## CAMPBELL BIOLOGY

TENTH EDITION

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## Photosynthetic Processes

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#### 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<sub>2</sub> and other inorganic molecules
- Almost all plants are photoautotrophs, using the energy of sunlight to make organic molecules





Other organisms also benefit from photosynthesis.

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





#### (a) Plants

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#### (b) Multicellular alga





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## (e) Purple sulfur bacteria

## C.B. Van Niel – 1930's

- Observed photosynthesis in purple sulfur bacteria
- $CO_2 + 2H_2S + light energy => (CH_2O) + H_2O + 2S$
- Van Niel then generalized this to the following reaction for all photosynthetic activity
- $CO_2 + 2H_2A + light energy => (CH_2O) + H_2O + 2A$

- 相對於autotrophs
- 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<sub>2</sub>

- 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



#### HOW COAL WAS FORMED

Before the dinosaurs, many giant plants died in swamps. Heat and pressure turned the dead plants into coal.

#### **PETROLEUM & NATURAL GAS FORMATION**

were buried under water and dirt.



Tiny sea plants and animals died and were buried on the ocean floor. Over time, they were covered by layers of silt and sand. Over millions of years, the remains were buried deeper and deeper. The enormous heat and pressure turned them into oil and gas. Today, we drill down through layers of sand, silt, and rock to reach the rock formations that contain oil and gas deposits.





# Concept 11.1: Photosynthesis converts light energy to the chemical energy of food

- Chloroplasts are structurally similar to and likely evolved from photosynthetic bacteria 藍綠菌
- The structural organization of these organelles allows for the chemical reactions of photosynthesis
  基質 stroma





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## Chloroplasts: The Sites of Photosynthesis in Plants

- Leaves are the major locations of photosynthesis
- Chloroplasts are found mainly in cells of the mesophyll, the interior tissue of the leaf
- Each mesophyll cell contains 30–40 chloroplasts
- CO<sub>2</sub> enters and O<sub>2</sub> exits the leaf through microscopic pores called stomata





- A chloroplast has an envelope of two membranes surrounding a dense fluid called the stroma
- Thylakoids are connected sacs in the chloroplast which compose a third membrane system
- Thylakoids may be stacked in columns called grana
- Chlorophyll, the pigment which gives leaves their green colour, resides in the thylakoid membranes





### 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 overall chemical change during photosynthesis is the reverse of the one that occurs during cellular respiration

## The Splitting of Water

 Chloroplasts split H<sub>2</sub>O into hydrogen and oxygen, incorporating the electrons of hydrogen into sugar molecules and releasing oxygen as a by-product



#### Photosynthesis as a Redox Process

- Photosynthesis reverses the direction of electron flow compared to respiration
- Photosynthesis is a redox process in which H<sub>2</sub>O is oxidized and CO<sub>2</sub> is reduced
- Photosynthesis is an endergonic process; the energy boost is provided by light



### 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<sub>2</sub>O
  - Release O<sub>2</sub>
  - Reduce the electron acceptor NADP+ to NADPH
  - Generate ATP from ADP by photophosphorylation

- The Calvin cycle (in the stroma) forms sugar from CO<sub>2</sub>, using ATP and NADPH
- The Calvin cycle begins with carbon fixation, incorporating CO<sub>2</sub> into organic molecules









### **BioFlix: The Carbon Cycle**



### **BioFlix: Photosynthesis**



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### Concept 11.2: The light reactions convert solar energy to the chemical energy of ATP and NADPH

- Chloroplasts are solar-powered chemical factories
- Their <u>thylakoids</u> 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



### 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



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### **Animation: Light and Pigments**



- 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 11.9



Slit moves to pass light of selected wavelength.

Green light The high transmittance (low absorption) reading indicates that chlorophyll absorbs very little green 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



(a) Absorption spectra



(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<sub>2</sub>
- He used the growth of aerobic bacteria clustered along the alga as a measure of O<sub>2</sub> production

#### oxygen seeking bacteria B. termo



#### (c) Engelmann's experiment

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### Why so many chlorophyll pigments?

In response to different wavelength in the environment!

- 1. shading
- 2. under forest

# Chl *b*/Chl *a* increases (Chl *b* content increases)

- Chlorophyll a is the main photosynthetic pigment
- Chlorophyll b, broaden the spectrum used for photosynthesis
- The difference in the absorption spectrum between chlorophyll a and b is due to a slight structural difference between the pigment molecules
- Accessory pigments called carotenoids absorb excessive light that would damage chlorophyll

Figure 11.11



CH<sub>3</sub> in chlorophyll *a* CHO in chlorophyll *b* 

Porphyrin ring: light-absorbing "head" of molecule; note magnesium atom at center

Hydrocarbon tail: interacts with <u>hydrophobic</u> <u>regions of proteins</u> inside thylakoid membranes of chloroplasts; H atoms not shown

### Video: Space-Filling Model of Chlorophyll a



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 Accessory pigments called carotenoids function in photoprotection; they absorb excessive light that would damage chlorophyll





# Sun Radiation Chlorophyll is the main photosynthetic pigment

**Photosynthetically** active radiation, often abbreviated PAR, designates the spectral range (wave band) of solar radiation from 400 to 700 nanometers that photosynthetic organisms are able to use in the process of photosynthesis.







