9

# Photosynthesis: Capturing Energy

Skip Moody/Dembinsky Photo Associates

**Photosynthesis.** These blue lupines (*Lupinus hirsutus*) and the trees behind them use light energy to power the processes that incorporate $CO_2$ into organic molecules. This photograph was taken in southern Michigan.

## KEY CONCEPTS

Light energy powers photosynthesis, which is essential to plants and most life on Earth.

Photosynthesis, which occurs in chloroplasts, is a redox process.

Light-dependent reactions convert light energy to the chemical energy of NADPH and ATP.

Carbon fixation reactions incorporate $CO_2$ into organic molecules.

Most photosynthetic organisms are photoautotrophs.

Look at all the living things that surround you—the trees, your pet goldfish, your own body. Most of that biomass is made up of carbon-based biological molecules. What is the ultimate source of all that carbon? Surprising to some, the source is carbon dioxide from the air. Your cells cannot take carbon dioxide from the air and incorporate it into organic molecules—but some plant cells can. They do this through **photosynthesis,** the sequence of events by which light energy is converted into the stored chemical energy of organic molecules. Photosynthesis is the first step in the flow of energy through most of the living world, capturing the vast majority of the energy that living organisms use. Photosynthesis not only sustains plants (see photograph) and other photosynthetic organisms such as algae and photosynthetic bacteria but also indirectly supports most nonphotosynthetic organisms such as animals, fungi, protozoa, and most bacteria. Each year photosynthetic organisms convert $CO_2$ into billions of tons of organic molecules. These molecules have two important roles in both photosynthetic and nonphotosynthetic organisms: they are both the building blocks of cells and, as we saw in Chapter 8, a source of chemical energy that fuels the metabolic reactions that sustain almost all life.

In this chapter we first examine how light energy is used in the synthesis of ATP and other molecules that temporarily hold chemical energy but are unstable and cannot be stockpiled in the cell. We then see how their energy powers the anabolic pathway by which a photosynthetic cell synthesizes stable organic molecules from the simple inorganic compounds $CO_2$ and water. Finally, we explore the role of photosynthesis in plants and in Earth's environment. ■

## LIGHT

### Learning Objective

1 Describe the physical properties of light, and explain the relationship between a wavelength of light and its energy.

Because most life on this planet depends on light, either directly or indirectly, it is important to understand the nature of light and its essential role in photosynthesis. Visible light represents a very small portion of a vast, continuous range of radiation called the *electromagnetic spectrum* (Fig. 9-1). All radiation in this spectrum travels as waves. A **wavelength** is the distance from one wave peak to the next. At one end of the electromagnetic spectrum are gamma rays, which have very short wavelengths measured in fractions of nanometers, or nm (1 nanometer equals $10^{-9}$ m, one billionth of a meter). At the other end of the spectrum are radio waves, with wavelengths so long they can be measured in kilometers. The portion of the electromagnetic spectrum from 380 to 760 nm is called the *visible spectrum,* because we humans can see it. The visible spectrum includes all the colors of the rainbow (Fig. 9-2); violet has the shortest wavelength, and red has the longest.

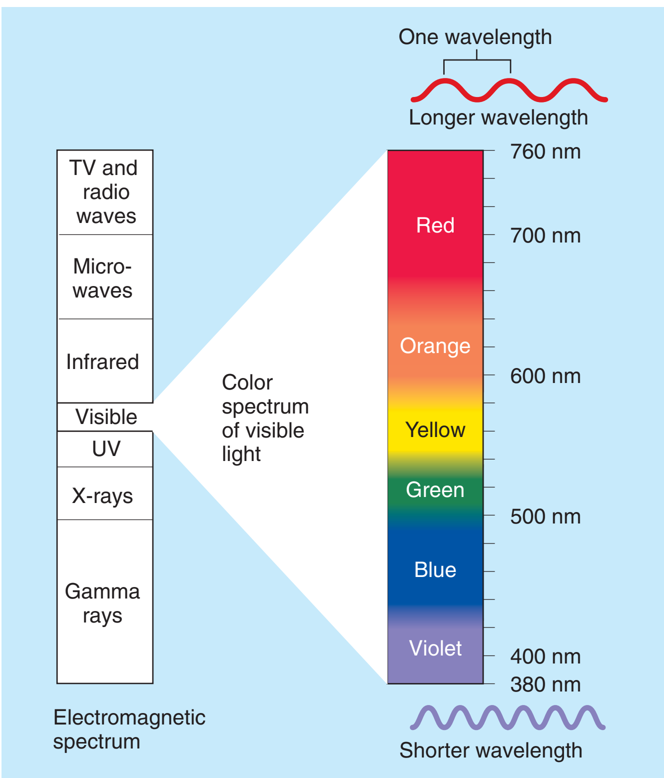



**Figure 9-1** ***Animated*** The electromagnetic spectrum

Waves in the electromagnetic spectrum have similar properties but different wavelengths. Radio waves are the longest (and least energetic) waves, with wavelengths as long as 20 km. Gamma rays are the shortest (and most energetic) waves. Visible light represents a small fraction of the electromagnetic spectrum and consists of a mixture of wavelengths ranging from about 380 to 760 nm. The energy from visible light is used in photosynthesis.

