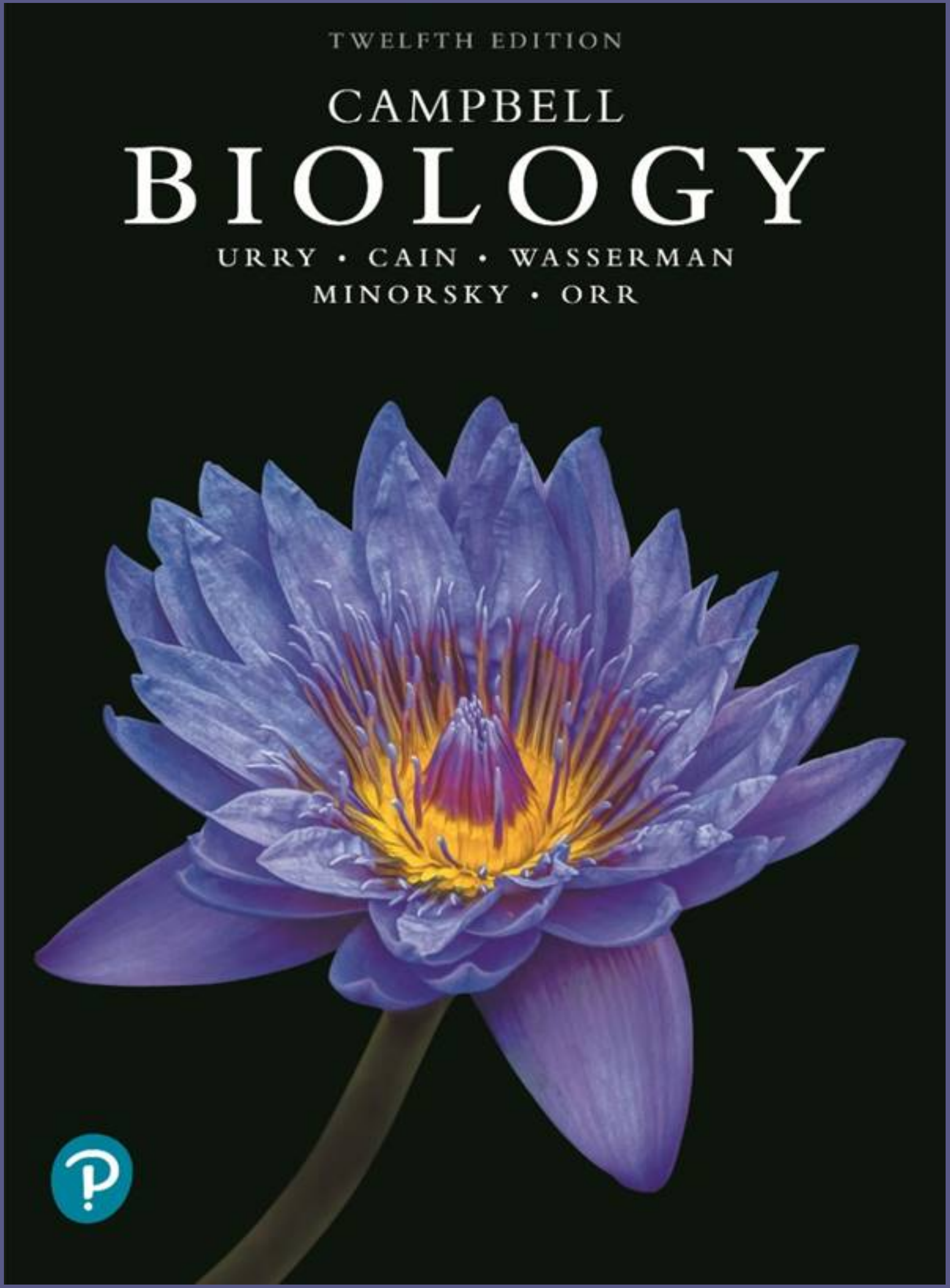


Chapter 10

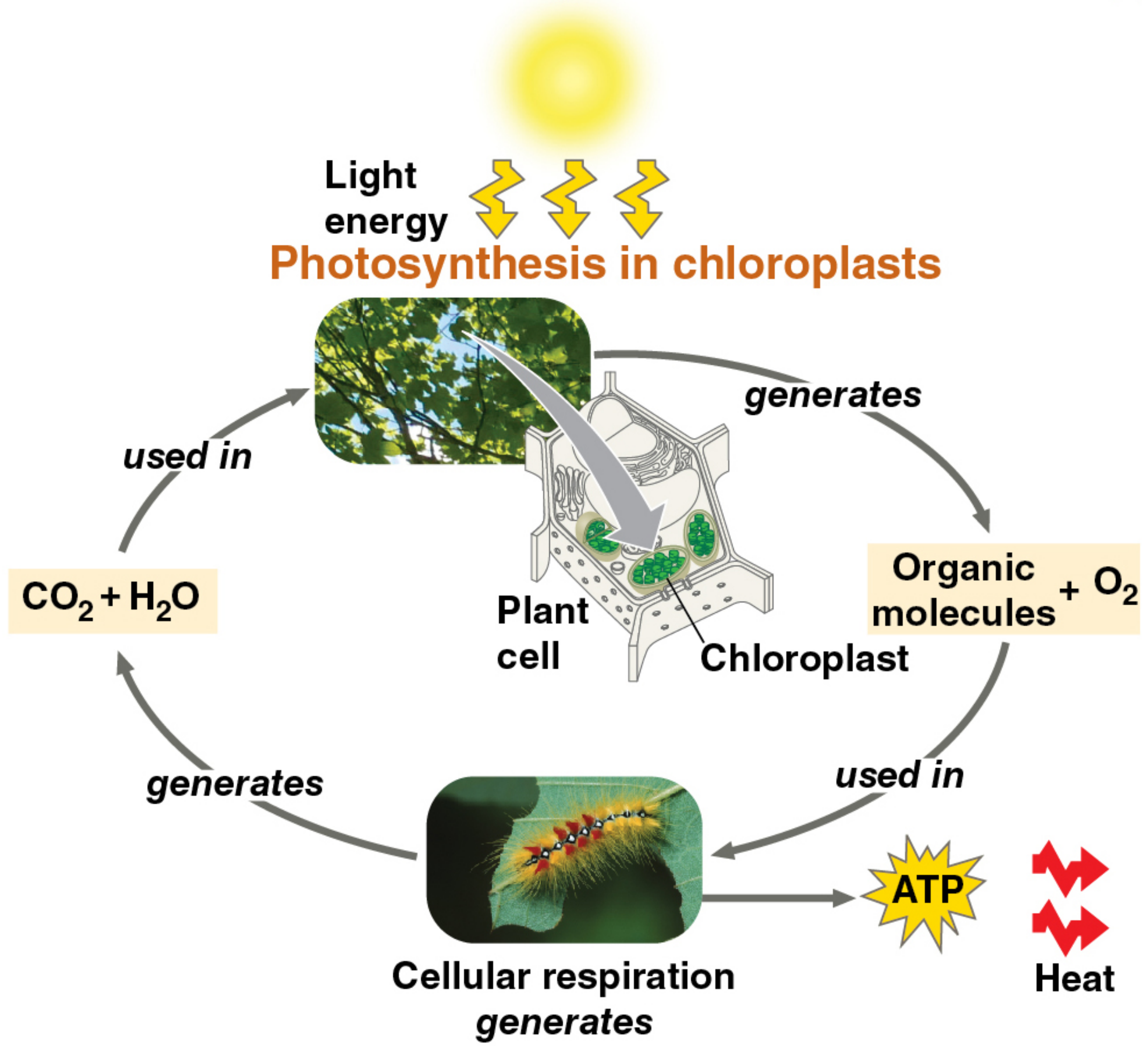
Photosynthesis

Lecture Presentations by
Nicole Tunbridge and
Kathleen Fitzpatrick

Figure 10.1a

Figure 10.1b

How do photosynthetic cells use light to change carbon dioxide and water into organic molecules and oxygen?



CONCEPT 10.1 Photosynthesis feeds the biosphere

- **Photosynthesis** is the process that converts solar energy into chemical energy within chloroplasts
- Photosynthesis nourishes almost the entire living world directly or indirectly

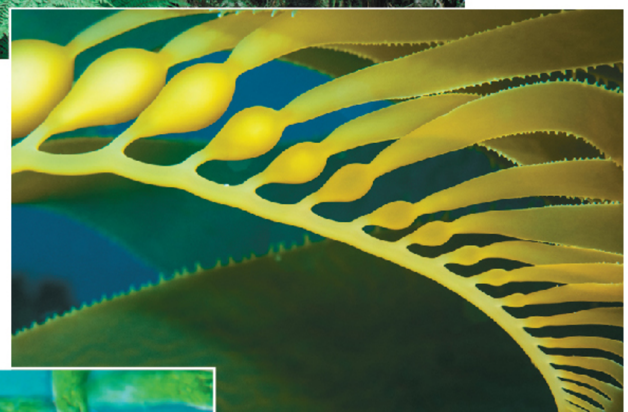
The Process That Feeds the Biosphere

- **Autotrophs** are “self-feeders” that sustain themselves without eating anything derived from other organisms
- Autotrophs are the producers of the biosphere; they produce organic molecules from CO_2 and other inorganic molecules

- Almost all plants are photoautotrophs, that is, they use the energy of sunlight to make organic molecules
- Photosynthesis also occurs in algae, certain other protists, and some prokaryotes

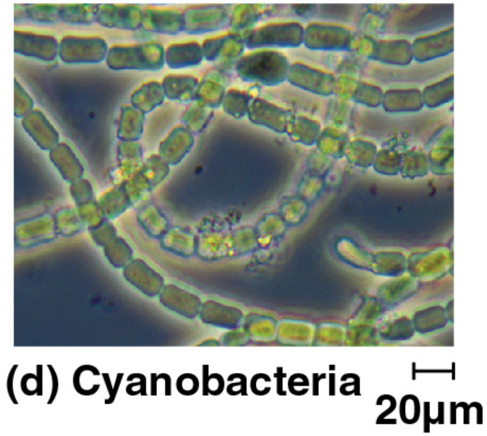
Figure 10.2

(a) Plants

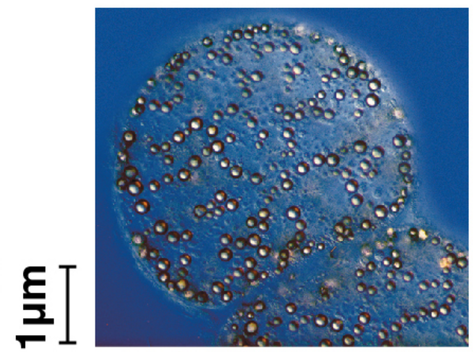


(b) Multicellular alga

(c) Unicellular protists



(d) Cyanobacteria



(e) Purple sulfur bacteria

- **Heterotrophs** obtain organic material from other organisms; they are the consumers of the biosphere
- Some consume other living things; others, called decomposers, eat dead organic material or feces

- Fossil fuels were formed from the remains of organisms that died hundreds of millions of years ago, representing ancient stores of the sun’s energy
- Almost all heterotrophs depend on photoautotrophs, either directly or indirectly, for food and O_2

CONCEPT 10.2: Photosynthesis converts light energy to the chemical energy of food

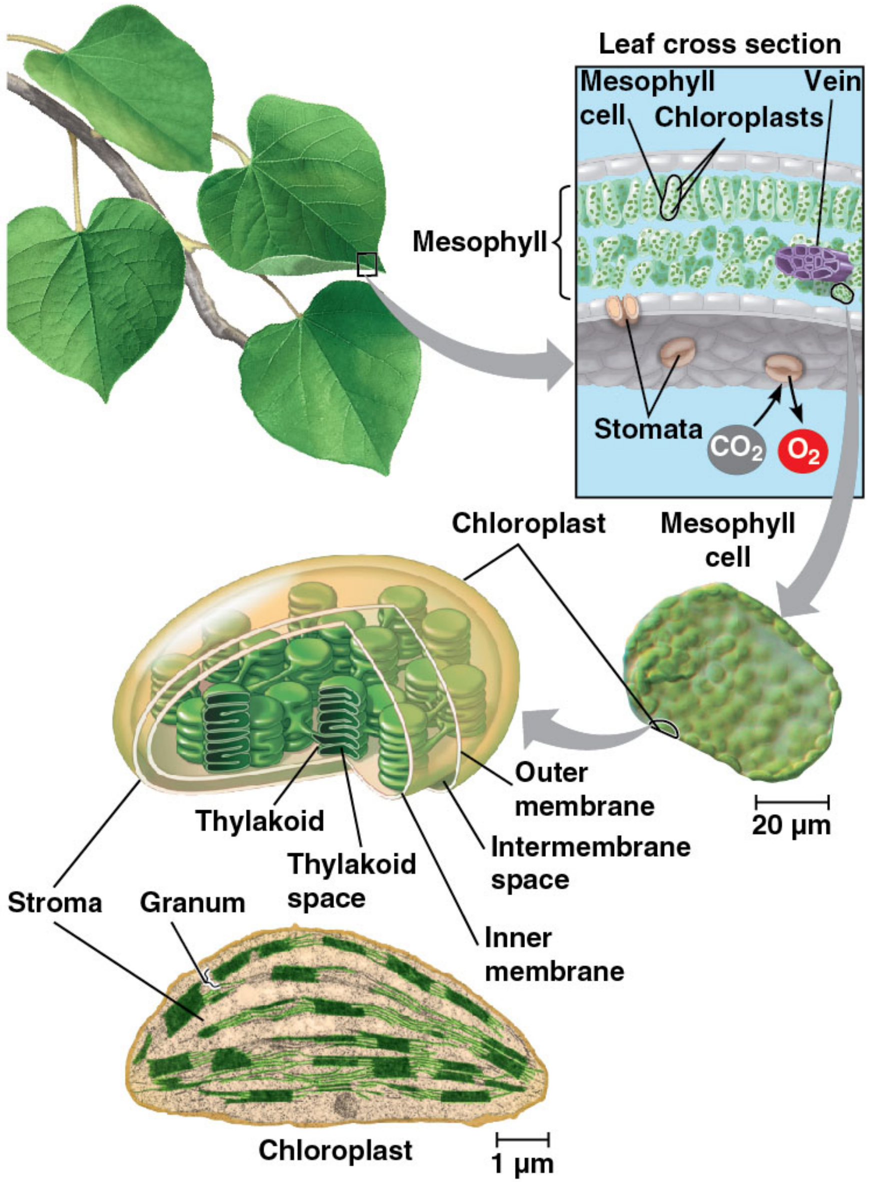
- Plants and other photosynthetic organisms contain organelles called **chloroplasts**
- Chloroplasts are structurally similar to and likely evolved from photosynthetic bacteria
- The structural organization of these organelles allows for the chemical reactions of photosynthesis

Chloroplasts: The Sites of Photosynthesis in Plants

- Most photosynthesis in plants occurs in the leaves
- Chloroplasts are found mainly in cells of the **mesophyll**, the interior tissue of the leaf
- CO_2 enters and O_2 exits the leaf through microscopic pores called **stomata**
- Veins transport water from the roots and export sugar to nonphotosynthetic parts of the plant

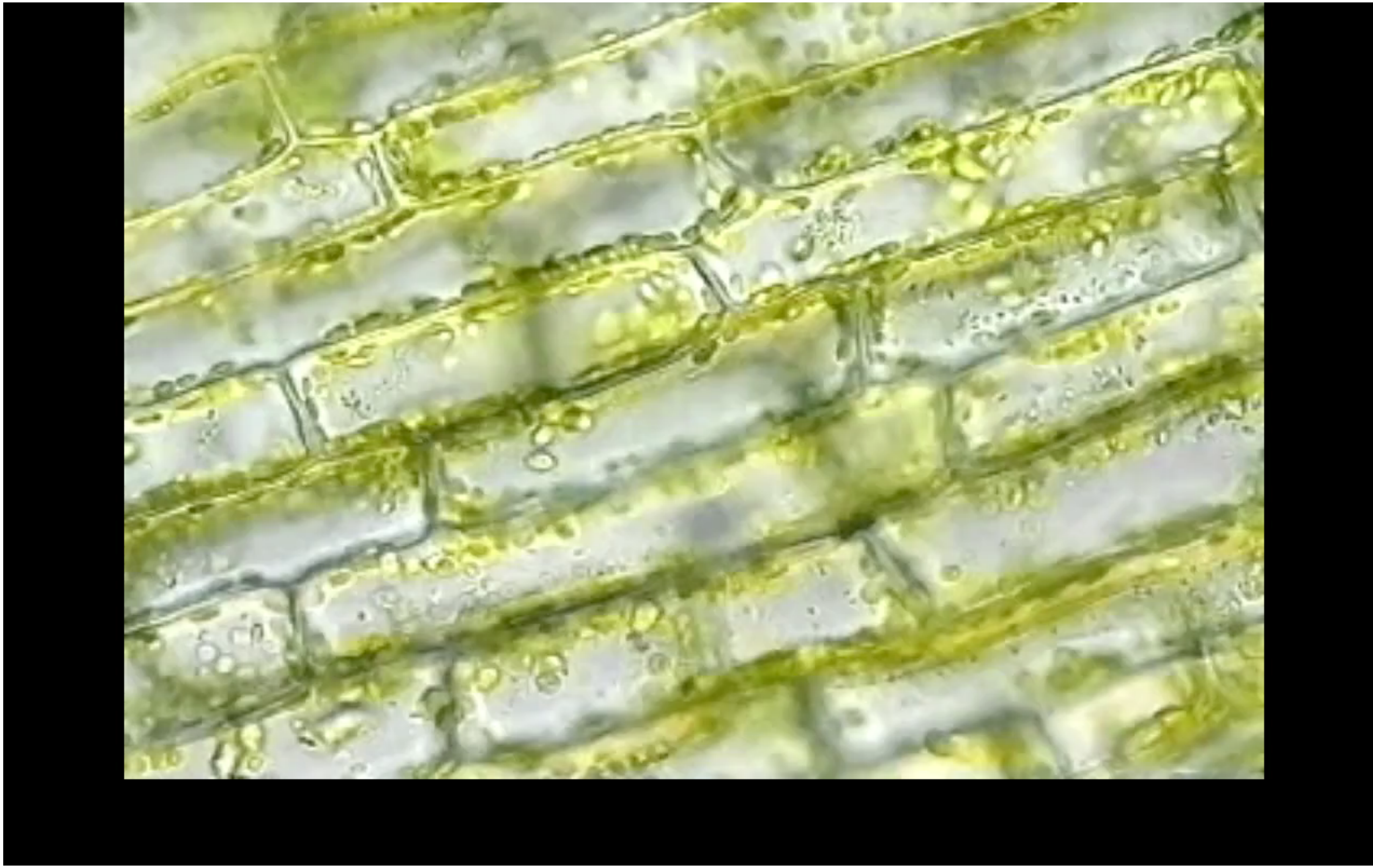
- A chloroplast has an envelope of two membranes surrounding a dense fluid called the **stroma**
- **Thylakoids** are connected sacs in the chloroplast that compose a third membrane system
- Thylakoids may be stacked in columns called grana
- **Chlorophyll**, the pigment that gives leaves their green color, resides in the thylakoid membranes