FIGURE 7.5 Light absorption and emission by chlorophyll. (A) Energy level diagram. Absorption or emission of light is indicated by vertical lines that connect the ground state with excited electron states. The blue and red absorption bands of chlorophyll (which absorb blue and red photons, respectively) correspond to the upward vertical arrows, signifying that energy absorbed from light causes the molecule to change from the ground state to an excited state. The downward-pointing arrow indicates fluorescence, in which the molecule goes from the lowest excited state to the ground state while re-emitting energy as a photon. (B) Spectra of absorption and fluorescence. The long-wavelength (red) absorption band of chlorophyll corre-sponds to light that has the energy required to cause the transition from the ground state to the first excited state. The short-wavelength (blue) absorption band corresponds to a transition to a higher excited state.



(A) Chlorophylls

CH.

ĊH,

ĊН

C-

**CH** 

0=

H.(



# Phycobiliprotein: 藻膽蛋白

■<u>藍緑藻</u>





### Phycoerthyrin



Phycocyanin



Allophycocyanin



Wavelength (nm)

### Phycobilisome藻膽蛋白體 in cyanobacteria

These antennae (called "**phycobilisomes**" in **Synechococcus**) are composed of pigment-proteins complexes arranged in such a way to capture light with a high efficiency. Pigments that are bound to antenna systems may have very different colours (such as green, blue, pink or orange) and this will determine the wavelengths of the solar spectrum that cells can efficiently harvest in the oceanic waters.

![](_page_61_Figure_2.jpeg)

![](_page_62_Figure_0.jpeg)

![](_page_63_Figure_0.jpeg)

Phycobiliproteins, bilin variation, and group III CA regulation.

![](_page_64_Figure_1.jpeg)

Kehoe D M PNAS 2010;107:9029-9030

![](_page_64_Picture_3.jpeg)

# complementary chromatic

Structure of a hemidiscoidal adaptation phycobilisome of Tolypothrix tenuis under different light conditions. (a) When illuminated by white light, the phycobilisome contains phycoerythrin, phycocyanin, and allophycocyanin. Energy absorbed by phycoerythrin is transferred to phycocyanin and allophycocyanin. The allophycocyanin core proteins are attached, via a linker protein, to the photosynthetic membrane, which is not shown. (b) When illuminated by red light, the phycobilisome undergoes complementary chromatic adaptation, in which phycoerythrin is no longer produced but additional phycocyanin is produced. (After R. MacColl and D. Guard-Friar, Phycobiliproteins, CRC Press, Boca Raton, FL, 1987)

![](_page_65_Figure_2.jpeg)

### **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

![](_page_67_Figure_1.jpeg)

![](_page_67_Picture_2.jpeg)

(a) Excitation of isolated chlorophyll molecule

(b) Fluorescence

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![](_page_68_Picture_1.jpeg)

(b) Fluorescence

#### Electron transport chain (ETC)

![](_page_69_Figure_1.jpeg)

![](_page_70_Figure_0.jpeg)

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### 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=Lhc (pigment molecules bound to proteins) transfer the energy of photons to the reaction center


(a) How a photosystem harvests light





(a) How a photosystem harvests light



(b) Structure of a photosystem

#### Photosystem II (PSII)

Photosystem II contains chlorophylls a and b and absorbs light at 680nm. This is a large protein complex that is located in the thylakoid membrane.



## LHC-II

- MOST ABUNDANT MEMBRANE PROTEIN IN CHLOROPLASTS OF GREEN PLANTS
- A TRANSMEMBRANE PROTEIN
- BINDS
  - ~ 7 CHLOROPHYLL a MOLECULES
  - ~ 5 CHLOROPHYLL b MOLECULES
  - TWO CAROTENOIDS

 COMPRISES ABOUT 50% OF ALL CHLOROPHYLL IN BIOSPHERE LH2 FROM Rs. acidophhilus







- 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



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- 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



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



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#### **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



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- There are 8 steps in linear electron flow:
  - 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<sup>+</sup>)













