CAMPBELL BIOLOGY IN FOCUS

URRY • CAIN • WASSERMAN • MINORSKY • REECE

8

Photosynthesis

Lecture Presentations by
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SECOND EDITION

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

Figure 8.1

- **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 O_2

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

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

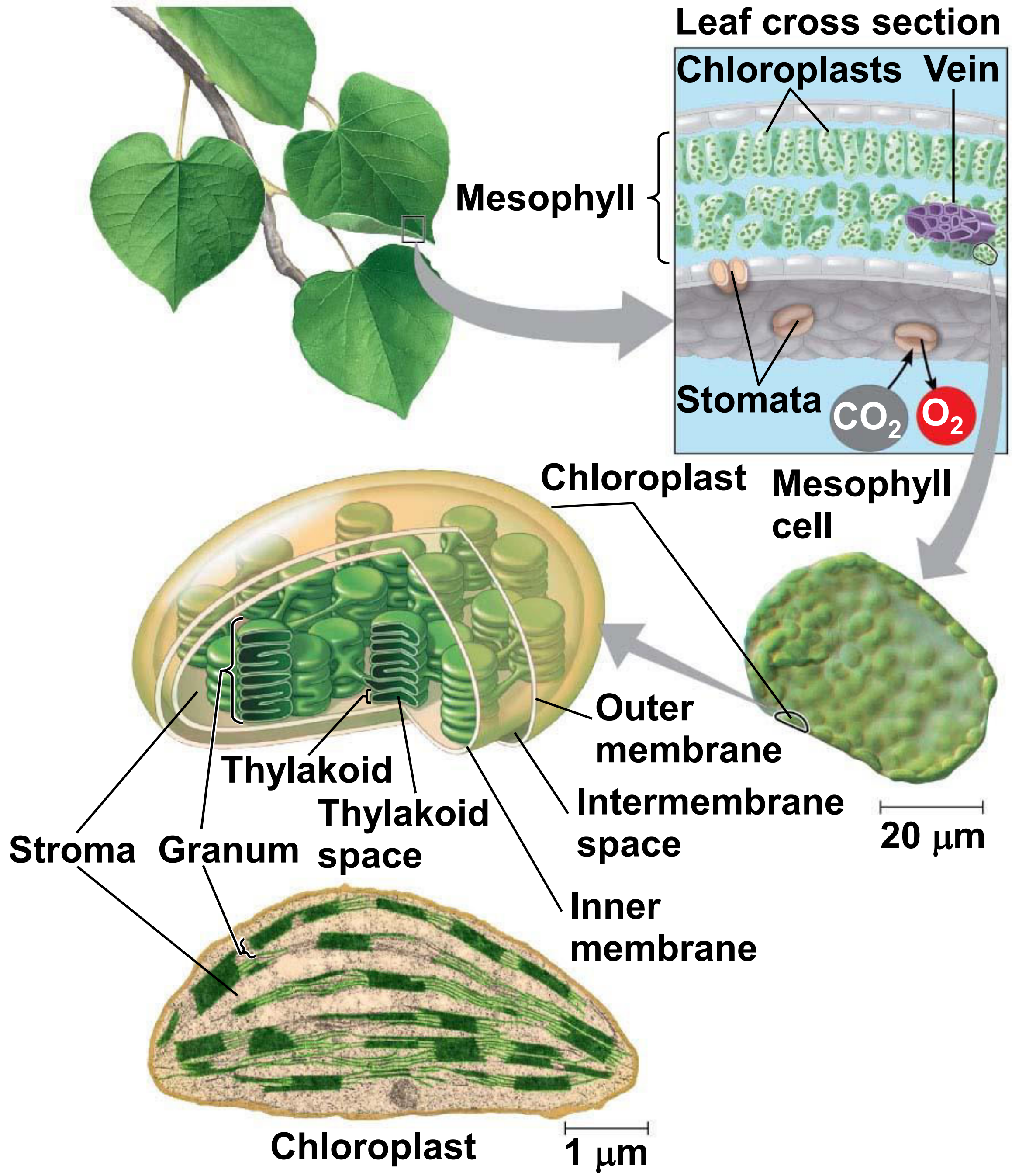
- The structural organization of photosynthetic cells includes enzymes and other molecules grouped together in a membrane
- This organization allows for the chemical reactions of photosynthesis to proceed efficiently
- Chloroplasts are structurally similar to and likely evolved from photosynthetic bacteria

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

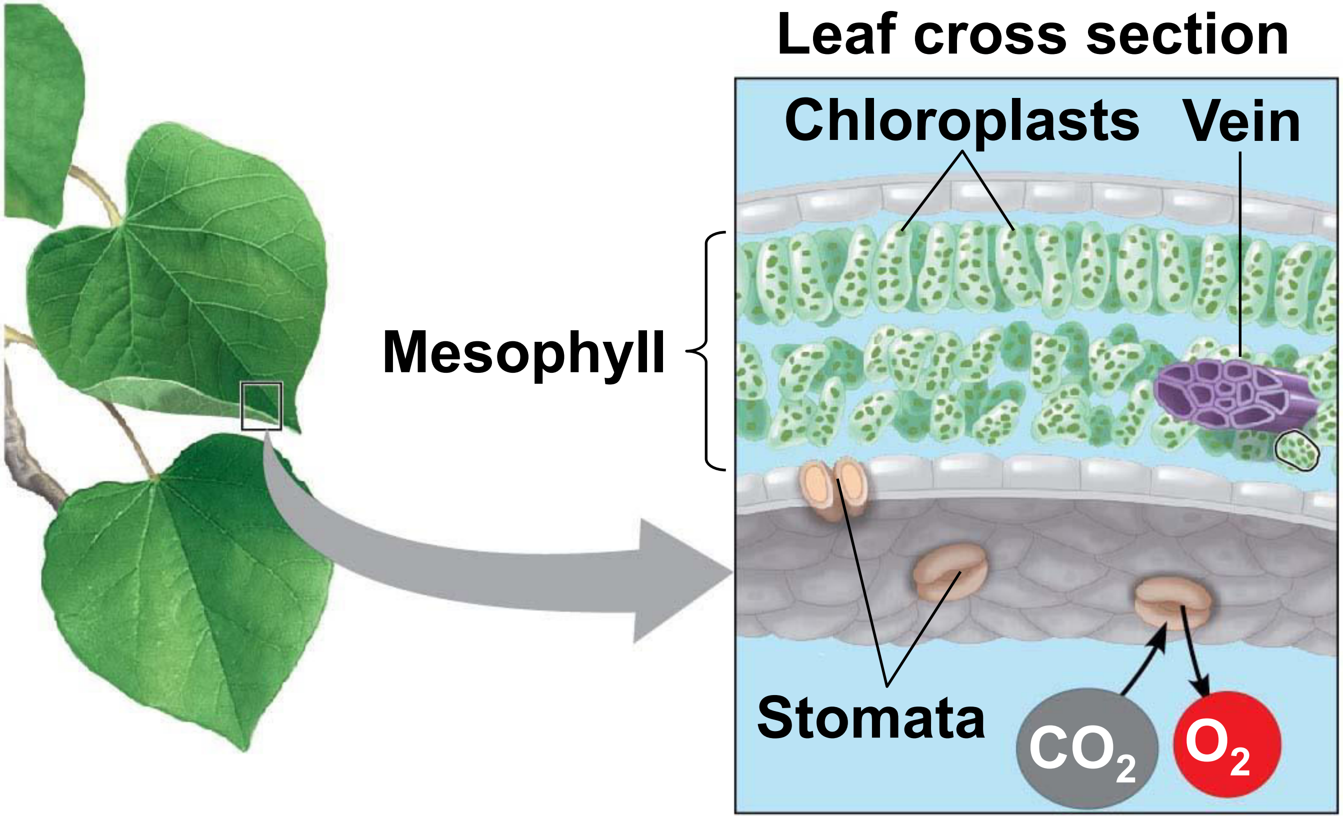
- CO_2 enters and O_2 exits the leaf through microscopic pores called **stomata**
- The chlorophyll is in the membranes of **thylakoids** (connected sacs in the chloroplast); thylakoids may be stacked in columns called grana
- Chloroplasts also contain **stroma**, a dense interior fluid

Figure 8.3



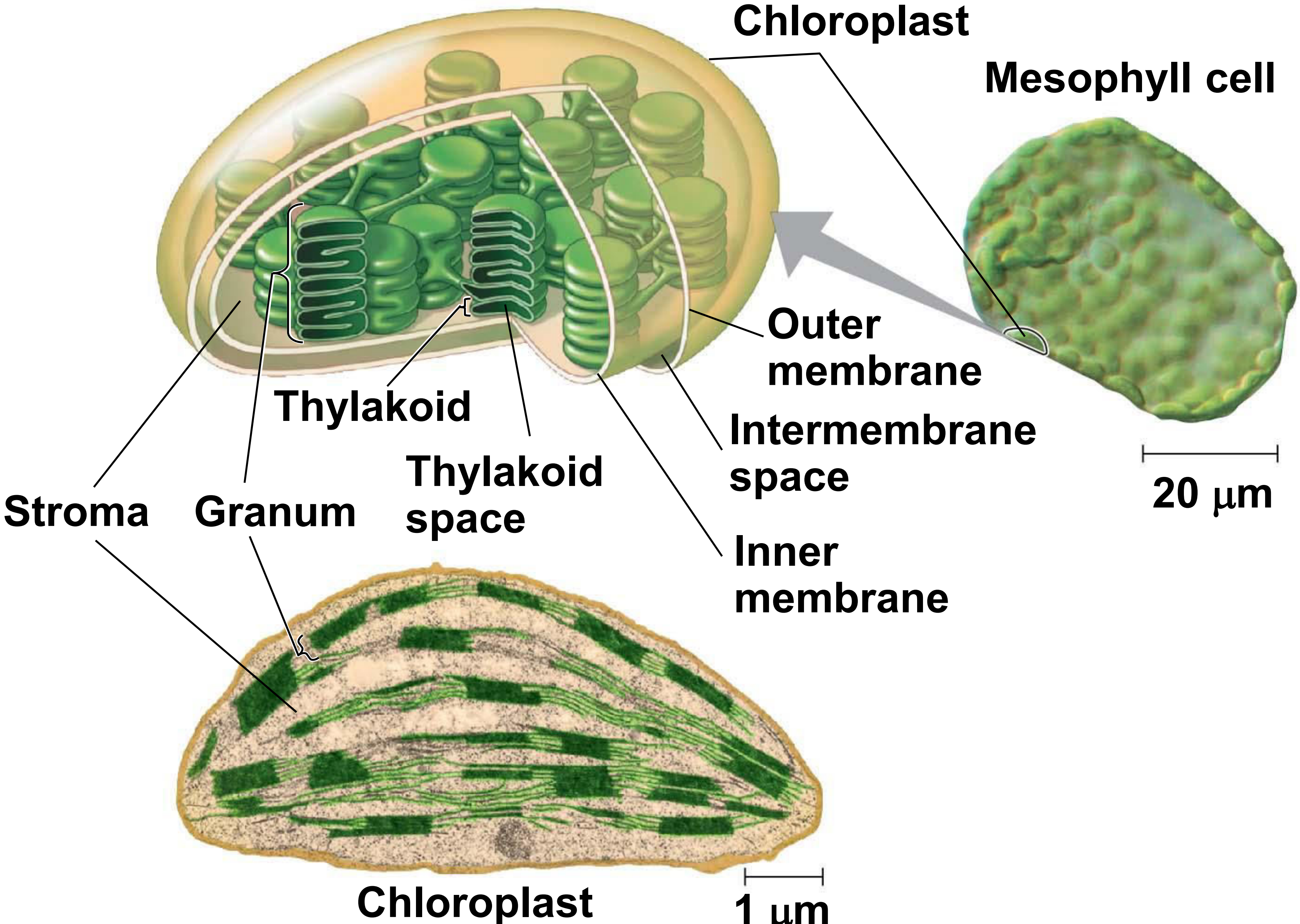
Leaf cross section
Chloroplasts
Vein
Mesophyll
Stomata
CO_2
O_2
Chloroplast
Mesophyll cell
Outer membrane
Intermembrane space
Inner membrane
Thylakoid
Thylakoid space
Stroma
Granum
20 μm
Chloroplast
1 μm

Figure 8.3-1



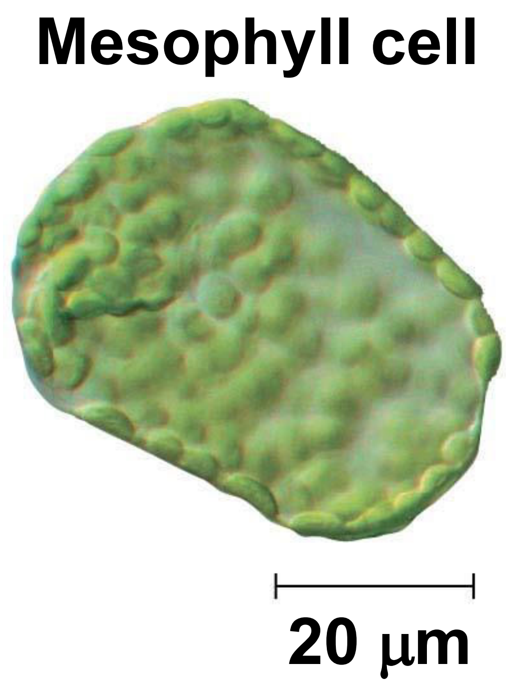
Leaf cross section
Chloroplasts
Vein
Mesophyll
Stomata
CO_2
O_2

Figure 8.3-2



Chloroplast
Mesophyll cell
Outer membrane
Intermembrane space
Inner membrane
Thylakoid
Thylakoid space
Stroma
Granum
20 μm
Chloroplast
1 μm

Figure 8.3-3



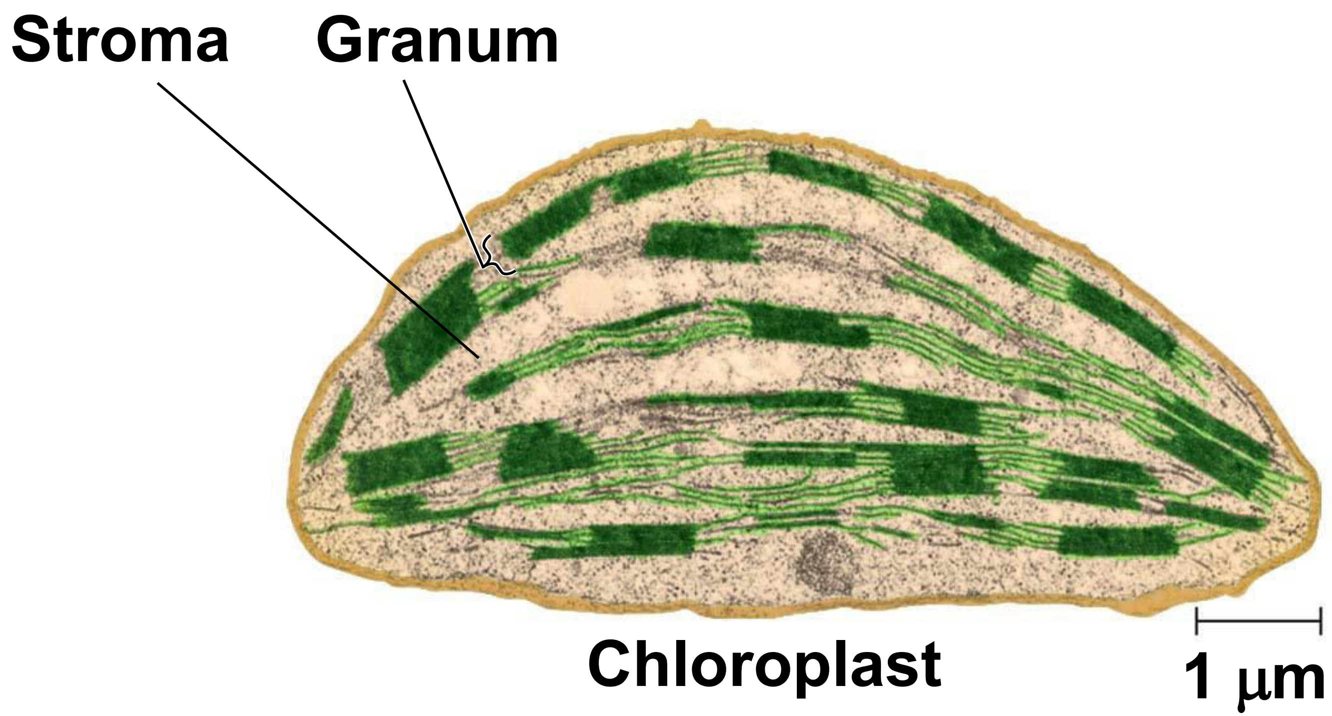
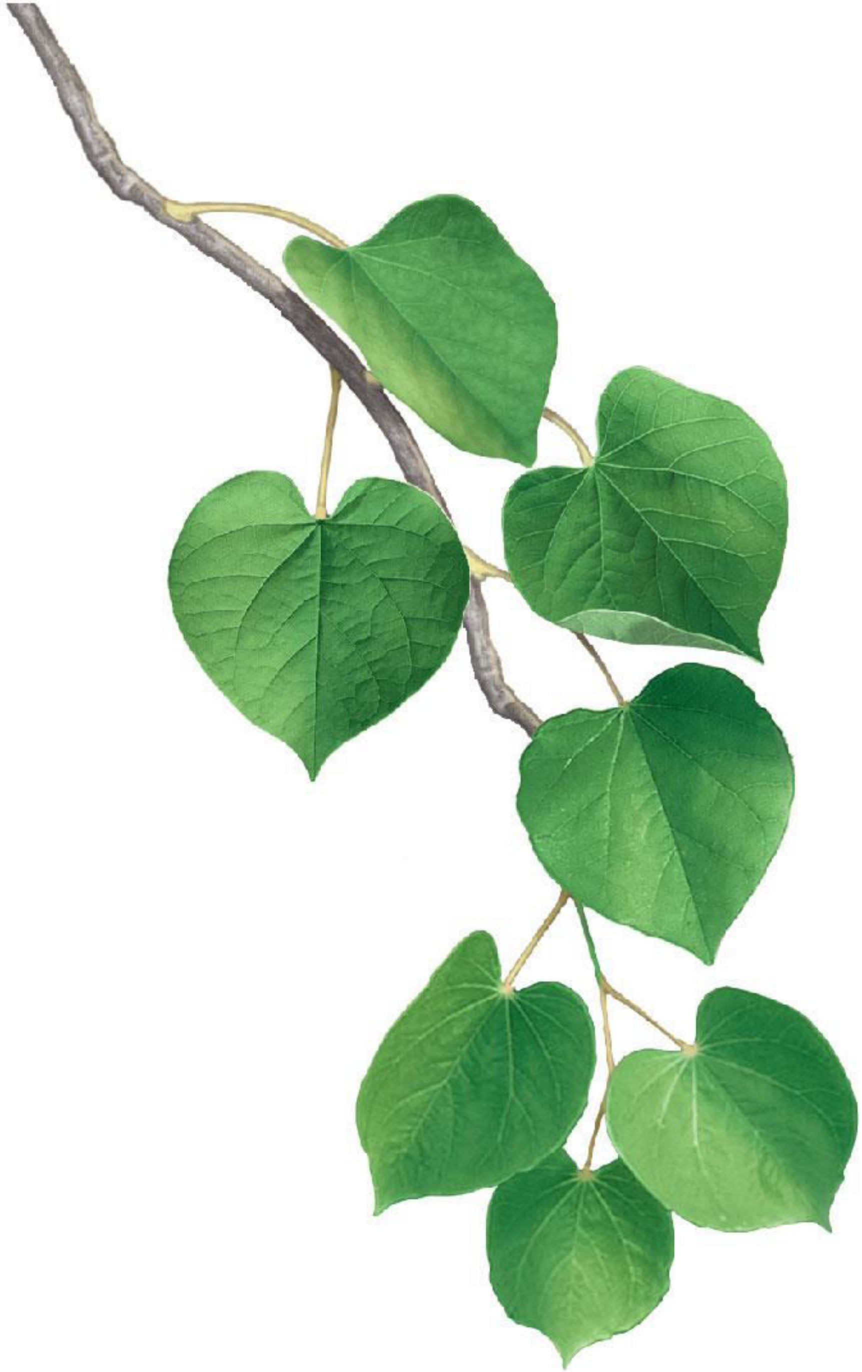

Stroma
Granum
Chloroplast
1 μm

Figure 8.3-5



Tracking Atoms Through Photosynthesis: *Scientific Inquiry*

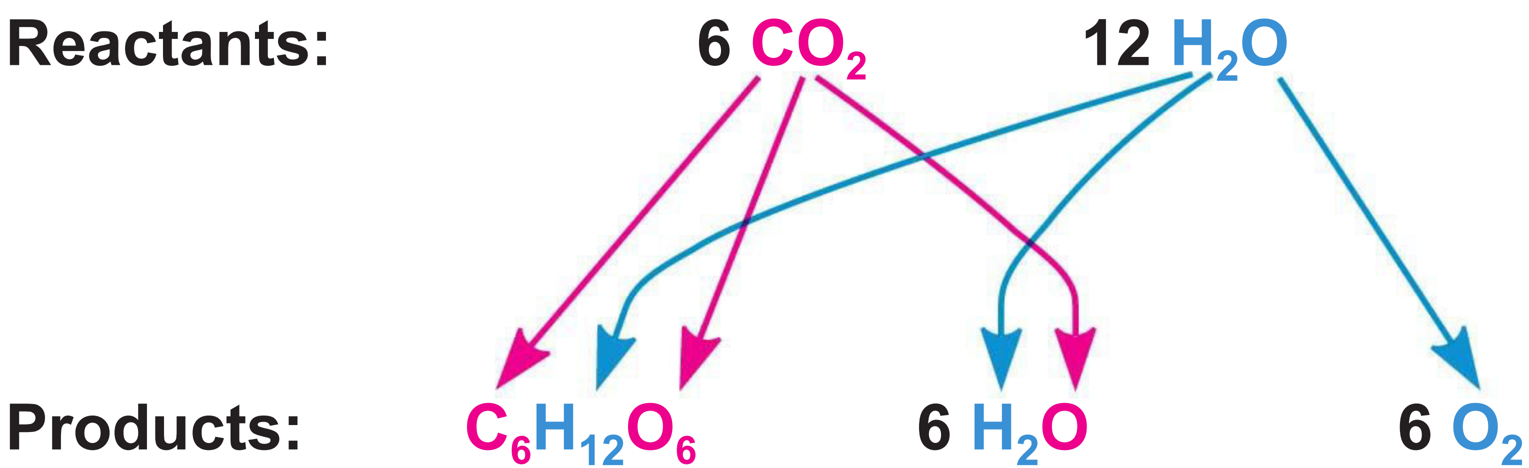
- Photosynthesis is a complex series of reactions that can be summarized as the following equation