Figure 10.3



Leaf cross section
Mesophyll cell
Vein
Chloroplasts
Mesophyll
Stomata
CO_2
O_2
Chloroplast
Mesophyll cell
20 µm
Outer membrane
Intermembrane space
Inner membrane
Thylakoid
Thylakoid space
Stroma
Granum
Chloroplast
1 µm

Video: Chloroplasts in Motion



Tracking Atoms Through Photosynthesis: *Scientific Inquiry*

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

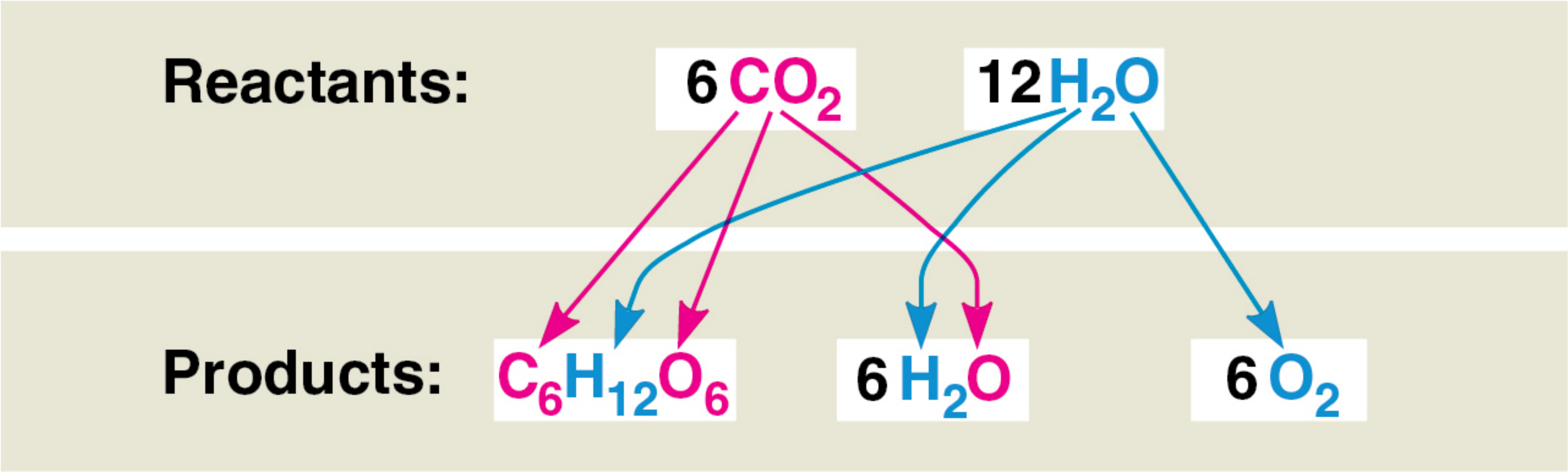
  $6\ CO_2 + 12\ H_2O + \text{Light energy} \rightarrow C_6H_{12}O_6 + 6\ O_2 + 6\ H_2O$

- The overall chemical change during photosynthesis is the reverse of cellular respiration

The Splitting of Water

- Chloroplasts split H_2O into hydrogen and oxygen, incorporating the electrons of hydrogen into sugar molecules and releasing O_2 as a by-product

Figure 10.4



- All photosynthetic organisms require a hydrogen source, but the source varies among organisms
  - For example, sulfur bacteria use H_2S instead of water, forming yellow globules of sulfur as a waste product

Photosynthesis as a Redox Process

- Photosynthesis reverses the direction of electron flow compared to respiration
- Photosynthesis is a redox process in which H_2O is oxidized and CO_2 is reduced
- Photosynthesis is an endergonic process; the energy boost is provided by light

Figure 10.UN01

becomes reduced

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

becomes oxidized

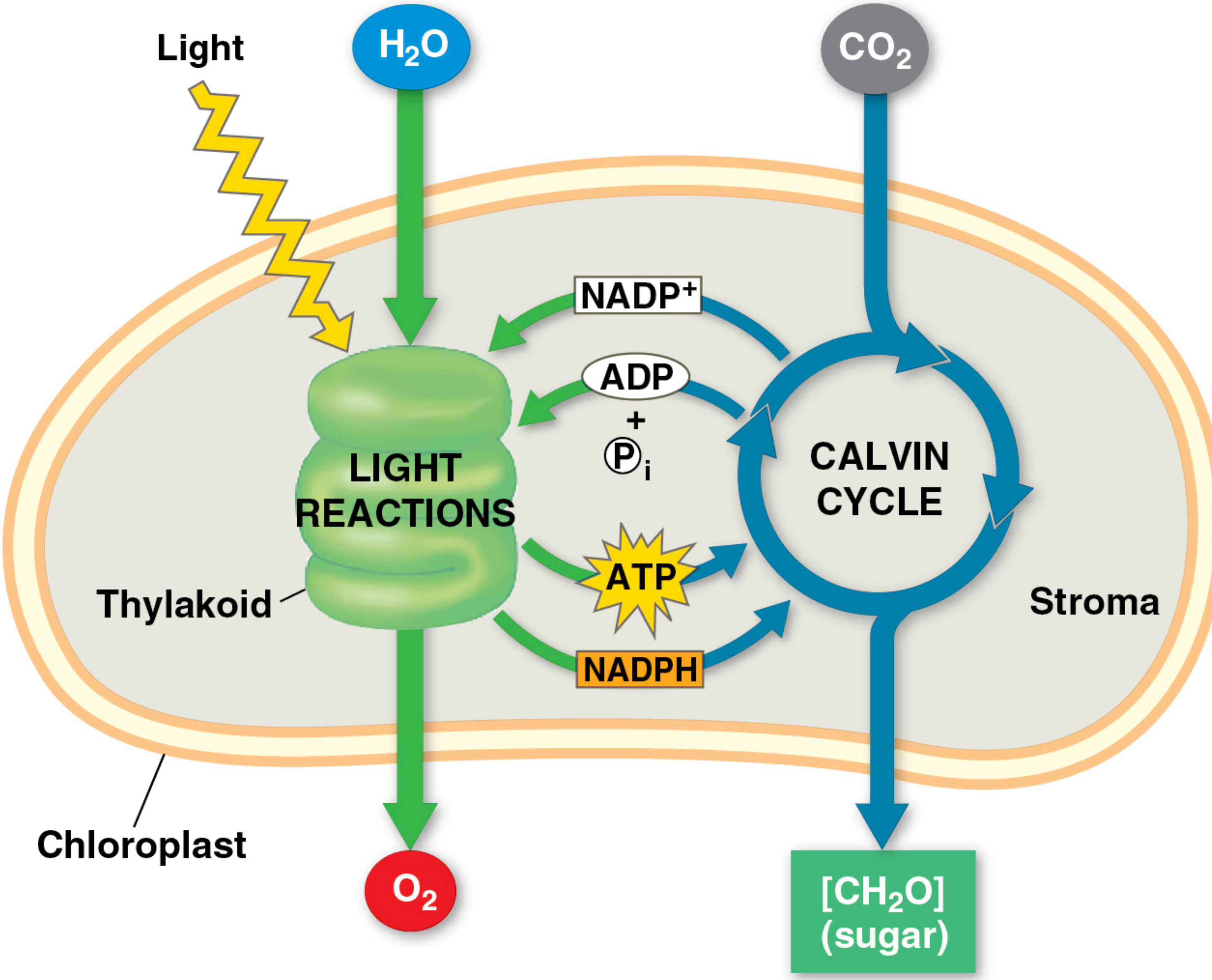
The Two Stages of Photosynthesis: *A Preview*

- Photosynthesis consists of the **light reactions** (the photo part) and **Calvin cycle** (the synthesis part)
- The light reactions (in the thylakoids)
  - Split H_2O, providing electrons and protons (H^+)
  - Release O_2 as a by-product
  - Reduce the electron acceptor **$NADP^+$** to **NADPH**
  - Generate ATP from ADP by **photophosphorylation**

- The Calvin cycle (in the stroma) makes sugar from CO_2, using the ATP and NADPH generated during the light reactions
- The Calvin cycle begins with **carbon fixation**, incorporating CO_2 into organic molecules
- It then reduces fixed carbon to carbohydrate by transferring electrons from NADPH

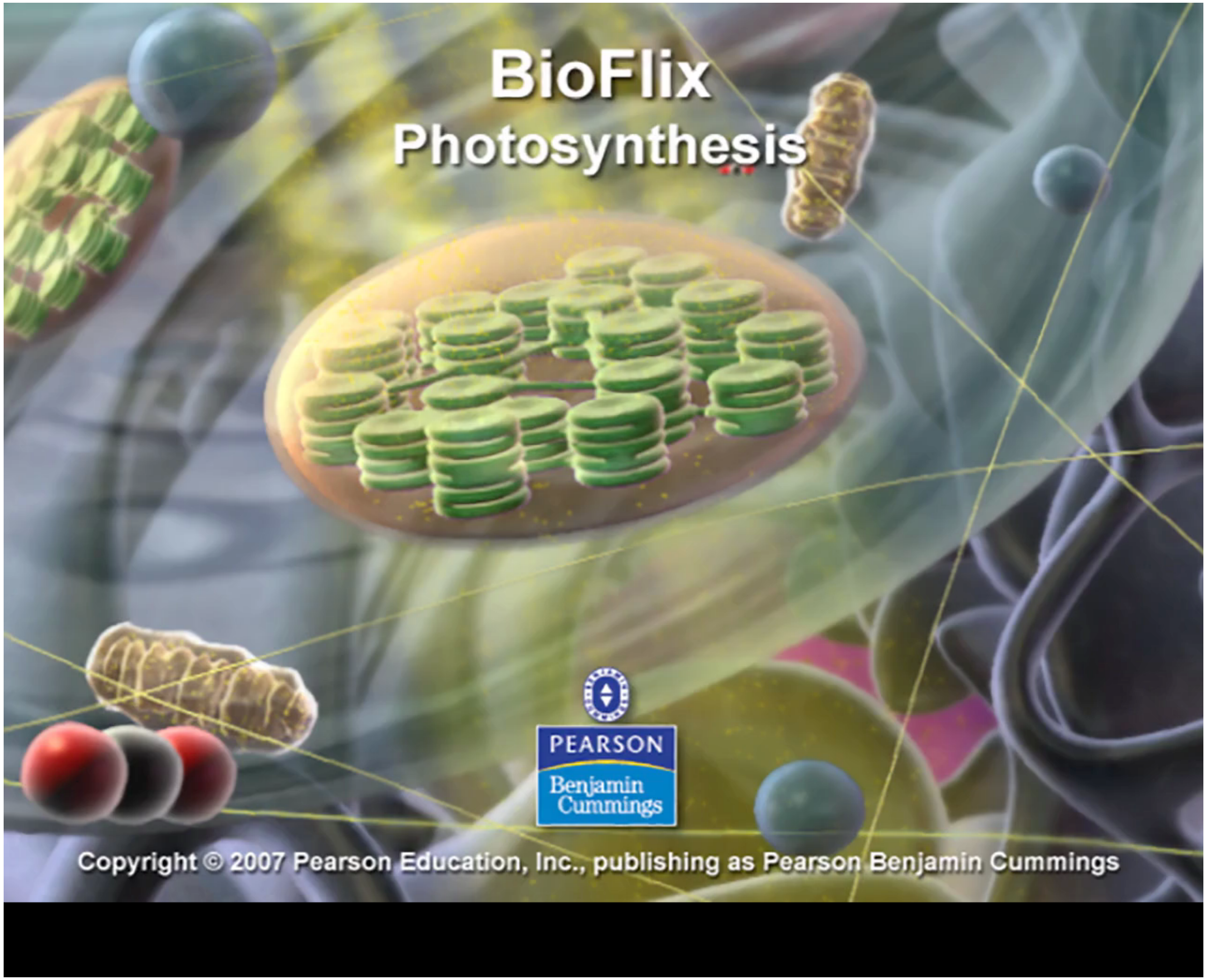
- Chloroplasts use light energy to make sugar by coordinating the two stages of photosynthesis
- The light reactions occur in the thylakoids and release NADPH and ATP to the stroma for use in the Calvin cycle

Figure 10.5



Light
H_2O
CO_2
$NADP^+$
ADP
+
Ⓟ$_i$
LIGHT
REACTIONS
CALVIN
CYCLE
ATP
NADPH
Thylakoid
Stroma
Chloroplast
O_2
$[CH_2O]$
(sugar)

Animation: Photosynthesis



CONCEPT 10.3: The light reactions convert solar energy to the chemical energy of ATP and NADPH

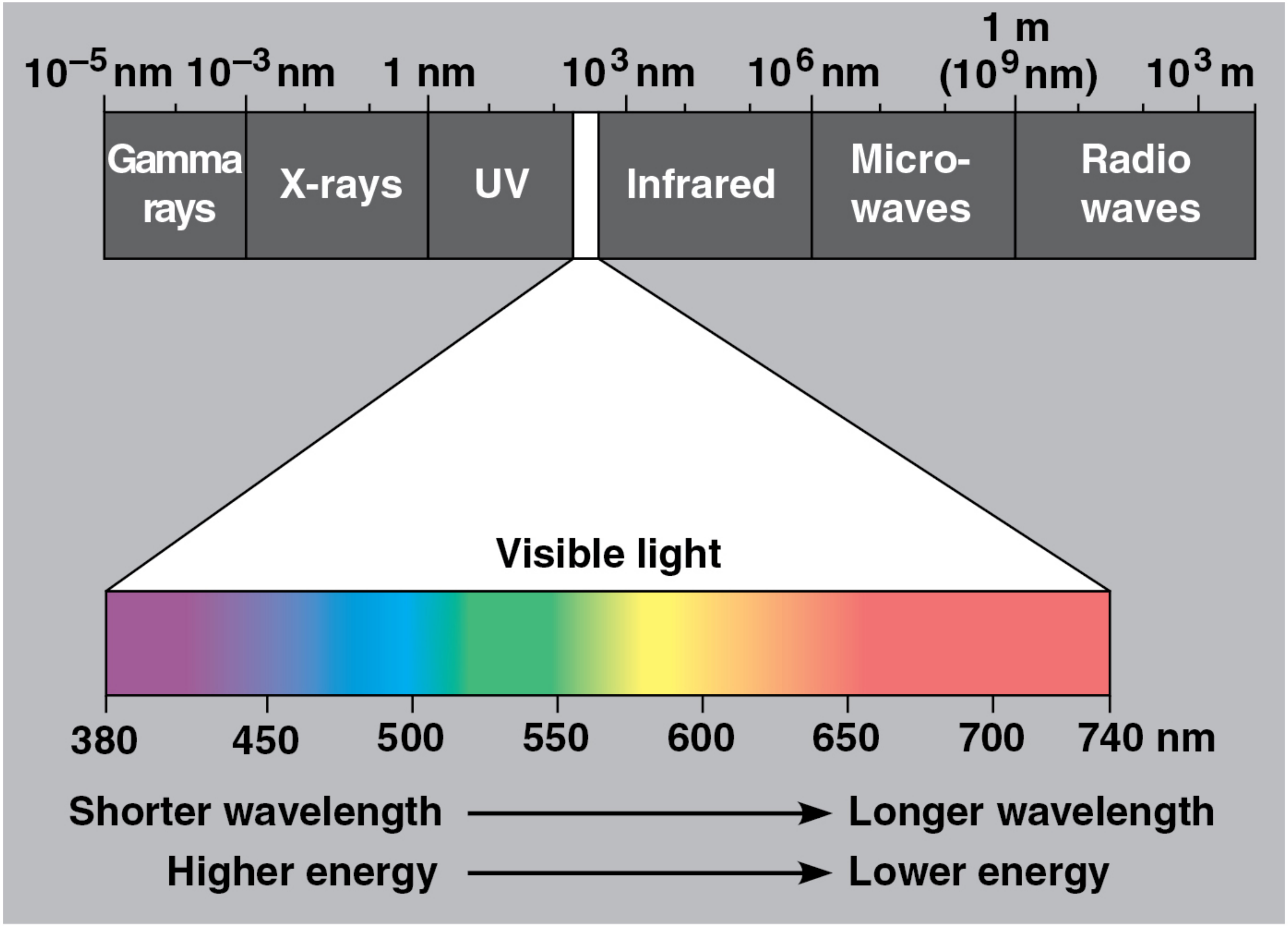
- Chloroplasts are solar-powered chemical factories
- Their thylakoids transform light energy into the chemical energy of ATP and NADPH

The Nature of Sunlight

- Light is electromagnetic energy, also called electromagnetic radiation
- Electromagnetic energy travels in rhythmic waves
- **Wavelength** is a measure of the distance between crests of electromagnetic waves
- It can range from less than a nanometer (gamma rays) to more than a kilometer (radio waves)

- The **electromagnetic spectrum** is the entire range of electromagnetic energy, or radiation
- **Visible light** (wavelengths 380 nm to 740 nm) drives photosynthesis and produces the colors seen by the human eye

