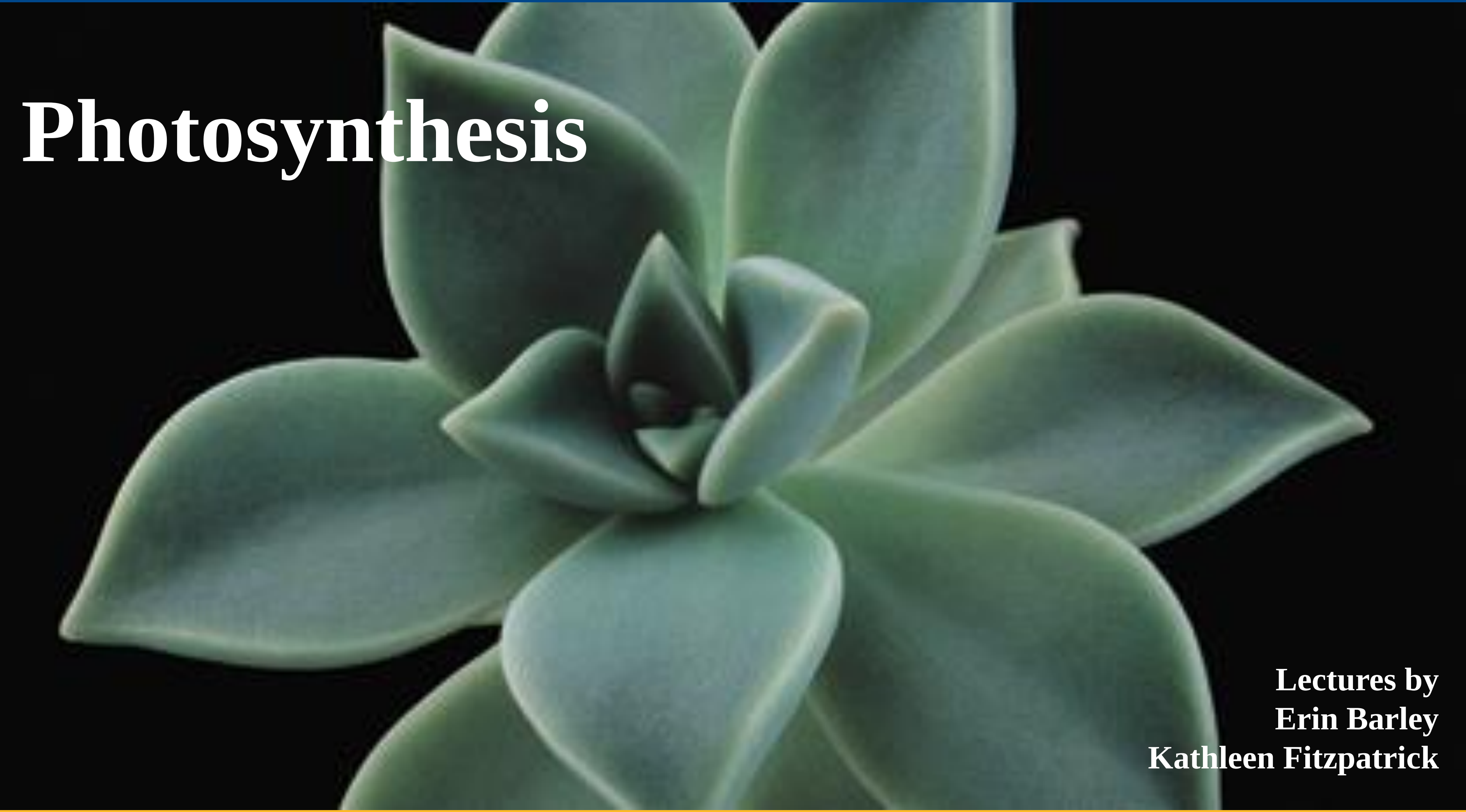
LECTURE PRESENTATIONS
For CAMPBELL BIOLOGY, NINTH EDITION
Jane B. Reece, Lisa A. Urry, Michael L. Cain, Steven A. Wasserman, Peter V. Minorsky, Robert B. Jackson

Chapter 10



Photosynthesis

Lectures by
Erin Barley
Kathleen Fitzpatrick

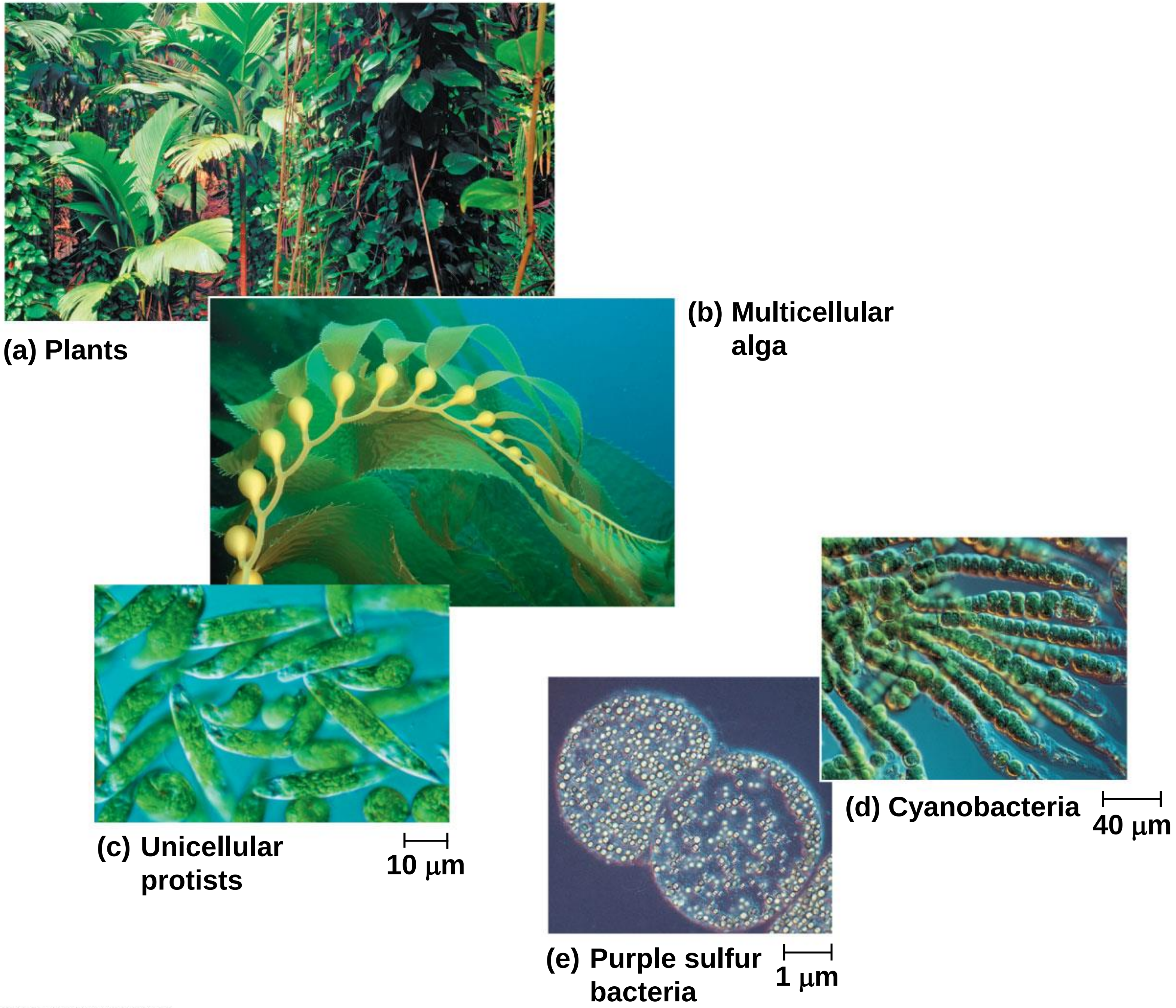
Overview: The Process That Feeds the Biosphere

- **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

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

Figure 10.2



(a) Plants
(b) Multicellular alga
(c) Unicellular protists
10 µm
(d) Cyanobacteria
40 µm
(e) Purple sulfur bacteria
1 µm

- **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

- The Earth's supply of fossil fuels was formed from the remains of organisms that died hundreds of millions of years ago
- In a sense, fossil fuels represent stores of solar energy from the distant past

Concept 10.1: Photosynthesis converts light energy to the chemical energy of food

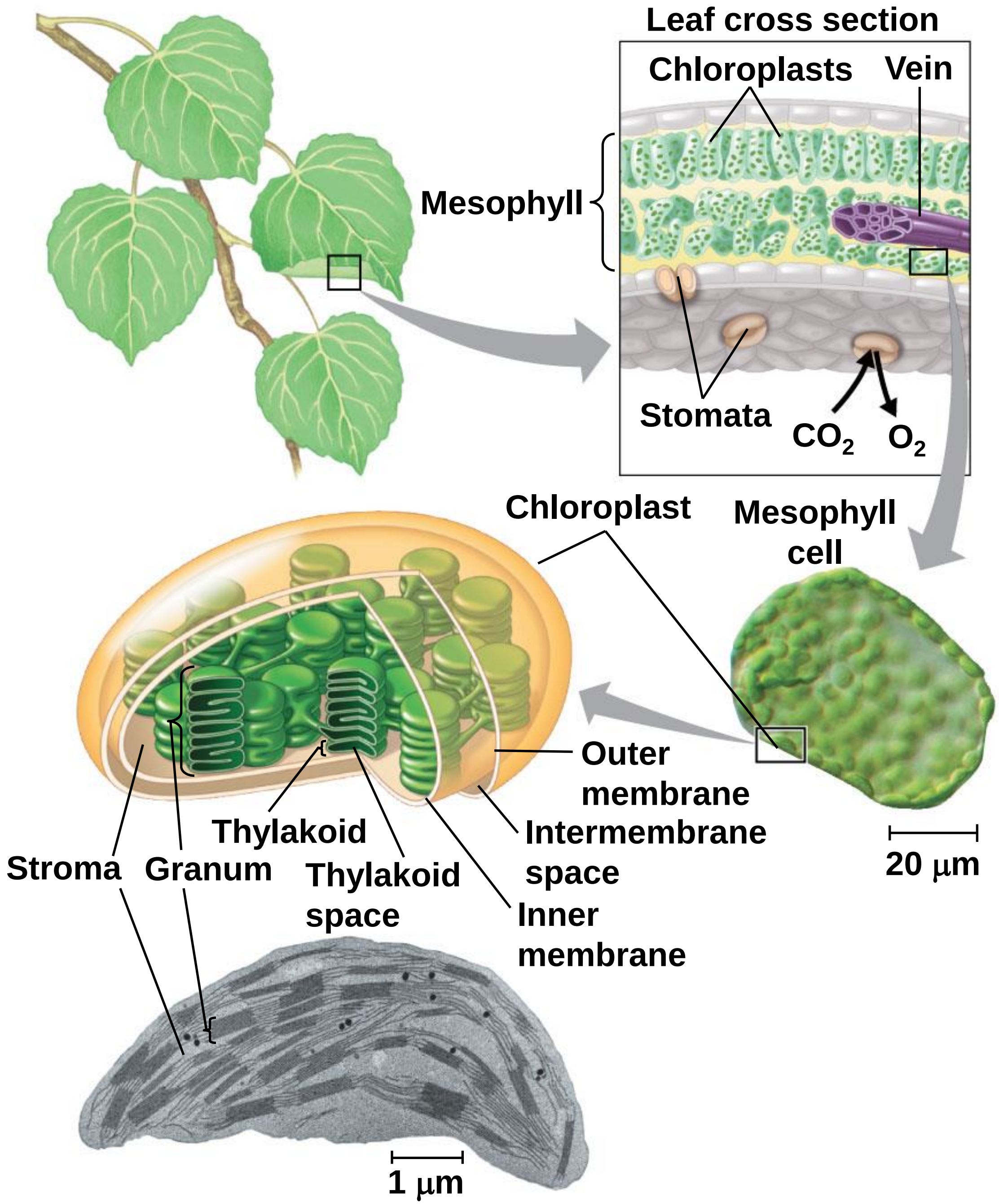
- Chloroplasts are structurally similar to and likely evolved from photosynthetic bacteria
- The structural organization of these cells allows for the chemical reactions of photosynthesis