Light is composed of small particles, or packets, of energy called **photons.** The energy of a photon is inversely proportional to its wavelength: Shorter-wavelength light has more energy per photon than longer-wavelength light.

Why does photosynthesis depend on light detectable by the human eye (visible light) rather than on some other wavelength of radiation? We can only speculate on the answer. Perhaps the reason is that radiation within the visible-light portion of the spectrum excites certain types of biological molecules, moving electrons into higher energy levels. Radiation with wavelengths longer than those of visible light does not have enough energy to excite these biological molecules. Radiation with wavelengths shorter than those of visible light is so energetic that it disrupts the bonds of many biological molecules. Thus, visible light has just the right amount of energy to cause the kinds of reversible changes in molecules that are useful in photosynthesis.

When a molecule absorbs a photon of light energy, one of its electrons becomes energized, which means that the electron shifts from a lower-energy atomic orbital to a high-energy orbital that is more distant from the atomic nucleus. One of two things then happens, depending on the atom and its surroundings (Fig. 9-3). The atom may return to its **ground state,** which is the condition in which all its electrons are in their normal, lowest-energy levels. When an electron returns to its ground state, its energy dissipates as heat or as an emission of light of a longer wavelength than the absorbed light; this emission of light is called **fluorescence.** Alternatively, the energized electron may leave the atom and be accepted by an electron acceptor molecule, which becomes reduced in the process; this is what occurs in photosynthesis.

Now that you understand some of the properties of light, let us consider the organelles that use light for photosynthesis.

### Review

- Why does photosynthesis require visible light?
- Which color of light has the longer wavelength, violet or red? Which color of light has the higher energy per photon, violet or red?

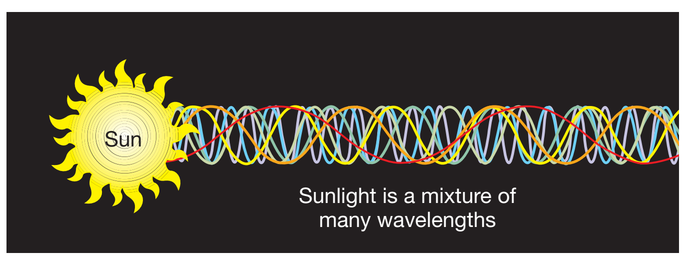



**Figure 9-2** Visible radiation emitted from the sun

Electromagnetic radiation from the sun includes ultraviolet radiation and visible light of varying colors and wavelengths.

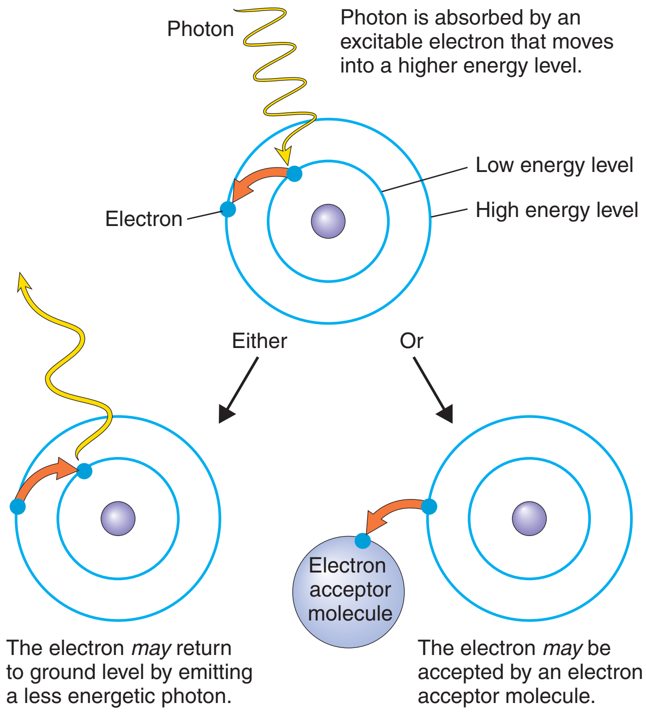



**Figure 9-3** Interactions between light and atoms or molecules

(*Top*) When a photon of light energy strikes an atom or a molecule of which the atom is a part, the energy of the photon may push an electron to an orbital farther from the nucleus (that is, into a higher energy level). (*Lower left*) If the electron returns to the lower, more stable energy level, the energy may be released as a less energetic, longer-wavelength photon, known as fluorescence (*shown*), or as heat. (*Lower right*) If the appropriate electron acceptors are available, the electron may leave the atom. During photosynthesis, an electron acceptor captures the energetic electron and passes it to a chain of acceptors.

## CHLOROPLASTS

### Learning Objectives

2 Diagram the internal structure of a chloroplast, and explain how its components interact and facilitate the process of photosynthesis.

3 Describe what happens to an electron in a biological molecule such as chlorophyll when a photon of light energy is absorbed.

