.
- C4 plants isolate CO_2 production spatially, CAM plants temporally.

Factors affecting photosynthesis

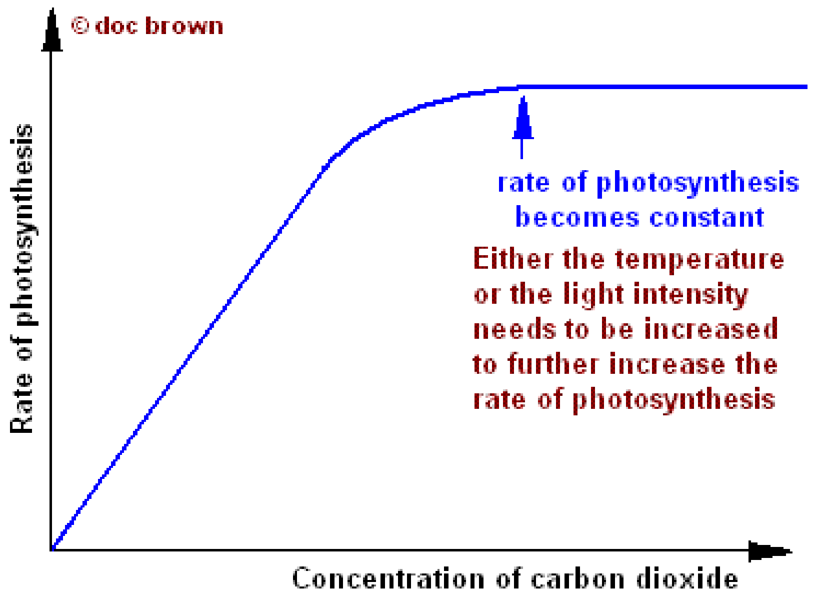
If factors affecting photosynthesis are optimum, then photosynthesis is rapid and therefore the plant grows faster. The most important factors among others are:

- CO_2 concentration of the air
- Light intensity
- Temperature
- Mineral elements
- Water
- O_2 concentration
- Chlorophyll amount

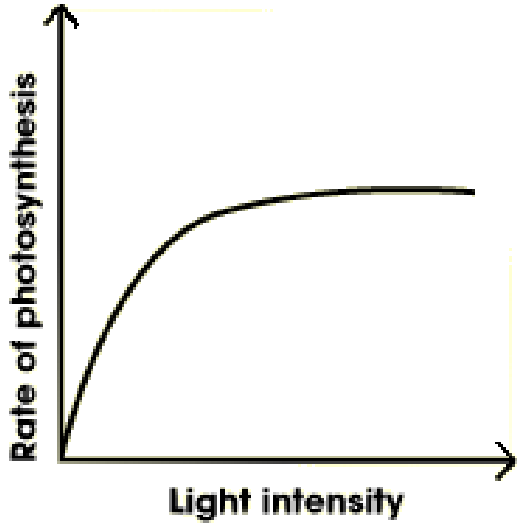
- CO_2 concentration: CO_2 ratio in the air is approximately 0.03%. If this amount is increased 10 times, photosynthesis also increased proportionally. However, if this ratio is also increased, photosynthesis can not increase anymore. In greenhouses CO_2 ratio is increased and thus plants perform photosynthesis more.

