

8

Photosynthesis

The Process That Feeds the Biosphere

- **Photosynthesis** is the process that converts solar energy into chemical energy
- Directly or indirectly, photosynthesis nourishes almost the entire living world

- **Autotrophs** sustain themselves without eating anything derived from other organisms
- Autotrophs are the producers of the biosphere, producing organic molecules from CO_2 and other inorganic molecules
- Almost all plants are photoautotrophs, using the energy of sunlight to make organic molecules

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Figure 8.1



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- **Heterotrophs** obtain their organic material from other organisms
- Heterotrophs are the consumers of the biosphere
- Almost all heterotrophs, including humans, depend on photoautotrophs for food and O₂

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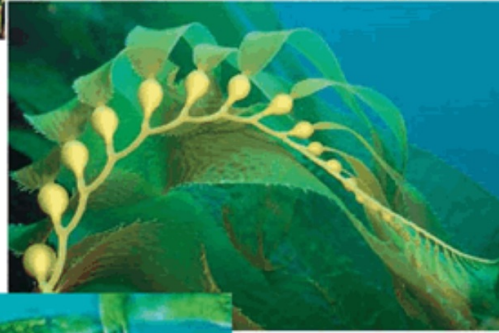
- Photosynthesis occurs in plants, algae, certain other protists, and some prokaryotes
- These organisms feed not only themselves but also most of the living world

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Figure 8.2



(a) Plants

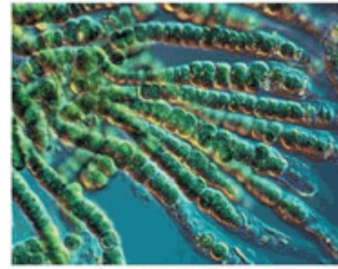


(b) Multicellular
alga



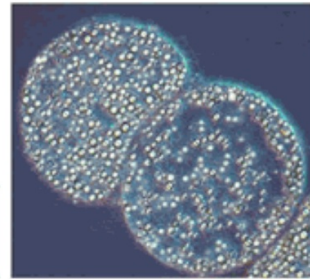
10
 μn

(c) Unicellular eukaryotes



40
 μn

(d) Cyanobacteria



1
 μn

(e) Purple sulfur
bacteria

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Concept 8.1: Photosynthesis converts light energy to the chemical energy of food

- The structural organization of photosynthetic cells includes enzymes and other molecules grouped together in a membrane
- This organization allows for the chemical reactions of photosynthesis to proceed efficiently
- Chloroplasts are structurally similar to and likely evolved from photosynthetic bacteria

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Chloroplasts: The Sites of Photosynthesis in Plants

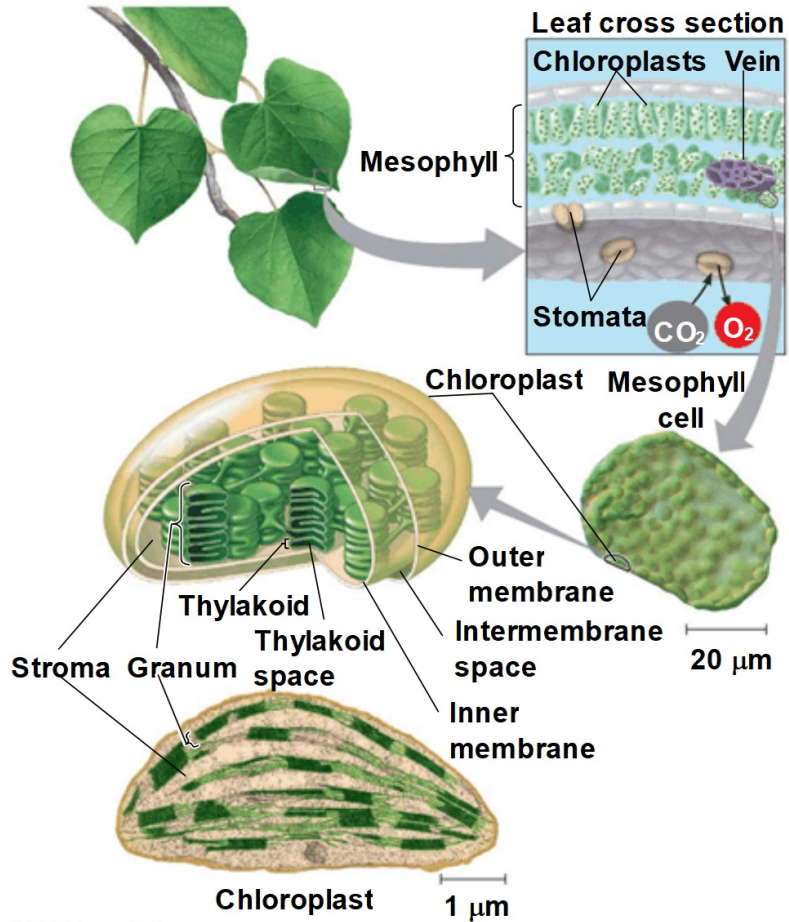
- Leaves are the major locations of photosynthesis
- Their green color is from **chlorophyll**, the green pigment within chloroplasts
- Chloroplasts are found mainly in cells of the **mesophyll**, the interior tissue of the leaf
- Each mesophyll cell contains 30–40 chloroplasts

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- CO₂ enters and O₂ exits the leaf through microscopic pores called **stomata**
- The chlorophyll is in the membranes of **thylakoids** (connected sacs in the chloroplast); thylakoids may be stacked in columns called grana
- Chloroplasts also contain **stroma**, a dense interior fluid

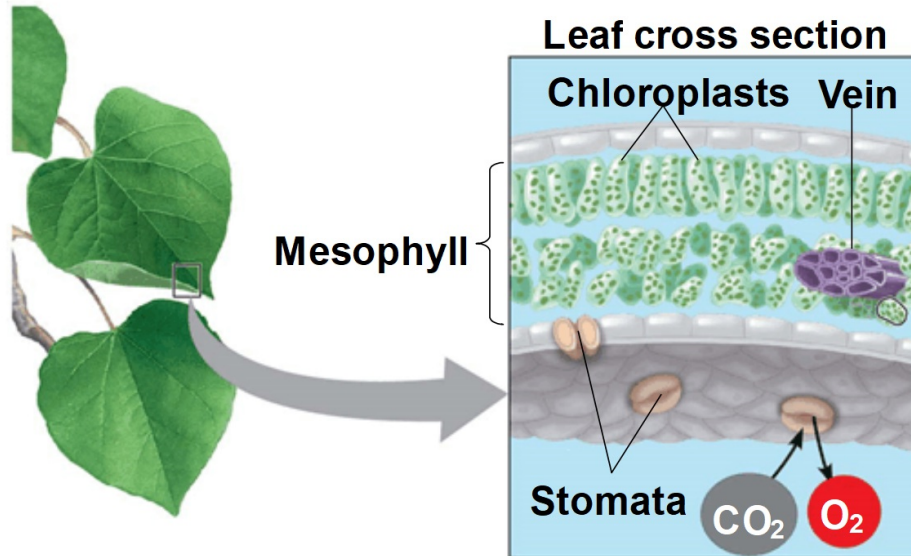
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Figure 8.3



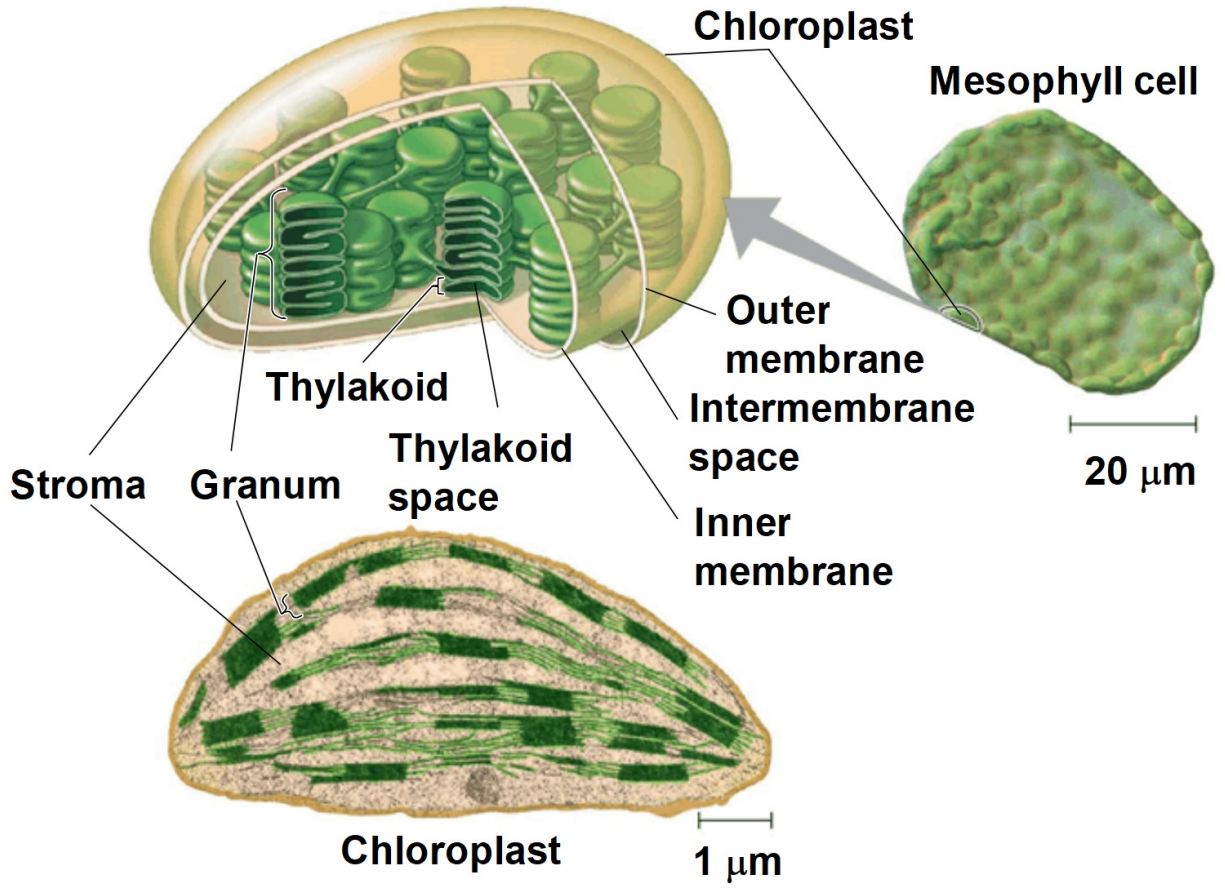
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Figure 8.3-1



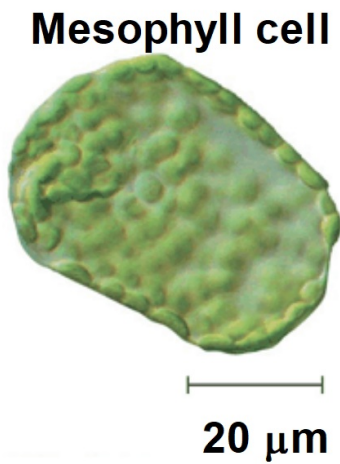
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Figure 8.3-2



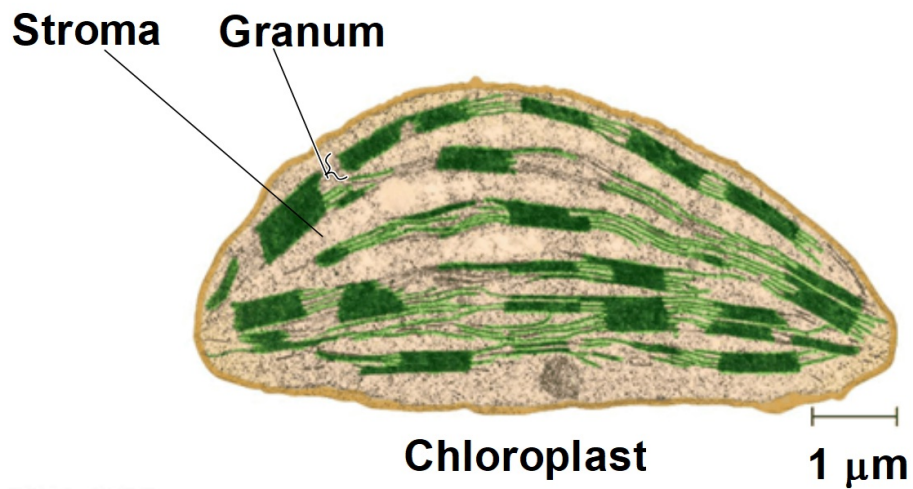
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Figure 8.3-3



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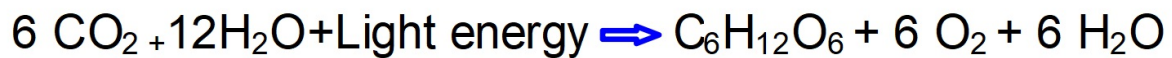
Figure 8.3-4



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Tracking Atoms Through Photosynthesis: *Scientific Inquiry*

- Photosynthesis is a complex series of reactions that can be summarized as the following equation



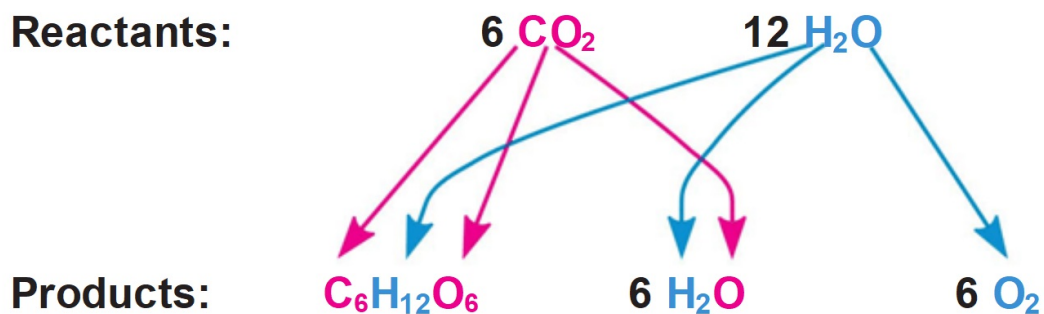
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The Splitting of Water

- Chloroplasts split H_2O into hydrogen and oxygen, incorporating the electrons of hydrogen into sugar molecules and releasing oxygen as a by-product

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Figure 8.4



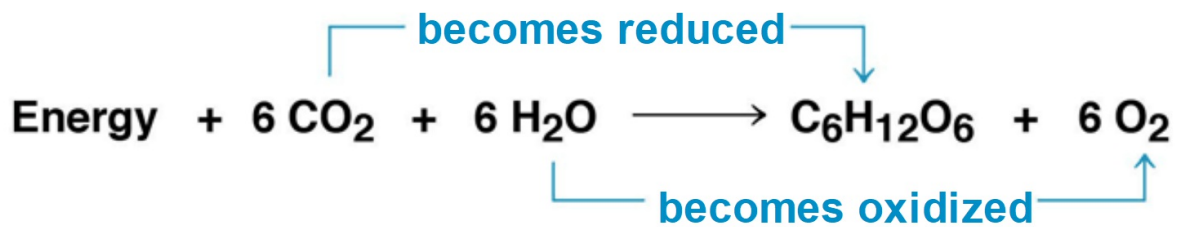
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Photosynthesis as a Redox Process

- Photosynthesis reverses the direction of electron flow compared to respiration
- Photosynthesis is a redox process in which H₂O is oxidized and CO₂ is reduced
- Photosynthesis is an endergonic process; the energy boost is provided by light

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Figure 8.UN01



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The Two Stages of Photosynthesis: *A Preview*

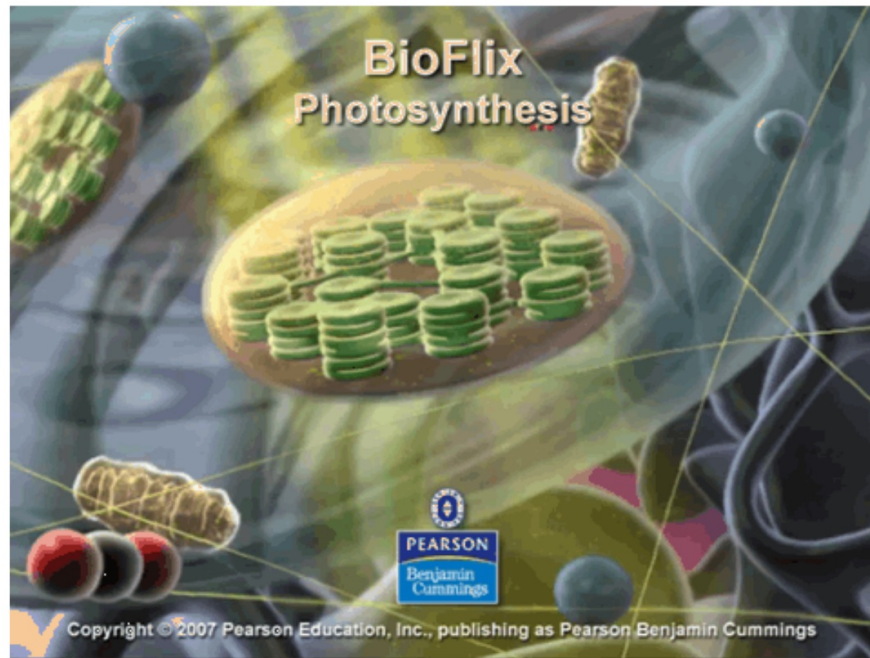
- Photosynthesis consists of the **light reactions** (the *photo* part) and **Calvin cycle** (the *synthesis* part)
- The light reactions (in the thylakoids)
 - Split H₂O
 - Release O₂
 - Reduce the electron acceptor, **NADP⁺**, to **NADPH**
 - Generate ATP from ADP by adding a phosphate group, **photophosphorylation**

