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 *photo*autotrophs, using the energy of sunlight to make organic molecules from H_2O and CO_2

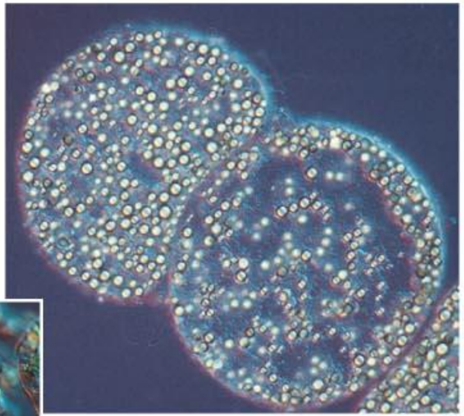
Fig. 10-2

(a) Plants

(b) Multicellular alga

(c) Unicellular protist 10 µm

(d) Cyanobacteria 40 µm



(e) Purple sulfur bacteria 1.5 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

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

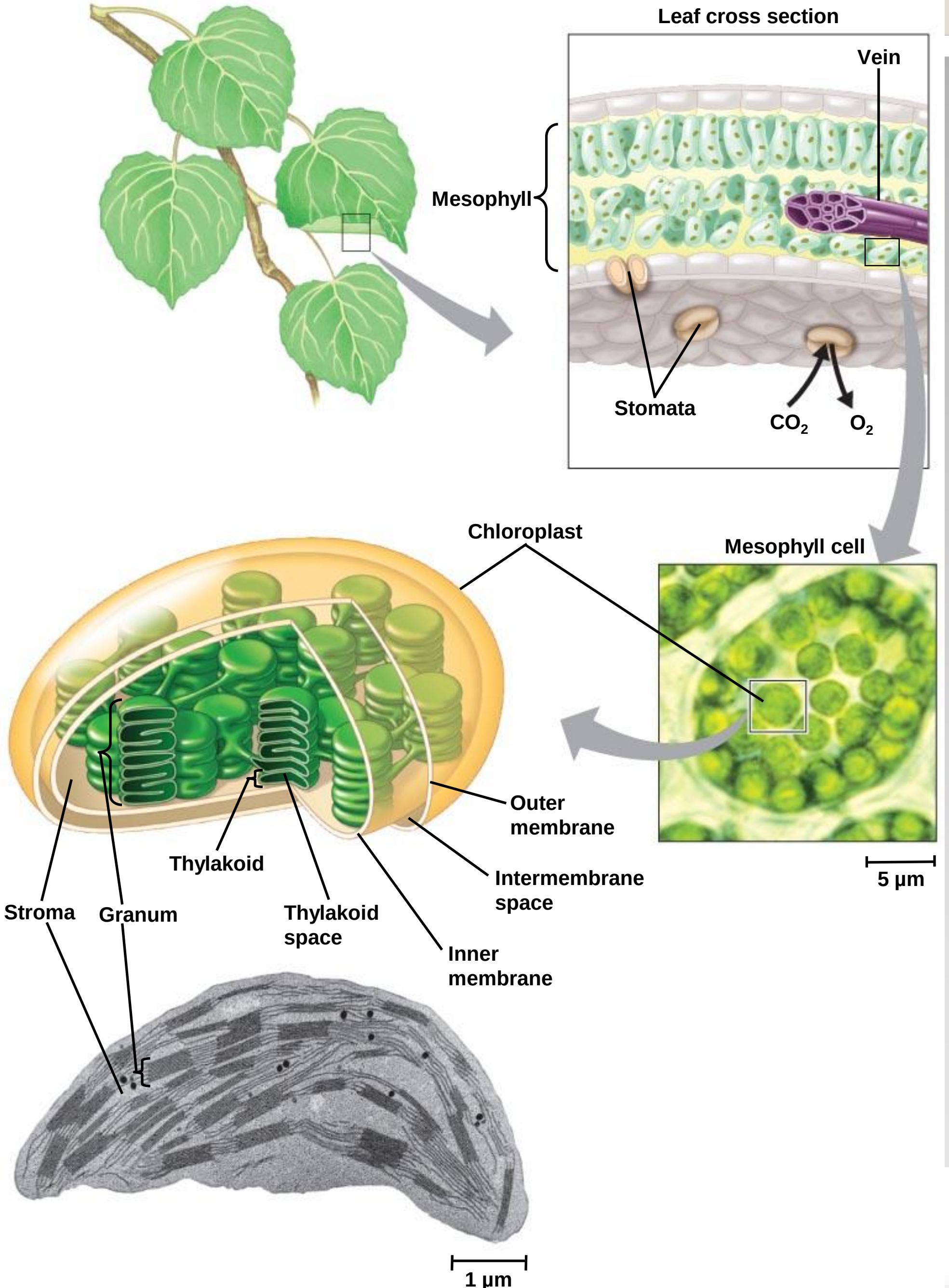
- Chloroplasts are structurally similar to and likely evolved from photosynthetic bacteria
- The structural organization of these cells allows for the chemical reactions of photosynthesis

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
- Light energy absorbed by chlorophyll drives the synthesis of organic molecules in the chloroplast
- CO_2 enters and O_2 exits the leaf through microscopic pores called **stomata**

- Chloroplasts are found mainly in cells of the **mesophyll**, the interior tissue of the leaf
- A typical mesophyll cell has 30–40 chloroplasts
- 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 fluid

Fig. 10-3



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

Photosynthesis 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

Photosynthesis as a Redox Process

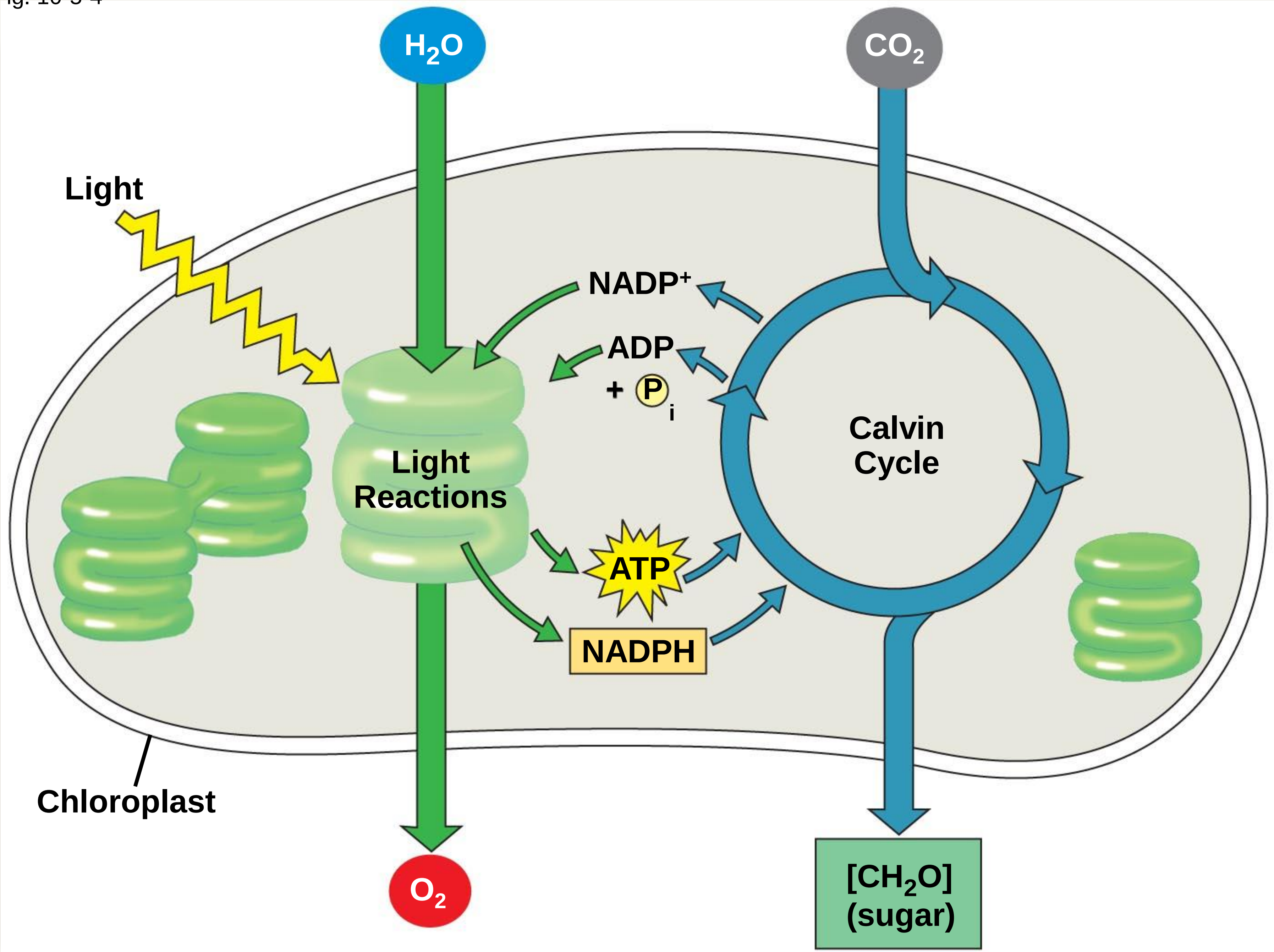
- Photosynthesis is a redox process in which H_2O is oxidized and CO_2 is reduced

The Two Stages of Photosynthesis

- 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

Fig. 10-5-4


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

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

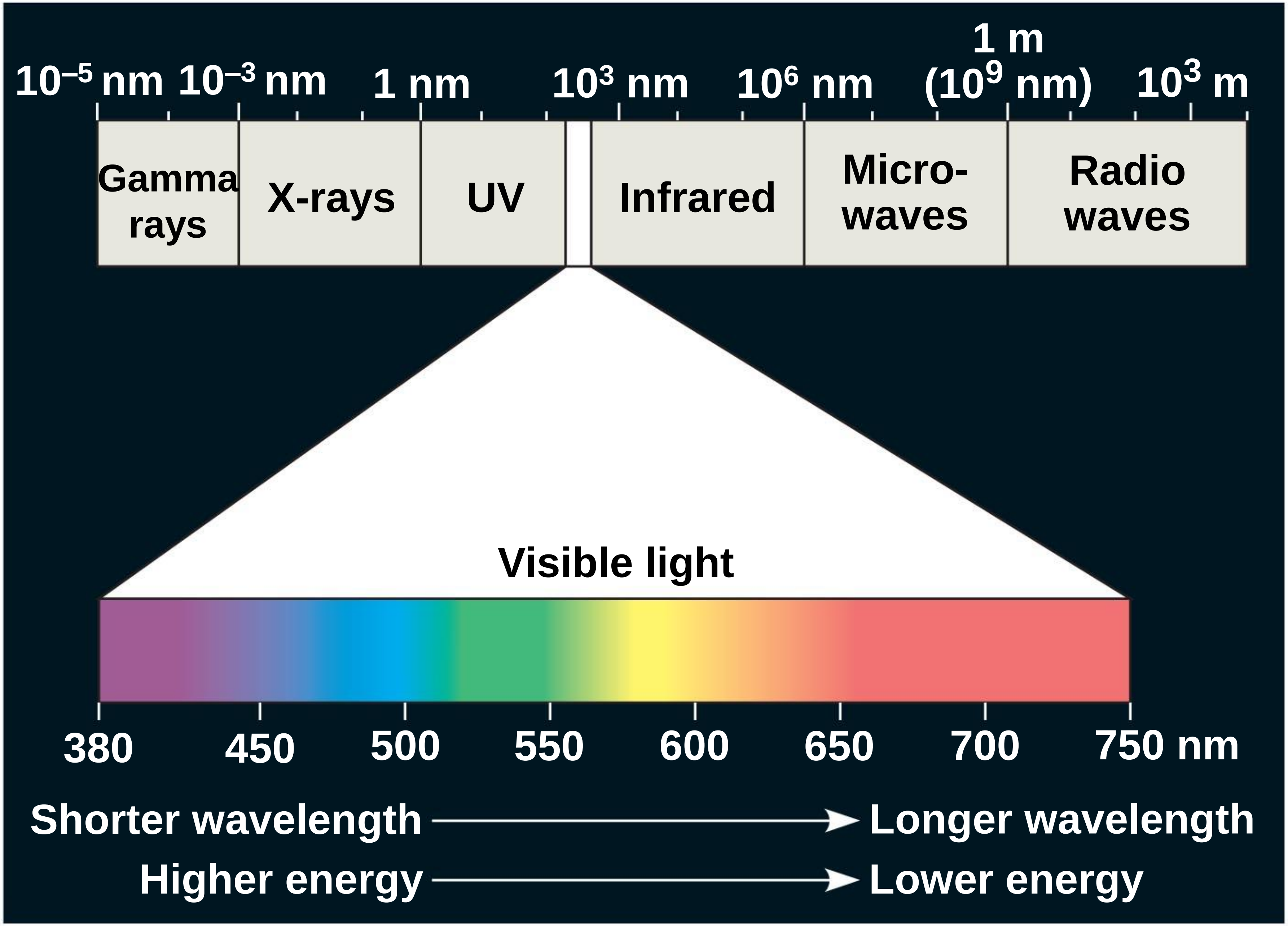
- Chloroplasts are solar-powered chemical factories
- Their thylakoids transform light energy into the chemical energy of ATP and NADPH