If you examine a section of leaf tissue in a microscope, you see that the green pigment, chlorophyll, is not uniformly distributed in the cell but is confined to organelles called **chloroplasts.** In plants, chloroplasts lie mainly inside the leaf in the cells of the **mesophyll,** a layer with many air spaces and a very high concentration of water vapor (Fig. 9-4a). The interior of the leaf exchanges gases with the outside through microscopic pores, called **stomata** (sing., *stoma*). Each mesophyll cell has 20 to 100 chloroplasts (Fig. 9-4b).

The chloroplast, like the mitochondrion, is enclosed by outer and inner membranes (Fig. 9-4c). The inner membrane encloses a fluid-filled region called the **stroma,** which contains most of the enzymes required to produce carbohydrate molecules. Suspended in the stroma is a third system of membranes that forms an interconnected set of flat, disclike sacs called **thylakoids.**

The thylakoid membrane encloses a fluid-filled interior space, the **thylakoid lumen.** In some regions of the chloroplast, thylakoid sacs are arranged in stacks called **grana** (sing., *granum*). Each granum looks something like a stack of coins, with each "coin" being a thylakoid. Some thylakoid membranes extend from one granum to another. Thylakoid membranes, like the inner mitochondrial membrane (see Chapter 8), are involved in ATP synthesis. (Photosynthetic prokaryotes have no chloroplasts, but thylakoid membranes are often arranged around the periphery of the cell as infoldings of the plasma membrane.)

### Chlorophyll is found in the thylakoid membrane

Thylakoid membranes contain several kinds of *pigments,* which are substances that absorb visible light. Different pigments absorb light of different wavelengths. **Chlorophyll,** the main pigment of photosynthesis, absorbs light primarily in the blue and red regions of the visible spectrum. Green light is not appreciably absorbed by chlorophyll. Plants usually appear green because some of the green light that strikes them is scattered or reflected.

A chlorophyll molecule has two main parts, a complex ring and a long side chain (Fig. 9-5). The ring structure, called a *porphyrin ring,* is made up of joined smaller rings composed of carbon and nitrogen atoms; the porphyrin ring absorbs light energy. The porphyrin ring of chlorophyll is strikingly similar to the heme portion of the red pigment hemoglobin in red blood cells. However, unlike heme, which contains an atom of iron in the center of the ring, chlorophyll contains an atom of magnesium in that position. The chlorophyll molecule also contains a long, hydrocarbon side chain that makes the molecule extremely nonpolar and anchors the chlorophyll in the membrane.

All chlorophyll molecules in the thylakoid membrane are associated with specific *chlorophyll-binding proteins;* biologists have identified about 15 different kinds. Each thylakoid membrane is filled with precisely oriented chlorophyll molecules and chlorophyll-binding proteins that facilitate the transfer of energy from one molecule to another.

There are several kinds of chlorophyll. The most important is **chlorophyll *a*,** the pigment that initiates the light-dependent reactions of photosynthesis. **Chlorophyll *b*** is an accessory pigment that also participates in photosynthesis. It differs from chlorophyll *a* only in a functional group on the porphyrin ring: The methyl group ($—CH_3$) in chlorophyll *a* is replaced in chlorophyll *b* by a terminal carbonyl group (—CHO). This difference shifts the wavelengths of light absorbed and reflected by chlorophyll *b,* making it appear yellow-green, whereas chlorophyll *a* appears bright green.

**(a)** This leaf cross section reveals that the mesophyll is the photosynthetic tissue. $CO_2$ enters the leaf through tiny pores or stomata, and $H_2O$ is carried to the mesophyll in veins.