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- The Calvin cycle (in the stroma) forms sugar from CO₂, using ATP and NADPH
- The Calvin cycle begins with **carbon fixation**, incorporating CO₂ into organic molecules

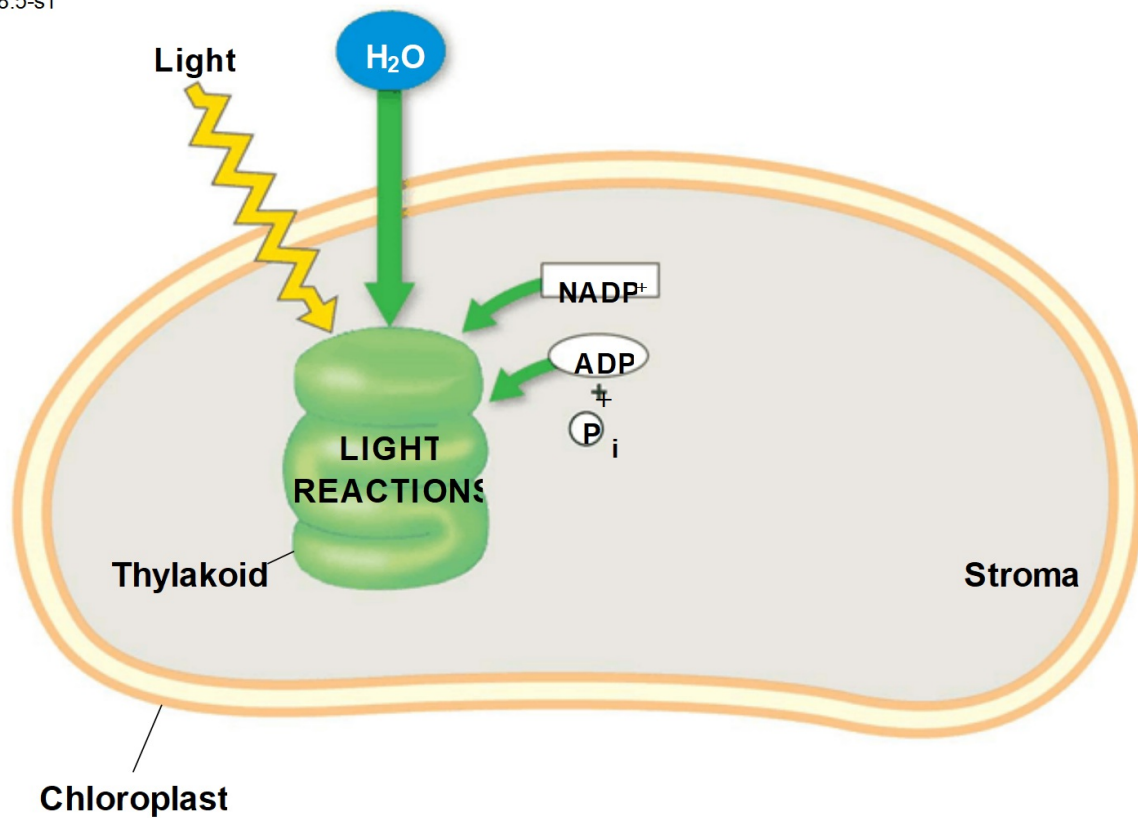
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Animation: Photosynthesis



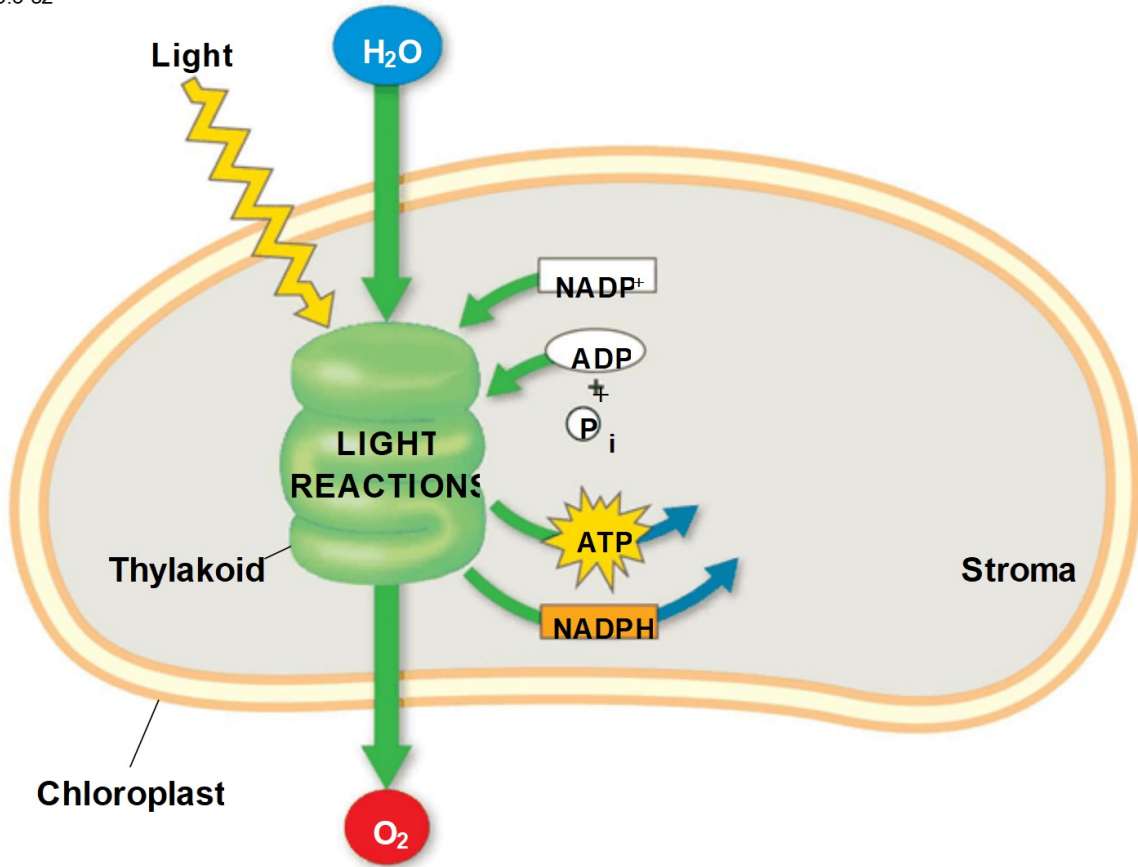
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Figure 8.5-s1



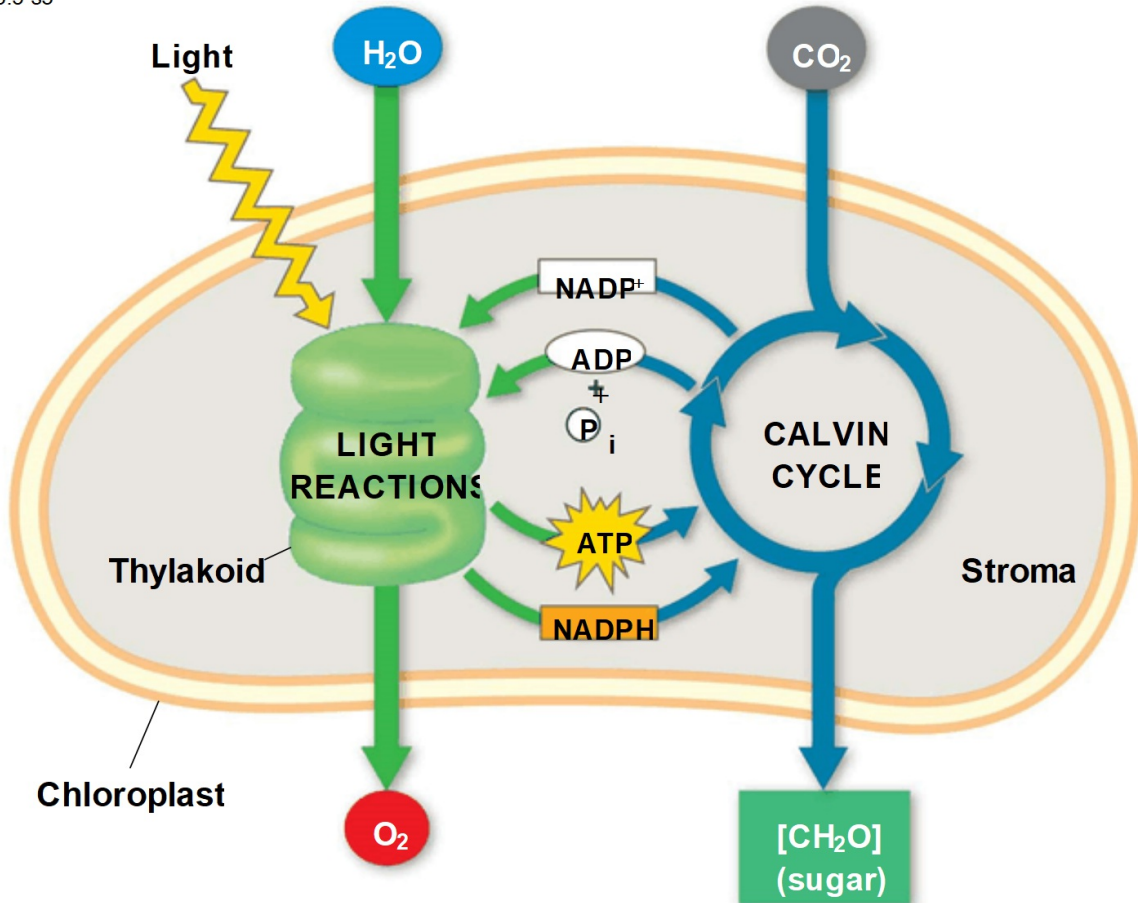
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Figure 8.5-s2



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Figure 8.5-s3



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Concept 8.2: The light reactions convert solar energy to the chemical energy of ATP and NADPH

- Chloroplasts are solar-powered chemical factories
- Their thylakoids transform light energy into the chemical energy of ATP and NADPH

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The Nature of Sunlight

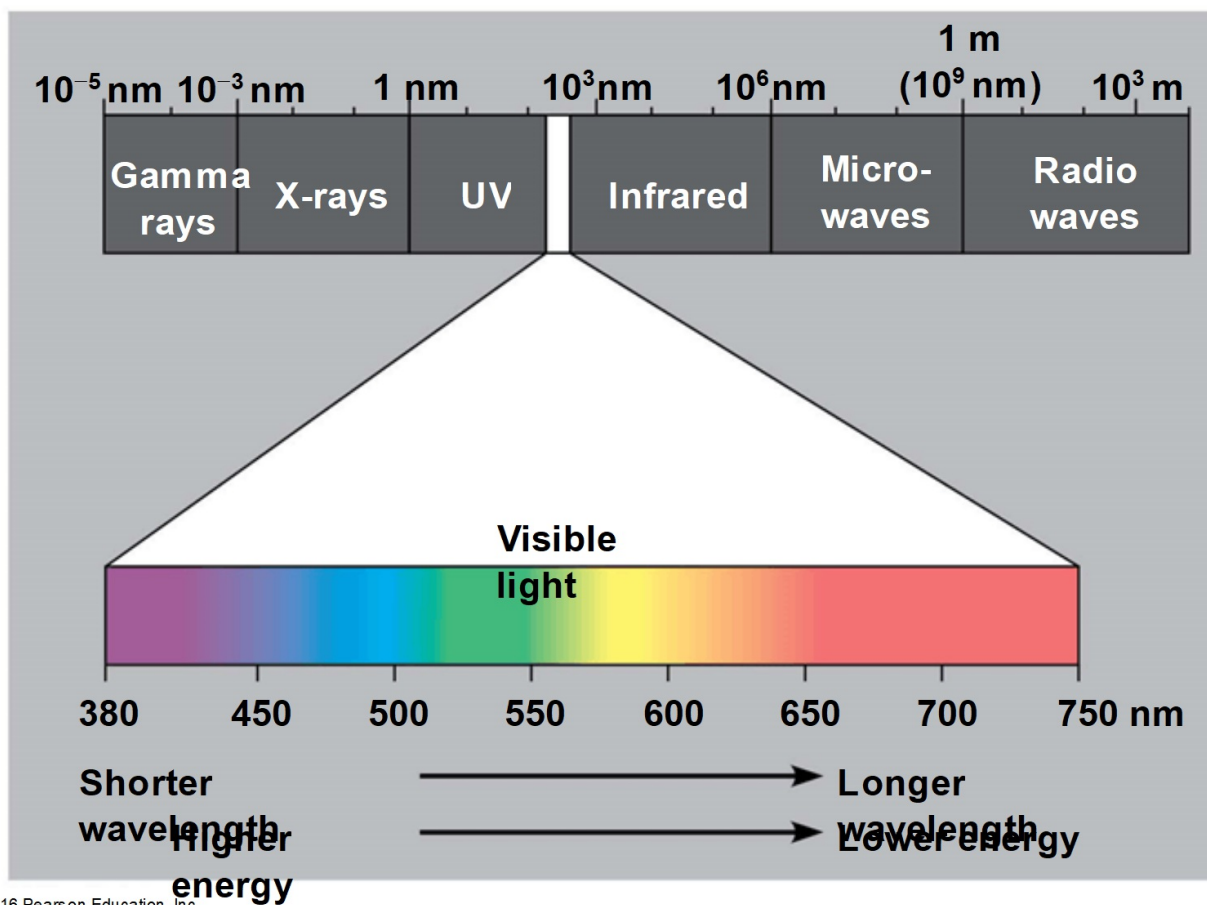
- Light is a form of electromagnetic energy, also called electromagnetic radiation
- Like other electromagnetic energy, light travels in rhythmic waves
- **Wavelength** is the distance between crests of waves
- Wavelength determines the type of electromagnetic energy

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- The **electromagnetic spectrum** is the entire range of electromagnetic energy, or radiation
- **Visible light** consists of wavelengths (including those that drive photosynthesis) that produce colors we can see
- Light also behaves as though it consists of discrete particles, called **photons**

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Figure 8.6



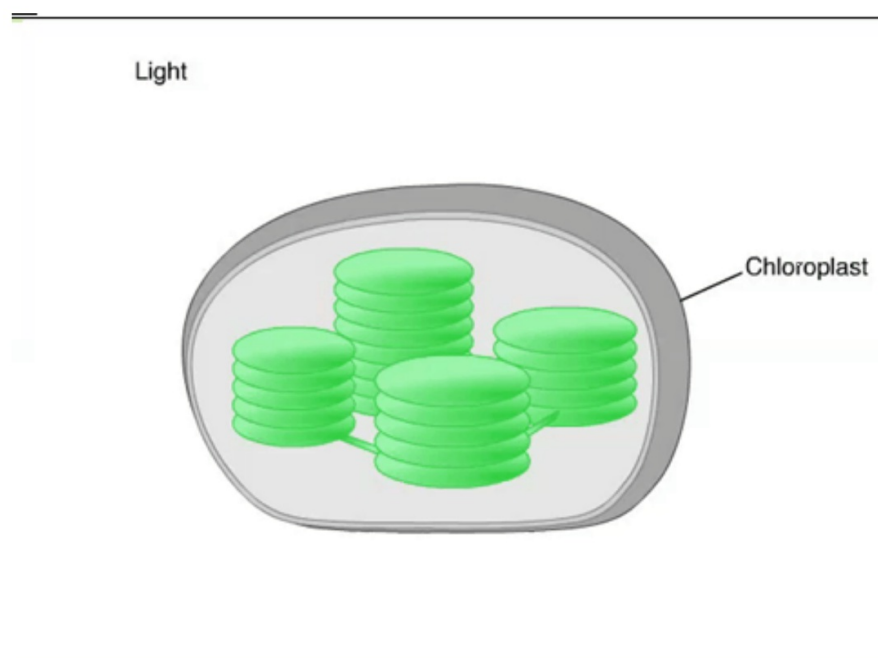
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Photosynthetic Pigments: The Light Receptors

- Pigments are substances that absorb visible light
- Different pigments absorb different wavelengths
- Wavelengths that are not absorbed are reflected or transmitted
- Leaves appear green because chlorophyll reflects and transmits green light