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 10.4


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
1 μm

Tracking Atoms Through Photosynthesis: *Scientific Inquiry*

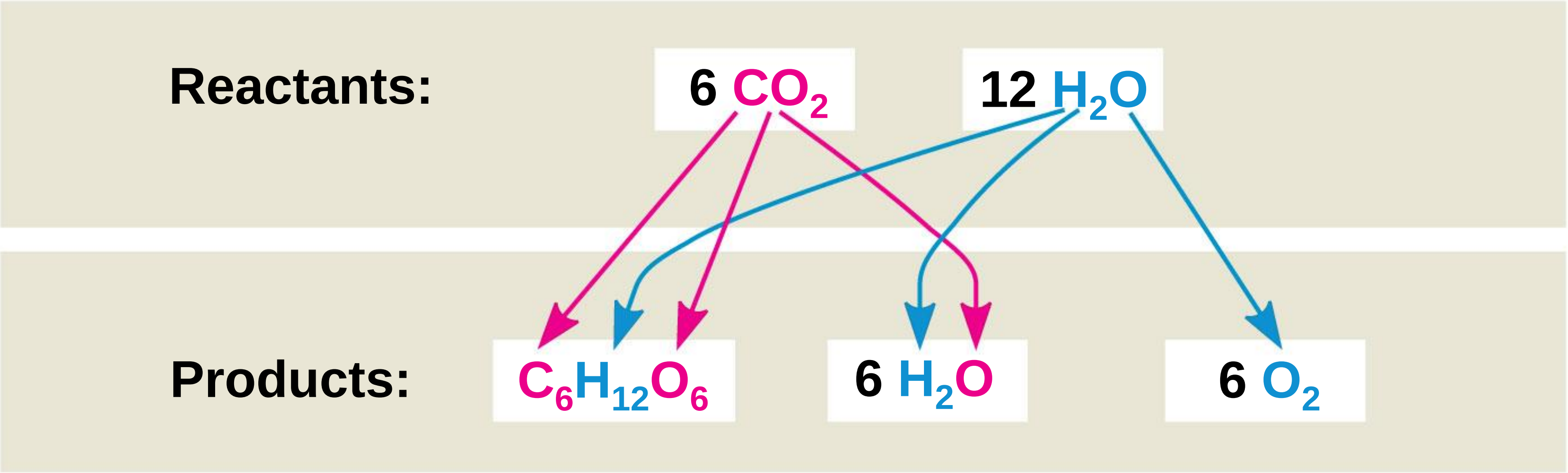
- Photosynthesis is a complex series of reactions that can be summarized as the following equation:

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

The 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 10.5



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

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

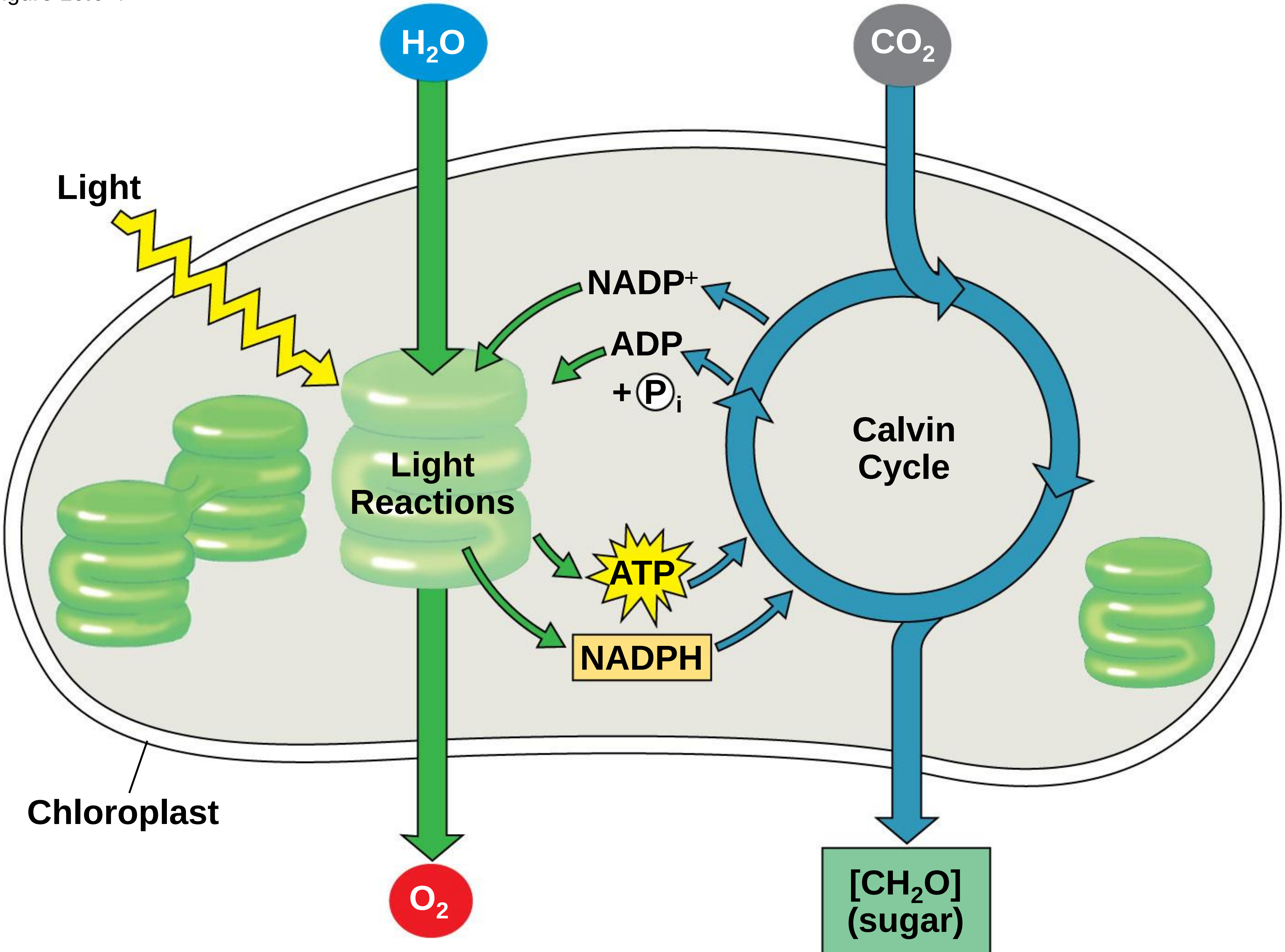
becomes oxidized

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
  - Release O_2
  - Reduce **NADP$^+$** to NADPH
  - Generate ATP from ADP by **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 10.6-4



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

Concept 10.2: The light reactions convert solar energy to the chemical energy of ATP and NADPH

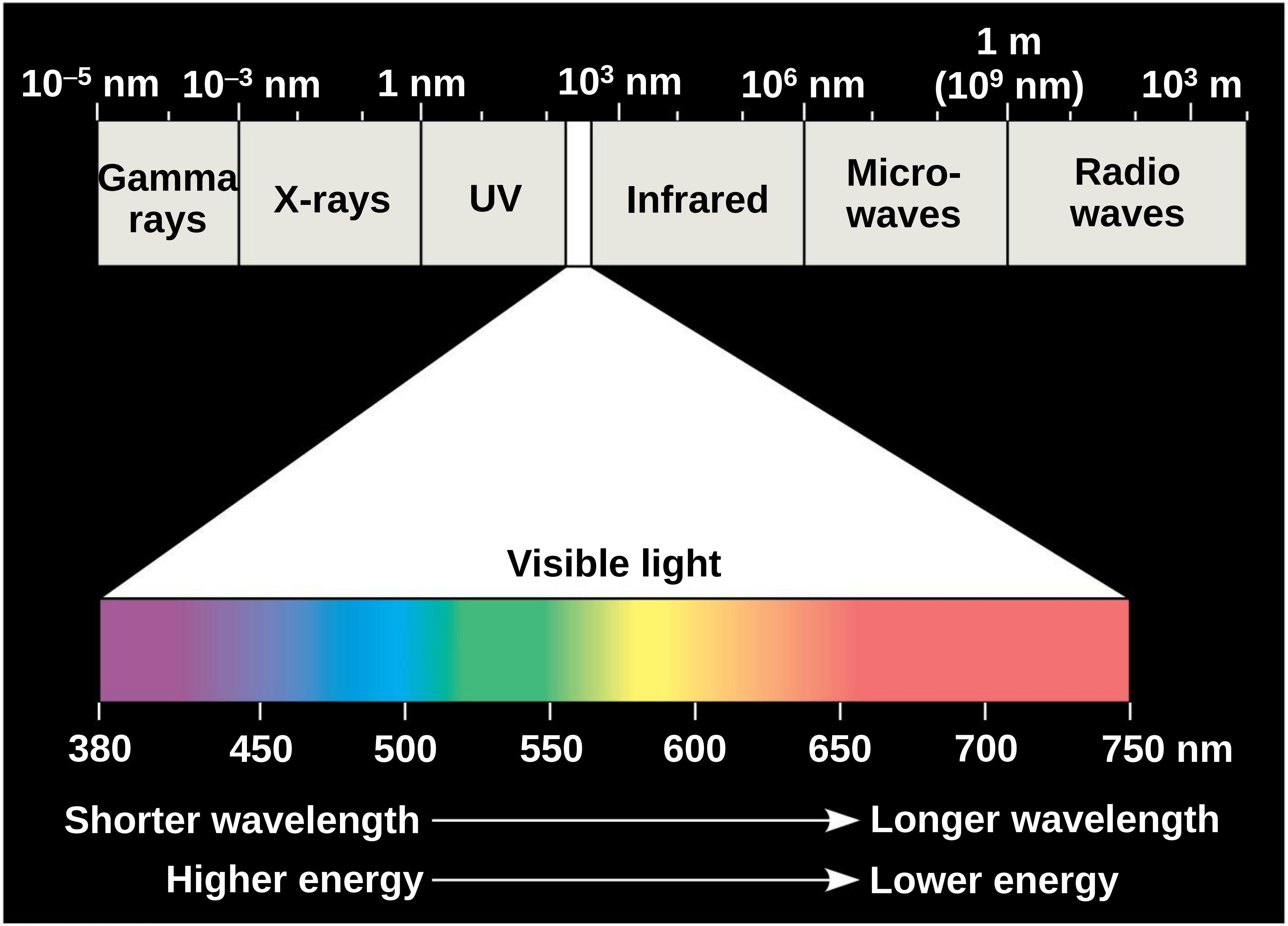
- Chloroplasts are solar-powered chemical factories
- Their thylakoids transform light energy into the chemical energy of ATP and NADPH

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**

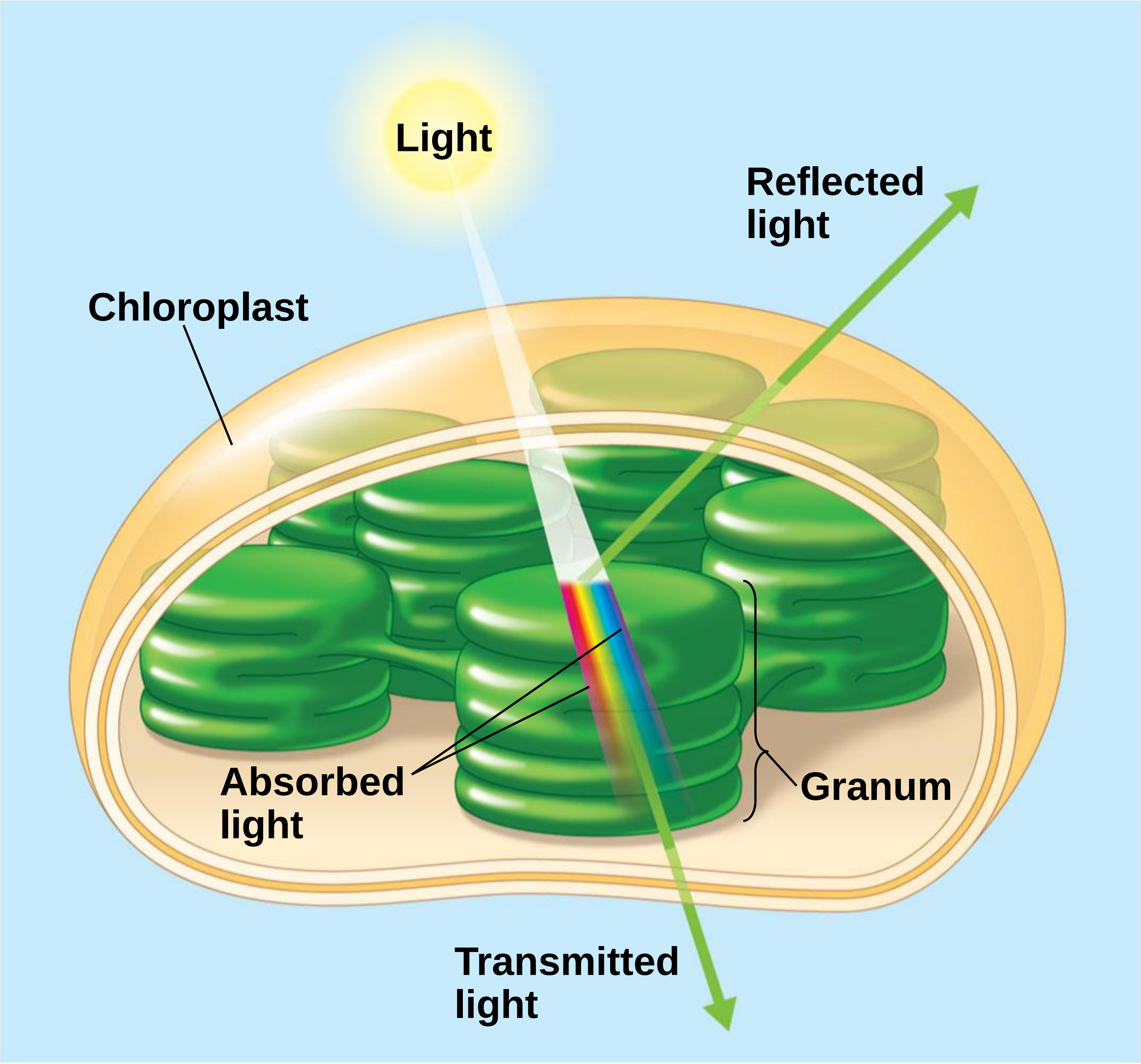
Figure 10.7


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
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

