Photosynthesis
Chapter 10

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

- **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

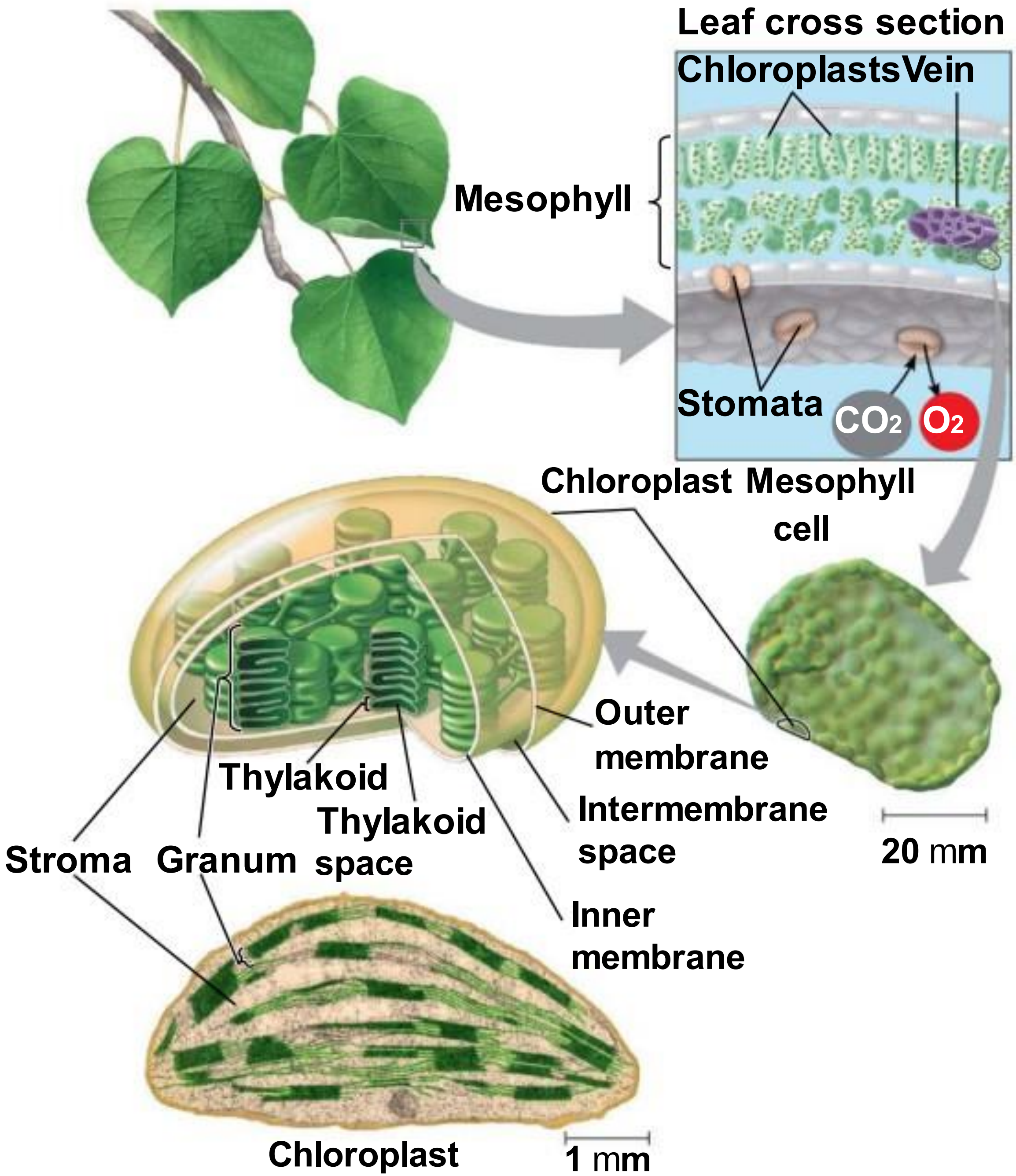
Photosynthesis converts light energy to the chemical energy of food

- 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

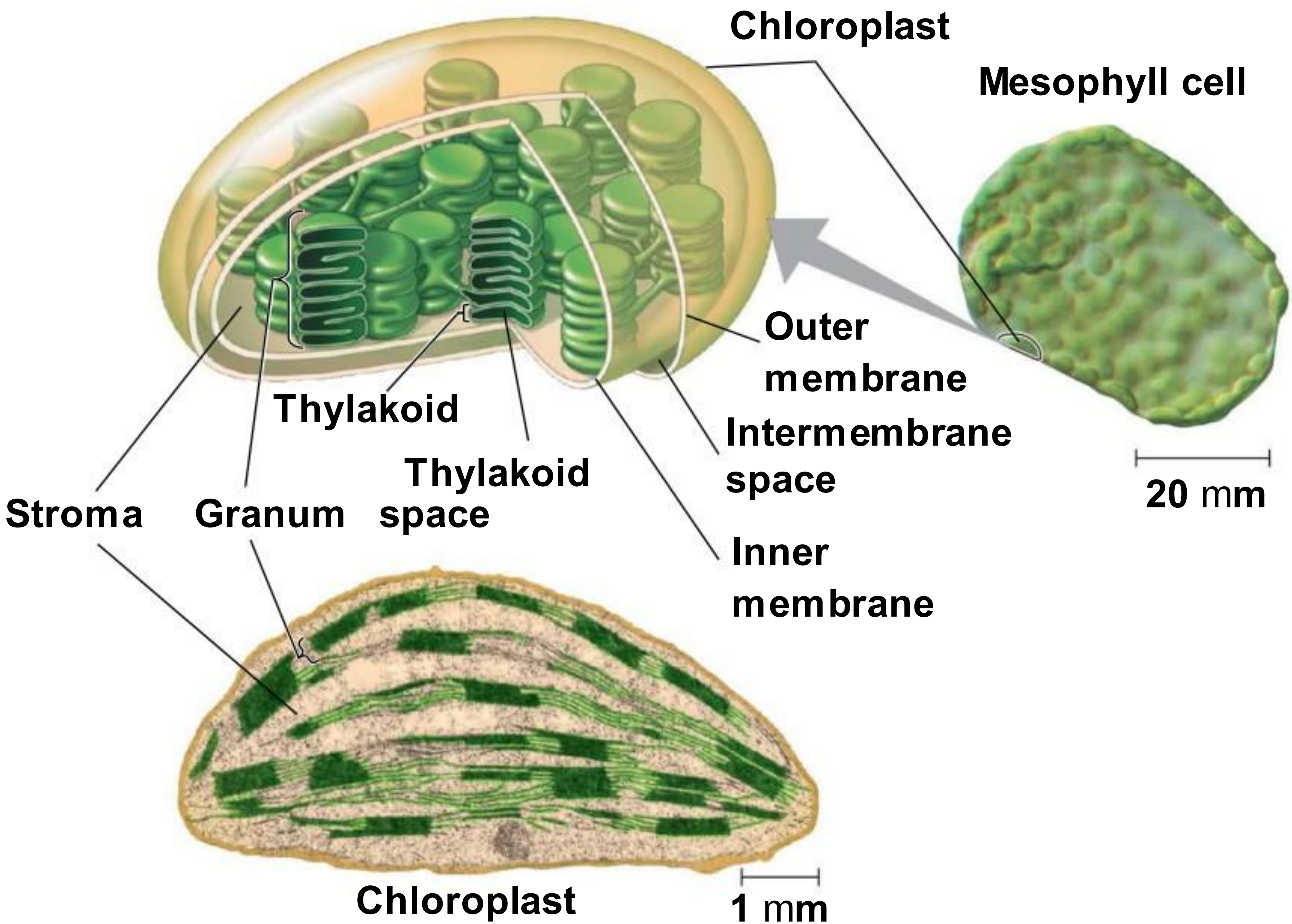
Chloroplasts: The Sites of Photosynthesis in Plants

- 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



Leaf cross section
Chloroplasts
Vein
Mesophyll
Stomata
CO2
O2
Chloroplast
Mesophyll cell
20 mm
Outer membrane
Intermembrane space
Inner membrane
Thylakoid
Thylakoid space
Stroma
Granum
Chloroplast
1 mm


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

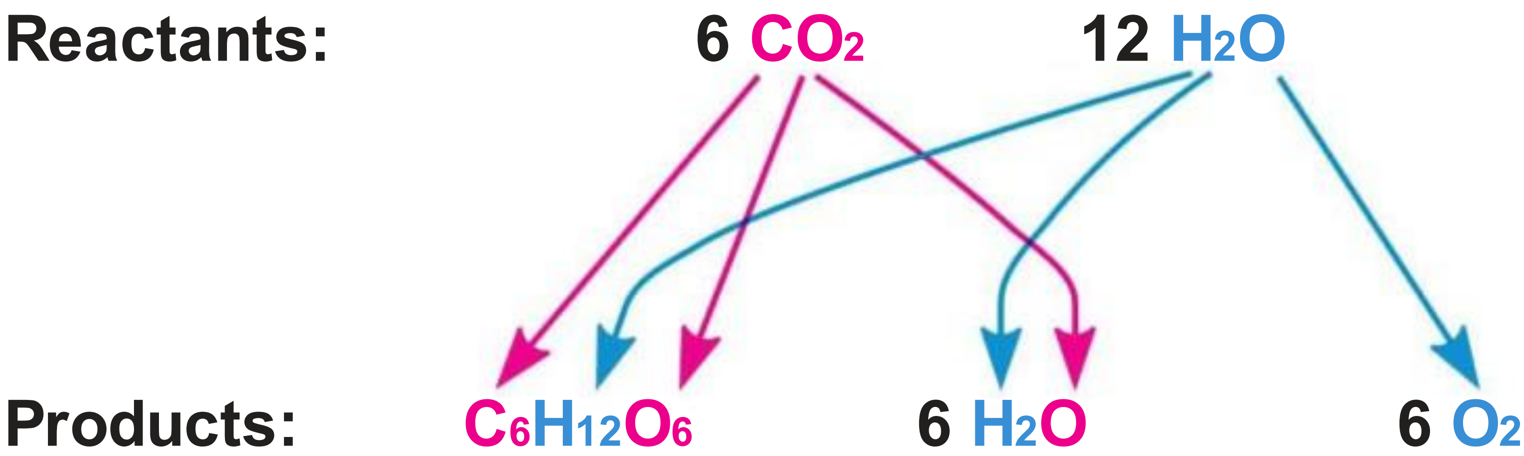
Tracking Atoms Through Photosynthesis: *Scientific Inquiry*

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

$6\ CO_2$ □ $12H_2O$ □ Light energy □ $C_6H_{12}O_6$ □ $6\ O_2$ □ $6\ H_2O$

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


Reactants:
6 CO_2
12 H_2O
Products:
$C_6H_{12}O_6$
6 H_2O
6 O_2

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

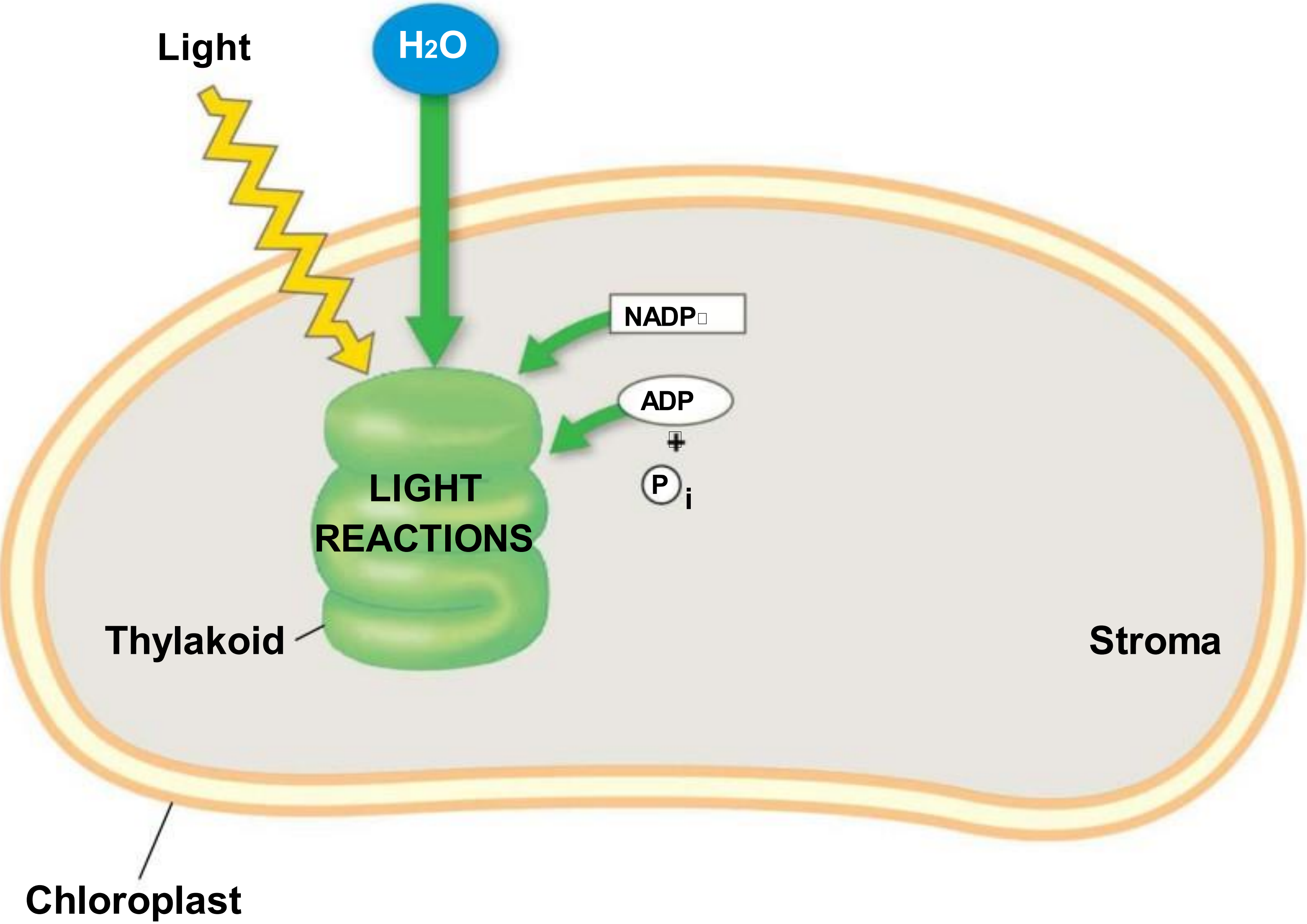
$$\text{Energy} + 6\,CO_2 + 6\,H_2O \longrightarrow C_6H_{12}O_6 + 6\,O_2$$