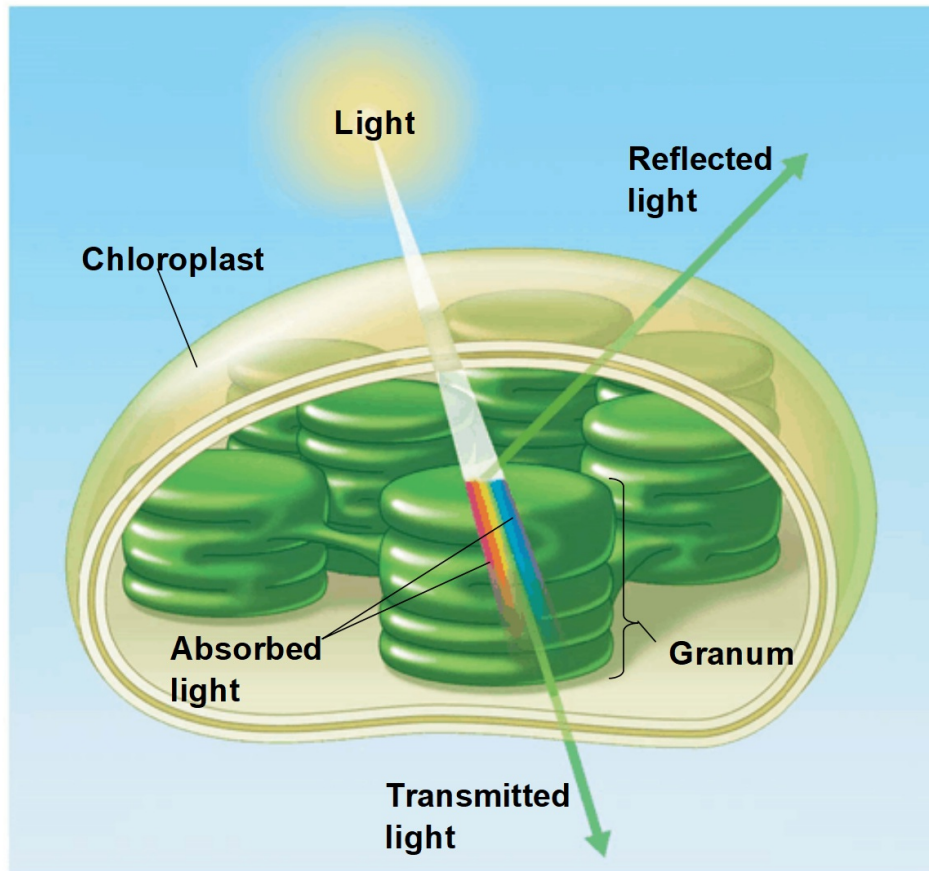
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Animation: Light and Pigments



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Figure 8.7



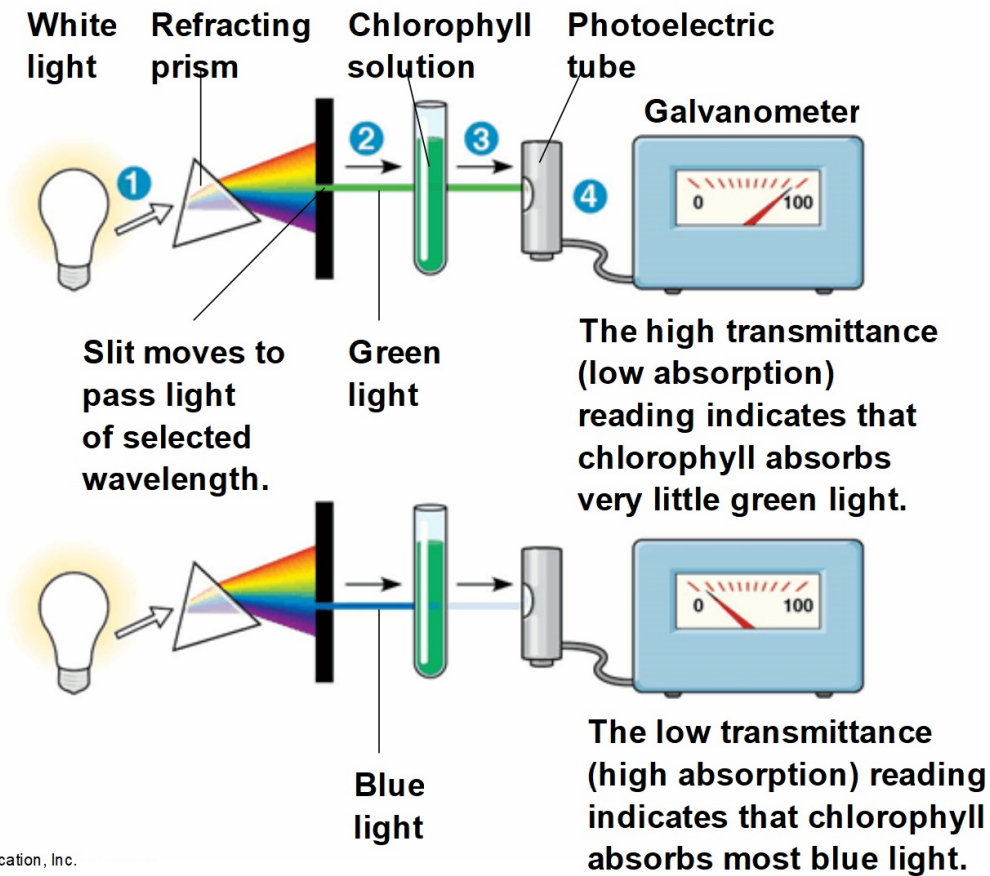
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- A **spectrophotometer** measures a pigment's ability to absorb various wavelengths
- This machine sends light through pigments and measures the fraction of light transmitted at each wavelength

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Figure 8.8

Technique

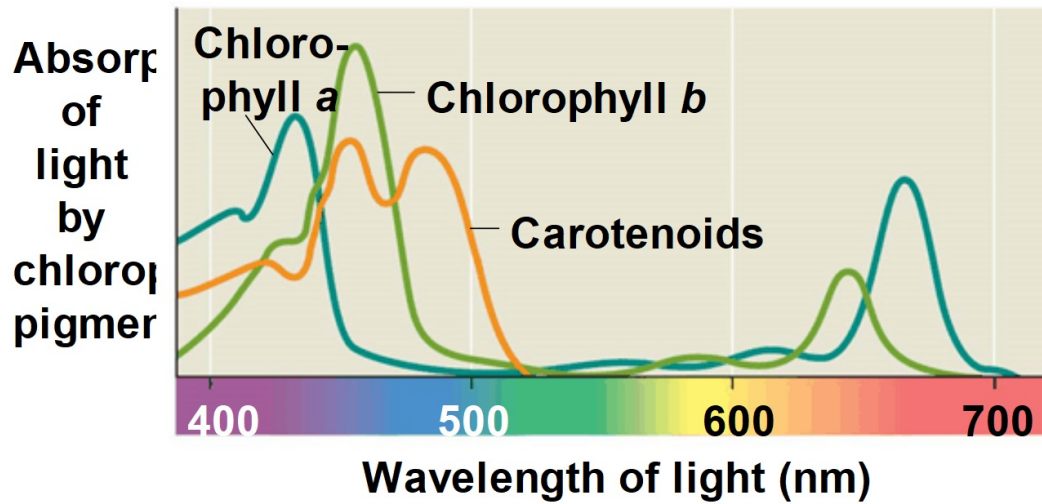


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- An **absorption spectrum** is a graph that plots a pigment's light absorption versus wavelength
- The absorption spectrum of **chlorophyll a** suggests that violet-blue and red light work best for photosynthesis
- Accessory pigments include **chlorophyll b** and a group of pigments called carotenoids

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Figure 8.9-1



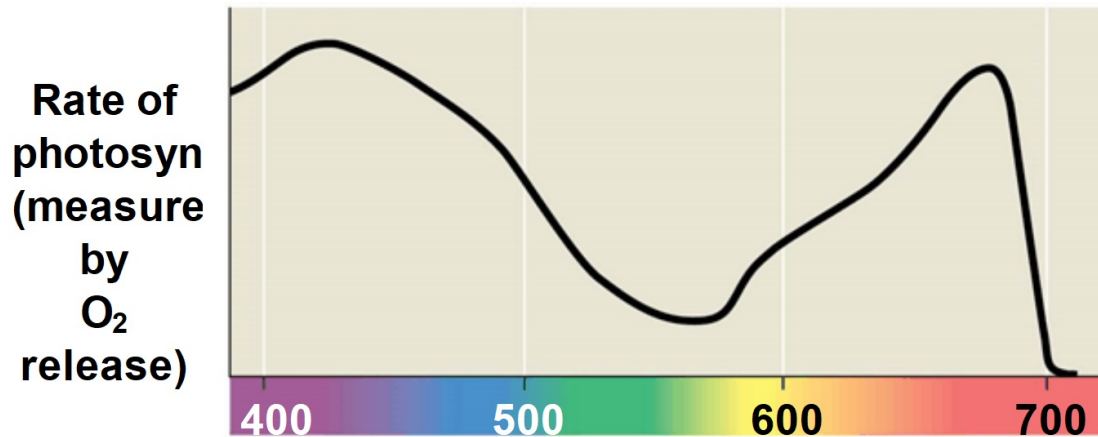
(a) Absorption spectra

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- An **action spectrum** profiles the relative effectiveness of different wavelengths of radiation in driving a process

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Figure 8.9-2



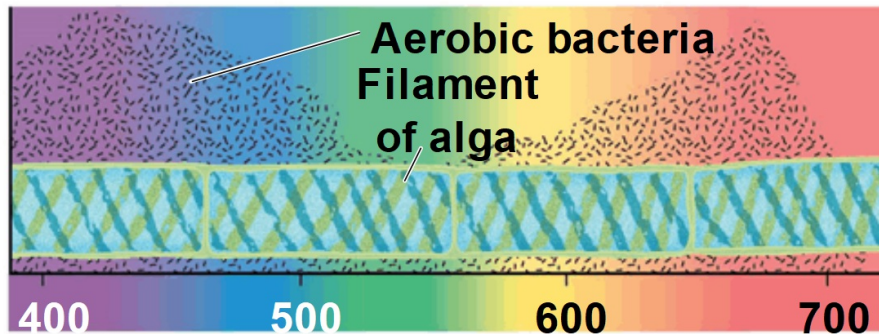
(b) Action spectrum

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- The action spectrum of photosynthesis was first demonstrated in 1883 by Theodor W. Engelmann
- In his experiment, he exposed different segments of a filamentous alga to different wavelengths
- Areas receiving wavelengths favorable to photosynthesis produced excess O₂
- He used the growth of aerobic bacteria clustered along the alga as a measure of O₂ production

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Figure 8.9-3



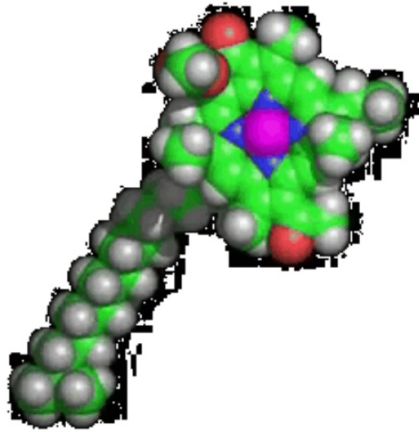
(c) Engelmann's experiment

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- Chlorophyll *a* is the main photosynthetic pigment
- Accessory pigments, such as chlorophyll *b*, broaden the spectrum used for photosynthesis
- A slight structural difference between chlorophyll *a* and chlorophyll *b* causes them to absorb slightly different wavelengths
- Accessory pigments called **carotenoids** absorb excessive light that would damage chlorophyll

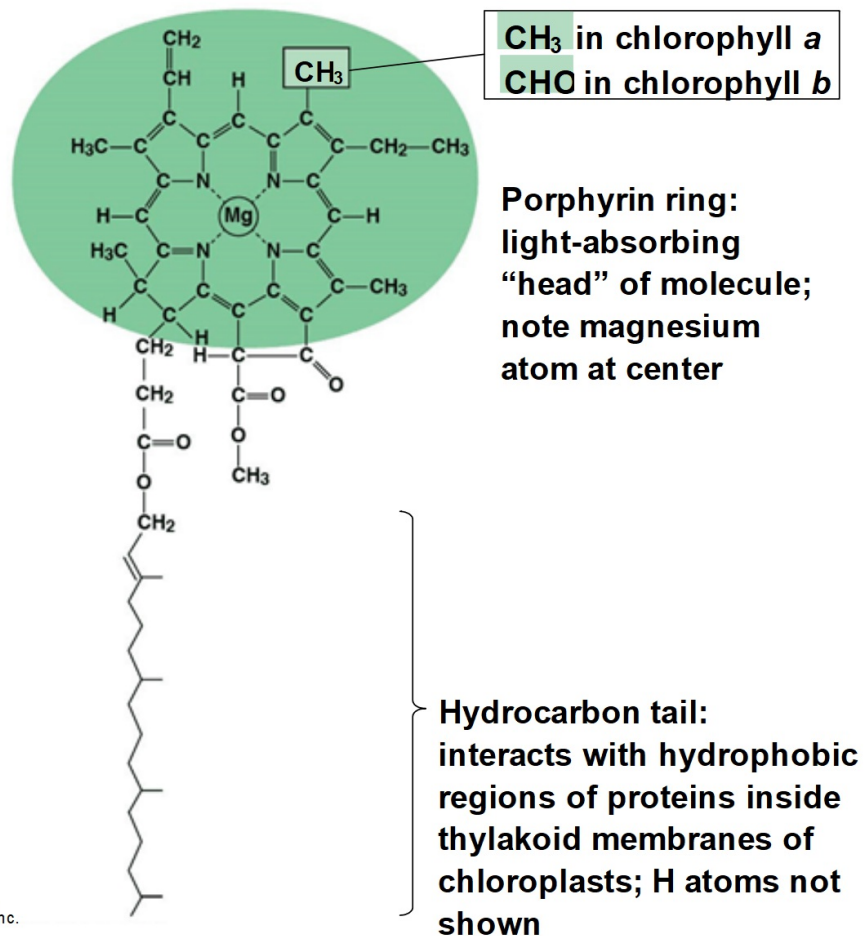
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Video: Chlorophyll Model



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Figure 8.10



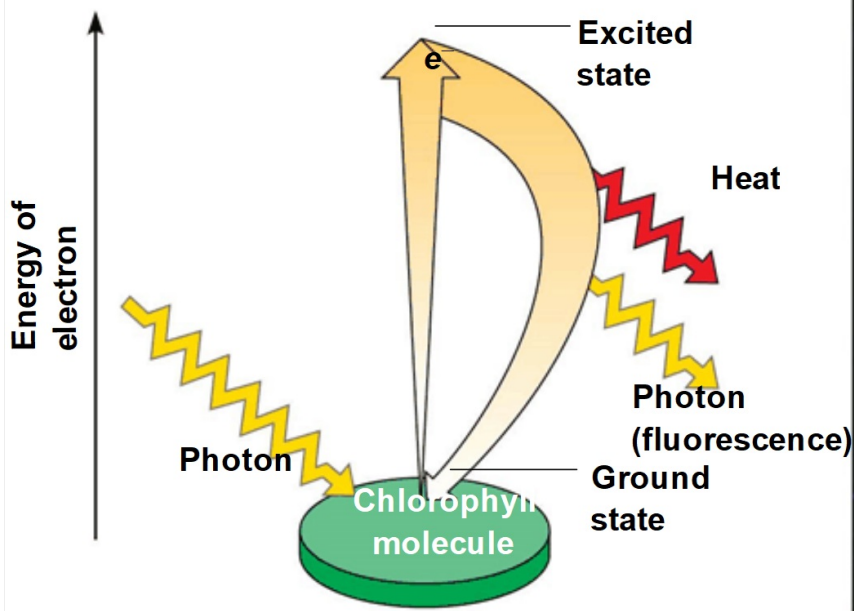
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Excitation of Chlorophyll by Light

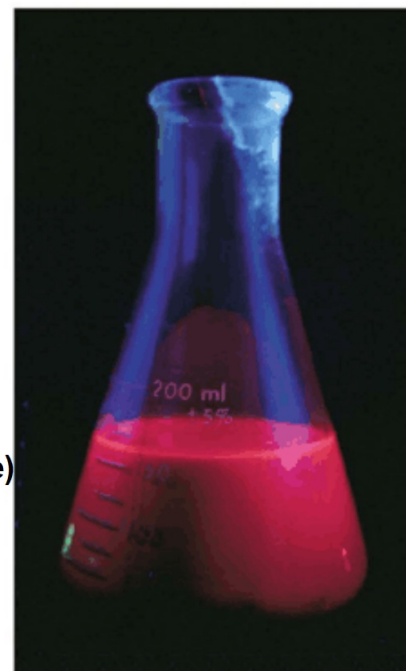
- When a pigment absorbs light, it goes from a ground state to an excited state, which is unstable
- When excited electrons fall back to the ground state, photons are given off, an afterglow called fluorescence
- If illuminated, an isolated solution of chlorophyll will fluoresce, giving off light and heat