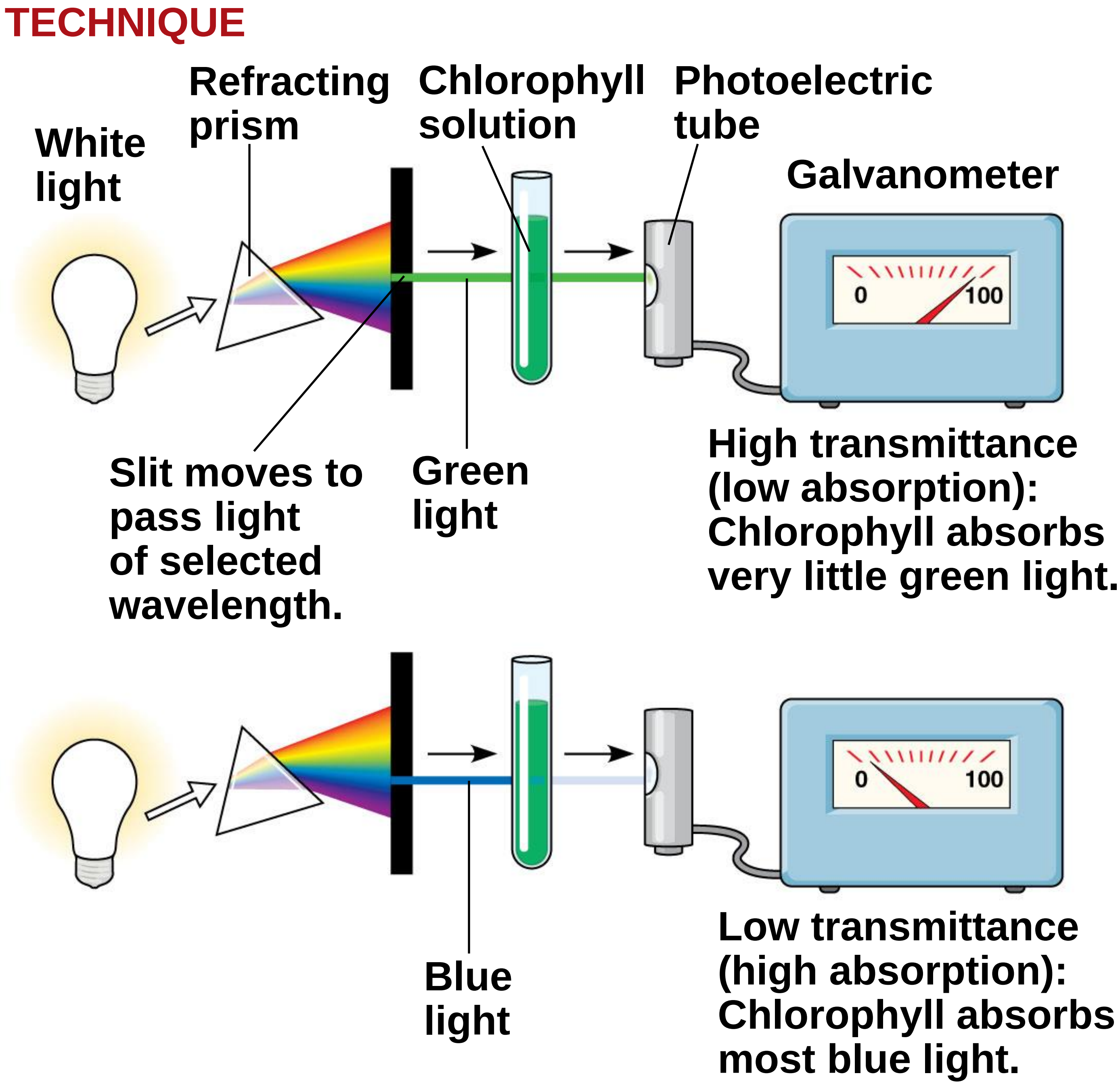
Figure 10.8



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

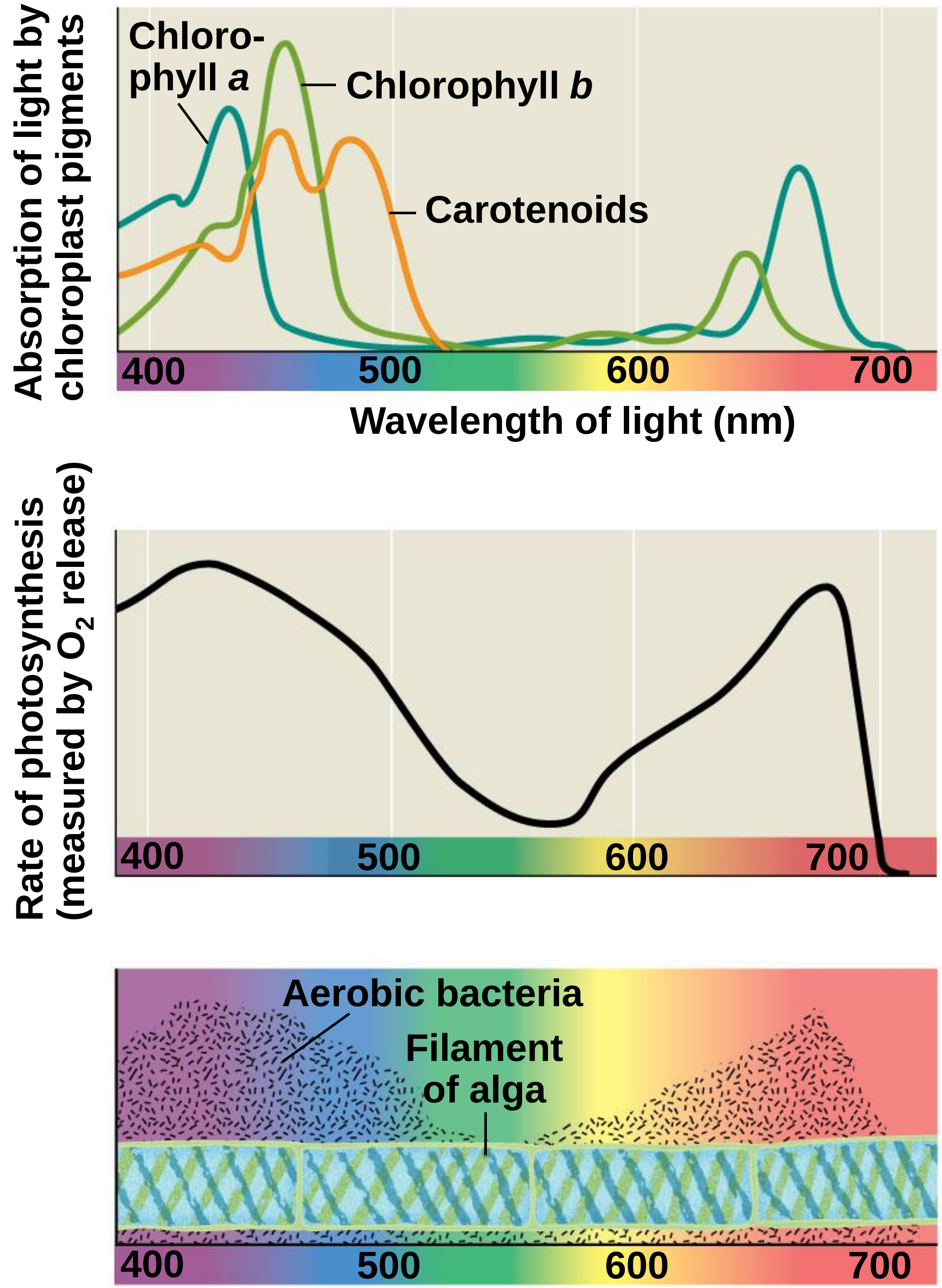
Figure 10.9


TECHNIQUE
White light
Refracting prism
Chlorophyll solution
Photoelectric tube
Galvanometer
0
100
Slit moves to pass light of selected wavelength.
Green light
High transmittance (low absorption): Chlorophyll absorbs very little green light.
0
100
Blue light
Low transmittance (high absorption): Chlorophyll absorbs most blue light.

- An **absorption spectrum** is a graph plotting a pigment's light absorption versus wavelength
- The absorption spectrum of **chlorophyll *a*** suggests that violet-blue and red light work best for photosynthesis
- An **action spectrum** profiles the relative effectiveness of different wavelengths of radiation in driving a process

Figure 10.10

RESULTS



(a) Absorption spectra

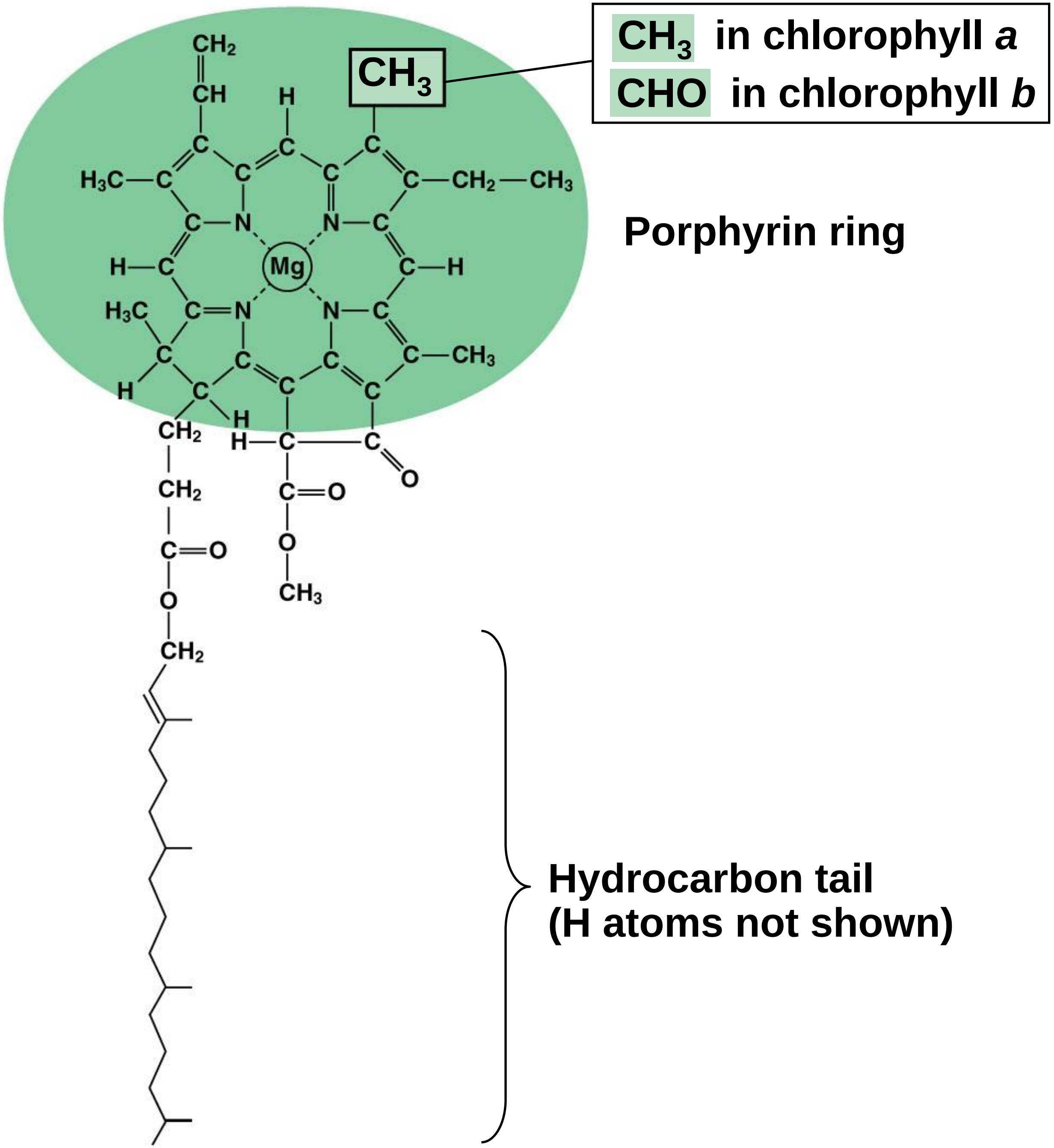
(b) Action spectrum

(c) Engelmann's experiment

- 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

- Chlorophyll *a* is the main photosynthetic pigment
- Accessory pigments, such as **chlorophyll *b***, broaden the spectrum used for photosynthesis
- Accessory pigments called **carotenoids** absorb excessive light that would damage chlorophyll