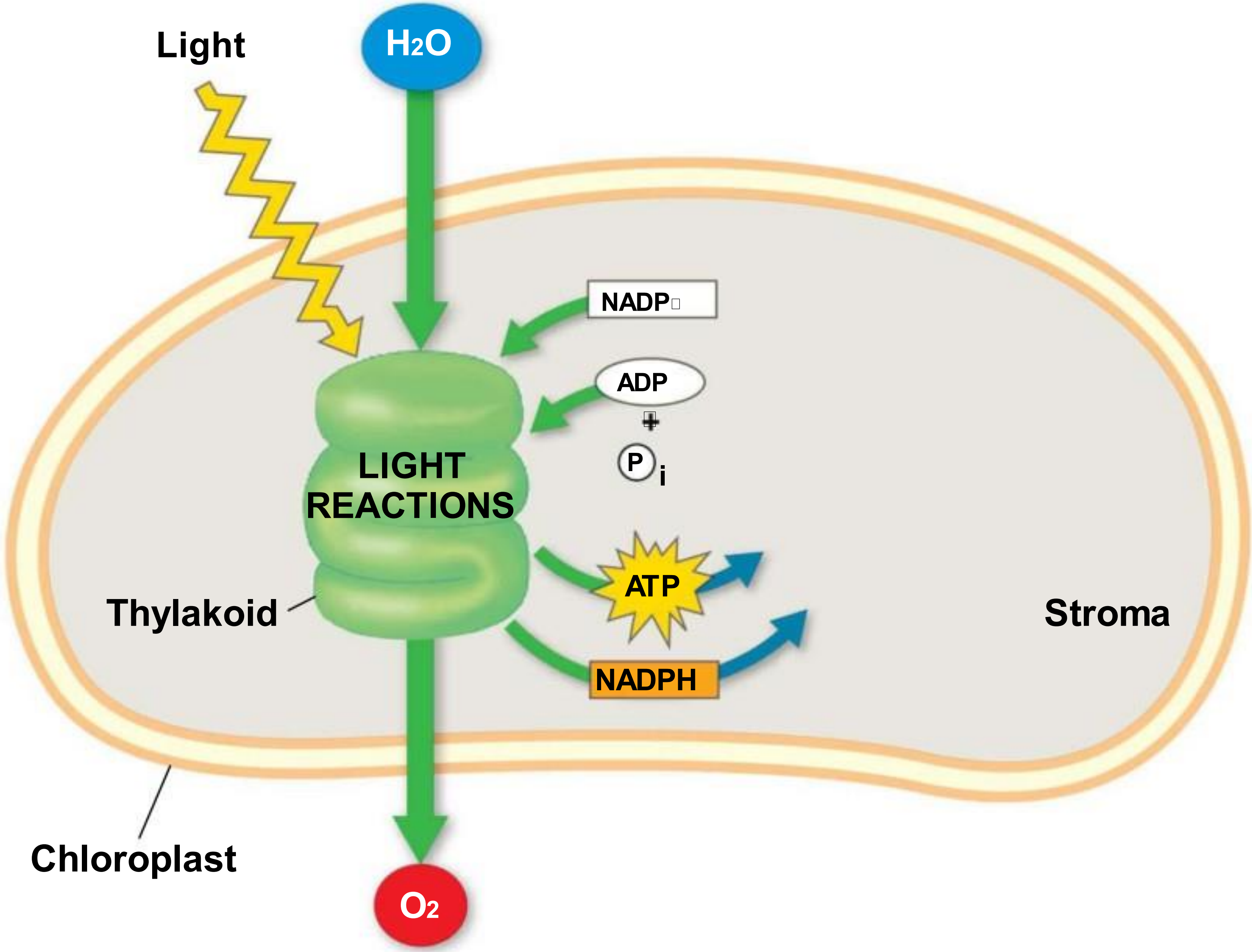
becomes oxidized

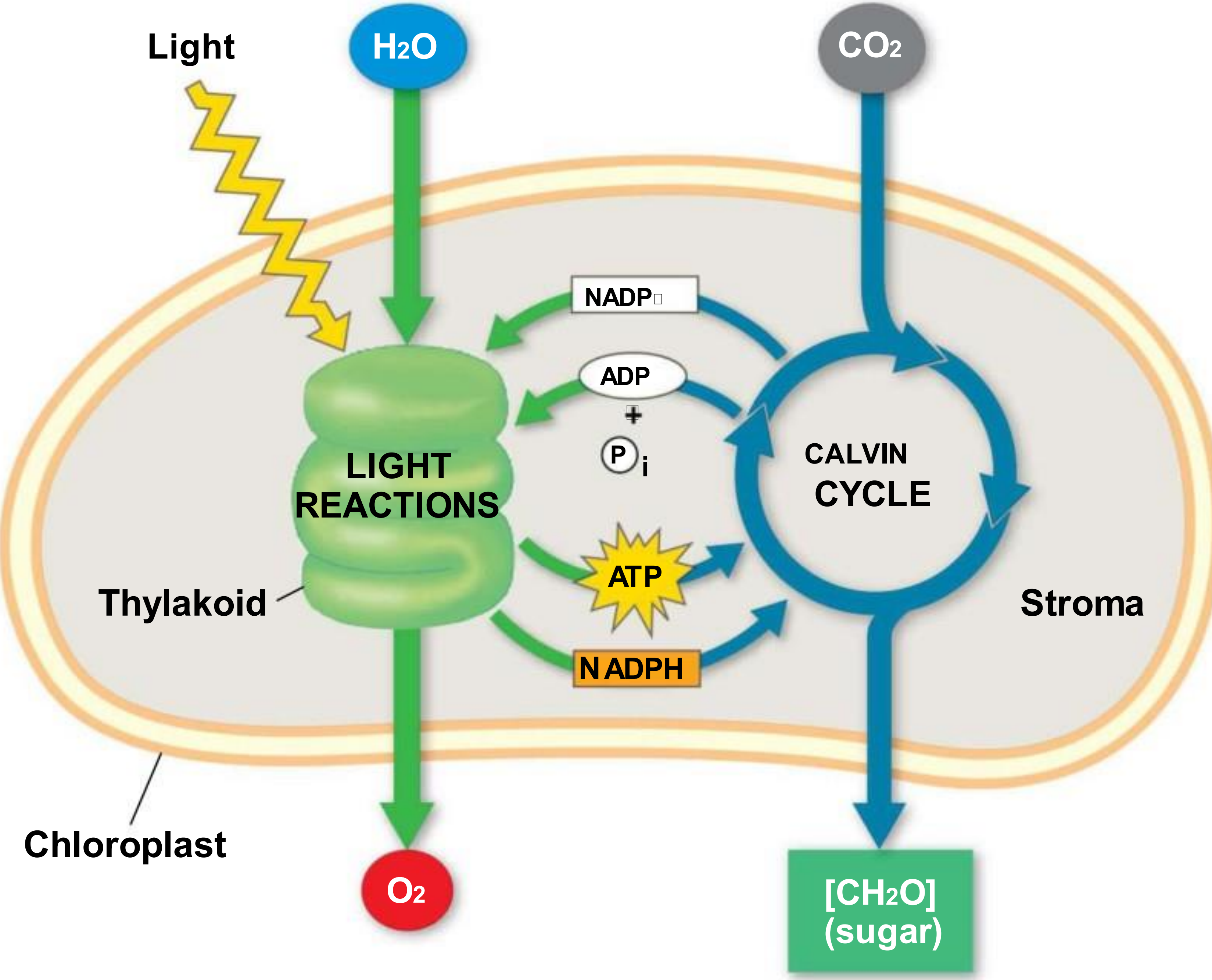
The Two Stages of Photosynthesis: *A Preview*

- 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


Light
H_2O
NADP
ADP
+
P_i
LIGHT REACTIONS
Thylakoid
Stroma
Chloroplast


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



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

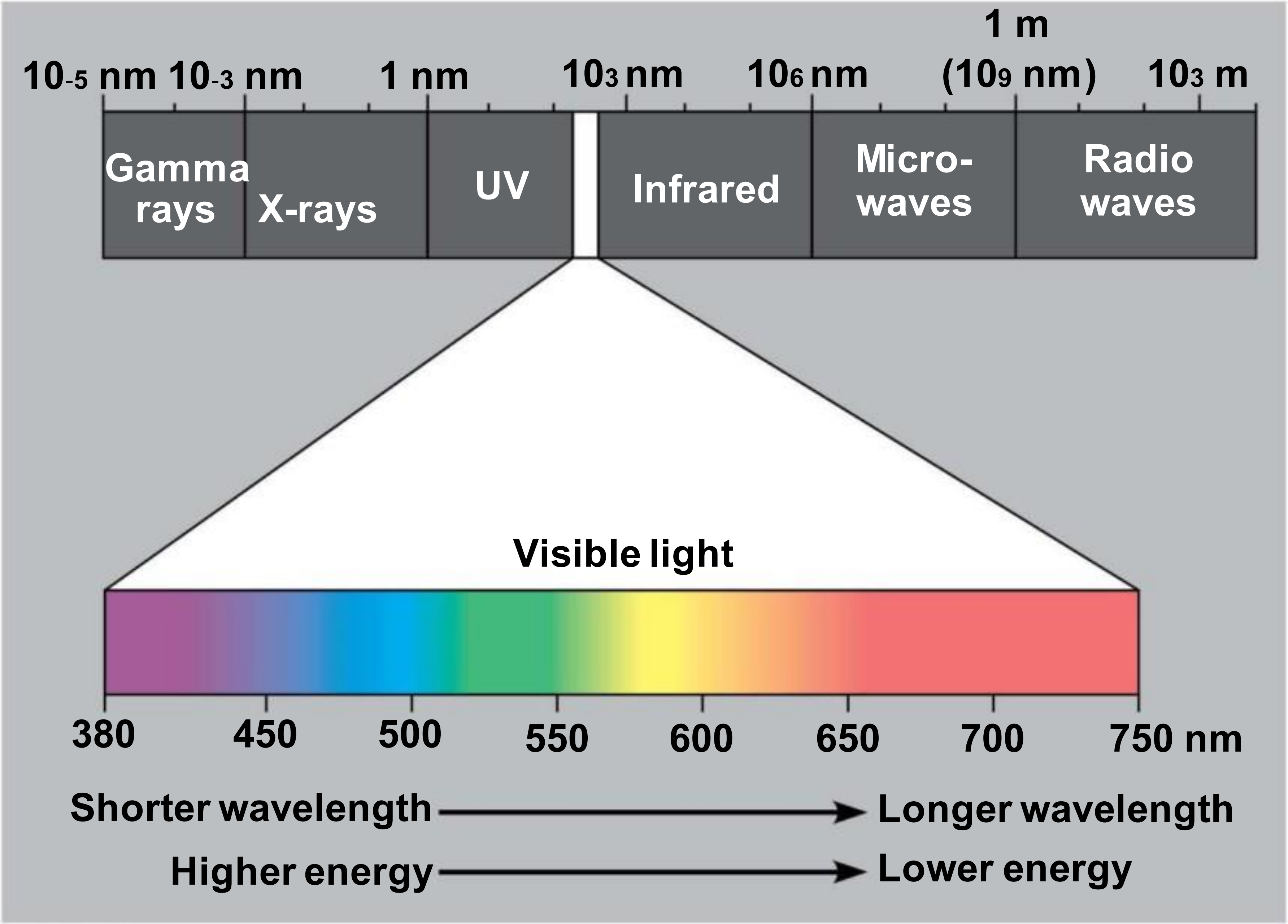
The light reactions convert solar energy to the chemical energy of ATP and NADPH

- 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**

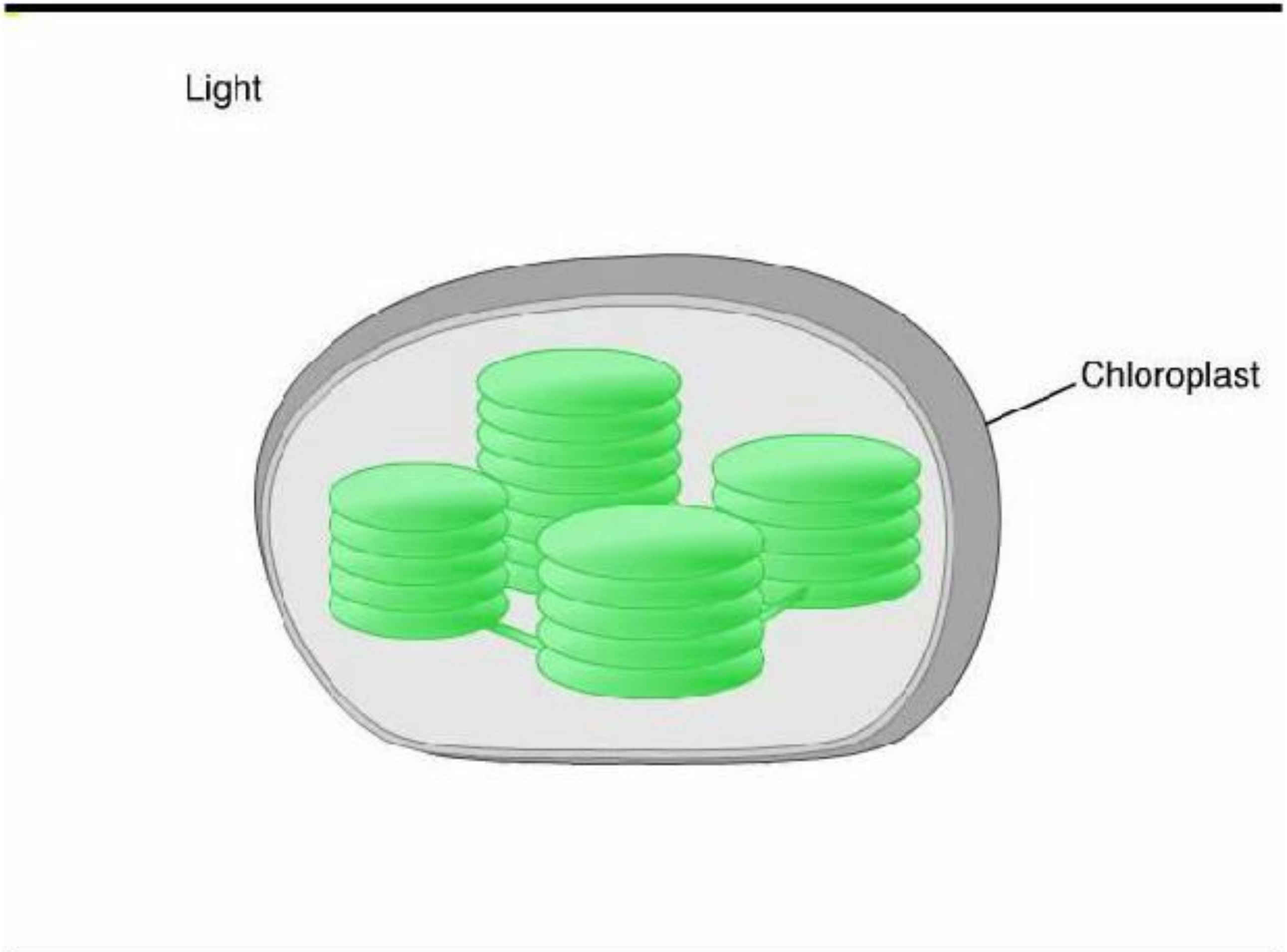


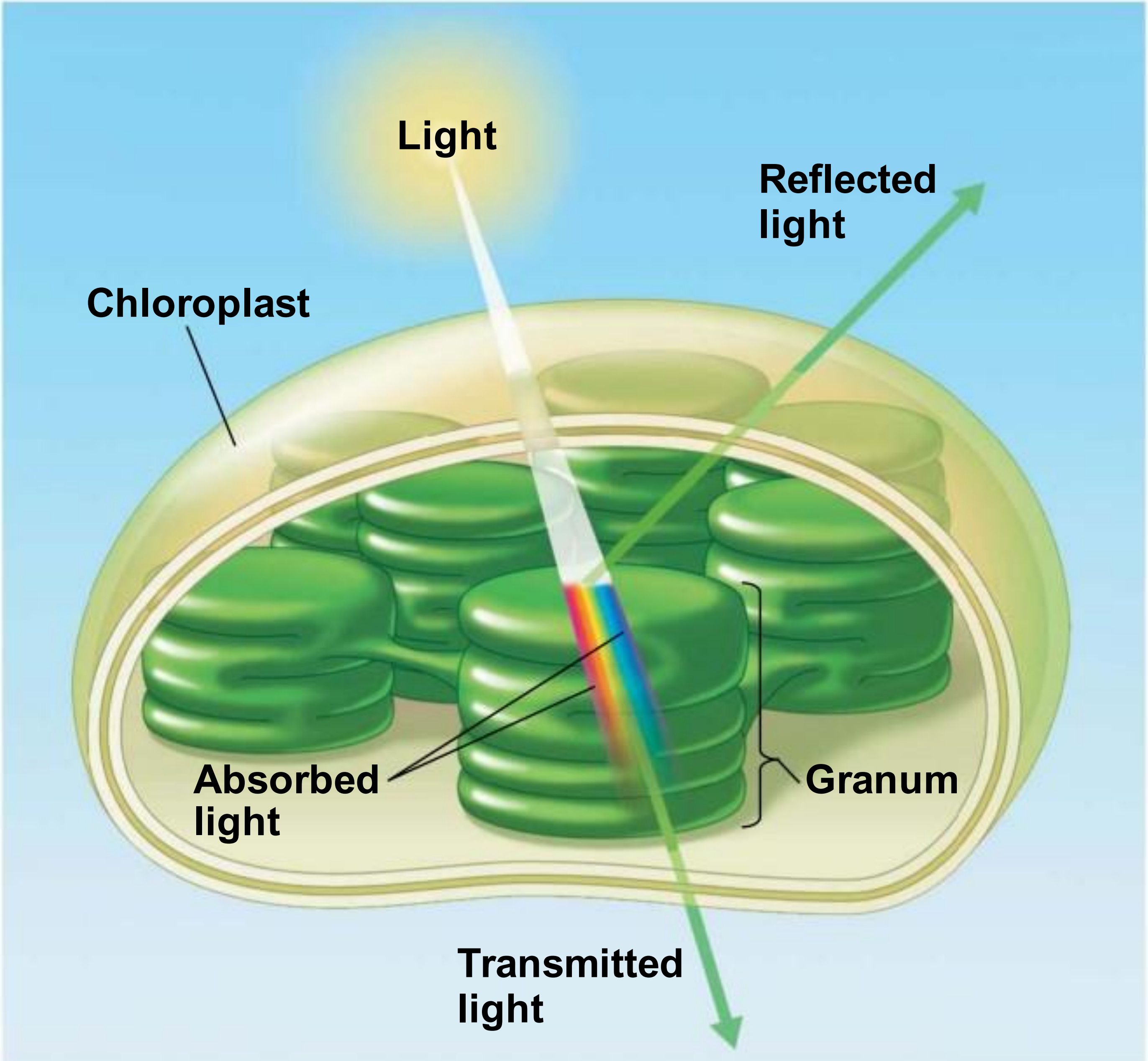
10-5 nm
10-3 nm
1 nm
103 nm
106 nm
1 m
(109 nm)
103 m
Gamma rays
X-rays
UV
Infrared
Micro-waves
Radio waves
Visible light
380
450
500
550
600
650
700
750 nm
Shorter wavelength
Longer wavelength
Higher energy
Lower energy