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Figure 8.11



(a) Excitation of isolated chlorophyll molecule



(b) Fluorescence

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(b) Fluorescence

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A Photosystem: A Reaction-Center Complex Associated with Light-Harvesting Complexes

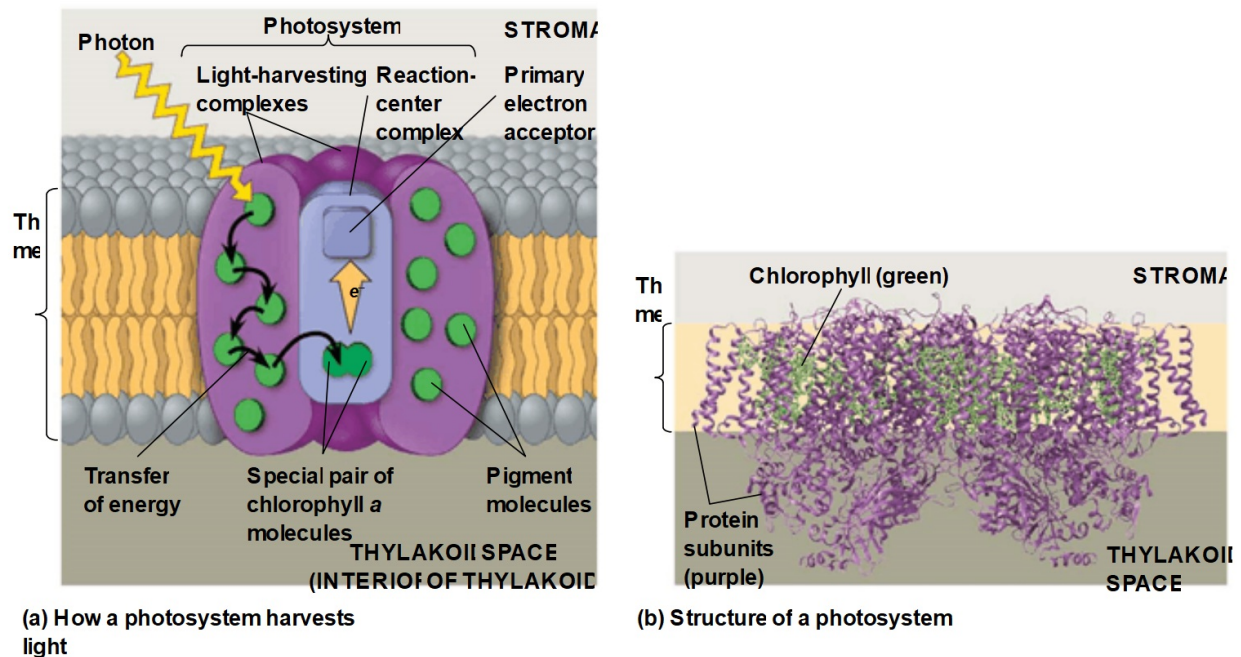
- A **photosystem** consists of a **reaction-center complex** (a type of protein complex) surrounded by light-harvesting complexes
- The **light-harvesting complexes** (pigment molecules bound to proteins) transfer the energy of photons to the reaction center

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- A **primary electron acceptor** in the reaction center accepts excited electrons and is reduced as a result
- Solar-powered transfer of an electron from a chlorophyll *a* molecule to the primary electron acceptor is the first step of the light reactions

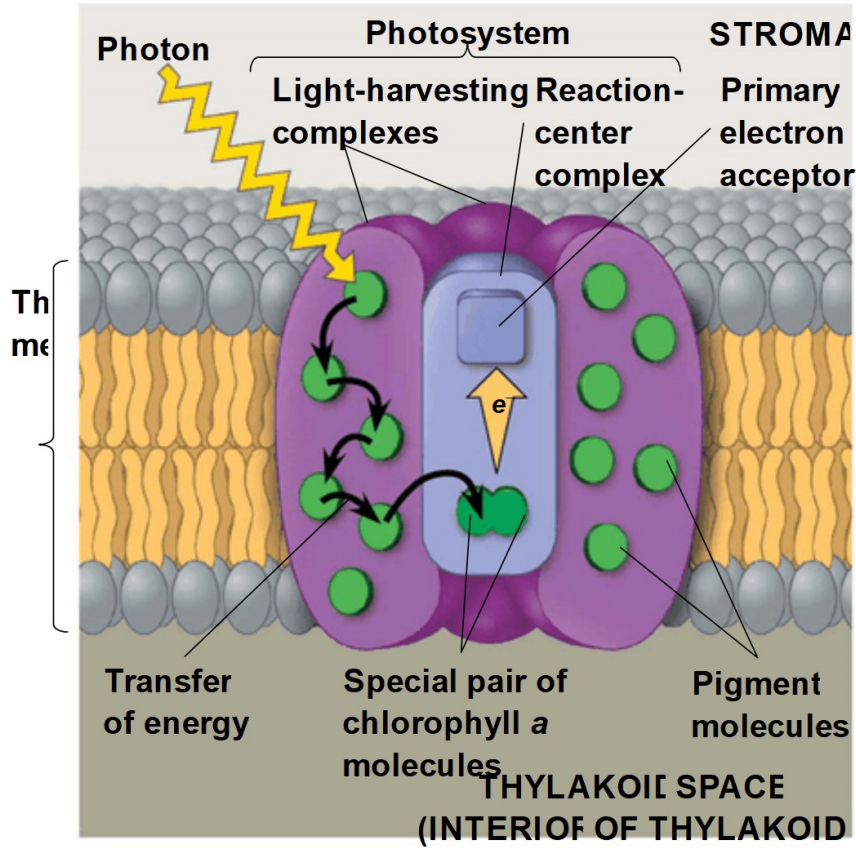
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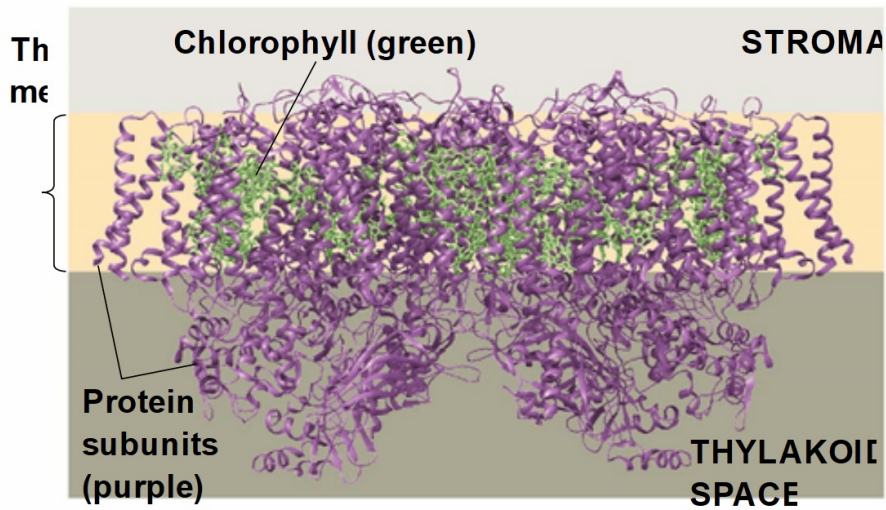
Figure 8.12-1



(a) How a photosystem harvests light

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Figure 8.12-2



(b) Structure of a photosystem

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- There are two types of photosystems in the thylakoid membrane
- **Photosystem II (PS II)** functions first (the numbers reflect order of discovery) and is best at absorbing a wavelength of 680 nm
- The reaction-center chlorophyll *a* of PS II is called P680

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- **Photosystem I (PS I)** is best at absorbing a wavelength of 700 nm
- The reaction-center chlorophyll *a* of PS I is called P700
- P680 and P700 are nearly identical, but their association with different proteins results in different light-absorbing properties

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Linear Electron Flow

- **Linear electron flow** involves the flow of electrons through the photosystems and other molecules embedded in the thylakoid membrane to produce ATP and NADPH using light energy

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- Linear electron flow can be broken down into a series of steps

A photon hits a pigment and its energy is passed among pigment molecules until it excites P680

An excited electron from P680 is transferred to the primary electron acceptor (we now call it P680⁺)

H₂O is split by enzymes, and the electrons are transferred from the hydrogen atoms to P680⁺, thus reducing it to P680; O₂ is released as a by-product

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Each electron “falls” down an electron transport chain from the primary electron acceptor of PS II to PS I

Energy released by the fall drives the creation of a proton gradient across the thylakoid membrane; diffusion of H^+ (protons) across the membrane drives ATP synthesis

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In PS I (like PS II), transferred light energy excites P700, causing it to lose an electron to an electron acceptor (we now call it P700⁺)

- P700⁺ accepts an electron passed down from PS II via the electron transport chain

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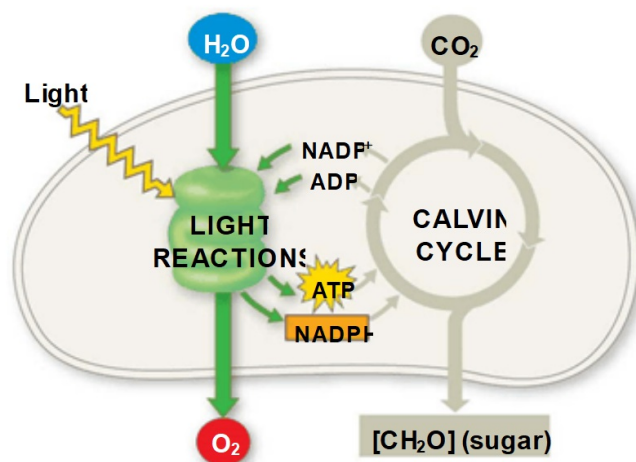
Excited electrons “fall” down an electron transport chain from the primary electron acceptor of PS I to the protein ferredoxin (Fd)

The electrons are transferred to NADP^+ , reducing it to NADPH, and become available for the reactions of the Calvin cycle

- This process also removes an H^+ from the stroma

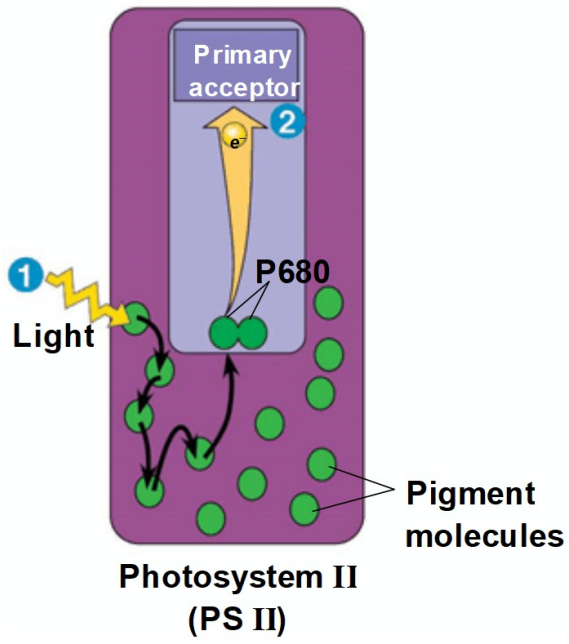
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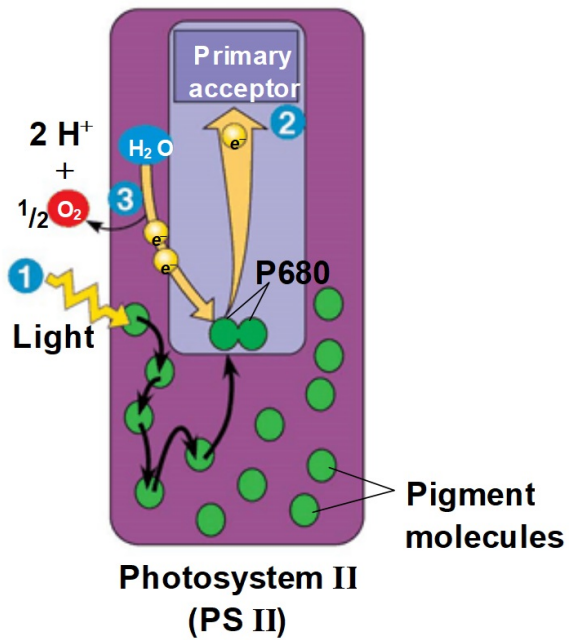
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Figure 8.13-s1



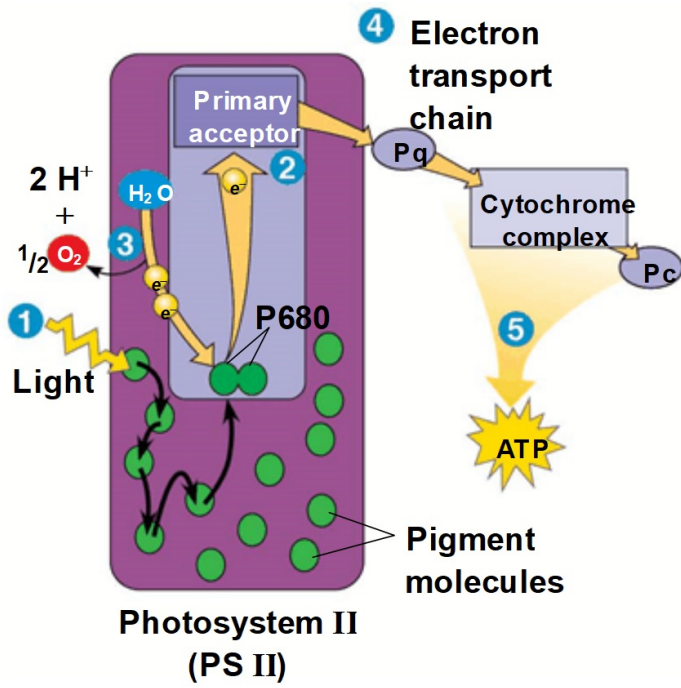
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Figure 8.13-s2



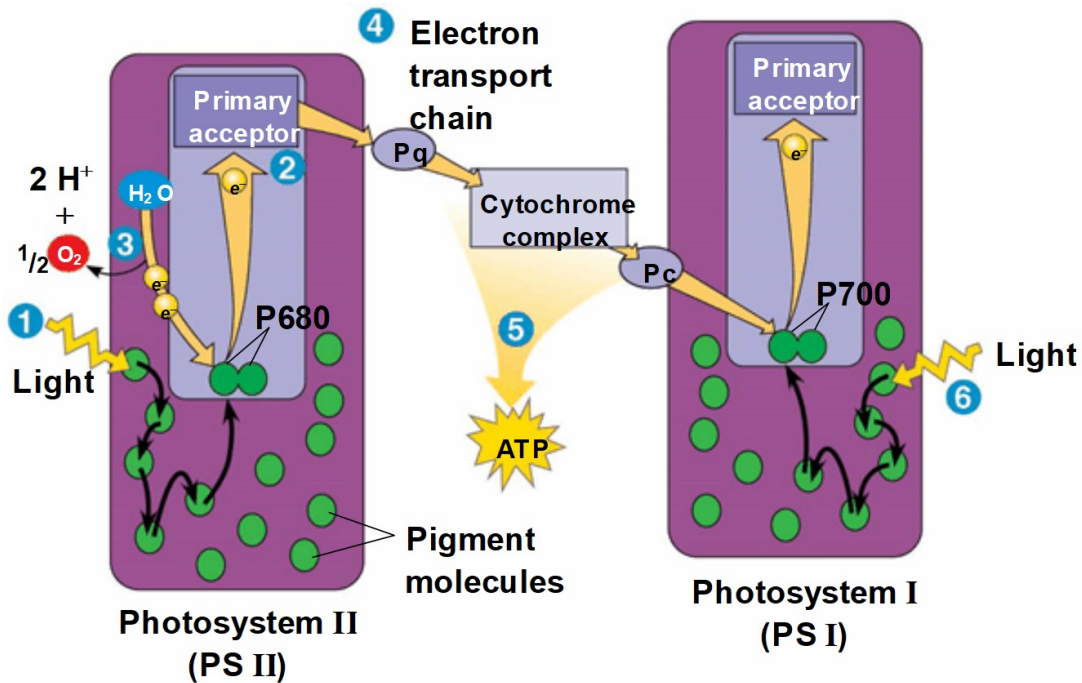
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Figure 8.13-s3