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

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

Figure 8.4



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 8.UN01

becomes reduced

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

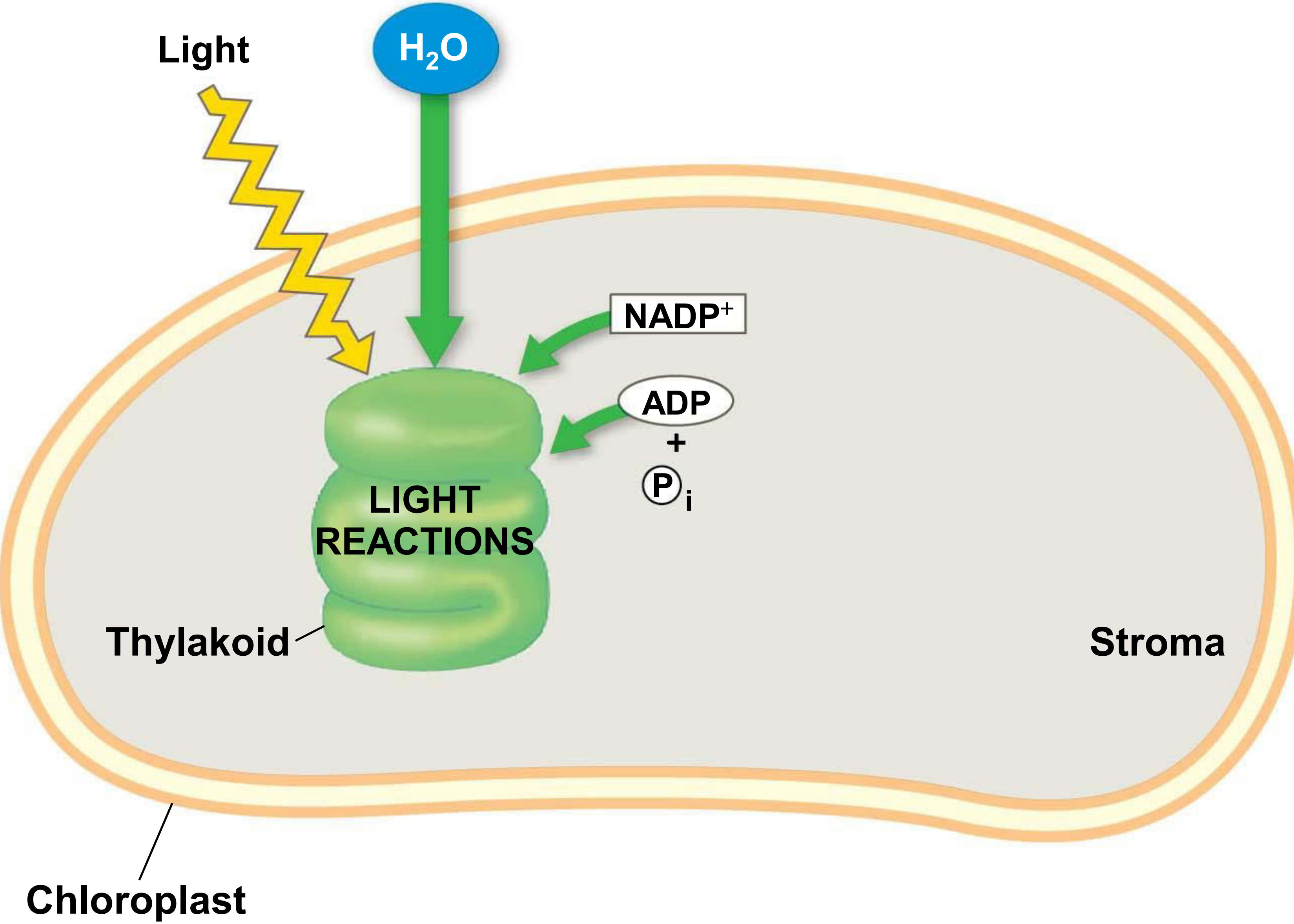
becomes oxidized

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
  - Release O_2
  - Reduce the electron acceptor, **$NADP^+$**, to **NADPH**
  - Generate ATP from ADP by adding a phosphate group, **photophosphorylation**

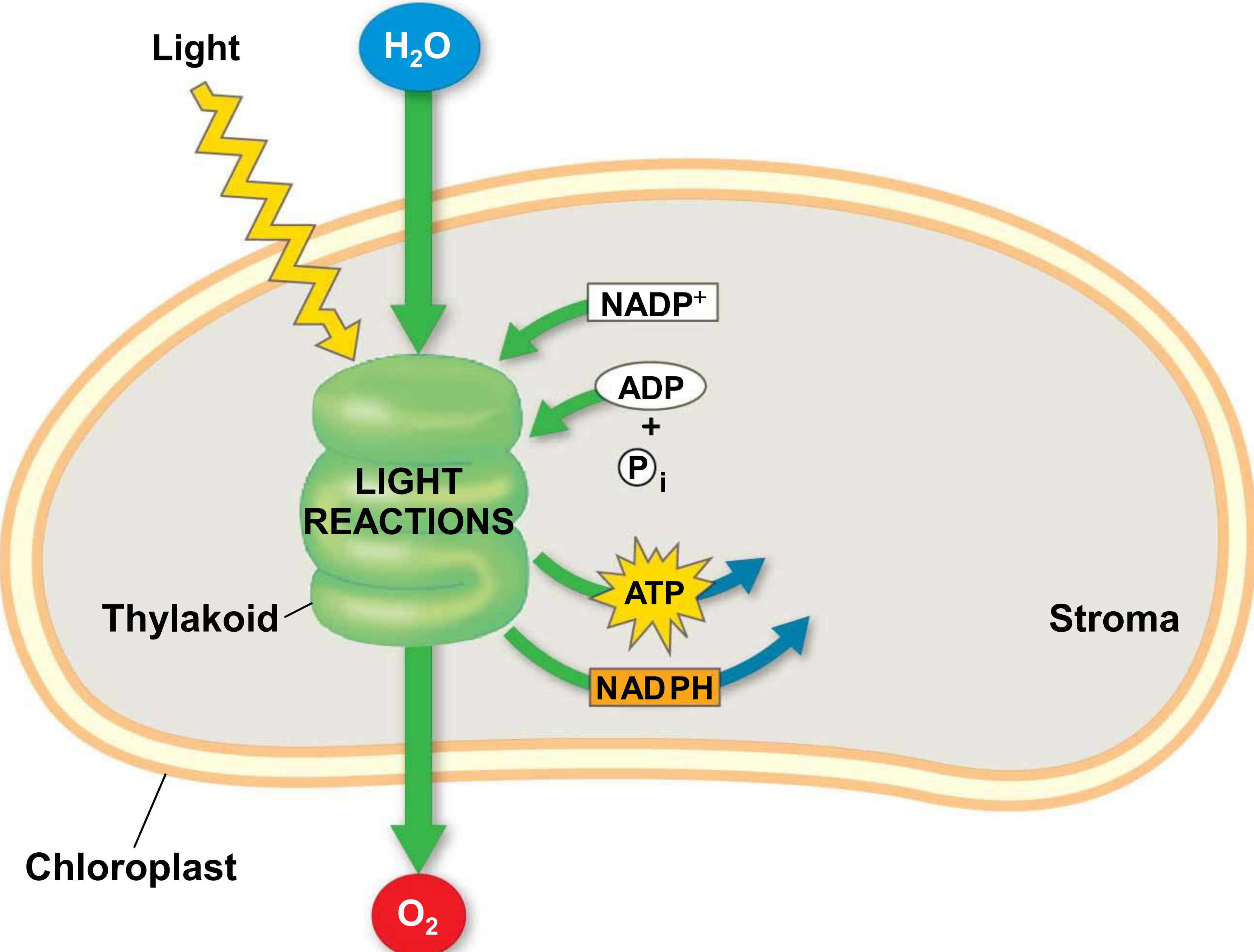
- The Calvin cycle (in the stroma) forms sugar from CO_2, using ATP and NADPH
- The Calvin cycle begins with **carbon fixation**, incorporating CO_2 into organic molecules

Figure 8.5-s1



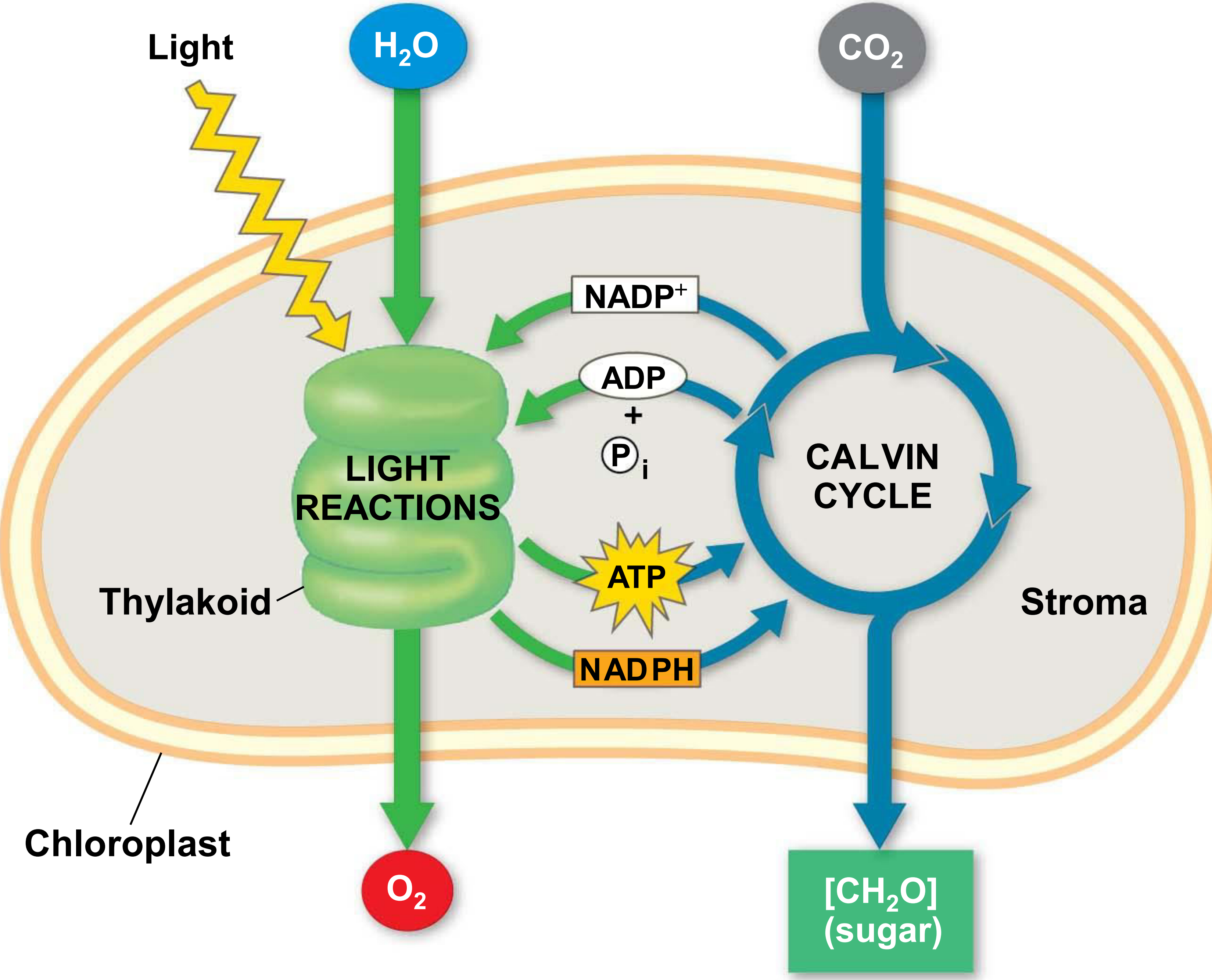
Light
H_2O
$NADP^+$
ADP
+
(P)i
LIGHT
REACTIONS
Thylakoid
Stroma
Chloroplast

Figure 8.5-s2



Light
H_2O
$NADP^+$
ADP
+
Ⓟi
LIGHT REACTIONS
ATP
NADPH
Thylakoid
Stroma
Chloroplast
O_2

Figure 8.5-s3



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

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

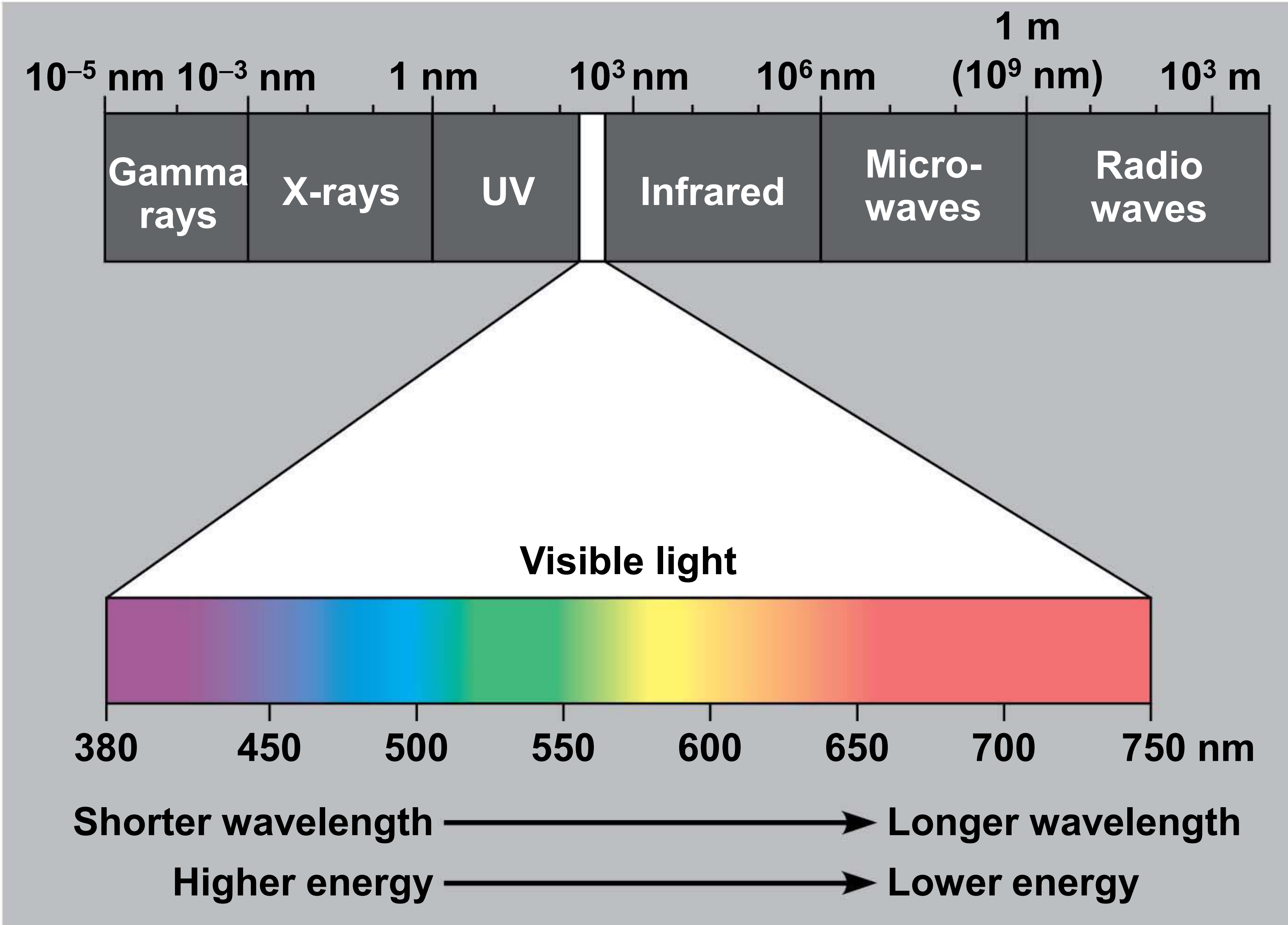
- Chloroplasts are solar-powered chemical factories
- Their thylakoids transform light energy into the chemical energy of ATP and NADPH

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

- 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**

Figure 8.6


10⁻⁵ nm
10⁻³ nm
1 nm
10³ nm
10⁶ nm
1 m
(10⁹ nm)
10³ m
Gamma rays
X-rays
UV
Infrared
Micro-waves
Radio waves
Visible light
380
450
500
550
600
650
700
750 nm
Shorter wavelength
Longer wavelength
Higher energy
Lower energy

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

Animation: Light and Pigments

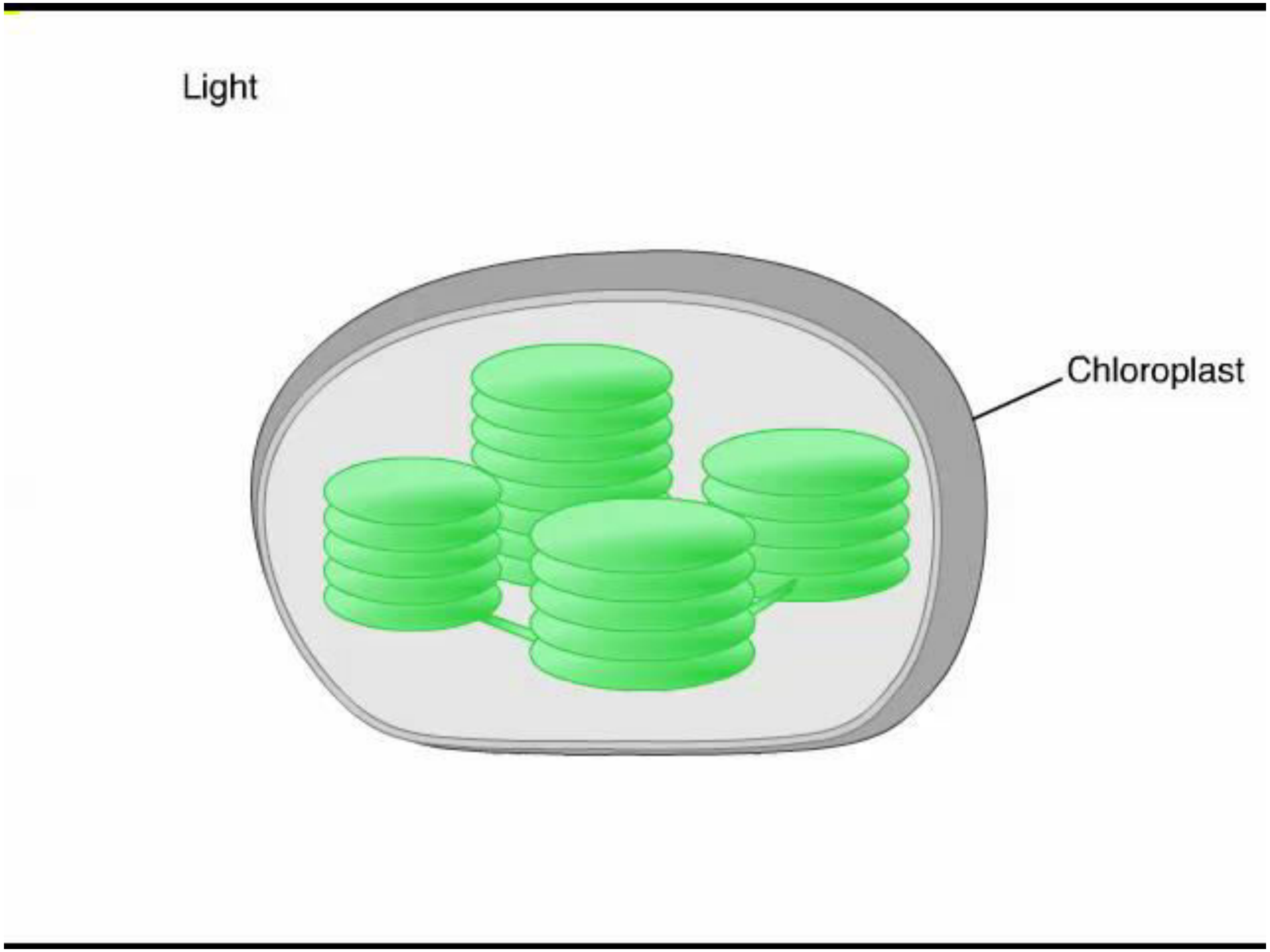
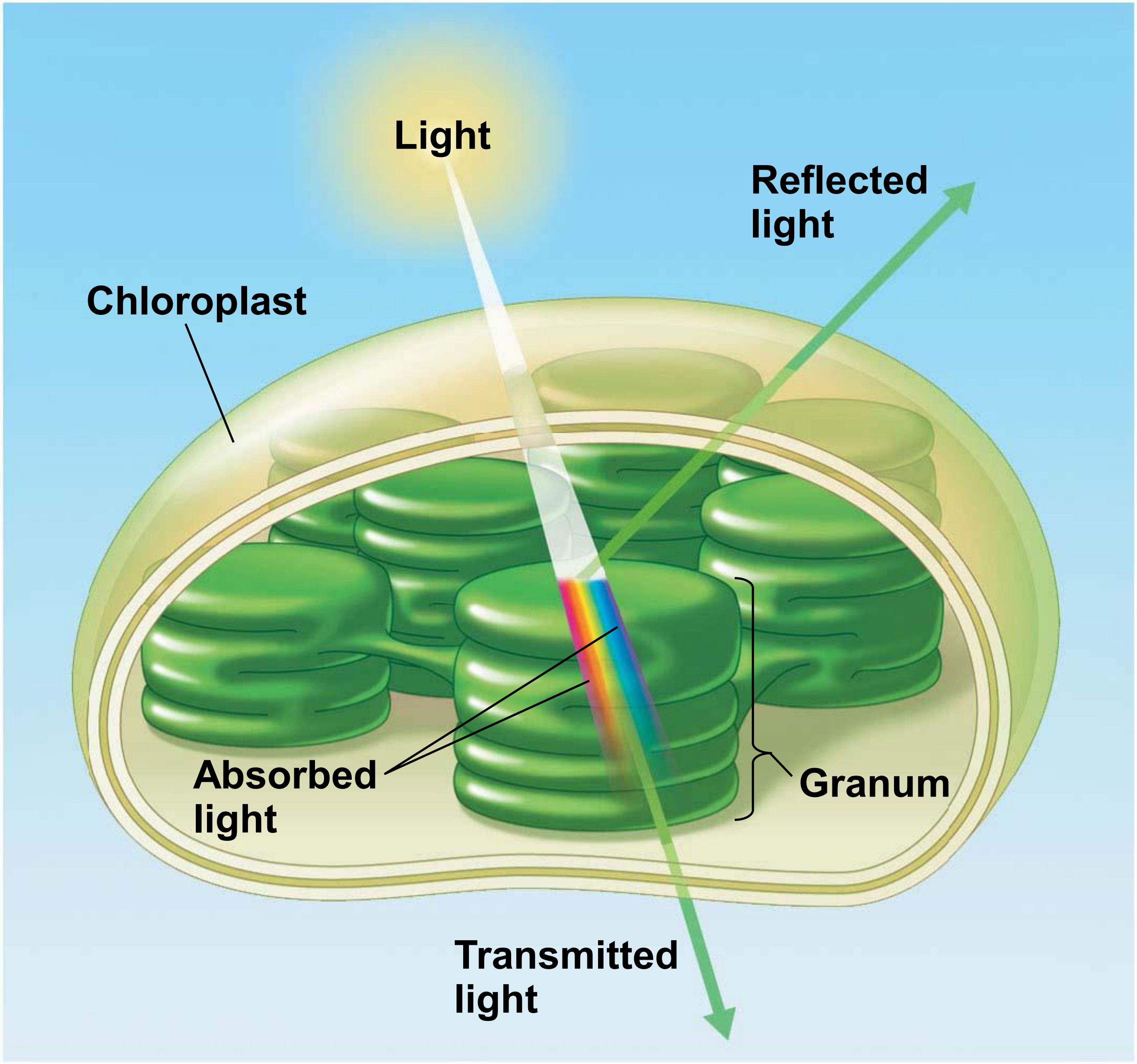
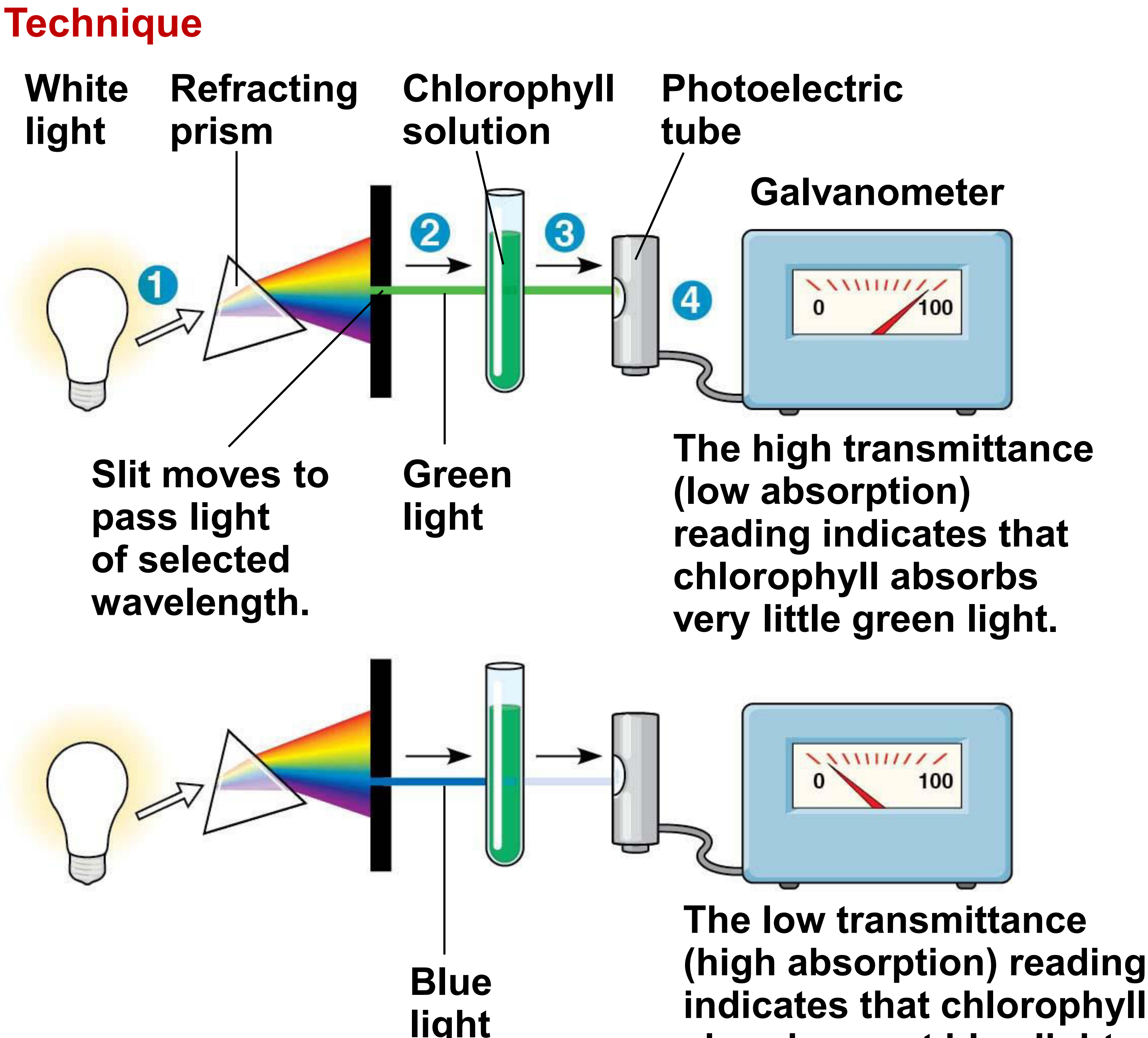


