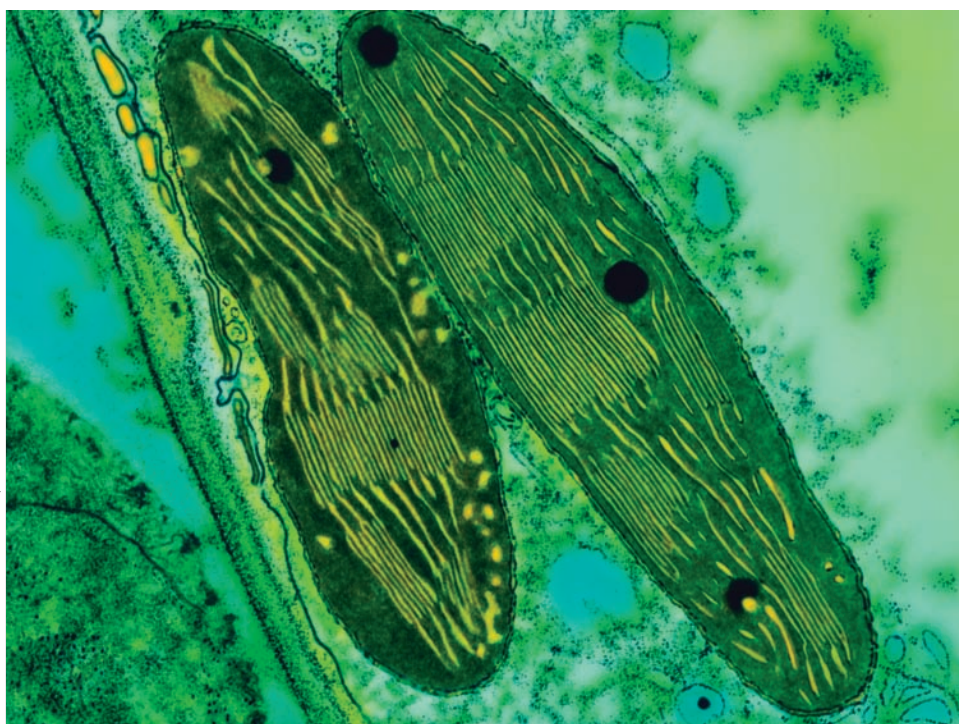Chloroplasts in the leaf of the pea plant *Pisum sativum* (colorized TEM). The light-dependent reactions of photosynthesis take place within the thylakoids of the chloroplasts (thylakoid membranes are shown in yellow).

Dr. Kari Lounatmaa/Science Photo Library/Photo Researchers, Inc.

9 Photosynthesis

WHY IT MATTERS

By the late 1880s, scientists realized that green algae and plants use light as a source of energy to make organic molecules. This conversion of light energy to chemical energy in the form of sugar and other organic molecules is called **photosynthesis.** The scientists also knew that these organisms release oxygen as part of their photosynthetic reactions. Among these scientists was a German botanist, Theodor Engelmann, who was curious about the particular colors of light used in photosynthesis. Was green light the most effective in promoting photosynthesis, as you might expect from looking at a plant, or were other colors used more?

Engelmann used only a light microscope and a glass prism to find the answer to this question. Yet his experiment stands today as a classic, both for the fundamental importance of his answer and for the simple but elegant methods he used to obtain it. Engelmann placed a strand of a green alga, *Spirogyra,* on a glass microscope slide, along with water containing bacteria that require oxygen to survive. He adjusted the prism so that it split a beam of light into its separate colors, which spread like a rainbow across the strand **(Figure 9.1).** After a short time, he noticed that the bacteria had begun to cluster around the algal

A glass prism breaks up a beam of light into a spectrum of colors, which are cast across a microscope slide.