#### The Z-scheme of the Light Reactions: An Energy Diagram



- H<sub>2</sub>O is split by enzymes, and the electrons are transferred from the hydrogen atoms to P680<sup>+</sup>, thus reducing it to P680
  - P680<sup>+</sup> is the strongest known biological oxidizing agent
  - O<sub>2</sub> 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
- 5. Energy released by the fall drives the creation of a proton gradient across the thylakoid membrane
  - Diffusion of H<sup>+</sup> (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<sup>+</sup> (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)
- 8. The electrons are then transferred to NADP<sup>+</sup> and reduce it to NADPH
  - The electrons of NADPH are available for the reactions of the Calvin cycle
  - This process also removes an H<sup>+</sup> from the stroma

 The energy changes of electrons during linear flow through the light reactions can be shown in a mechanical analogy



### **Cyclic Electron Flow**

- In cyclic electron flow, electrons cycle back from Fd to the PS I reaction center
- Cyclic electron flow uses only photosystem I and produces ATP, but not NADPH
- No oxygen is released



- 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

# Cyclic Electron Flow



- Electron in Photosystem I is excited and transferred to ferredoxin that shuttles the electron to the cytochrome complex.
- The electron then travels down the electron chain and re-enters photosystem I

## Green tide



# 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



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- 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<sub>2</sub>O to NADPH








# Concept 11.3: The Calvin cycle uses the chemical energy of ATP and NADPH to reduce CO<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub>
- The Calvin cycle has three phases
  - 1. Carbon fixation (catalyzed by rubisco)
  - 2. Reduction
  - 3. Regeneration of the CO<sub>2</sub> acceptor (RuBP)









## Concept 11.4: 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<sub>2</sub>O but also limits photosynthesis
- The closing of stomata reduces access to CO<sub>2</sub> and causes O<sub>2</sub> to build up
- These conditions favor an apparently wasteful process called photorespiration

# Rubisco: Ribulose-1,5-bisphosphate carboxylase/oxygenase



## **Photorespiration: C2 cycle**









# 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<sub>2</sub> and more CO<sub>2</sub>
- 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<sub>4</sub> Plants

- C<sub>4</sub> plants minimize the cost of photorespiration by incorporating CO<sub>2</sub> into four-carbon compounds
- There are two distinct types of cells in the leaves of C<sub>4</sub> plants:
  - Bundle-sheath cells are arranged in tightly packed sheaths around the veins of the leaf
  - Mesophyll cells are loosely packed between the bundle sheath and the leaf surface

- Sugar production in C<sub>4</sub> plants occurs in a threestep process:
  - 1. The production of the four carbon precursors is catalyzed by the enzyme **PEP carboxylase** in the mesophyll cells
    - PEP carboxylase has a higher affinity for CO<sub>2</sub> than rubisco does; it can fix CO<sub>2</sub> even when CO<sub>2</sub> concentrations are low

- 2. These four-carbon compounds are exported to bundle-sheath cells
- 3. Within the bundle-sheath cells, they release CO<sub>2</sub> that is then used in the Calvin cycle



Sugar

Vascular

tissue



#### The C<sub>4</sub> pathway



- Since the Industrial Revolution in the 1800s, CO<sub>2</sub> levels have risen greatly
- Increasing levels of CO<sub>2</sub> may affect C<sub>3</sub> and C<sub>4</sub> 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<sub>2</sub> into organic acids
- Stomata close during the day, and CO<sub>2</sub> is released from organic acids and used in the Calvin cycle

Figure 11.21





Sugarcane



#### Pineapple

## 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<sub>2</sub> in our atmosphere

Figure 11.22a



#### LIGHT REACTIONS

- Are carried out by molecules in the thylakoid membranes
- Convert light energy to the chemical energy of ATP and NADPH
- Split H<sub>2</sub>O and release O<sub>2</sub> to the atmosphere

#### **CALVIN CYCLE REACTIONS**

- Take place in the stroma
- Use ATP and NADPH to convert CO<sub>2</sub> to the sugar G3P
- Return ADP, inorganic phosphate, and NADP<sup>+</sup> to the light reactions

#### MAKE CONNECTIONS The Working Cell

Flow of Genetic Information in the Cell: DNA  $\rightarrow$  RNA  $\rightarrow$  Protein (Chapters 5–7) Movement Across Cell Membranes (Chapter 7) Energy Transformations in the Cell: Photosynthesis and Cellular Respiration (Chapters 8–11)







Figure 11.23c



	350 ppm CO <sub>2</sub>	600 ppm CO <sub>2</sub>	1,000 ppm CO <sub>2</sub>
Average dry mass of one corn plant (g)	91	89	80
Average dry mass of one velvetleaf plant (g)	35	48	54



Corn plant surrounded by invasive velvetleaf plants










## porphyrin ring



## - phytol tail

Chlorophylls consist of a light-absorbing with a magnesium atom at the center and a long phytol tail that anchors the molecule in a membrane (Figure 1). They absorb light in the blue and red parts of the spectrum, but the green wavelengths are transmitted or reflected.