Figure 8.7


Light
Reflected light
Chloroplast
Absorbed light
Granum
Transmitted light

- 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

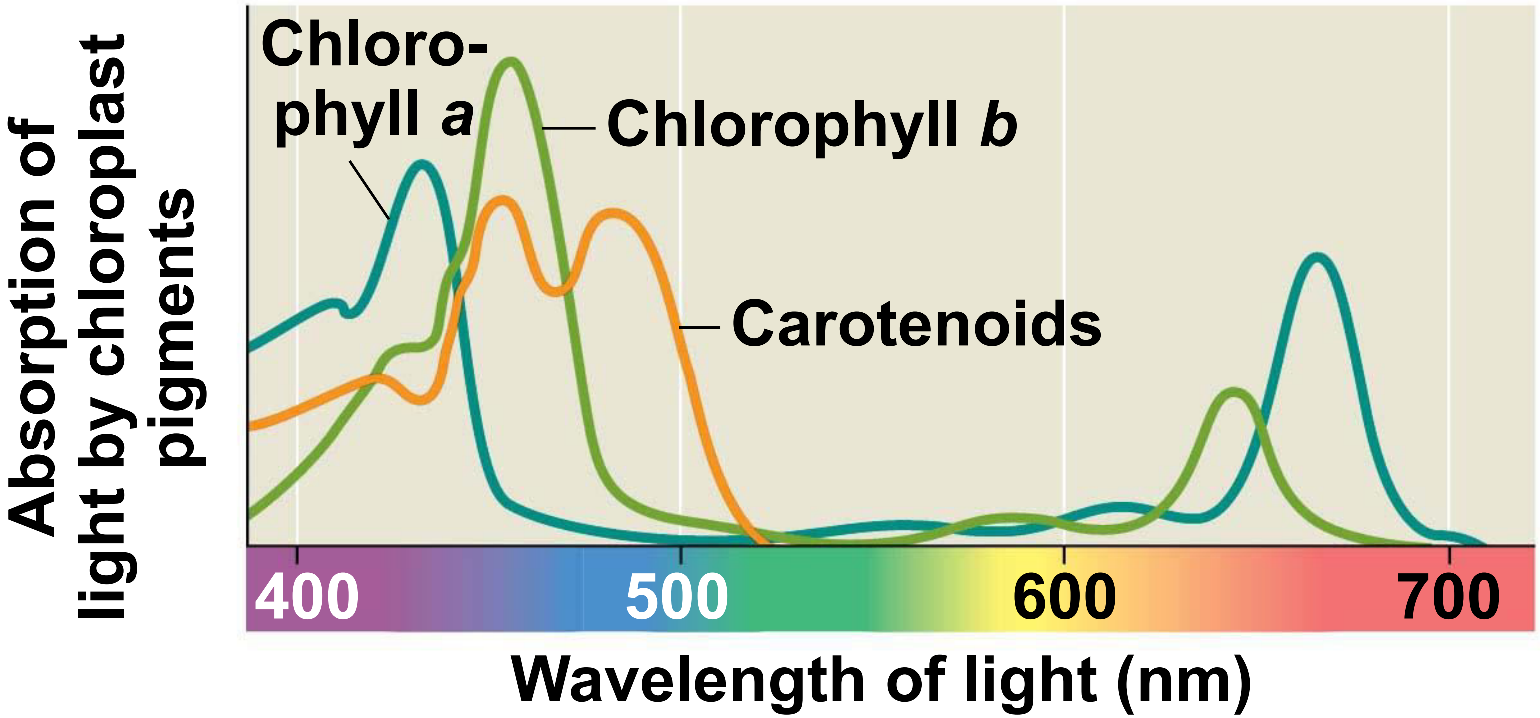
Figure 8.8



Technique
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.

- 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

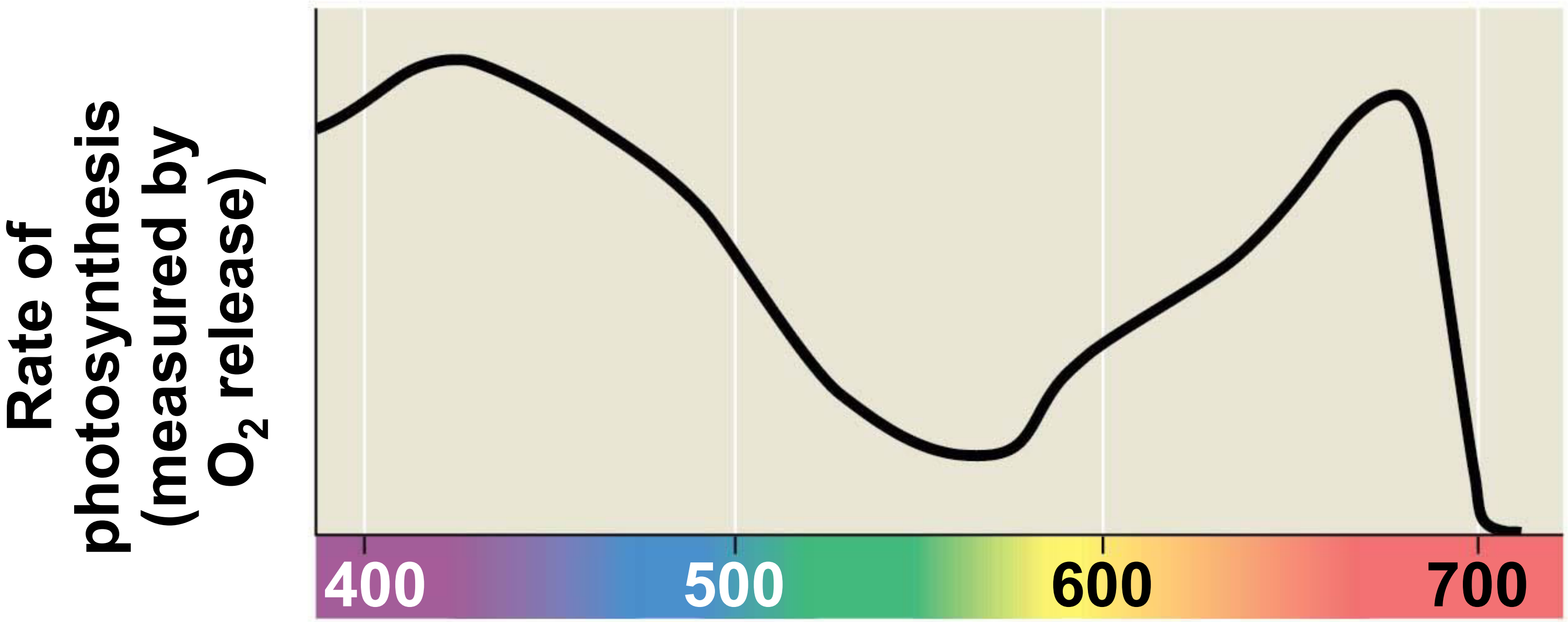
Figure 8.9-1



(a) Absorption spectra

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

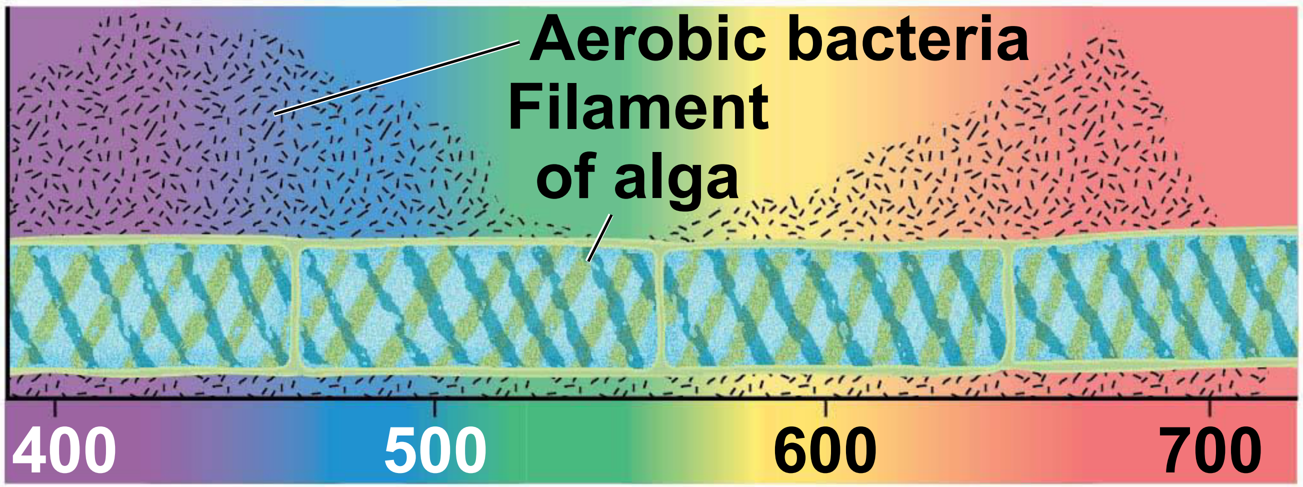
Figure 8.9-2



(b) Action spectrum

- 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 O_2
- He used the growth of aerobic bacteria clustered along the alga as a measure of O_2 production

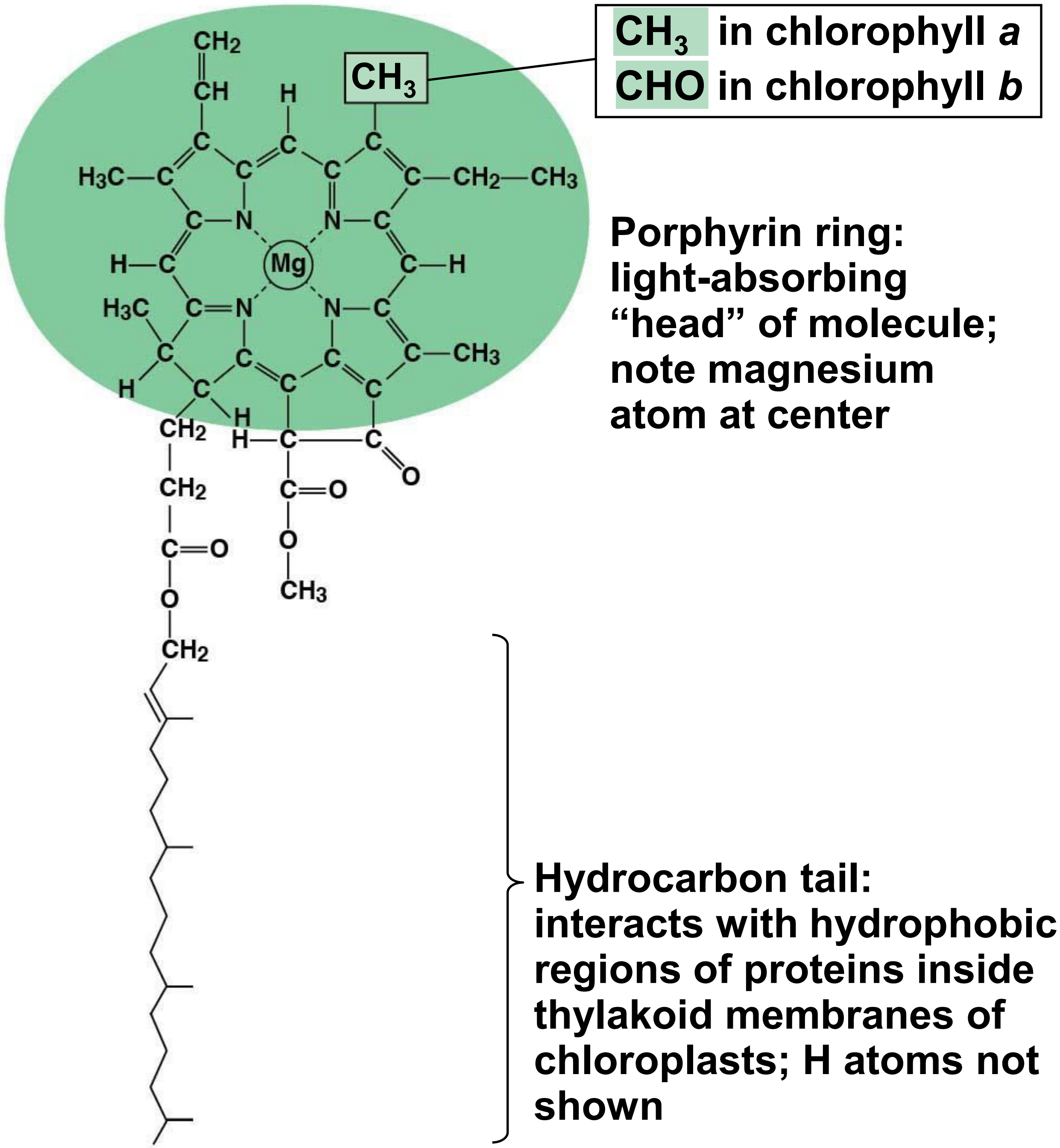
Figure 8.9-3



(c) Engelmann's experiment

- 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

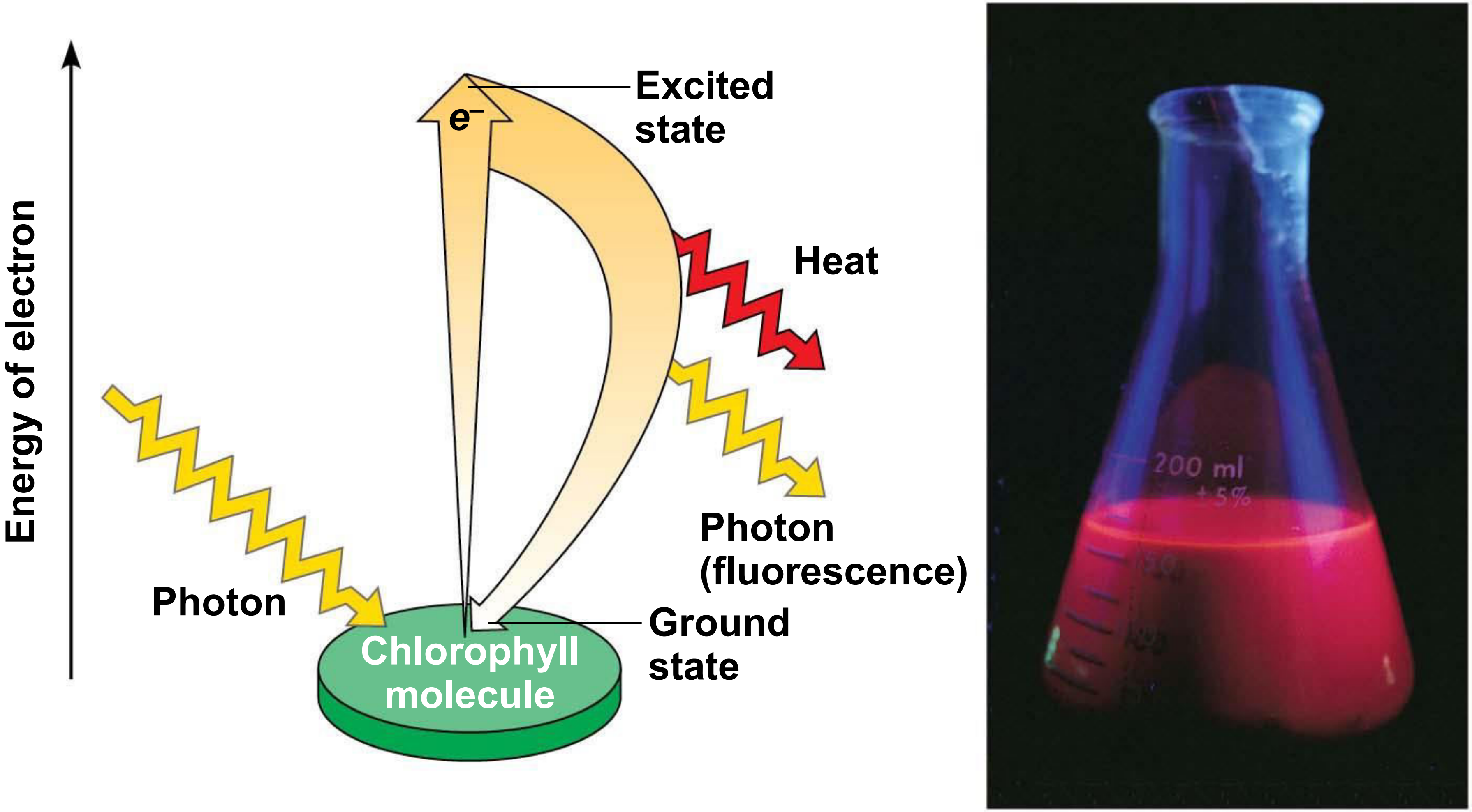
Figure 8.10


CH2
CH
H
CH3
H3C—C
C—CH2—CH3
C—N
N—C
H—C
Mg
C—H
H3C
C=N
N—C
C—CH3
H
H
CH2
H—C
C=O
O
CH2
C=O
O
CH3
CH2
CH3 in chlorophyll a
CHO in chlorophyll b
Porphyrin ring: light-absorbing "head" of molecule; note magnesium atom at center
Hydrocarbon tail: interacts with hydrophobic regions of proteins inside thylakoid membranes of chloroplasts; H atoms not shown