Figure 10.6

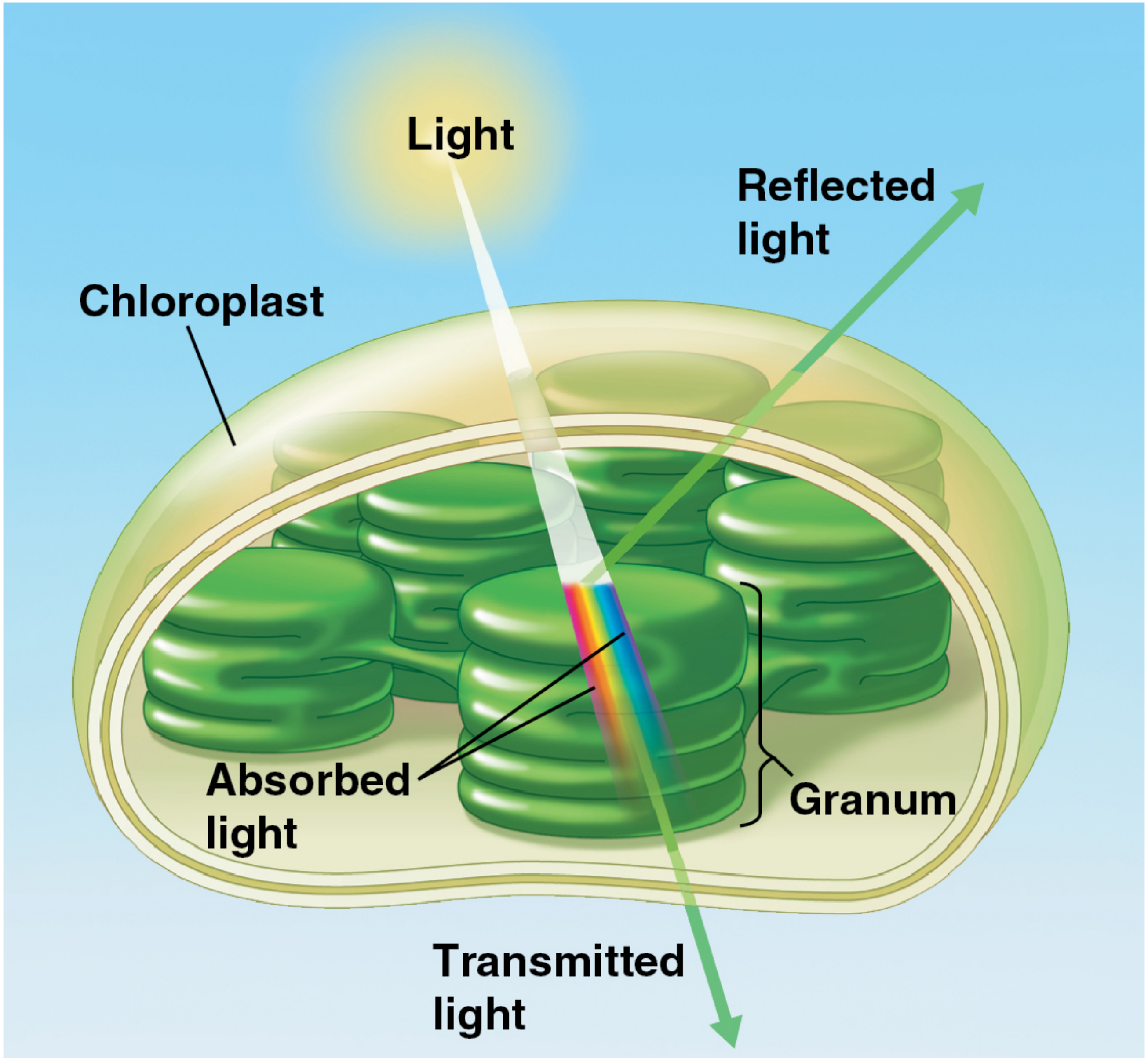

1 m
10^{-5} nm
10^{-3} nm
1 nm
10^{3} nm
10^{6} nm
(10^{9} nm)
10^{3} m
Gamma rays
X-rays
UV
Infrared
Micro-waves
Radio waves
Visible light
380
450
500
550
600
650
700
740 nm
Shorter wavelength
Longer wavelength
Higher energy
Lower energy

- Light also behaves as though it consists of discrete particles, called **photons**
- Each photon has a fixed quantity of energy which is inversely related to the wavelength of light; shorter wavelengths have more energy per photon of light

Photosynthetic Pigments: The Light Receptors

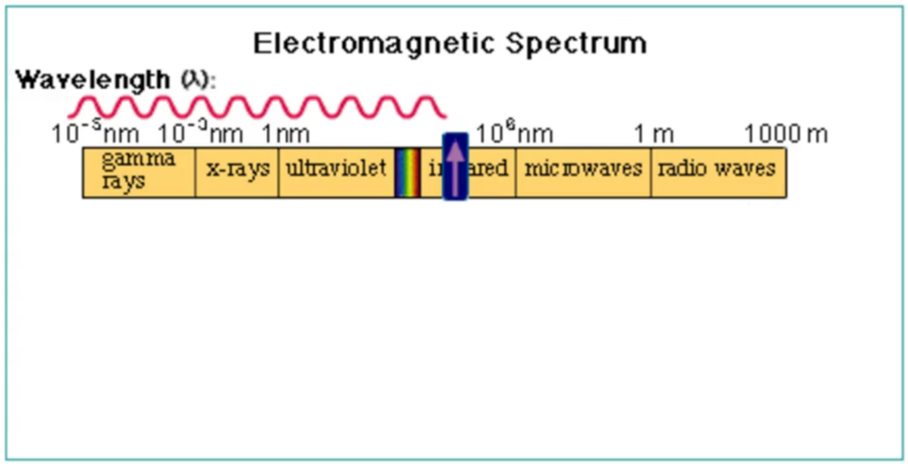
- Pigments are substances that absorb visible light
- Different pigments absorb different wavelengths, and the wavelengths that are absorbed disappear
- Wavelengths that are not absorbed are reflected or transmitted
  - For example, most leaves appear green because chlorophyll absorbs violet-blue and red light while reflecting and transmitting green light

Figure 10.7


Light
Reflected light
Chloroplast
Absorbed light
Granum
Transmitted light

Animation: Light Energy and Pigments

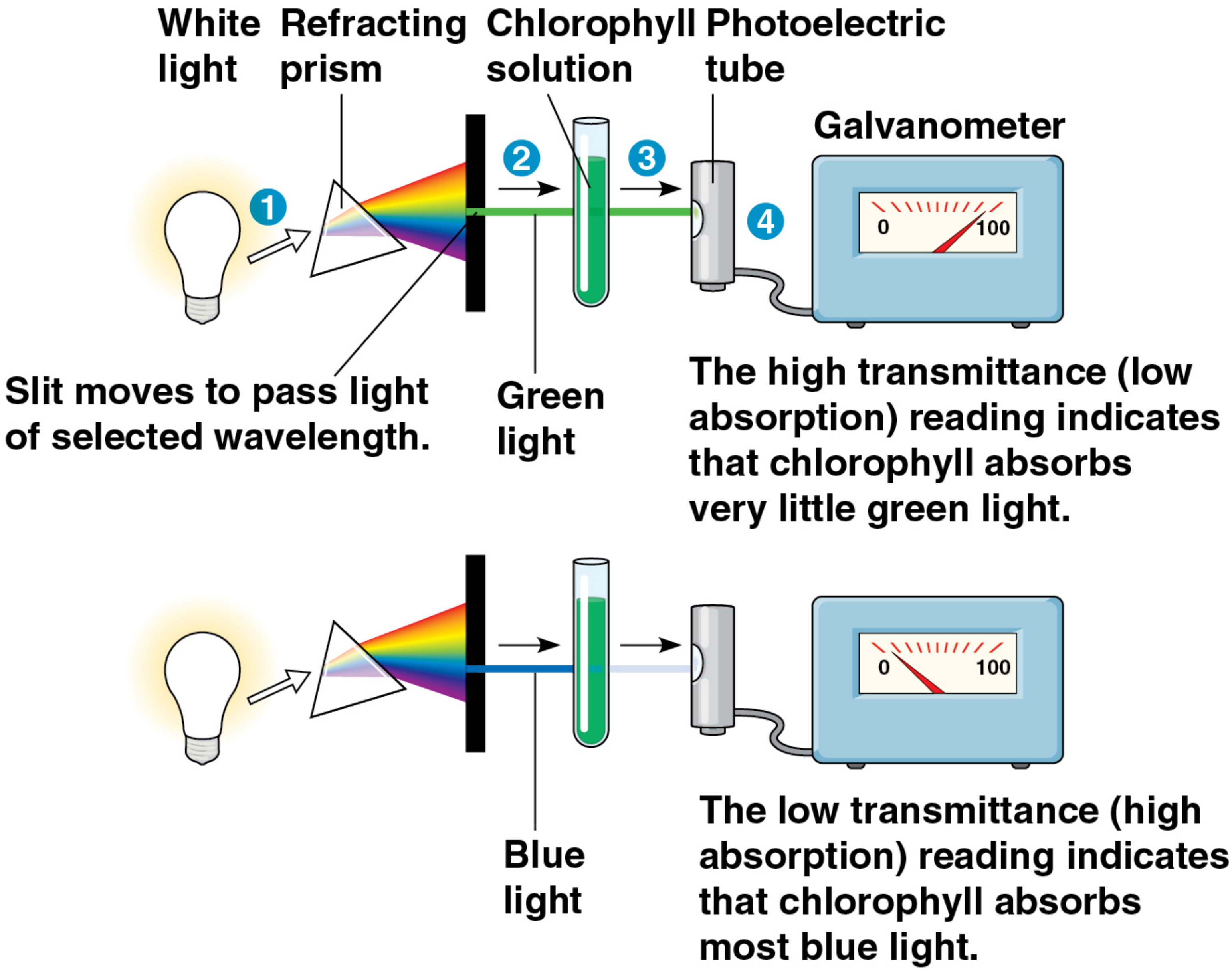
Light Energy and Pigments



[redacted]

- A **spectrophotometer** measures a pigment’s ability to absorb various wavelengths
- It sends light through pigments and measures the fraction of light transmitted at each wavelength
- An **absorption spectrum** is a graph plotting a pigment’s light absorption versus wavelength

Figure 10.8

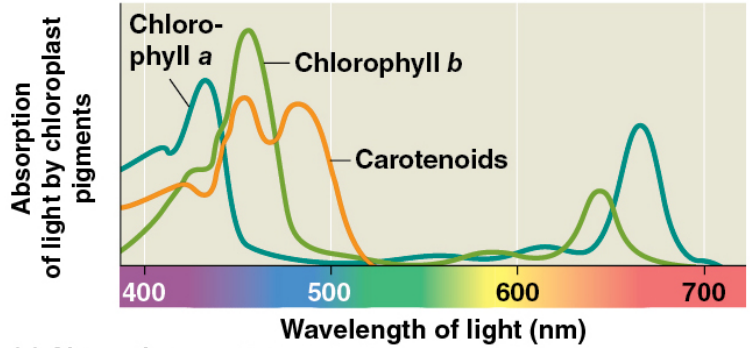


White light
Refracting prism
Chlorophyll solution
Photoelectric tube
Galvanometer
1
2
3
4
0
100
Slit moves to pass light of selected wavelength.
Green light
The high transmittance (low absorption) reading indicates that chlorophyll absorbs very little green light.
0
100
Blue light
The low transmittance (high absorption) reading indicates that chlorophyll absorbs most blue light.

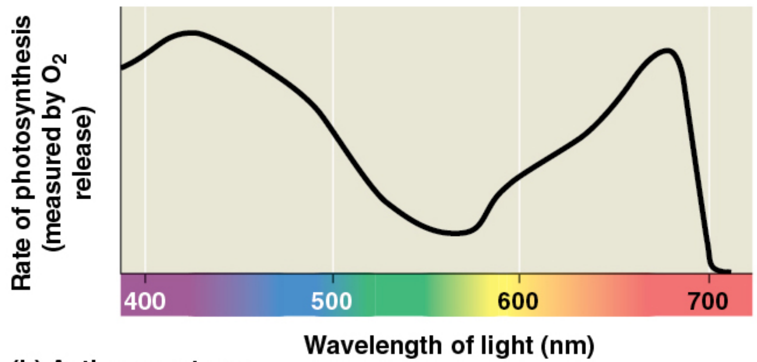
- Three types of pigments in chloroplasts include:
  - **Chlorophyll *a***, the key light-capturing pigment that participates directly in light reactions
  - **Chlorophyll *b***, an accessory pigment
  - Carotenoids, a separate group of accessory pigments

- The absorption spectrum of chlorophyll *a* indicates that violet-blue and red light will work best for photosynthesis, while green is the least effective
- The **action spectrum** for photosynthesis, a profile of the relative effectiveness of different wavelengths, confirms the effectiveness of violet-blue and red light

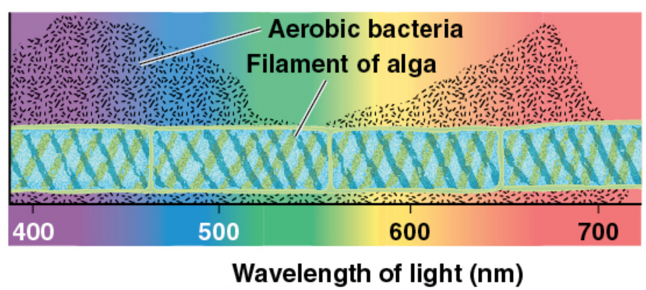
- The action spectrum of photosynthesis was first demonstrated in 1883 by Theodor W. Engelmann
- He exposed different segments of a filamentous alga to different wavelengths of light and used the growth of aerobic bacteria as a measure of O_2 production



(a) Absorption spectra



(b) Action spectrum



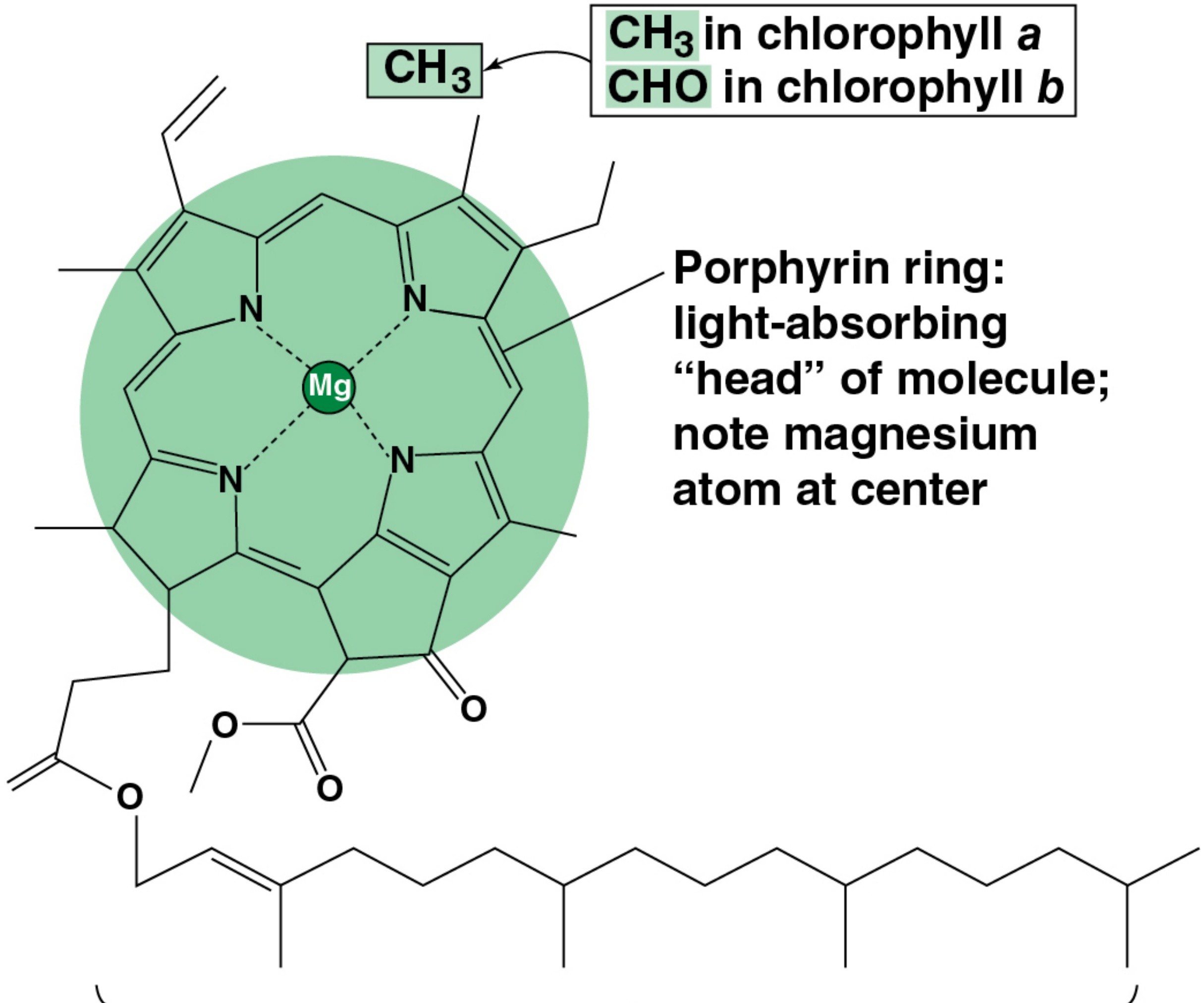
(c) Engelmann's experiment

Data from T. W. Engelmann, *Bacterium photometricum*. Ein Beitrag zur vergleichenden Physiologie des Licht-und Farbensinnes, *Archiv. für Physiologie* 30:95–124 (1883).