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

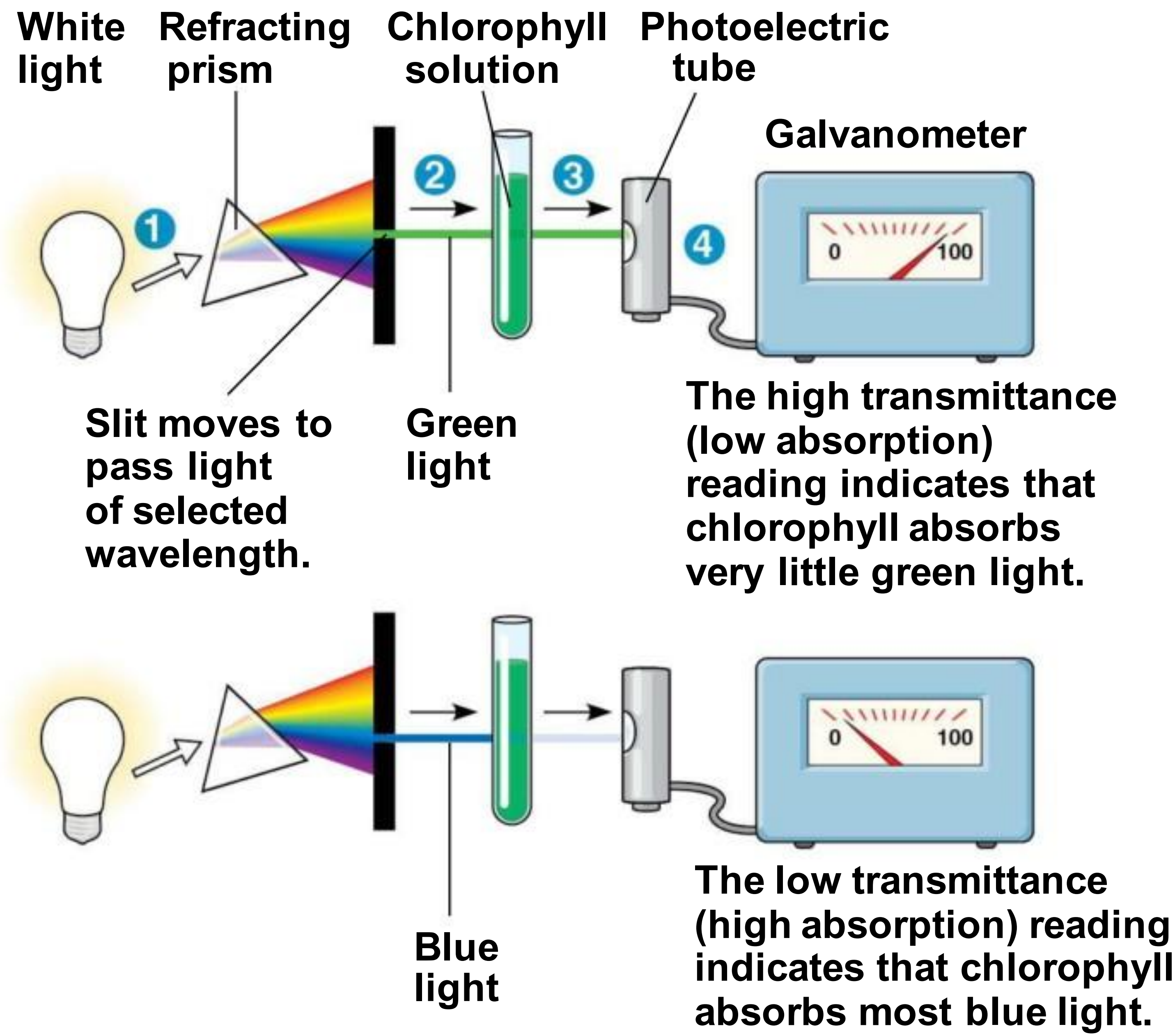
Animation: Light and Pigments



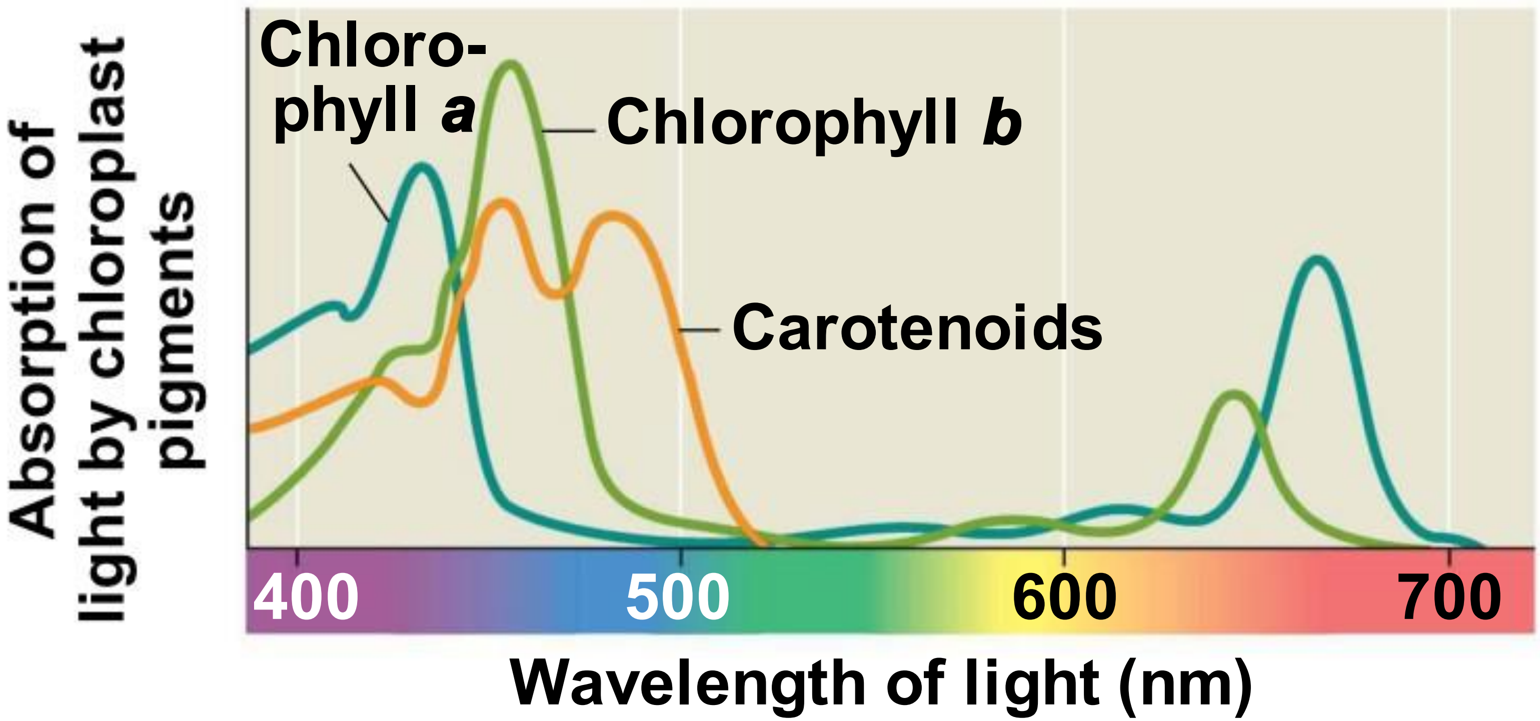

Light
Reflected light
Chloroplast
Absorbed light
Granum
Transmitted light

- 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

Technique

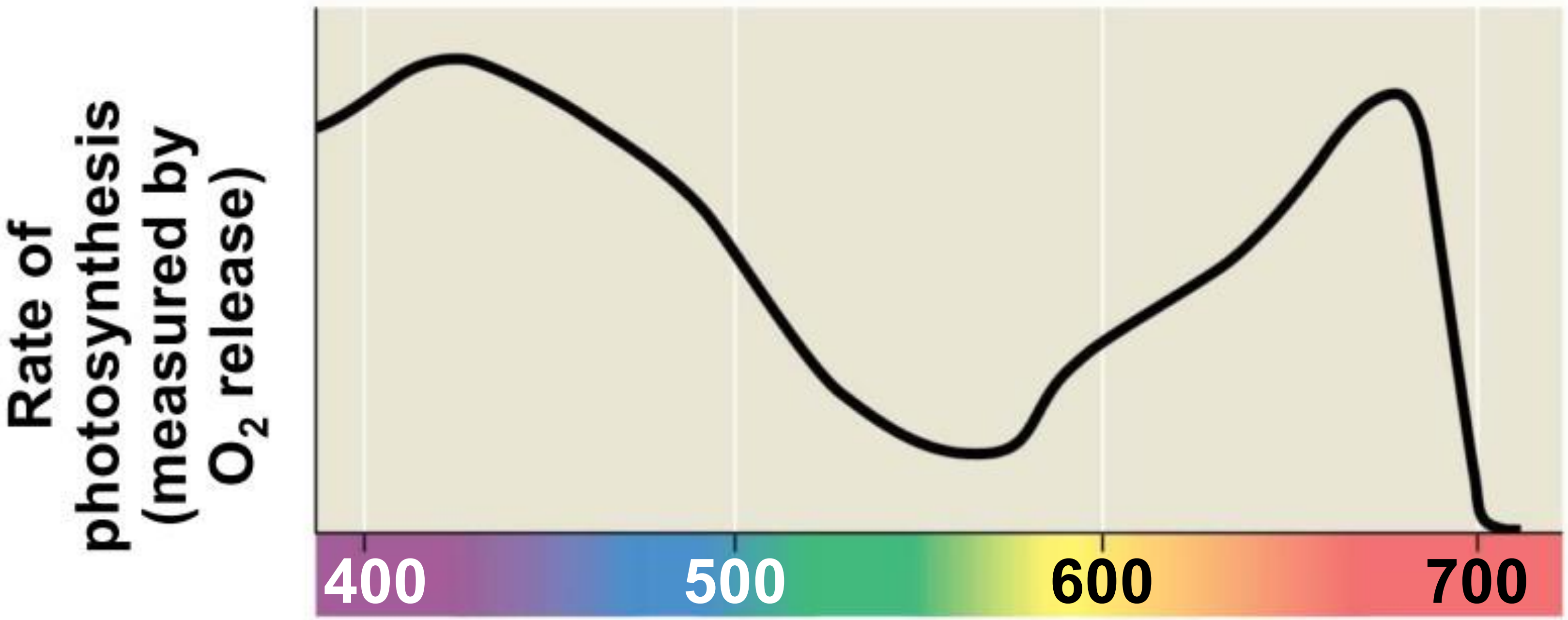

White light
Refracting prism
Chlorophyll solution
Photoelectric tube
Galvanometer
1
2
3
4
0
100
Slit moves to pass light of selected wavelength.
Green light
The high transmittance (low absorption) reading indicates that chlorophyll absorbs very little green light.
0
100
Blue light
The low transmittance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