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

Figure 8.11



(a) Excitation of isolated chlorophyll molecule

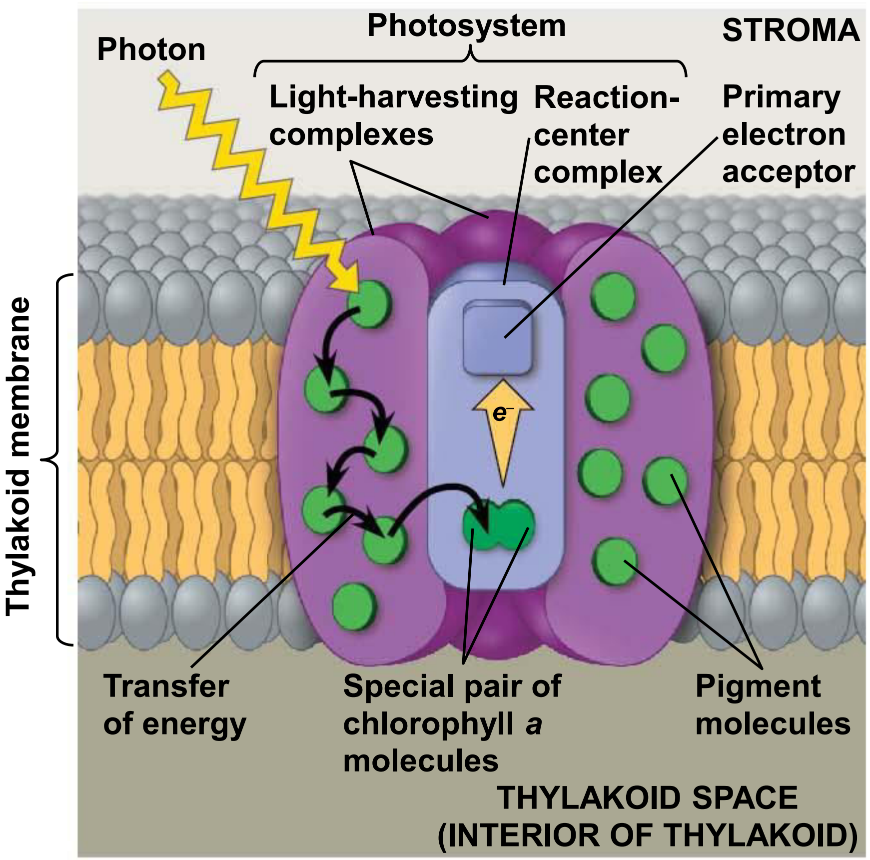
(b) Fluorescence

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

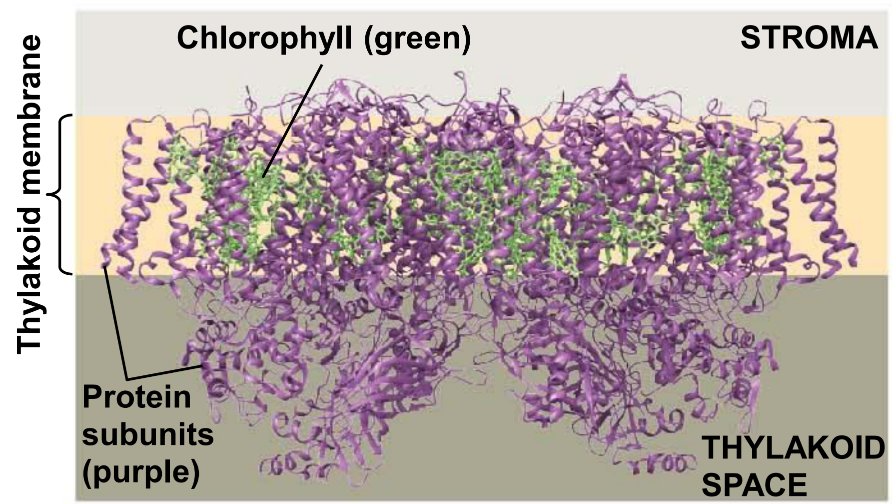
- A **photosystem** consists of a **reaction-center complex** (a type of protein complex) surrounded by light-harvesting complexes
- The **light-harvesting complexes** (pigment molecules bound to proteins) transfer the energy of photons to the reaction center

- 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 8.12

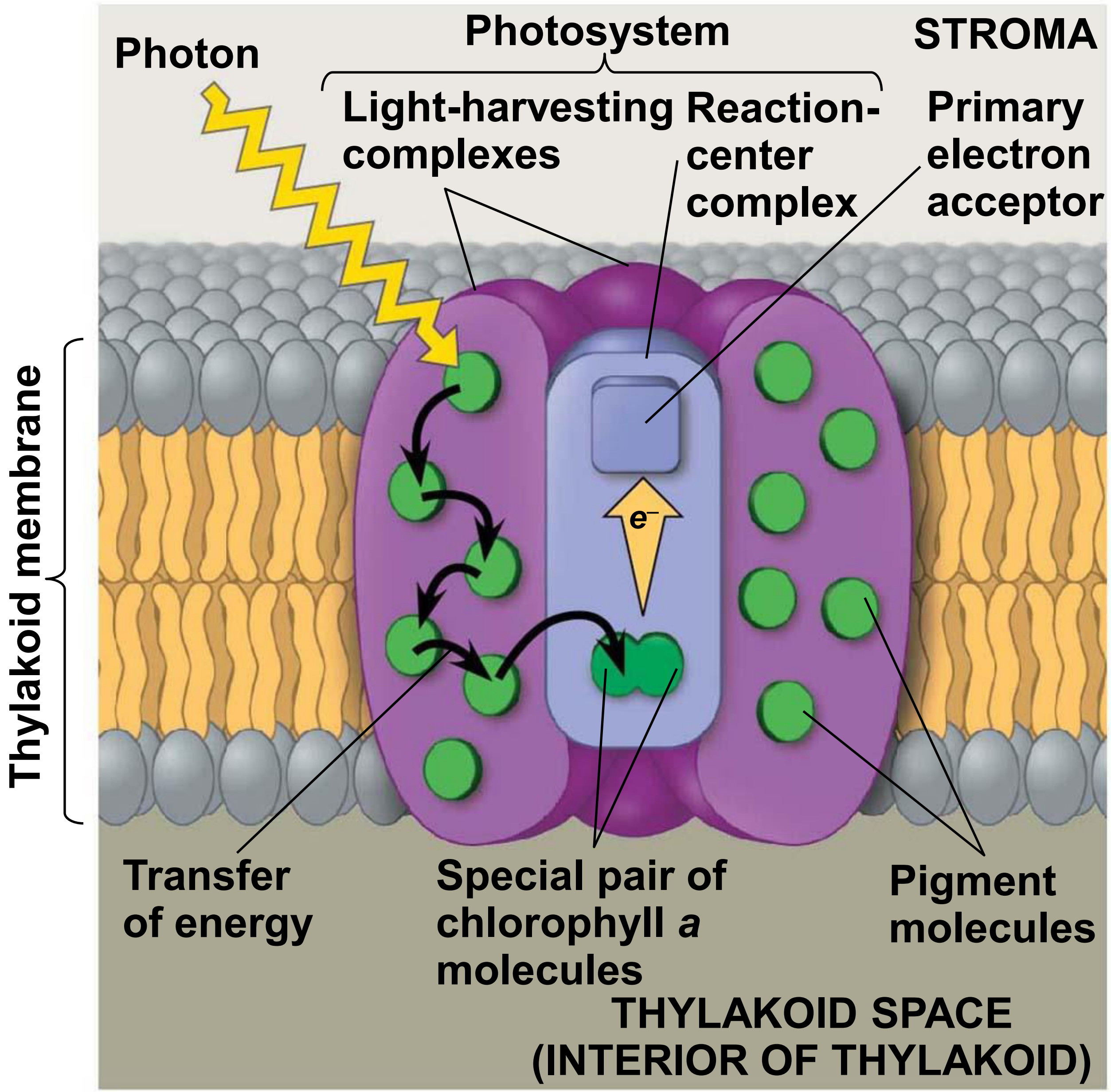


(a) How a photosystem harvests light



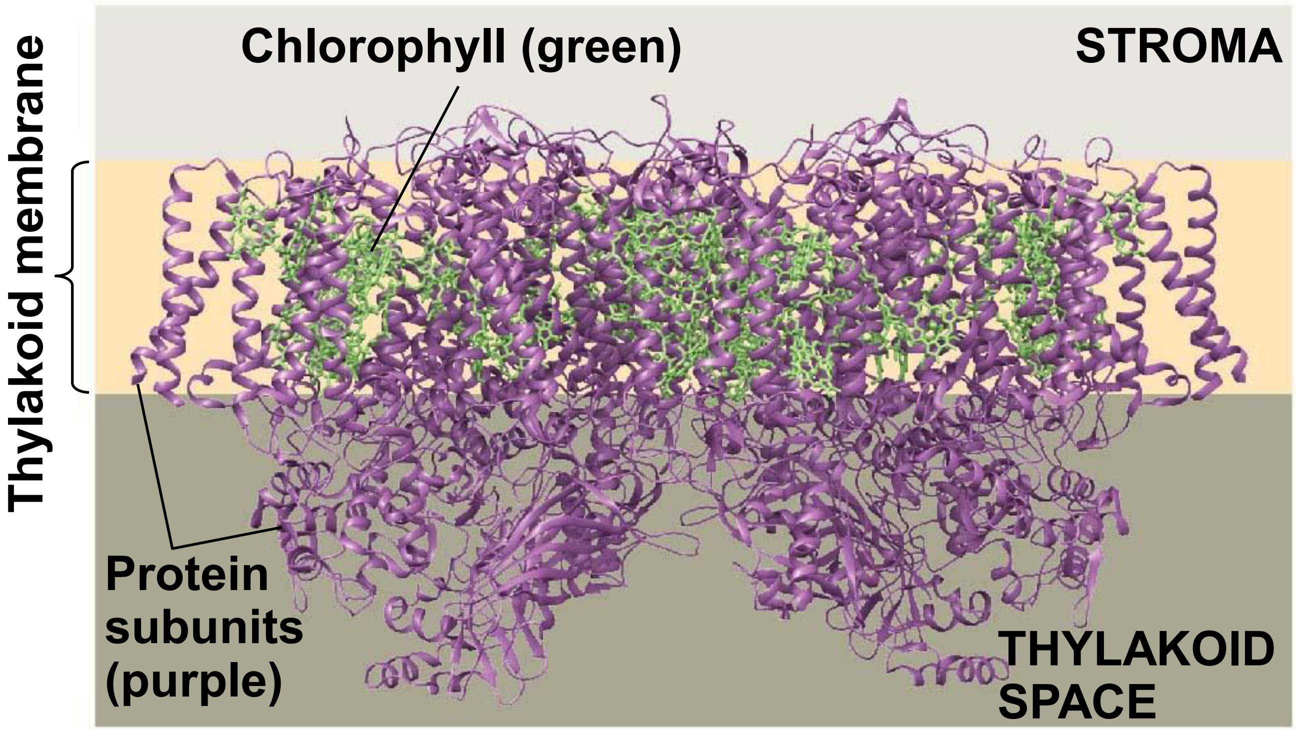
(b) Structure of a photosystem

Figure 8.12-1



(a) How a photosystem harvests light

Figure 8.12-2



(b) Structure of a photosystem

- 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

- **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

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

- Linear electron flow can be broken down into a series of steps
    1. A photon hits a pigment 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 now call it $P680^+$)
    3. H_2O is split by enzymes, and the electrons are transferred from the hydrogen atoms to $P680^+$, thus reducing it to P680; O_2 is released as a by-product

4. Each electron “falls” down an electron transport chain from the primary electron acceptor of PS II to PS I
5. 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

6. 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

7. Excited electrons “fall” down an electron transport chain from the primary electron acceptor of PS I to the protein ferredoxin (Fd)
8. 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