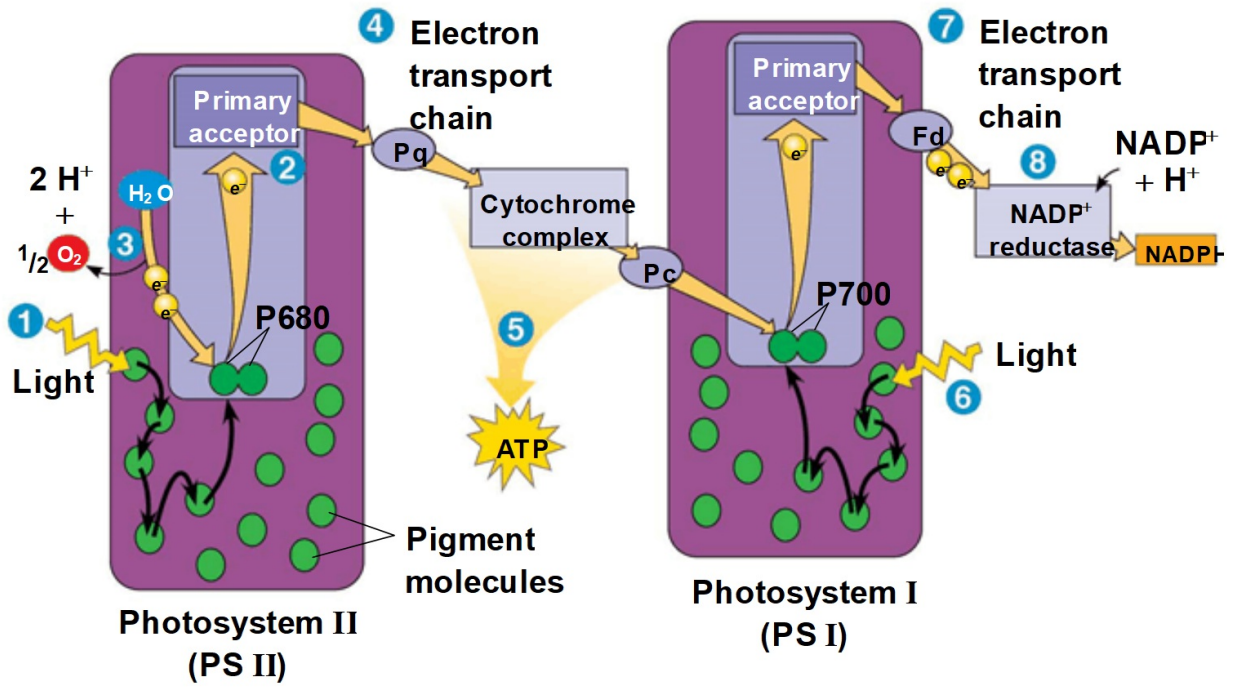
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Figure 8.13-s5

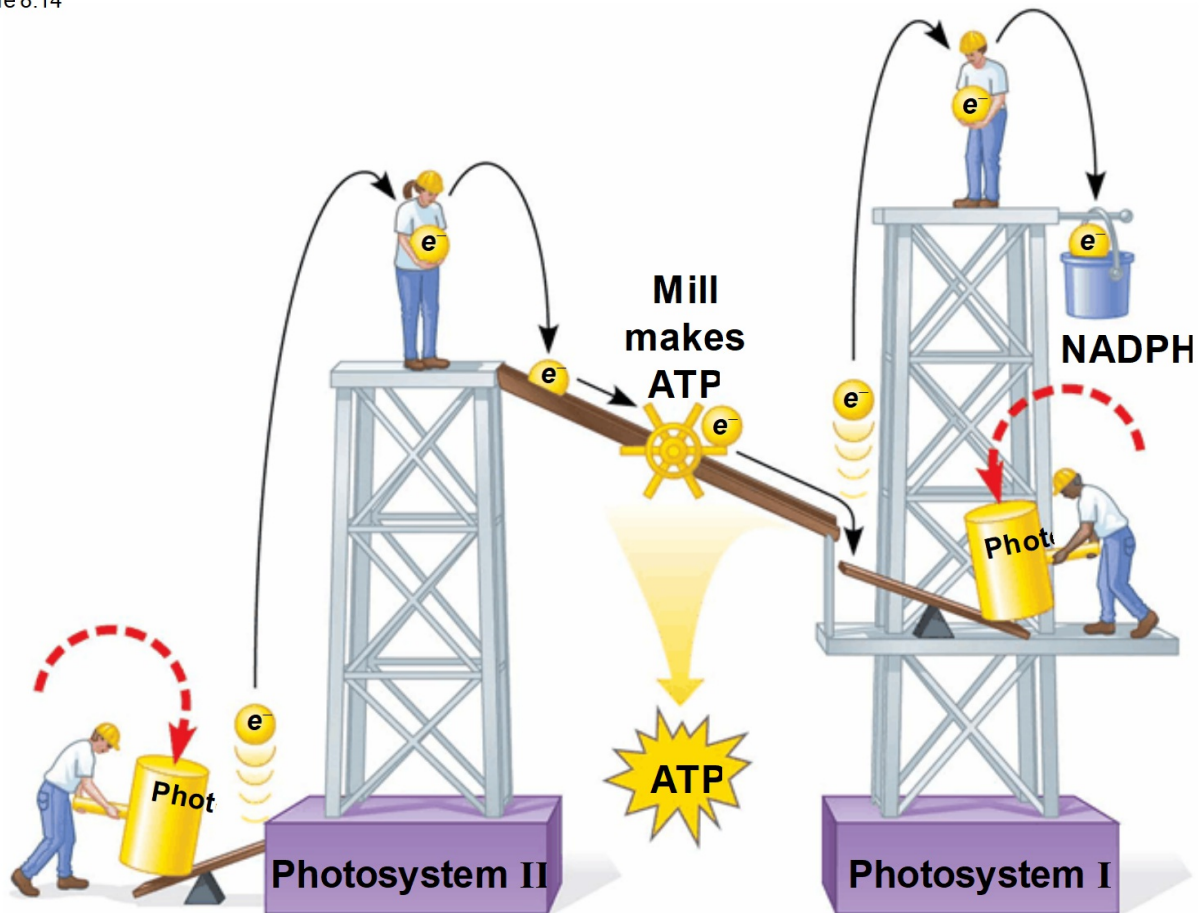


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- The energy changes of electrons during linear flow can be represented in a mechanical analogy

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Figure 8.14



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A Comparison of Chemiosmosis in Chloroplasts and Mitochondria

- Chloroplasts and mitochondria generate ATP by chemiosmosis but use different sources of energy
- Mitochondria transfer chemical energy from food to ATP; chloroplasts transform light energy into the chemical energy of ATP

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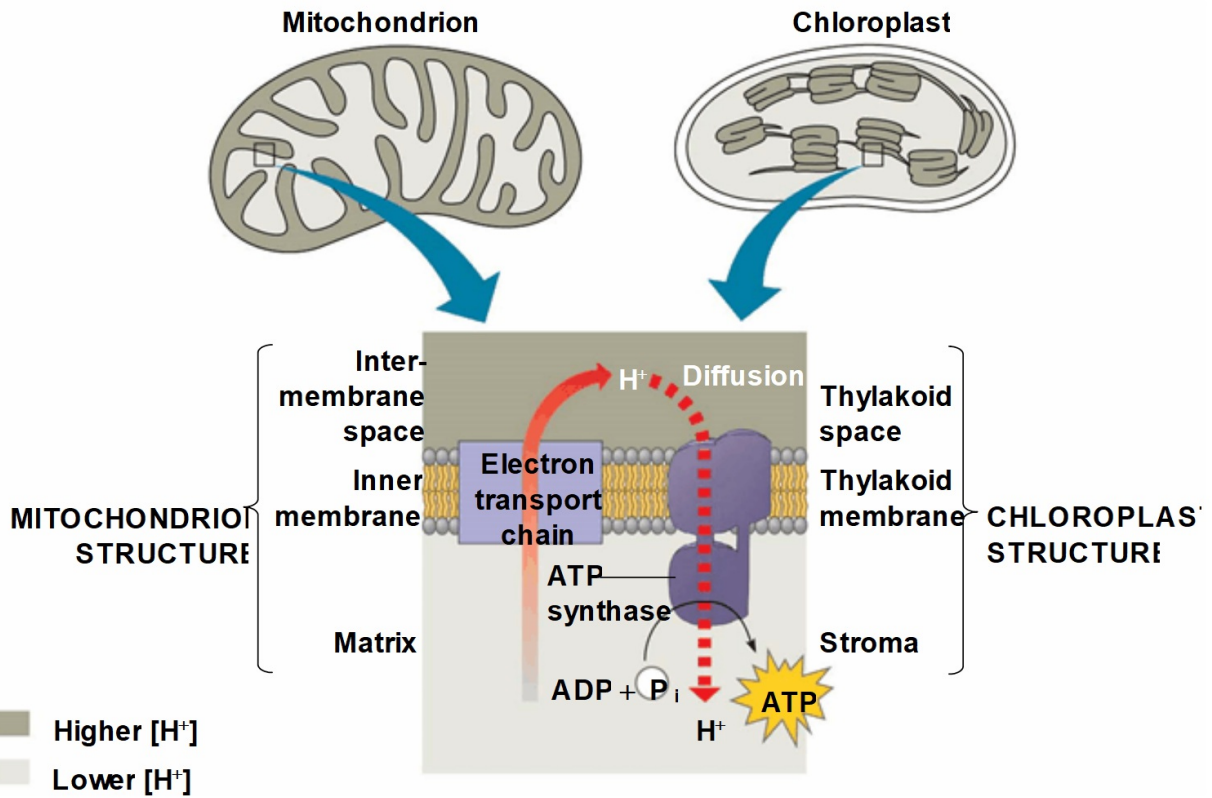
- Spatial organization of chemiosmosis differs between chloroplasts and mitochondria but there are also similarities
- Both use the energy generated by an electron transport chain to pump protons (H^+) across a membrane against their concentration gradient
- Both rely on the diffusion of protons through ATP synthase to drive the synthesis of ATP

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- In mitochondria, protons are pumped to the intermembrane space and drive ATP synthesis as they diffuse back into the mitochondrial matrix
- In chloroplasts, protons are pumped into the thylakoid space and drive ATP synthesis as they diffuse back into the stroma

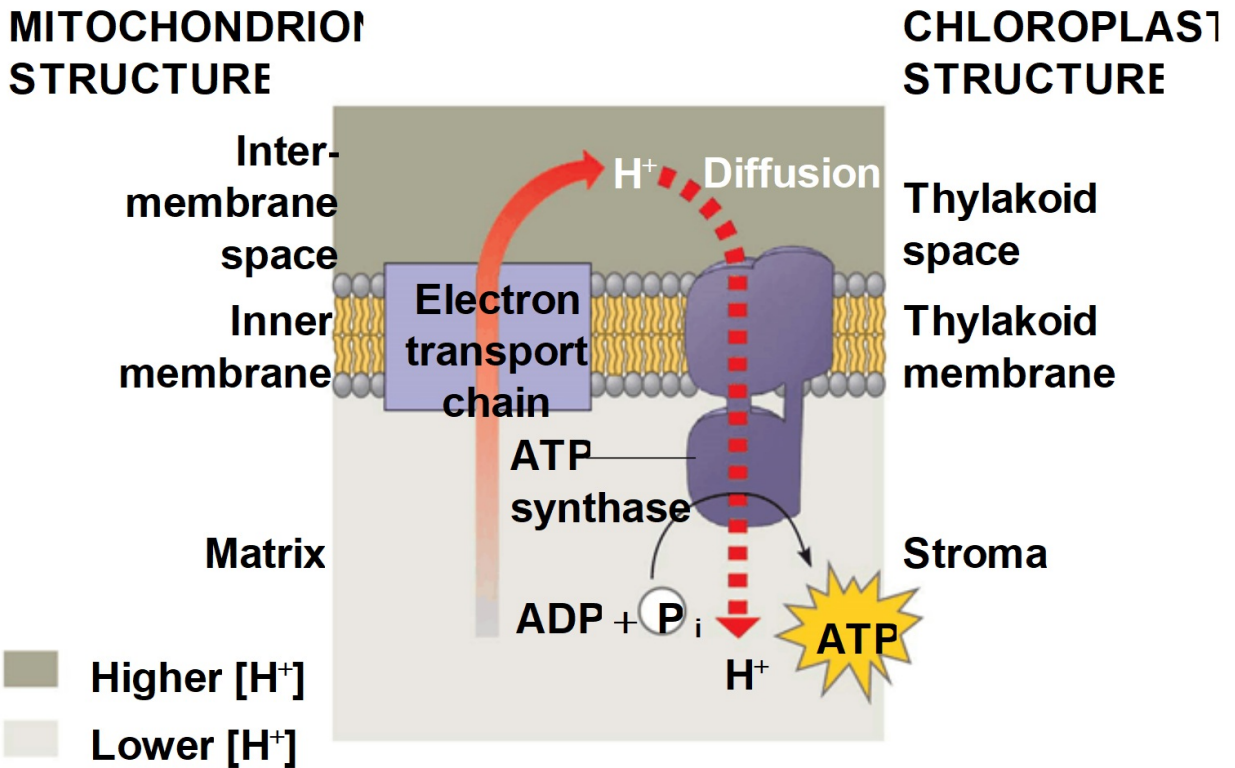
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Figure 8.15



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Figure 8.15-1

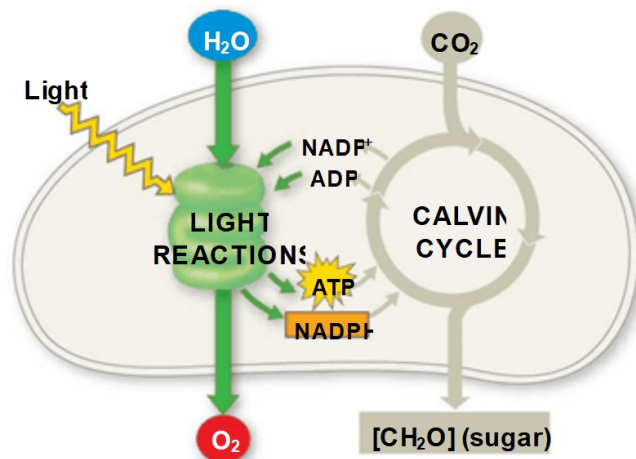


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- The light reactions of photosynthesis generate ATP and increase the potential energy of electrons by moving them from H_2O to NADPH
- ATP and NADPH are produced on the side of the thylakoid membrane facing the stroma, where the Calvin cycle takes place
- The Calvin cycle uses ATP and NADPH to power the synthesis of sugar from CO_2

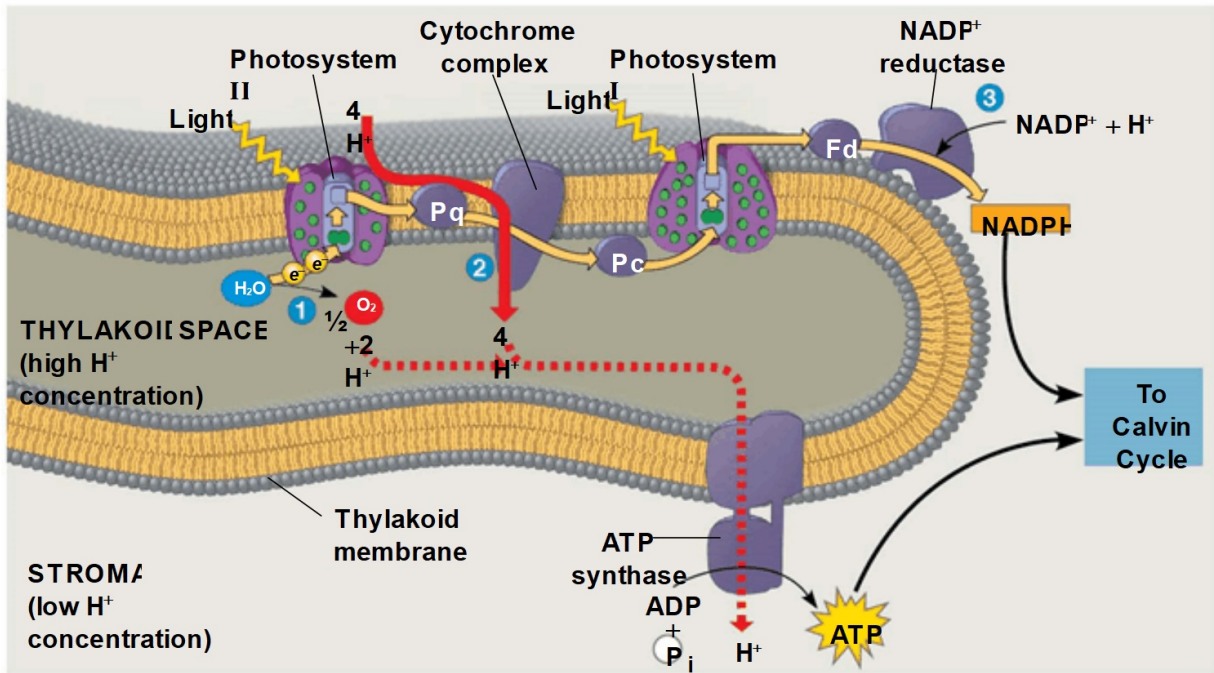
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Figure 8.UN02