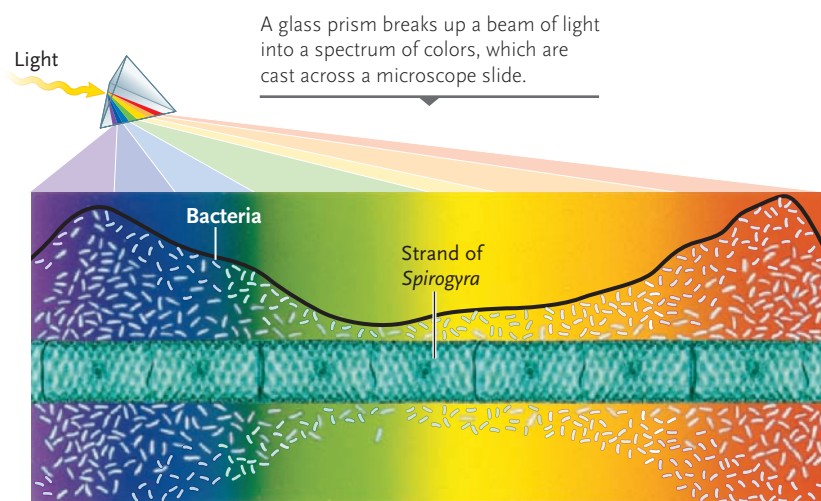Light

Bacteria

Strand of *Spirogyra*

Figure 9.1

Engelmann's 1882 experiment revealing the action spectrum of light used in photosynthesis by *Spirogyra*, a green alga. The aerobic bacteria clustered along the algal strand in the regions where oxygen was released in greatest quantity—the regions in which photosynthesis proceeded at the greatest rate. Those regions corresponded to the colors (wavelengths) of light being absorbed most effectively by the alga—in this case, violet and red.

strand in different locations. The largest clusters were under the blue and violet light at one end of the strand and the red light at the other end. Very few bacteria were found in the green light. Evidently, violet, blue, and red light caused the most oxygen to be released, and Engelmann concluded that these colors of light—rather than green—were used most effectively in photosynthesis.

Engelmann used the distribution of bacteria to construct a curve called an *action spectrum* for the wavelengths of light falling on the *Spirogyra;* it shows the relative effect of each color of light on photosynthesis (black curve in Figure 9.1). Engelmann's results were so accurate that an action spectrum obtained from *Spirogyra* with modern equipment fits closely with his bacterial distribution. However, his results were so advanced for his time that they remained controversial for some 60 years, until instruments that directly measure the effects of different wavelengths of light became available.

Scientists now know that photosynthetic organisms, which include plants, some protists (the algae), and some archaeans and bacteria, absorb the radiant energy of sunlight and convert it into chemical energy. The organisms use the chemical energy to convert simple inorganic raw materials—water, carbon dioxide (CO_2) from the air, and inorganic minerals from the soil—into complex organic molecules. Photosynthesis is still not completely understood, so it remains a subject of active research today.

This chapter begins with an overview of the photosynthetic reactions. We then examine light and light absorption and the reactions that use absorbed energy to make organic molecules from inorganic substances. This chapter focuses primarily on photosynthesis in

plants and green algae; other eukaryotic photosynthesizers have individual variations on the process (see Chapter 26). Prokaryotic photosynthesis is described in Chapter 25.

9.1 Photosynthesis: An Overview

Plants and other photosynthetic organisms are the *primary producers* of Earth; they convert the energy of sunlight into chemical energy and use it to assemble simple inorganic raw materials into complex organic molecules. Primary producers use some of the organic molecules they make as an energy source for their own activities. But they also serve—directly or indirectly—as a food source for *consumers,* the animals that live by eating plants or other animals. Eventually, the bodies of both primary producers and consumers provide chemical energy for bacteria, fungi, and other *decomposers.*

Photosynthesizers and other organisms that use energy to make all of their required organic molecules from CO_2 and other inorganic sources such as water are called **autotrophs** (*autos* = self; *trophos* = feeding). Autotrophs that use light as the energy source to make organic molecules by photosynthesis are called **photoautotrophs.** Consumers and decomposers, which need a source of organic molecules to survive, are called **heterotrophs** (*hetero* = different).