**(b)** Notice the numerous chloroplasts in this LM of plant cells.

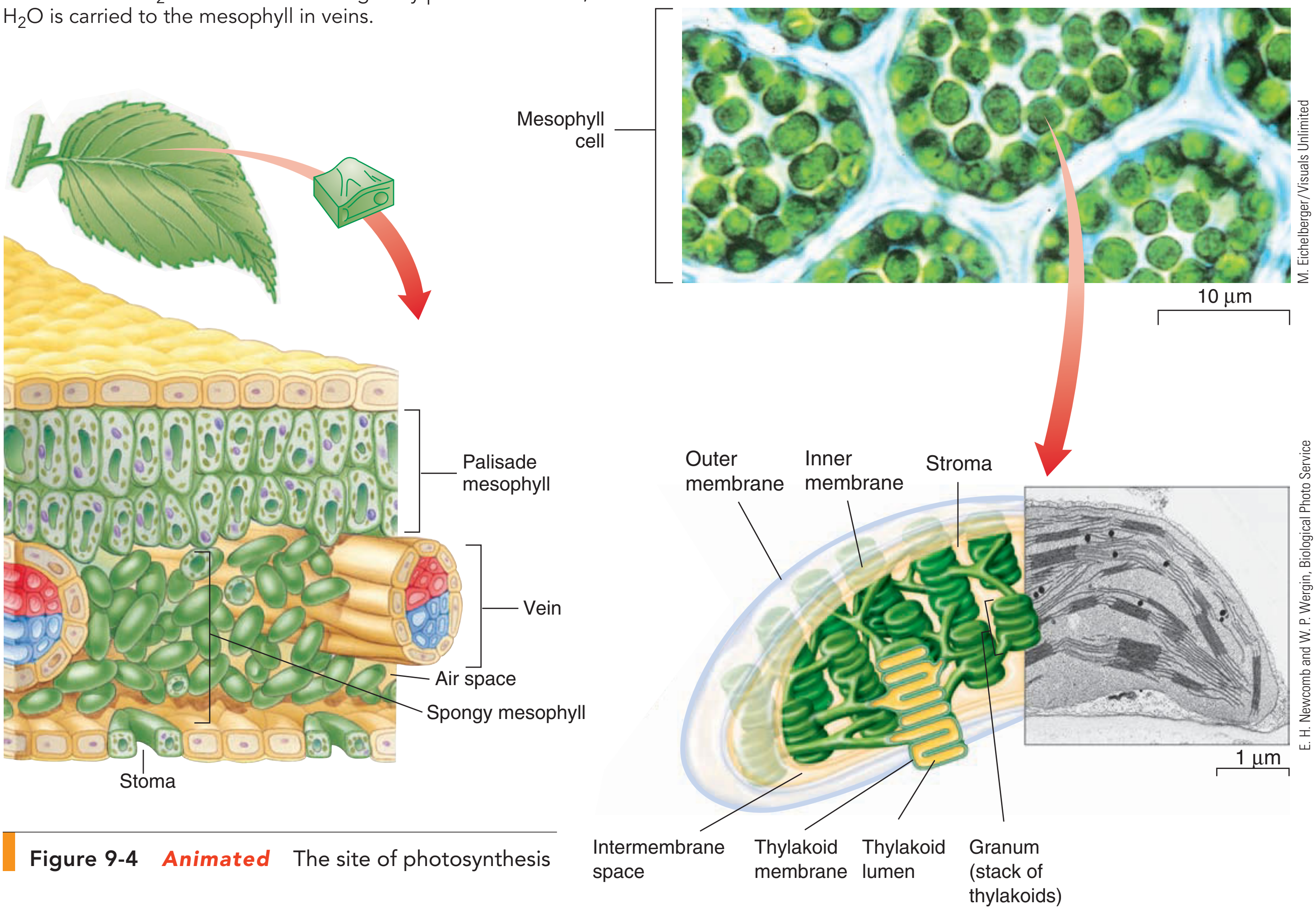



**Figure 9-4** ***Animated*** The site of photosynthesis

**(c)** In the chloroplast, pigments necessary for the light-capturing reactions of photosynthesis are part of thylakoid membranes, whereas the enzymes for the synthesis of carbohydrate molecules are in the stroma.

Chloroplasts have other accessory photosynthetic pigments, such as **carotenoids,** which are yellow and orange (see Fig. 3-14). Carotenoids absorb different wavelengths of light than chlorophyll, thereby expanding the spectrum of light that provides energy for photosynthesis. Chlorophyll may be excited by light directly by energy passed to it from the light source, or indirectly by energy passed to it from accessory pigments that have become excited by light. When a carotenoid molecule is excited, its energy can be transferred to chlorophyll *a.* Carotenoids also protect chlorophyll and other parts of the thylakoid membrane from excess light energy that could easily damage the photosynthetic components. (High light intensities often occur in nature.)

## Chlorophyll is the main photosynthetic pigment

As you have seen, the thylakoid membrane contains more than one kind of pigment. An instrument called a *spectrophotometer* measures the relative abilities of different pigments to absorb different wavelengths of light. The **absorption spectrum** of a pigment is a plot of its absorption of light of different wavelengths. Figure 9-6a shows the absorption spectra for chlorophylls *a* and *b.*

An **action spectrum** of photosynthesis is a graph of the relative effectiveness of different wavelengths of light. To obtain an action spectrum, scientists measure the rate of photosynthesis at each wavelength for leaf cells or tissues exposed to monochromatic light (light of one wavelength) (Fig. 9-6b).

In a classic biology experiment, the German biologist T. W. Engelmann obtained the first action spectrum in 1883. Engelmann's experiment, described in Figure 9-7, took advantage of the shape of the chloroplast in a species of the green alga *Spirogyra.* Its long, filamentous strands are found in freshwater habitats, especially slow-moving or still waters. *Spirogyra* cells each contain a long, spiral-shaped, emerald-green chloroplast embedded in the cytoplasm. Engelmann exposed these cells to a color spectrum produced by passing light through a prism. He hypothesized that if chlorophyll were indeed responsible for photosynthesis, the process would take place most rapidly in the areas where the chloroplast was illuminated by the colors most strongly absorbed by chlorophyll.