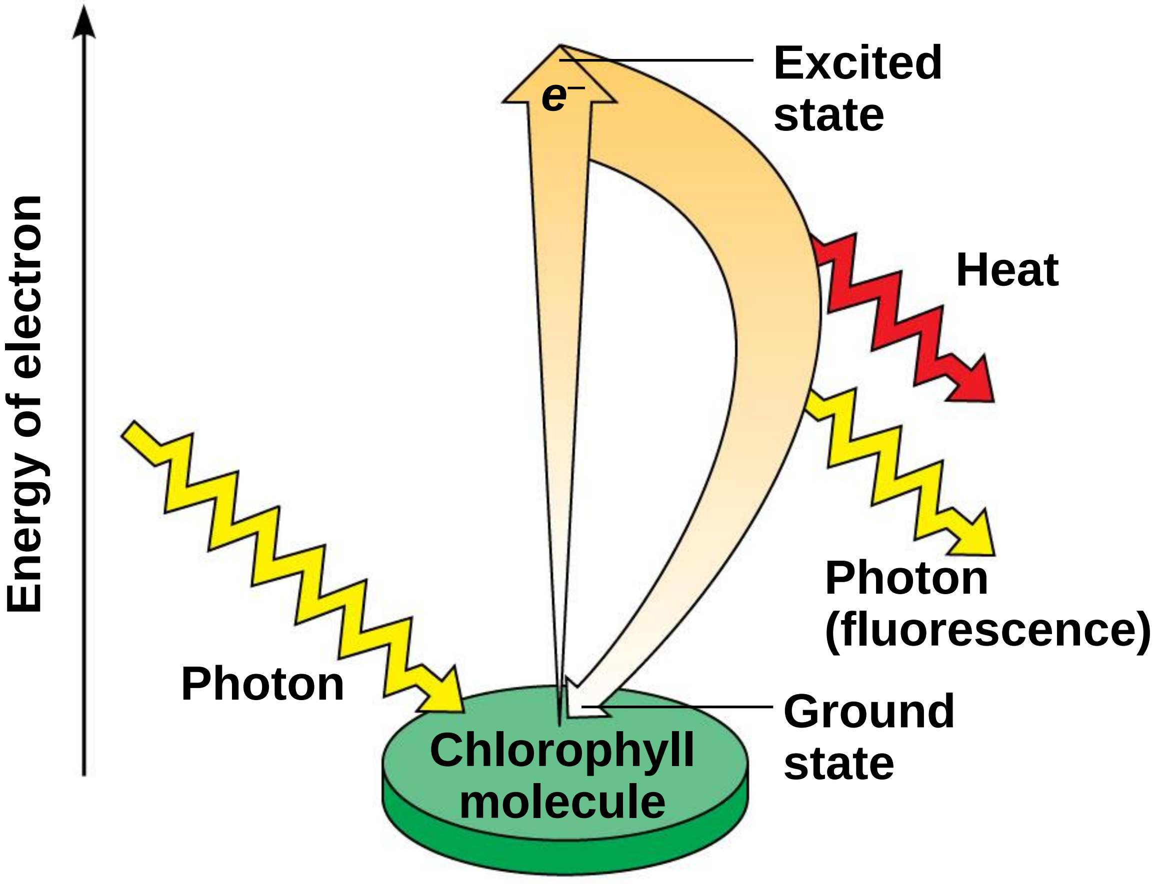
Figure 10.11


CH3 in chlorophyll a
CHO in chlorophyll b
Porphyrin ring
Hydrocarbon tail
(H atoms not shown)
Mg

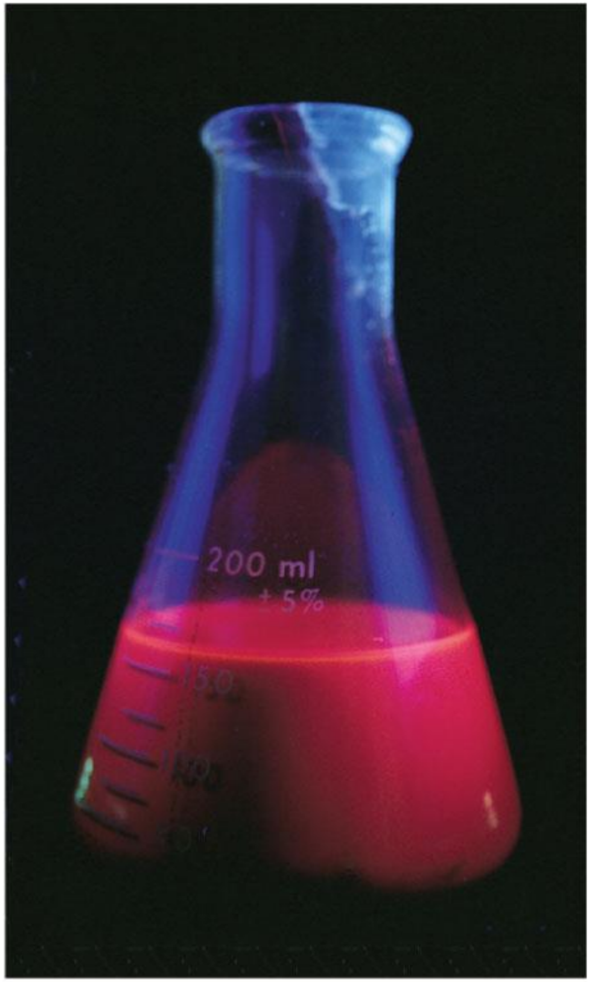
Excitation of Chlorophyll by Light

- 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 10.12



(a) Excitation of isolated chlorophyll molecule

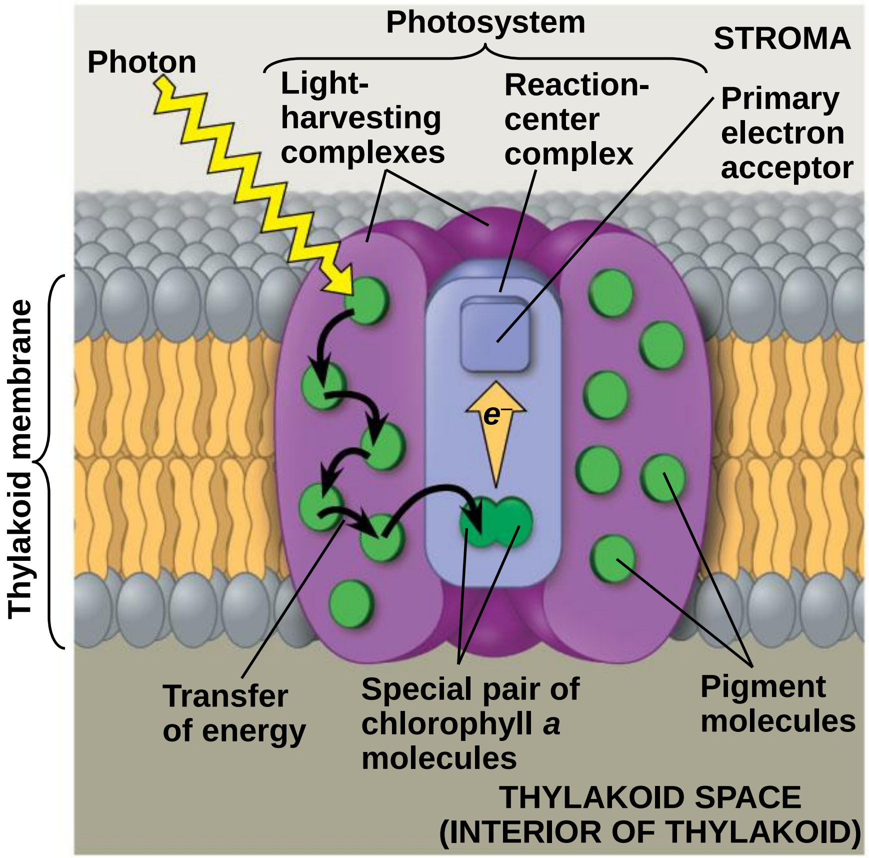


(b) Fluorescence

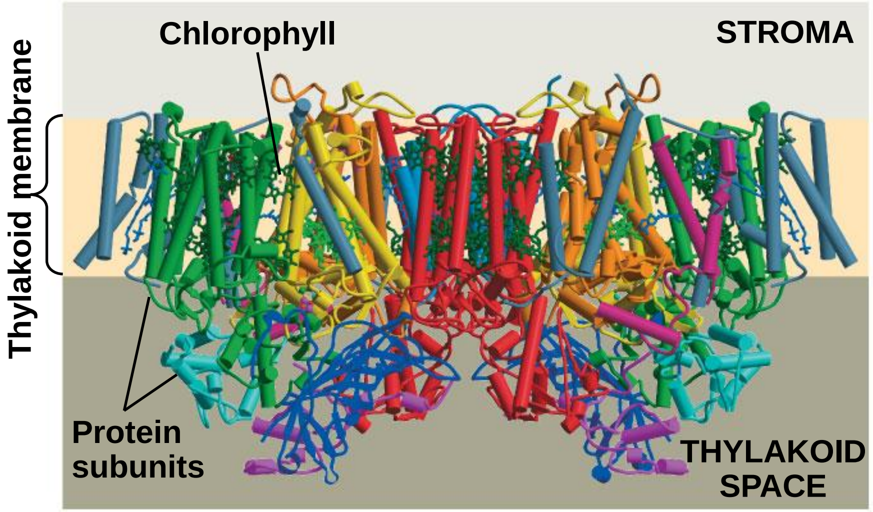
A Photosystem: A Reaction-Center Complex Associated with Light-Harvesting Complexes

- 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

Figure 10.13



(a) How a photosystem harvests light



(b) Structure of photosystem II

- 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

- 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

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

- 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 $P680^+$)

- $P680^+$ is a very strong oxidizing agent
- 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 of this reaction

- 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

- In PS I (like PS II), transferred light energy excites P700, which loses an electron to an electron acceptor
- $P700^+$ (P700 that is missing an electron) accepts an electron passed down from PS II via the electron transport chain

- Each electron “falls” down an electron transport chain from the primary electron acceptor of PS I to the protein ferredoxin (Fd)
- The electrons are then transferred to $NADP^+$ and reduce it to NADPH
- The electrons of NADPH are available for the reactions of the Calvin cycle
- This process also removes an H^+ from the stroma

