Chapter 10

Photosynthesis

Lectures by
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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
• **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
• CO₂ enters and O₂ 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
Tracking Atoms Through Photosynthesis: Scientific Inquiry

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

\[ 6 \text{CO}_2 + 12 \text{H}_2\text{O} + \text{Light energy} \rightarrow \text{C}_6\text{H}_{12}\text{O}_6 + 6 \text{O}_2 + 6 \text{H}_2\text{O} \]
The Splitting of Water

- Chloroplasts split $\text{H}_2\text{O}$ into hydrogen and oxygen, incorporating the electrons of hydrogen into sugar molecules and releasing oxygen as a by-product.
Figure 10.5

Reactants:
6 \( \text{CO}_2 \)  
12 \( \text{H}_2\text{O} \)

Products:
\( \text{C}_6\text{H}_{12}\text{O}_6 \)  
6 \( \text{H}_2\text{O} \)  
6 \( \text{O}_2 \)
**Photosynthesis as a Redox Process**

- Photosynthesis reverses the direction of electron flow compared to respiration.
- Photosynthesis is a redox process in which $\text{H}_2\text{O}$ is oxidized and $\text{CO}_2$ is reduced.
- Photosynthesis is an endergonic process; the energy boost is provided by light.
Energy + 6 CO₂ + 6 H₂O → C₆H₁₂O₆ + 6 O₂

becomes reduced

becomes oxidized
The Two Stages of Photosynthesis:
A Preview

• Photosynthesis consists of the light reactions (the \textit{photo} part) and Calvin cycle (the \textit{synthesis} part)

• The light reactions (in the thylakoids)
  – Split H\textsubscript{2}O
  – Release O\textsubscript{2}
  – Reduce \textbf{NADP}^{+} to NADPH
  – Generate ATP from ADP by \textit{photophosphorylation}
• The Calvin cycle (in the stroma) forms sugar from CO\textsubscript{2}, using ATP and NADPH
• The Calvin cycle begins with **carbon fixation**, incorporating CO\textsubscript{2} into organic molecules
Light Reactions

Calvin Cycle

\[ \text{[CH}_2\text{O]} \text{ (sugar)} \]

\[ \text{ATP} \]

\[ \text{ADP} + P_i \]

\[ \text{NADP}^+ \]

\[ \text{H}_2\text{O} \]

\[ \text{CO}_2 \]

\[ \text{O}_2 \]

Chloroplast

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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

- Gamma rays
- X-rays
- UV
- Infrared
- Microwaves
- Radio waves

Visible light

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

Chloroplast

Light

Reflected light

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

Slit moves to pass light of selected wavelength.

Green light

High transmittance (low absorption): Chlorophyll absorbs very little green light.

Blue light

Low transmittance (high absorption): Chlorophyll absorbs most blue light.

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• 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.
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

Hydrocarbon tail (H atoms not shown)

Porphyrin ring

CH$_3$ in chlorophyll $a$

CHO in chlorophyll $b$
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) 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

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• 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$_2$O 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

**Photosystem II (PS II)**

1. Light

2. Primary acceptor

3. $2 \text{H}^+ + \frac{1}{2} \text{O}_2 \rightarrow \text{H}_2\text{O}

4. Electron transport chain

5. Cytochrome complex

6. ATP

7. Electron transport chain

8. NADP$^+ + \text{H}^+$

**Photosystem I (PS I)**

- Primary acceptor
- Cytochrome complex
- Fd
- NADP$^+$ reductase
- NADPH

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Figure 10.15

Photosystem II

Mill makes ATP

ATP

NADPH

e⁻ → e⁻ → e⁻ → e⁻ → e⁻ → e⁻

Photosystem II

Photosystem I

Photon

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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

Photosystem I

Primary acceptor
Cytochrome complex
Pc
ATP

Photosystem II

Primary acceptor
Cytochrome complex
Pq

Fd

NADP⁺ reductase
NADP⁺ + H⁺
NADPH

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• 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

Intermembrane space

Thylakoid space

Inner membrane

Thylakoid membrane

Matrix

Stroma

Electron transport chain

ATP synthase

H^+ Diffusion

ADP + P_i → 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 H₂O to NADPH
Figure 10.18