- The action spectrum for photosynthesis is broader than the absorption spectrum of chlorophyll
- Accessory pigments, such as chlorophyll *b*, broaden the spectrum used for photosynthesis
- The difference in the absorption spectrum between chlorophyll *a* and *b* is due to a slight structural difference between the pigment molecules

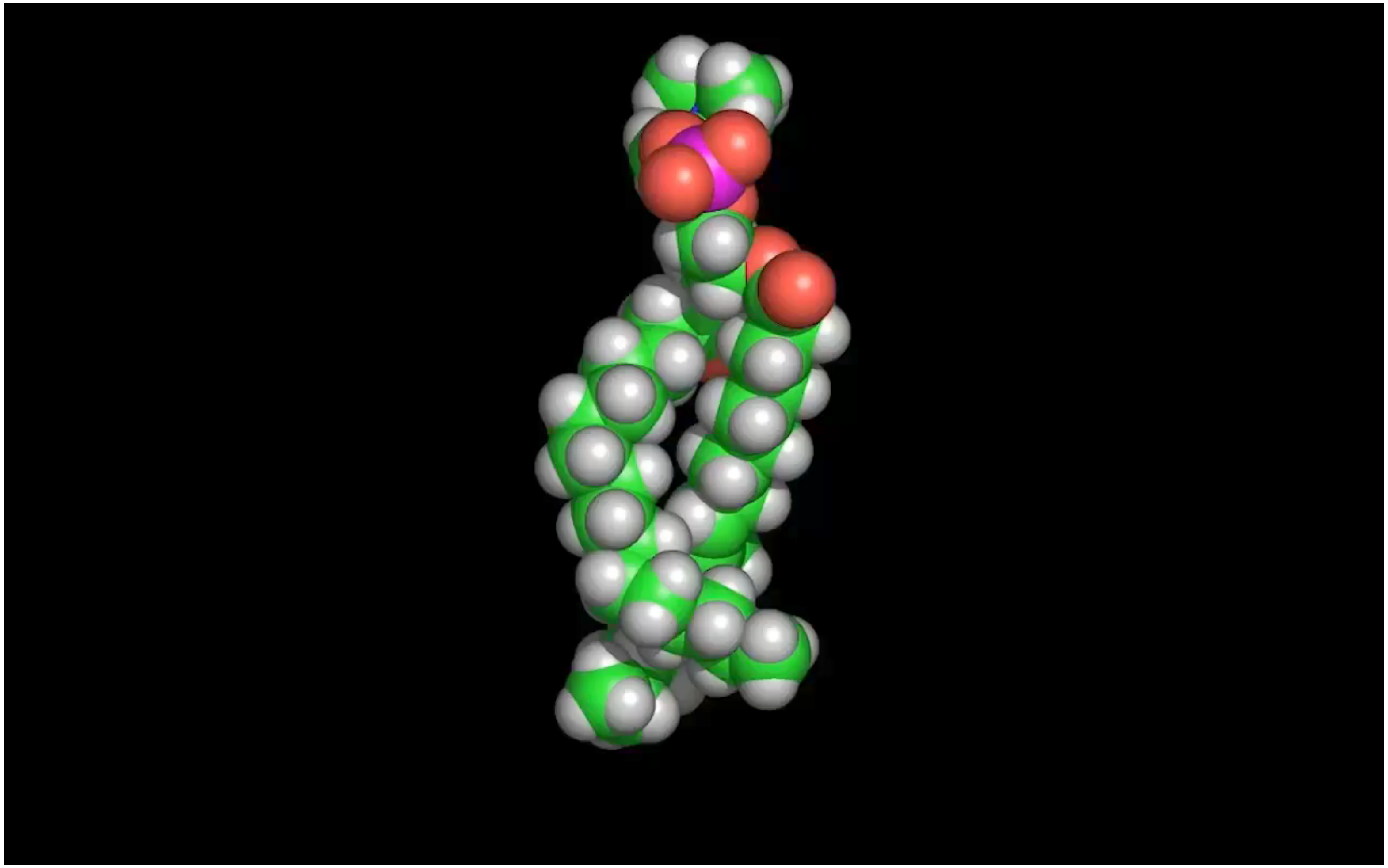
Figure 10.10

Chlorophyll *a* and *b* differ in only one functional group:



Hydrocarbon tail: interacts with hydrophobic regions of proteins inside thylakoid membranes of chloroplasts

Animation: Space-Filling Model of Chlorophyll



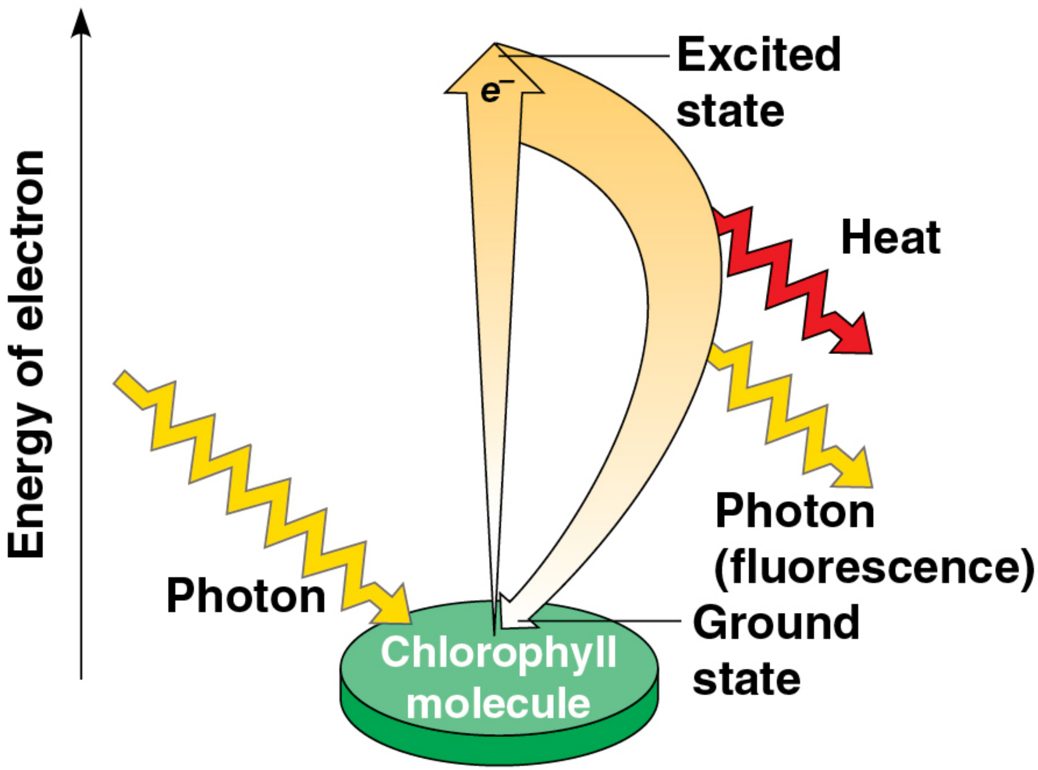
- In the last decade, two other forms of chlorophyll were discovered—chlorophyll *d* and chlorophyll *f*—that absorb higher wavelengths of light
- The cyanobacterium, *Chroococcidiopsis thermalis*, uses chlorophyll *f* in place of chlorophyll *a* in shaded conditions

- Other accessory pigments called **carotenoids**, are yellow or orange because they absorb violet and blue-green light
- Carotenoids broaden the spectrum for photosynthesis
- Some are also photoprotective, that is, they absorb excessive light that would otherwise damage chlorophyll or react with oxygen

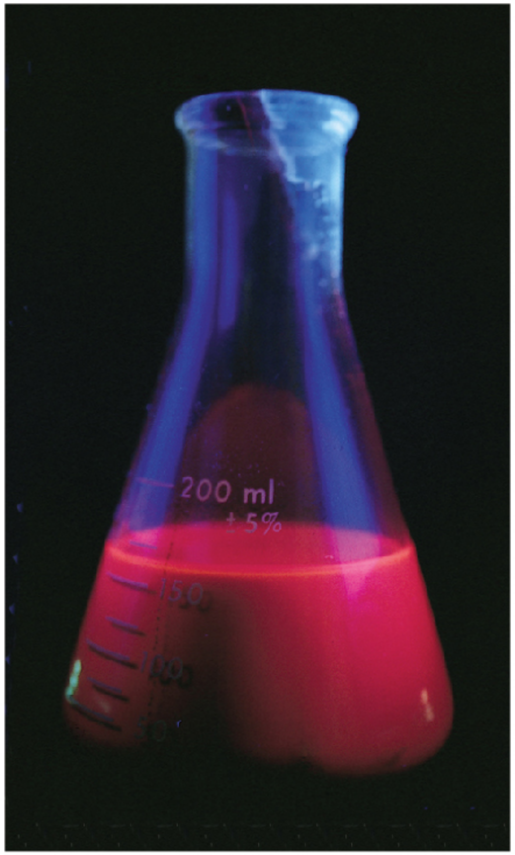
Excitation of Chlorophyll by Light

- When a pigment molecule absorbs light, one of its electrons goes from a ground state to an excited state, which is unstable
- In isolation, excited electrons fall back to the ground state, releasing excess energy as heat or light, an afterglow called fluorescence

Figure 10.11



(a) Excitation of isolated chlorophyll molecule



(b) Fluorescence

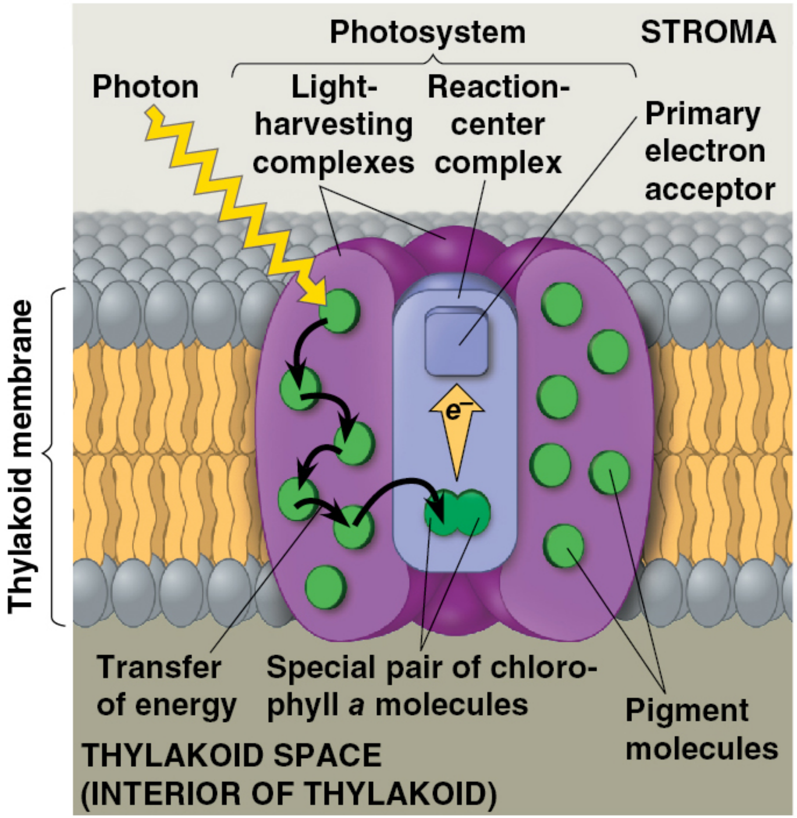
A Photosystem: A Reaction-Center Complex Associated with Light-Harvesting Complexes

- A **photosystem** consists of a reaction-center complex surrounded by light-harvesting complexes
- The **reaction-center complex** is an association of proteins holding a special pair of chlorophyll *a* molecules and a primary electron acceptor

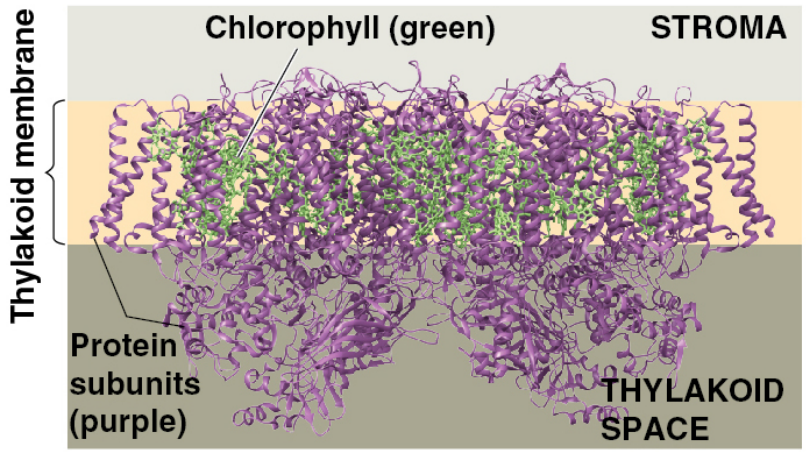
- The **light-harvesting complex** consists of various pigment molecules bound to proteins
- Light-harvesting complexes transfer the energy of photons to the chlorophyll *a* molecules in the reaction-center complex
- These chlorophyll *a* molecules are special because they can transfer an excited electron to a different molecule

- 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

Figure 10.12



(a) How a photosystem harvests light



(b) Structure of a photosystem

- There are two types of photosystems in the thylakoid membrane, numbered in order of their discovery
  - **Photosystem II (PS II)** is called P680 because its reaction-center chlorophyll a is best at absorbing light with a wavelength of 680 nm
  - **Photosystem I (PS I)** is called P700 because its reaction-center chlorophyll a is best at absorbing light with a wavelength of 700 nm

Linear Electron Flow

- During the light reactions, there are two possible routes for electron flow: cyclic and linear
- **Linear electron flow**, the primary pathway, involves both photosystems and produces ATP and NADPH using light energy

- There are eight steps in linear electron flow:
  1. A photon hits a pigment in a light-harvesting complex of PS II, and its energy is passed among pigment molecules until it excites P680
  2. An excited electron from P680 is transferred to the primary electron acceptor; we refer to the oxidized form as $P680^+$

3. An enzyme catalyzes the split of H_2O into two electrons, two hydrogen ions (H^+) and an oxygen atom
   - The electrons are transferred to the $P680^+$ pair, reducing it back to P680
   - The H^+ are released into the thylakoid space
   - The oxygen atom combines with another oxygen atom generated by the splitting of a different H_2O and forms O_2

4. Electrons are passed in a series of redox reactions from the primary electron acceptor of PS II down an electron transport chain to PS I
    - The electron transport chain includes the electron carrier plastoquinone (Pq), a cytochrome complex, and a protein called plastocyanin (Pc)
    - Energy released by electron transfer is used to pump H^+ into the thylakoid space, creating a proton gradient across the thylakoid membrane

5. Potential energy stored in the proton gradient drives production of ATP by chemiosmosis
6. In PS I (like PS II), transferred light energy excites P700, which loses an electron to the primary electron acceptor
   - $P700^+$ (P700 that is missing an electron) accepts an electron passed down from PS II via the electron transport chain

7. Electrons are passed from the primary electron acceptor of PS I down a second electron transport chain to the protein ferredoxin (Fd)
   - There is no proton gradient or ATP produced by this electron transport chain

8. The enzyme $NADP^+$ reductase catalyzes the transfer of electrons from Fd to $NADP^+$
   - Two electrons are needed to reduce $NADP^+$ to NADPH
   - The electrons of NADPH are at a higher energy level than they were in H_2O, so are more readily available for the reactions of the Calvin cycle
   - The formation of NADPH also removes an H^+ from the stroma