Figure 10.14-5

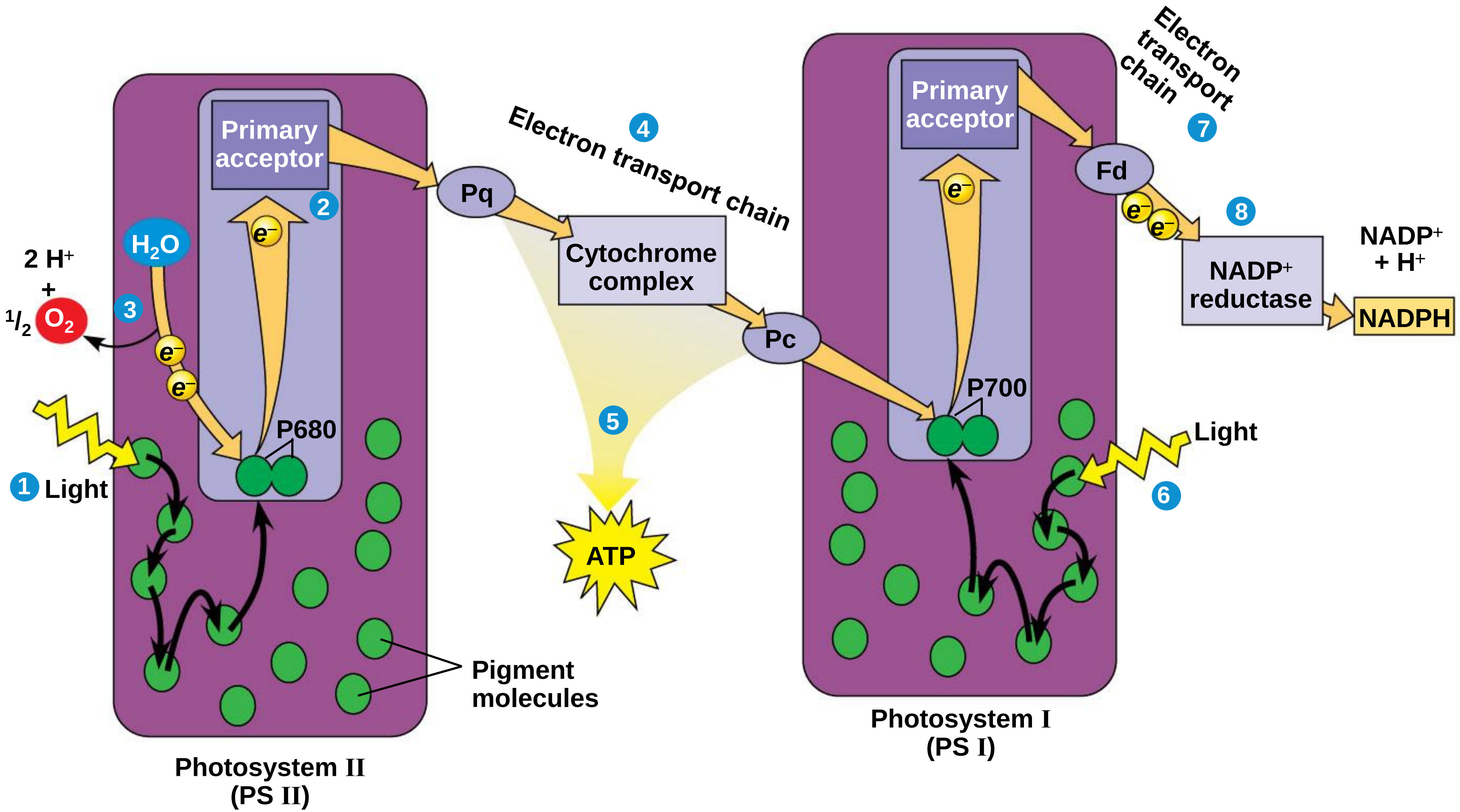
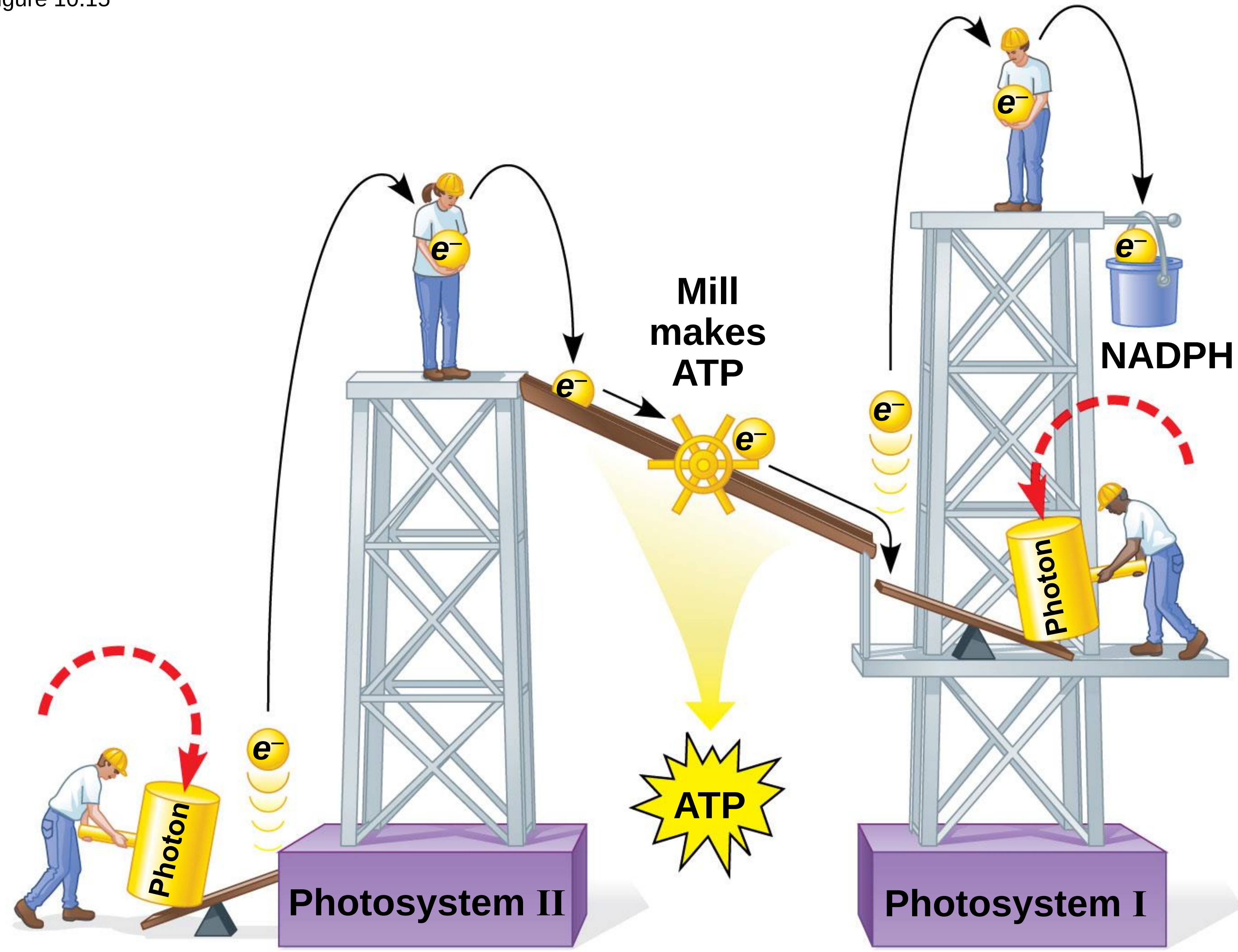


Figure 10.15

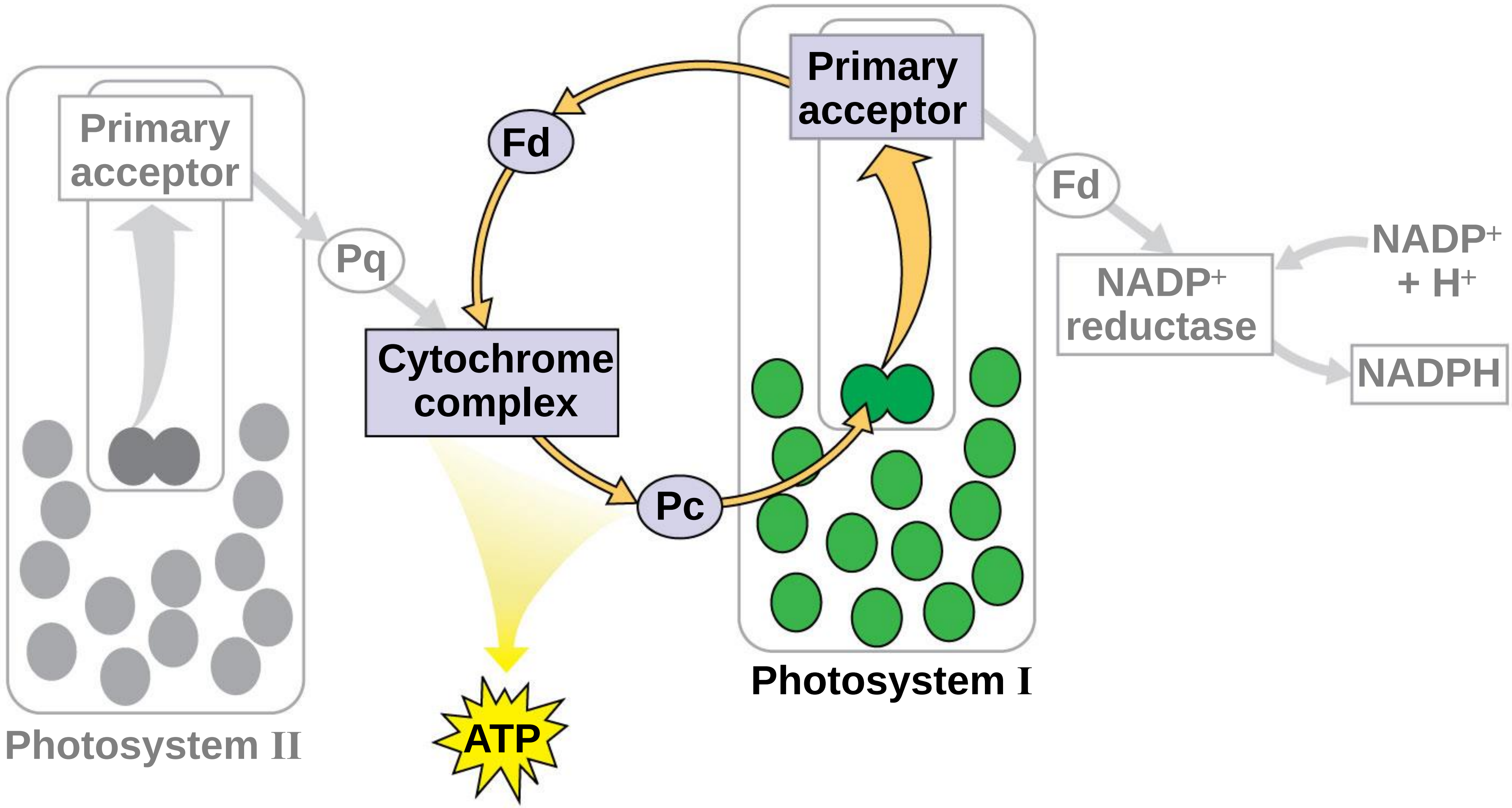


Mill makes ATP
NADPH
e⁻
Photon
ATP
Photosystem II
Photosystem I

Cyclic Electron Flow

- **Cyclic electron flow** uses only photosystem I and produces ATP, but not NADPH
- No oxygen is released
- Cyclic electron flow generates surplus ATP, satisfying the higher demand in the Calvin cycle

Figure 10.16


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

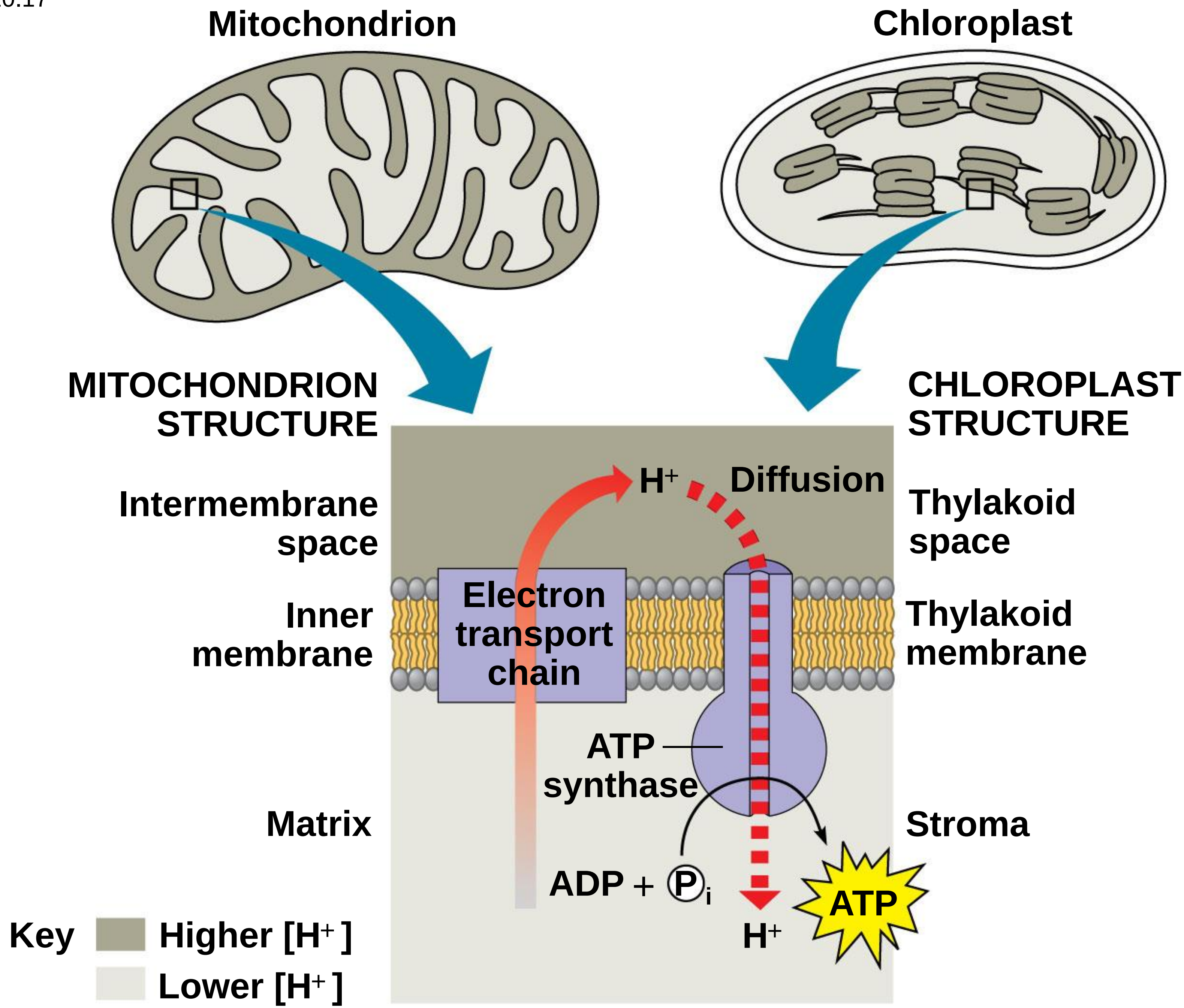
- Some organisms such as purple sulfur bacteria have PS I but not PS II
- Cyclic electron flow is thought to have evolved before linear electron flow
- Cyclic electron flow may protect cells from light-induced damage