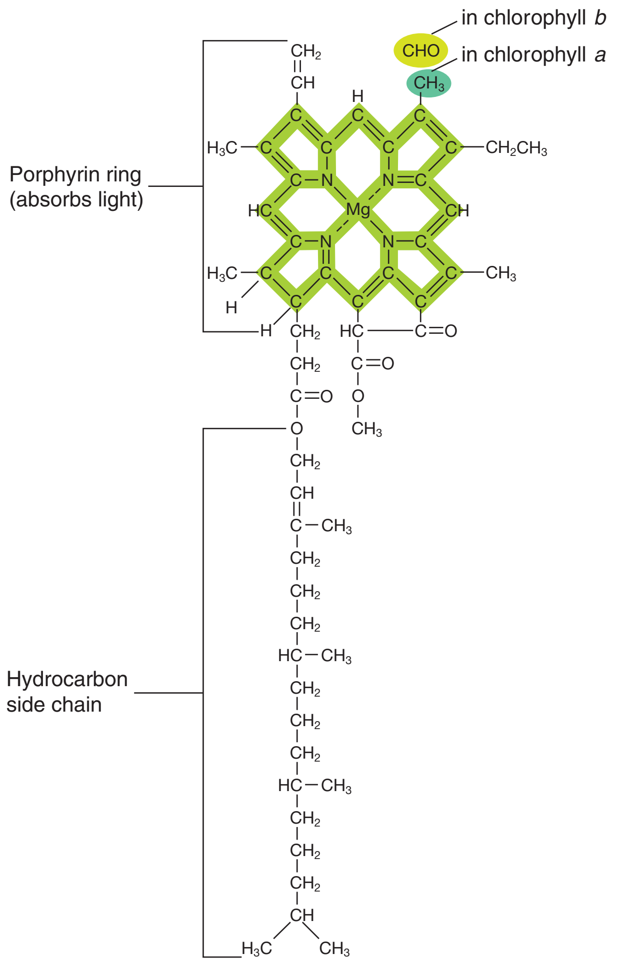
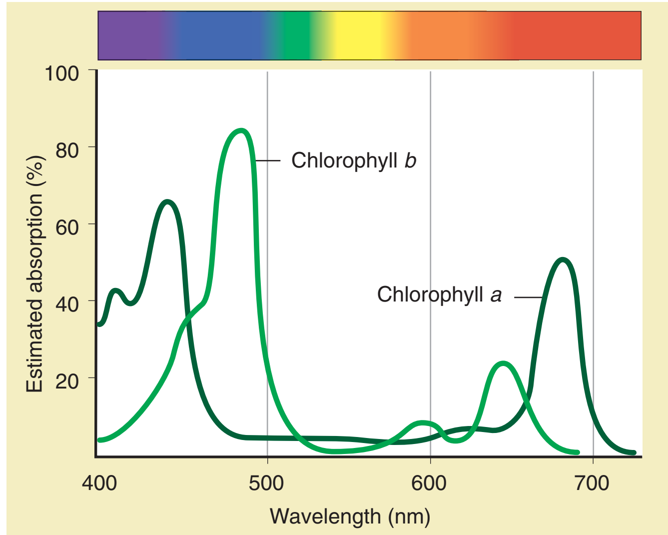
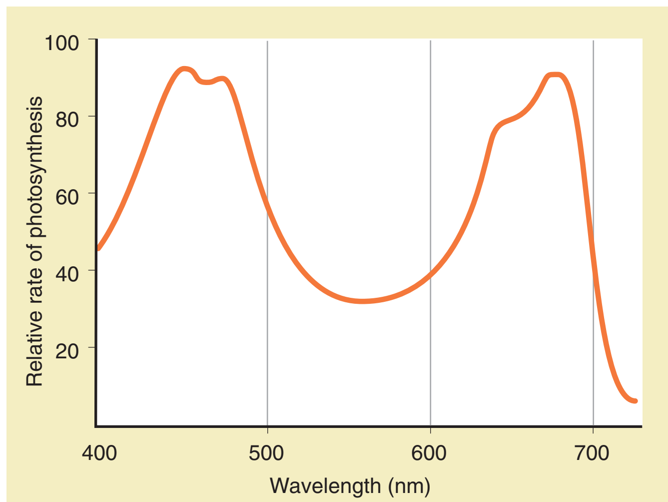



**Figure 9-5** The structure of chlorophyll

Chlorophyll consists of a porphyrin ring and a hydrocarbon side chain. The porphyrin ring, with a magnesium atom in its center, contains a system of alternating double and single bonds; these are commonly found in molecules that strongly absorb certain wavelengths of visible light and reflect others (chlorophyll reflects green). Notice that at the top right corner of the diagram, the methyl group (—$CH_3$) distinguishes chlorophyll *a* from chlorophyll *b*, which has a carbonyl group (—CHO) in this position. The hydrophobic hydrocarbon side chain anchors chlorophyll to the thylakoid membrane.




**(a)** Chlorophylls *a* and *b* absorb light mainly in the blue (422 to 492 nm) and red (647 to 760 nm) regions.




**(b)** The action spectrum of photosynthesis indicates the effectiveness of various wavelengths of light in powering photosynthesis. Many plant species have action spectra for photosynthesis that resemble the generalized action spectrum shown here.