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**

Fig. 10-6



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

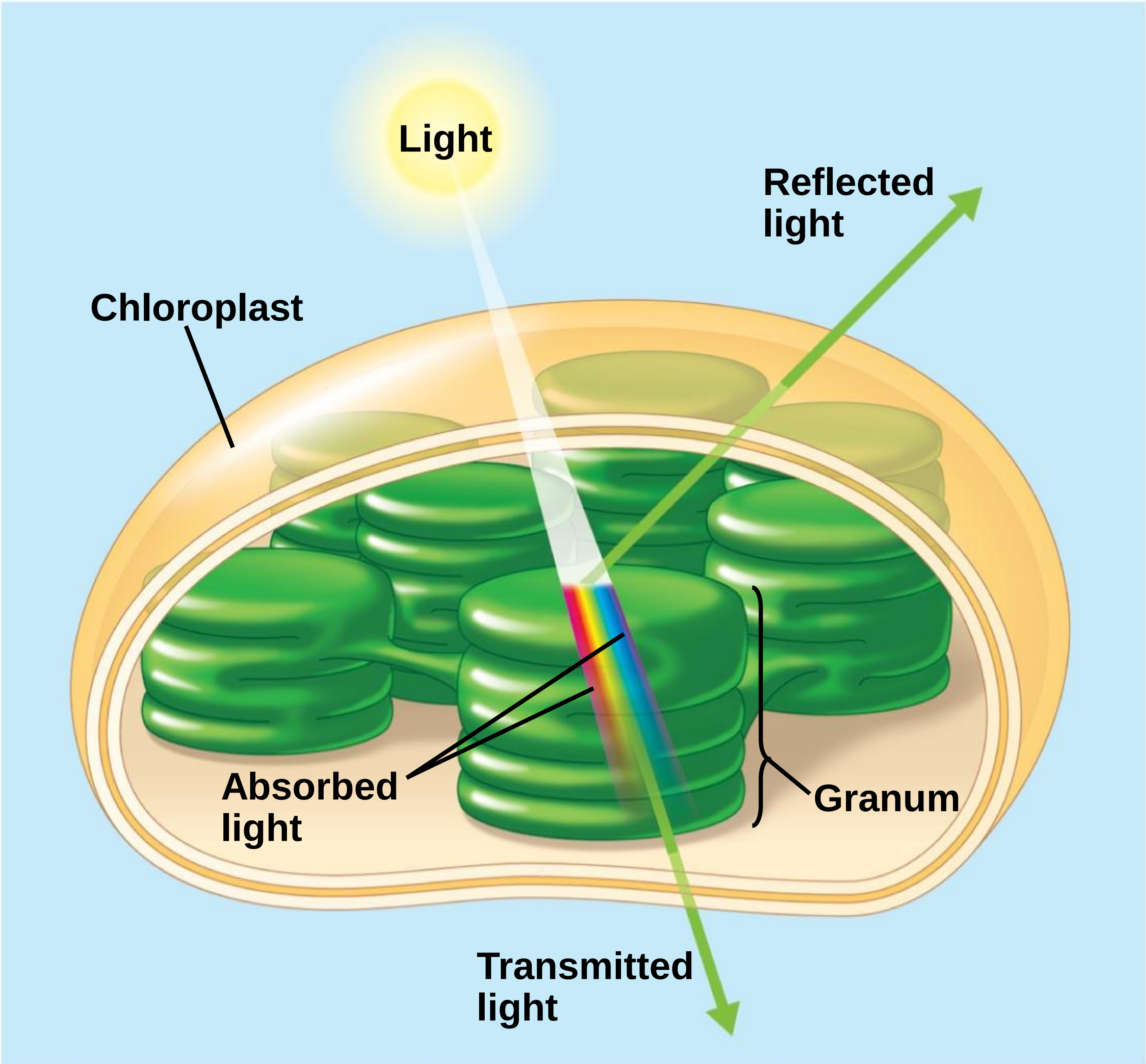
Photosynthetic Pigments: The Light Receptors