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 also shows 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 as they diffuse back into the stroma

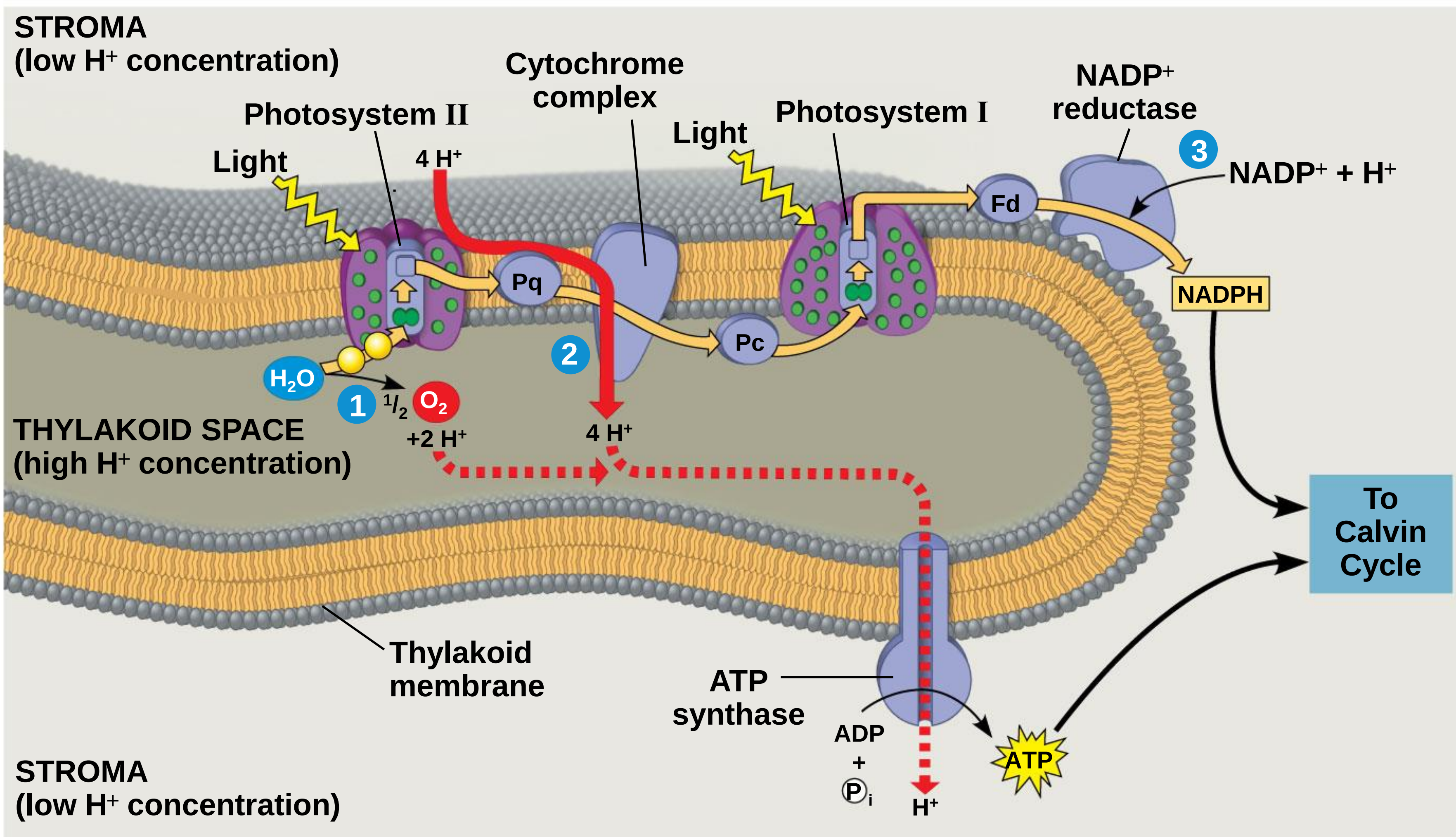
Figure 10.17



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

- ATP and NADPH are produced on the side facing the stroma, where the Calvin cycle takes place
- In summary, light reactions generate ATP and increase the potential energy of electrons by moving them from H_2O to NADPH

Figure 10.18



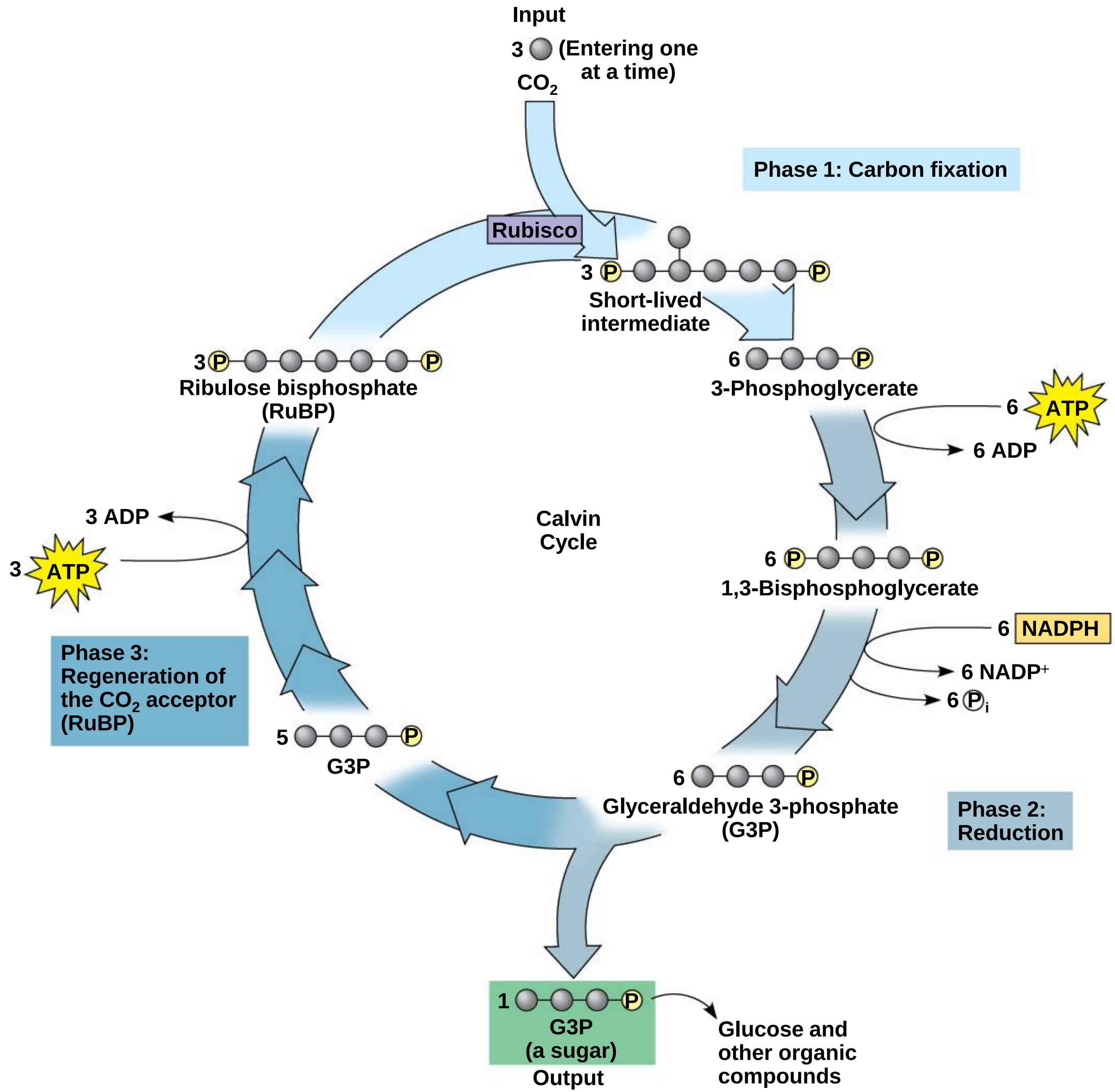
STROMA
(low H+ concentration)
Photosystem II
Light
4 H+
Cytochrome complex
Light
Photosystem I
NADP+ reductase
3
NADP+ + H+
Fd
Pq
Pc
NADPH
2
H2O
1
1/2 O2
+2 H+
4 H+
THYLAKOID SPACE
(high H+ concentration)
To Calvin Cycle
Thylakoid membrane
ATP synthase
ADP
+
Pi
H+
ATP
STROMA
(low H+ concentration)

Concept 10.3: 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
- The cycle 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 1 G3P, the cycle must take place three times, fixing 3 molecules of CO_2
- The Calvin cycle has three phases
  - **Carbon fixation** (catalyzed by **rubisco**)
  - **Reduction**
  - **Regeneration of the CO_2 acceptor (RuBP)**

Figure 10.19-3



Concept 10.4: Alternative mechanisms of carbon fixation have evolved in hot, arid climates

- Dehydration is a problem for 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**

Photorespiration: An Evolutionary Relic?

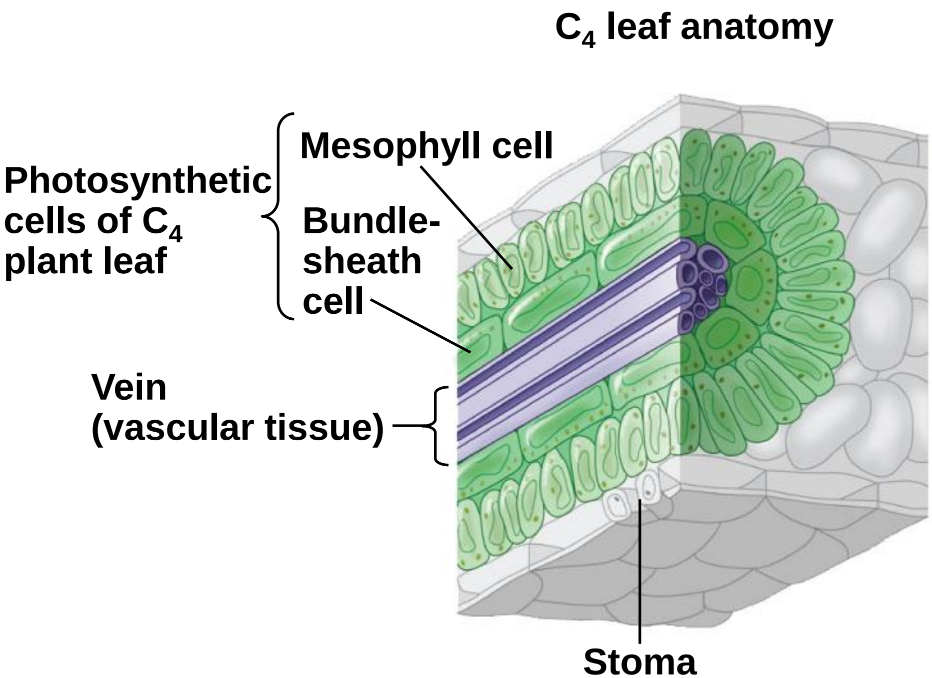
- In most plants (**C_3 plants**), initial fixation of CO_2, via rubisco, forms a three-carbon compound (3-phosphoglycerate)
- In photorespiration, rubisco adds O_2 instead of CO_2 in the Calvin cycle, producing a two-carbon compound
- Photorespiration consumes O_2 and organic fuel and releases CO_2 without producing 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
- In many plants, photorespiration is a problem because on a hot, dry day it can drain as much as 50% of the carbon fixed by the Calvin cycle