As the pathway of energy flow proceeds from primary producers to decomposers, the organic molecules made by photosynthesis are broken down into inorganic molecules again, and the chemical energy captured in photosynthesis is released as heat. Thus the energy required for life flows from the sun through plants, animals, and decomposers, and finally is released as heat. Because the reactions capturing light energy are the first step in this pathway, photosynthesis is the vital link between the energy of sunlight and the vast majority of living organisms.

Electrons Play a Primary Role in Photosynthesis

Photosynthesis proceeds in two stages, each involving multiple reactions. In the first stage, the **light-dependent reactions,** the energy of sunlight is absorbed and converted into chemical energy in the form of two substances: ATP and NADPH. ATP is the main energy source for plant cells, and NADPH (nicotinamide adenine dinucleotide phosphate) carries electrons pushed to high energy levels by absorbed light. In the second stage of photosynthesis, the **light-independent reactions** (also called the *Calvin cycle*), these electrons are used as a source of energy to convert inorganic CO_2 to an organic form, a process called **CO_2 fixation.** The conversion is a reduction, in which electrons are added to CO_2;

as part of the reduction, protons are also added to CO_2 (reduction and oxidation are discussed in Section 8.1). With the added electrons and protons (H^+), CO_2 is converted to a carbohydrate, with carbon, hydrogen, and oxygen atoms in the ratio $1\,C:2\,H:1\,O$. Carbohydrate units are often symbolized as $(CH_2O)_n$, with the "n" indicating that different carbohydrates are formed from different multiples of the carbohydrate unit.

In plants, algae, and one group of photosynthetic bacteria (the cyanobacteria), the source of electrons and protons for CO_2 fixation is the most abundant substance on Earth: water. Oxygen generated from the splitting of water is released to the environment as a by-product:

$$2\,H_2O \rightarrow 4\,H^+ + 4\,e^- + O_2$$
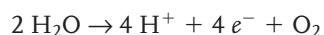
Thus plants, algae, and cyanobacteria use three resources that are readily available—sunlight, water, and CO_2—to produce almost all the organic matter on Earth and to supply the oxygen of our atmosphere.

In the organisms able to split water, the two reactions shown above are combined and multiplied by 6 to produce a six-carbon carbohydrate such as glucose:

$$6\,CO_2 + 12\,H_2O \rightarrow C_6H_{12}O_6 + 6\,O_2 + 6\,H_2O$$
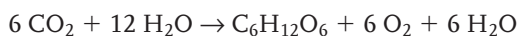
Note that water appears on both sides of the equation; it is both consumed as a reactant and generated as a product in photosynthesis.

The water-splitting reaction probably developed even before oxygen-consuming organisms appeared, evolving first in photosynthetic bacteria that resembled present-day cyanobacteria. The oxygen released by the reaction profoundly changed the atmosphere, allowing aerobic respiration, in which oxygen serves as the final acceptor for electrons removed in cellular oxidations. The existence of all animals depends on the oxygen provided by the water-splitting reaction of photosynthesis.

Glucose is often shown as the only product of photosynthesis. Glucose is the major product of photosynthesis; other monosaccharides, disaccharides, polysaccharides, lipids, and amino acids are also produced. In fact, all the organic molecules of plants are assembled as direct or indirect products of photosynthesis.