Figure 8.UN02

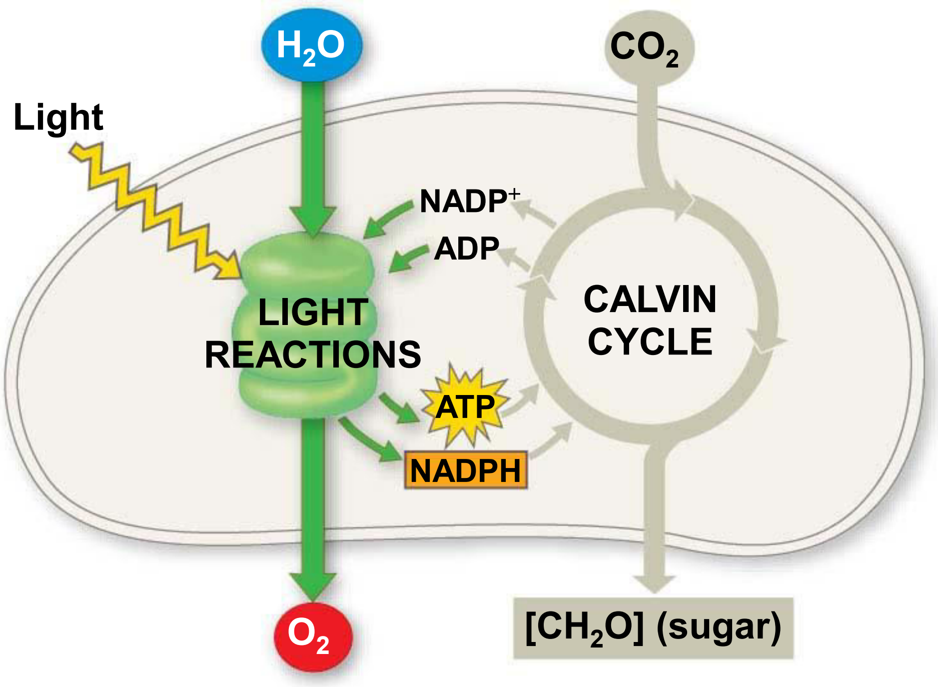


Figure 8.13-s1

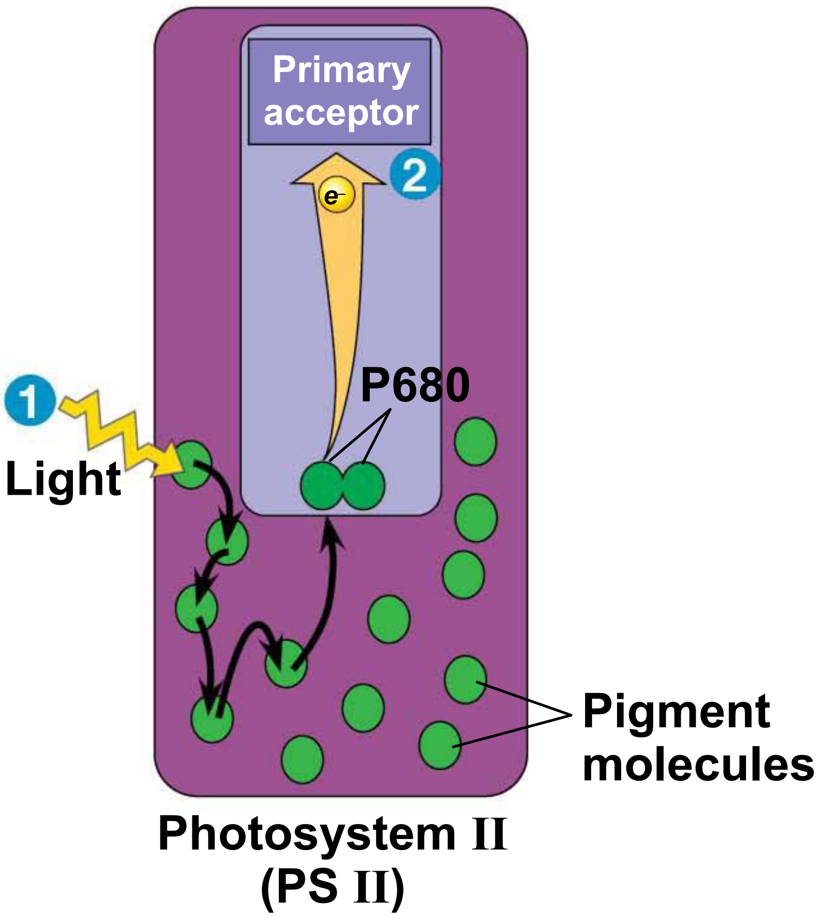


Figure 8.13-s2

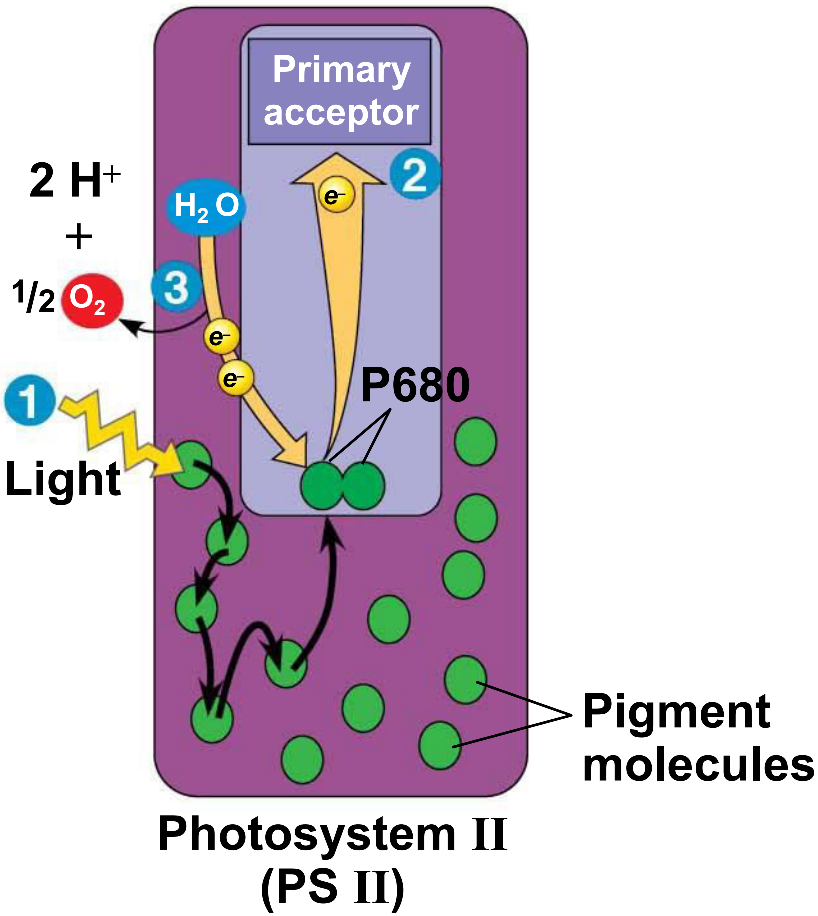


Figure 8.13-s3

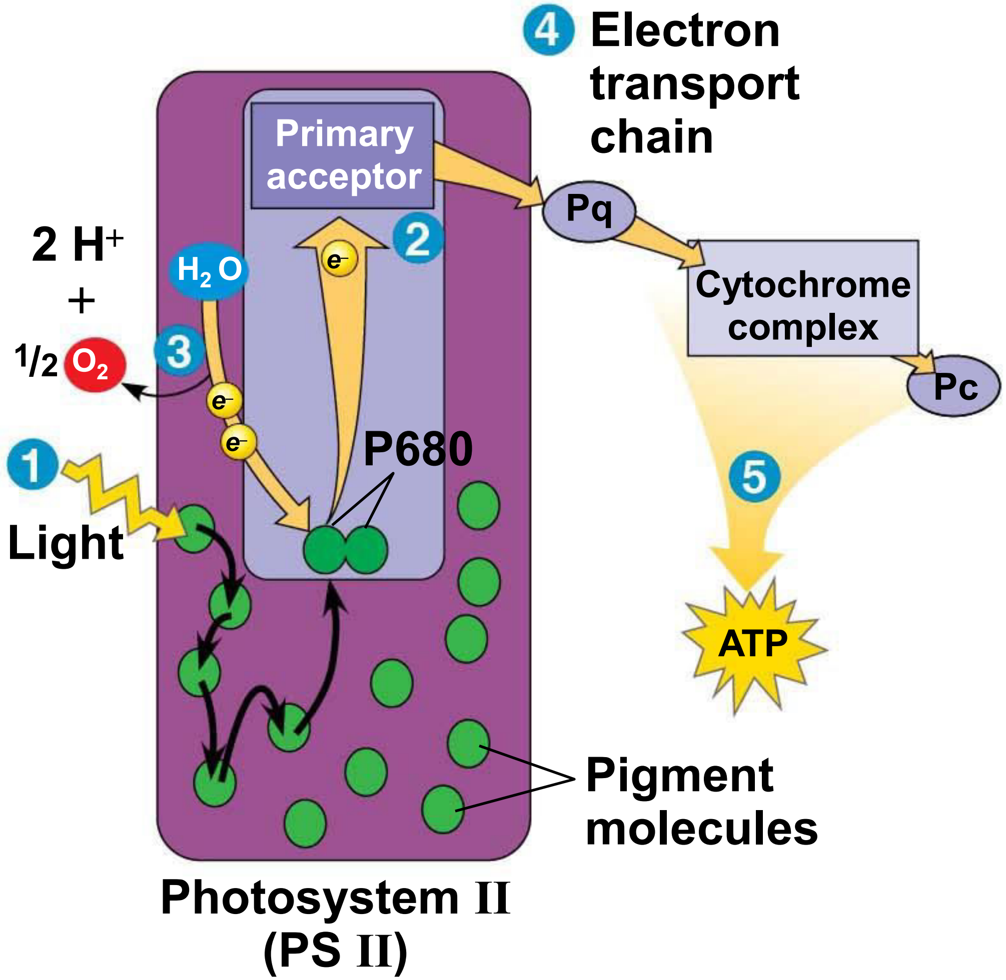


Figure 8.13-s4

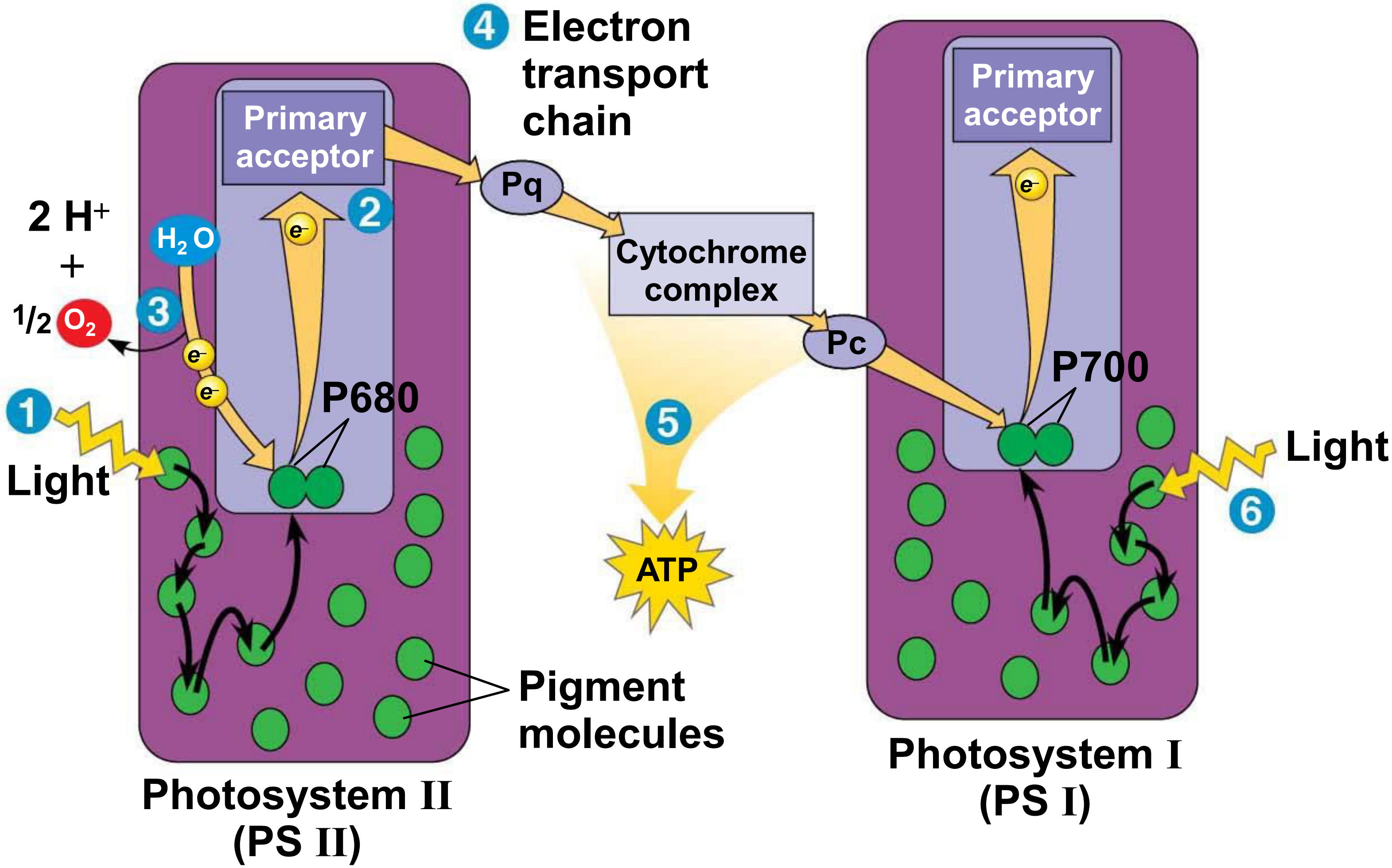
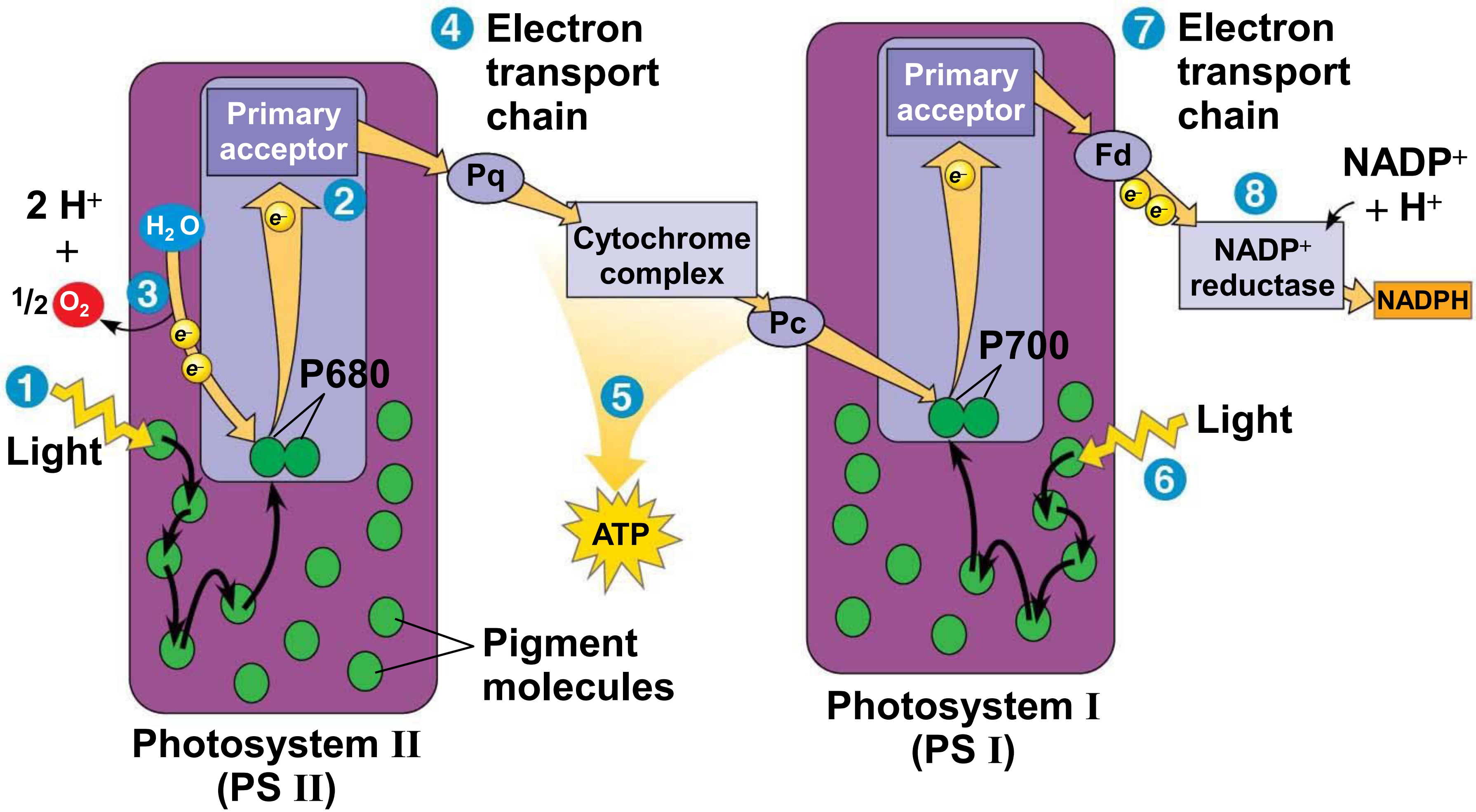
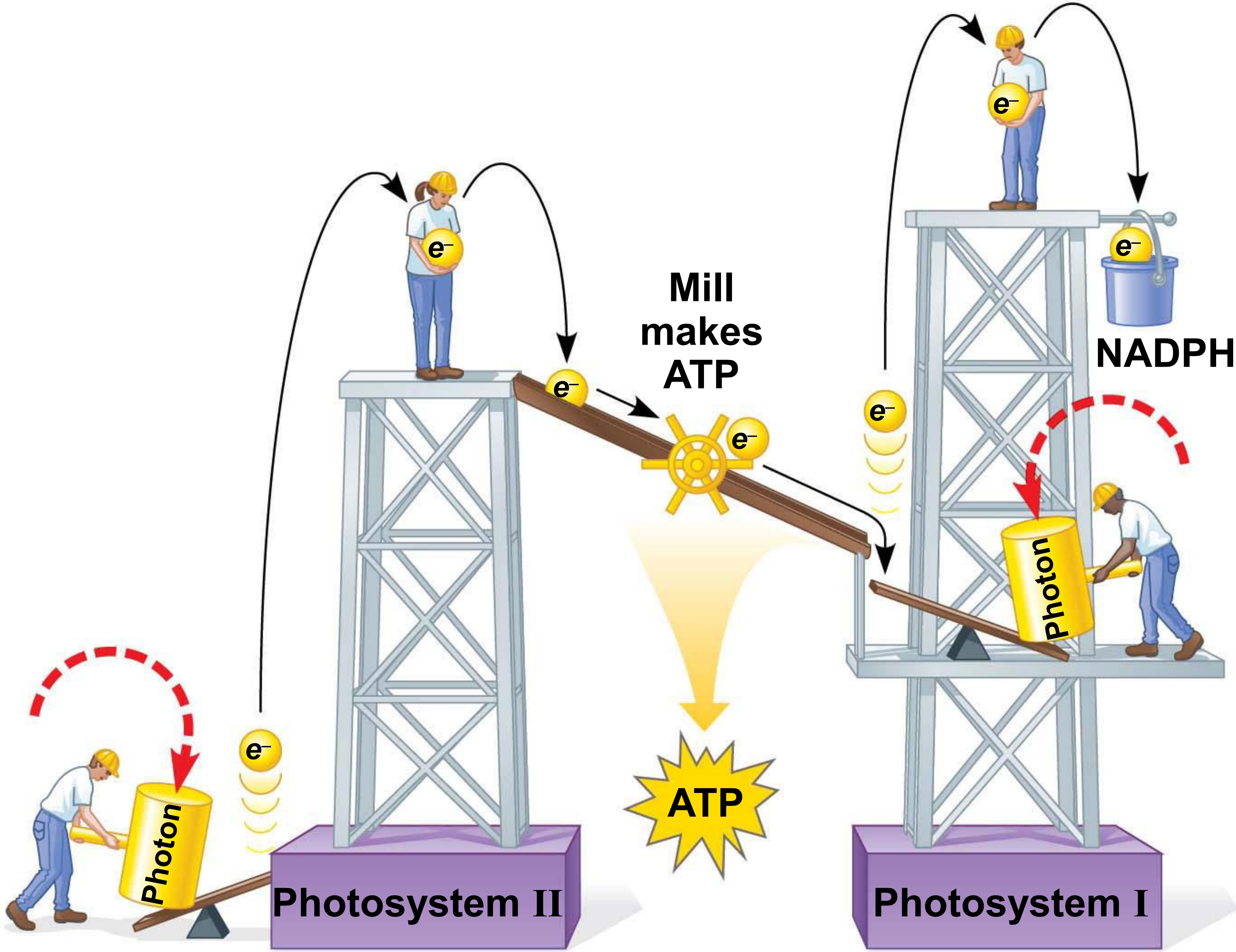


Figure 8.13-s5



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

Figure 8.14



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

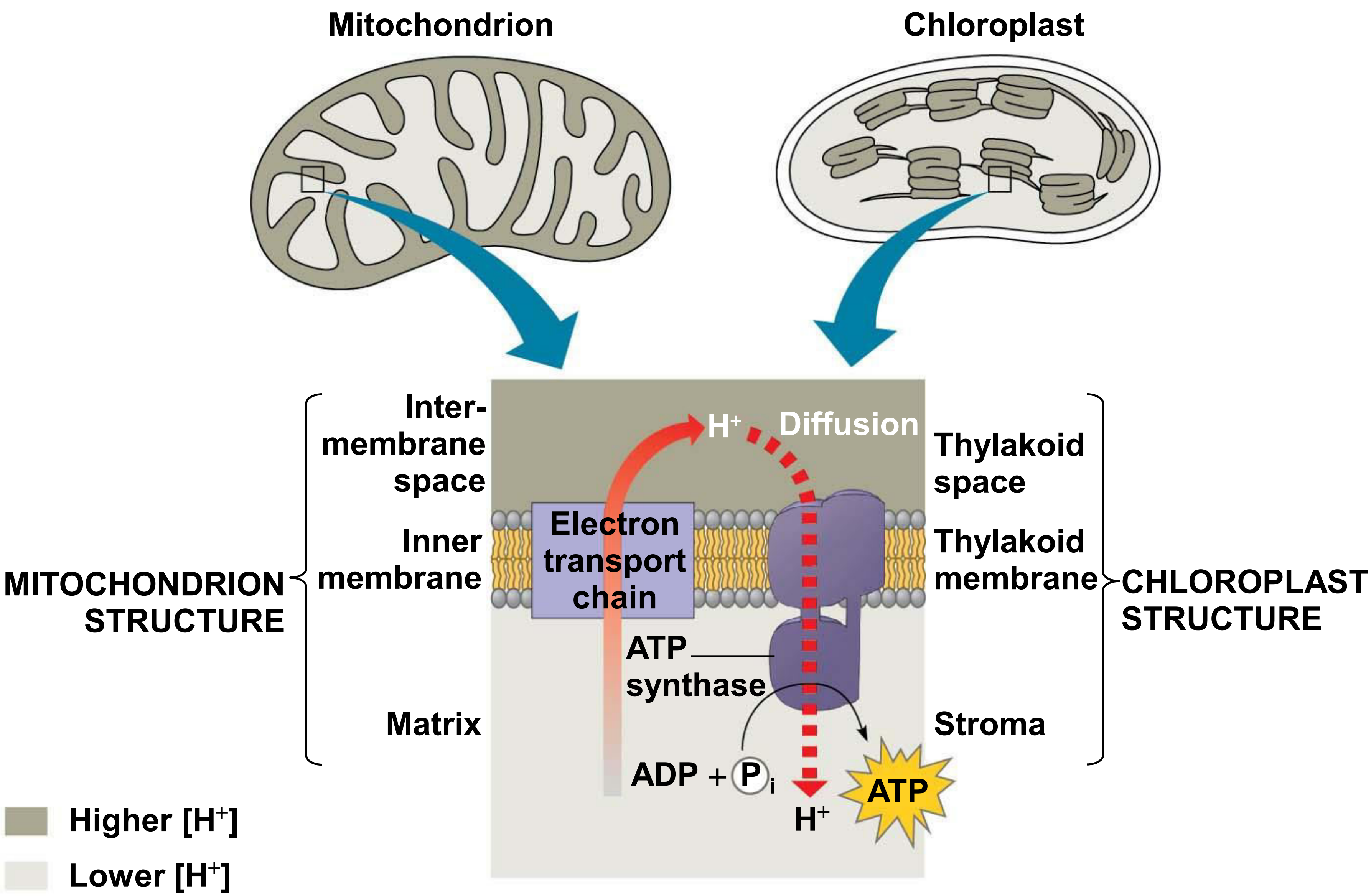
A Comparison of Chemiosmosis in Chloroplasts and Mitochondria

- 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

- 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

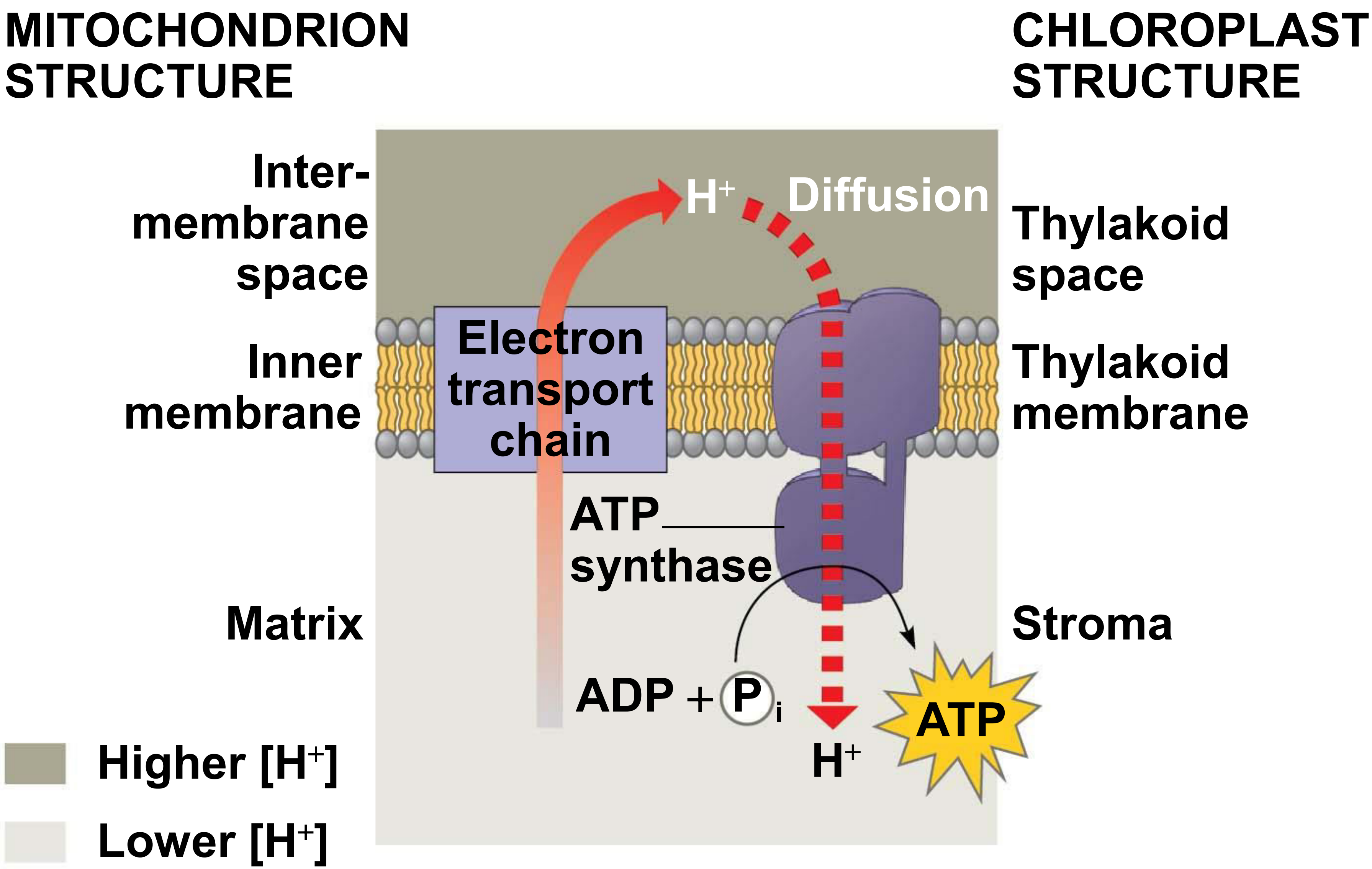
- In mitochondria, protons are pumped to the intermembrane space and drive ATP synthesis as they diffuse back into the mitochondrial matrix
- In chloroplasts, protons are pumped into the thylakoid space and drive ATP synthesis as they diffuse back into the stroma

Figure 8.15



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

Figure 8.15-1


MITOCHONDRION STRUCTURE
CHLOROPLAST STRUCTURE
Inter-membrane space
Inner membrane
Matrix
H+
Diffusion
Electron transport chain
ATP synthase
ADP + P i
H+
ATP
Thylakoid space
Thylakoid membrane
Stroma
Higher [H+]
Lower [H+]

- 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

Figure 8.UN02

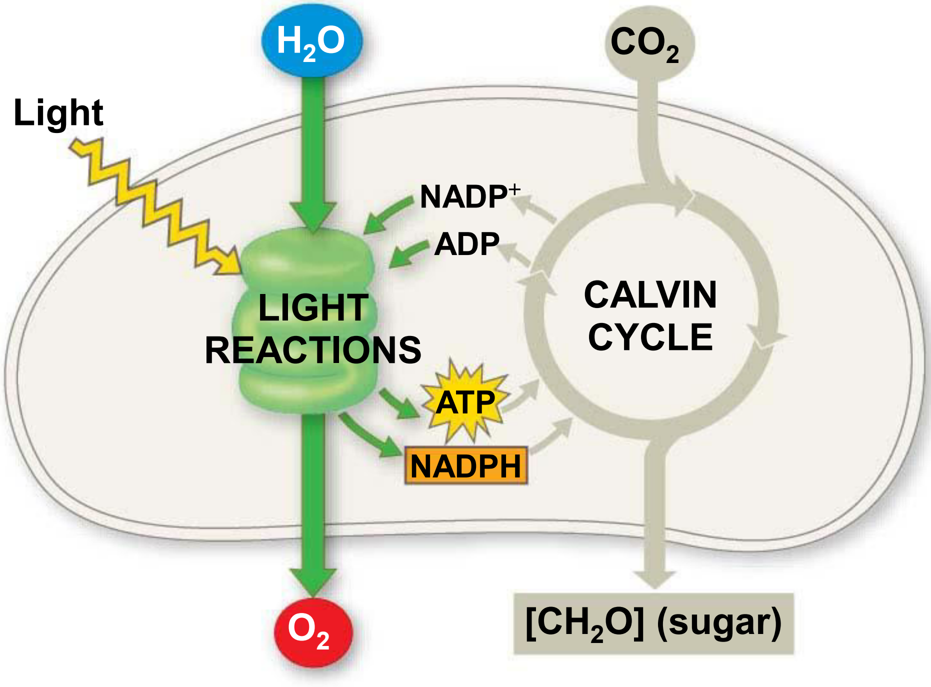
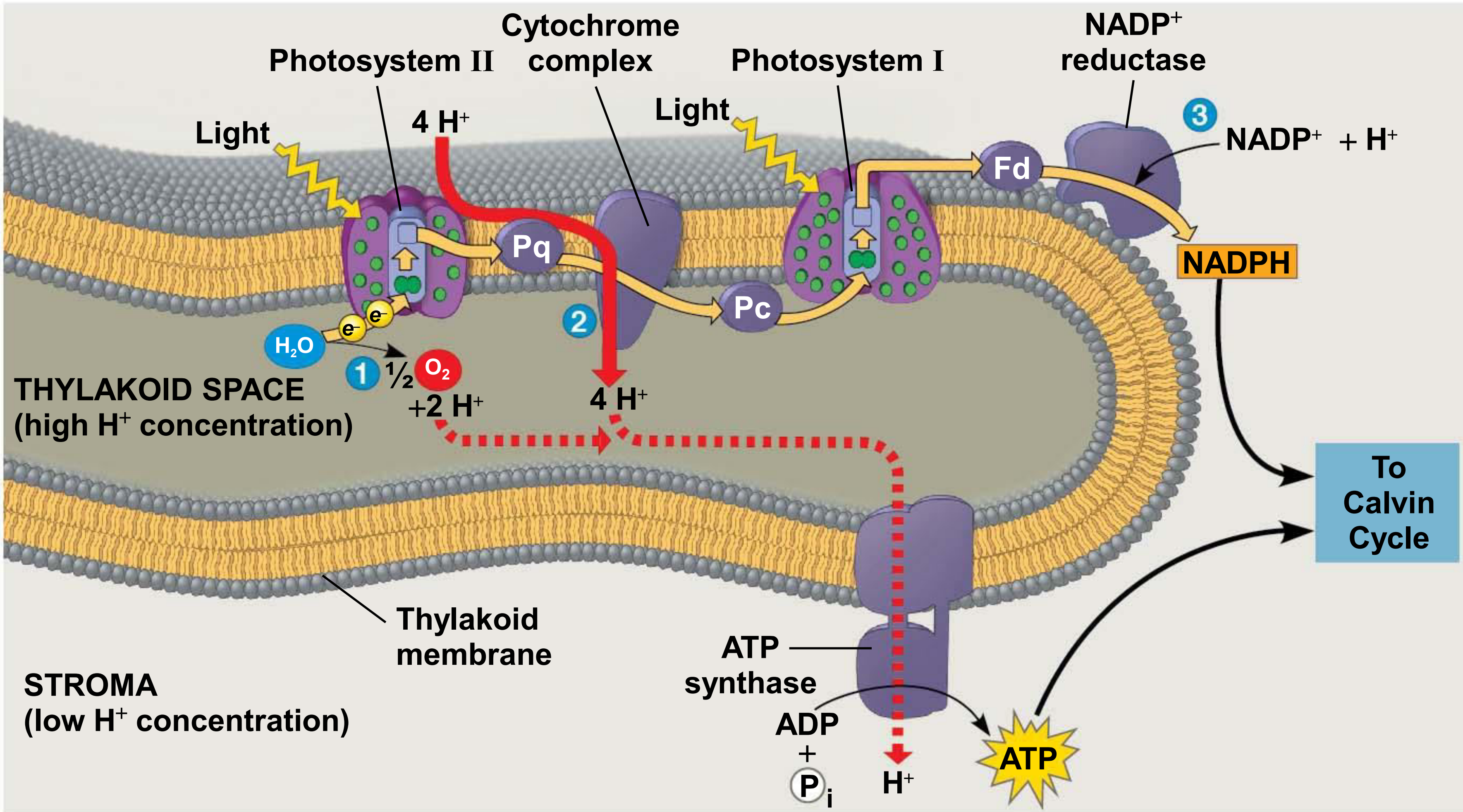
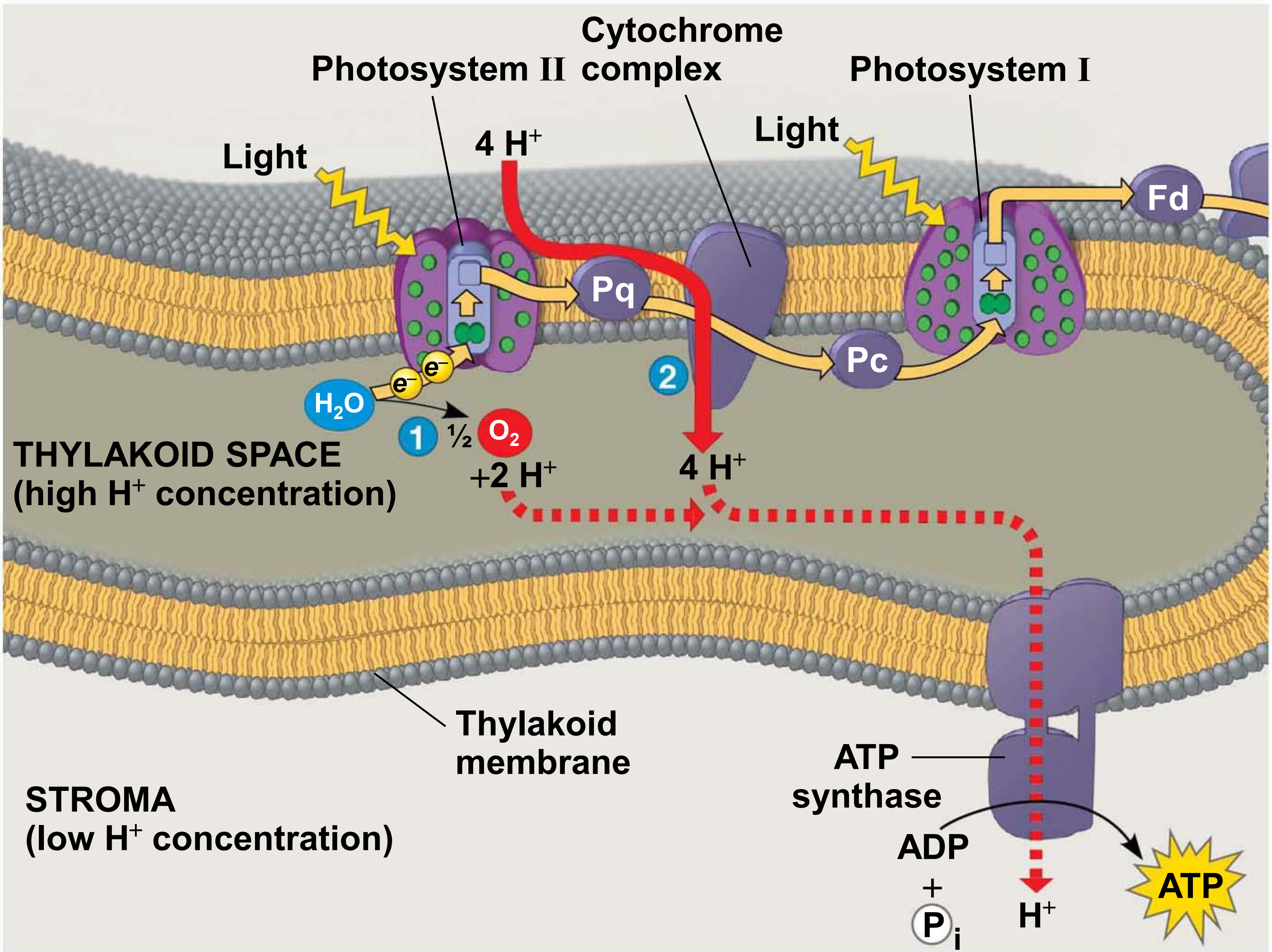