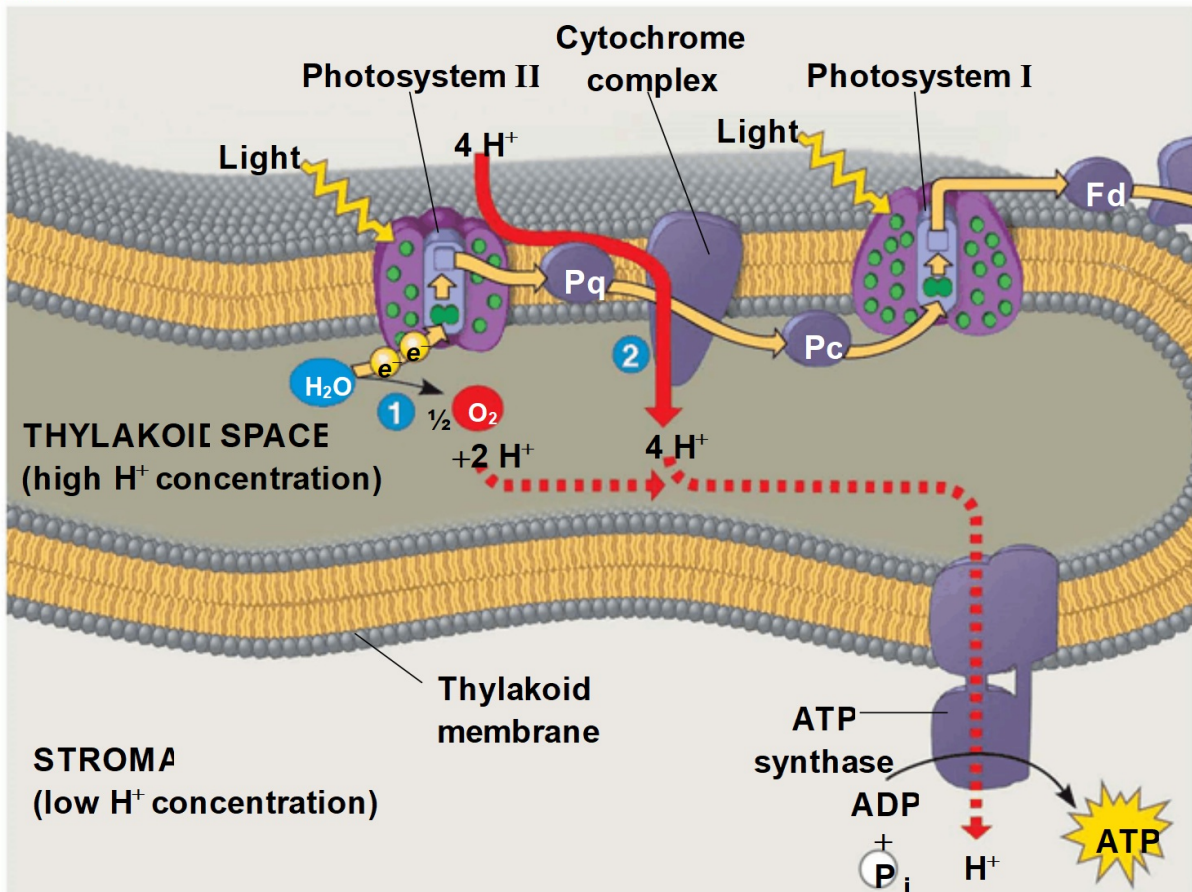
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Figure 8.16



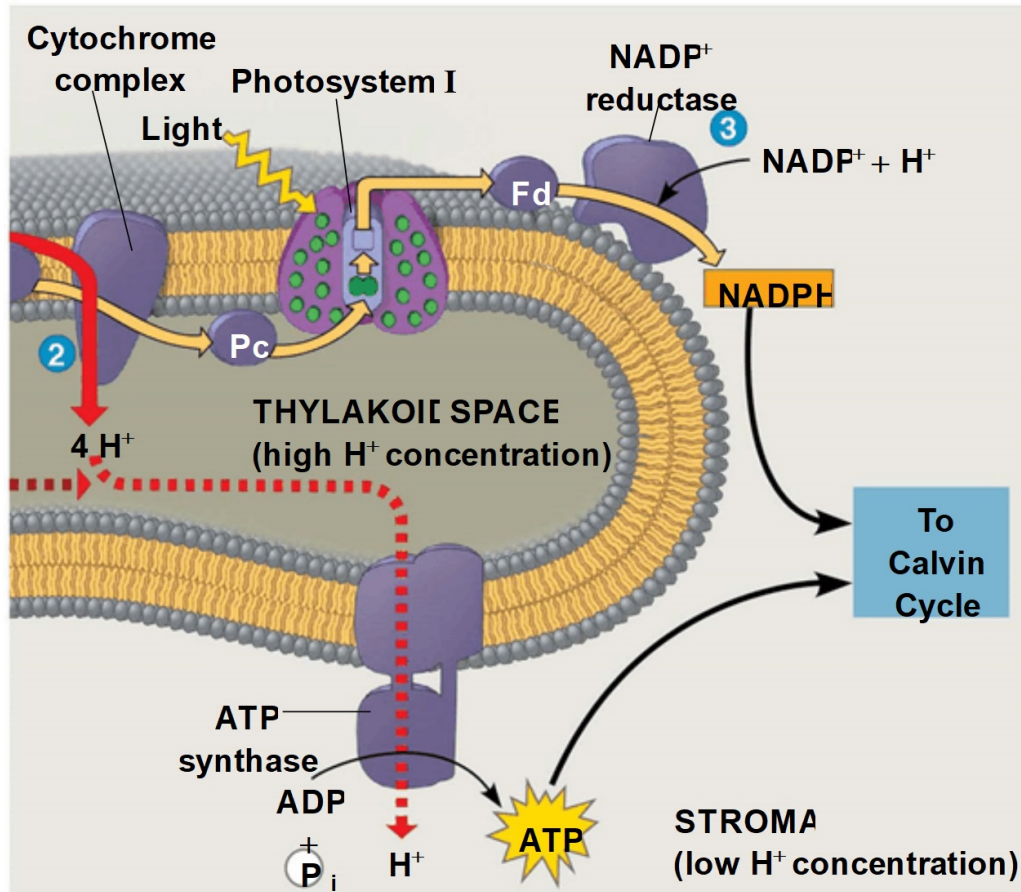
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Figure 8.16-1



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Figure 8.16-2



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Concept 8.3: The Calvin cycle uses the chemical energy of ATP and NADPH to reduce CO₂ to sugar

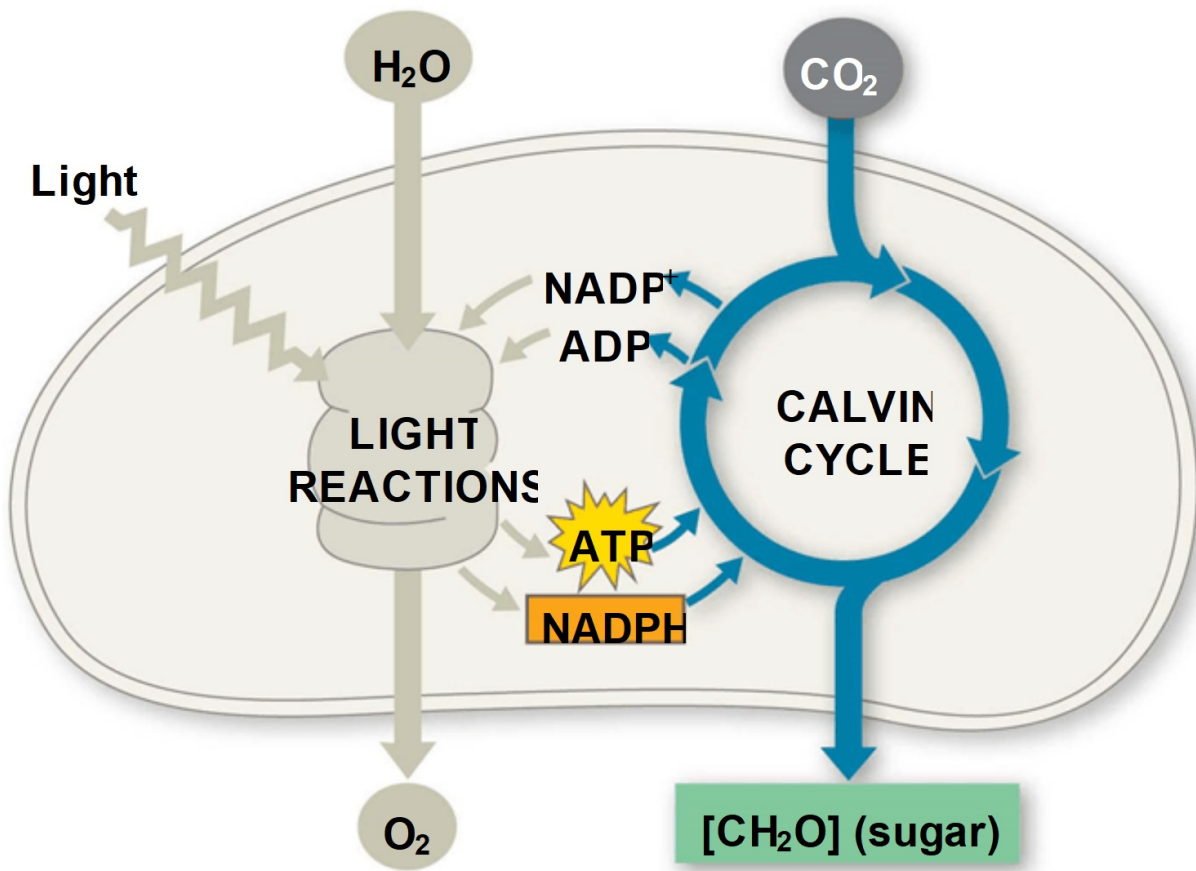
- The Calvin cycle, like the citric acid cycle, regenerates its starting material after molecules enter and leave the cycle
- Unlike the citric acid cycle, the Calvin cycle is anabolic
- It builds sugar from smaller molecules by using ATP and the reducing power of electrons carried by NADPH

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- Carbon enters the cycle as CO_2 and leaves as a sugar named **glyceraldehyde 3-phosphate (G3P)**
- For net synthesis of one G3P, the cycle must take place three times, fixing three molecules of CO_2
- The Calvin cycle has three phases
 - Carbon fixation
 - Reduction
 - Regeneration of the CO_2 acceptor

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Figure 8.UN03

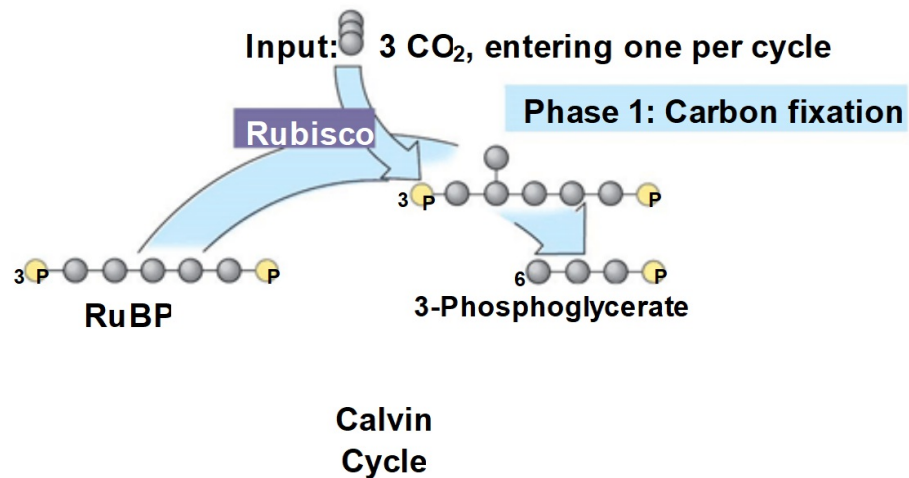


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- **Phase 1, carbon fixation**, involves the incorporation of the CO_2 molecules into ribulose biphosphate (RuBP) using the enzyme **rubisco**
- The product is 3-phosphoglycerate

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Figure 8.17-s1

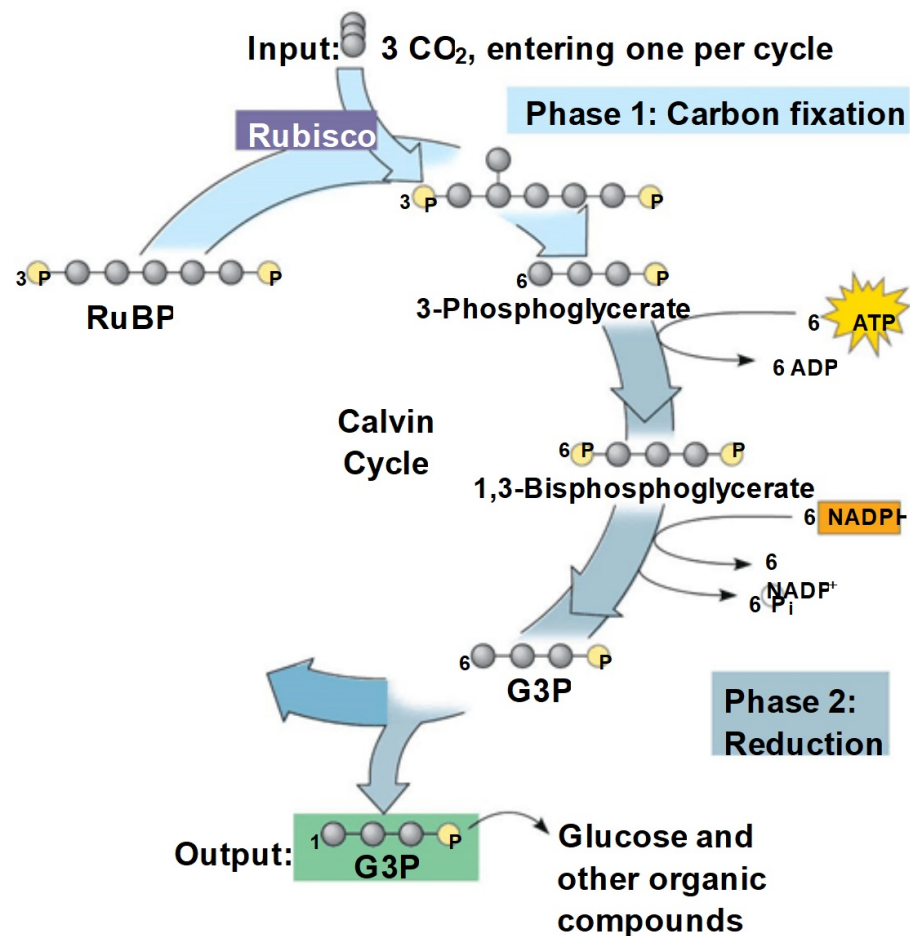


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- **Phase 2, reduction**, involves the reduction and phosphorylation of 3-phosphoglycerate to G3P
- Six ATP and six NADPH are required to produce six molecules of G3P, but only one exits the cycle for use by the cell

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Figure 8.17-s2

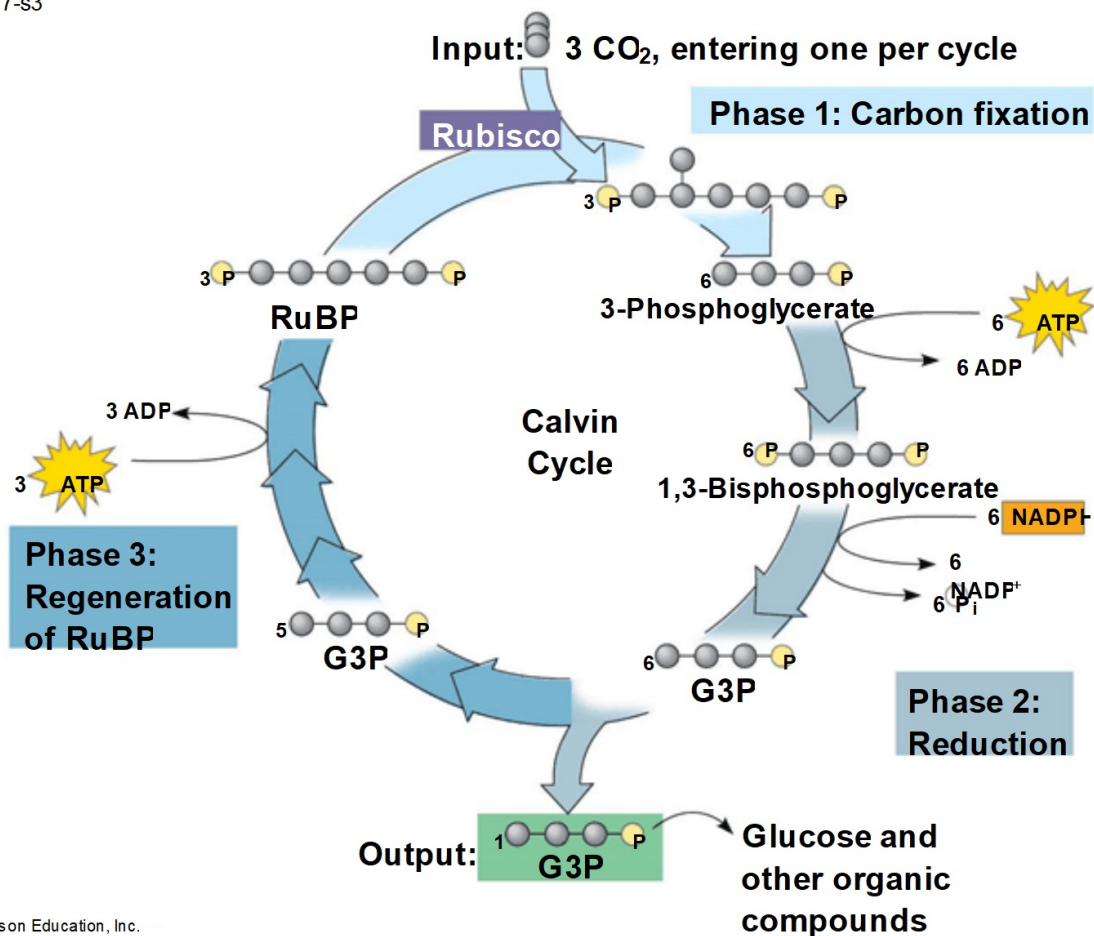


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- **Phase 3, regeneration**, involves the rearrangement of the five remaining molecules of G3P to regenerate the initial CO₂ receptor, RuBP
- Three additional ATP are required to power this step