Figure 10.UN02

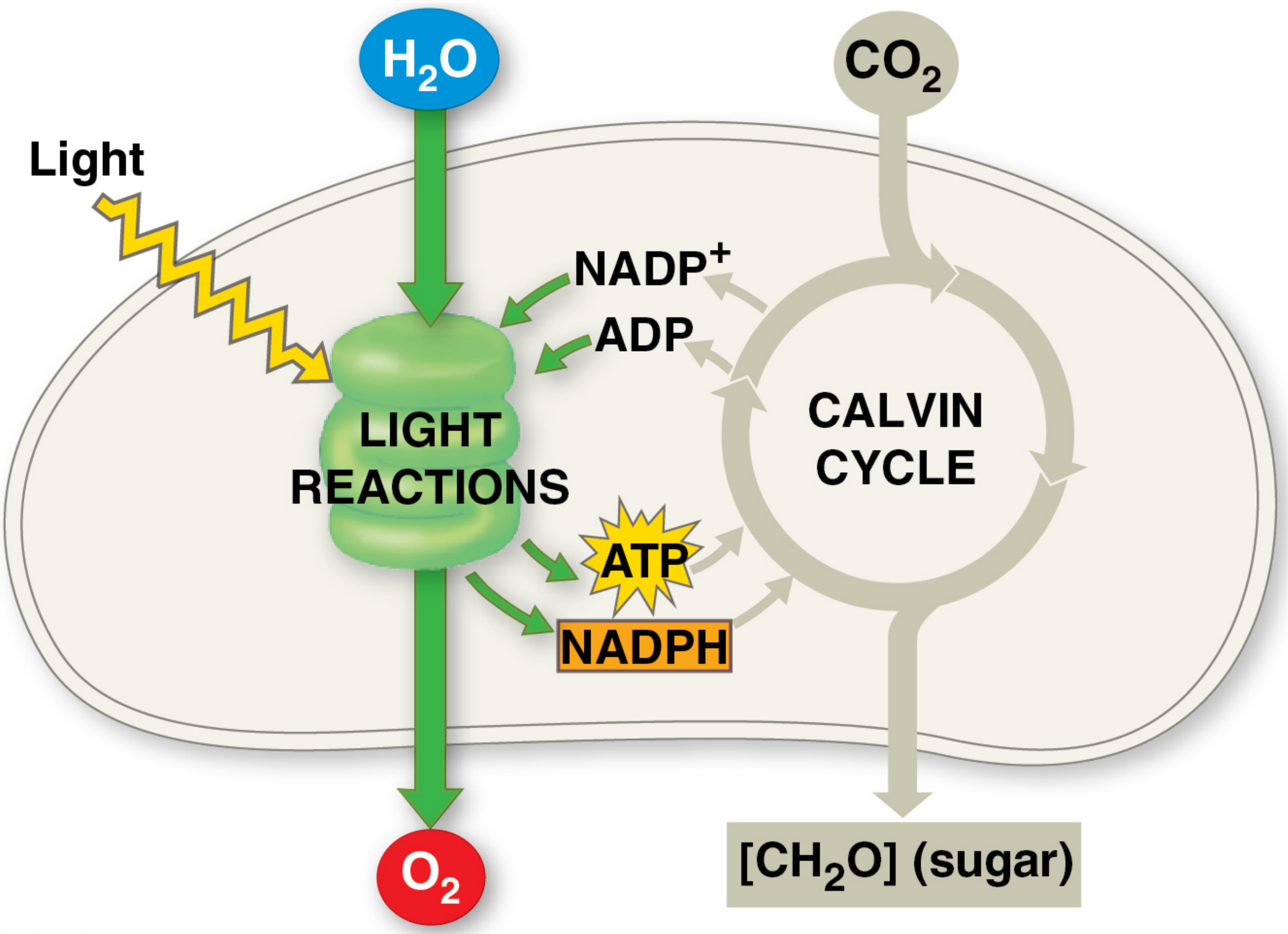
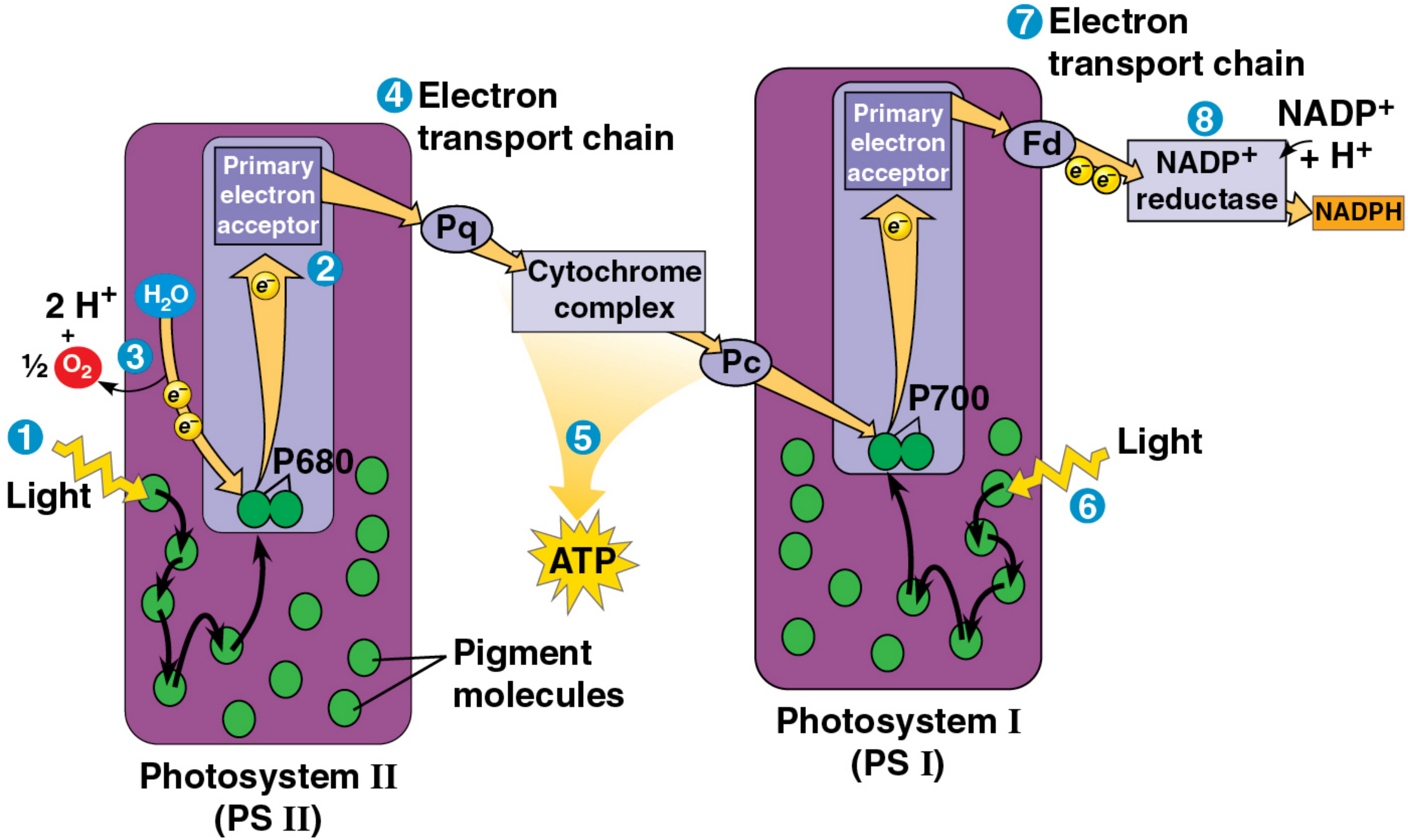


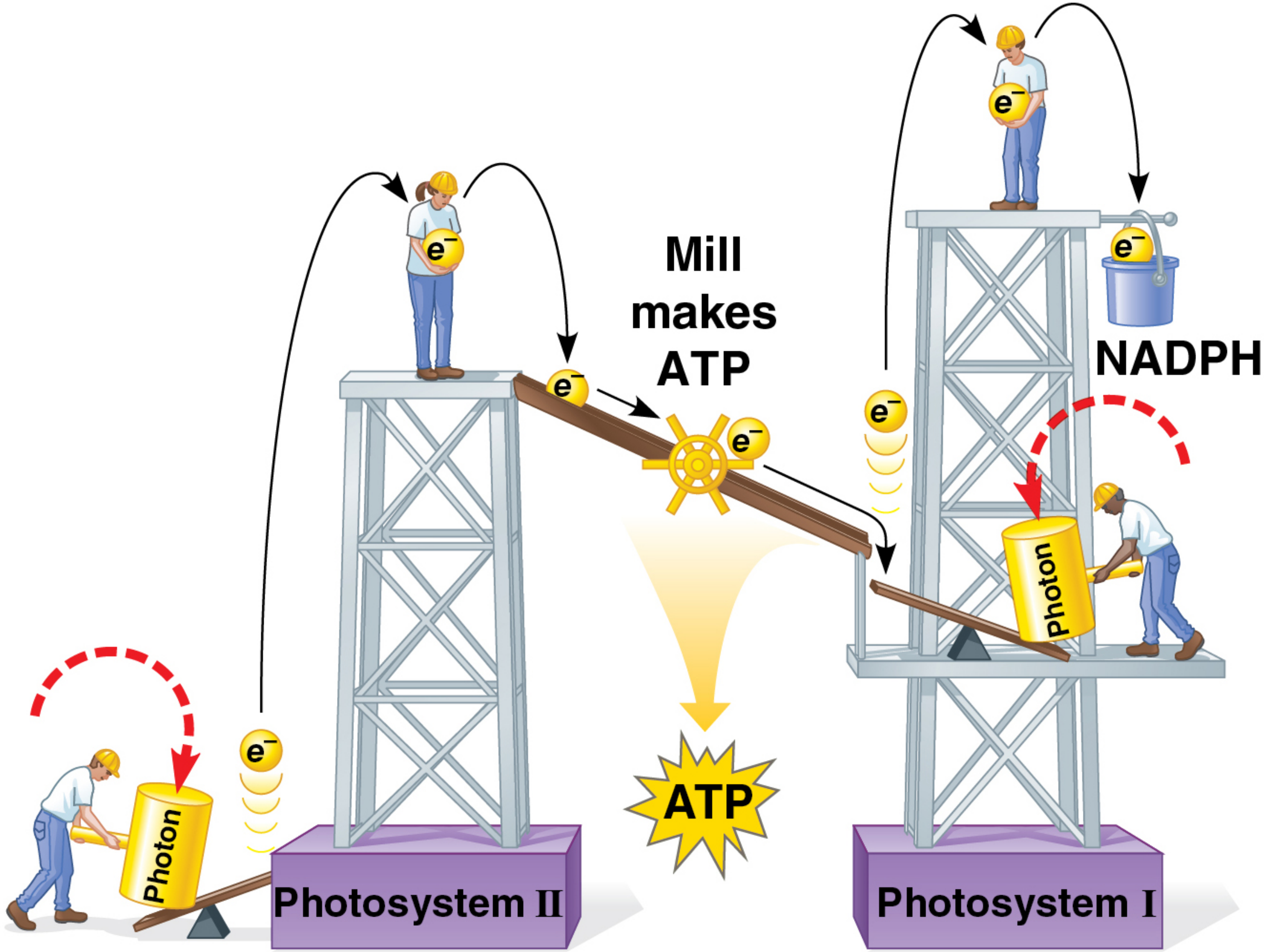
Figure 10.13



4 Electron transport chain
7 Electron transport chain
Primary electron acceptor
Primary electron acceptor
Pq
Cytochrome complex
Pc
Fd
8
NADP+ reductase
NADP+ + H+
NADPH
2
e−
2 H+ + ½ O2
H2O
3
e−
e−
1
Light
P680
5
ATP
P700
Light
6
Pigment molecules
Photosystem II (PS II)
Photosystem I (PS I)

- Light reactions use solar power to generate ATP and NADPH, providing the chemical energy and reducing power needed by the Calvin cycle to make sugar
- The energy changes of electrons during linear flow through the light reactions can be shown in a mechanical analogy

Figure 10.14

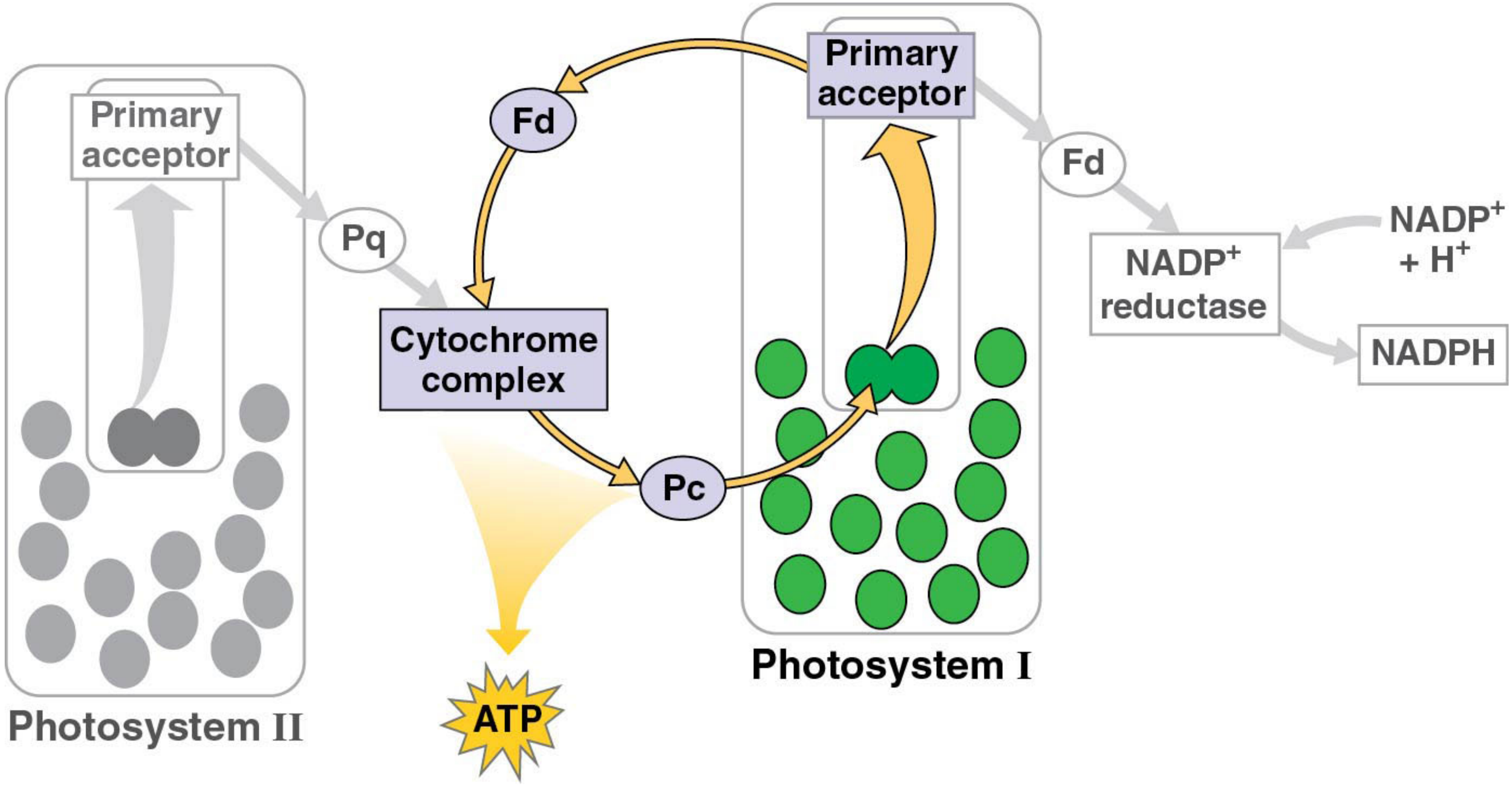


e⁻
Mill
makes
ATP
NADPH
Photon
ATP
Photosystem II
Photosystem I

Cyclic Electron Flow

- In **cyclic electron flow**, photoexcited electrons cycle back from Fd to the cytochrome complex instead of being transferred to $NADP^+$
- Electrons are passed to a P700 chlorophyll in the PS I reaction center via the plastocyanin molecule (Pc)
- Cyclic electron flow uses only photosystem I
- It produces ATP, but no NADPH or oxygen results from this process

Figure 10.15


Primary acceptor
Pq
Photosystem II
Fd
Cytochrome complex
Pc
ATP
Primary acceptor
Photosystem I
Fd
NADP+ reductase
NADP+ + H+
NADPH

- Several groups of photosynthetic bacteria have only a single photosystem related to either PS II or PS I
- For these organisms, cyclic electron flow is the only means of generating ATP during photosynthesis
- Photosynthesis may have first evolved in the ancestors of these bacteria in a form similar to cyclic electron flow

- Cyclic electron flow is probably, in part an "evolutionary leftover" in organisms with both photosystems
- Cyclic electron flow may have some photoprotective capability; plants that do not have it grow well in low light, but cannot grow well in intense light

A Comparison of Chemiosmosis in Chloroplasts and Mitochondria

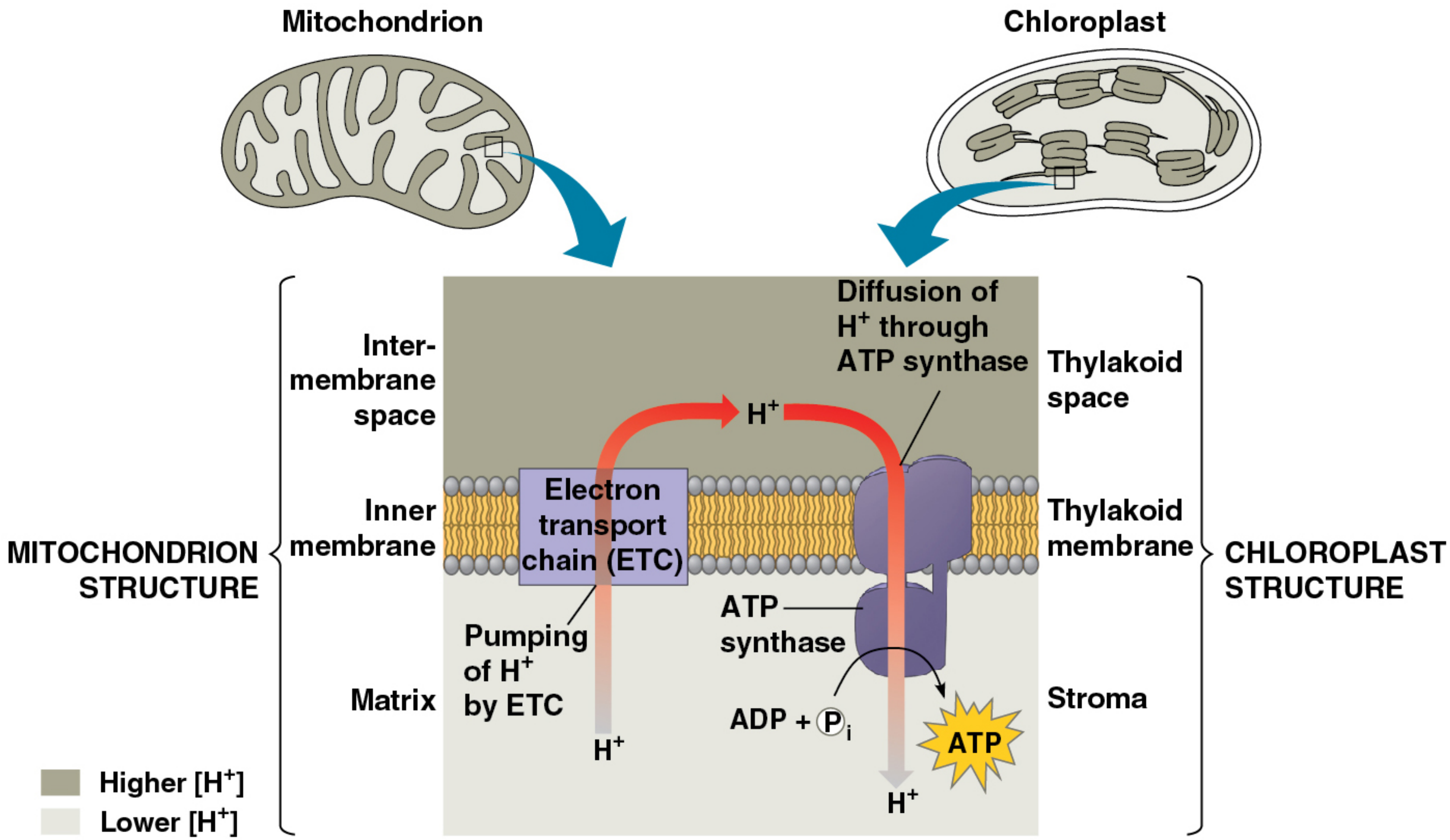
- Chloroplasts and mitochondria both generate ATP by chemiosmosis
  - Electron transport chains pump protons (H^+) across a membrane as electrons are passed through carriers with progressively higher electron affinity
  - ATP synthase couples the diffusion of H^+ down their gradient to the phosphorylation of ADP to ATP

- Some of the electron carriers, including iron-containing proteins called cytochromes, are very similar in mitochondria and chloroplasts
- The ATP synthase complexes are also very similar

- Photophosphorylation differs from oxidative phosphorylation in a few key ways
  - In chloroplasts, high energy electrons drop down the transport chain from water, while in mitochondria, they are extracted from organic molecules
  - Mitochondria transfer chemical energy from food to ATP; chloroplasts transform light energy into the chemical energy of ATP

- Although the spatial organization of chemiosmosis differs slightly, there are similarities
  - 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 on the stroma side of the membrane as they diffuse back into the stroma