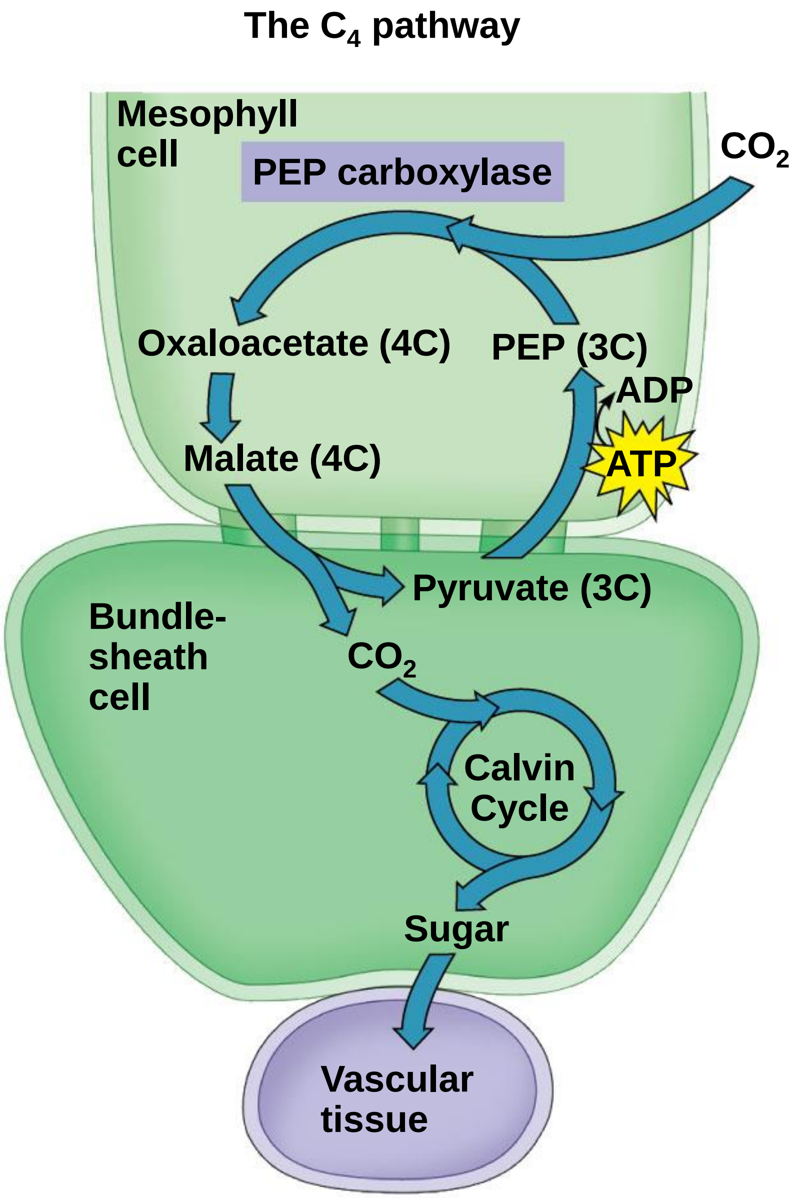
C_4 Plants

- **C_4 plants** minimize the cost of photorespiration by incorporating CO_2 into four-carbon compounds in mesophyll cells
- This step requires the enzyme **PEP carboxylase**
- PEP carboxylase has a higher affinity for CO_2 than rubisco does; it can fix CO_2 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 10.20



C4 leaf anatomy
Photosynthetic cells of C4 plant leaf
Mesophyll cell
Bundle-sheath cell
Vein (vascular tissue)
Stoma



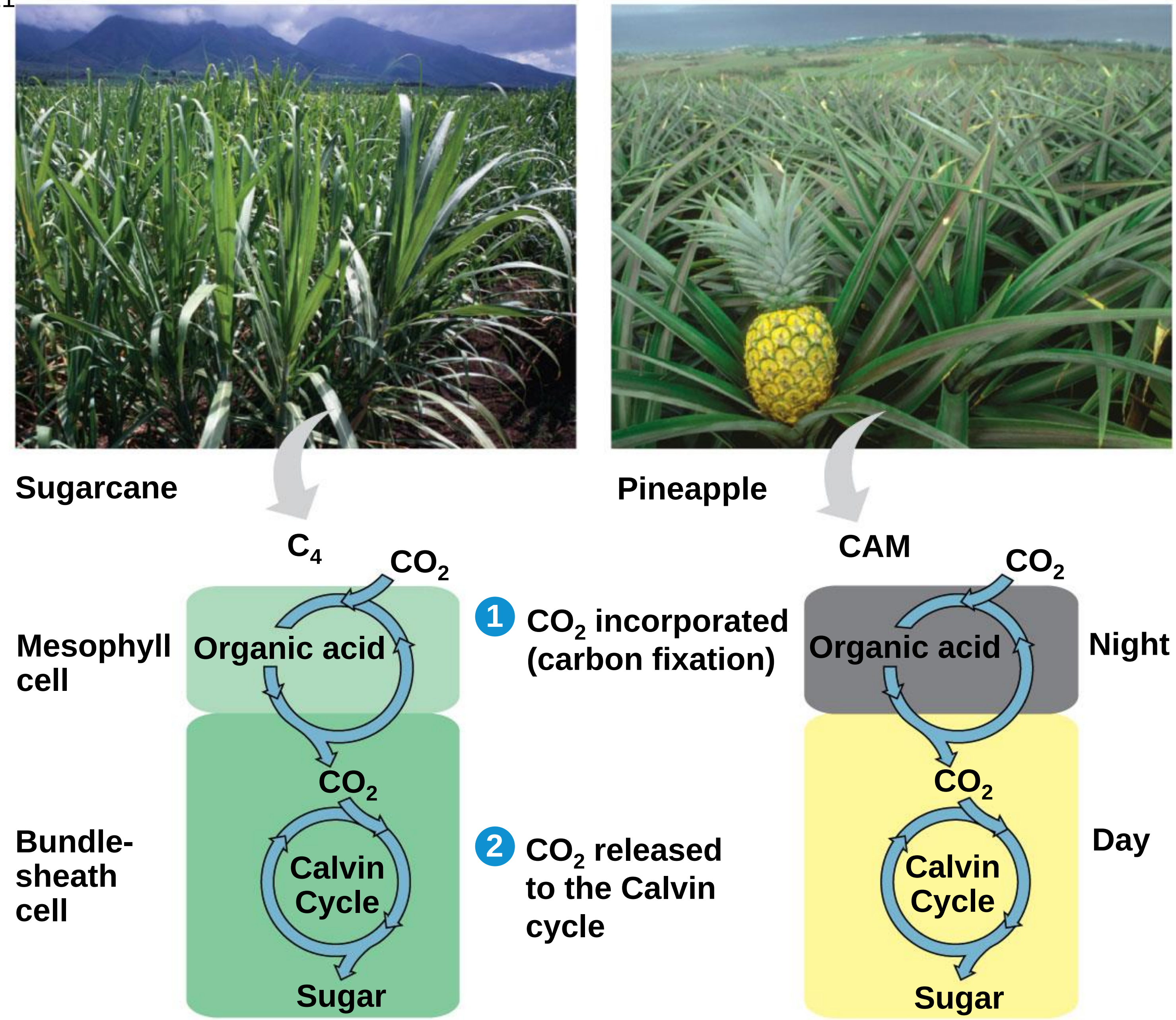
The C4 pathway
Mesophyll cell
PEP carboxylase
CO2
Oxaloacetate (4C)
PEP (3C)
ADP
ATP
Malate (4C)
Pyruvate (3C)
Bundle-sheath cell
CO2
Calvin Cycle
Sugar
Vascular tissue

- In the last 150 years since the Industrial Revolution, CO_2 levels have risen greatly
- Increasing levels of CO_2 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

CAM Plants

- Some plants, including 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 10.21



(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 structures such as roots, tubers, seeds, and fruits
- In addition to food production, photosynthesis produces the O_2 in our atmosphere

Figure 10.22

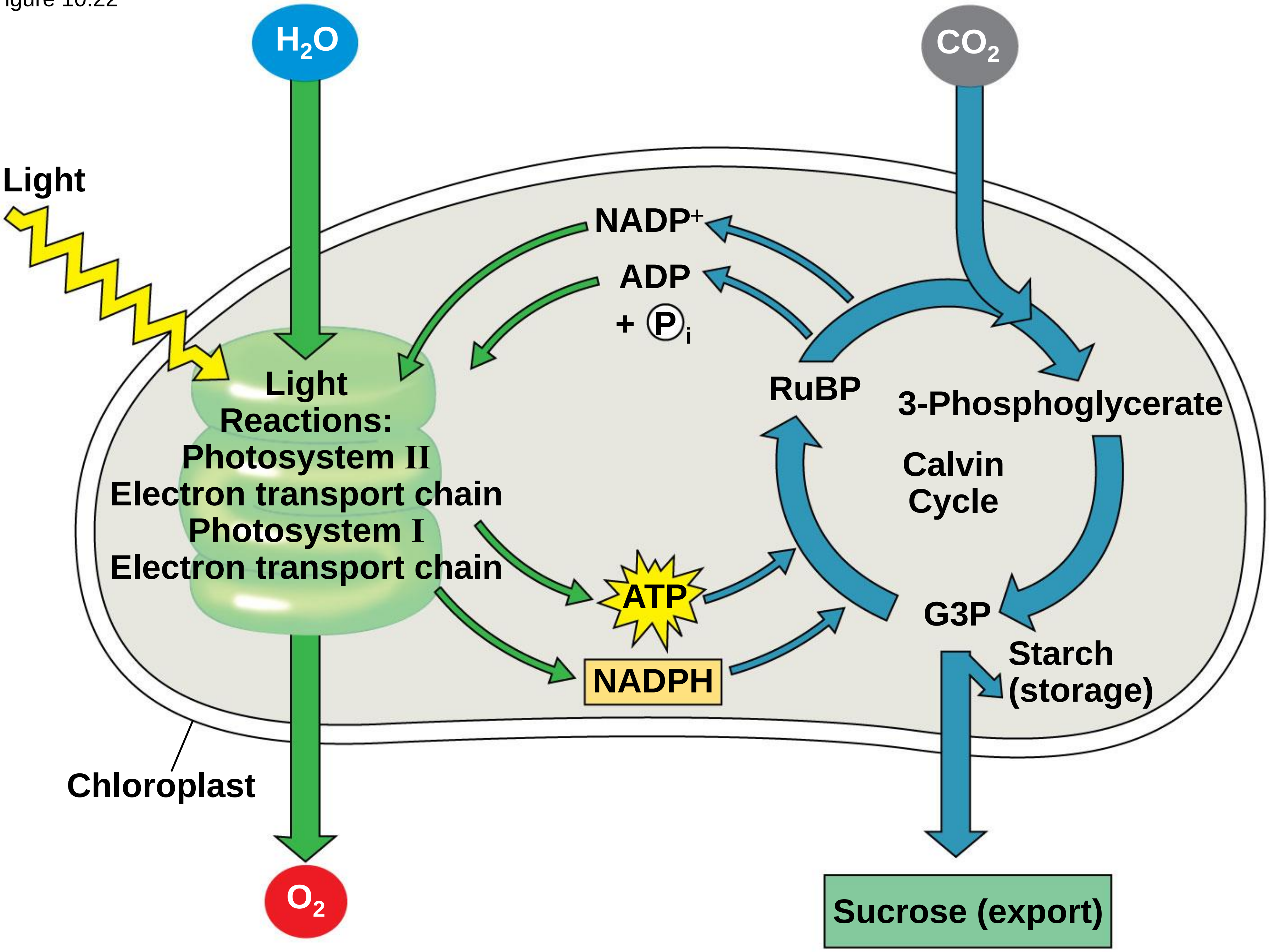

H2O
CO2
Light
NADP+
ADP
+ Pi
Light
Reactions:
Photosystem II
Electron transport chain
Photosystem I
Electron transport chain
RuBP
3-Phosphoglycerate
Calvin
Cycle
ATP
NADPH
G3P
Starch
(storage)
Chloroplast
O2
Sucrose (export)