**Figure 9-6** A comparison of the absorption spectra for chlorophylls *a* and *b* with the action spectrum for photosynthesis

Yet how could photosynthesis be measured in those technologically unsophisticated days? Engelmann knew that photosynthesis produces oxygen and that certain motile bacteria are attracted to areas of high oxygen concentration. He determined the action spectrum of photosynthesis by observing that the bacteria swam toward the parts of the *Spirogyra* filaments in the blue and red regions of the spectrum. How did Engelmann know bacteria were not simply attracted to blue or red light? Engelmann exposed bacteria to the spectrum of visible light in the absence of *Spirogyra* as a control. The bacteria showed no preference for any particular wavelength of light. Because the action spectrum of photosynthesis closely matched the absorption spectrum of chlorophyll, Engelmann concluded that chlorophyll in the chloroplasts (and not another compound in another organelle) is responsible for photosynthesis. Numerous studies using sophisticated instruments have since confirmed Engelmann's conclusions.

If you examine Figure 9-6 closely, you will observe that the action spectrum of photosynthesis does not parallel the absorption spectrum of chlorophyll exactly. This difference occurs because accessory pigments, such as carotenoids, transfer some of the energy of excitation produced by green light to chlorophyll molecules. The presence of these accessory photosynthetic pigments can be demonstrated by chemical analysis of almost any

## SUMMARY WITH KEY TERMS

### Learning Objectives

1 Describe the physical properties of light, and explain the relationship between a wavelength of light and its energy (page 192).

- Light consists of particles called **photons** that move as waves.
- Photons with shorter **wavelengths** have more energy than those with longer wavelengths.

2 Diagram the internal structure of a chloroplast, and explain how its components interact and facilitate the process of photosynthesis (page 193).

- In plants, **photosynthesis** occurs in chloroplasts, which are located mainly within **mesophyll** cells inside the leaf.
- **Chloroplasts** are organelles enclosed by a double membrane; the inner membrane encloses the **stroma** in which membranous, saclike **thylakoids** are suspended. Each thylakoid encloses a **thylakoid lumen.** Thylakoids arranged in stacks are called **grana.**
- **Chlorophyll *a*, chlorophyll *b*, carotenoids,** and other photosynthetic pigments are components of the thylakoid membranes of chloroplasts.

3 Describe what happens to an electron in a biological molecule such as chlorophyll when a photon of light energy is absorbed (page 193).

- Photons excite biological molecules such as chlorophyll and other photosynthetic pigments, causing one or more electrons to become energized. These energized electrons may be accepted by electron acceptor compounds.
- The combined **absorption spectra** of chlorophylls *a* and *b* are similar to the **action spectrum** for photosynthesis.

4 Describe photosynthesis as a redox process (page 196).

- During photosynthesis, light energy is captured and converted to the chemical energy of carbohydrates; hydrogens from water are used to reduce carbon, and oxygen derived from water becomes oxidized, forming molecular oxygen.

5 Distinguish between the light-dependent reactions and carbon fixation reactions of photosynthesis (page 196).

- In the **light-dependent reactions,** electrons energized by light are used to generate **ATP** and **NADPH;** these compounds provide energy for the formation of carbohydrates during the **carbon fixation reactions.**

**ThomsonNOW™ Learn more about photosynthesis in plants by clicking on the figures in ThomsonNOW.**

6 Describe the flow of electrons through photosystems I and II in the noncyclic electron transport pathway and the products produced. Contrast this with cyclic electron transport (page 198).

- **Photosystems I** and **II** are the two types of photosynthetic units involved in photosynthesis. Each photosystem includes chlorophyll molecules and accessory pigments organized with pigment-binding proteins into **antenna complexes.**
- Only a special pair of chlorophyll *a* molecules in the **reaction center** of an antenna complex give up energized electrons to a nearby electron acceptor. **P700** is the reaction center for photosystem I; **P680** is the reaction center for photosystem II.
- During the noncyclic light-dependent reactions, known as **noncyclic electron transport,** ATP and NADPH are formed.
- Electrons in photosystem I are energized by the absorption of light and passed through an **electron transport chain** to $NADP^+$, forming NADPH. Electrons given up by P700 in photosystem I are replaced by electrons from P680 in photosystem II.
- A series of redox reactions takes place as energized electrons are passed along the electron transport chain from photosystem II to photosystem I. Electrons given up by P680 in photosystem II are replaced by electrons made available by the **photolysis** of $H_2O$; oxygen is released in the process.
- During **cyclic electron transport,** electrons from photosystem I are eventually returned to photosystem I. ATP is produced by chemiosmosis, but no NADPH or oxygen is generated.

**ThomsonNOW™ Experience the process of noncyclic electron transport by clicking on the figure in ThomsonNOW.**

7 Explain how a proton ($H^+$) gradient is established across the thylakoid membrane and how this gradient functions in ATP synthesis (page 198).