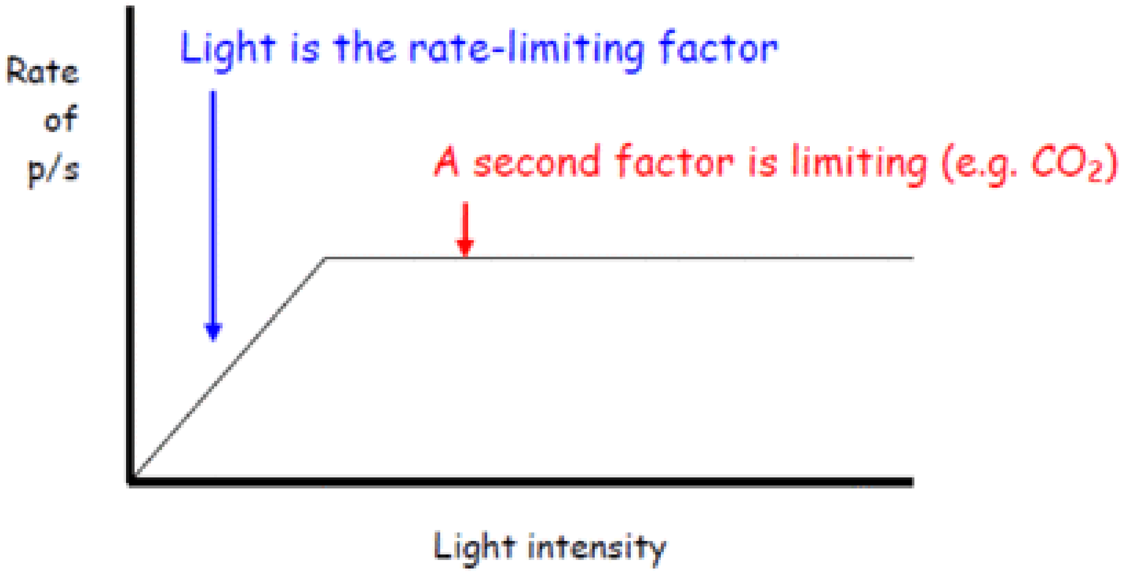


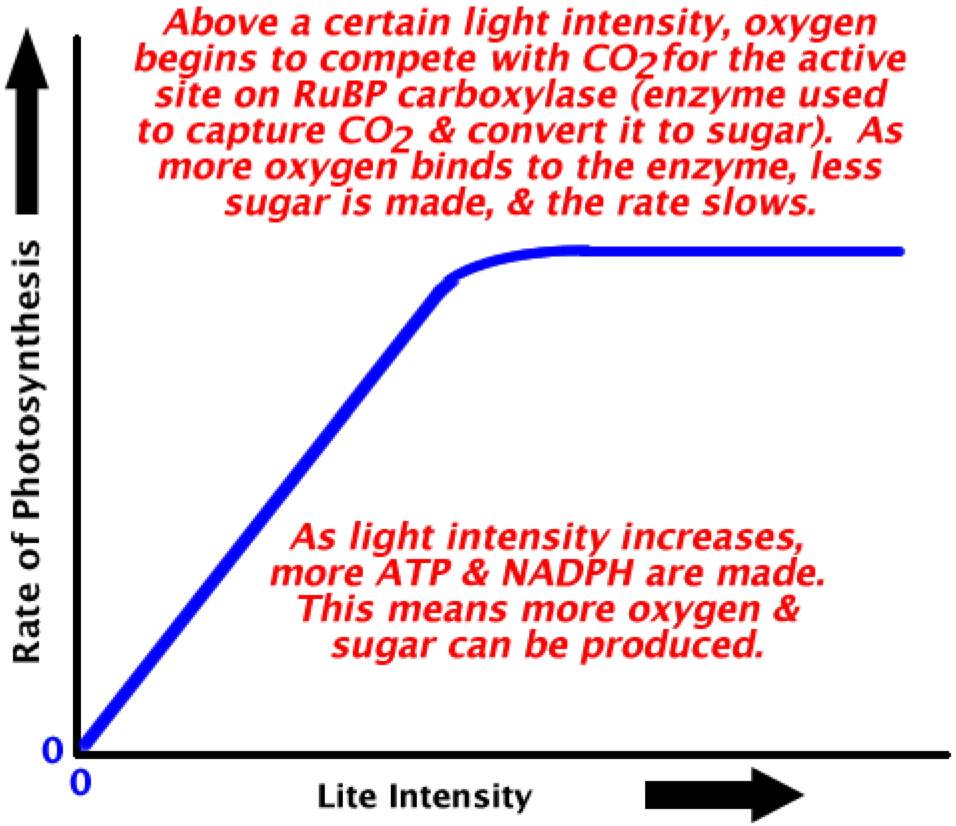
Even if there is plenty of light, a plant cannot perform photosynthesis if there is insufficient carbon dioxide.