Figure 8.16



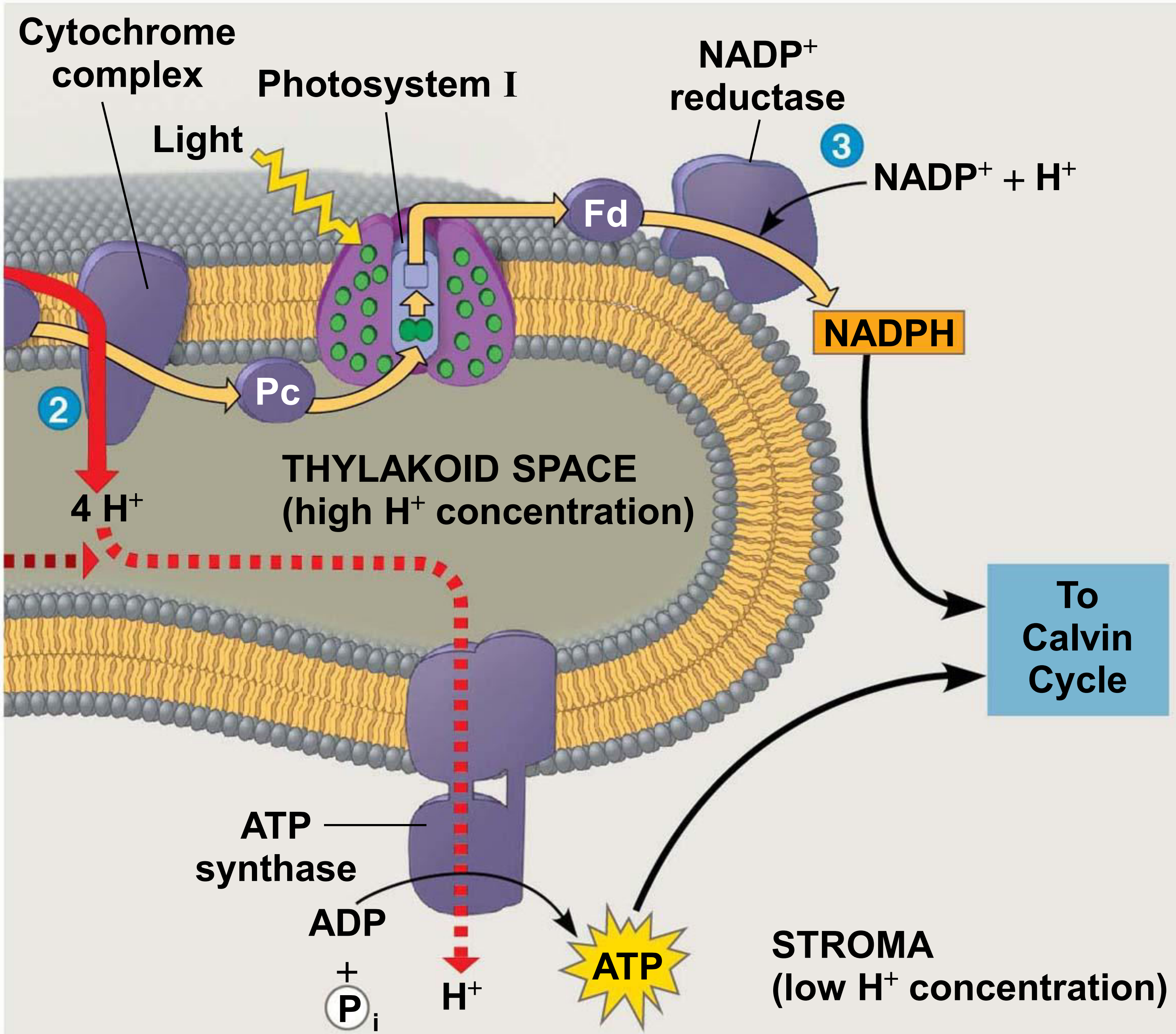
Photosystem II
Cytochrome complex
Photosystem I
NADP+ reductase
Light
4 H+
Light
3
NADP+ + H+
Fd
Pq
NADPH
Pc
e−
e−
2
H2O
1
½ O2
+2 H+
4 H+
THYLAKOID SPACE
(high H+ concentration)
To Calvin Cycle
Thylakoid membrane
ATP synthase
STROMA
(low H+ concentration)
ADP
+
P i
H+
ATP

Figure 8.16-1



Cytochrome complex
Photosystem II
Photosystem I
Light
4 H+
Light
Fd
Pq
Pc
e−
e−
H2O
1
½ O2
2
THYLAKOID SPACE (high H+ concentration)
+2 H+
4 H+
Thylakoid membrane
ATP synthase
STROMA (low H+ concentration)
ADP
+
P i
H+
ATP

Figure 8.16-2



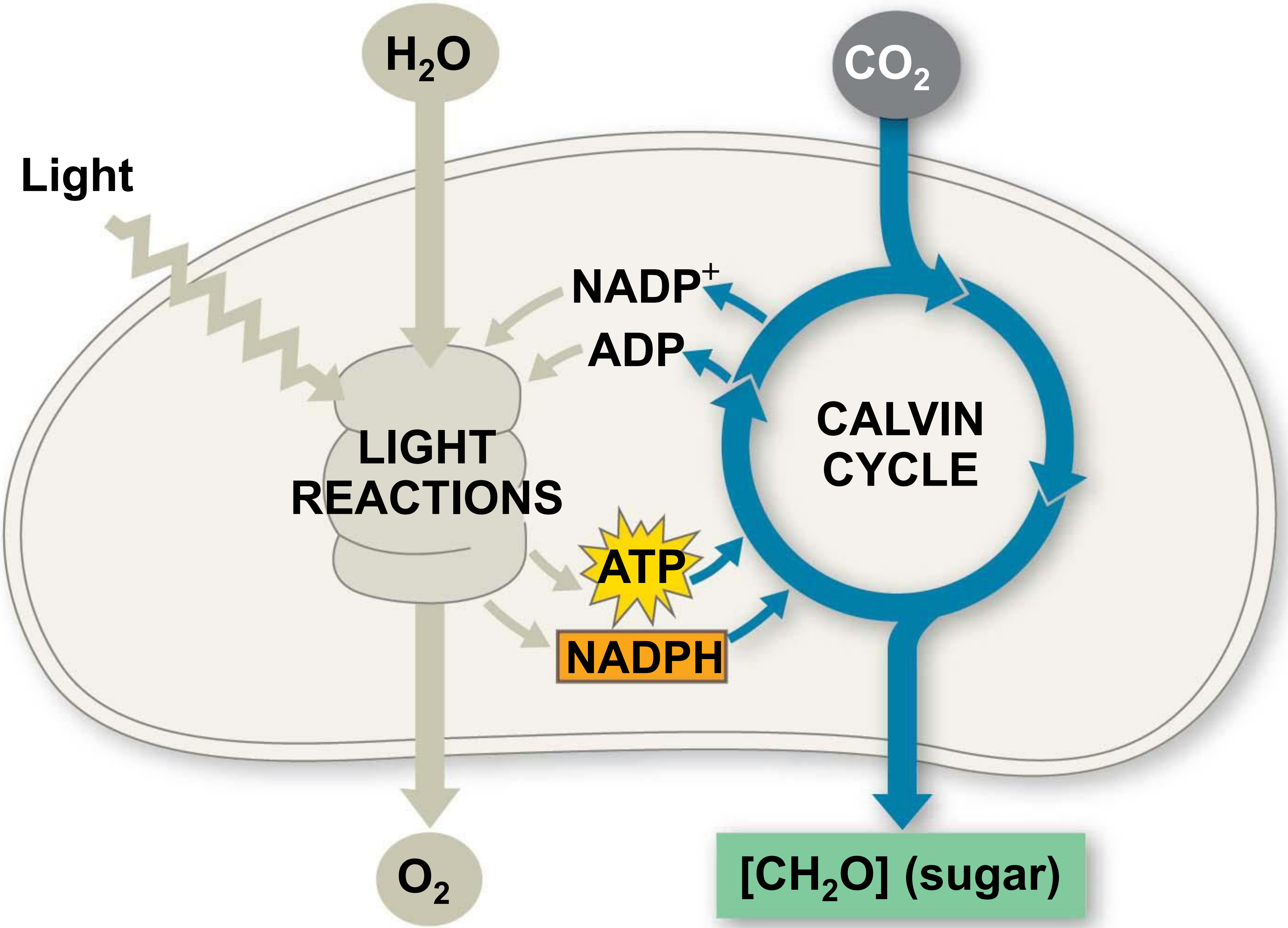
Cytochrome complex
Photosystem I
Light
NADP+ reductase
3
NADP+ + H+
Fd
NADPH
Pc
2
4 H+
THYLAKOID SPACE
(high H+ concentration)
To Calvin Cycle
ATP synthase
ADP
+
P i
H+
ATP
STROMA
(low H+ concentration)

Concept 8.3: 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
- 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

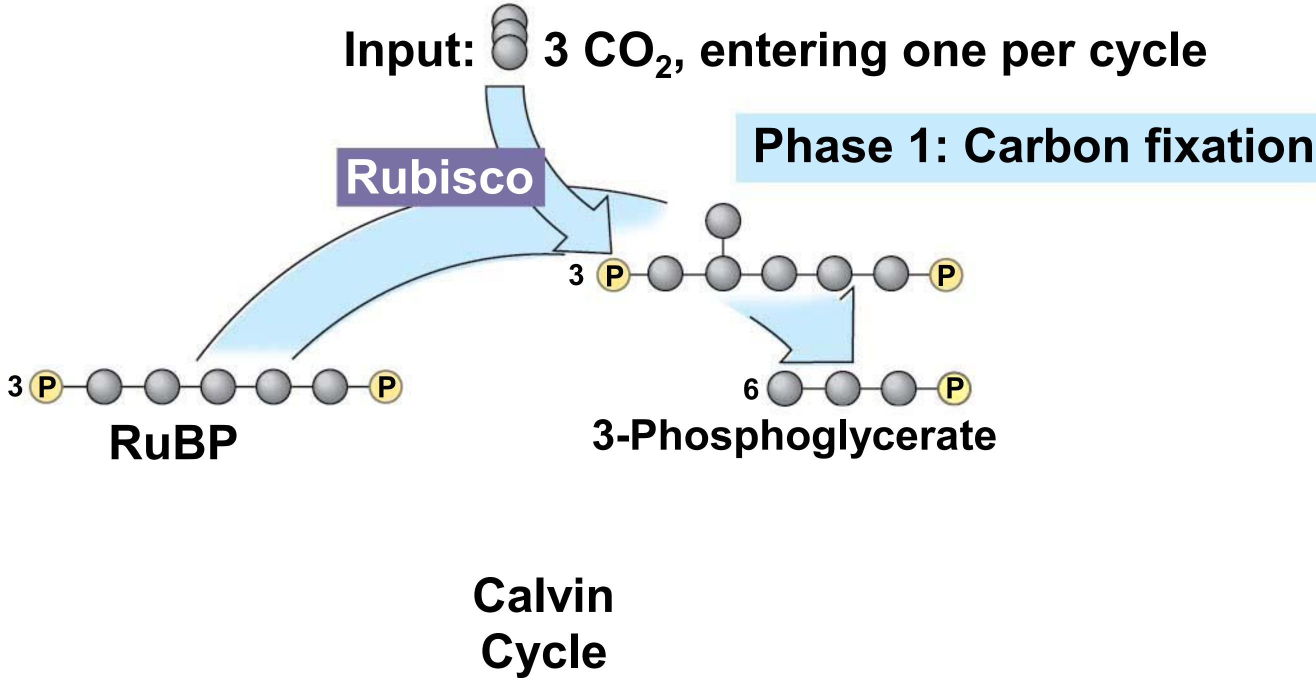
- Carbon enters the cycle as CO_2 and leaves as a sugar named **glyceraldehyde 3-phospate** (**G3P**)
- For net synthesis of one G3P, the cycle must take place three times, fixing three molecules of CO_2
- The Calvin cycle has three phases
  - Carbon fixation
  - Reduction
  - Regeneration of the CO_2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

Figure 8.UN03



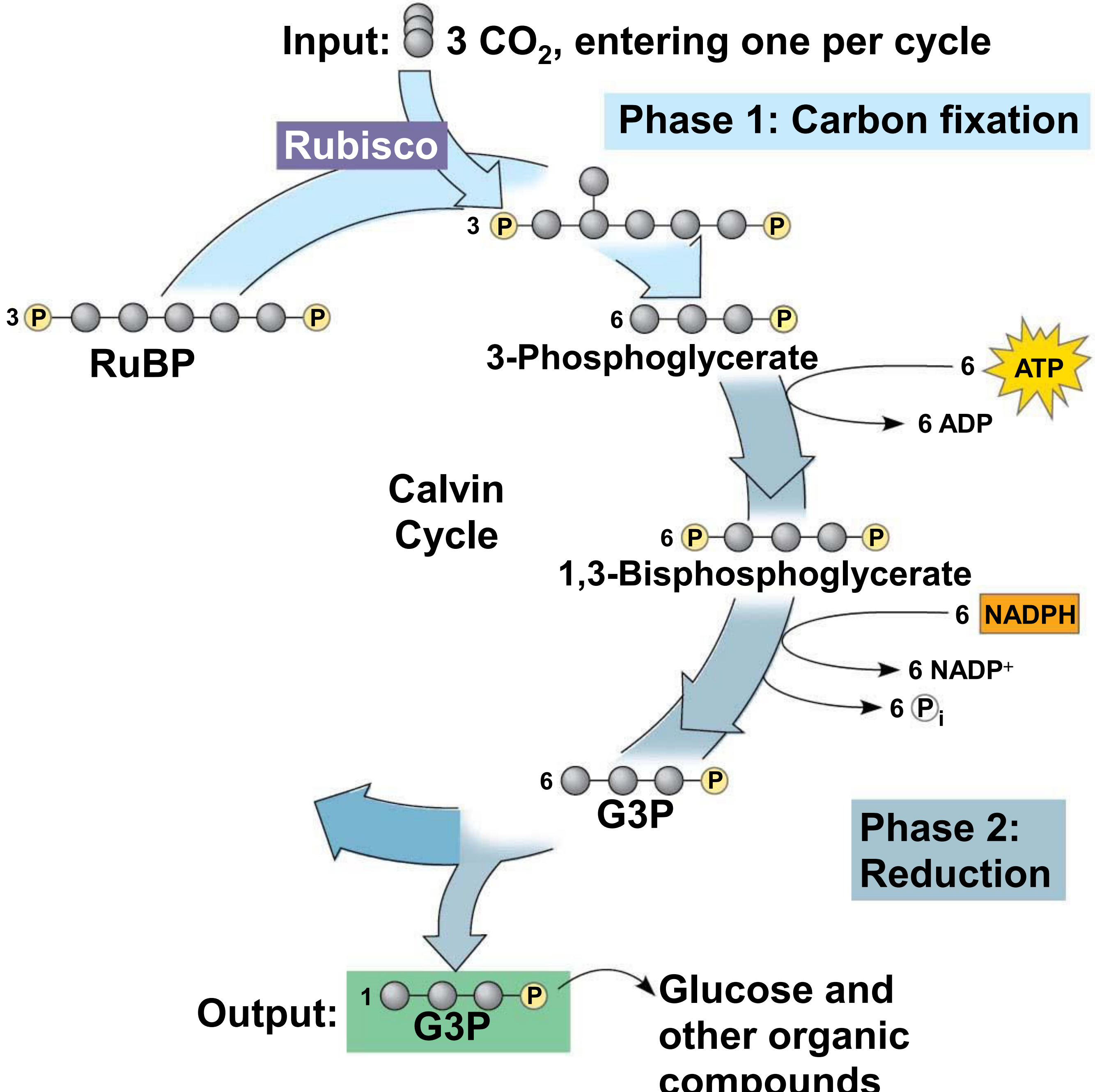
- **Phase 1**, **carbon fixation**, involves the incorporation of the CO_2 molecules into ribulose bisphosphate (RuBP) using the enzyme **rubisco**
- The product is 3-phosphoglycerate

Figure 8.17-s1



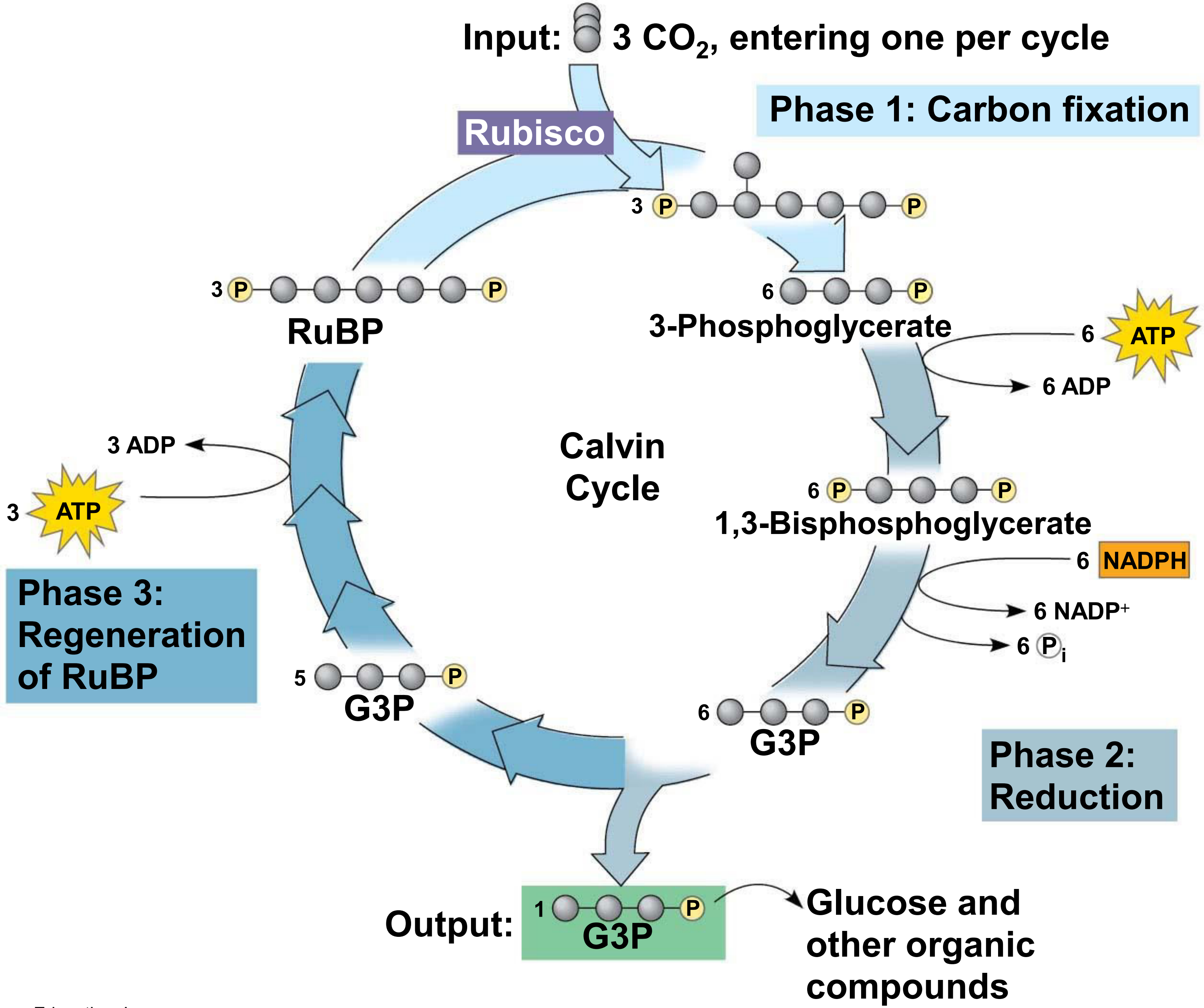
- **Phase 2**, **reduction**, involves the reduction and phosphorylation of 3-phosphoglycerate to G3P
- Six ATP and six NADPH are required to produce six molecules of G3P, but only one exits the cycle for use by the cell