Originally, investigators thought that the O_2 released by photosynthesis came from the CO_2 entering the process. The fact that it comes from water was first established in the 1940s, when researchers used a heavy isotope of oxygen, ^{18}O, to trace the pathways of the atoms through photosynthesis. A substance containing heavy ^{18}O can be distinguished readily from the same substance containing the normal isotope, ^{16}O. When a photosynthetic organism was supplied with water containing ^{18}O, the heavy isotope showed up in the O_2 given off in photosynthesis. However, if the organisms were supplied with carbon dioxide con-
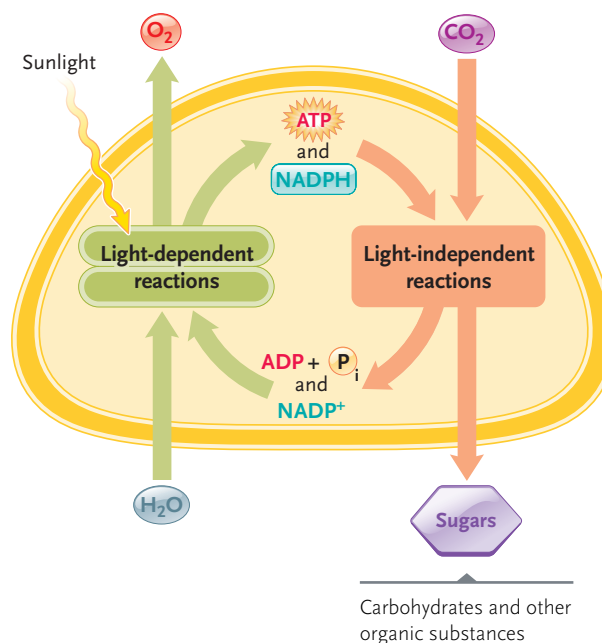
Figure 9.2
The light-dependent and light-independent reactions of photosynthesis, and their interlinking reactants and products. Both series of reactions occur in the chloroplasts of plants and algae.

taining ^{18}O, the heavy isotope showed up in the carbohydrate and water molecules assembled during the reactions—but not in the oxygen gas. This experiment, and other similar experiments using different isotopes, revealed where each atom of the reactants end up in products:
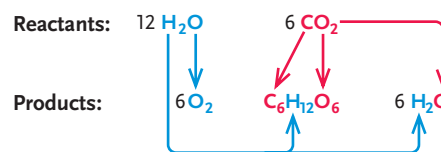
Figure 9.2 summarizes the relationships of the light-dependent and light-independent reactions. Notice that the ATP and NADPH produced by the light-dependent reactions, along with CO_2, are the reactants of the light-independent reactions. The ADP, inorganic phosphate (P_i), and $NADP^+$ produced by the light-independent reactions, along with H_2O, are the reactants for the light-dependent reactions. The light-dependent and light-independent reactions thus form a cycle in which the net inputs are H_2O and CO_2, and the net outputs are organic molecules and O_2.

In Eukaryotes, Photosynthesis Takes Place in Chloroplasts

In eukaryotes, the photosynthetic reactions take place in the chloroplasts of plants and algae; in cyanobacteria, the reactions are distributed between the plasma membrane and the cytosol.

Figure 9.3
The membranes and compartments of chloroplasts.

Craig Tuttle/Corbis

Cutaway of a small section from the leaf

Leaf's upper surface

Photosynthetic cells

CO_2

Stoma

O_2
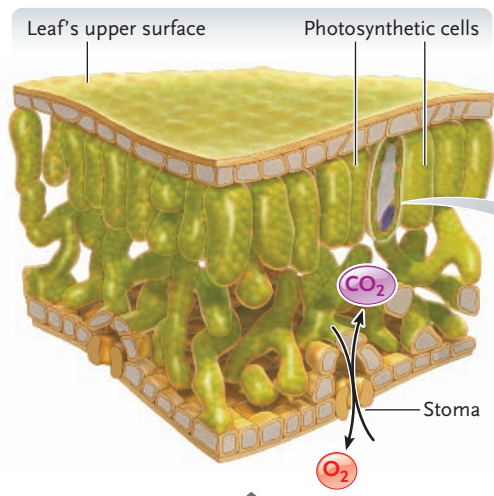
The leaf's surfaces enclose many photosynthetic cells. Stomata are minute openings through which O_2 and CO_2 are exchanged with the surrounding atmosphere.