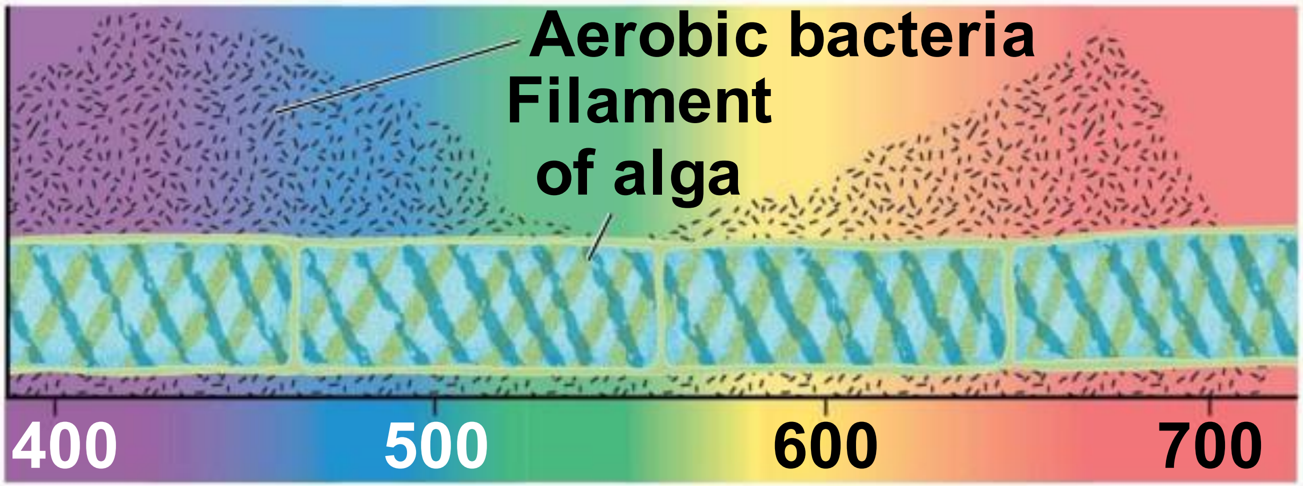
(a) Absorption spectra

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



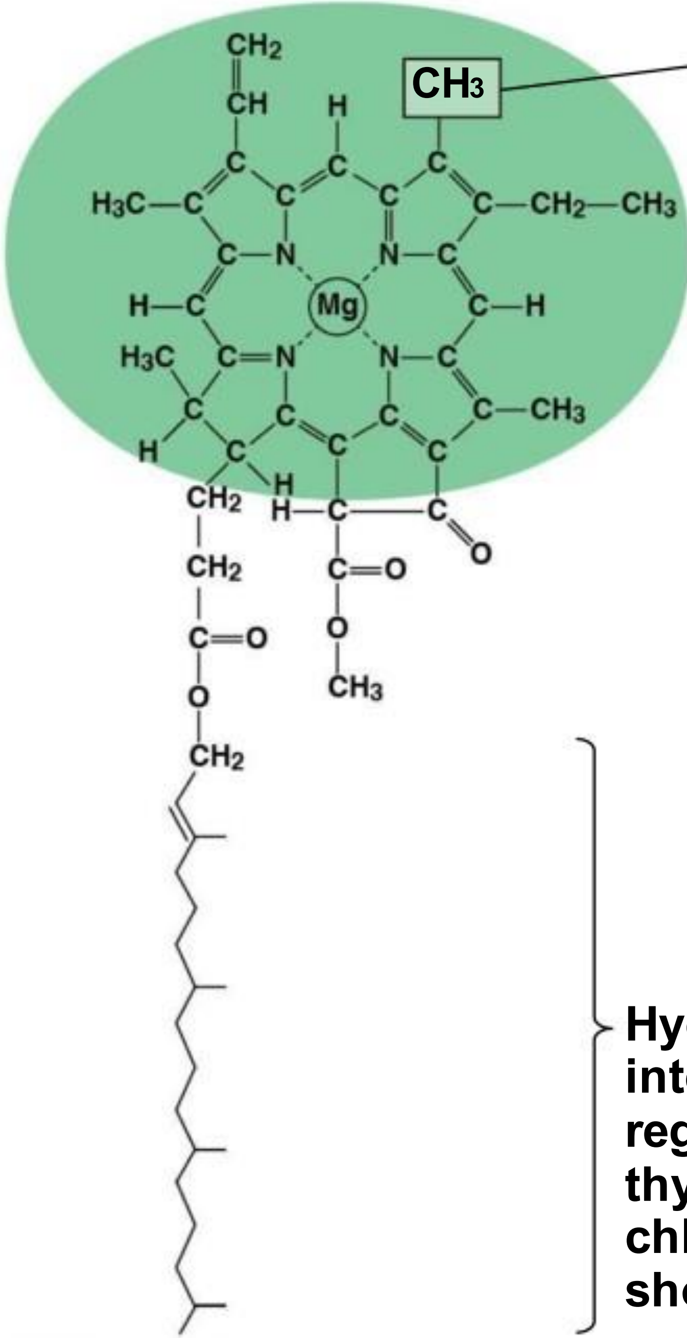
(b) Action spectrum

- 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



(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



CH_3 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

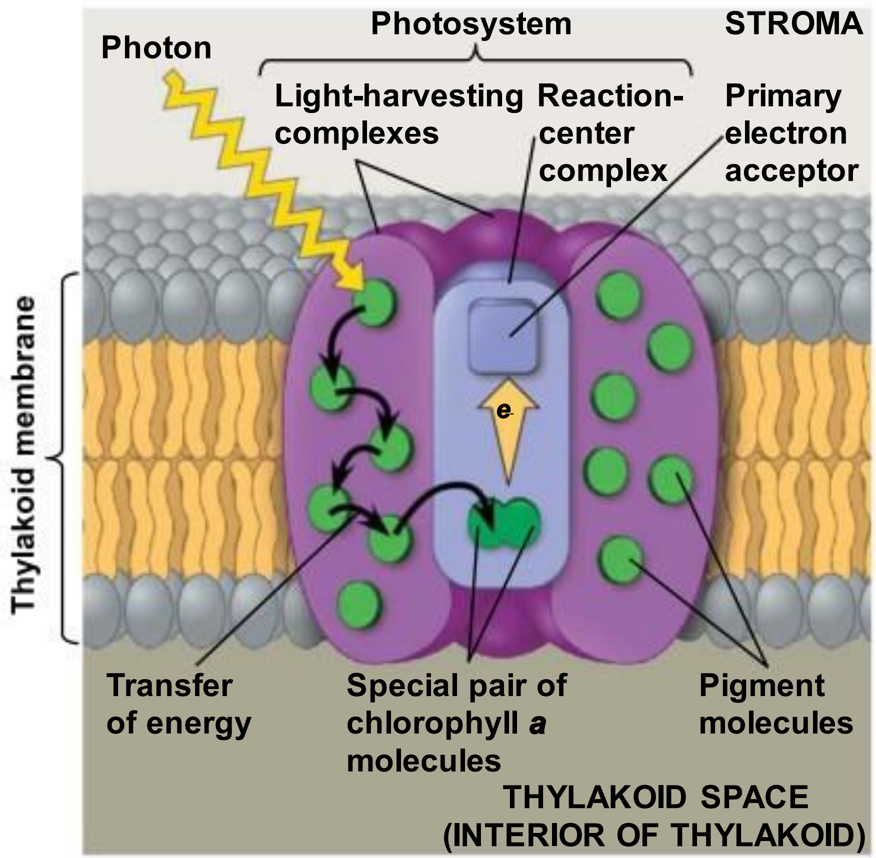
Excitation of Chlorophyll by Light

- 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

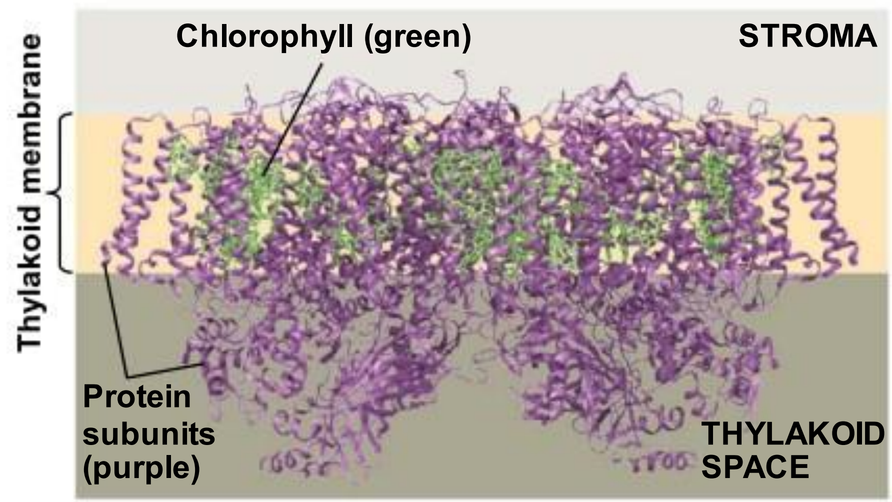
A Photosystem: A Reaction-Center Complex Associated with Light-Harvesting Complexes

- 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

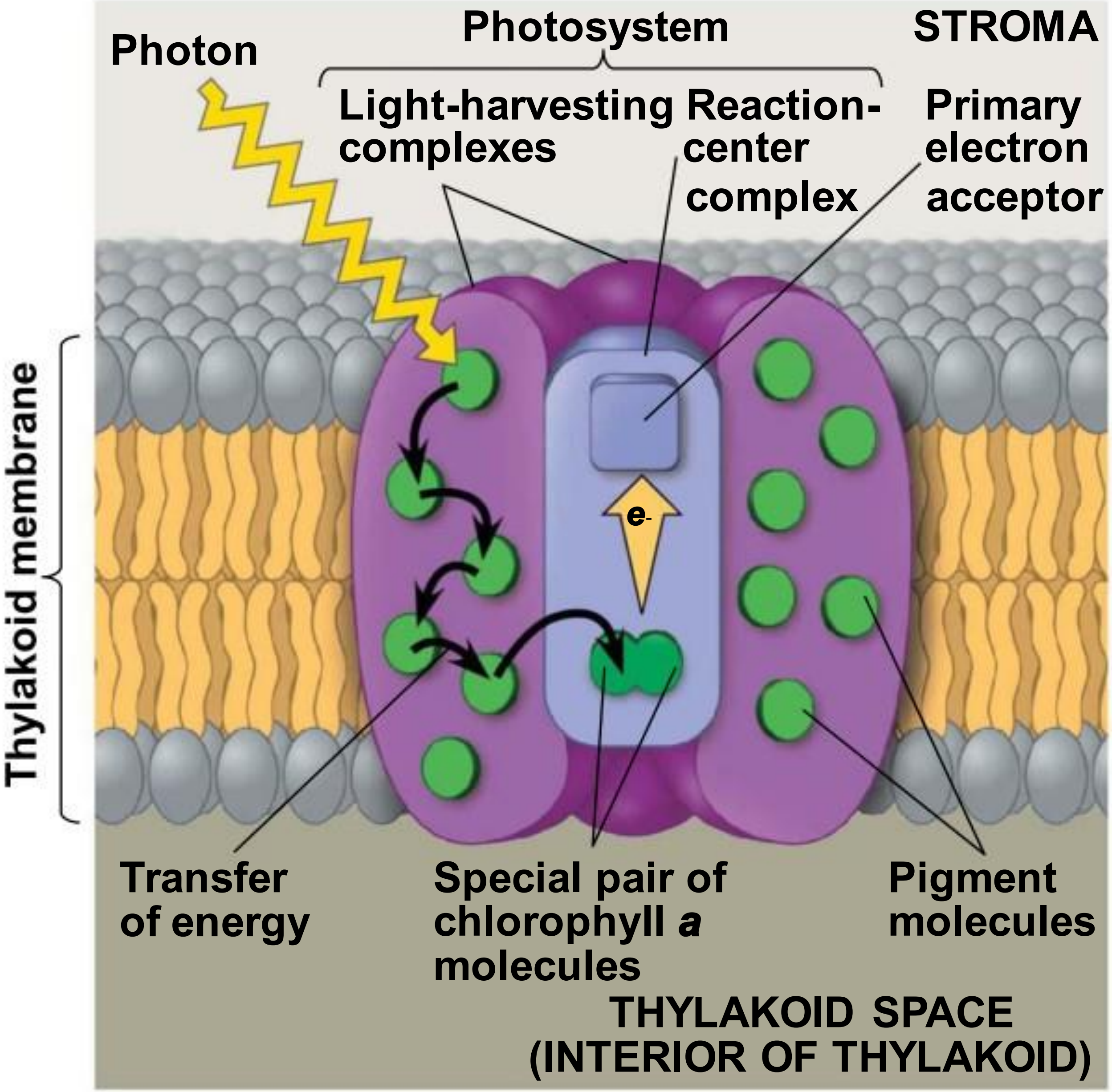
- A **primary electron acceptor** in the reaction center accepts excited electrons and is reduced as a result
- Solar-powered transfer of an electron from a chlorophyll *a* molecule to the primary electron acceptor is the first step of the light reactions



(a) How a photosystem harvests light



(b) Structure of a photosystem



(a) How a photosystem harvests light

- 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

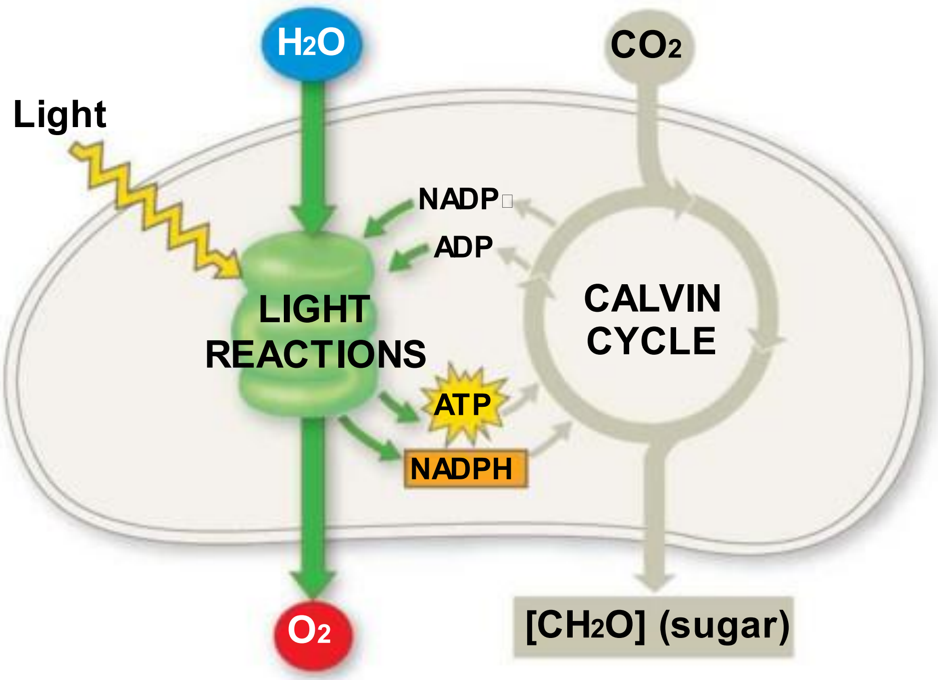
- Linear electron flow can be broken down into a series of steps

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

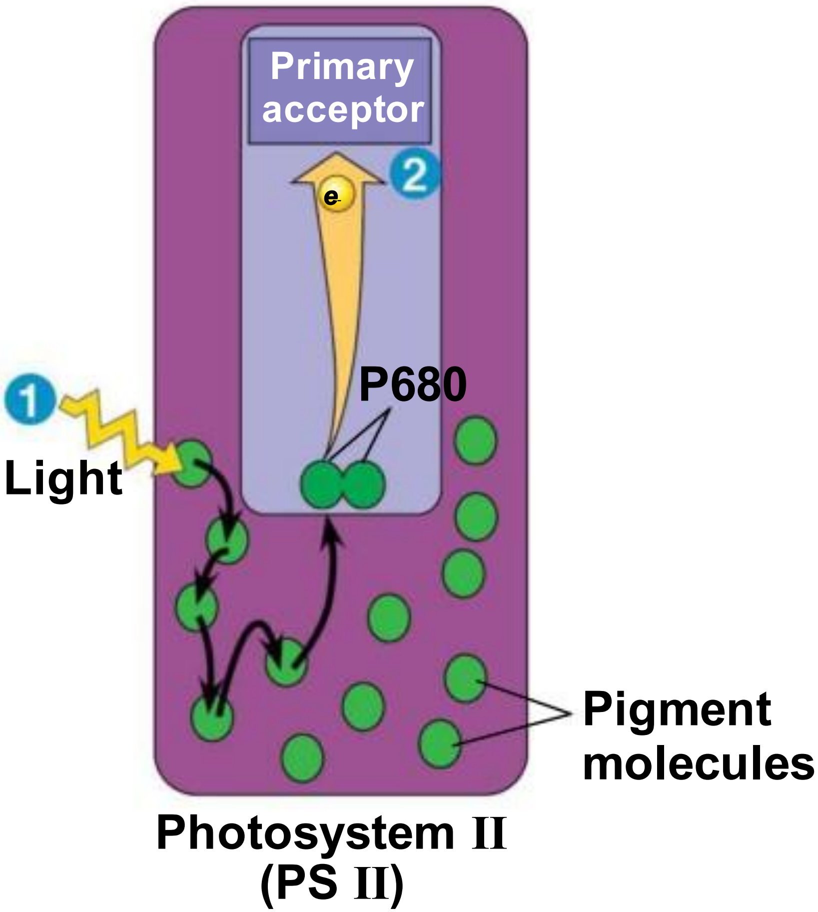
4. Each electron "falls" down an electron transport chain from the primary electron acceptor of PS II to PS I
5. Energy released by the fall drives the creation of a proton gradient across the thylakoid membrane; diffusion of H^+ (protons) across the membrane drives ATP synthesis