- 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

PLAY

Animation: Light and Pigments

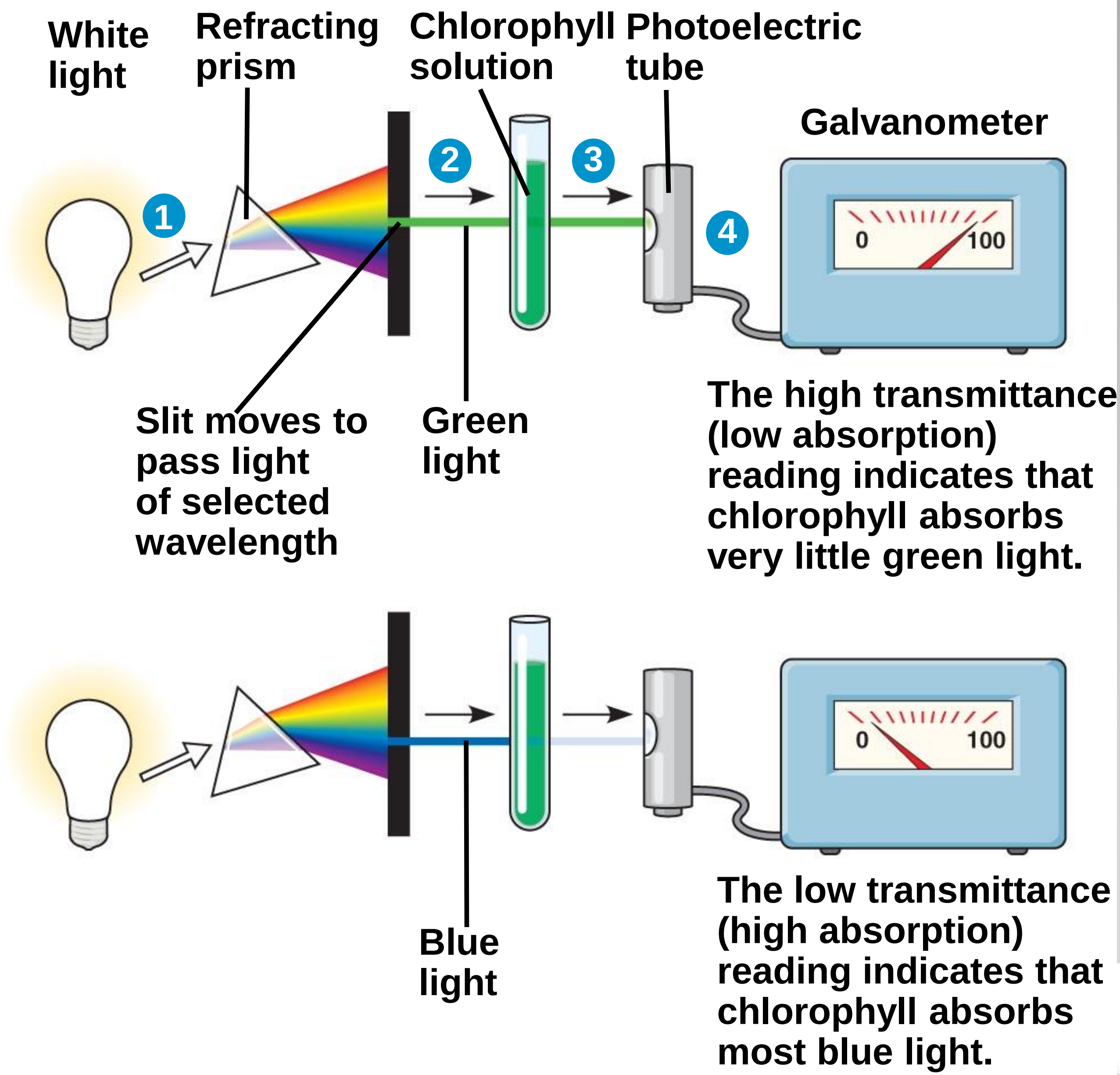
Fig. 10-7


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

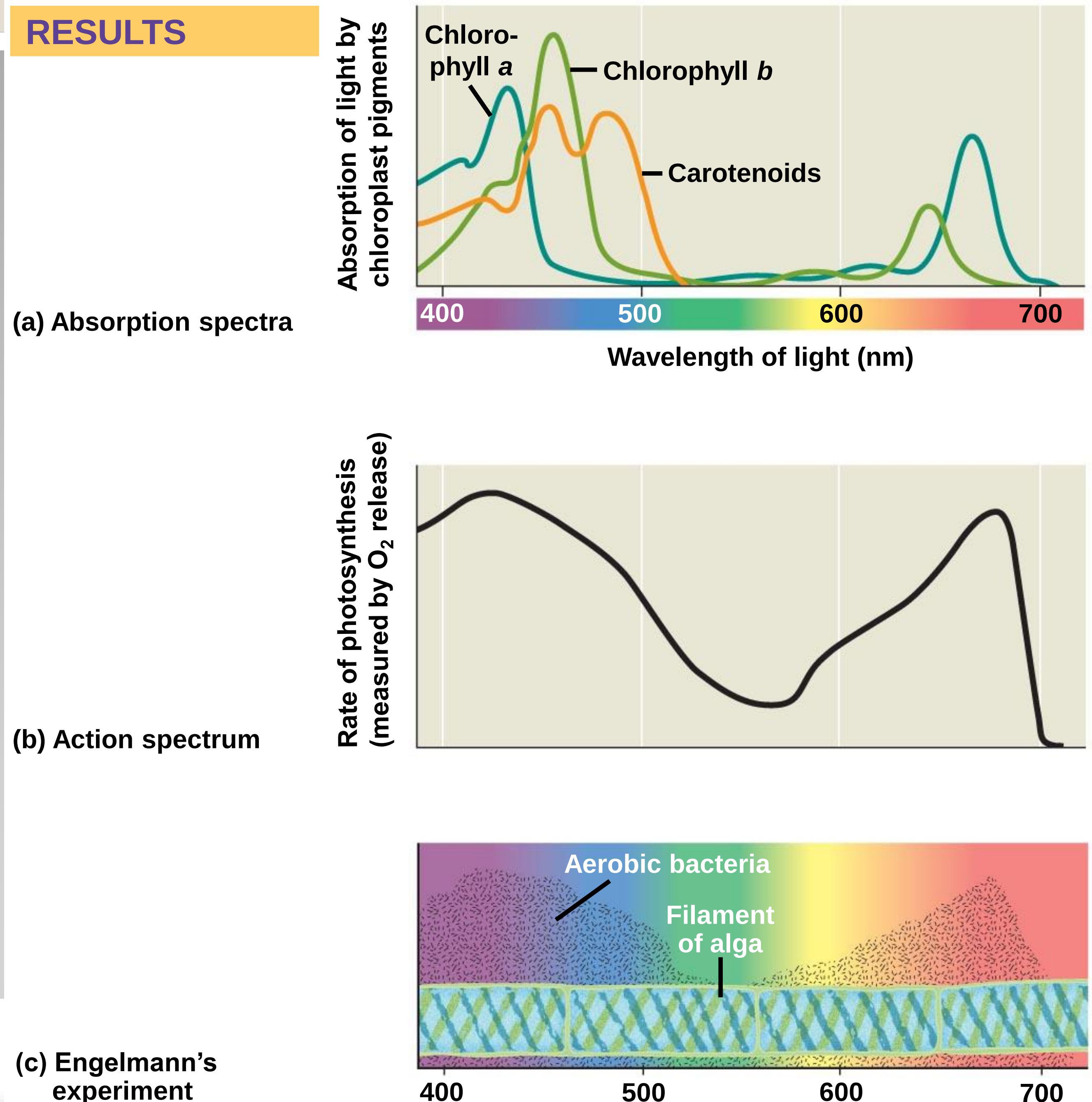
Fig. 10-8

TECHNIQUE



- 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

Fig. 10-9



(a) Absorption spectra

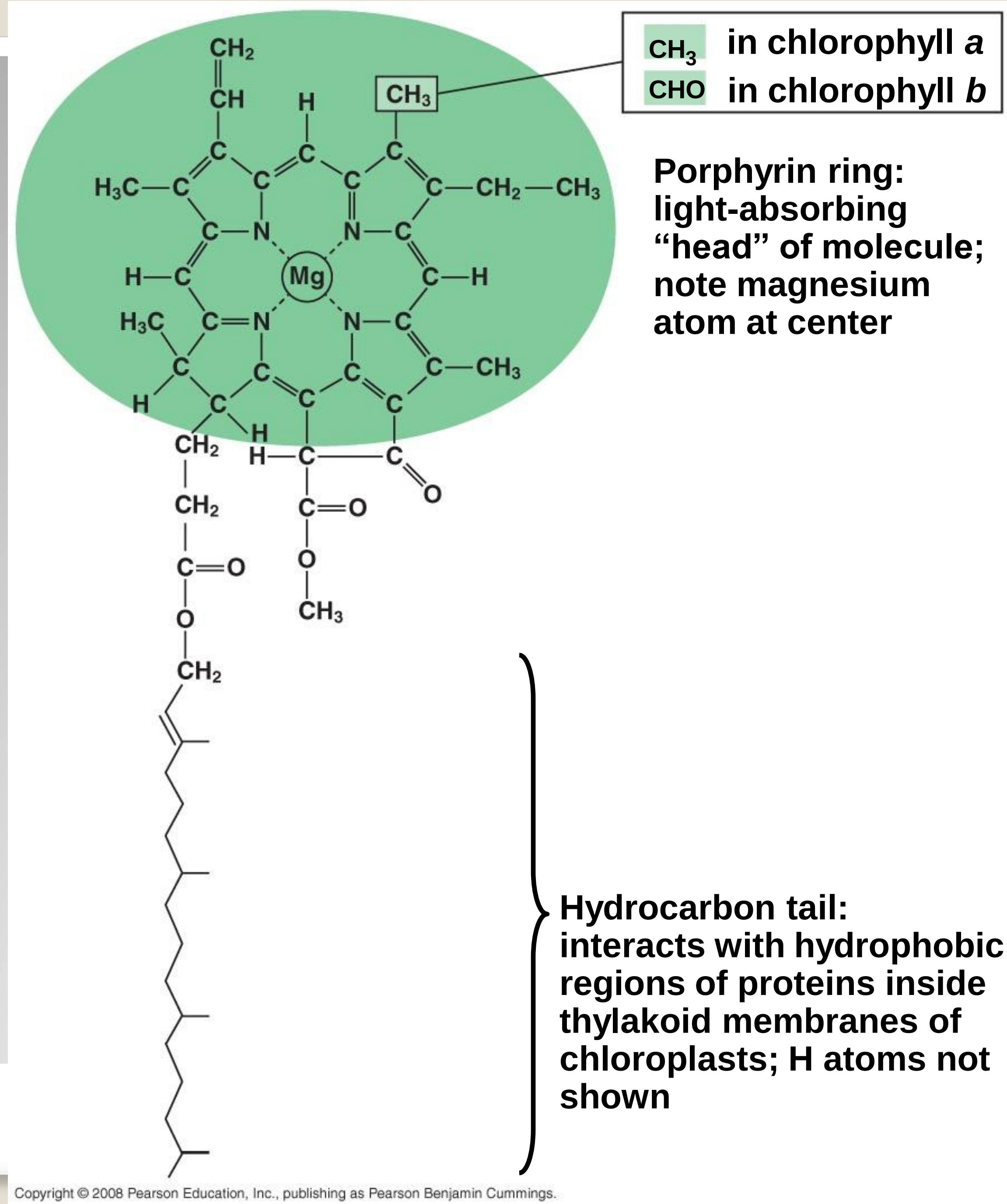
(b) Action spectrum

(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

Fig. 10-10


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
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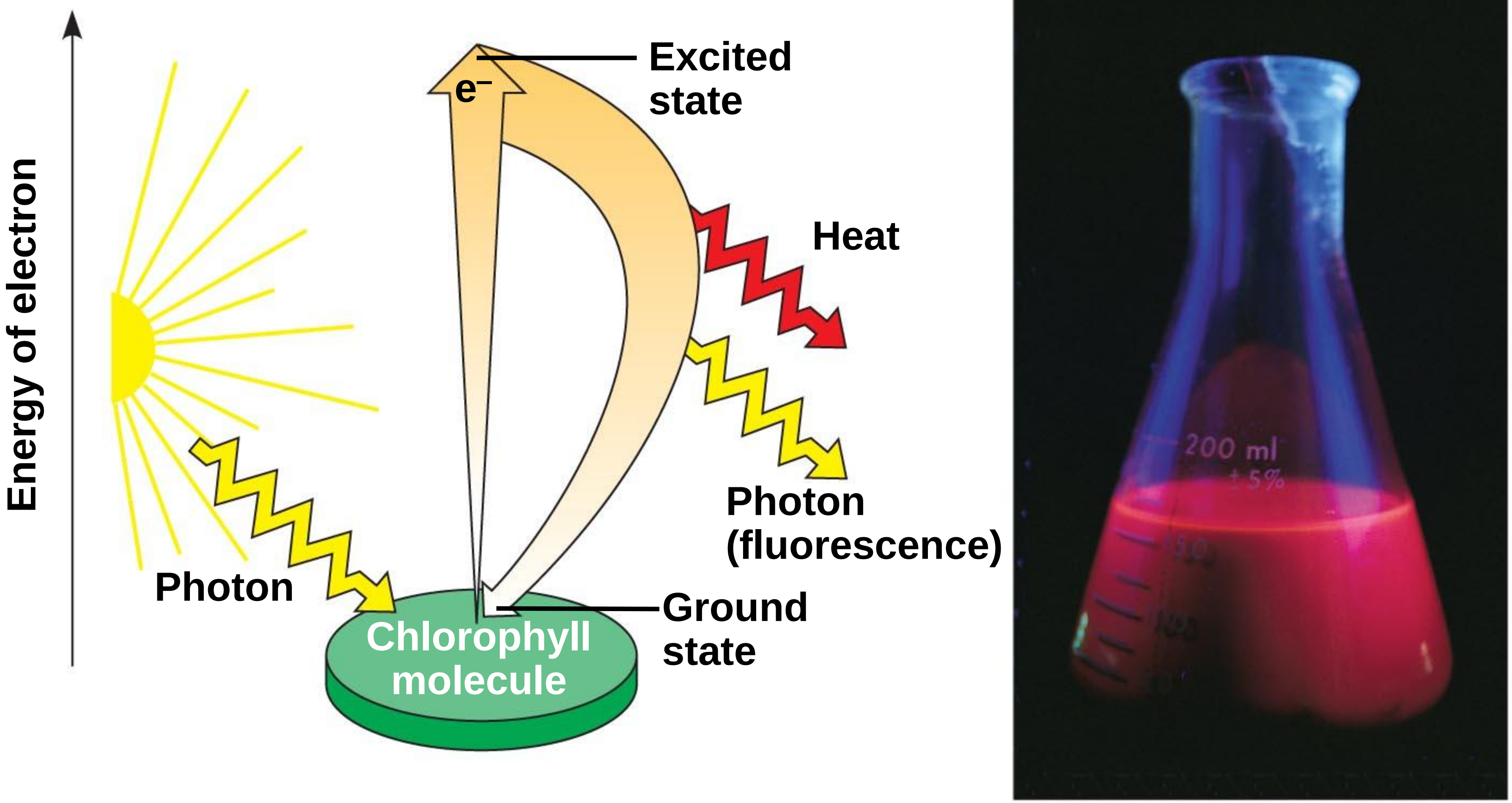
Excitation of Chlorophyll by Light

- 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

Fig. 10-11



(a) Excitation of isolated chlorophyll molecule

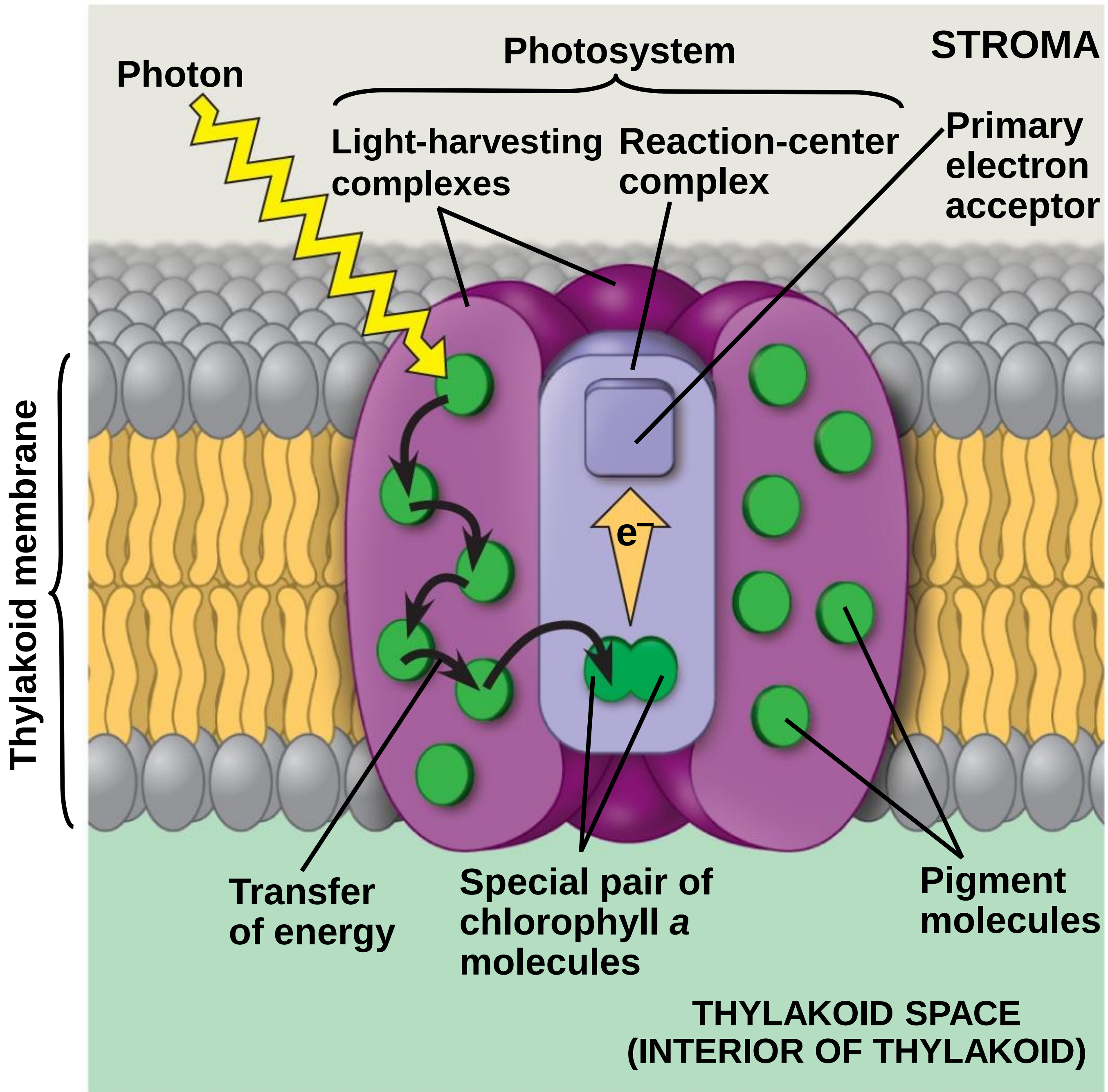
(b) Fluorescence

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

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

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

Fig. 10-12


Photon
Photosystem
STROMA
Light-harvesting complexes
Reaction-center complex
Primary electron acceptor
e⁻
Thylakoid membrane
Transfer of energy
Special pair of chlorophyll *a* molecules
Pigment molecules
THYLAKOID SPACE (INTERIOR OF THYLAKOID)