Figure 10.16


Mitochondrion
Chloroplast
MITOCHONDRION STRUCTURE
Inter-membrane space
Inner membrane
Matrix
Electron transport chain (ETC)
Pumping of H+ by ETC
H+
H+
Diffusion of H+ through ATP synthase
ATP synthase
ADP + P i
ATP
H+
Thylakoid space
Thylakoid membrane
Stroma
CHLOROPLAST STRUCTURE
Higher [H+]
Lower [H+]

- Both ATP and NADPH are produced on the stroma side of the thylakoid membrane, making them available for sugar synthesis in the Calvin cycle

Figure 10.UN03

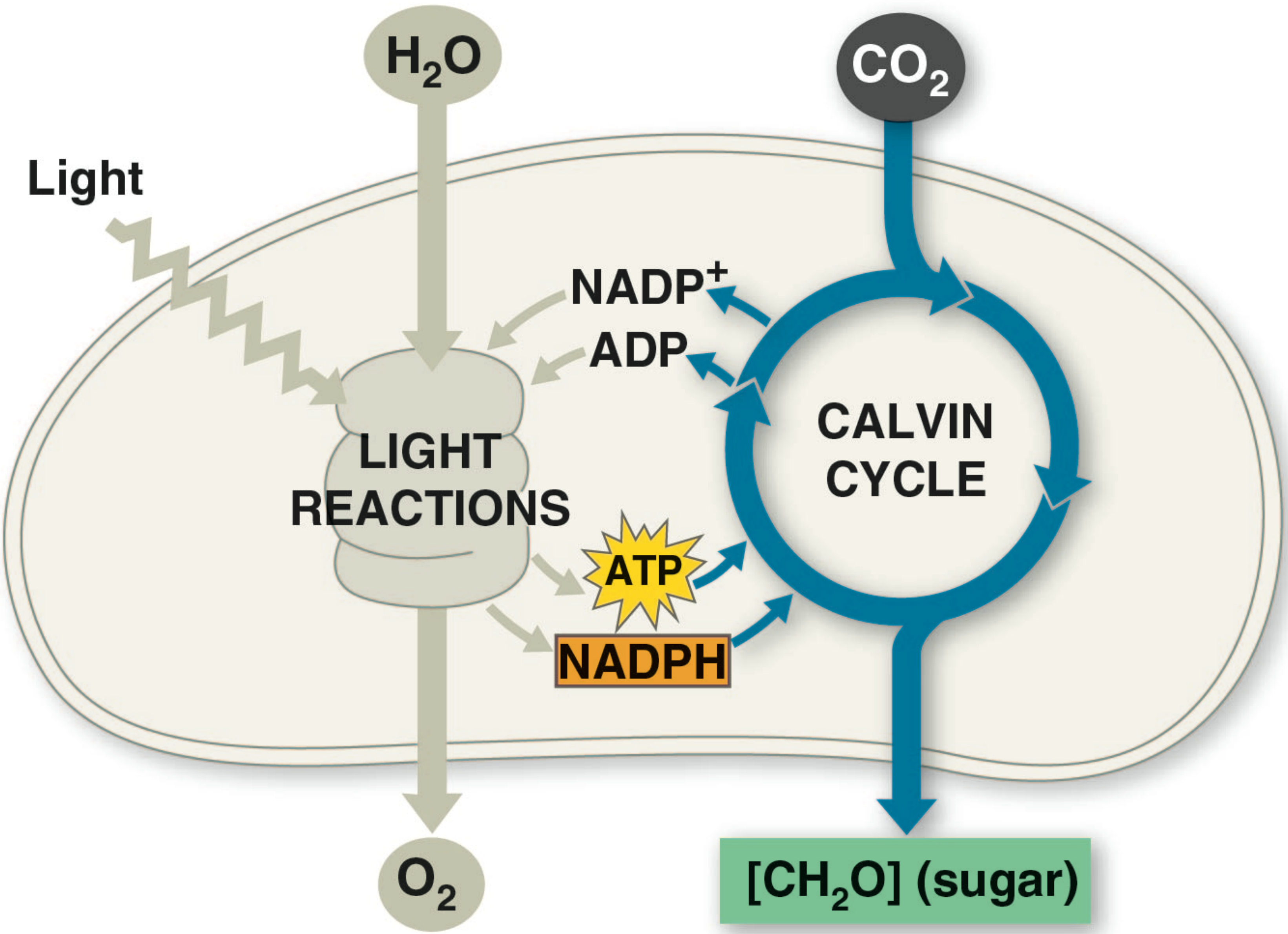
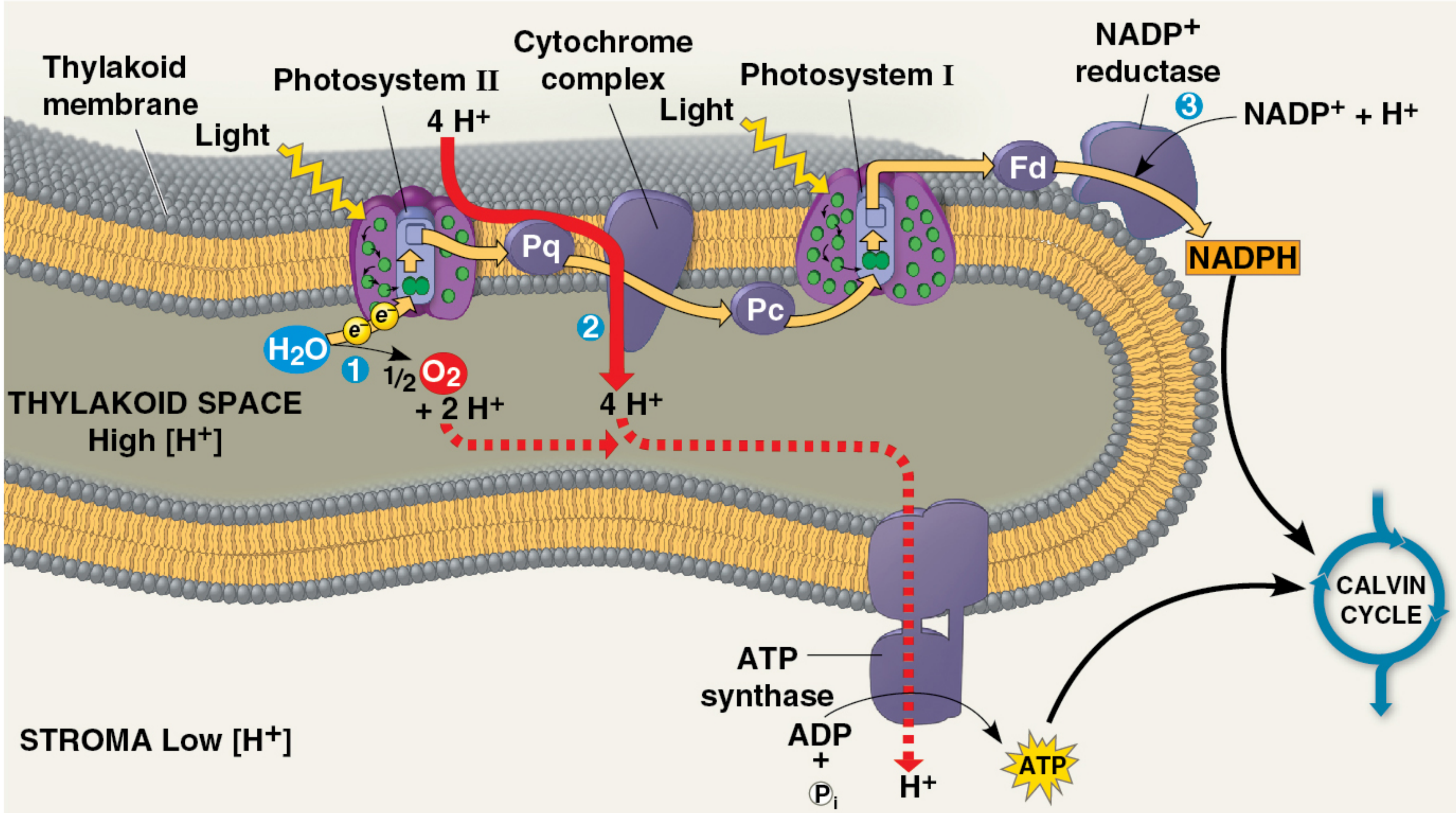


Figure 10.17



Thylakoid membrane
Light
Photosystem II
4 H+
Cytochrome complex
Light
Photosystem I
NADP+ reductase
3
NADP+ + H+
Fd
NADPH
Pq
Pc
2
e−
e−
H2O
1
1/2 O2
+ 2 H+
4 H+
THYLAKOID SPACE
High [H+]
CALVIN CYCLE
ATP synthase
ADP
+
Pi
H+
ATP
STROMA Low [H+]

Animation: The Light Reactions

Animation: The Light Reactions

CONCEPT 10.4: The Calvin cycle uses the chemical energy of ATP and NADPH to reduce CO_2 to sugar

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

- Carbon enters the cycle as CO_2 and leaves as a sugar named **glyceraldehyde 3-phospate (G3P)**
- For net synthesis of one G3P, the cycle must take place three times, fixing three molecules of CO_2, one for each turn of the cycle
- The Calvin cycle has three phases: carbon fixation, reduction, and regeneration of the CO_2 acceptor

Phase 1: Carbon fixation

- The binding of CO_2 to a five-carbon sugar named ribulose bisphosphate (RuBP) is catalyzed by RuBP carboxylase-oxygenase, or **rubisco**
- The six-carbon intermediate molecule is immediately split into two molecules of 3-phosphoglycerate (for each CO_2 fixed)

Phase 2: Reduction

- Each molecule of 3-phosphoglycerate is altered through phosphorylation by six ATP and reduction by six NADPH to ultimately produce a G3P sugar
- For every three CO_2 molecules that enter the cycle, six molecules of G3P are formed
- Only one of these can be counted as a net gain of carbohydrate

Phase 3: Regeneration of the CO_2 acceptor (RuBP)

- The remaining five molecules of G3P are rearranged in a complex series of reactions yielding three molecules of RuBP
- Three additional molecules of ATP are used to facilitate the regeneration of RuBP

Figure 10.UN04

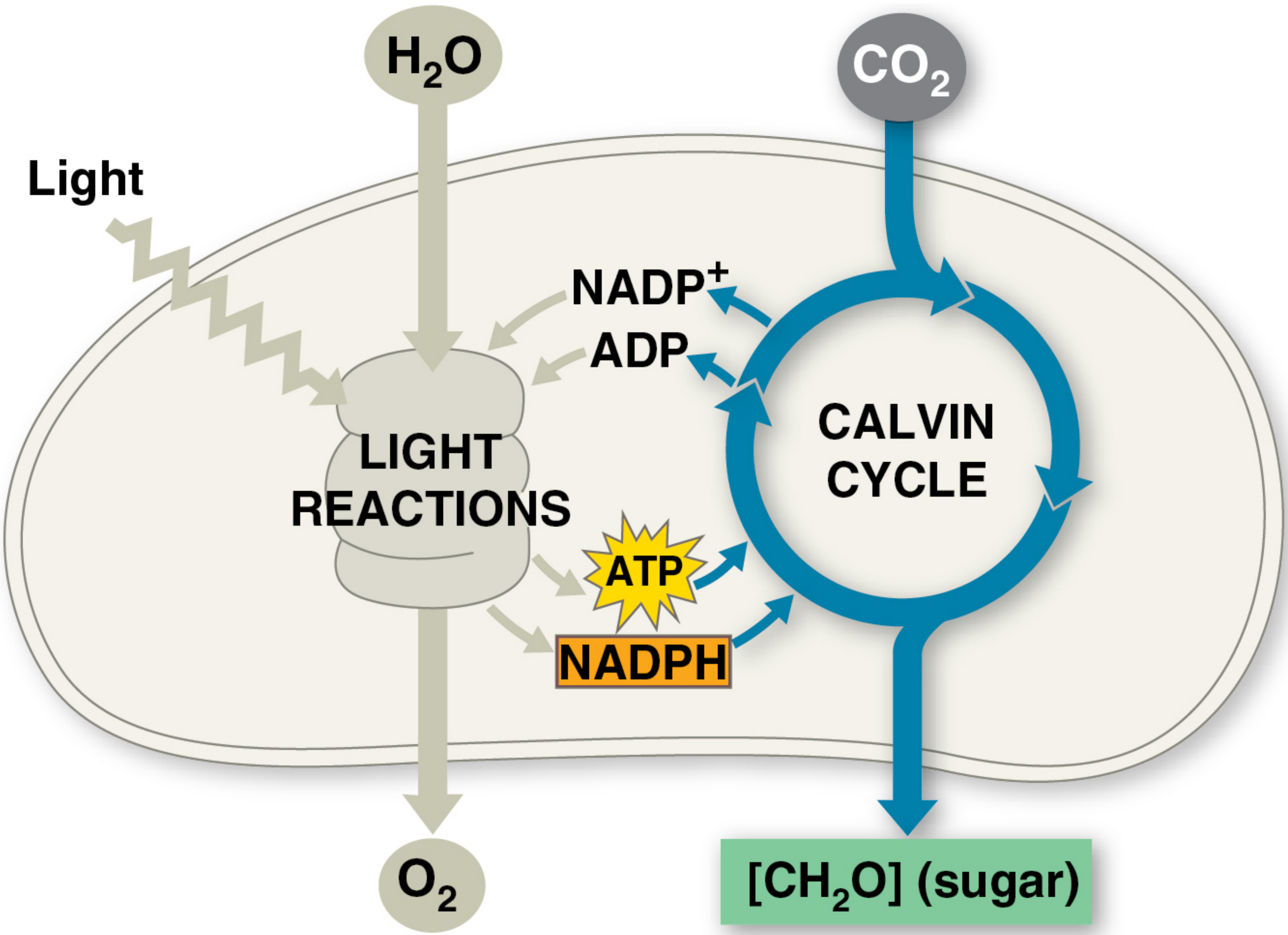
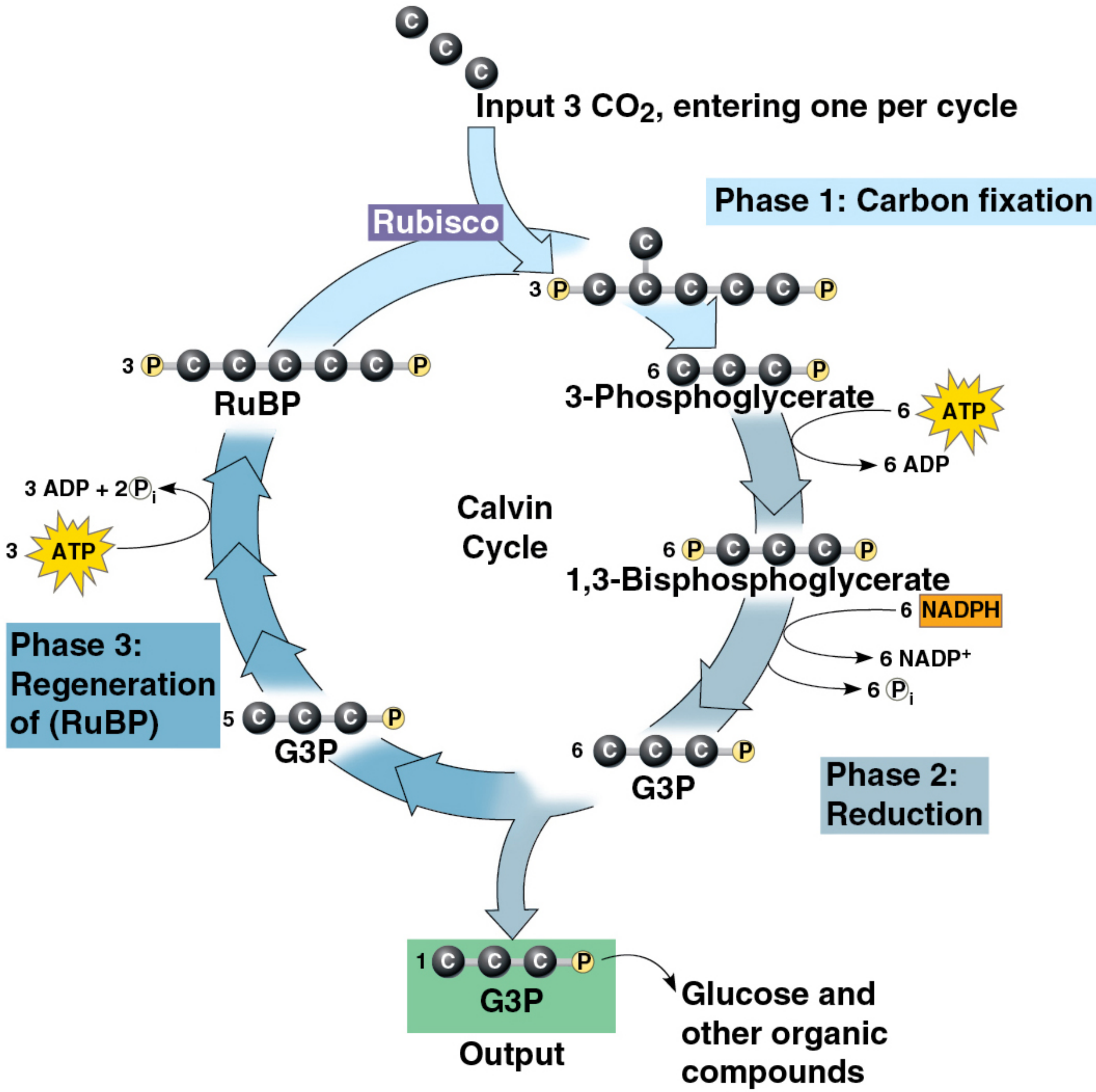