- **Photophosphorylation** is the synthesis of ATP coupled to the transport of electrons energized by photons of light. Some of the energy of the electrons is used to pump protons across the thylakoid membrane, providing the energy to generate ATP by **chemiosmosis.**
- As protons diffuse through **ATP synthase,** an enzyme complex in the thylakoid membrane, ADP is phosphorylated to form ATP.

8 Summarize the three phases of the Calvin cycle, and indicate the roles of ATP and NADPH in the process (page 202).

- The **carbon fixation reactions** proceed by way of the **Calvin cycle,** also known as the **$C_3$ pathway.**
- In the $CO_2$ uptake phase of the Calvin cycle, $CO_2$ is combined with **ribulose bisphosphate (RuBP),** a five-carbon sugar, by the enzyme ribulose bisphosphate carboxylase/oxygenase, commonly known as **rubisco,** forming the three-carbon molecule **phosphoglycerate (PGA).**
- In the carbon reduction phase of the Calvin cycle, the energy and reducing power of ATP and NADPH are used to convert PGA molecules to **glyceraldehyde-3-phosphate (G3P).** For every 6 $CO_2$ molecules fixed, 12 molecules of G3P are produced, and 2 molecules of G3P leave the cycle to produce the equivalent of 1 molecule of glucose.
- In the RuBP regeneration phase of the Calvin cycle, the remaining G3P molecules are modified to regenerate RuBP.

**ThomsonNOW™ See the Calvin cycle in action by clicking on the figure in ThomsonNOW.**

9 Discuss how photorespiration reduces photosynthetic efficiency (page 202).

- In **photorespiration,** $C_3$ plants consume oxygen and generate $CO_2$ by degrading Calvin cycle intermediates but do not produce ATP. Photorespiration is significant on bright, hot, dry days when plants close their stomata, conserving water but preventing the passage of $CO_2$ into the leaf.

10 Compare the $C_4$ and CAM pathways (page 202).

- In the **$C_4$ pathway,** the enzyme **PEP carboxylase** binds $CO_2$ effectively, even when $CO_2$ is at a low concentration. $C_4$ reactions take place within mesophyll cells. The $CO_2$ is fixed in **oxaloacetate,** which is then converted to malate. The malate moves into a **bundle sheath cell,** and $CO_2$ is removed from it. The released $CO_2$ then enters the Calvin cycle.
- The **crassulacean acid metabolism (CAM) pathway** is similar to the $C_4$ pathway. PEP carboxylase fixes carbon at night in the mesophyll cells, and the Calvin cycle occurs during the day in the same cells.

**ThomsonNOW™ See a comparison of the $C_3$ and $C_4$ pathways by clicking on the figure in ThomsonNOW.**

11 Contrast photoautotrophs and chemoheterotrophs with respect to their energy and carbon sources (page 206).

- **Photoautotrophs** use light as an energy source and are able to incorporate atmospheric $CO_2$ into pre-existing carbon skeletons. **Chemoheterotrophs** obtain energy by oxidizing chemicals and obtain carbon as organic molecules from other organisms.

12 State the importance of photosynthesis in a plant and to other organisms (page 207).

- Photosynthesis is the ultimate source of all chemical energy and organic molecules available to photoautotrophs, such as plants, and to virtually all other organisms as well. It also constantly replenishes the supply of oxygen in the atmosphere, vital to all aerobic organisms.

## Summary Reactions for Photosynthesis

The light-dependent reactions (noncyclic electron transport):

$$12\ H_2O + 12\ NADP^+ + 18\ ADP + 18\ P_i \xrightarrow[\text{Chlorophyll}]{\text{Light}} 6\ O_2 + 12\ NADPH + 18\ ATP$$

The carbon fixation reactions (Calvin cycle):

$$12\ NADPH + 18\ ATP + 6\ CO_2 \longrightarrow C_6H_{12}O_6 + 12\ NADP^+ + 18\ ADP + 18\ P_i + 6\ H_2O$$

By canceling out the common items on opposite sides of the arrows in these two coupled equations, we obtain the simplified overall equation for photosynthesis:

$$\underset{\text{Carbon dioxide}}{6\ CO_2} + \underset{\text{Water}}{12\ H_2O} \xrightarrow[\text{Chlorophyll}]{\text{Light energy}} \underset{\text{Glucose}}{C_6H_{12}O_6} + \underset{\text{Oxygen}}{6\ O_2} + \underset{\text{Water}}{6\ H_2O}$$