- 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

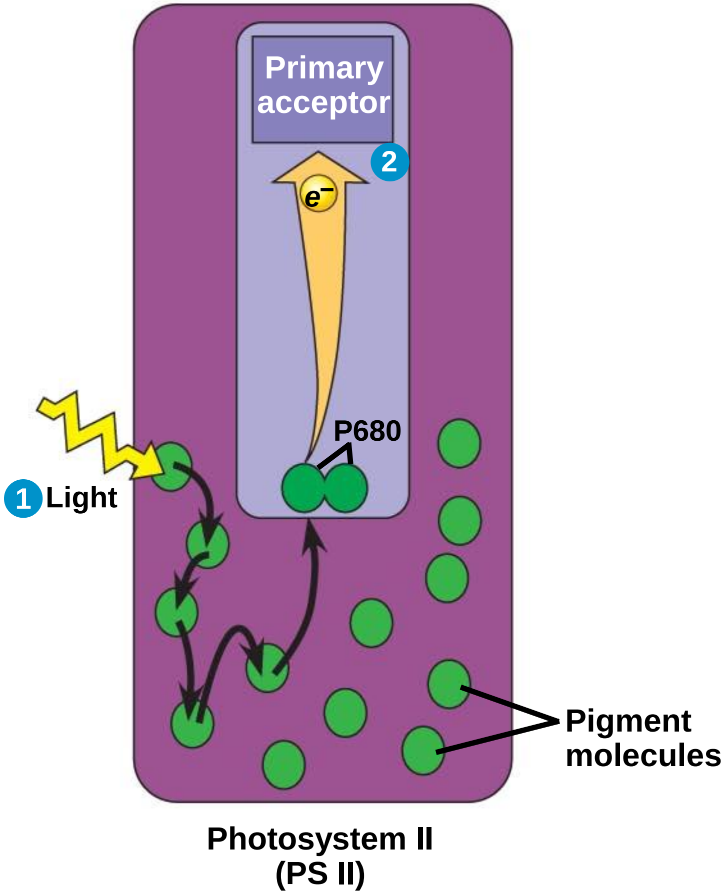
- **Photosystem I (PS I)** is best at absorbing a wavelength of 700 nm
- The reaction-center chlorophyll *a* of PS I is called P700

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

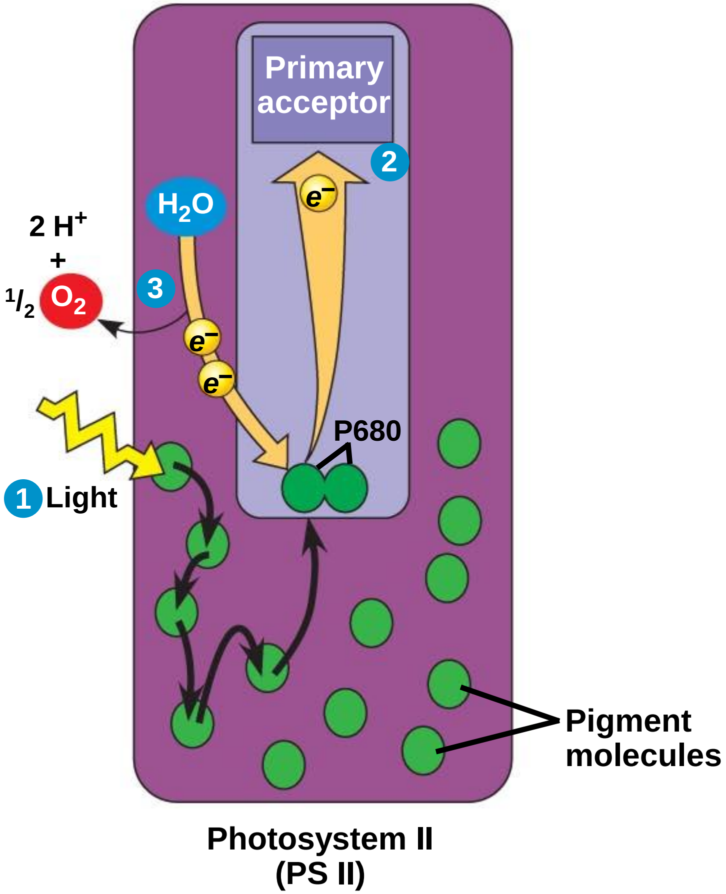
Fig. 10-13-1



Primary acceptor
2
e⁻
P680
1 Light
Pigment molecules
Photosystem II (PS II)

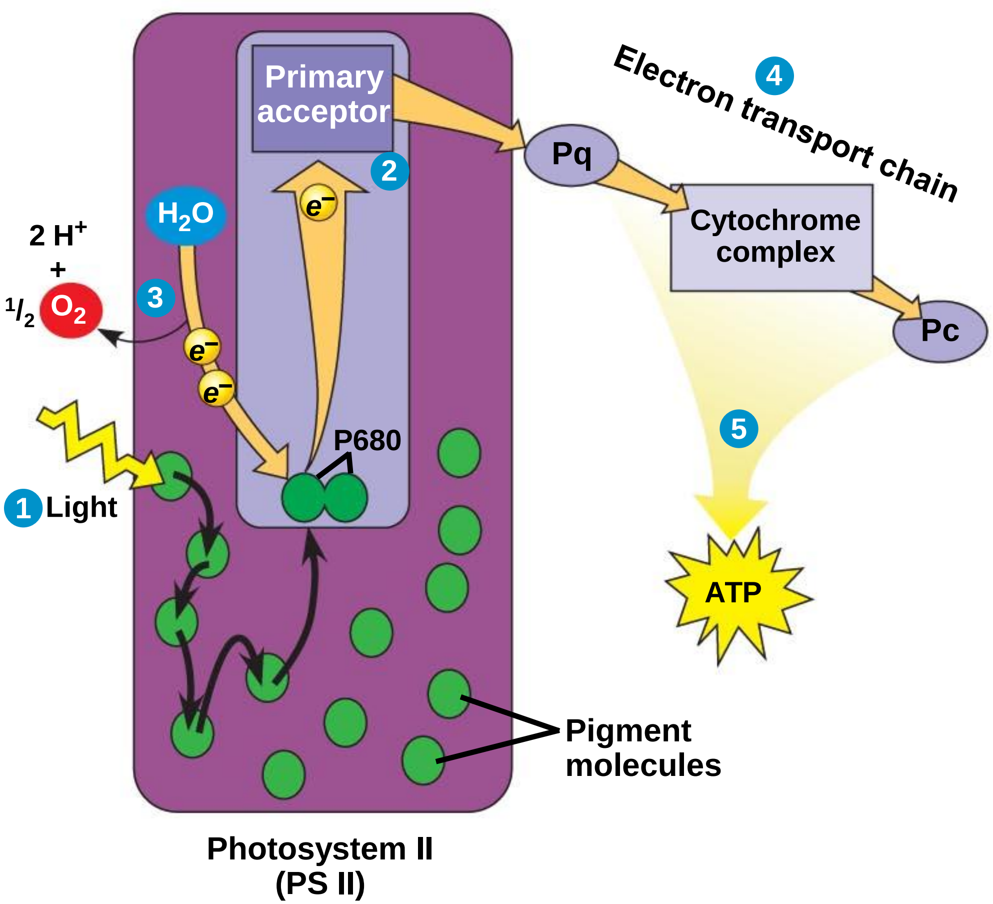
- $P680^+$ (P680 that is missing an electron) is a very strong oxidizing agent
- H_2O is split by enzymes, and the electrons are transferred from the hydrogen atoms to $P680^+$, thus reducing it to P680
- O_2 is released as a by-product of this reaction

Fig. 10-13-2


Primary
acceptor
2
H_2O
2 H^+
+
$^1/_2$ O_2
3
e^-
e^-
e^-
P680
1 Light
Pigment
molecules
Photosystem II
(PS II)

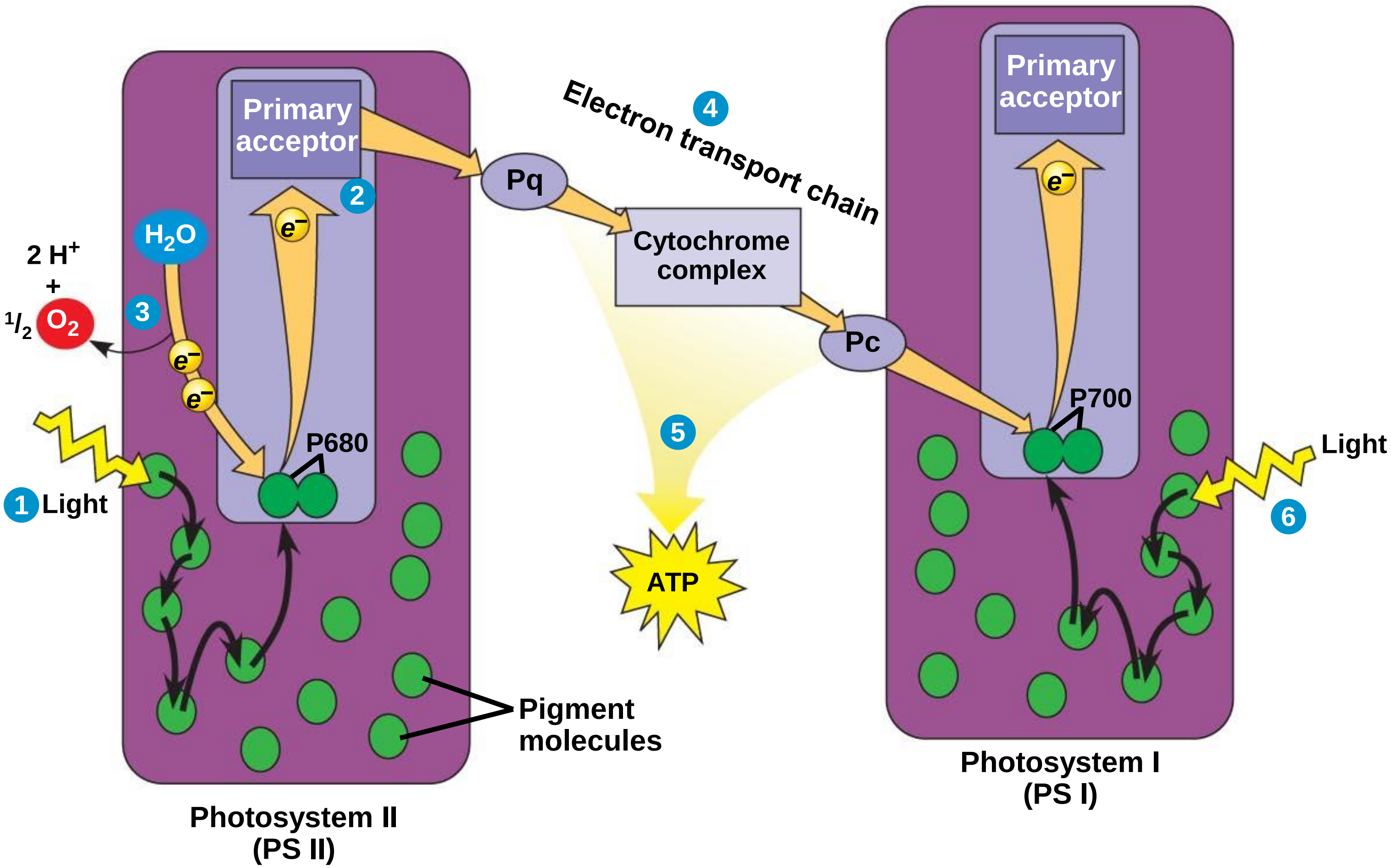
- Each electron “falls” down an electron transport chain from the primary electron acceptor of PS II to PS I
- Energy released by the fall drives the creation of a proton gradient across the thylakoid membrane
- Diffusion of H^+ (protons) across the membrane drives ATP synthesis