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Figure 8.17-s3



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Evolution of Alternative Mechanisms of Carbon Fixation in Hot, Arid Climates

- Adaptation to dehydration is a problem for land plants, sometimes requiring trade-offs with other metabolic processes, especially photosynthesis
 - On hot, dry days, plants close stomata, which conserves H₂O but also limits photosynthesis
 - The closing of stomata reduces access to CO₂ and causes O₂ to build up
 - These conditions favor an apparently wasteful process called photorespiration

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- In most plants (**C₃ plants**), initial fixation of CO₂,
 - via rubisco, forms a three-carbon compound (3-phosphoglycerate)
 - In **photorespiration**, rubisco adds O₂ instead of CO₂ in the Calvin cycle, producing a two-carbon compound

Photorespiration decreases photosynthetic output by consuming ATP, O₂, and organic fuel and releasing CO₂ without producing any ATP or sugar

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- Photorespiration may be an evolutionary relic because rubisco first evolved at a time when the atmosphere had far less O₂ and more CO₂
- Photorespiration limits damaging products of light reactions that build up in the absence of the Calvin cycle

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C₄ Plants

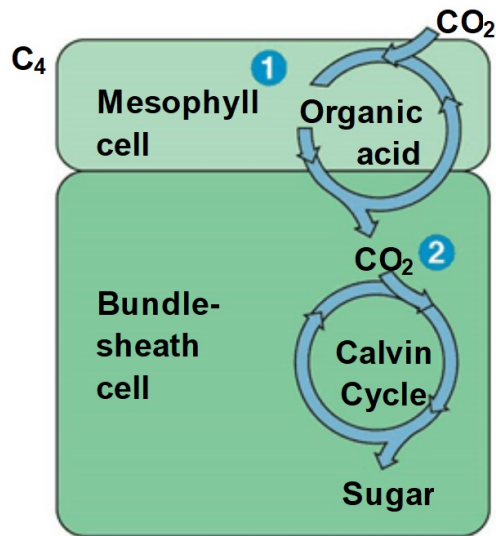
- **C₄ plants** minimize the cost of photorespiration by incorporating CO₂ into a four-carbon compound
- An enzyme in the mesophyll cells has a high affinity for CO₂ and can fix carbon even when CO₂ concentrations are low
- These four-carbon compounds are exported to bundle-sheath cells, where they release CO₂ that is then used in the Calvin cycle

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Figure 8.18a



Sugarcane



(a) Spatial separation of steps

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Figure 8.18-1



Sugarcane

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CAM Plants

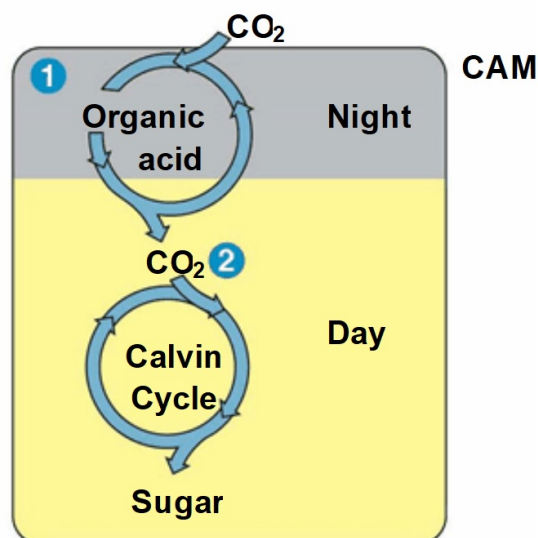
- Some plants, including pineapples and many cacti and succulents, use **crassulacean acid metabolism (CAM)** to fix carbon
- **CAM plants** open their stomata at night, incorporating CO₂ into organic acids
- Stomata close during the day, and CO₂ is released from organic acids and used in the Calvin cycle

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Figure 8.18b



Pineapple



(b) Temporal separation of steps

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Pineapple

- The C_4 and CAM pathways are similar in that they both incorporate carbon dioxide into organic intermediates before entering the Calvin cycle
 - In C_4 plants, carbon fixation and the Calvin cycle occur in different cells
 - In CAM plants, these processes occur in the same cells, but at different times of the day

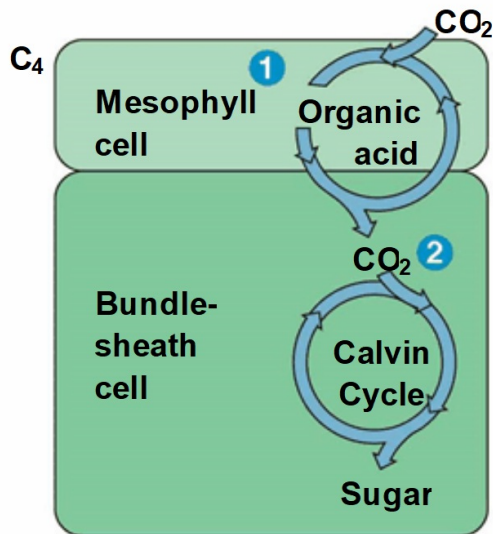
Figure 8.18



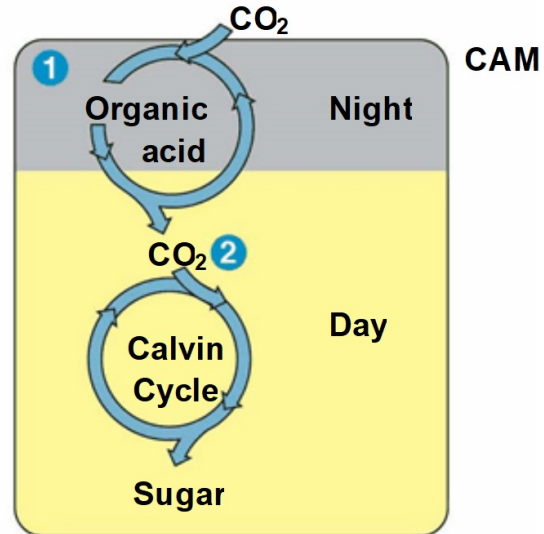
Sugarcane



Pineapple



(a) Spatial separation of steps



(b) Temporal separation of steps

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The Importance of Photosynthesis: *A Review*

- The energy entering chloroplasts as sunlight gets stored as chemical energy in organic compounds
- Sugar made in the chloroplasts supplies chemical energy and carbon skeletons to synthesize the organic molecules of cells
- Plants store excess sugar as starch in the chloroplasts and in structures such as roots, tubers, seeds, and fruits
- In addition to food production, photosynthesis produces the O₂ in our atmosphere

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Figure 8.19

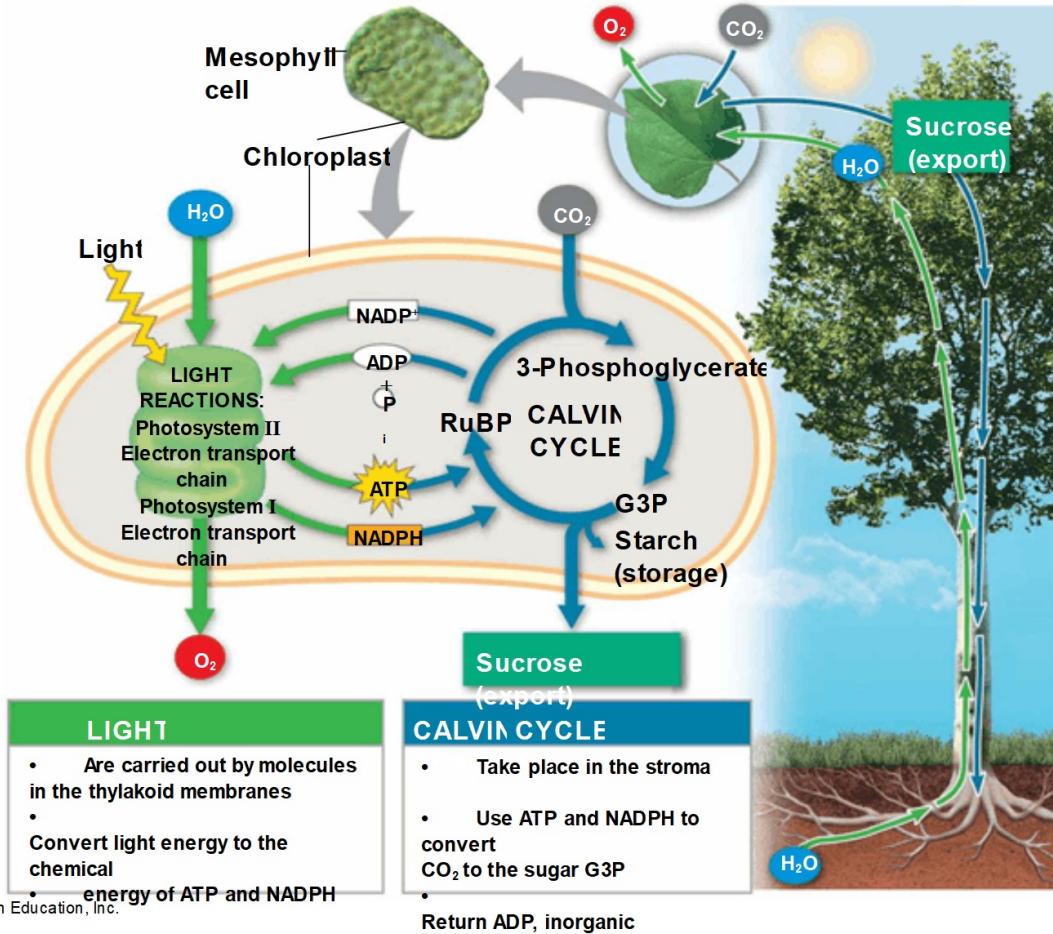


Figure 8.19-1

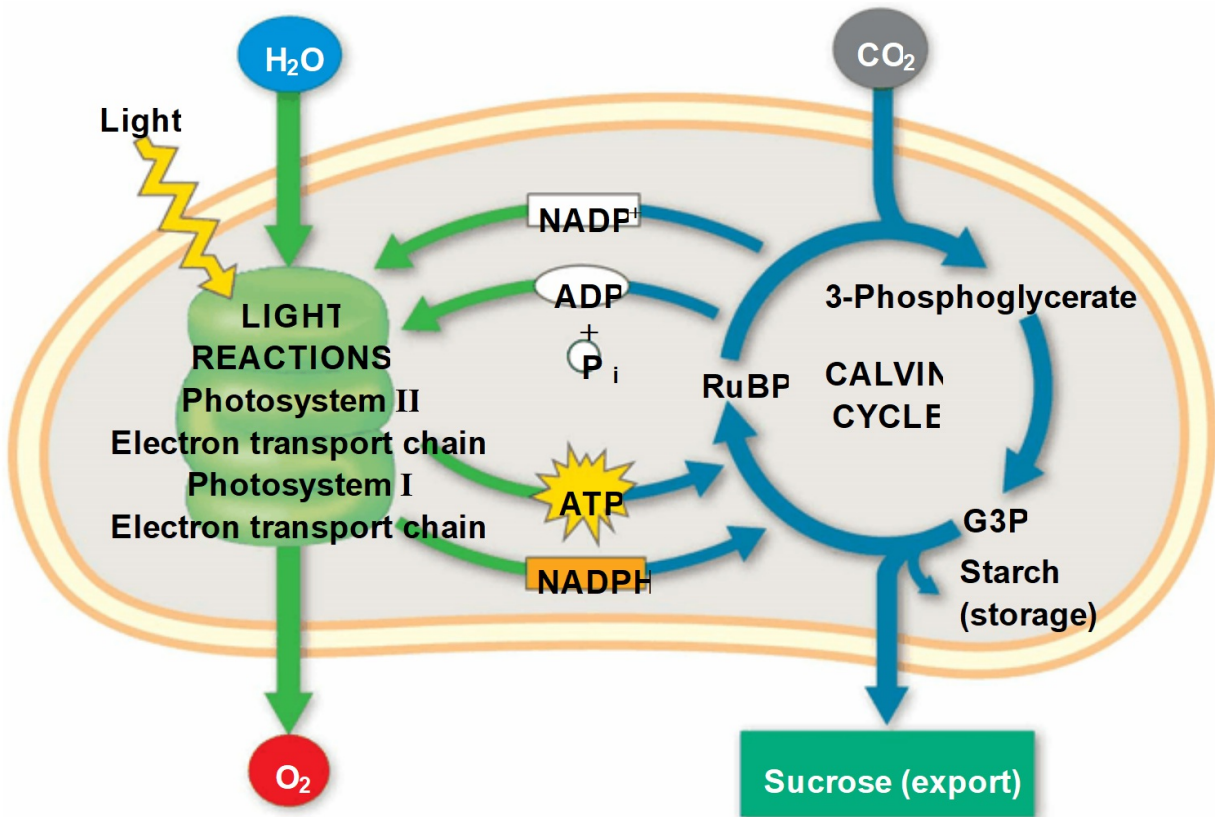
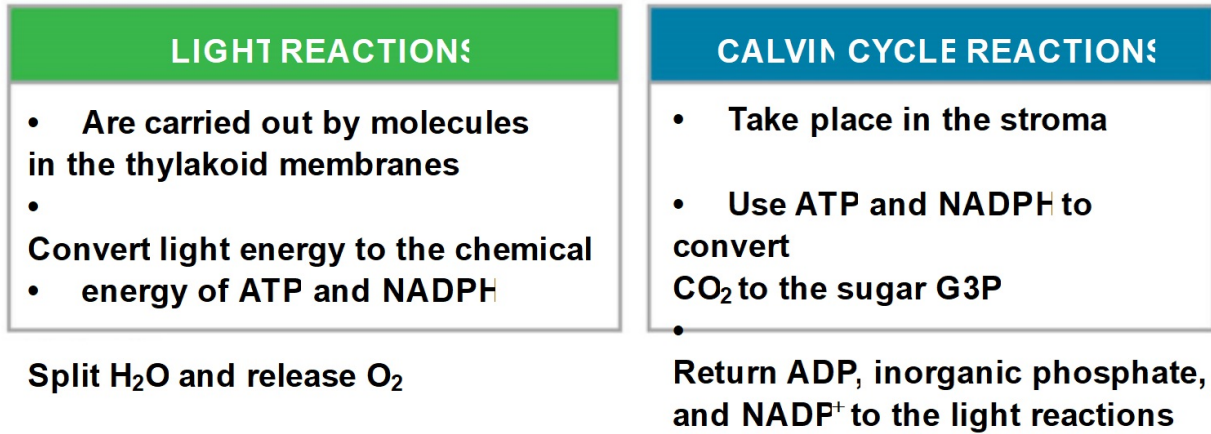