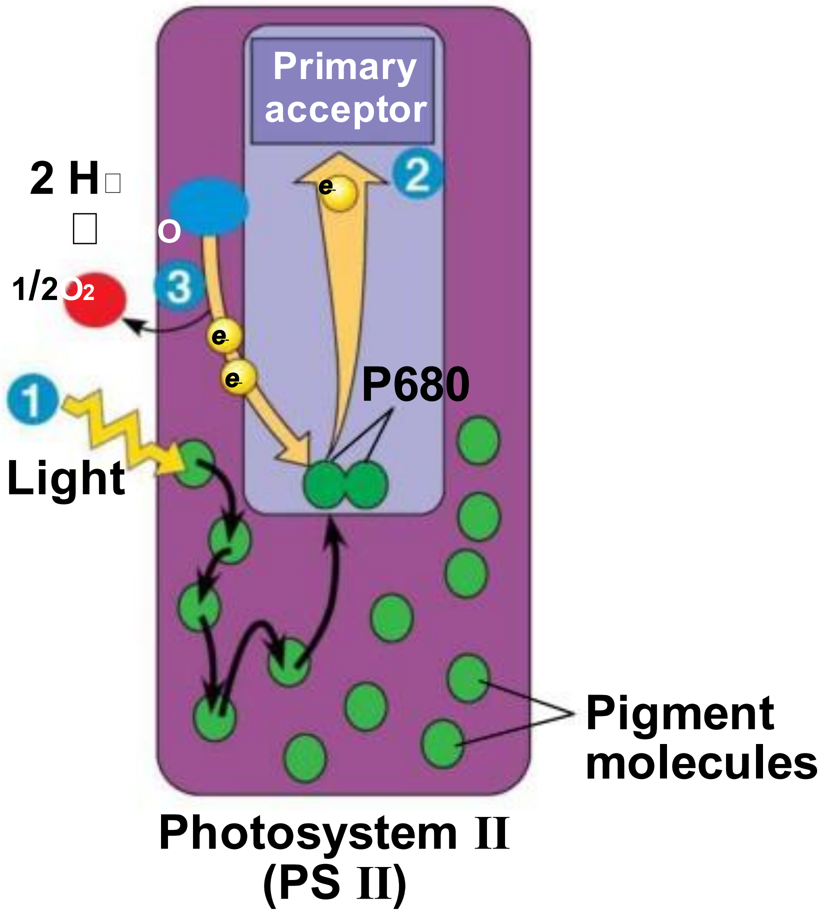
6. In PS I (like PS II), transferred light energy excites P700, causing it to lose an electron to an electron acceptor (we now call it $P700^{+}$)
   - $P700^{+}$ accepts an electron passed down from PS II via the electron transport chain

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



H_2O
CO_2
Light
NADP
ADP
LIGHT REACTIONS
CALVIN CYCLE
ATP
NADPH
O_2
$[CH_2O]$ (sugar)


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



Primary acceptor
2 H
O
1/2 O2
e
3
2
1
Light
P680
Pigment molecules
Photosystem II (PS II)

Figure 8.13-s3

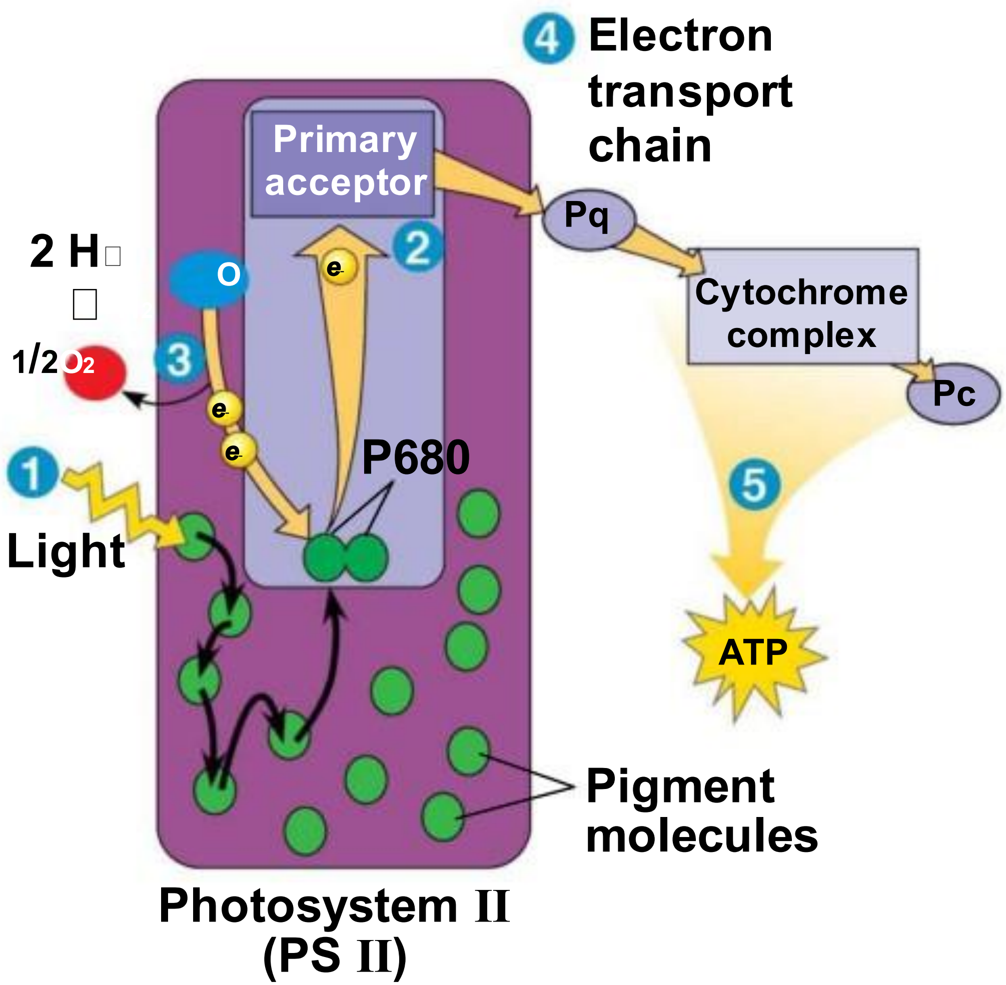
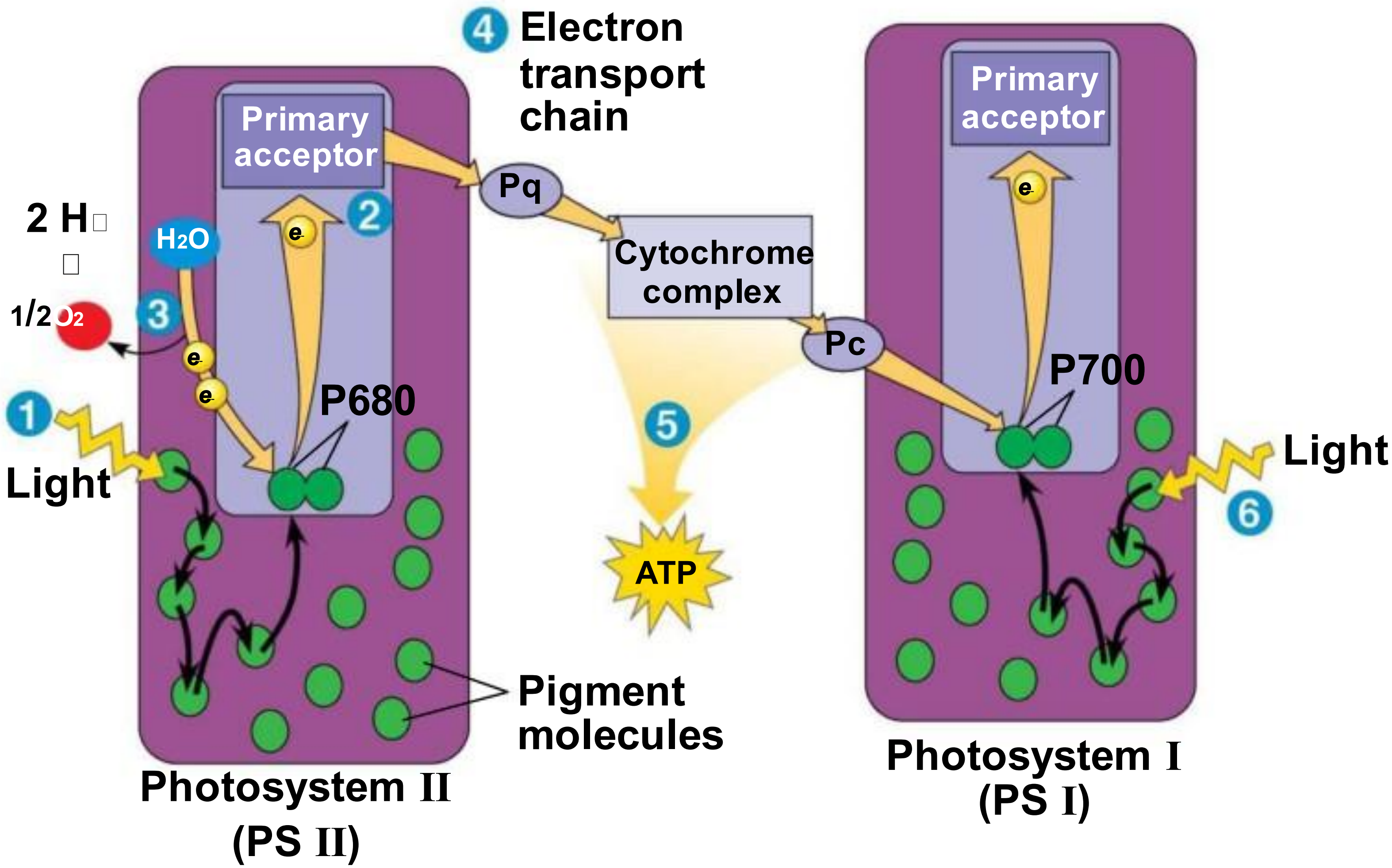
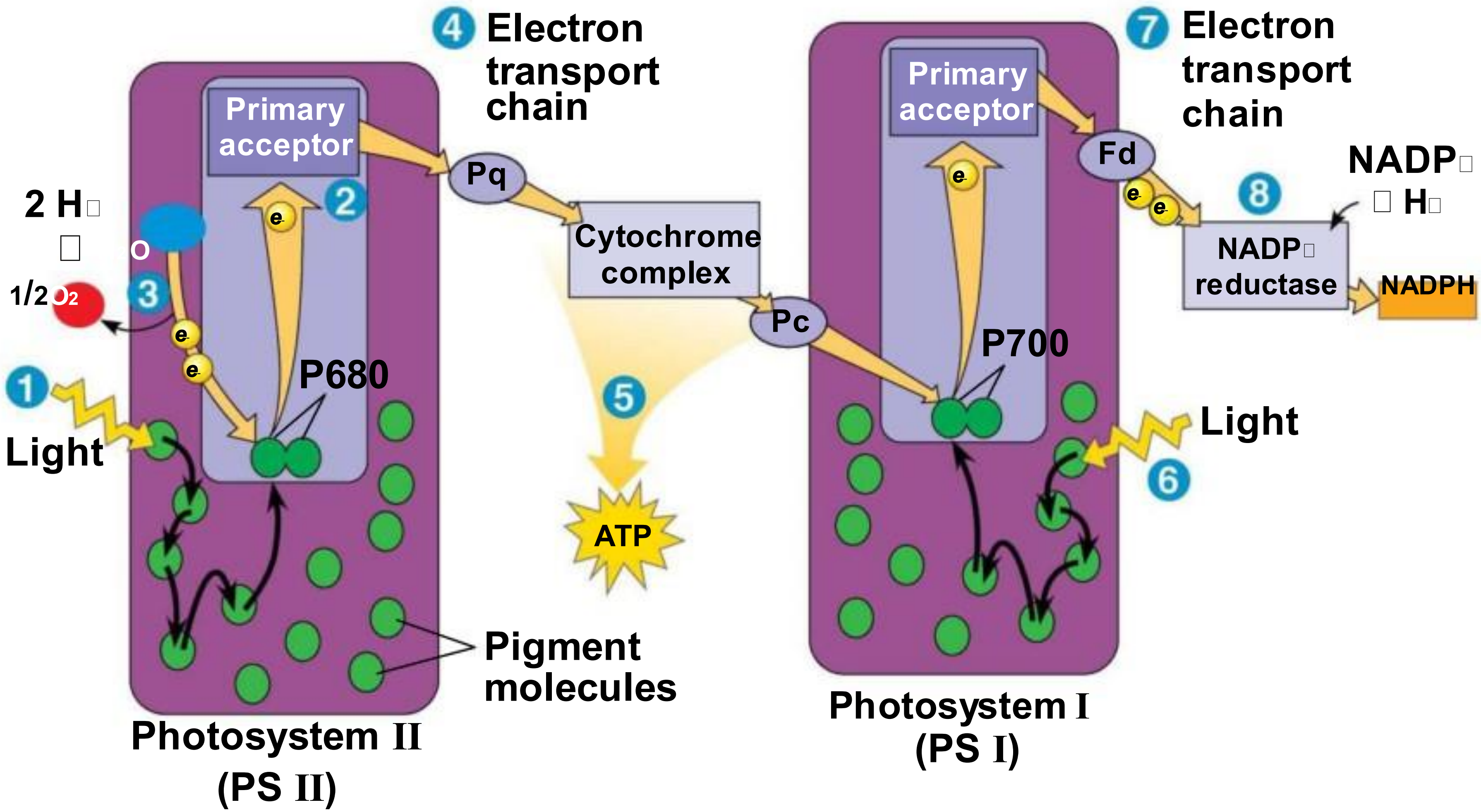


Figure 8.13-s4





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

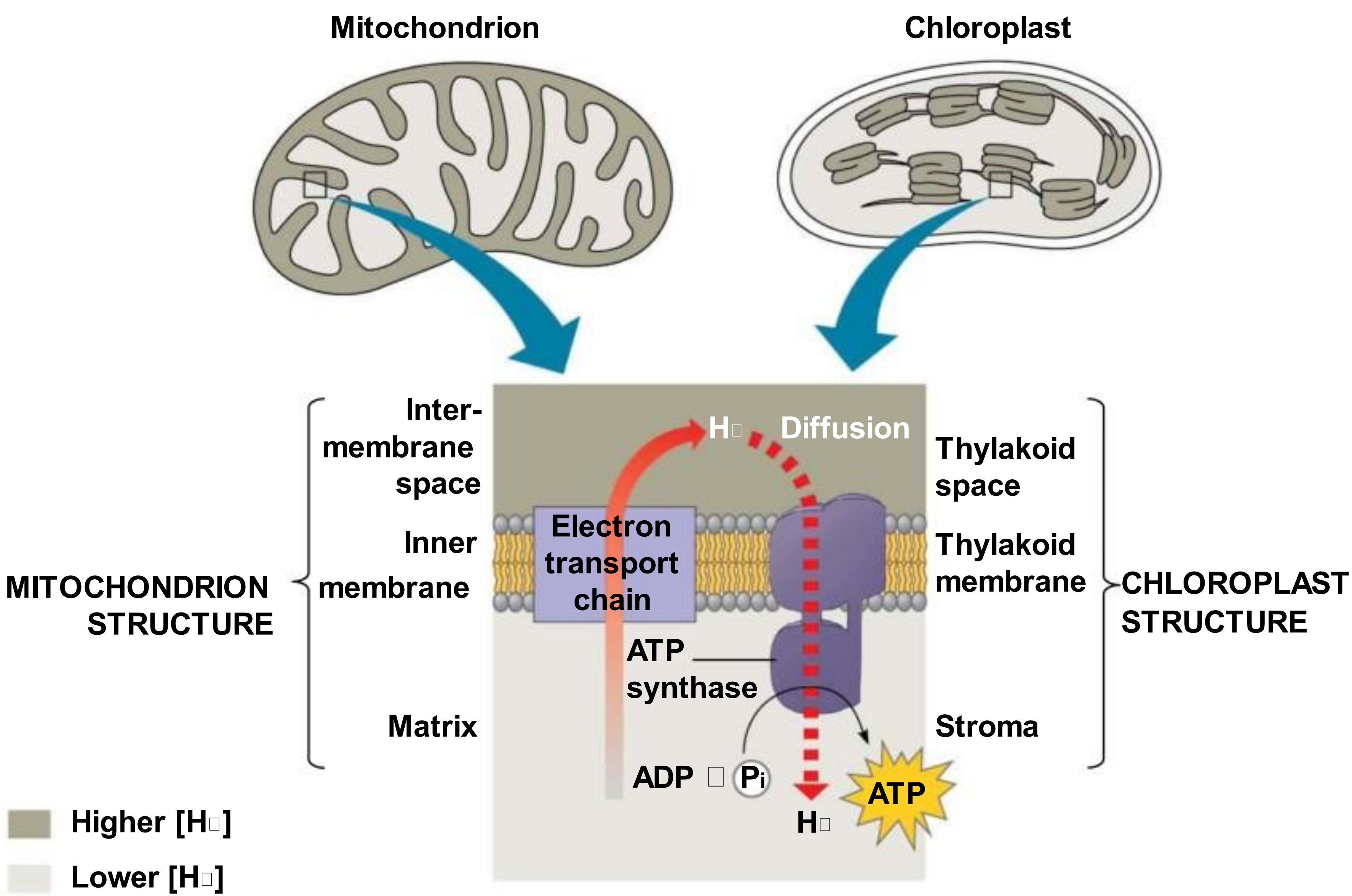
- The energy changes of electrons during linear flow can be represented in a mechanical analogy