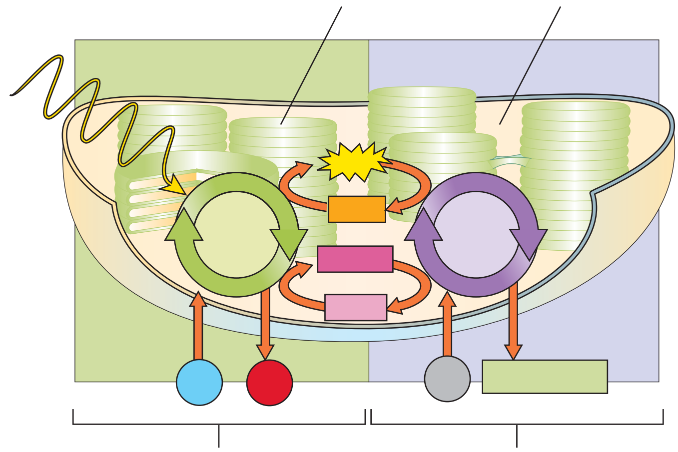
# TEST YOUR UNDERSTANDING

1. Where is chlorophyll located in the chloroplast? (a) thylakoid membranes (b) stroma (c) matrix (d) thylakoid lumen (e) between the inner and outer membranes
2. In photolysis, some of the energy captured by chlorophyll is used to split (a) $CO_2$ (b) ATP (c) NADPH (d) $H_2O$ (e) both b and c
3. Light is composed of particles of energy called (a) carotenoids (b) reaction centers (c) photons (d) antenna complexes (e) photosystems
4. The relative effectiveness of different wavelengths of light in photosynthesis is demonstrated by (a) an action spectrum (b) photolysis (c) carbon fixation reactions (d) photoheterotrophs (e) an absorption spectrum
5. In plants, the final electron acceptor in noncyclic electron flow is (a) $NADP^+$ (b) $CO_2$ (c) $H_2O$ (d) $O_2$ (e) G3P
6. Most plants contain, in addition to chlorophyll, accessory photosynthetic pigments such as (a) PEP (b) G3P (c) carotenoids (d) PGA (e) $NADP^+$
7. The part of a photosystem that absorbs light energy is its (a) antenna complexes (b) reaction center (c) terminal quinone electron acceptor (d) pigment-binding protein (e) thylakoid lumen
8. In ________________, electrons that have been energized by light contribute their energy to add phosphate to ADP, producing ATP. (a) crassulacean acid metabolism (b) the Calvin cycle (c) photorespiration (d) $C_4$ pathways (e) photophosphorylation
9. In ________________, there is a one-way flow of electrons to $NADP^+$, forming NADPH. (a) crassulacean acid metabolism (b) the Calvin cycle (c) photorespiration (d) cyclic electron transport (e) noncyclic electron transport
10. The mechanism by which electron transport is coupled to ATP production by means of a proton gradient is called (a) chemiosmosis (b) crassulacean acid metabolism (c) fluorescence (d) the $C_3$ pathway (e) the $C_4$ pathway
11. In photosynthesis in eukaryotes, the transfer of electrons through a sequence of electron acceptors provides energy to pump protons across the (a) chloroplast outer membrane (b) chloroplast inner membrane (c) thylakoid membrane (d) inner mitochondrial membrane (e) plasma membrane
12. The inputs for ________________ are $CO_2$, NADPH, and ATP. (a) cyclic electron transport (b) the carbon fixation reactions (c) noncyclic electron transport (d) photosystems I and II (e) chemiosmosis
13. The Calvin cycle begins when $CO_2$ reacts with (a) phosphoenolpyruvate (b) glyceraldehyde-3-phosphate (c) ribulose bisphosphate (d) oxaloacetate (e) phosphoglycerate
14. The enzyme directly responsible for almost all carbon fixation on Earth is (a) rubisco (b) PEP carboxylase (c) ATP synthase (d) phosphofructokinase (e) ligase
15. In $C_4$ plants, $C_4$ and $C_3$ pathways occur at different ________________; whereas in CAM plants, CAM and $C_3$ pathways occur at different ________________. (a) times of

day; locations within the leaf (b) seasons; locations (c) locations; times of day (d) locations; seasons (e) times of day; seasons

16. An organism characterized as a photoautotroph obtains energy from ________________ and carbon from ________________. (a) light; organic molecules (b) light; $CO_2$ (c) organic molecules; organic molecules (d) organic molecules; $CO_2$ (e) $O_2$; $CO_2$

17. Label the figure. Use Figure 9-8 to check your answers.



## CRITICAL THINKING

1. Must all autotrophs use light energy? Explain.
2. Only some plant cells have chloroplasts, but all actively metabolizing plant cells have mitochondria. Why?
3. Explain why the proton gradient formed during chemiosmosis represents a state of low entropy. (You may wish to refer to the discussion of entropy in Chapter 7.)
4. The electrons in glucose have relatively high free energies. How did they become so energetic?
5. What strategies may be employed in the future to increase world food supply? Base your answer on your knowledge of photosynthesis and related processes.
6. What would life be like for photoautotrophs if there were no chemoheterotrophs? For chemoheterotrophs if there were no photoautotrophs?
7. What might you suspect if scientists learned that a distant planet has an atmosphere that is 15% molecular oxygen?
8. **Evolution Link.** Propose an explanation for the fact that bacteria, chloroplasts, and mitochondria all have ATP synthase complexes.
9. **Analyzing Data.** Examine Figure 9-6. Imagine a photosynthetic pigment that would be able to absorb the wavelengths of light under-utilized in plant photosynthesis. What possible colors might that pigment likely be (i.e., what colors/wavelengths might it reflect)?