Figure 8.17-s2



- **Phase 3**, **regeneration**, involves the rearrangement of the five remaining molecules of G3P to regenerate the initial CO_2 receptor, RuBP
- Three additional ATP are required to power this step

Figure 8.17-s3



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 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

- In most plants (**C_3 plants**), initial fixation of CO_2, via rubisco, forms a three-carbon compound (3-phosphoglycerate)
- In **photorespiration**, rubisco adds O_2 instead of CO_2 in the Calvin cycle, producing a two-carbon compound
- Photorespiration decreases photosynthetic output by consuming ATP, O_2, and organic fuel and releasing CO_2 without producing any ATP or sugar

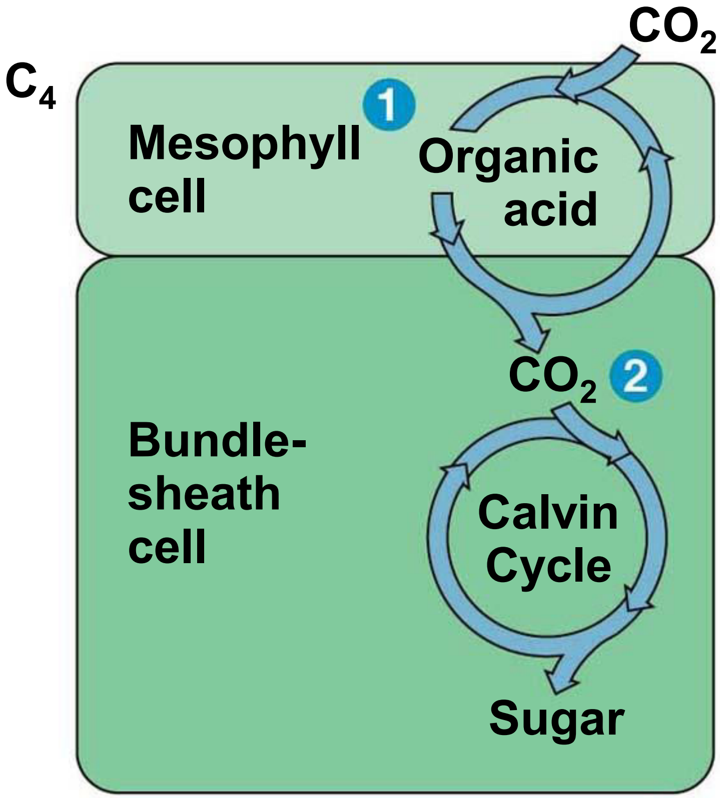
- Photorespiration may be an evolutionary relic because rubisco first evolved at a time when the atmosphere had far less O_2 and more CO_2
- Photorespiration limits damaging products of light reactions that build up in the absence of the Calvin cycle

C_4 Plants

- **C_4 plants** minimize the cost of photorespiration by incorporating CO_2 into a four-carbon compound
- An enzyme in the mesophyll cells has a high affinity for CO_2 and can fix carbon even when CO_2 concentrations are low
- These four-carbon compounds are exported to bundle-sheath cells, where they release CO_2 that is then used in the Calvin cycle

Figure 8.18a

Sugarcane



(a) Spatial separation of steps

Figure 8.18-1

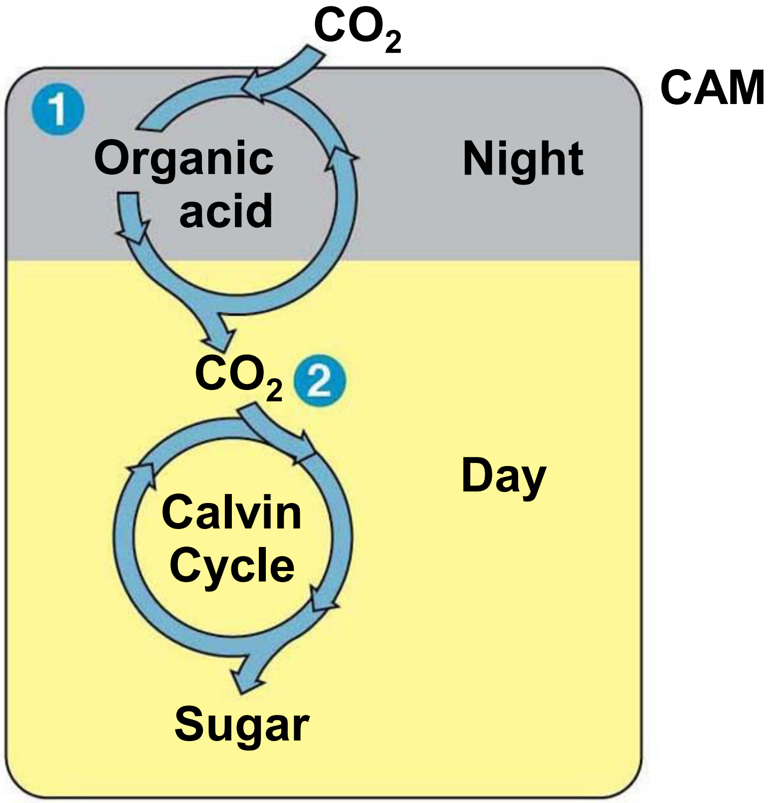
Sugarcane

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 CO_2 into organic acids
- Stomata close during the day, and CO_2 is released from organic acids and used in the Calvin cycle

Figure 8.18b

Pineapple



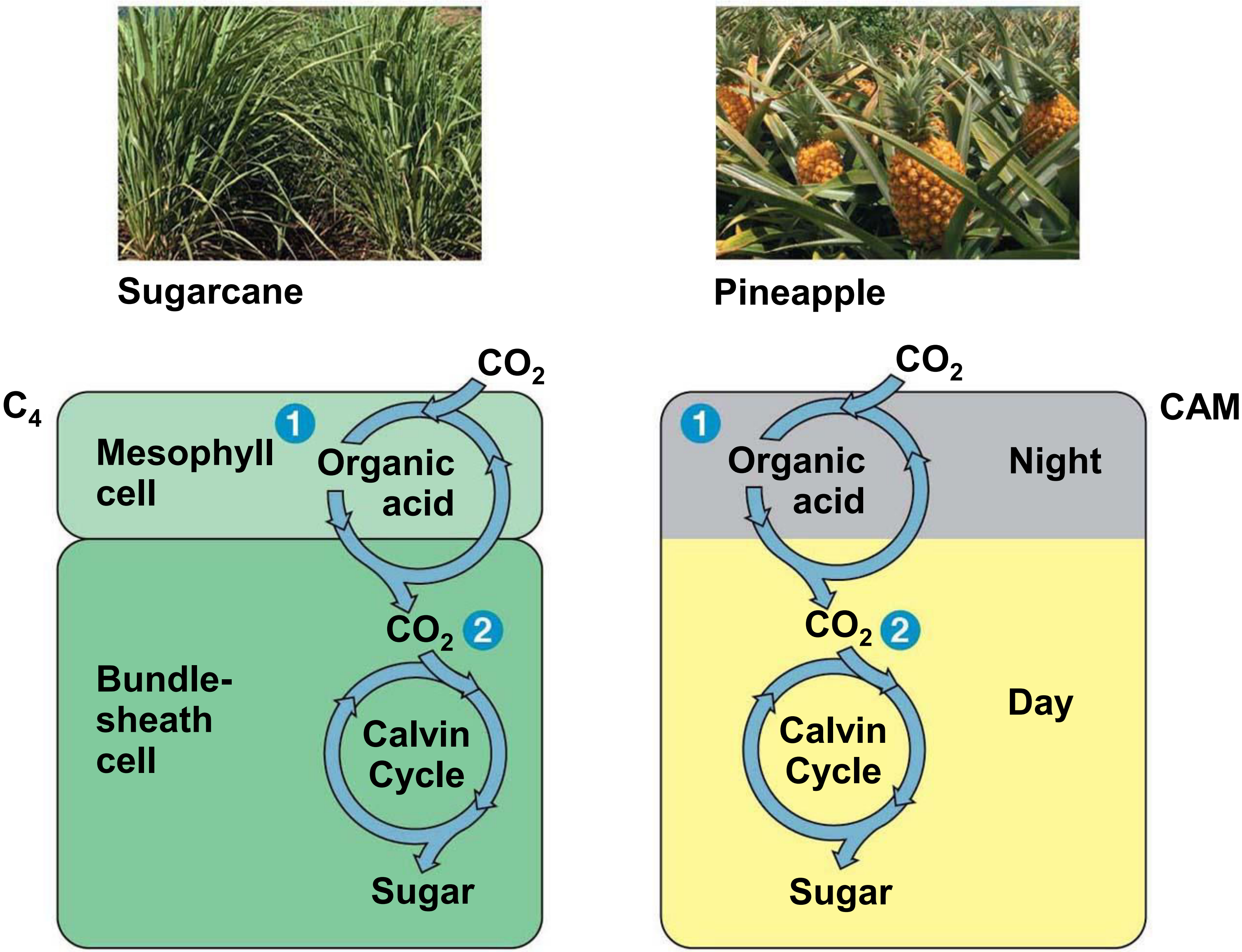
(b) Temporal separation of steps

Figure 8.18-2

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

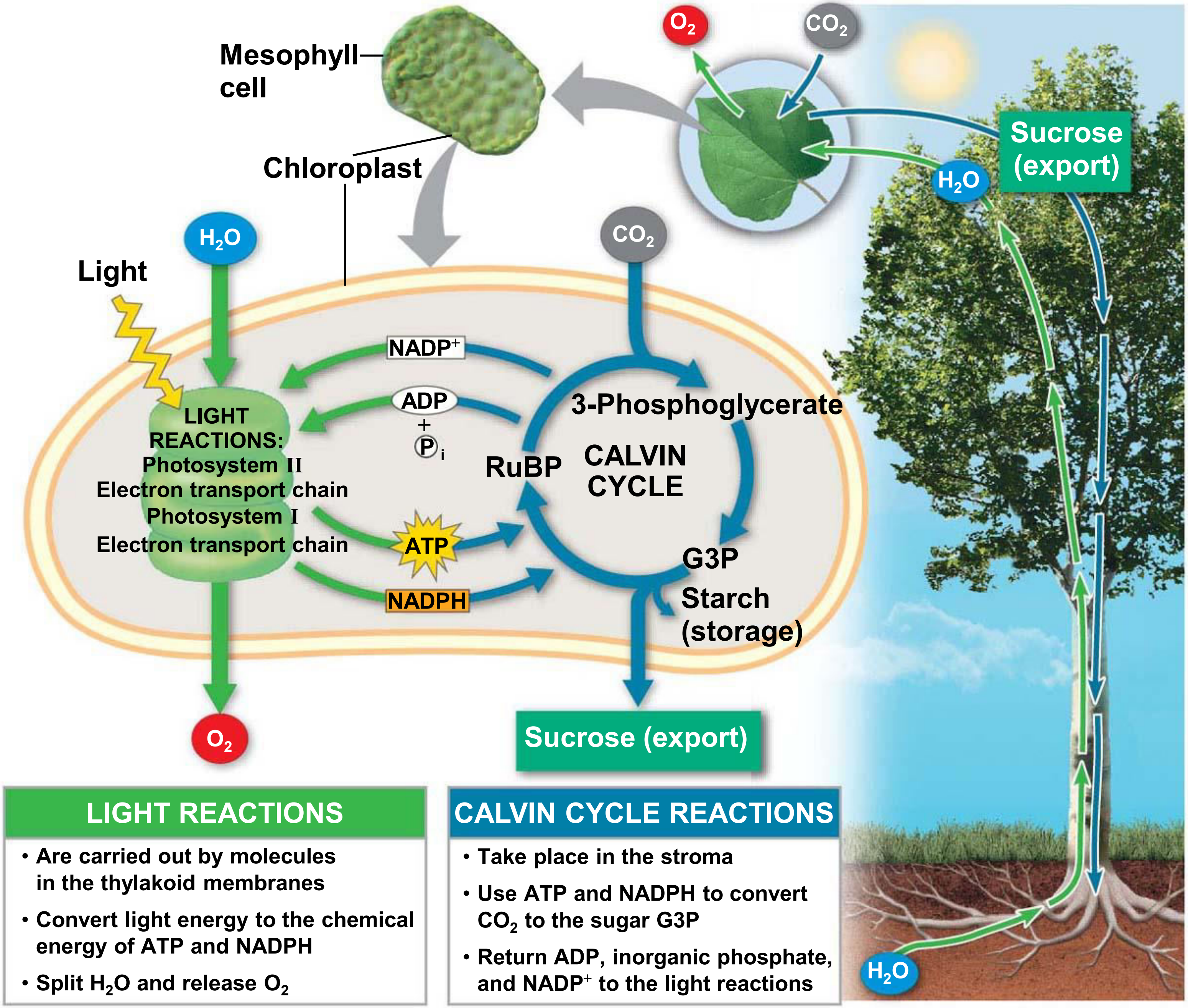


(a) Spatial separation of steps **(b) Temporal separation of steps**

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 O_2 in our atmosphere

Figure 8.19



Mesophyll cell
Chloroplast
O_2
CO_2
Sucrose (export)
H_2O
Light
LIGHT REACTIONS:
Photosystem II
Electron transport chain
Photosystem I
Electron transport chain
$NADP^+$
ADP
+
Ⓟi
ATP
NADPH
3-Phosphoglycerate
RuBP
CALVIN CYCLE
G3P
Starch (storage)
Sucrose (export)
LIGHT REACTIONS
• Are carried out by molecules in the thylakoid membranes
• Convert light energy to the chemical energy of ATP and NADPH
• Split H_2O and release O_2
CALVIN CYCLE REACTIONS
• Take place in the stroma
• Use ATP and NADPH to convert CO_2 to the sugar G3P
• Return ADP, inorganic phosphate, and $NADP^+$ to the light reactions

Figure 8.19-1

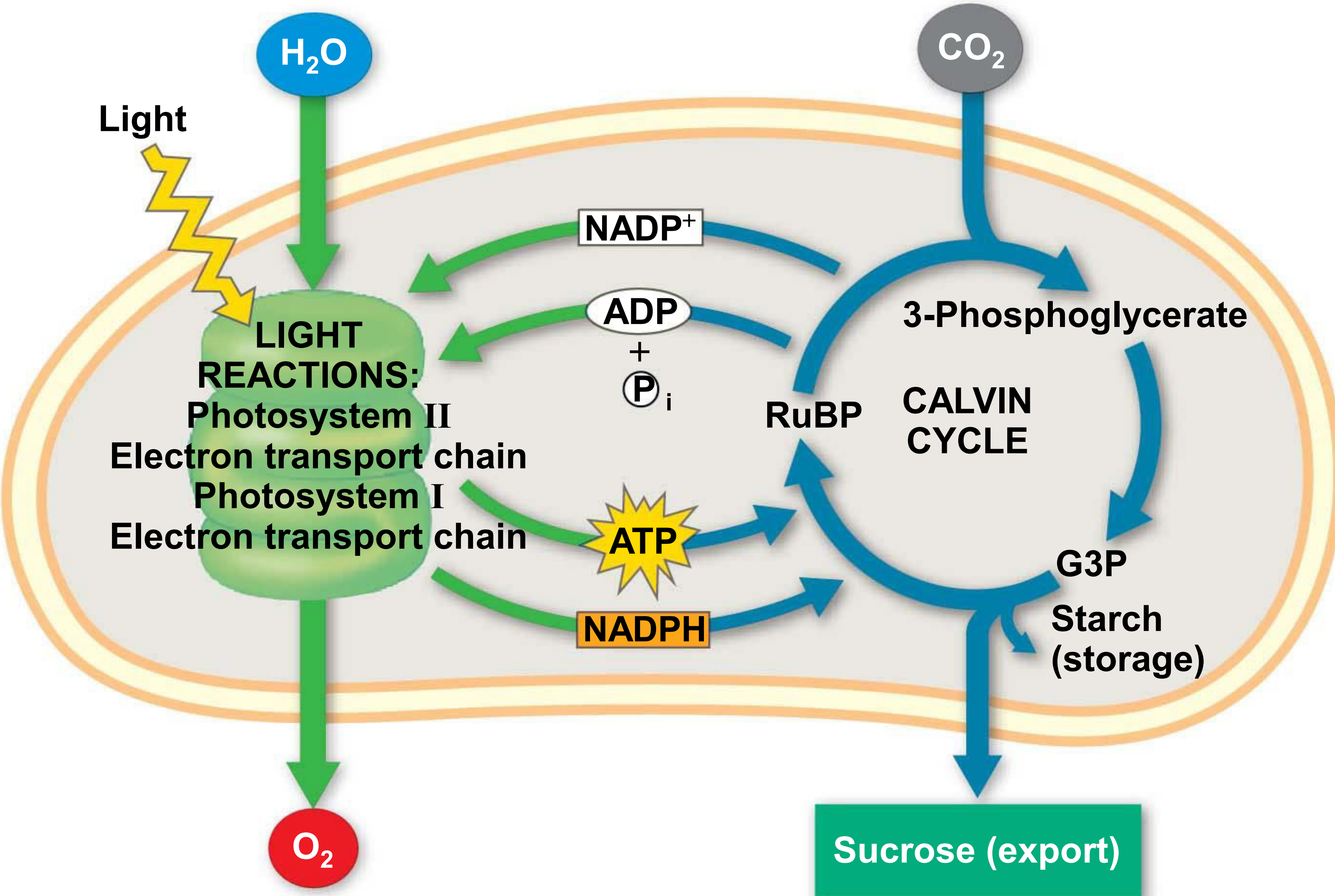

H_2O
Light
CO_2
NADP+
ADP
+
P i
LIGHT
REACTIONS:
Photosystem II
Electron transport chain
Photosystem I
Electron transport chain
ATP
NADPH
RuBP
3-Phosphoglycerate
CALVIN
CYCLE
G3P
Starch
(storage)
O_2
Sucrose (export)

Figure 8.19-2

LIGHT REACTIONS	CALVIN CYCLE REACTIONS
• Are carried out by molecules in the thylakoid membranes • Convert light energy to the chemical energy of ATP and NADPH • Split H_2O and release O_2	• Take place in the stroma • Use ATP and NADPH to convert CO_2 to the sugar G3P • Return ADP, inorganic phosphate, and $NADP^+$ to the light reactions