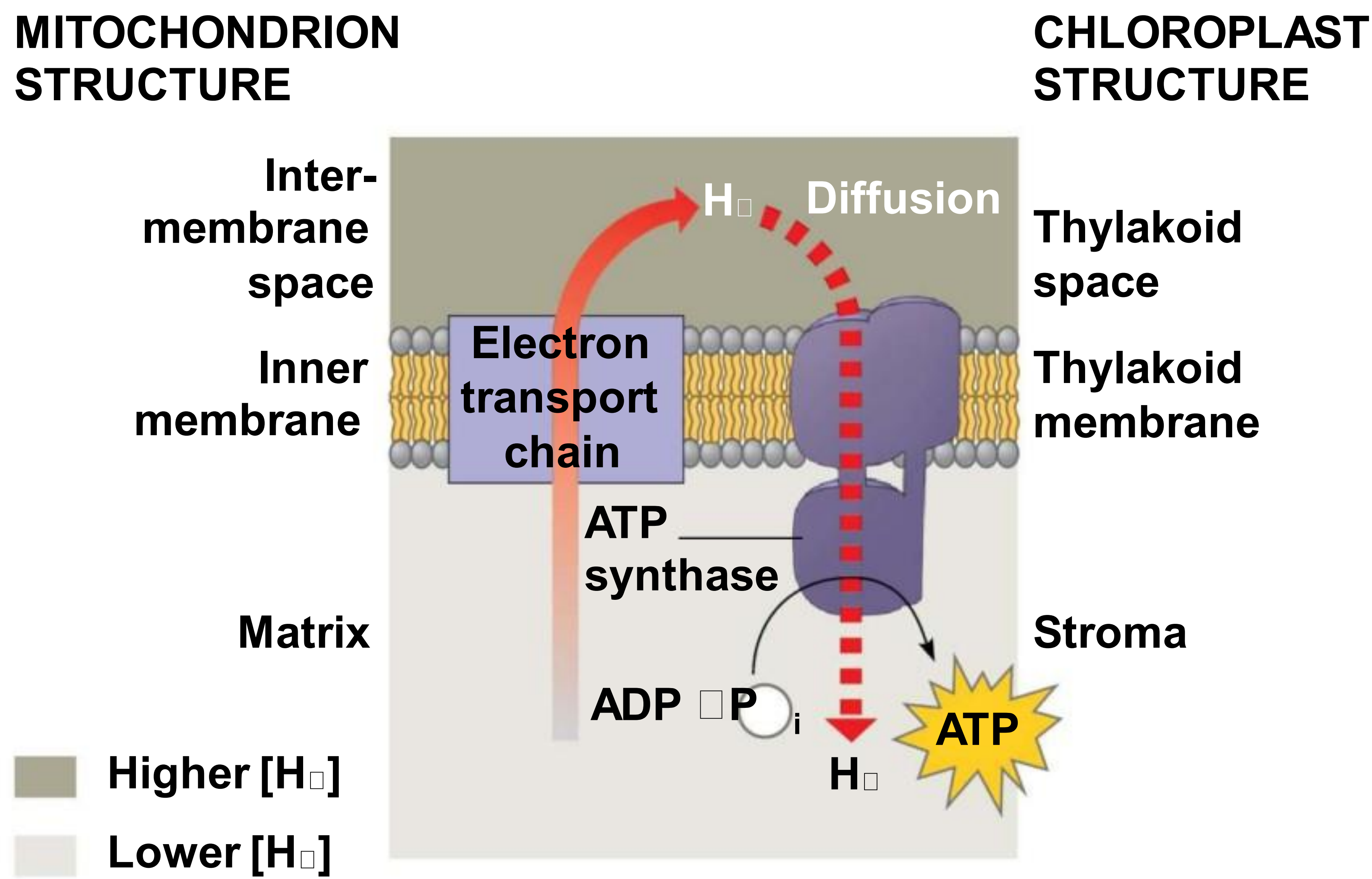
A Comparison of Chemiosmosis in Chloroplasts and Mitochondria

- 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

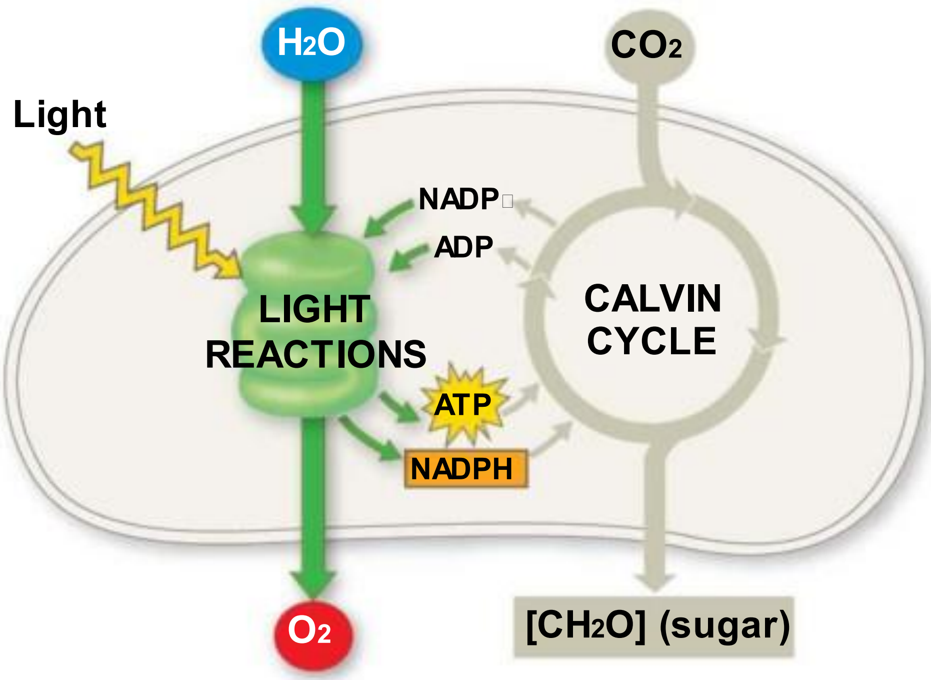
- Spatial organization of chemiosmosis differs between chloroplasts and mitochondria but there are also similarities
- Both use the energy generated by an electron transport chain to pump protons (H^+) across a membrane against their concentration gradient
- Both rely on the diffusion of protons through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

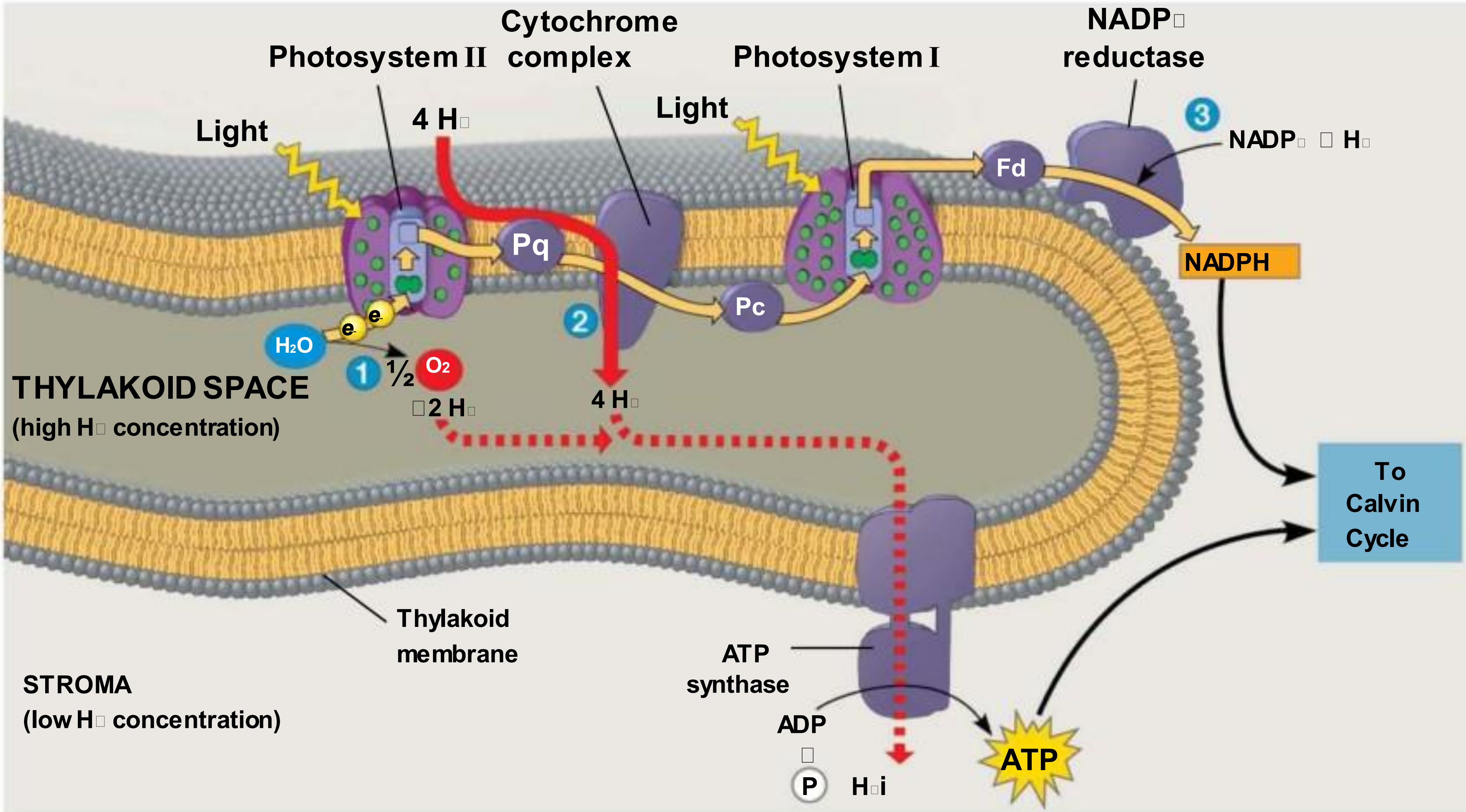

Mitochondrion
Chloroplast
MITOCHONDRION STRUCTURE
Inter-membrane space
Inner membrane
Matrix
H□
Diffusion
Electron transport chain
ATP synthase
ADP □ Pi
H□
ATP
Thylakoid space
Thylakoid membrane
Stroma
CHLOROPLAST STRUCTURE
Higher [H□]
Lower [H□]

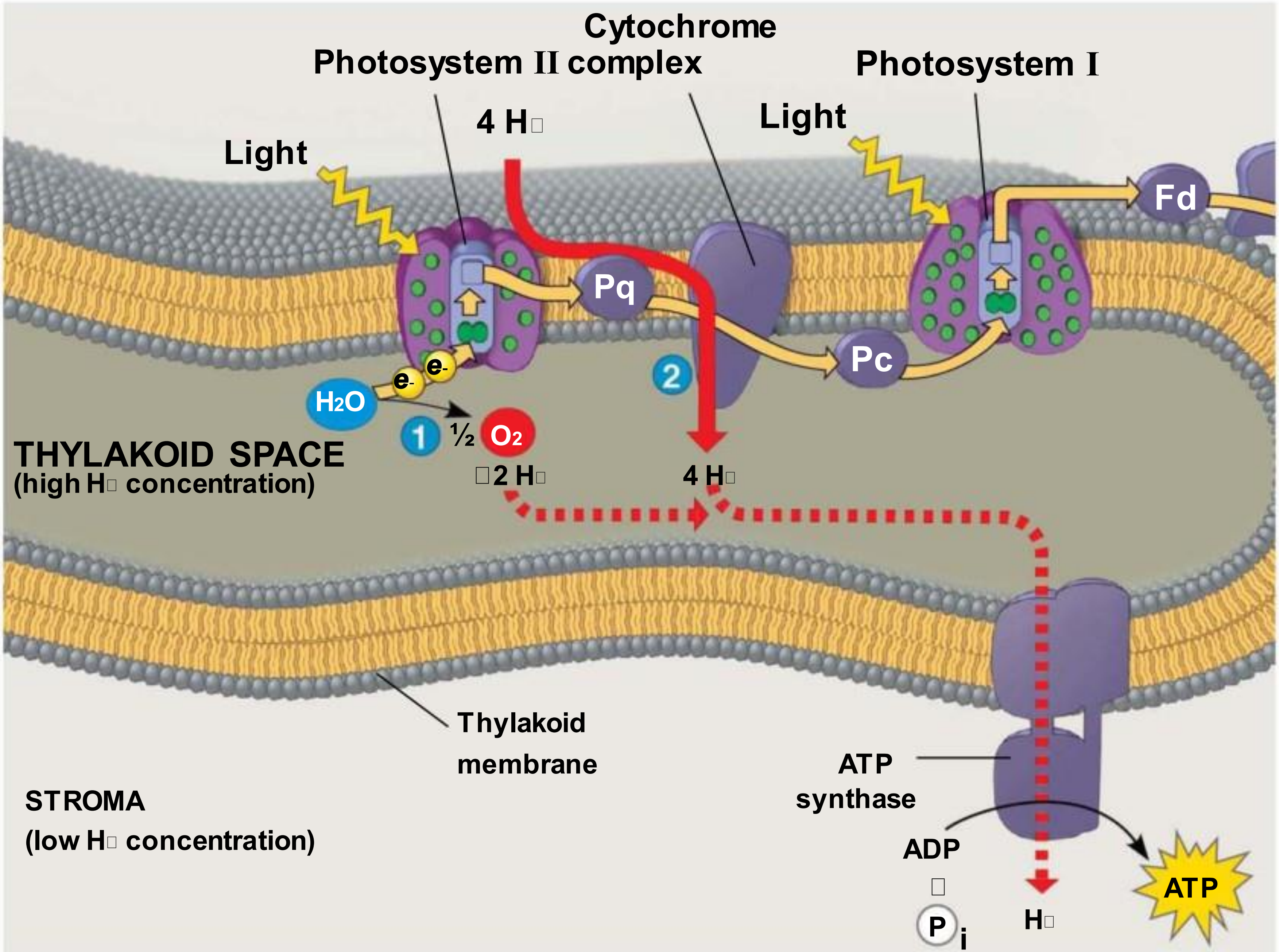

MITOCHONDRION STRUCTURE
CHLOROPLAST STRUCTURE
Inter-membrane space
H+
Diffusion
Thylakoid space
Inner membrane
Electron transport chain
Thylakoid membrane
ATP synthase
Matrix
Stroma
ADP + P i
ATP
H+
Higher [H+]
Lower [H+]