One of the photosynthetic cells, with green chloroplasts

Large central vacuole

Nucleus

Cutaway view of a chloroplast

Outer membrane

Inner membrane

Thylakoids
• light absorption by chlorophylls and carotenoids
• electron transfer
• ATP synthesis by ATP synthase

Stroma (space around thylakoids)
• light-independent reactions

Granum

Stromal lamellae

Thylakoid lumen

Thylakoid membrane

Chloroplasts from individual algal and plant groups differ in structural details. The chloroplasts of plants and green algae are formed from three membranes that enclose three compartments inside the organelles (**Figure 9.3;** chloroplast structure is also described in Section 5.4). An *outer mem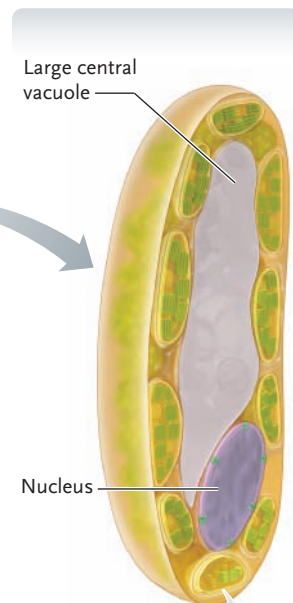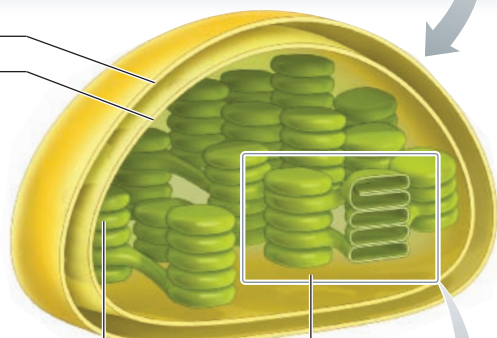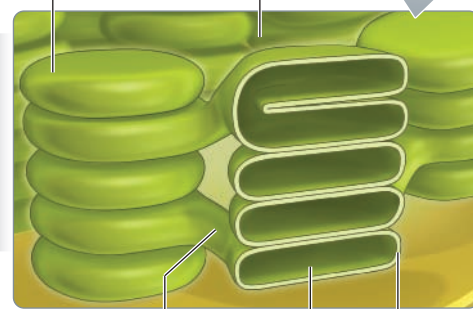brane* covers the entire surface of the organelle. An *inner membrane* lies just inside the outer membrane. Between the outer and inner membranes is an *intermembrane compartment*. The fluid within the inner membrane is the *stroma*. Within the stroma is the third membrane system, the *thylakoid membranes,* which form flattened, closed sacs called *thylakoids*. The space enclosed by a thylakoid is called the *thylakoid lumen*.

In green algae and higher plants, thylakoids are arranged into stacks called *grana* (singular, *granum;* shown in Figure 9.3). The grana are interconnected by flattened, tubular membranes called *stromal lamellae*. The stromal lamellae probably link the thylakoid lumens into a single continuous space within the stroma.

The thylakoid membranes and stromal lamellae house the molecules that carry out the light-dependent reactions of photosynthesis, including the pigments, electron transfer carriers, and ATP synthase enzymes for ATP production. The light-independent reactions are concentrated in the stroma.

In higher plants, the CO_2 required for photosynthesis diffuses to cells containing chloroplasts after entering the plant through *stomata,* minute "air valves" in leaves and stems. The O_2 produced in photosynthesis diffuses from the cells and exits through the stomata, as does water. Water and minerals required for photosynthesis are absorbed by the roots and transported to cells containing chloroplasts through tubular conductive vessels; the organic products of photosynthesis are distributed to all parts of the plant by other vessels (see Chapter 32).

Study Break

1. What are the two stages of photosynthesis?
2. In which organelle does photosynthesis take place in plants? Where in that organelle are the two stages of photosynthesis carried out?

9.2 The Light-Dependent Reactions of Photosynthesis

In this section we discuss the light-dependent reactions (also referred to more simply as the light reactions), in which light energy is converted to chemical energy. The light-dependent reactions involve two main processes: (1) light absorption and (2) synthesis of NADPH and ATP. We will describe these processes

in turn. Through the discussion, it may be useful for you to refer to the summary Figure 9.2 periodically to keep the bigger picture in perspective.