Fig. 10-13-3


Primary acceptor
2
Electron transport chain
4
Pq
Cytochrome complex
Pc
H_2O
$2 H^+$
+
$^1/_2$ O_2
3
e⁻
e⁻
e⁻
P680
1 Light
5
ATP
Pigment molecules
Photosystem II (PS II)

- 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

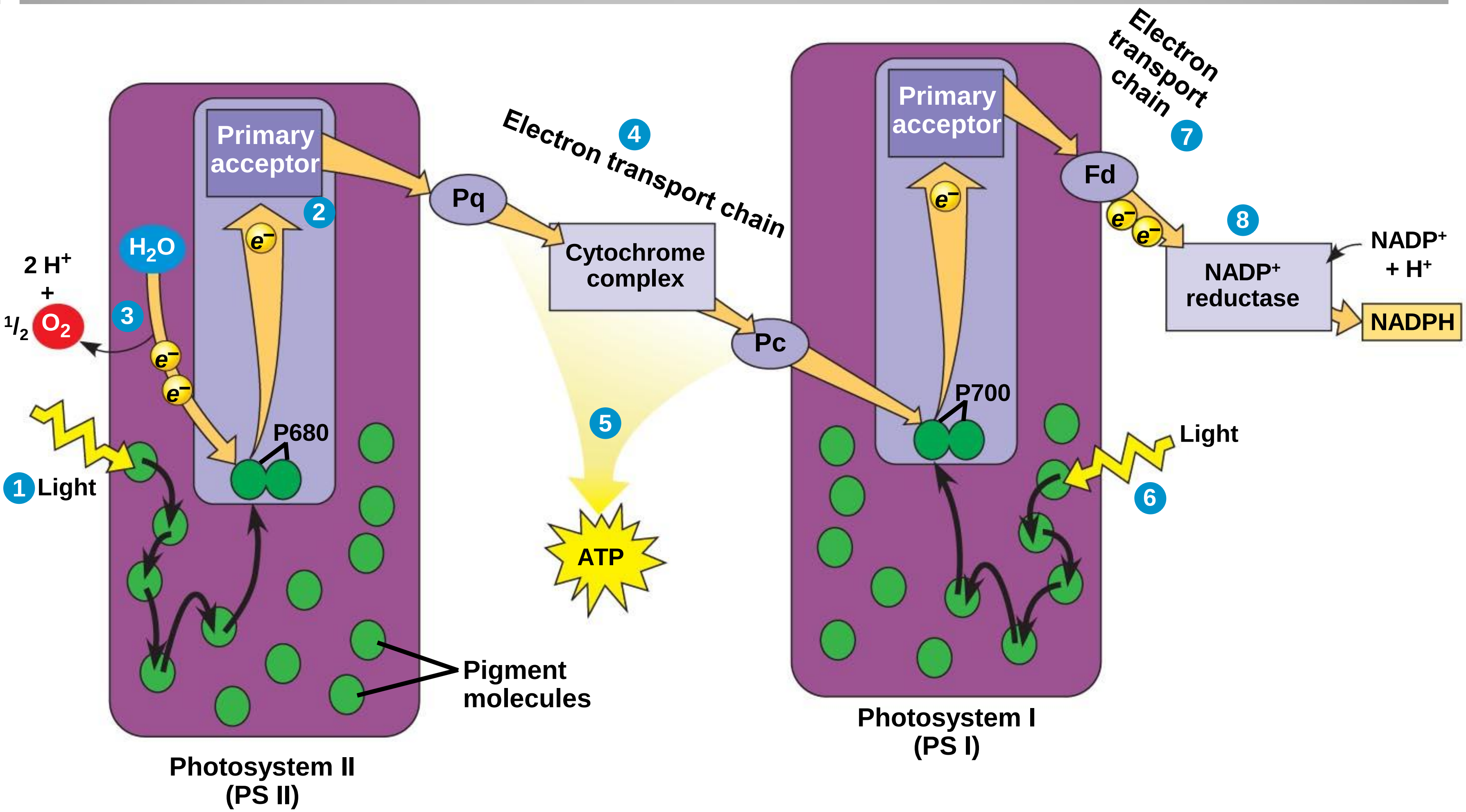
Fig. 10-13-4



Primary acceptor
2
H2O
2 H+
+
1/2 O2
3
e–
e–
e–
P680
1 Light
Pq
4
Electron transport chain
Cytochrome complex
Pc
5
ATP
Pigment molecules
Photosystem II (PS II)
Primary acceptor
e–
P700
Light
6
Photosystem I (PS I)

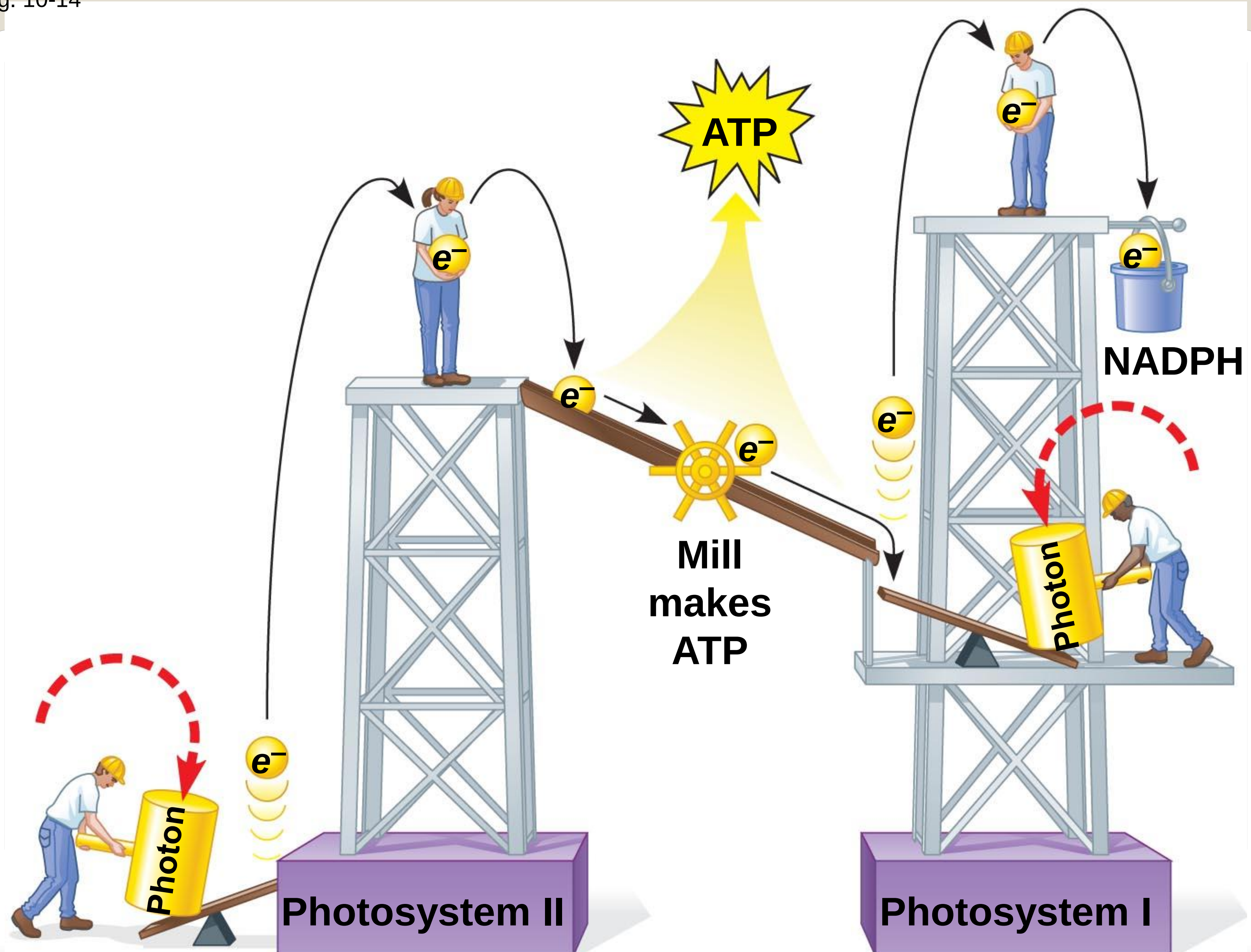
- Each electron “falls” down an electron transport chain from the primary electron acceptor of PS I to the protein ferredoxin (Fd)
- The electrons are then transferred to $NADP^+$ and reduce it to NADPH
- The electrons of NADPH are available for the reactions of the Calvin cycle

Fig. 10-13-5



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

Fig. 10-14

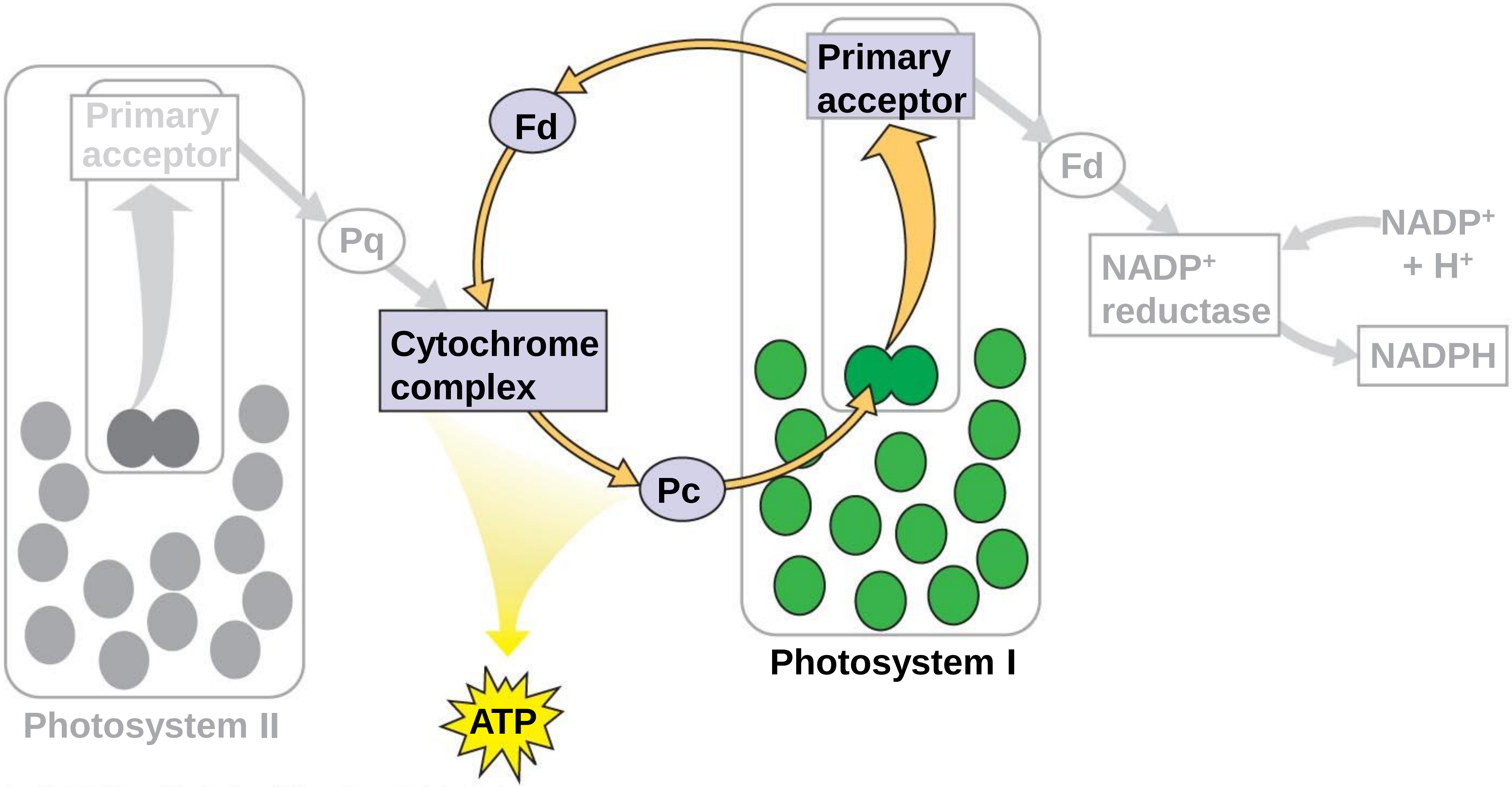


ATP
e⁻
e⁻
e⁻
e⁻
e⁻
e⁻
e⁻
NADPH
Mill makes ATP
Photon
Photon
Photosystem II
Photosystem I