- 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

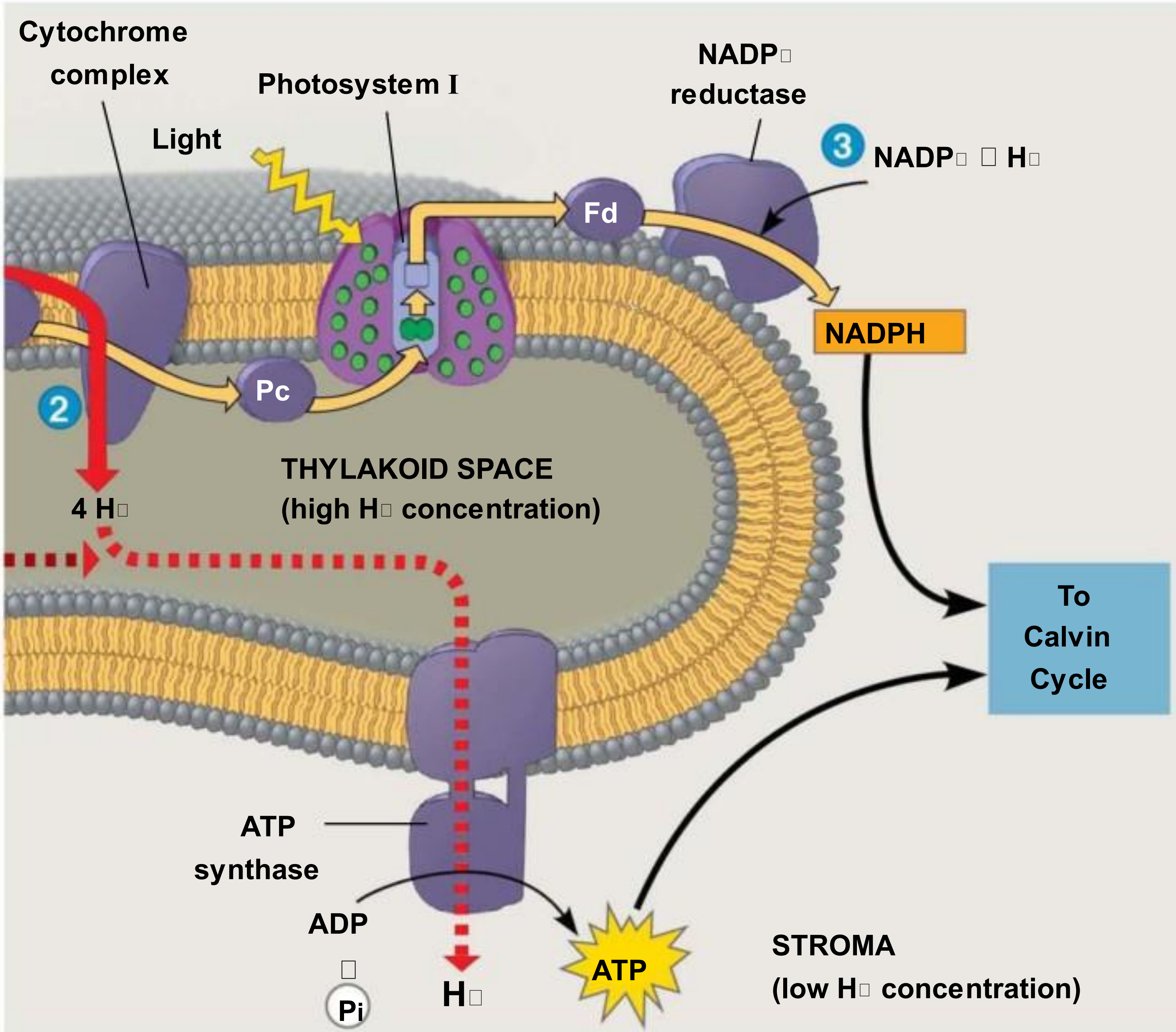


H_2O
CO_2
Light
NADP
ADP
LIGHT REACTIONS
CALVIN CYCLE
ATP
NADPH
O_2
$[CH_2O]$ (sugar)


Cytochrome complex
Photosystem II
Photosystem I
NADP+ reductase
Light
4 H+
Light
3
NADP+ + H+
Fd
Pq
NADPH
Pc
2
H_2O
e-
e-
1
½ O_2
+2 H+
4 H+
THYLAKOID SPACE
(high H+ concentration)
To Calvin Cycle
Thylakoid membrane
ATP synthase
STROMA
(low H+ concentration)
ADP
+
P
H+i
ATP



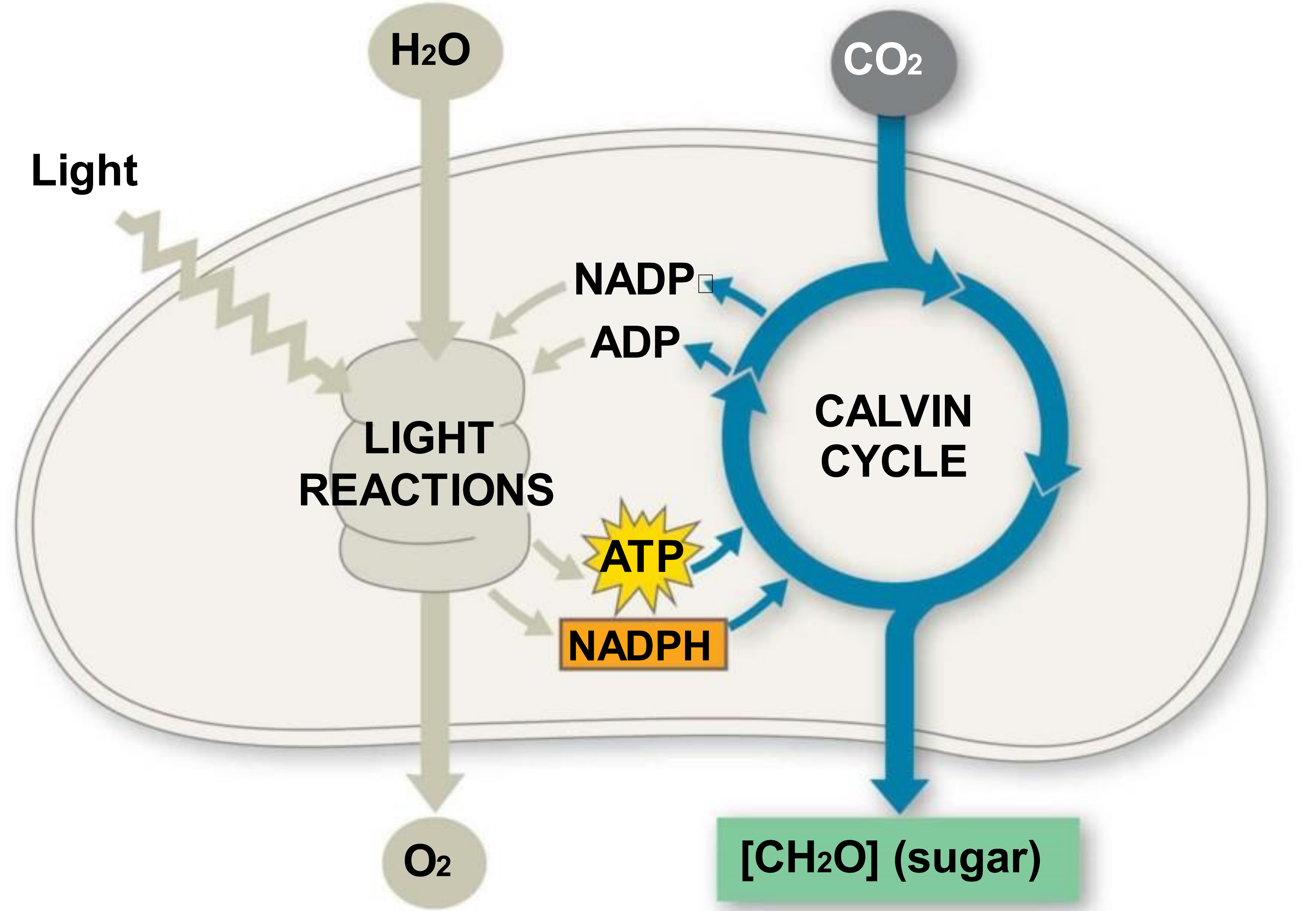
Cytochrome complex
Photosystem II
Photosystem I
Light
4 H
Light
Fd
Pq
Pc
e-
e-
H2O
2
1
½ O2
THYLAKOID SPACE
(high H concentration)
2 H
4 H
Thylakoid membrane
ATP synthase
STROMA
(low H concentration)
ADP
P i
H
ATP


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

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

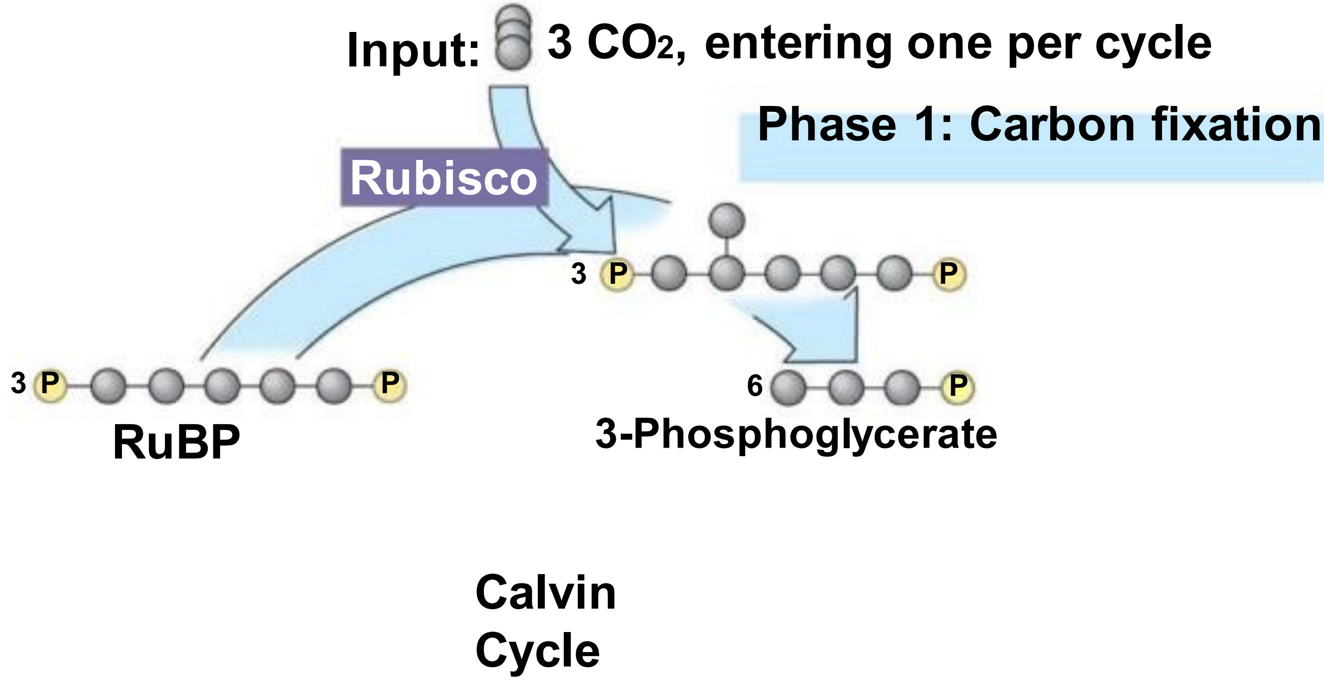
- The Calvin cycle, like the citric acid cycle, regenerates its starting material after molecules enter and leave the cycle
- Unlike the citric acid cycle, the Calvin cycle is anabolic
- It builds sugar from smaller molecules by using ATP and the reducing power of electrons carried by NADPH

- 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

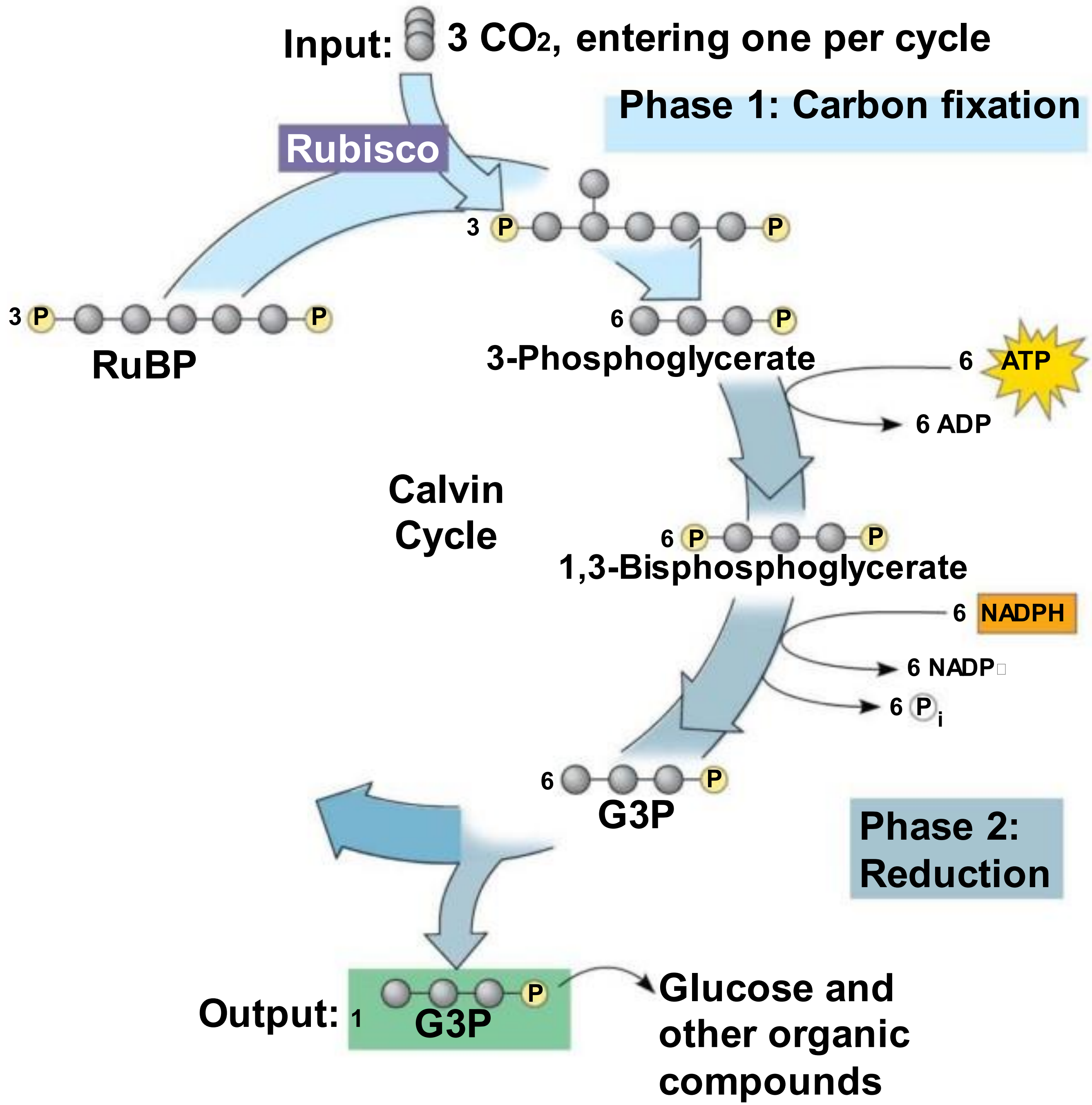


H_2O
CO_2
Light
NADP
ADP
LIGHT REACTIONS
CALVIN CYCLE
ATP
NADPH
O_2
[CH_2O] (sugar)