Figure 10.18

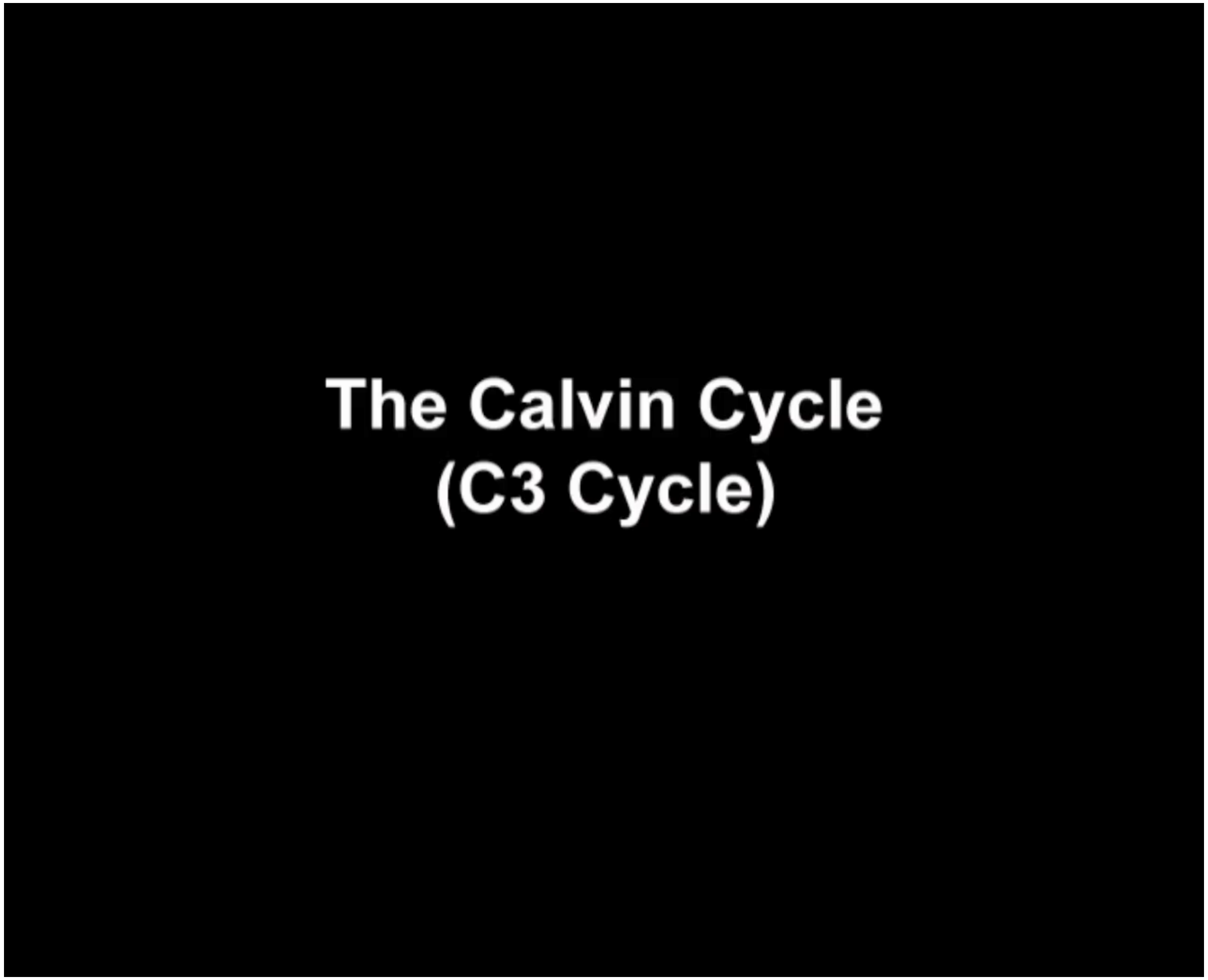


Input 3 CO_2, entering one per cycle
Phase 1: Carbon fixation
Rubisco
3 P C C C C C C P
6 C C C P
3-Phosphoglycerate
6 ATP
6 ADP
3 P C C C C C P
RuBP
3 ADP + 2 P_i
3 ATP
Calvin Cycle
6 P C C C P
1,3-Bisphosphoglycerate
6 NADPH
6 $NADP^+$
6 P_i
Phase 3: Regeneration of (RuBP)
5 C C C P
G3P
6 C C C P
G3P
Phase 2: Reduction
1 C C C P
G3P
Output
Glucose and other organic compounds

Animation: The Calvin Cycle

[redacted]

Animation: The Calvin Cycle



- For the net synthesis of one G3P molecule, the Calvin cycle consumes nine molecules of ATP and six molecules of NADPH
- The light reactions regenerate the ATP and NADPH
- The G3P is the starting molecule for metabolic pathways that synthesize other organic molecules, including glucose, sucrose, and other carbohydrates

CONCEPT 10.5: Alternative mechanisms of carbon fixation have evolved in hot, arid climates

- Dehydration is a major challenge of terrestrial life for plants, particularly in arid climates
- Plants have metabolic adaptations to help conserve water; but these adaptations often involve trade-offs

- One important trade-off is the balance between photosynthesis and water conservation
  - On hot, dry days, plants close stomata, which conserves H_2O but also limits photosynthesis
  - The closing of stomata reduces access to CO_2 and causes O_2 to build up
  - These conditions favor an apparently wasteful process called photorespiration

Photorespiration: An Evolutionary Relic?

- Most plants are **C_3 plants**, in which the initial fixation of CO_2, via rubisco, forms a three-carbon compound (3-phosphoglycerate)
- In **photorespiration**, rubisco binds with O_2 instead of CO_2, producing a two-carbon compound

- Photorespiration is costly because it consumes O_2 and organic fuel without producing any ATP or sugar
- It is thought to be an evolutionary relic because rubisco first evolved at a time when the atmosphere had far less O_2 and more CO_2
- Photorespiration may provide some protection from the damaging products of the light reactions that build up when the Calvin cycle slows due to low CO_2

- In many plants, photorespiration drains away as much as 50% of the carbon fixed by the Calvin cycle
- In some plant species, alternate modes of carbon fixation have evolved to minimize photorespiration and optimize the Calvin cycle

C_4 Plants

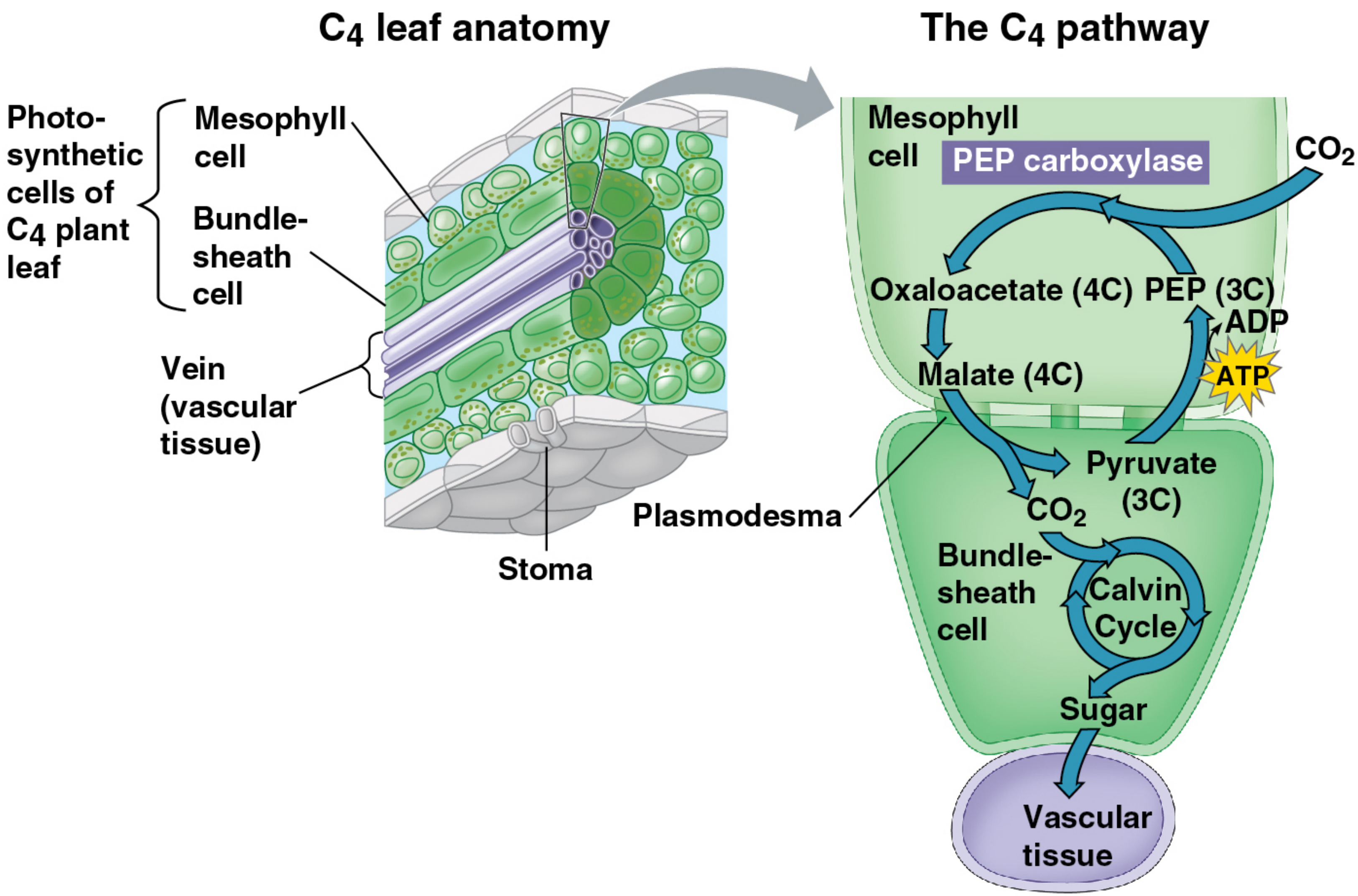
- **C_4 plants** minimize the cost of photorespiration by incorporating CO_2 into a four-carbon compound as the first product of the Calvin cycle
- C_4 has evolved several times and is used by several thousand species in at least 19 different families
- Important agricultural examples include sugarcane and corn

- In hot, dry weather, C_4 plants partially close their stomata, conserving water but reducing CO_2
- Photosynthesis begins in mesophyll cells, but is completed in **bundle-sheath cells**, cells arranged in tightly packed sheaths around the leaf veins

- Sugar production in C_4 plants occurs in a three-step process
  1. The production of the four-carbon precursors is catalyzed by the enzyme **PEP carboxylase** in the mesophyll cells
     - PEP carboxylase has a higher affinity for CO_2 than rubisco does; it can fix CO_2 even when CO_2 concentrations are low

2. The four-carbon compounds are exported to bundle-sheath cells through plasmodesmata
3. Within the bundle-sheath cells, CO_2 is released from the four-carbon compound and then used in the Calvin cycle
   - Pyruvate is transported to the mesophyll cells where one ATP is used to convert it back to PEP
   - This ATP is generated using cyclic electron flow

Figure 10.19



C4 leaf anatomy
The C4 pathway
Photo-
synthetic
cells of
C4 plant
leaf
Mesophyll
cell
Bundle-
sheath
cell
Vein
(vascular
tissue)
Stoma
Plasmodesma
Mesophyll
cell
PEP carboxylase
CO2
Oxaloacetate (4C)
PEP (3C)
ADP
ATP
Malate (4C)
Pyruvate
(3C)
CO2
Bundle-
sheath
cell
Calvin
Cycle
Sugar
Vascular
tissue

- CO_2 levels have drastically increased since the Industrial Revolution began in the 1800s, and continue to rise today due to human activities
- Increasing CO_2 and temperature may affect C_3 and C_4 plants differently, perhaps changing the relative abundance of these species
- The effects of such changes are unpredictable and a cause for concern

- Suitable agricultural land is decreasing due to the effects of climate change, while the world population and demand for food continue to increase
- C_4 photosynthesis uses less water and resources than C_3 photosynthesis
- Scientists have genetically modified rice, a C_3 plant, to carry out C_4 photosynthesis for an estimated 30–50% increase in yield for given water and resources

CAM Plants

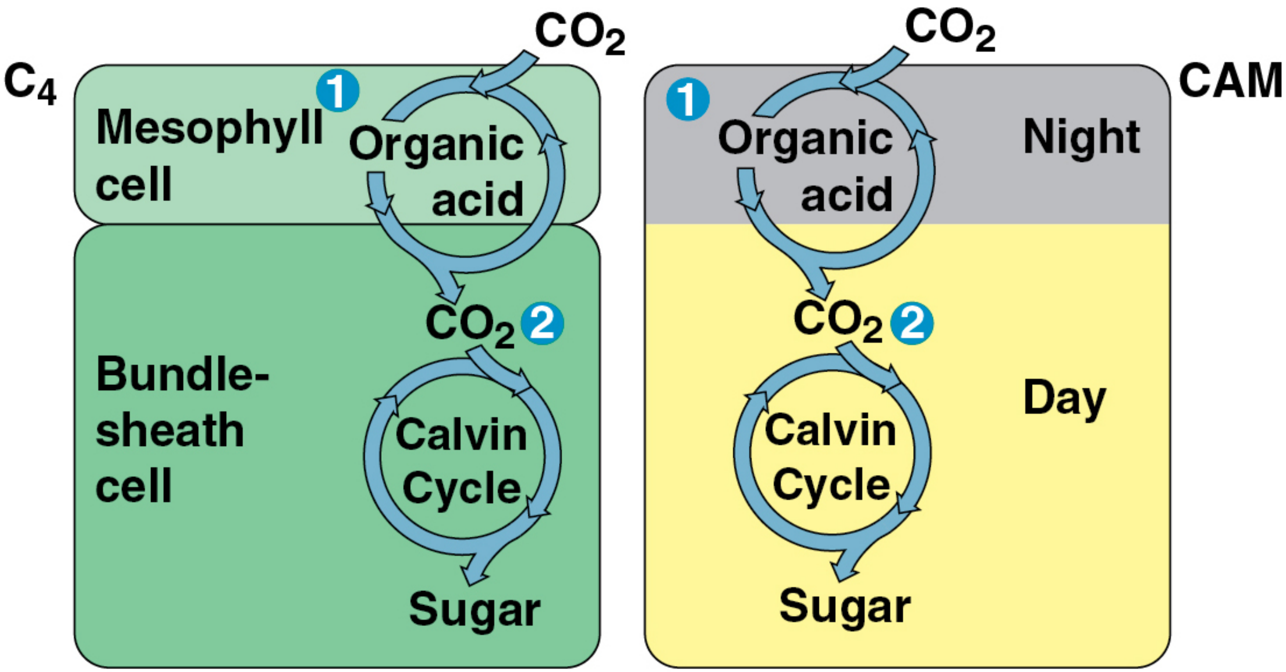
- Some plants, including succulents, conserve water by using **crassulacean acid metabolism (CAM)** to fix carbon
- **CAM plants** open their stomata at night, and incorporate CO_2 into organic acids that are stored in the vacuoles
- Stomata close during the day, and CO_2 is released from organic acids and used in the Calvin cycle

- The CAM pathway is similar to the C_4 pathway in that they both incorporate CO_2 into organic intermediates before it enters the Calvin cycle
- The C_4 pathway structurally separates the initial steps of carbon fixation from the Calvin cycle
- In the CAM pathway, these steps occur in the same cell, but are separated in time

Figure 10.20

Sugarcane

Pineapple



(a) Spatial separation of steps

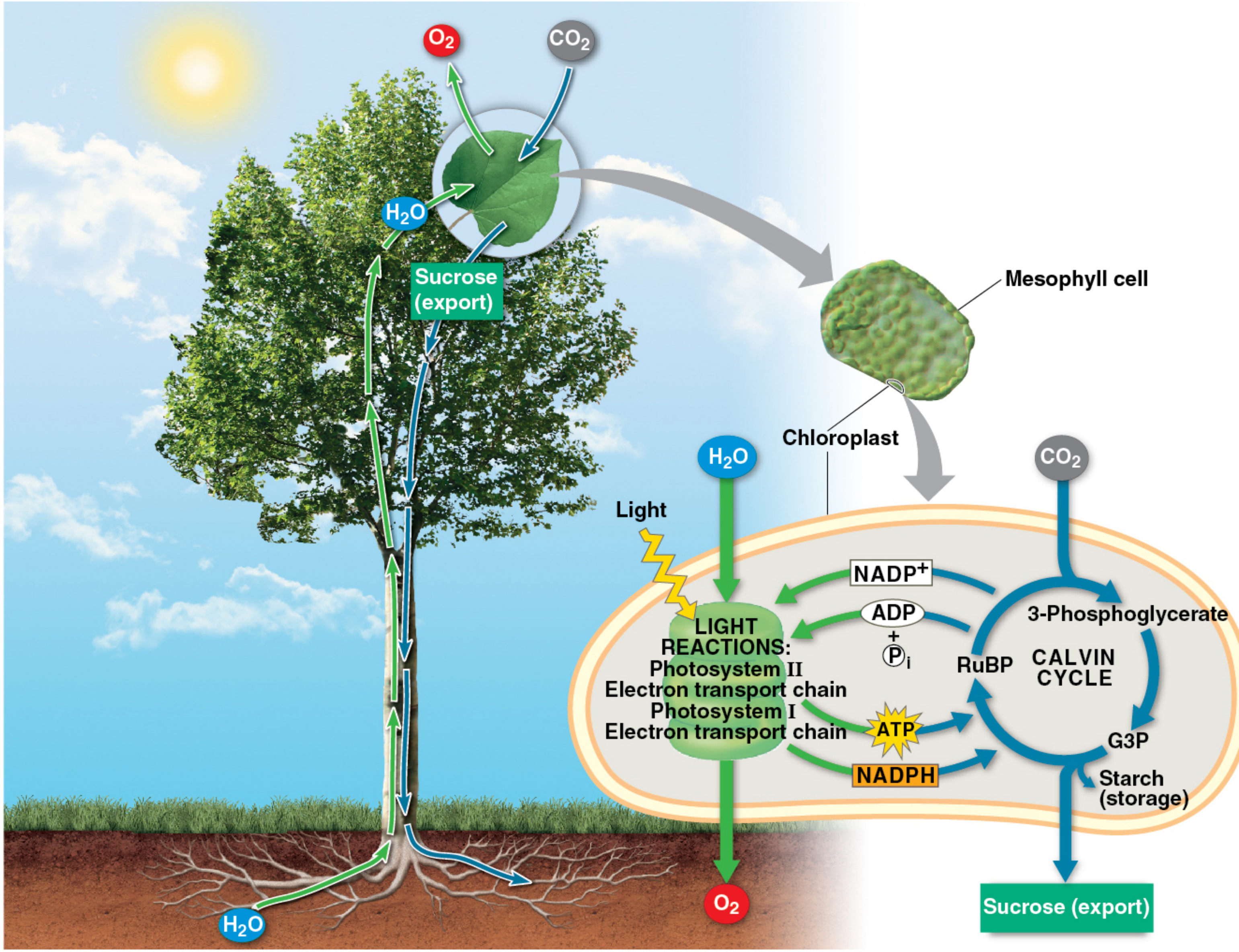
(b) Temporal separation of steps

Animation: Photosynthesis in Dry Climates

CONCEPT 10.6: Photosynthesis is essential for life on Earth: 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 in the form of starch in chloroplasts and other structures such as roots, tubers, seeds, and fruits