Cyclic Electron Flow

- **Cyclic electron flow** uses only photosystem I and produces ATP, but not NADPH
- Cyclic electron flow generates surplus ATP, satisfying the higher demand in the Calvin cycle

Fig. 10-15


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

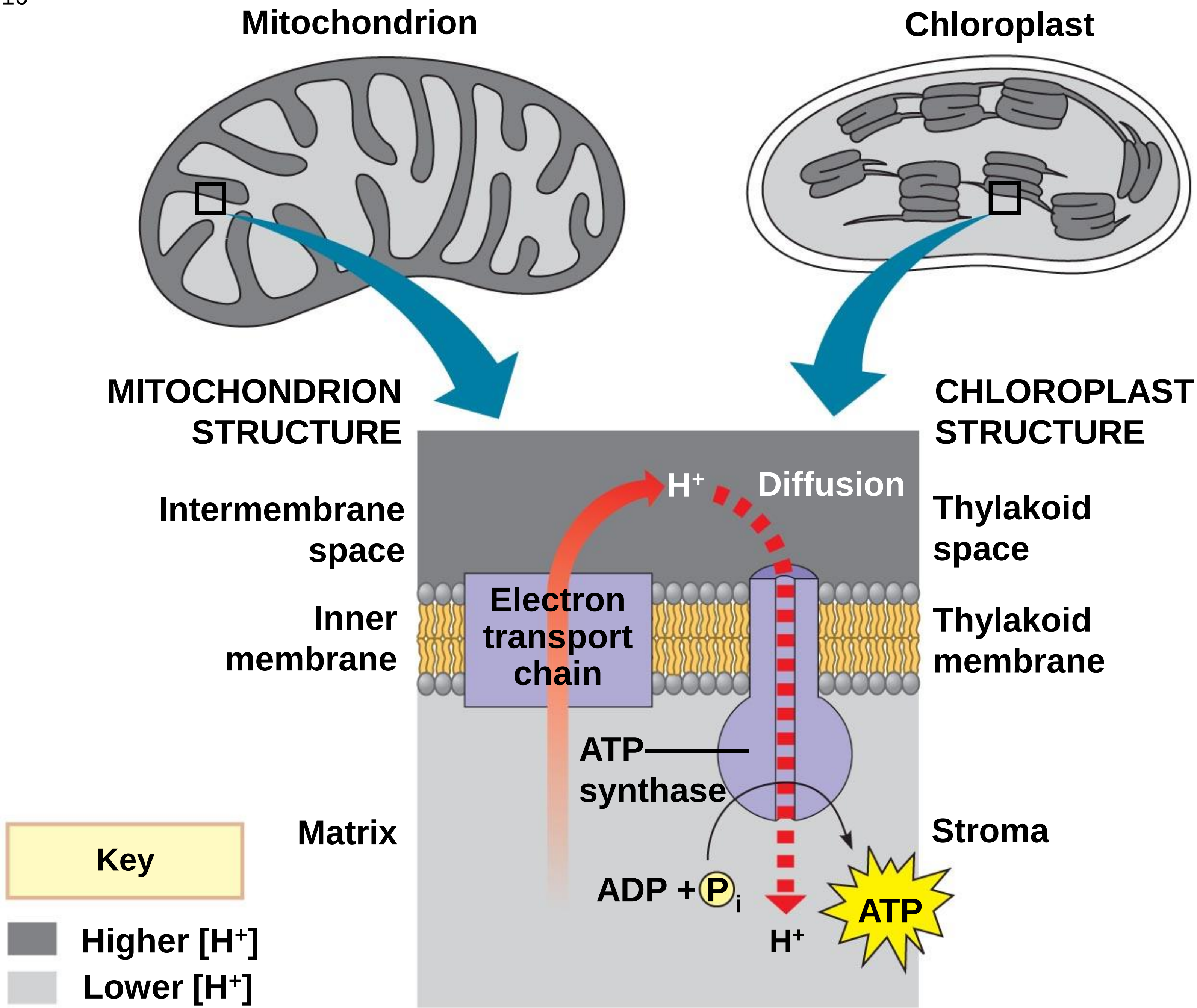
- Some organisms such as purple sulfur bacteria have PS I but not PS II
- Cyclic electron flow is thought to have evolved before linear electron flow
- Cyclic electron flow may protect cells from light-induced damage

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

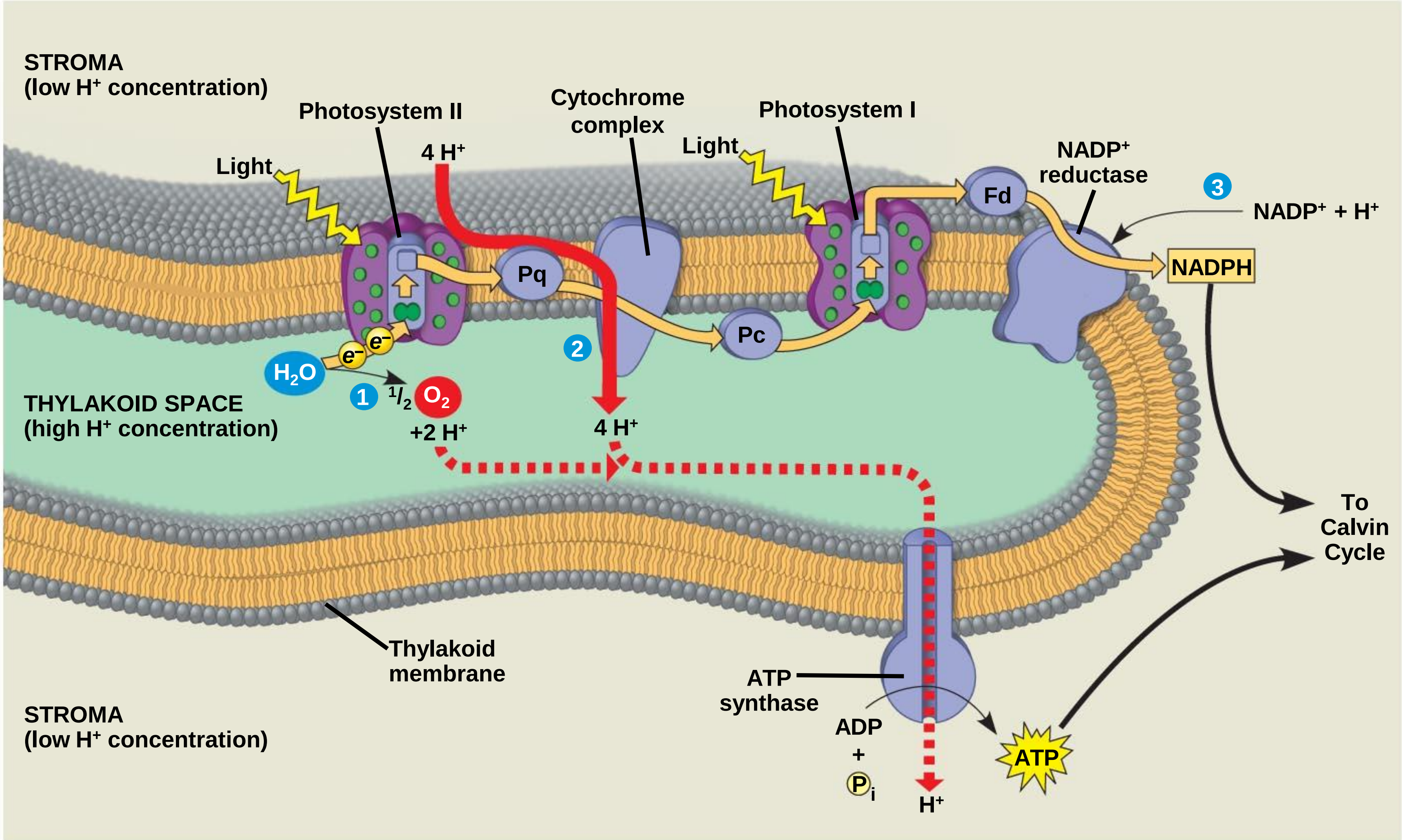
- In mitochondria, protons are pumped to the intermembrane space and drive ATP synthesis as they diffuse back into the mitochondrial matrix
- In chloroplasts, protons are pumped into the thylakoid space and drive ATP synthesis as they diffuse back into the stroma

Fig. 10-16


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

Fig. 10-17



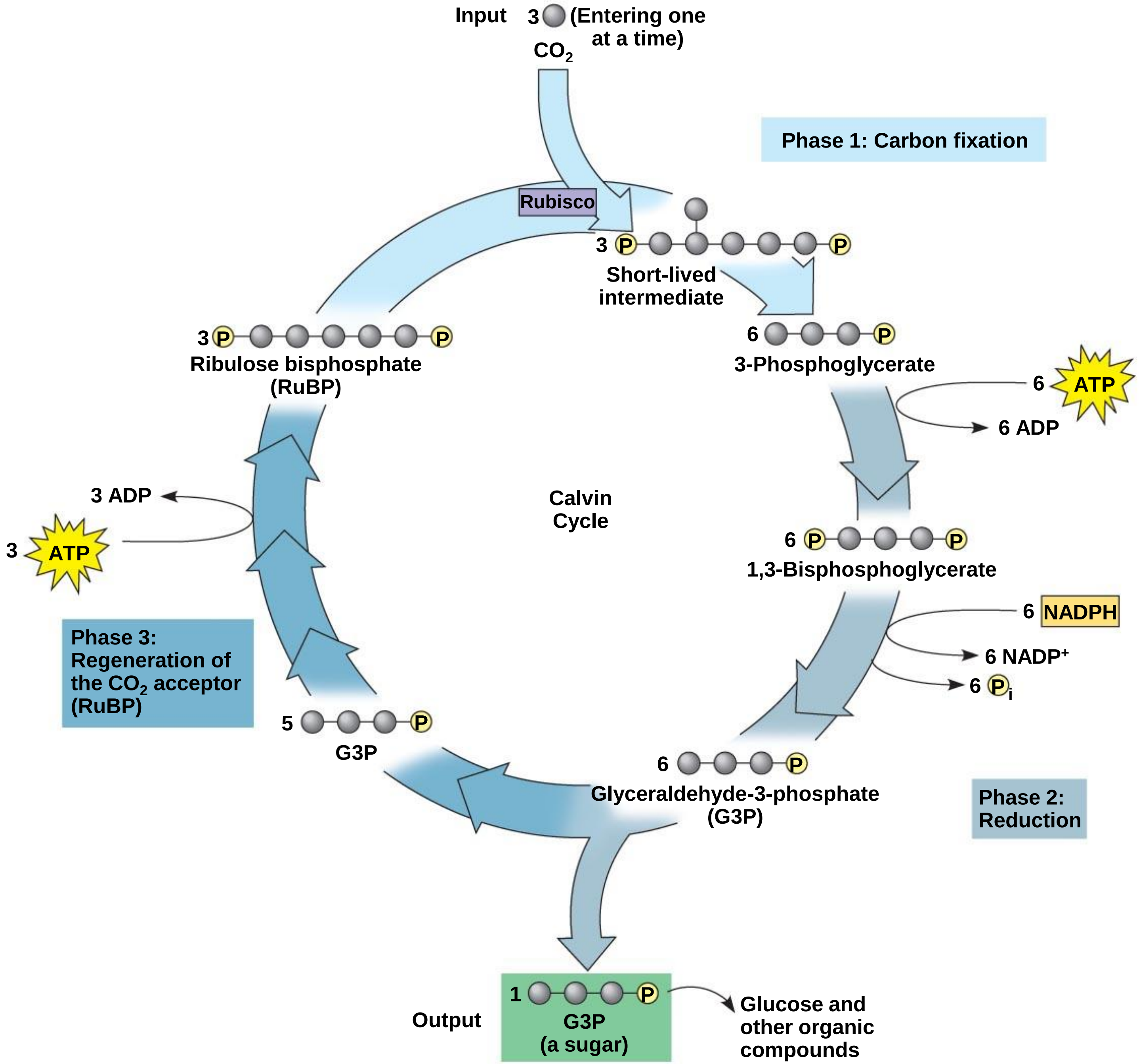
STROMA
(low H+ concentration)
Photosystem II
Cytochrome complex
Photosystem I
Light
4 H+
Light
NADP+ reductase
Fd
3
NADP+ + H+
Pq
NADPH
Pc
2
H2O
e–
e–
1
1/2 O2
THYLAKOID SPACE
(high H+ concentration)
+2 H+
4 H+
To Calvin Cycle
Thylakoid membrane
ATP synthase
STROMA
(low H+ concentration)
ADP
+
Pi
ATP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