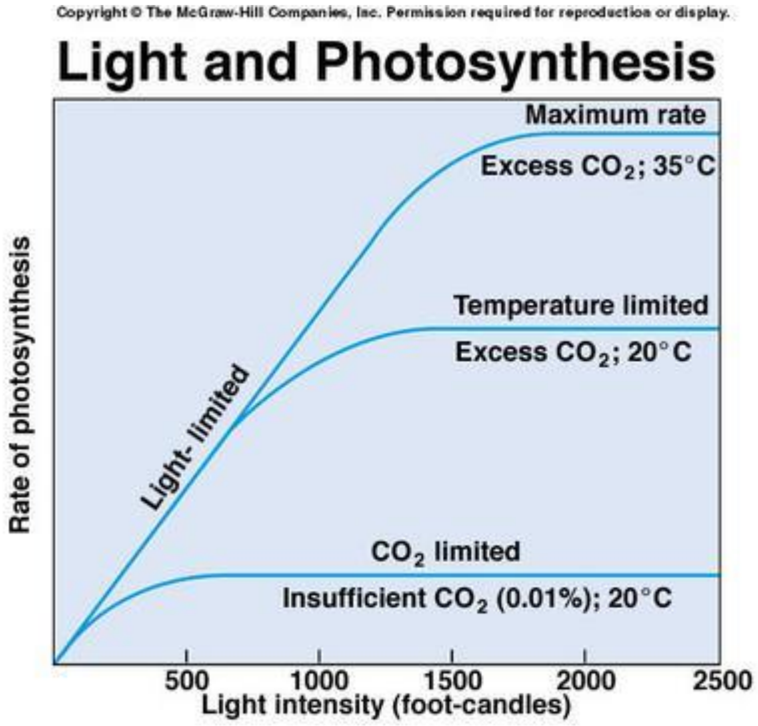


- Light intensity: Without enough light, a plant cannot perform photosynthesis very quickly, even if there is plenty of water and carbon dioxide. Increasing the light intensity will boost the speed of photosynthesis. However in too intense light photosynthesis will not increase any longer. In addition, if sufficient CO_2 is not present, then photosynthesis rate will not increase.