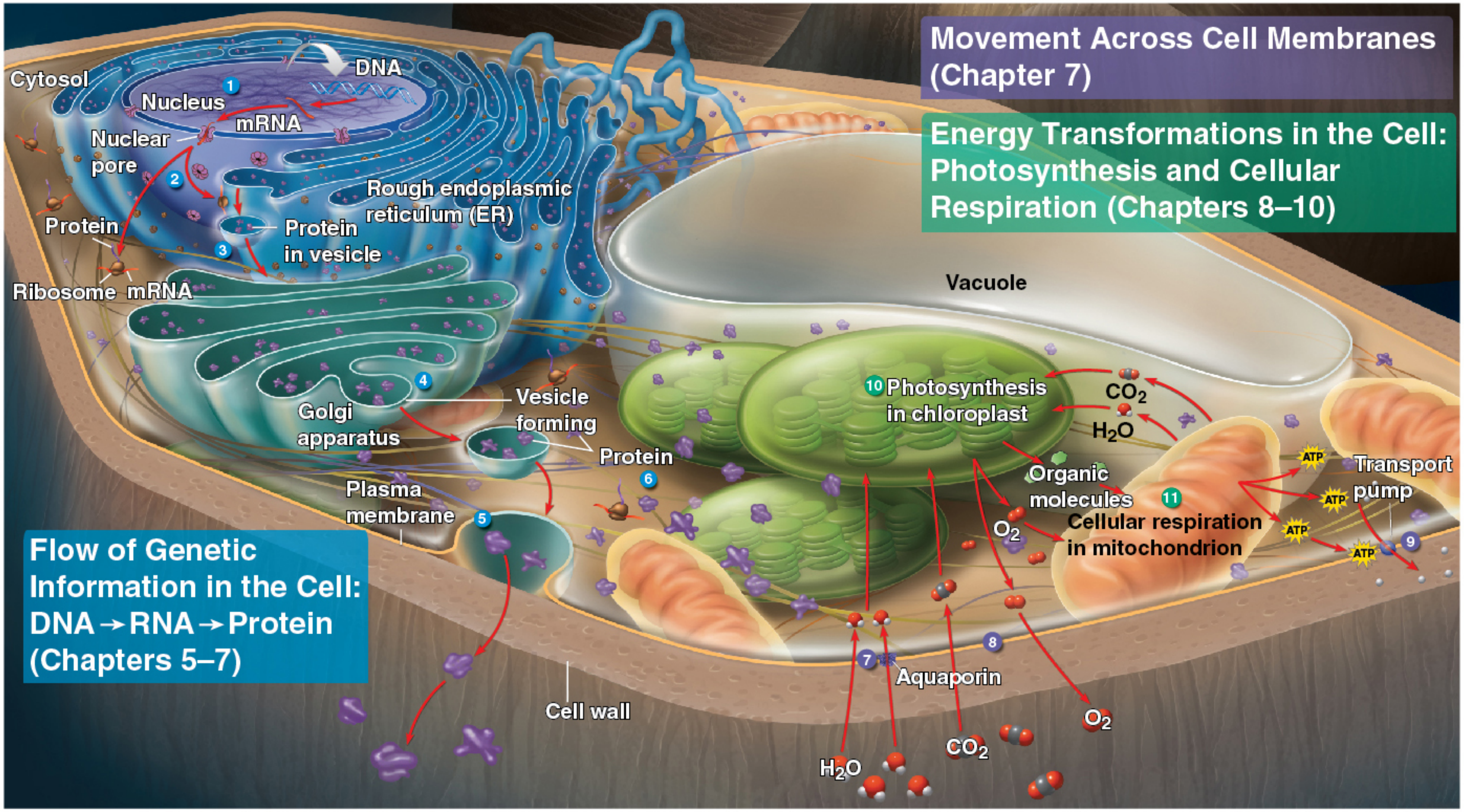
Figure 10.21



O_2
CO_2
H_2O
Sucrose (export)
Mesophyll cell
Chloroplast
H_2O
CO_2
Light
$NADP^+$
ADP
+
P_i
3-Phosphoglycerate
LIGHT REACTIONS:
Photosystem II
Electron transport chain
Photosystem I
Electron transport chain
RuBP
CALVIN CYCLE
ATP
G3P
NADPH
Starch (storage)
O_2
Sucrose (export)
H_2O

Figure 10.22

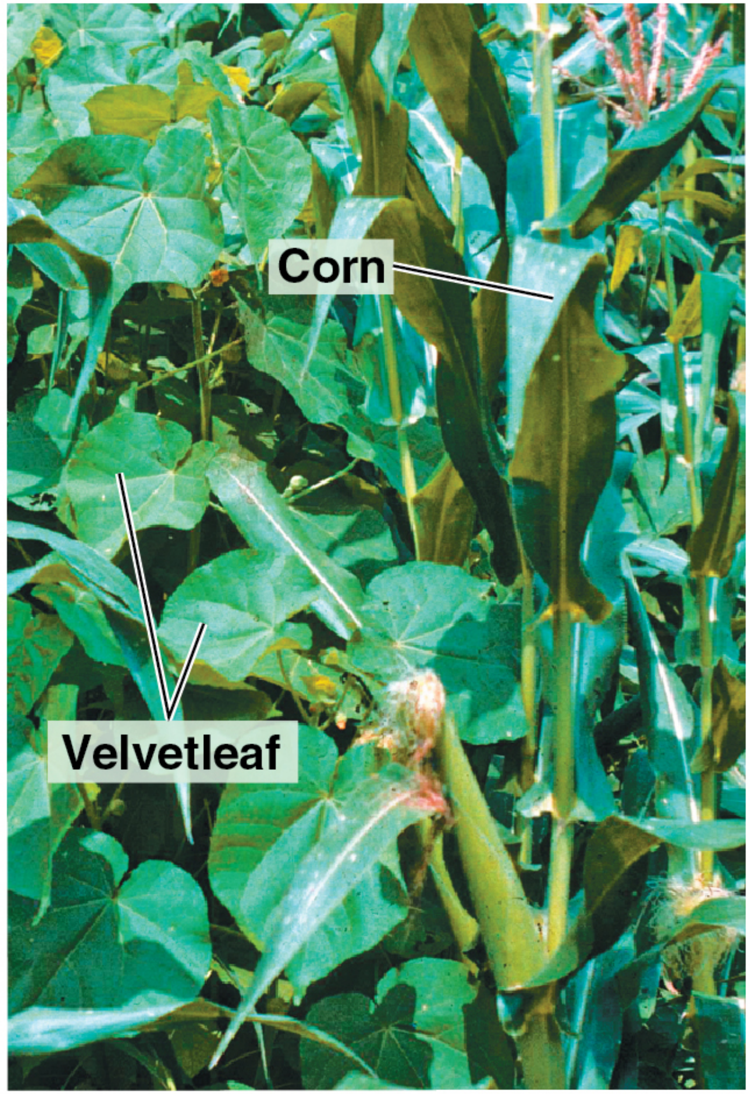
MAKE CONNECTIONS: The Working Cell



Data from the Experiment

	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 CO_2 enrichment on the growth and competitiveness of C_3 and C_4 weed and crop plants, *Weed Science* 28(1):71–75 (1980).



Corn plant surrounded by invasive velvetleaf plants

Figure 10.UN06

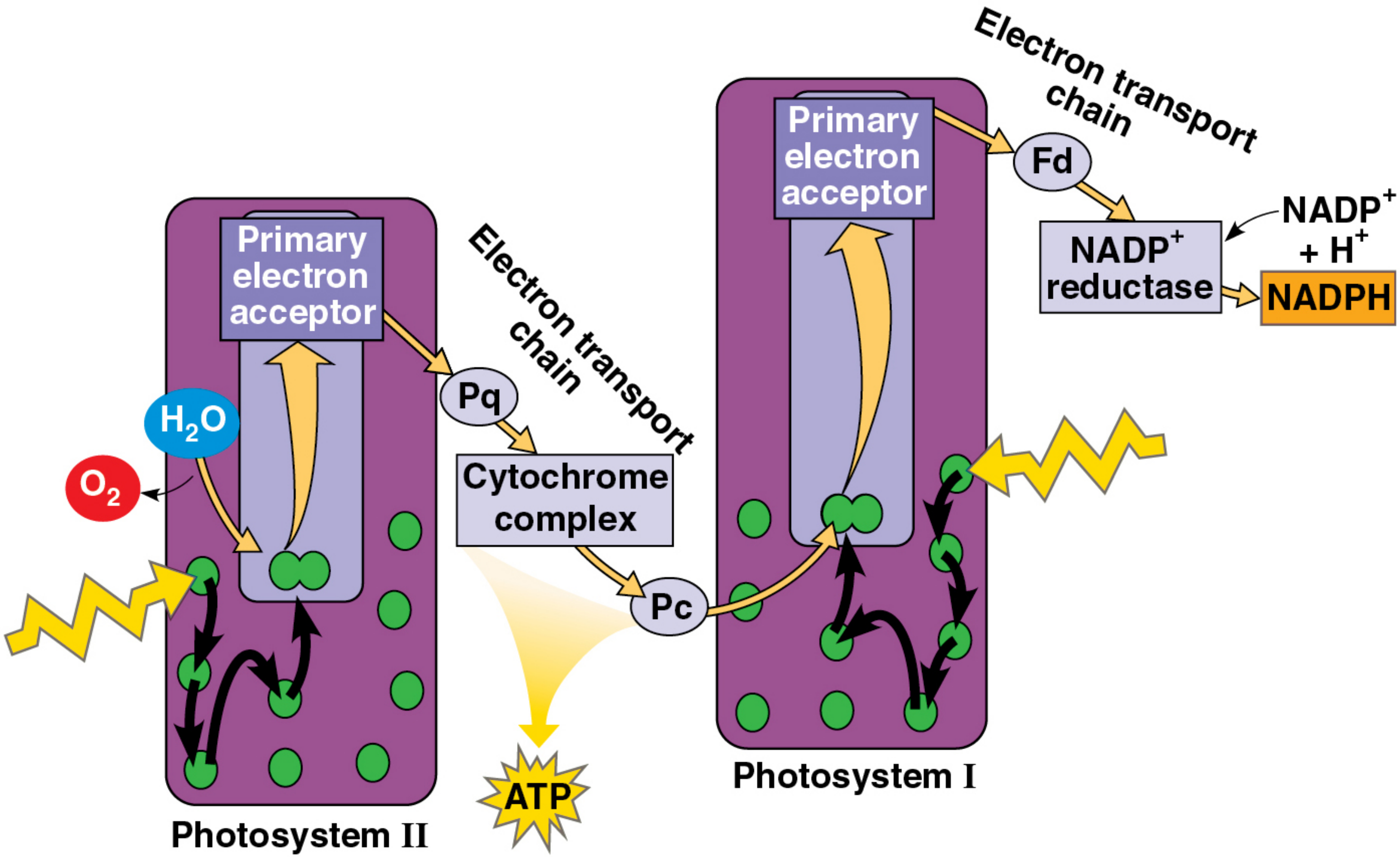


Figure 10.UN07

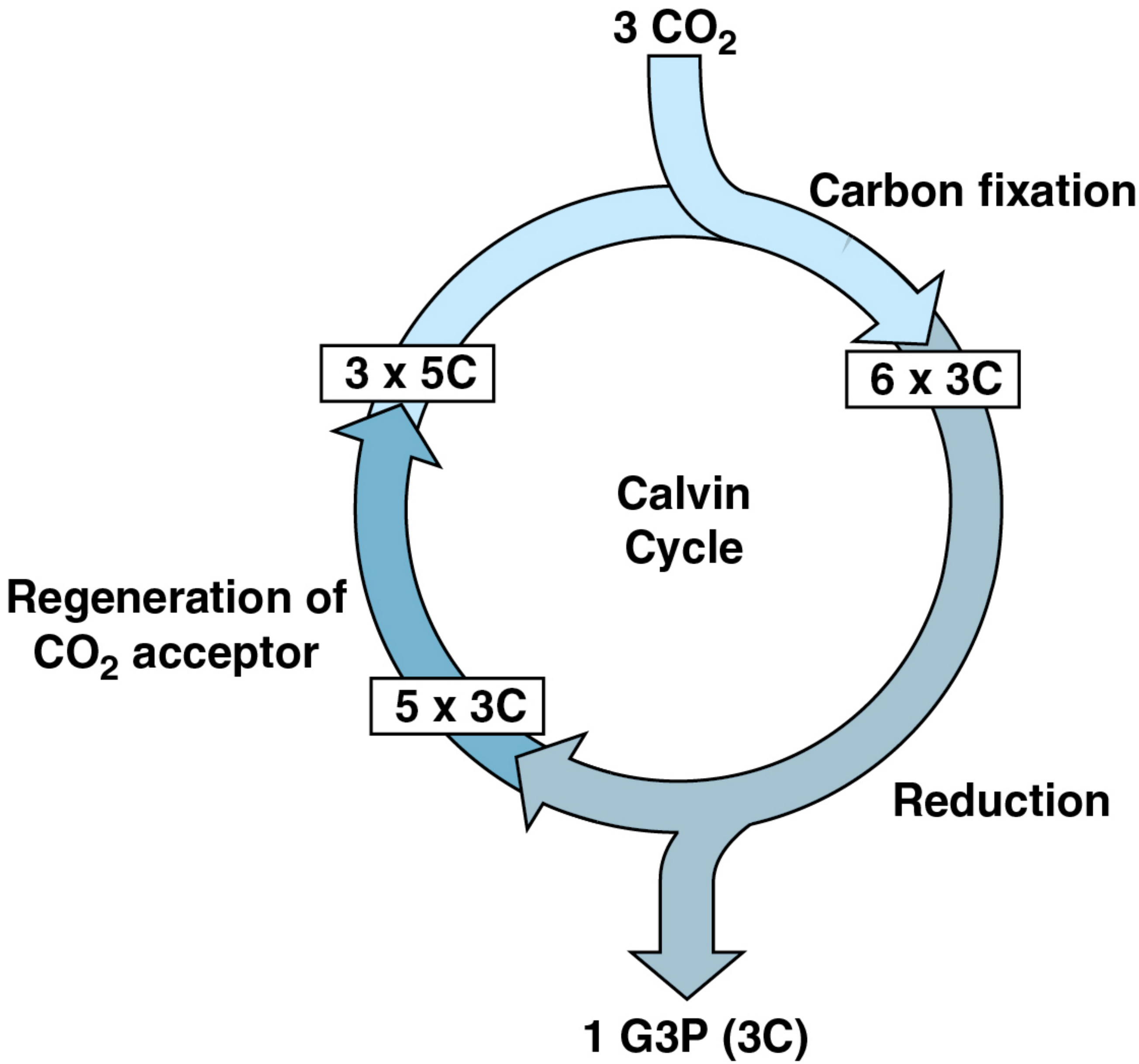


Figure 10.UN08

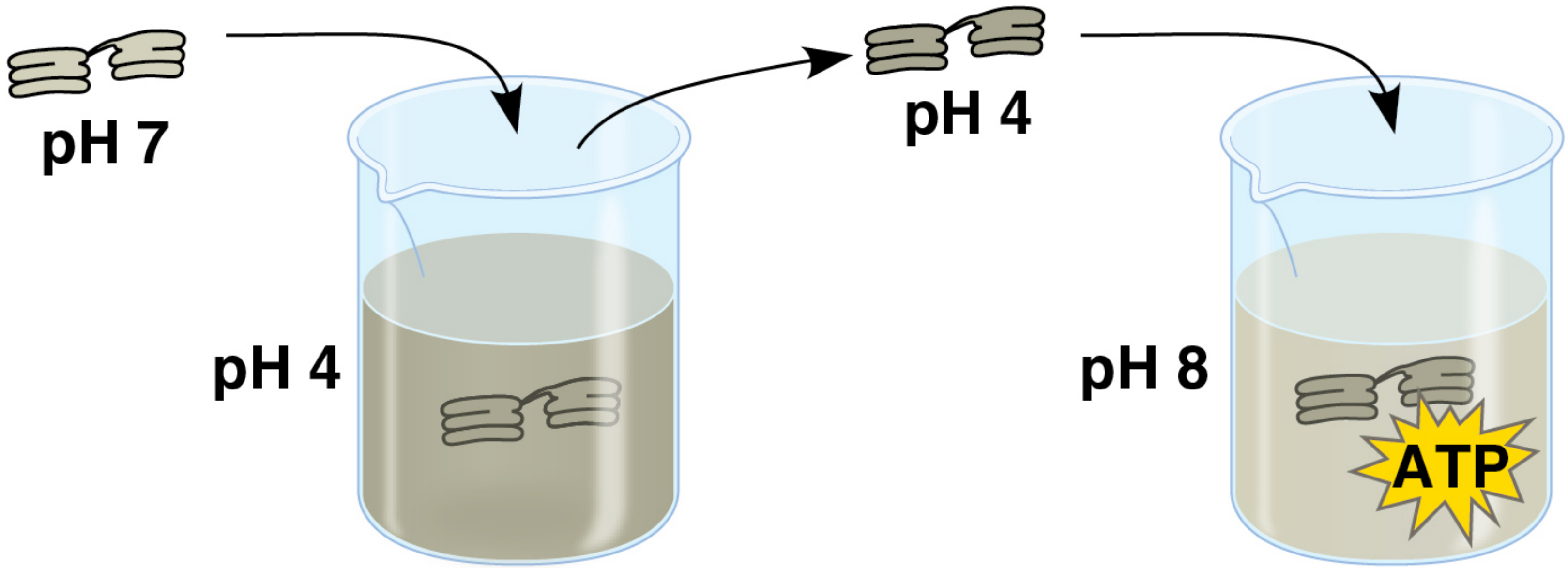


Figure 10.UN09