Figure 8.19-2



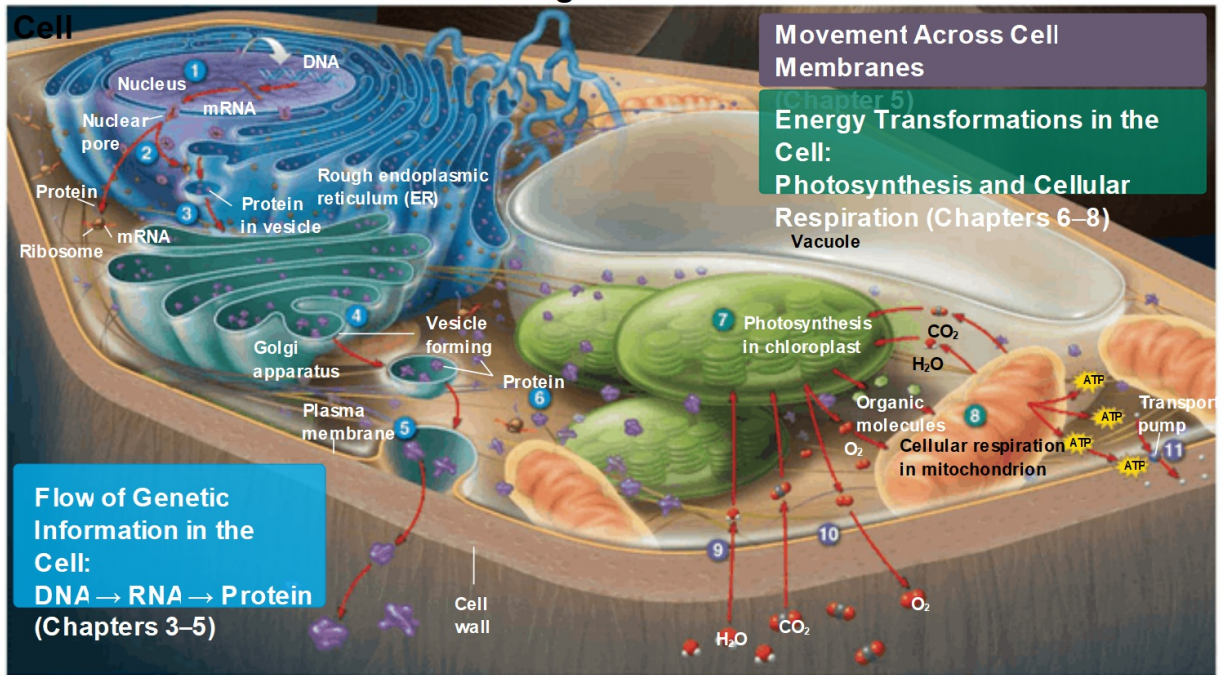
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- Photosynthesis is one of many important processes conducted by a working plant cell

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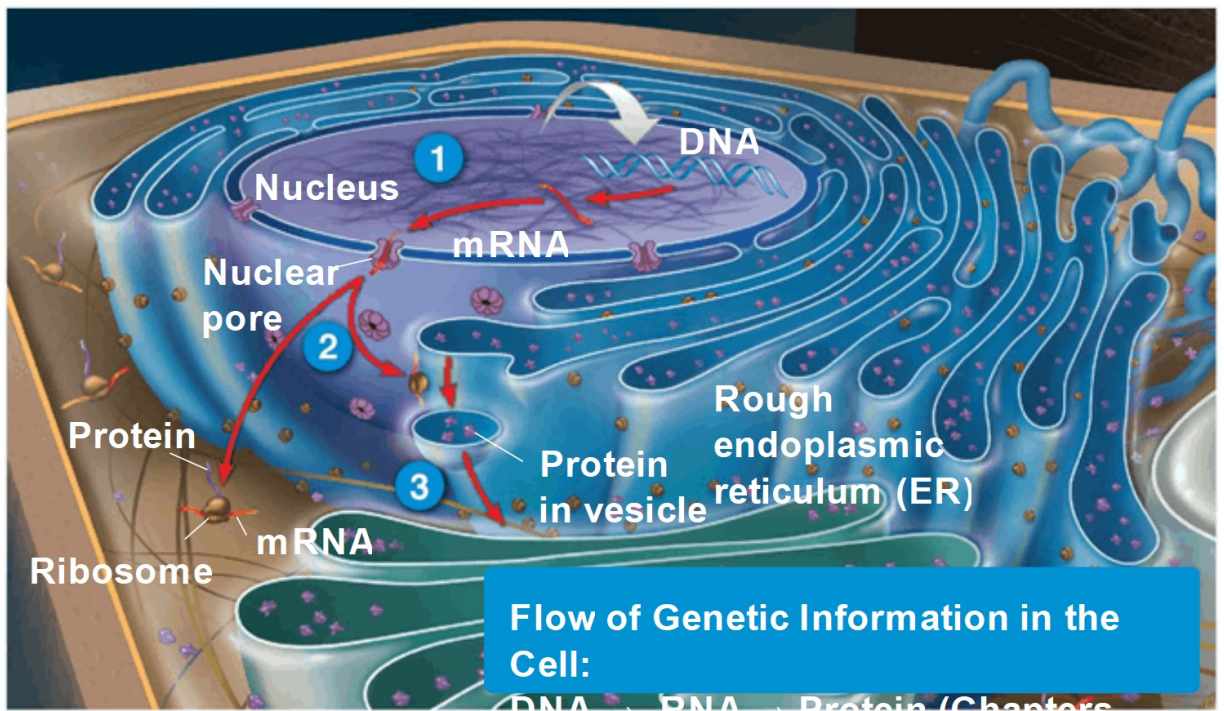
Figure 8.20

MAKE CONNECTIONS The Working



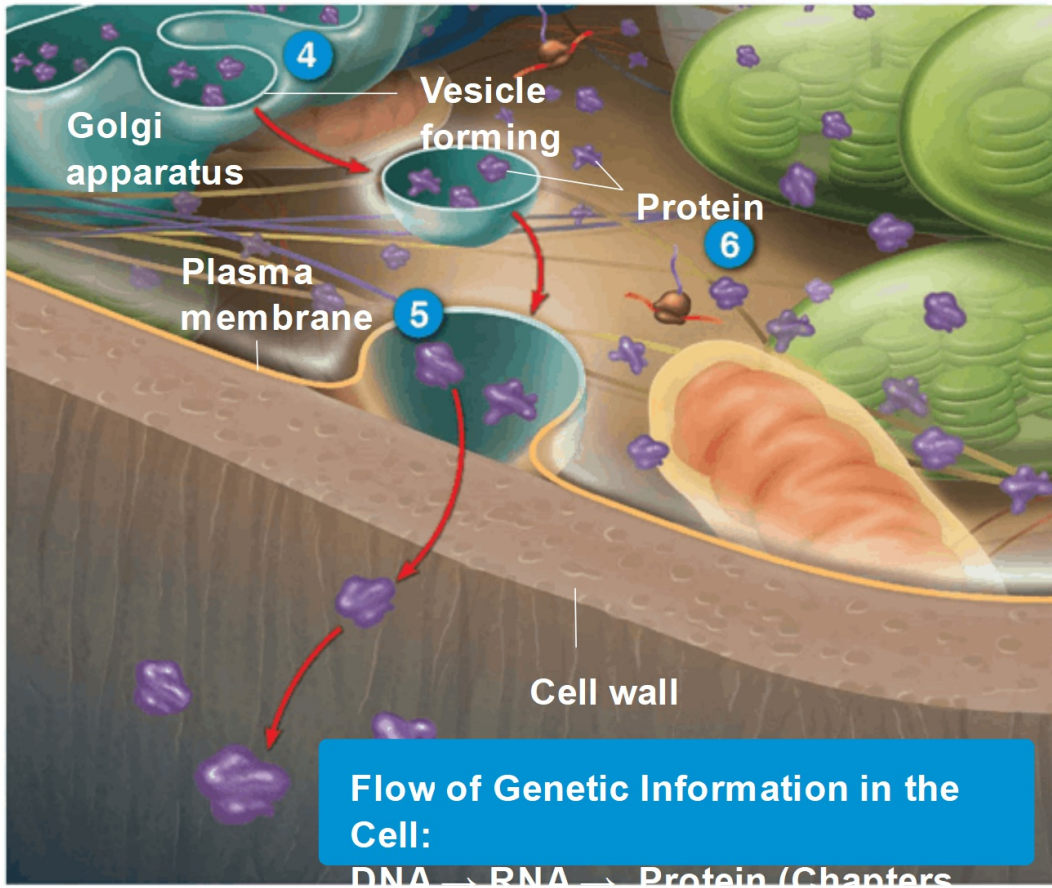
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Figure 8.20-1



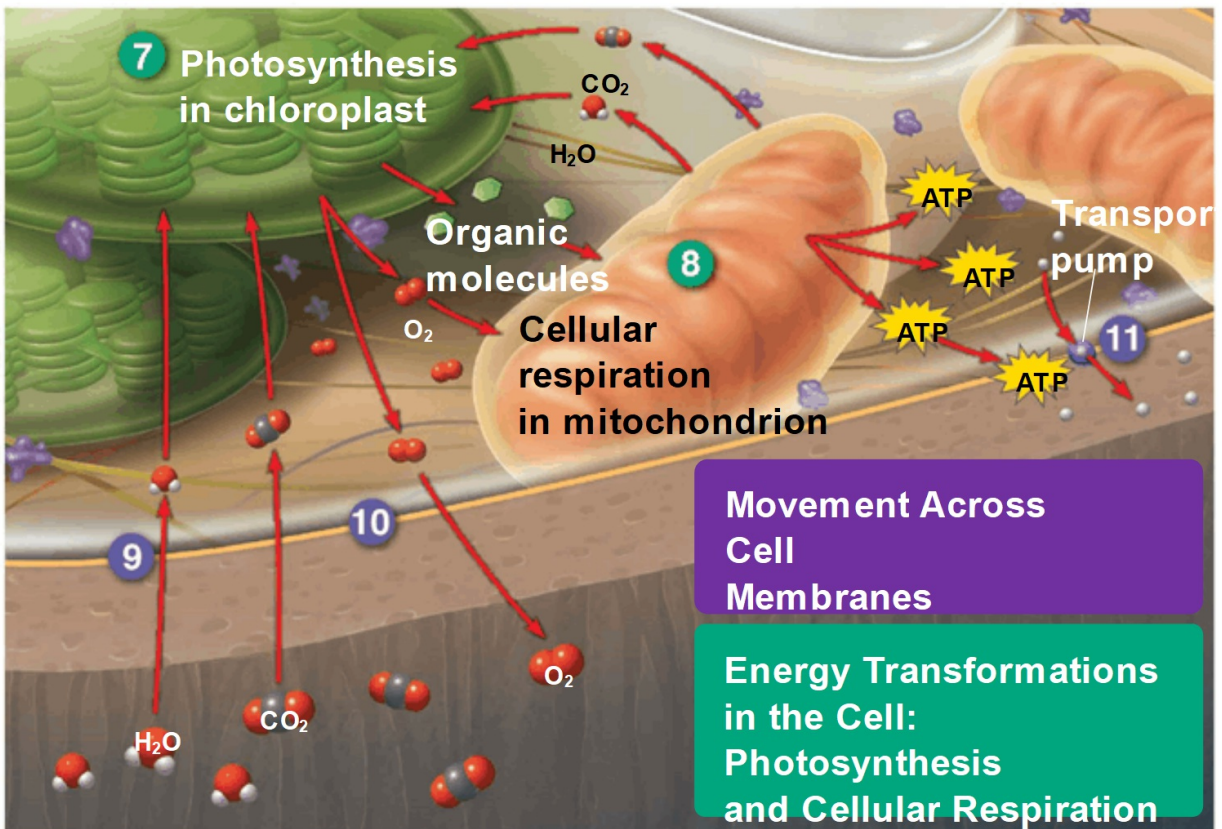
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Figure 8.20-2



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Figure 8.20-3



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Figure 8.UN04-1

	350 ppm CO ₂	600 ppm CO ₂	1,000 ppm CO ₂
Average dry mass of one corn plant (g)	91	89	80
Average dry mass of one velvetleaf plant (g)	35	48	54

Data from D. T. Patterson and E. P. Flint, Potential effects of global atmospheric CO₂ enrichment on the growth and competitiveness of C₃ and C₄ weed and crop plants, *Weed Science* 28(1): 71–75 (1980).

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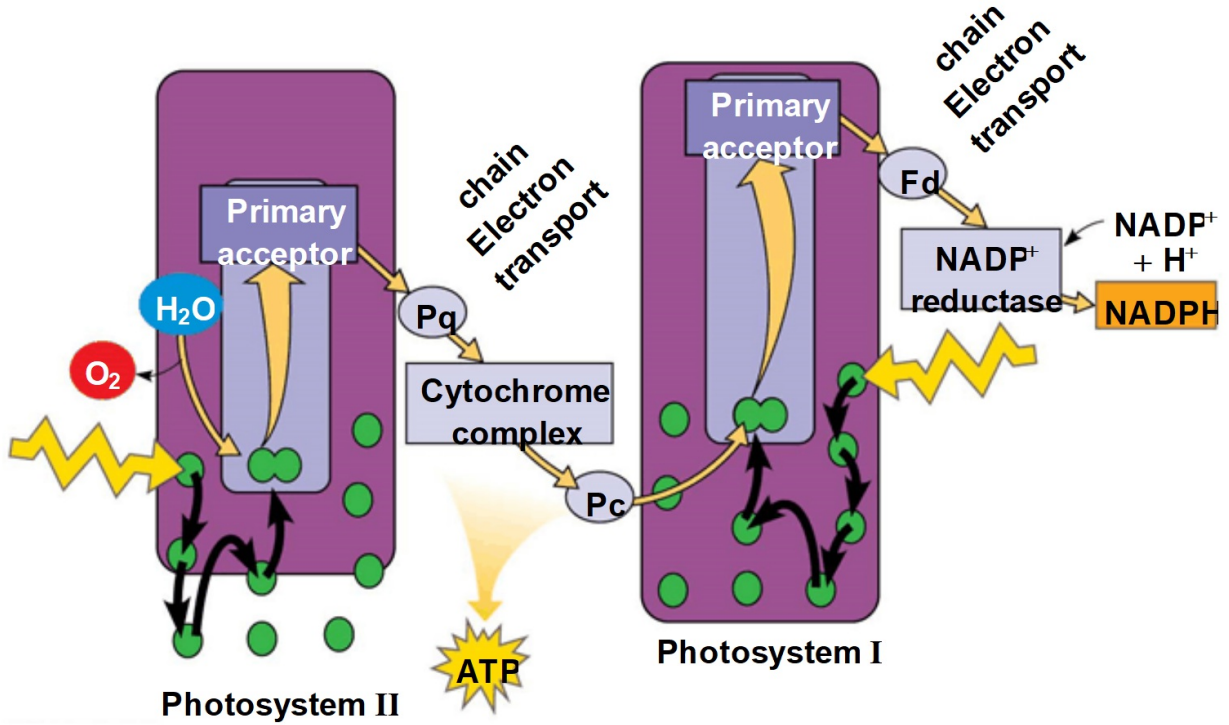
Figure 8.UN04-2



▶ **Corn plant surrounded
by invasive velvetleaf
plants**

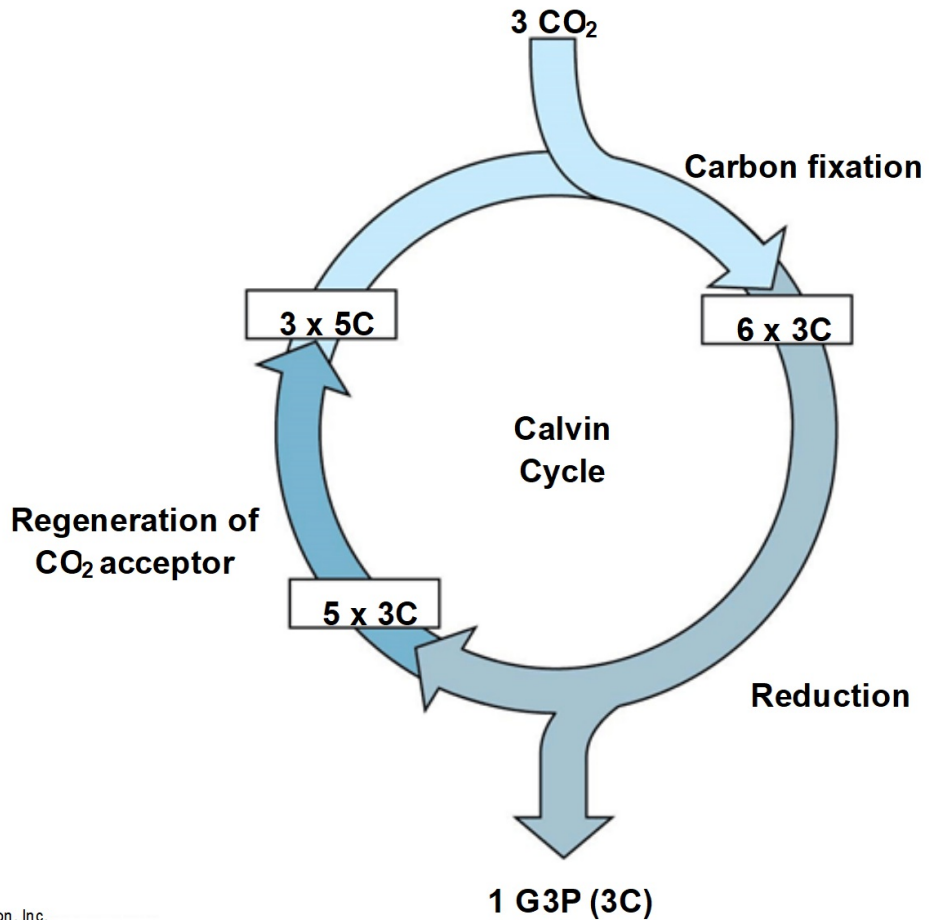
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Figure 8.UN05



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Figure 8.UN06



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Figure 8.UN07