Above a certain light intensity, oxygen begins to compete with CO_2 for the active site on RuBP carboxylase (enzyme used to capture CO_2 & convert it to sugar). As more oxygen binds to the enzyme, less sugar is made, & the rate slows.
As light intensity increases, more ATP & NADPH are made. This means more oxygen & sugar can be produced.
Rate of Photosynthesis
0
0
Lite Intensity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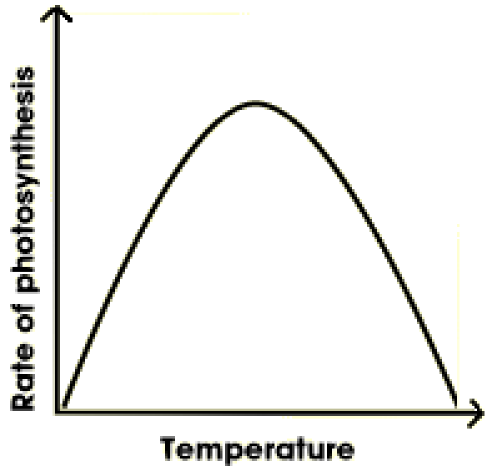
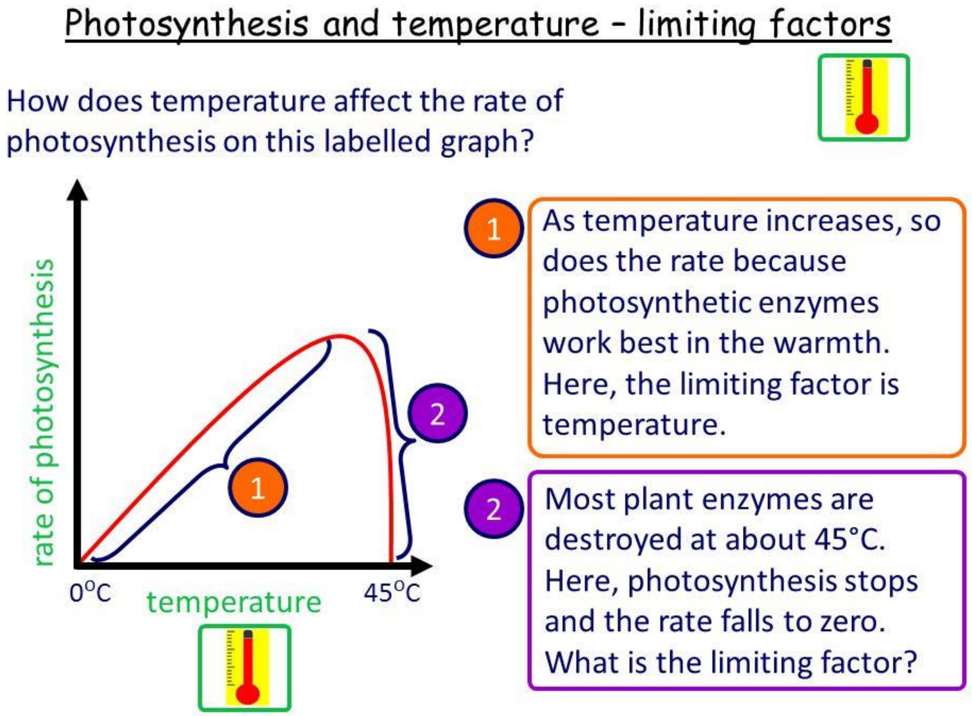
Light and Photosynthesis
Maximum rate
Excess CO_2; 35°C
Temperature limited
Excess CO_2; 20°C
Light- limited
CO_2 limited
Insufficient CO_2 (0.01%); 20°C
Rate of photosynthesis
500
1000
1500
2000
2500
Light intensity (foot-candles)

Temperature: If it gets too cold, the rate of photosynthesis will decrease. And also, plants cannot perform photosynthesis if it gets too hot. The effect of temperature varies accroding to the climate. In general, photosynthesis stops in plants growing in the tropics or subtropics aslightly above the freezng point of water. However it continues in plants growing in temperate regions till the freezing point of water. The optimal temperature for photosynthesis in most plants is between +20 and +30°C.





- Mineral elements: Minerals such as Mg, Fe, Mn, K andN has to be present at a sufficient level for photosynthesis.

- Water: Without water, photosynthesis can not be performed. Plants need water both to survive and also as a hydrogen source. A plant uses 1% of water that it gets for photosynthesis.

- O_2 concentration: The atmosphere has 21% oxygen. Above this percentage photosynthesis halts and below it increases.

- Chlorophyll amount: Increase in chlorophyll amount affects photosynthesis positively.

COMPARISON OF PHOTOSYNTHESIS WITH CELLULAR RESPIRATION

	CELLULAR RESPIRATION	PHOTOSYNTHESIS
a) Used substance:	Glucose, lipids, proteins, O_2	CO_2, H_2O
b) Final product:	CO_2, H_2O, Energy	Glucose, H_2O, O_2
c) Chemical change:	Breakdown of organic molecules	Production of organic molecules
d) Occurs when?	Continuously	During daylight
e) Where:	In all living cells	In cells that contain chlorophyll
f) General formula:	A) Cellular respiration: $C_6H_{12}O_6$ + $6O_2 \rightarrow 6CO_2$ + $6H_2O$ + 38 ATP (via enzyme)	Solar energy B) Photosynthesis: $6CO_2 + 12H_2O \rightarrow C_6H_{12}O_6 + 6H_2O + 6O_2$ (via solar energy)