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

Figure 8.20

MAKE CONNECTIONS: The Working Cell

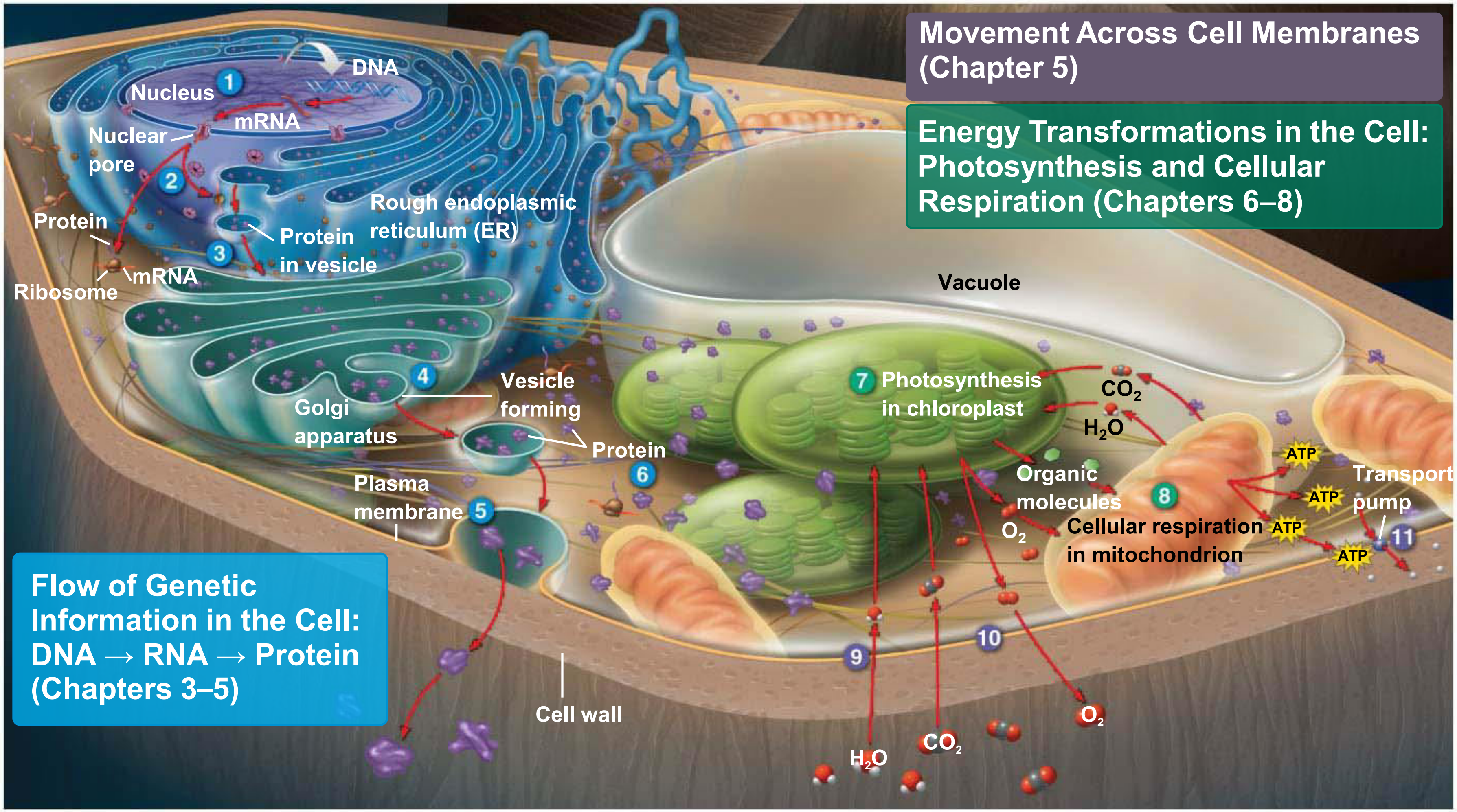


Figure 8.20-1

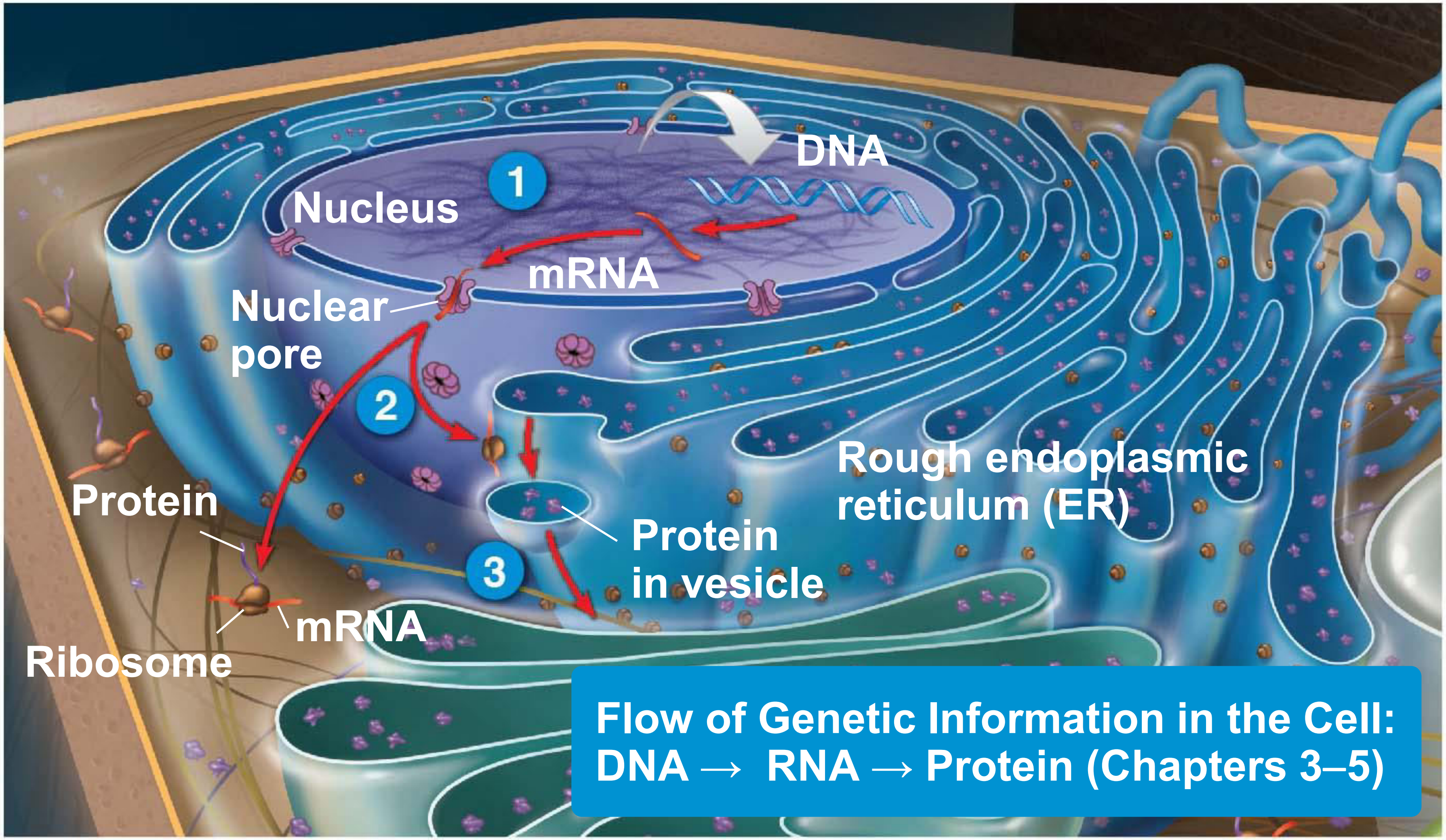

DNA
1
Nucleus
mRNA
Nuclear pore
2
Protein
Protein in vesicle
Rough endoplasmic reticulum (ER)
3
mRNA
Ribosome
Flow of Genetic Information in the Cell:
DNA → RNA → Protein (Chapters 3–5)

Figure 8.20-2

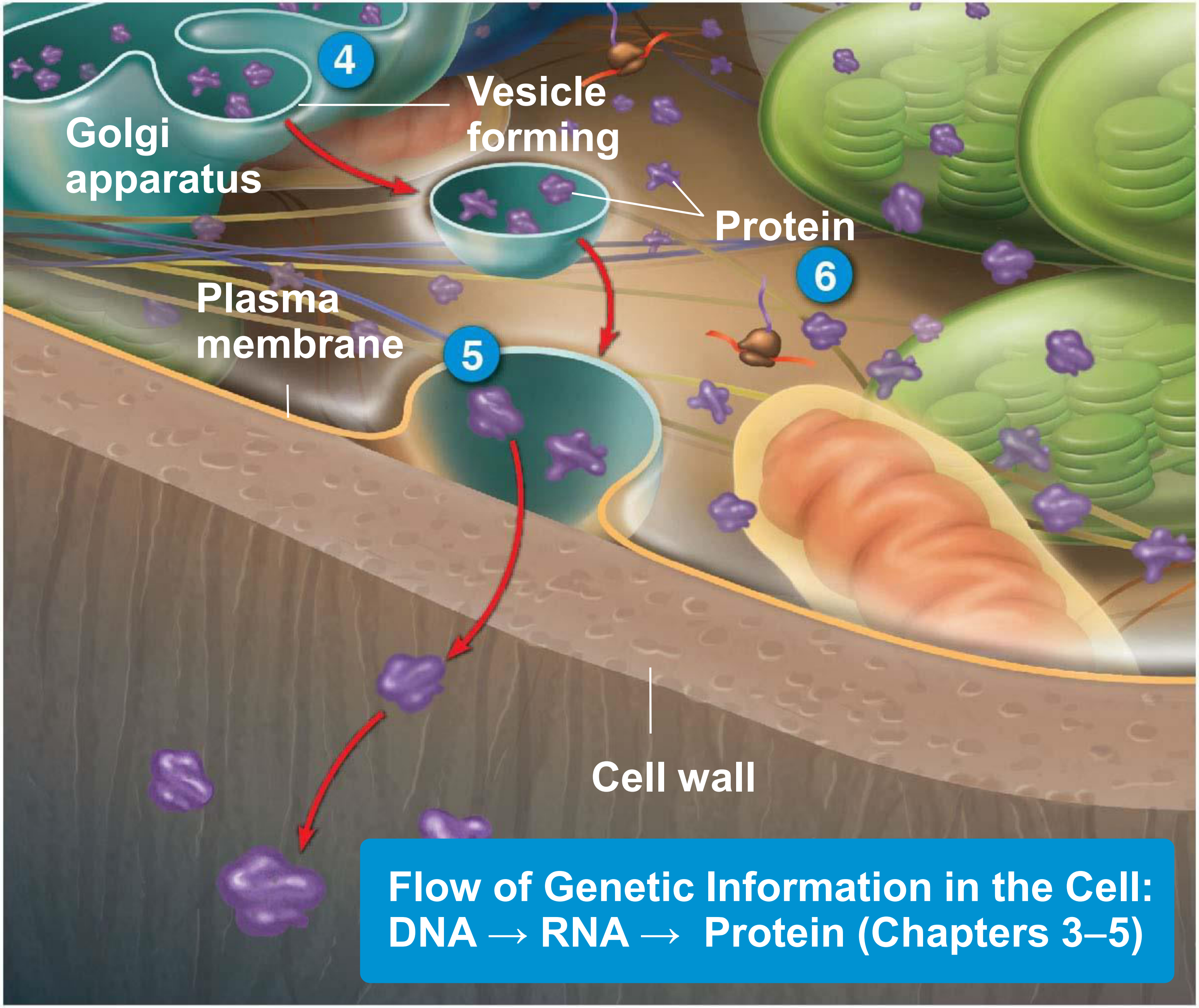

4
Vesicle forming
Golgi apparatus
Protein
6
Plasma membrane
5
Cell wall
Flow of Genetic Information in the Cell:
DNA → RNA → Protein (Chapters 3–5)

Figure 8.20-3

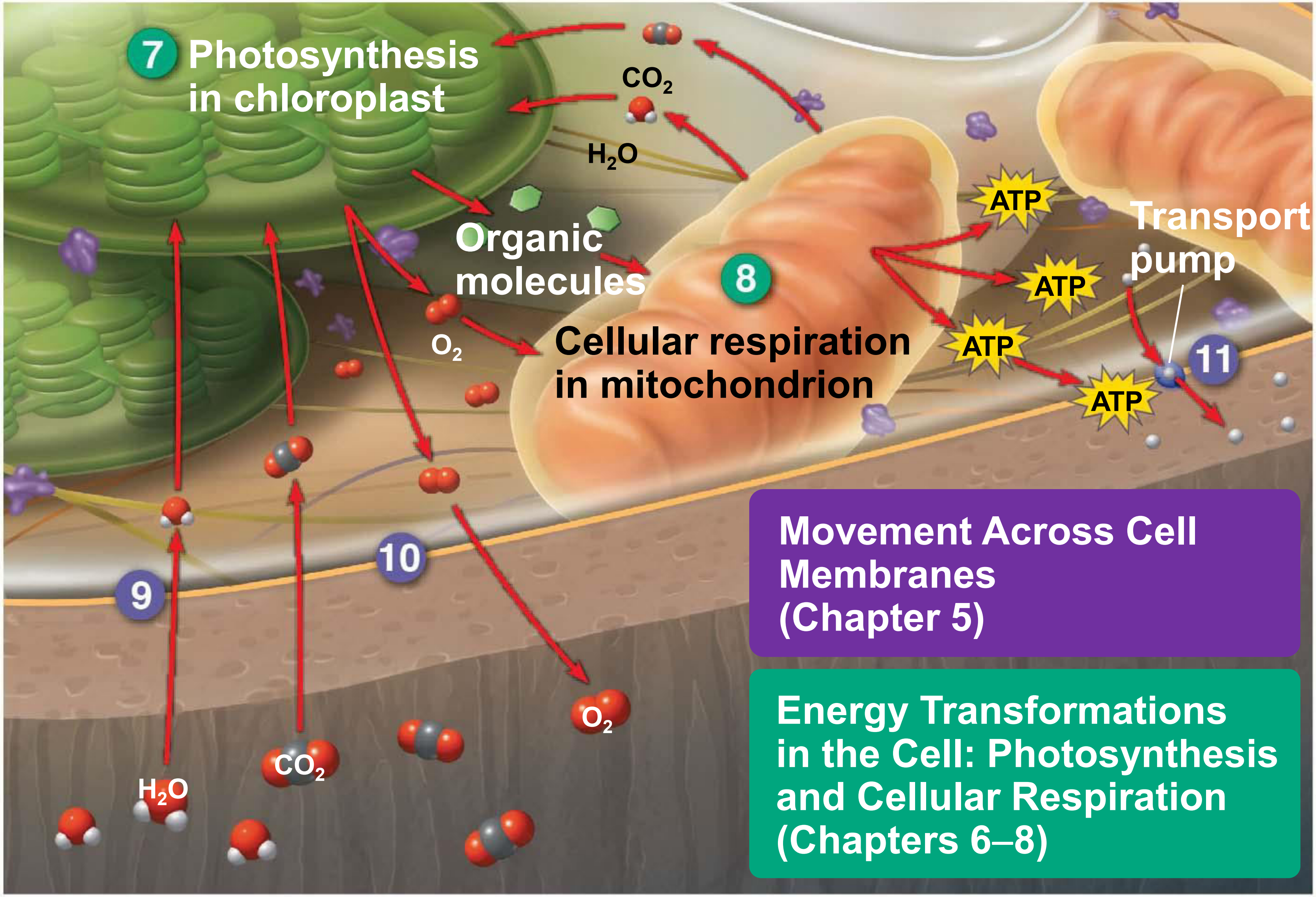

7 Photosynthesis in chloroplast
CO_2
H_2O
Organic molecules
O_2
8
Cellular respiration in mitochondrion
ATP
ATP
ATP
ATP
Transport pump
11
10
9
O_2
CO_2
H_2O
Movement Across Cell Membranes (Chapter 5)
Energy Transformations in the Cell: Photosynthesis and Cellular Respiration (Chapters 6–8)

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 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).

Figure 8.UN05

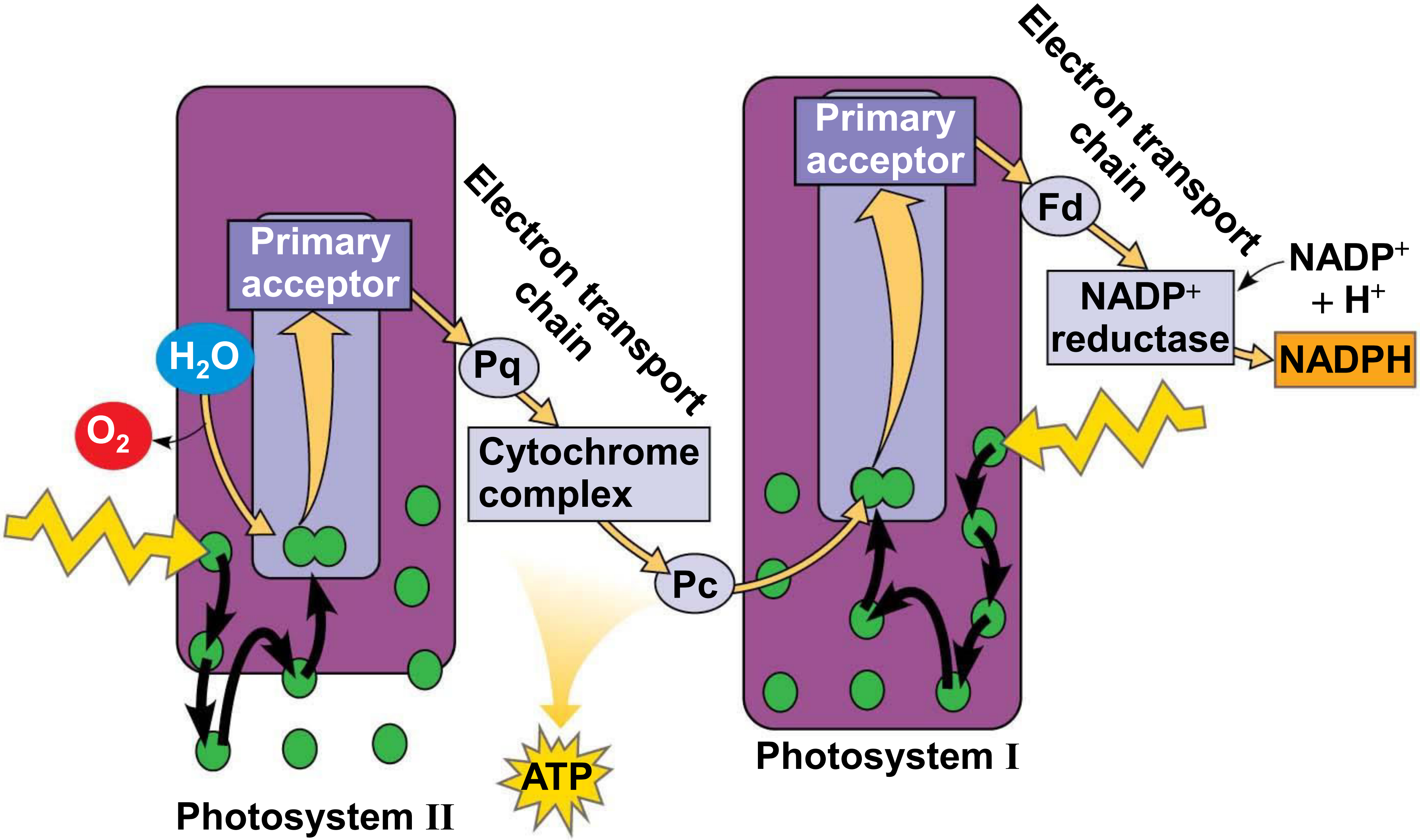


Figure 8.UN06

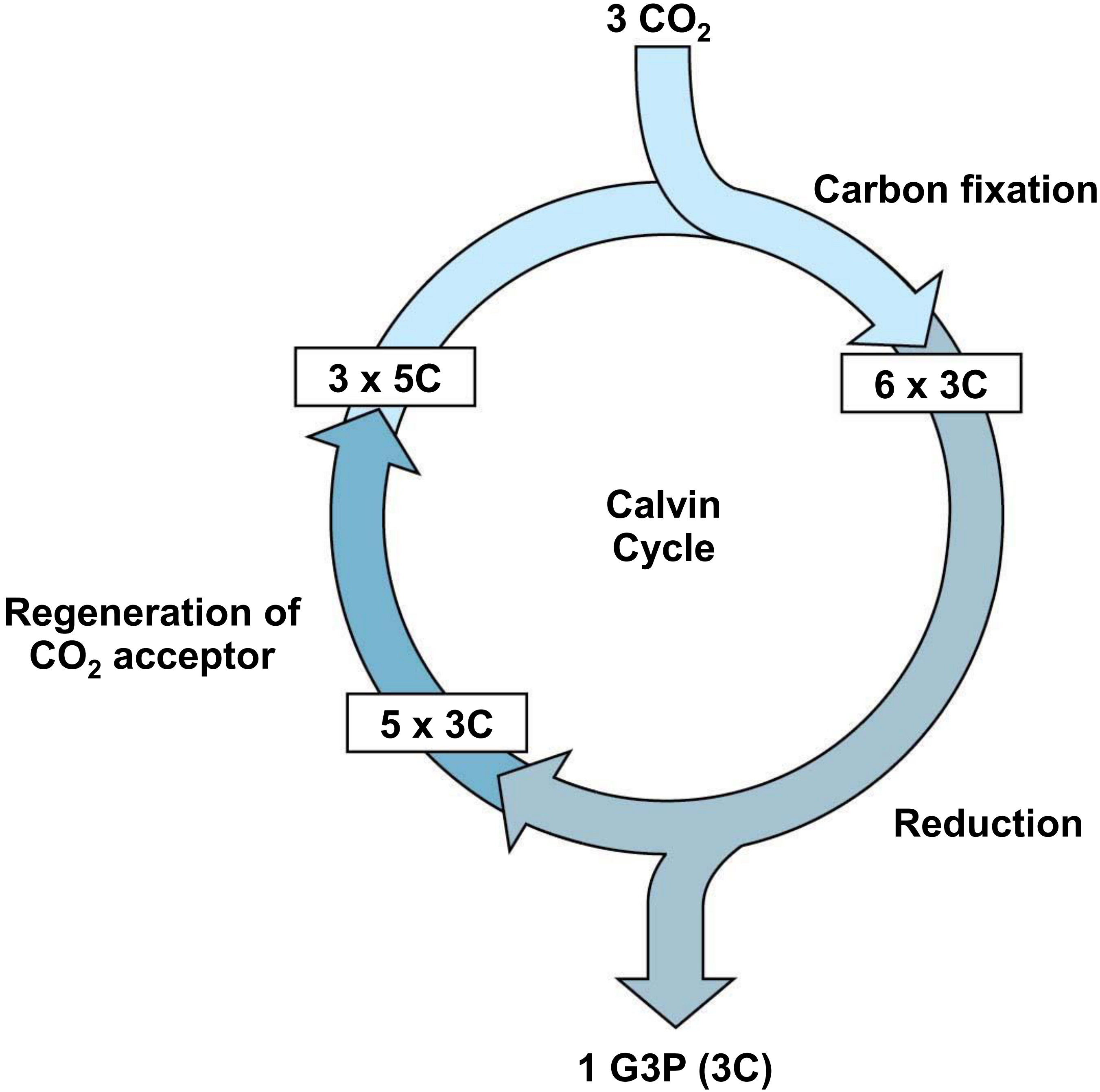


Figure 8.UN07

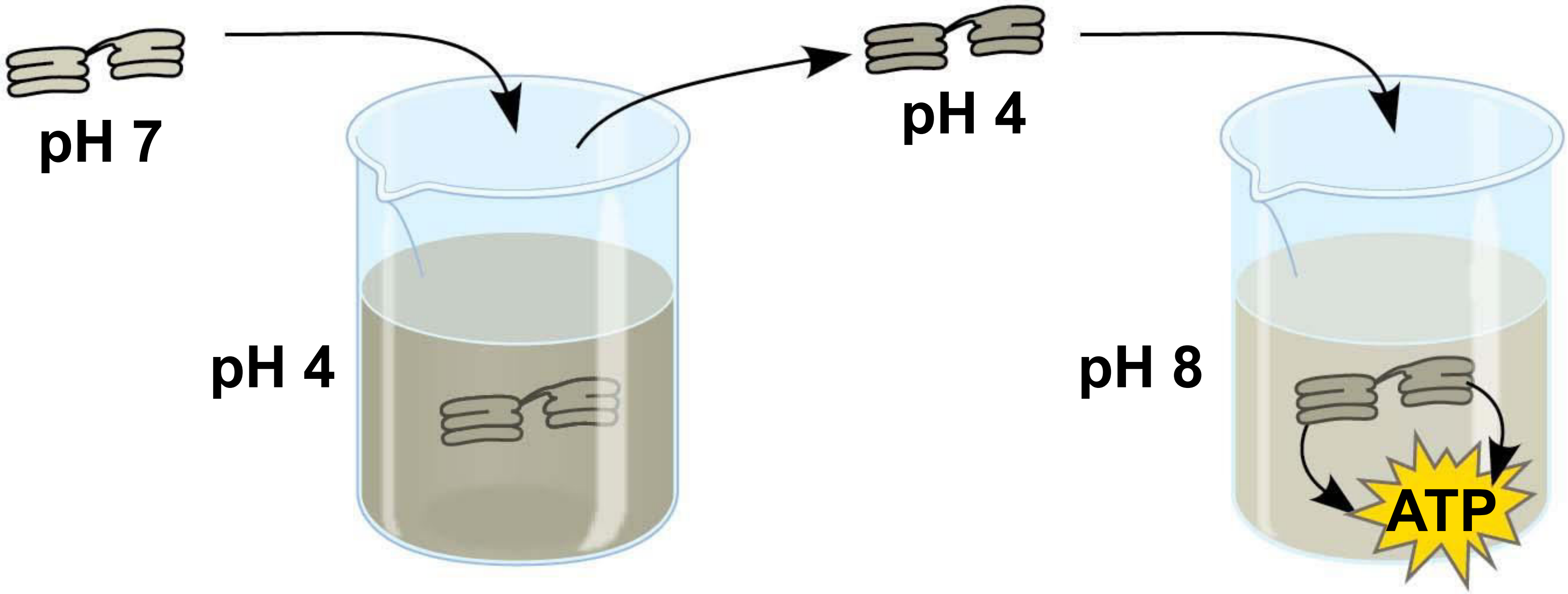


Figure 8.UN08