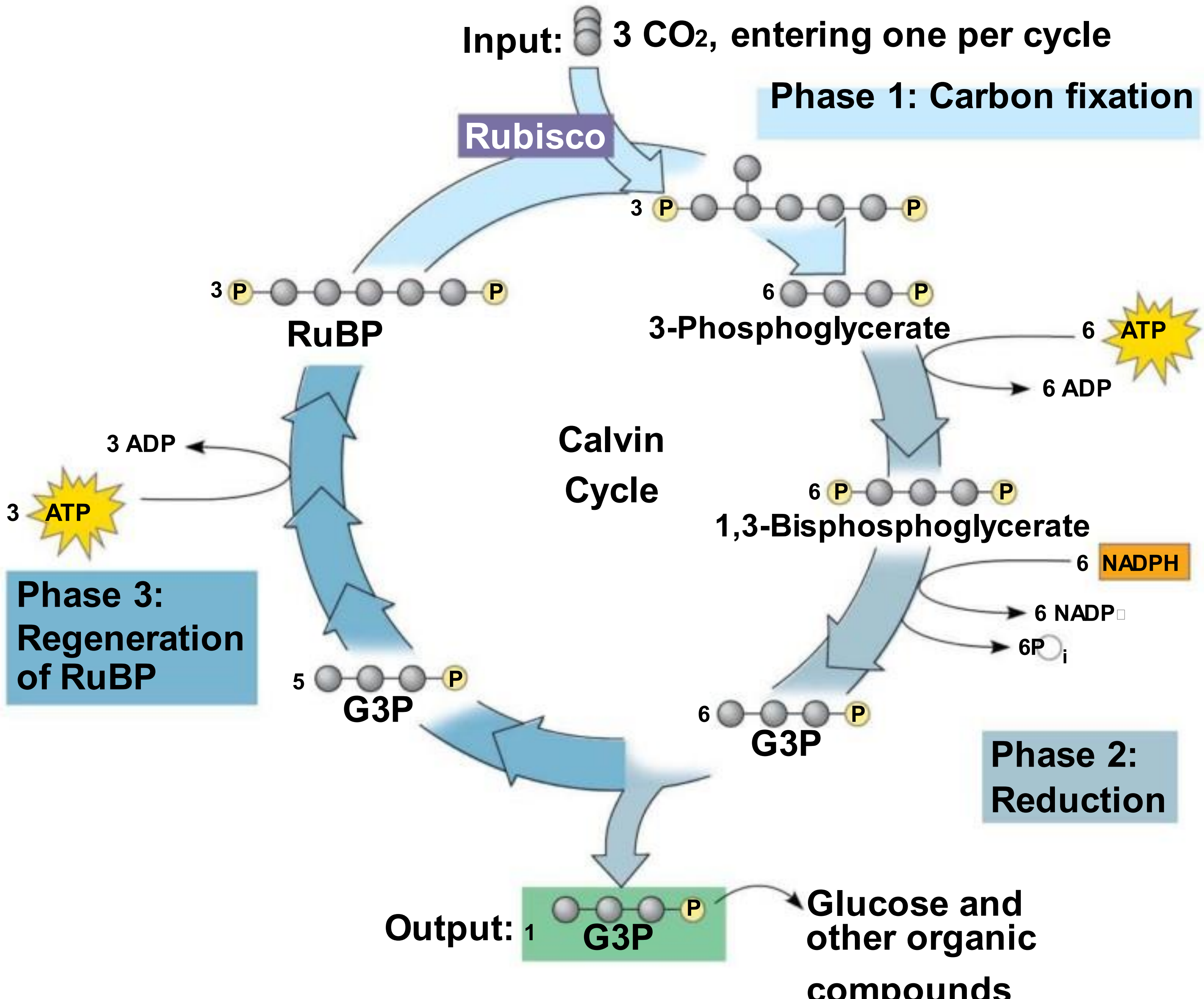
- **Phase 1**, **carbon fixation**, involves the incorporation of the CO_2 molecules into ribulose bisphosphate (RuBP) using the enzyme **rubisco**
- The product is 3-phosphoglycerate


Input:
3 CO_2, entering one per cycle
Phase 1: Carbon fixation
Rubisco
3 P P
3 P P
6 P
RuBP
3-Phosphoglycerate
Calvin
Cycle

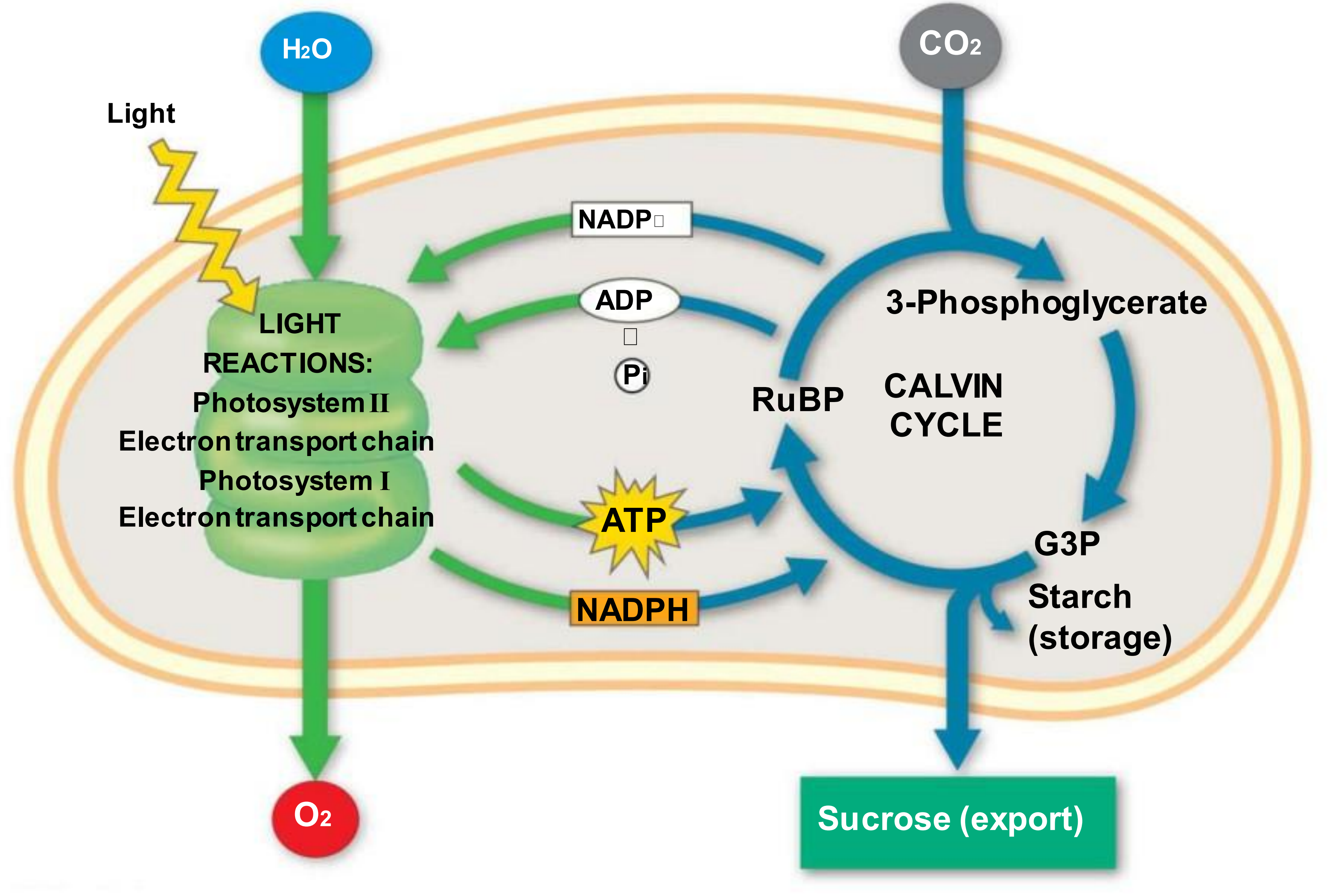
- **Phase 2**, **reduction**, involves the reduction and phosphorylation of 3-phosphoglycerate to G3P
- Six ATP and six NADPH are required to produce six molecules of G3P, but only one exits the cycle for use by the cell


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

- **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



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



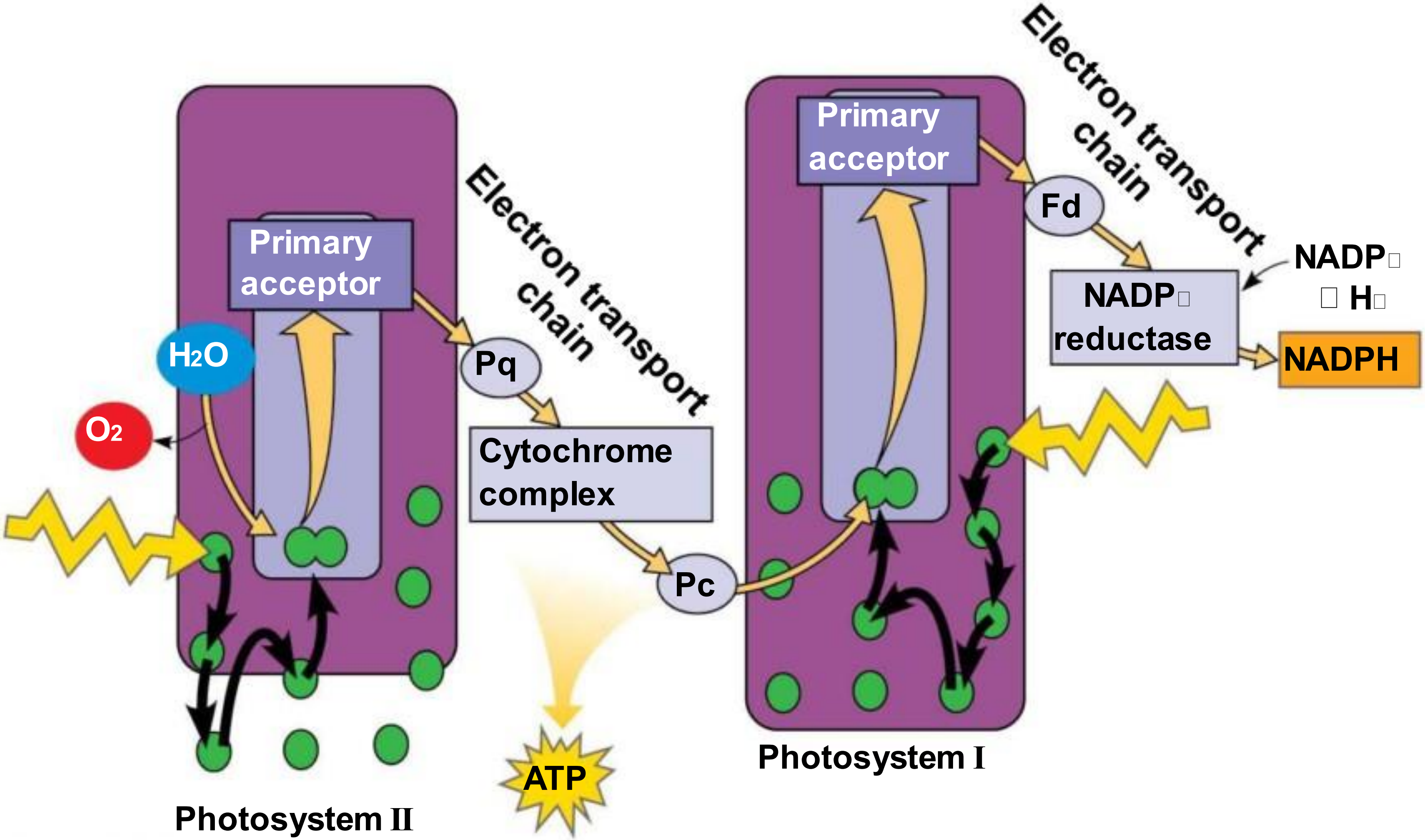
H_2O
CO_2
Light
NADP
ADP
Pi
LIGHT
REACTIONS:
Photosystem II
Electron transport chain
Photosystem I
Electron transport chain
ATP
NADPH
3-Phosphoglycerate
RuBP
CALVIN
CYCLE
G3P
Starch
(storage)
O_2
Sucrose (export)

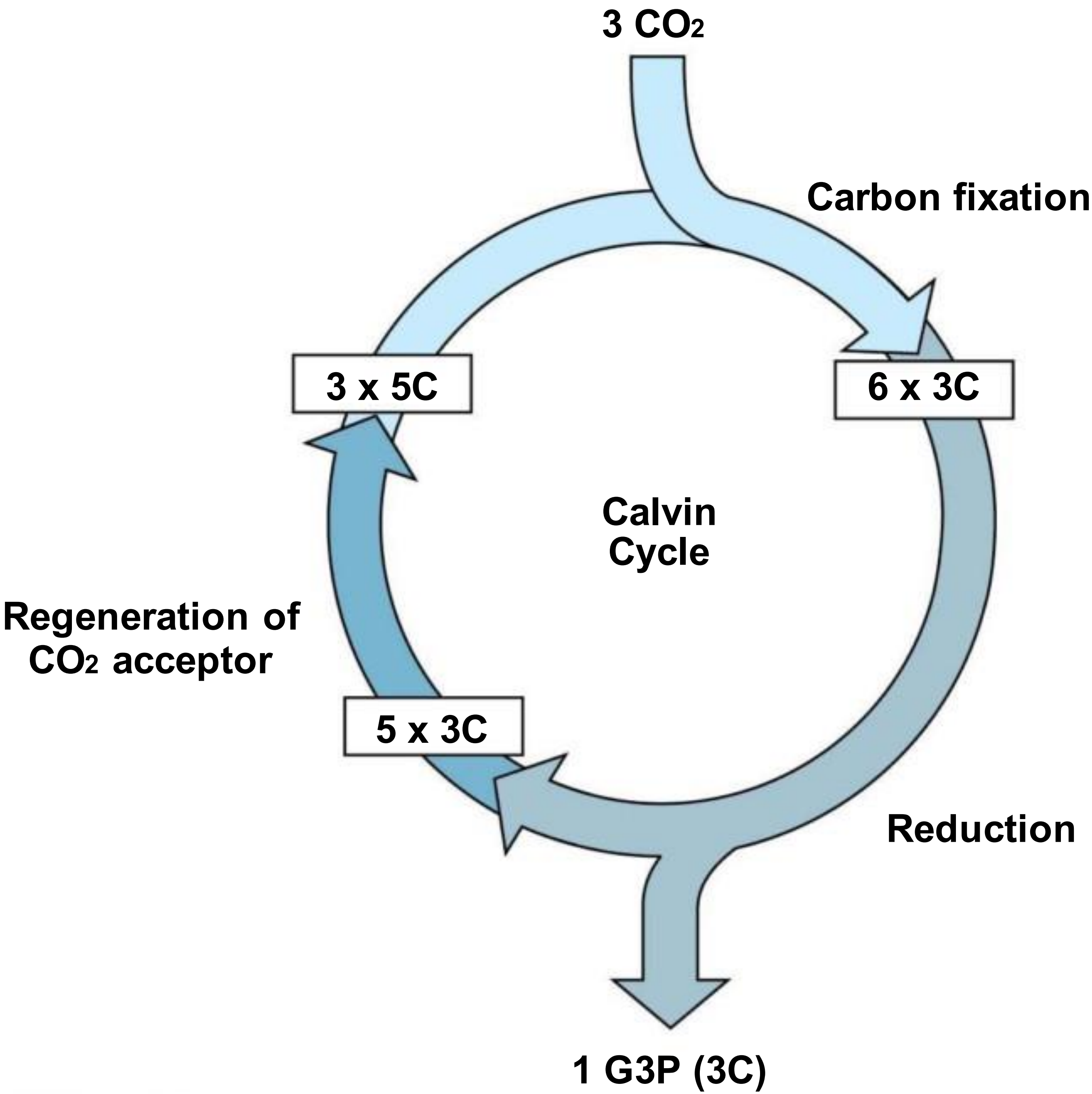
LIGHT REACTIONS

- 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


Electron transport chain
Primary acceptor
Pq
Cytochrome complex
Pc
ATP
H_2O
O_2
Photosystem II
Primary acceptor
Fd
Electron transport chain
NADP□ reductase
NADP□
□ H□
NADPH
Photosystem I


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