Figure 10.UN02

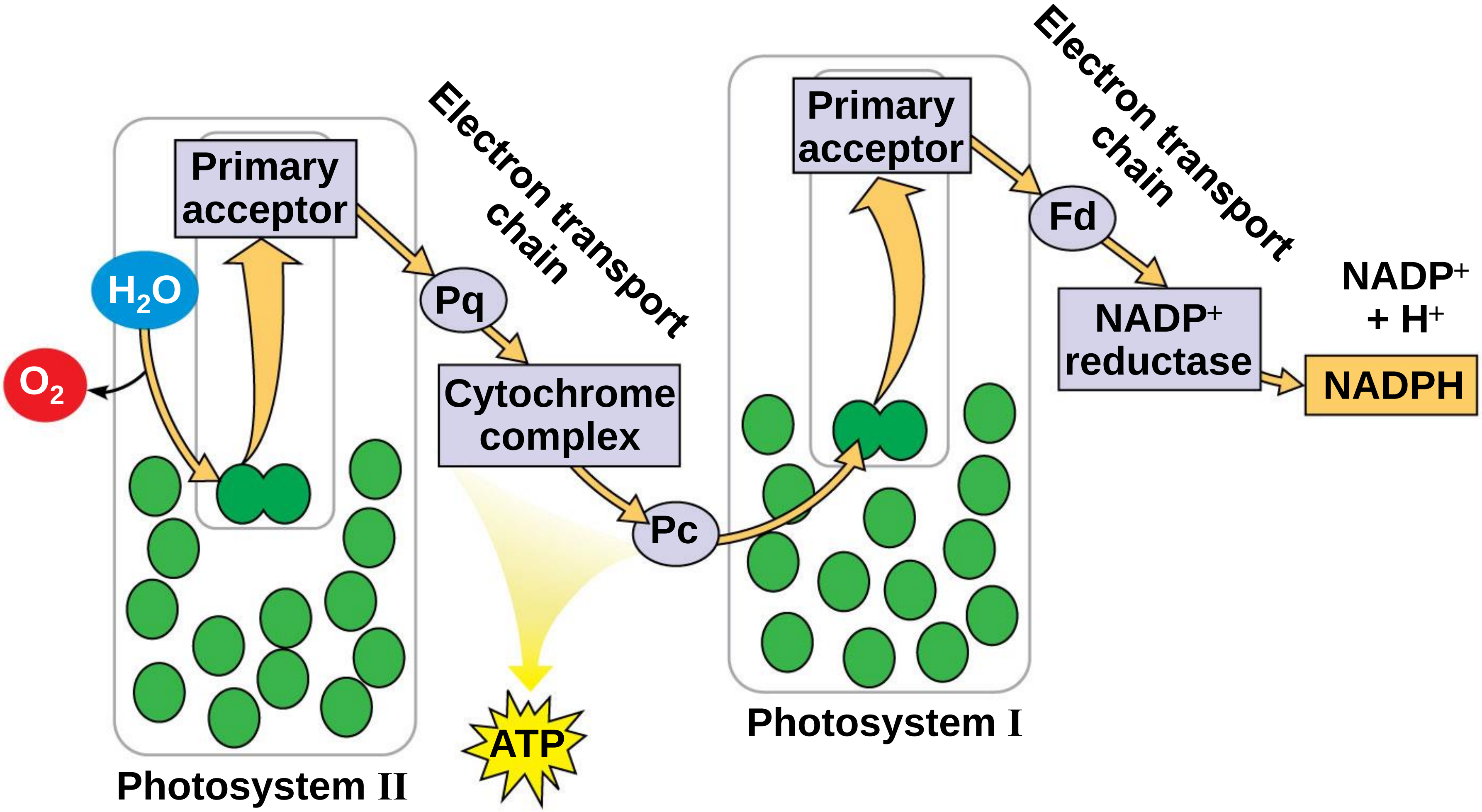


Figure 10.UN03

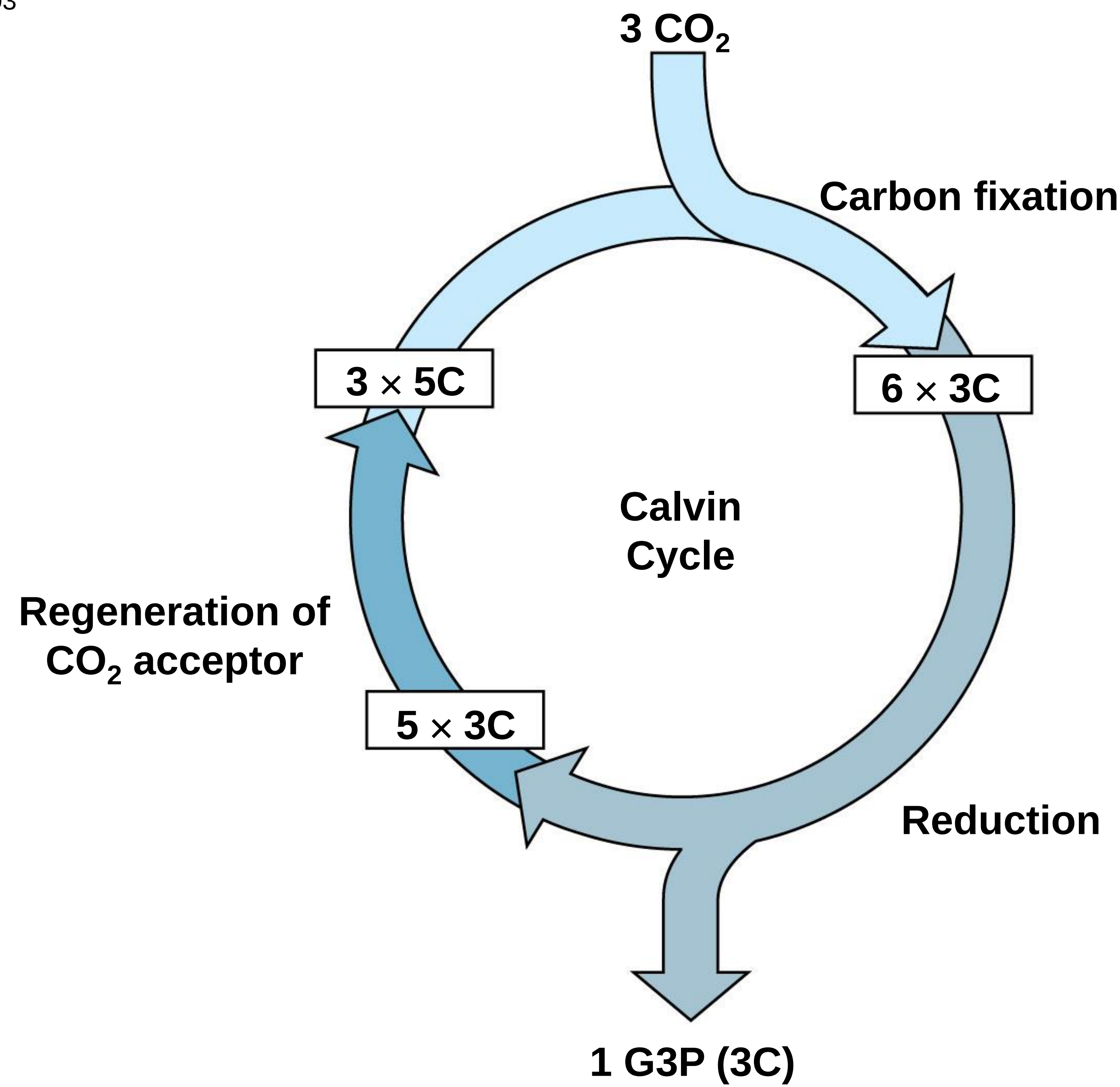


Figure 10.UN04

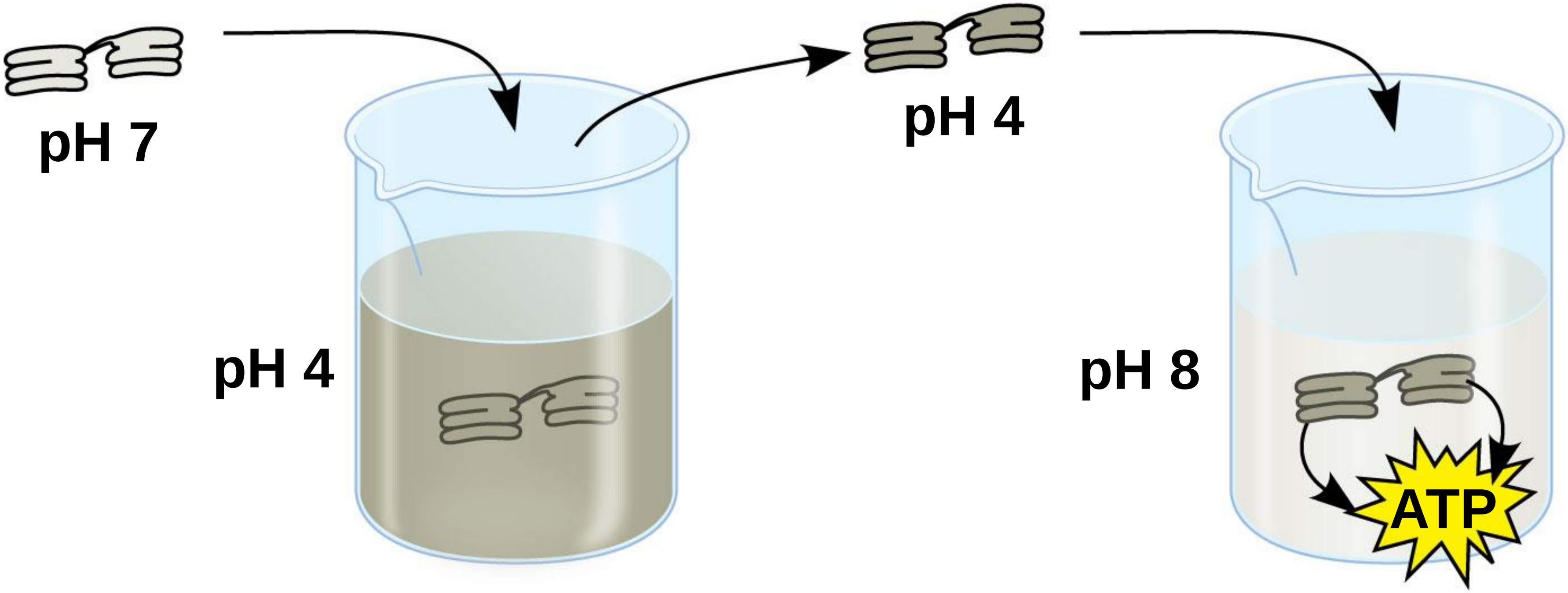


Figure 10.UN07

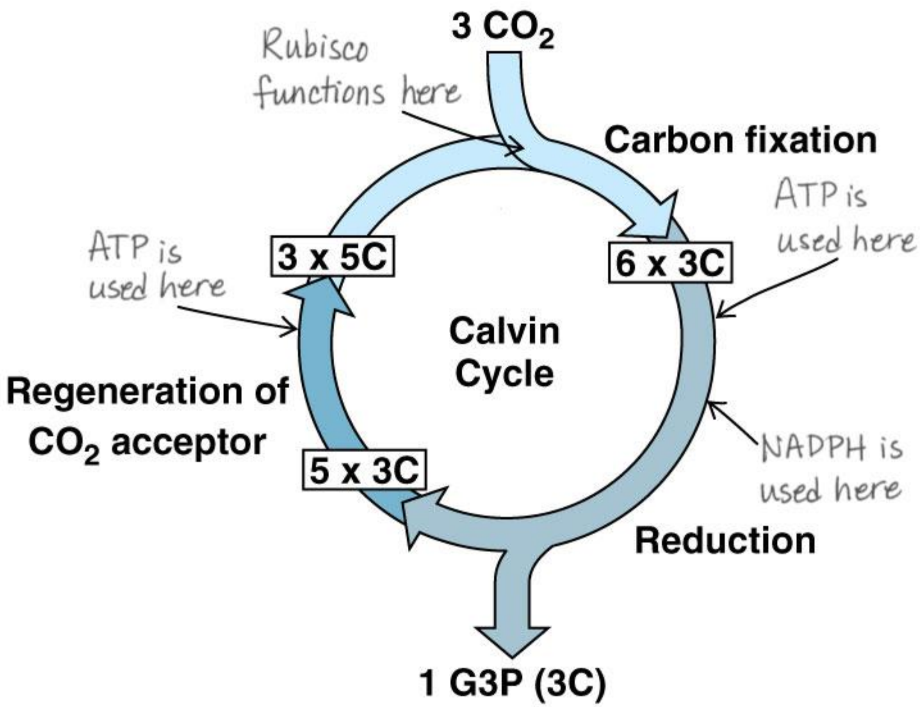


Figure 10.UN08