The Calvin cycle uses ATP and NADPH to convert 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)**

Fig. 10-18-3


Input
3 (Entering one at a time)
CO2
Phase 1: Carbon fixation
Rubisco
3 P P
Short-lived intermediate
3 P P
Ribulose bisphosphate (RuBP)
6 P
3-Phosphoglycerate
6 ATP
6 ADP
3 ADP
3 ATP
Calvin Cycle
6 P P
1,3-Bisphosphoglycerate
6 NADPH
6 NADP+
6 Pi
Phase 3: Regeneration of the CO2 acceptor (RuBP)
5 P
G3P
6 P
Glyceraldehyde-3-phosphate (G3P)
Phase 2: Reduction
1 P
Output
G3P (a sugar)
Glucose and other organic compounds

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 a seemingly wasteful process called photorespiration

Photorespiration

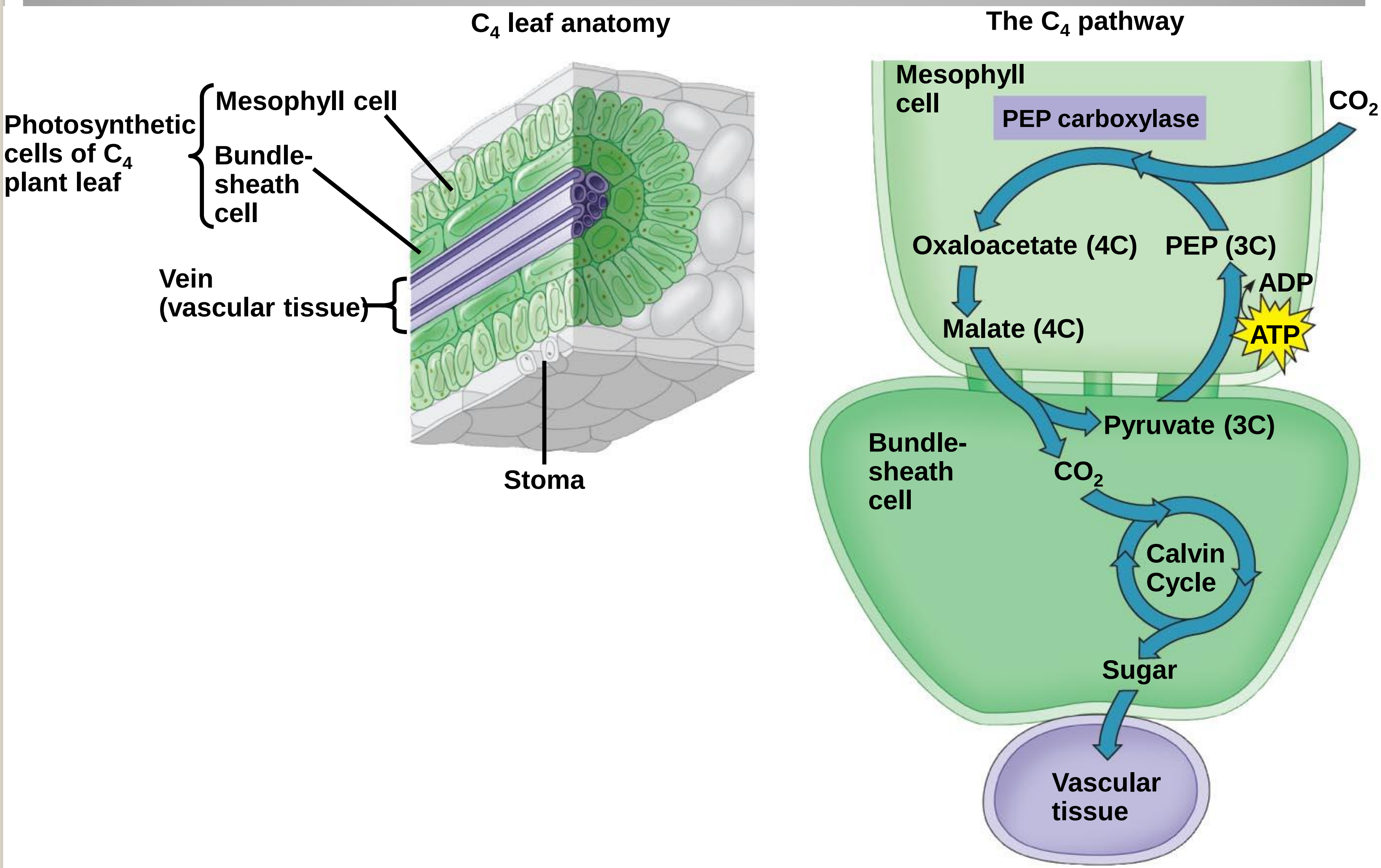
- In most plants (**C_3 plants**), initial fixation of CO_2, via rubisco, forms a three-carbon compound
- In **photorespiration**, rubisco adds O_2 instead of CO_2 in the Calvin cycle
- Photorespiration consumes O_2 and organic fuel and releases CO_2 without producing ATP or sugar

- 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

Fig. 10-19

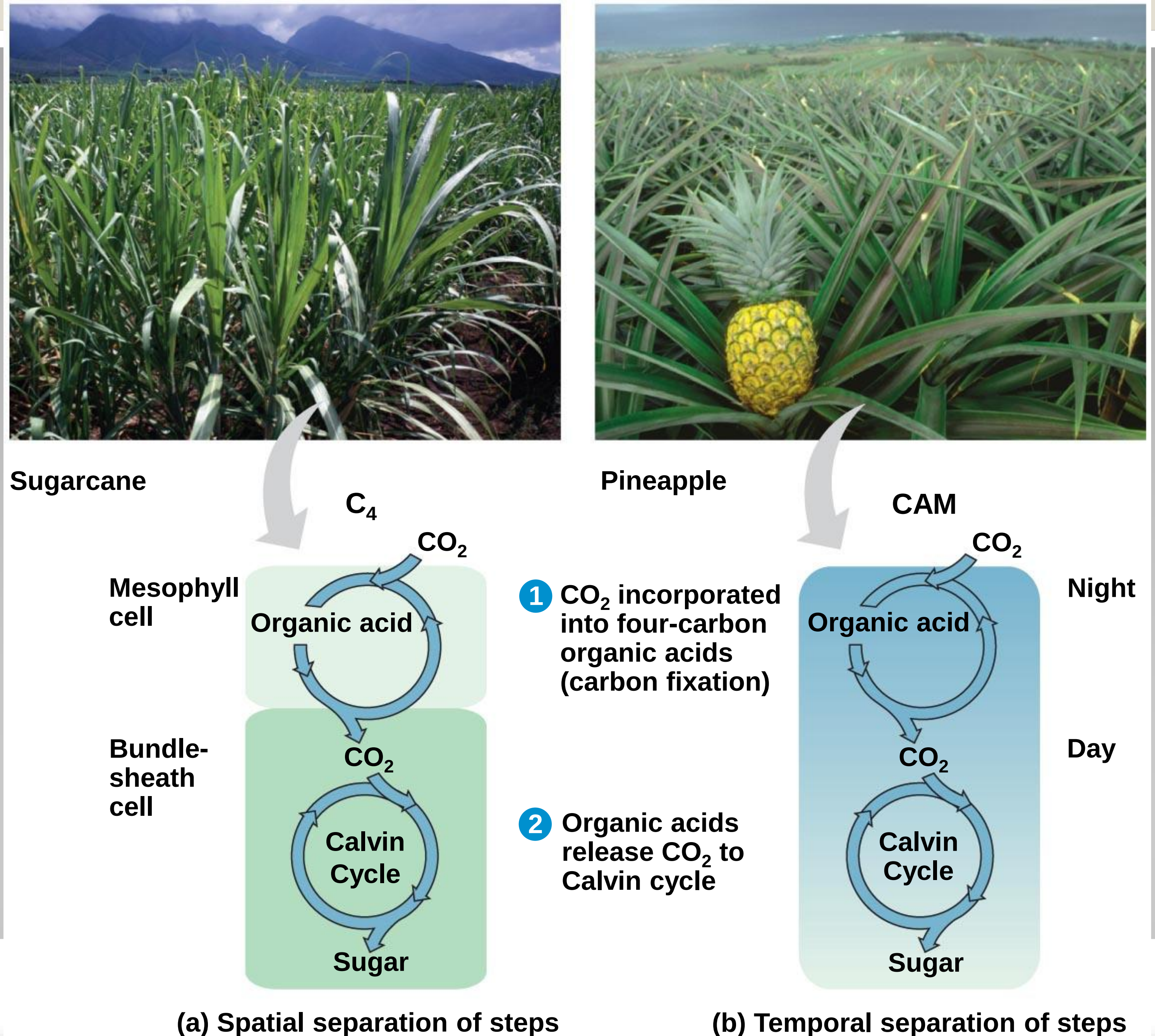


C_4 leaf anatomy
Photosynthetic cells of C_4 plant leaf
Mesophyll cell
Bundle-sheath cell
Vein (vascular tissue)
Stoma
The C_4 pathway
Mesophyll cell
PEP carboxylase
CO_2
Oxaloacetate (4C)
PEP (3C)
ADP
Malate (4C)
ATP
Pyruvate (3C)
Bundle-sheath cell
CO_2
Calvin Cycle
Sugar
Vascular tissue