**STROMA** (low H⁺ concentration)

**THYLAKOID SPACE** (high H⁺ concentration)

**Photosystem II**

1. **Light**
   - **H₂O** → **1/2 O₂** + **2 H⁺**

2. **4 H⁺**

**Cytochrome complex**

3. **NADP⁺ reductase**
   - **NADP⁺ + H⁺**

**Photosystem I**

4. **ATP synthase**
   - **ADP + P** → **ATP**

**Thylakoid membrane**

**To Calvin Cycle**
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-phosphate (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)
Phase 1: Carbon fixation

Rubisco

3 \[\text{CO}_2\] (Entering one at a time)

Short-lived intermediate

3 \[\text{P} \]

6

ADP

ATP

3 \[\text{P} \]

1,3-Bisphosphoglycerate

6

NADPH

6 NADP⁺

6 \[\text{P} \]

Glyceraldehyde 3-phosphate (G3P)

Phase 2: Reduction

G3P

Glucose and other organic compounds

Output

Phase 3: Regeneration of the CO₂ acceptor (RuBP)

Ribulose bisphosphate (RuBP)

3 \[\text{P} \]

5 G3P

3 ADP

3 ATP

Input

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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<sub>3</sub> plants), initial fixation of CO<sub>2</sub>, via rubisco, forms a three-carbon compound (3-phosphoglycerate)
- In photorespiration, rubisco adds O<sub>2</sub> instead of CO<sub>2</sub> in the Calvin cycle, producing a two-carbon compound
- Photorespiration consumes O<sub>2</sub> and organic fuel and releases CO<sub>2</sub> 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.
**C₄ Plants**

- **C₄ plants** minimize the cost of photorespiration by incorporating CO₂ into four-carbon compounds in mesophyll cells.
- This step requires the enzyme **PEP carboxylase**.
- PEP carboxylase has a higher affinity for CO₂ than rubisco does; it can fix CO₂ even when CO₂ concentrations are low.
- These four-carbon compounds are exported to **bundle-sheath cells**, where they release CO₂ that is then used in the Calvin cycle.
Photosynthetic cells of $C_4$ plant leaf

Mesophyll cell

Bundle-sheath cell

Vein (vascular tissue)

Stoma

C$_4$ leaf anatomy

The $C_4$ pathway

Mesophyll cell

PEP carboxylase

Oxaloacetate (4C) → PEP (3C)

Malate (4C) → Pyruvate (3C)

CO$_2$ → Sugar

Calvin Cycle

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
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

Sugarcane

Mesophyll cell

Bundle-sheath cell

CO₂

Organic acid

Sugar

CO₂

Calvin Cycle

Sugar

(b) Temporal separation of steps

Pineapple

CAM

CO₂

Organic acid

Sugar

CO₂

Calvin Cycle

Sugar

1. CO₂ incorporated (carbon fixation)

2. CO₂ released to the Calvin cycle
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 $\text{O}_2$ in our atmosphere.
Light

Reactions:
Photosystem II
Electron transport chain
Photosystem I
Electron transport chain

RuBP
3-Phosphoglycerate
Calvin Cycle
G3P
Starch (storage)

NADP$^+$
ADP + $P_i$

ATP
NADPH

H$_2$O
CO$_2$

O$_2$

Chloroplast

SUcrose (export)
Figure 10.UN02

Photosystem II

- Primary acceptor
- Electron transport chain
- H$_2$O
- O$_2$

Photosystem I

- Primary acceptor
- Electron transport chain
- Fd
- NADP$^+$ reductase
- NADP$^+$ + H$^+$
- NADPH

Cytochrome complex

ATP
Regeneration of CO$_2$ acceptor

Carbon fixation

Calvin Cycle

Reduction

1 G3P (3C)

3 CO$_2$

3 × 5C

5 × 3C

6 × 3C

3 × 3C
Figure 10.UN08

High $H^+$ concentration ($pH=4$)

Low $H^+$ concentration ($pH=8$)

$ADP + P_i \rightarrow ATP$