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

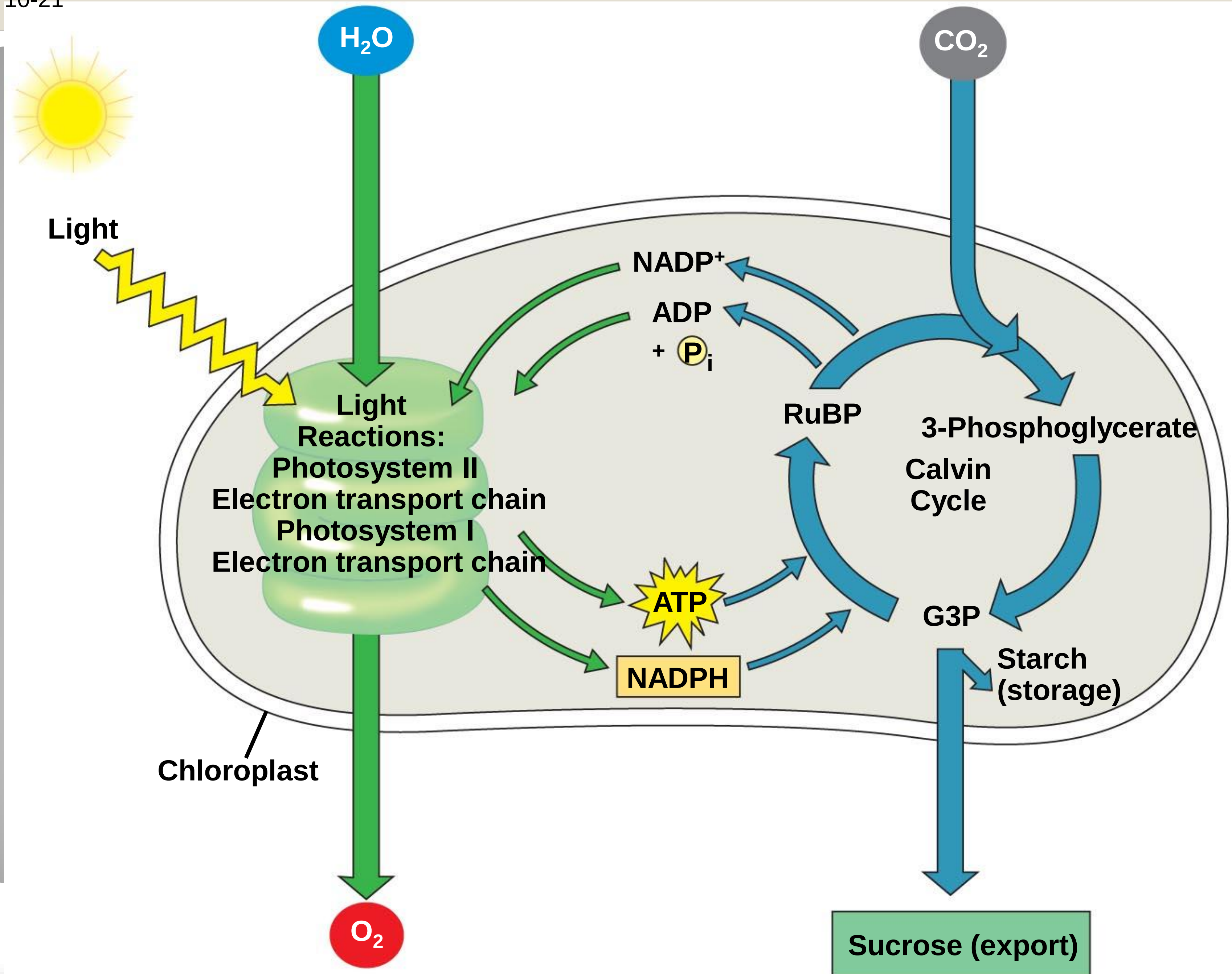
Fig. 10-20


Sugarcane
Pineapple
C_4
CAM
CO_2
Mesophyll cell
Organic acid
Bundle-sheath cell
CO_2
Calvin Cycle
Sugar
1 CO_2 incorporated into four-carbon organic acids (carbon fixation)
2 Organic acids release CO_2 to Calvin cycle
CO_2
Night
Organic acid
Day
CO_2
Calvin Cycle
Sugar
(a) Spatial separation of steps
(b) Temporal separation of steps

The Importance of Photosynthesis: *A Review*

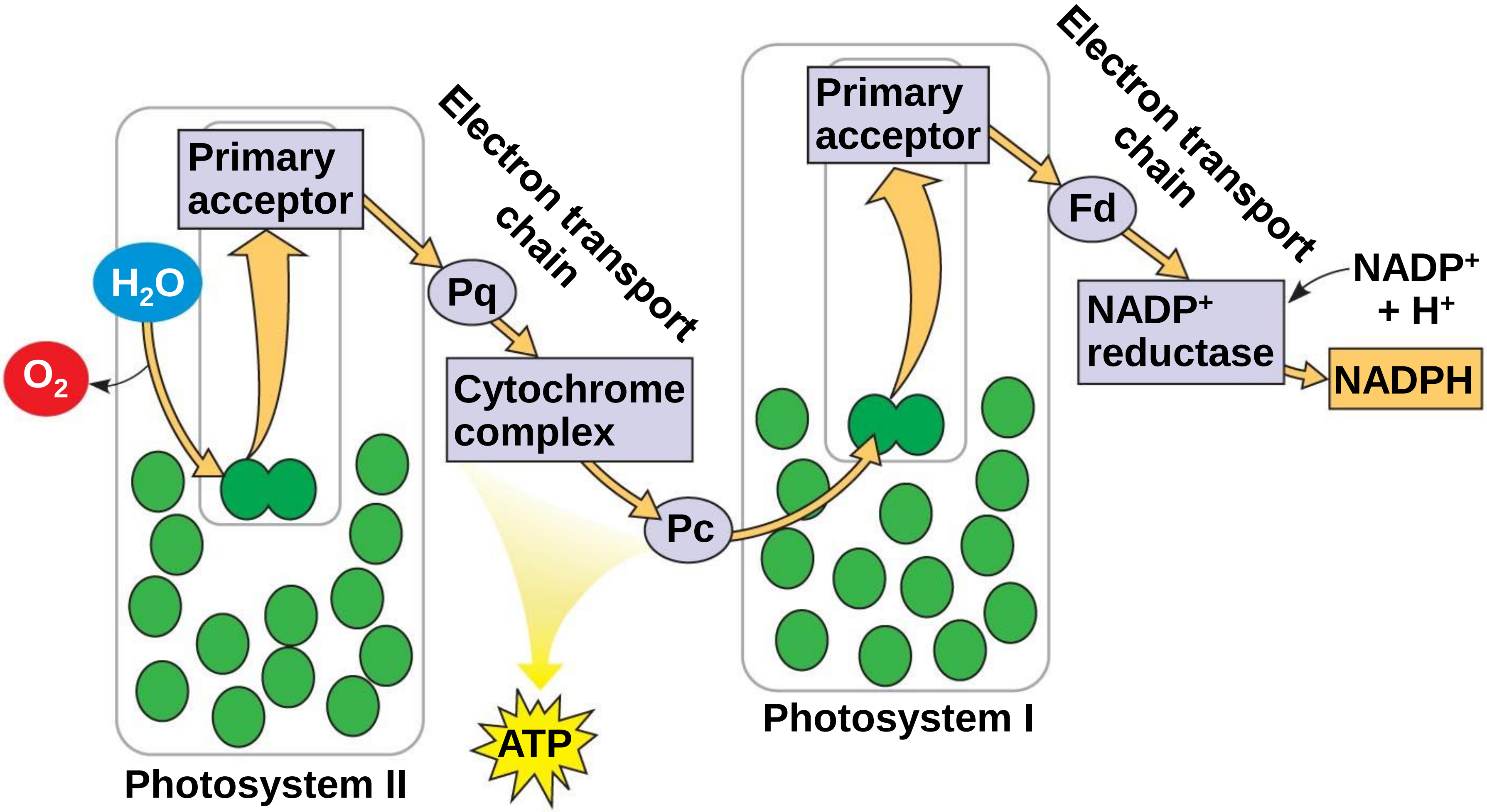
- The energy entering chloroplasts as sunlight gets stored as chemical energy in organic compounds
- Sugar made in the chloroplasts supplies chemical energy and carbon skeletons to synthesize the organic molecules of cells
- Plants store excess sugar as starch in structures such as roots, tubers, seeds, and fruits
- In addition to food production, photosynthesis produces the O_2 in our atmosphere

Fig. 10-21



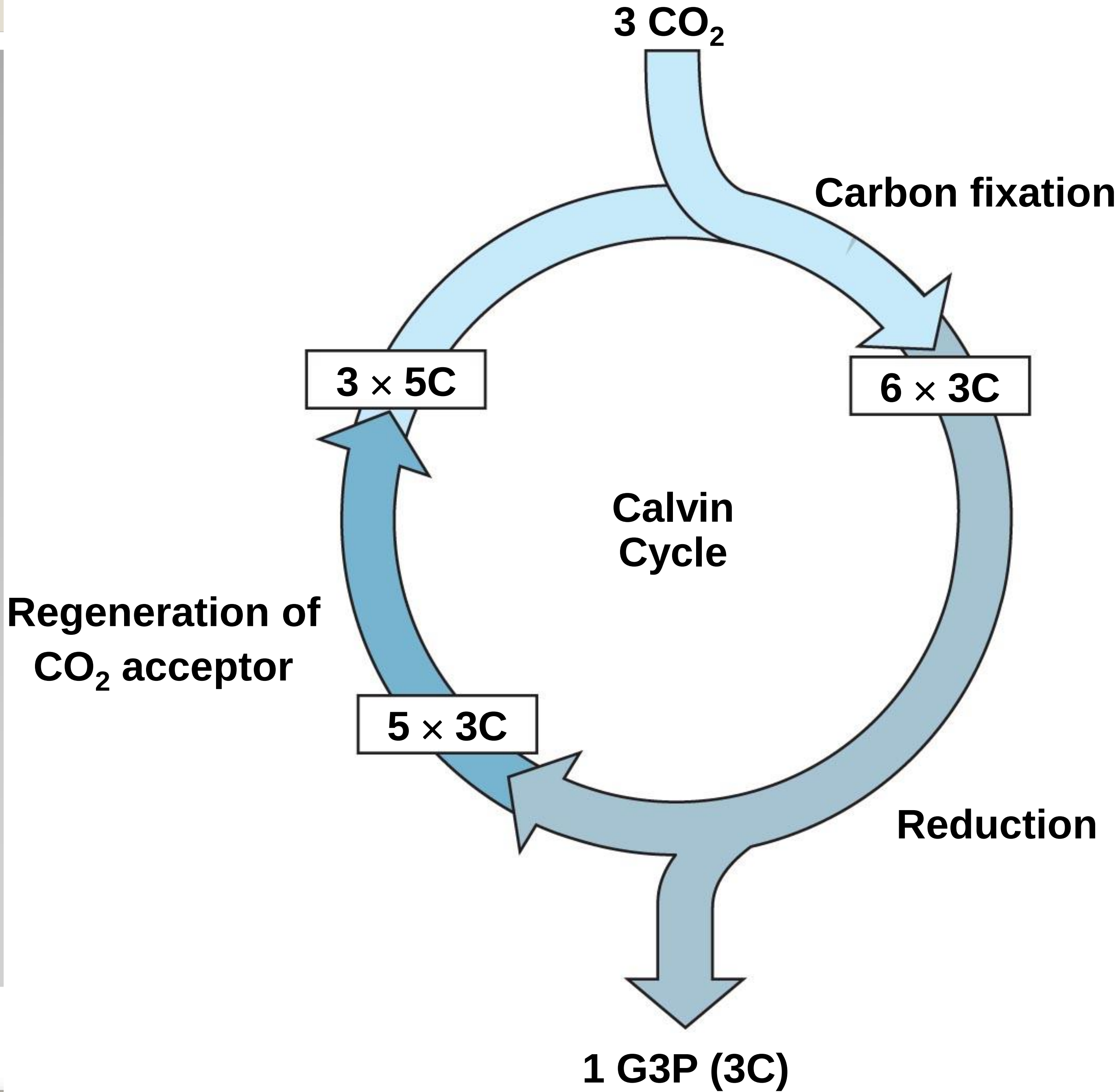
H2O
CO2
Light
NADP+
ADP
+ Pi
Light
Reactions:
Photosystem II
Electron transport chain
Photosystem I
Electron transport chain
RuBP
3-Phosphoglycerate
Calvin
Cycle
ATP
G3P
NADPH
Starch
(storage)
Chloroplast
O2
Sucrose (export)

Fig. 10-UN1



Primary acceptor
Electron transport chain
Pq
Cytochrome complex
Pc
H2O
O2
ATP
Photosystem II
Primary acceptor
Electron transport chain
Fd
NADP+ reductase
NADP+ + H+
NADPH
Photosystem I

Fig. 10-UN2


3 CO_2
Carbon fixation
3 × 5C
6 × 3C
Calvin Cycle
Regeneration of CO_2 acceptor
5 × 3C
Reduction
1 G3P (3C)