Electrons in Pigment Molecules Absorb Light Energy in Photosynthesis

The first process in photosynthesis is light absorption. What is light? Visible light is a form of radiant energy. It makes up a small part of the **electromagnetic spectrum (Figure 9.4),** which ranges from radio waves to gamma rays. The various forms of electromagnetic radiation differ in *wavelength*—the horizontal distance between the crests of successive waves. Radio

waves have wavelengths in the range of 10 meters to hundreds of kilometers, and gamma rays have wavelengths in the range of one hundredth to one millionth of a nanometer. The average wavelength for an FM radio station, for example, is 3 m. Generally, the shorter the wavelength, the greater the energy of the radiation.

The radiation we detect as visible light has wavelengths between about 700 nm, seen as red light, and 400 nm, seen as blue light. We see the entire spectrum of wavelengths from 700 to 400 nm, combined together, as white light. Although radiated in apparently continuous beams that follow a wave path through space, the energy of light interacts with matter in discrete units called *photons*. Each photon contains a fixed amount of energy that is inversely proportional to its wavelength: the shorter the wavelength, the greater the energy of a photon.

In photosynthesis, light is absorbed by molecules of green pigments called **chlorophylls** (*chloros* = yellow-green; *phyllon* = leaf) and yellow-orange pigments called **carotenoids** (*carota* = carrot). These pigment molecules are embedded in the thylakoid membranes of chloroplasts.

Pigment molecules such as chlorophyll appear colored to an observer because they absorb the energy of visible light at certain wavelengths and transmit or reflect other wavelengths. The color of a pigment is produced by the transmitted or reflected light. Plants look green because chlorophyll absorbs blue and red light most strongly and transmits or reflects most of the wavelengths in between; we see the reflected light as green. This green light, as demonstrated by Engel-

a. Visible spectrum

400-nm wavelength

700-nm wavelength

Barker Blankenship/FPG/Getty Images
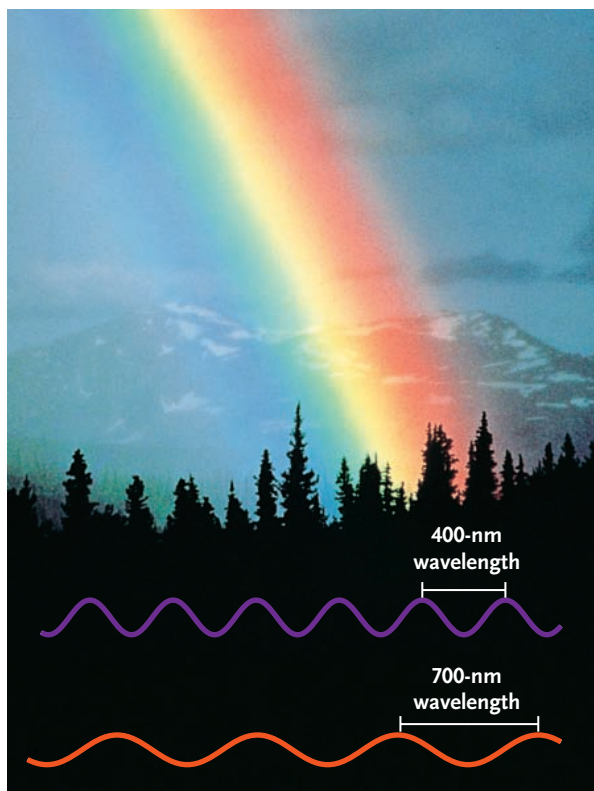
Figure 9.4
The electromagnetic spectrum and the visible wavelengths used as the energy source for photosynthesis. **(a)** Examples of wavelengths, showing the difference between the longest and shortest wavelengths of visible light. **(b)** The entire electromagnetic spectrum, ranging from gamma rays to radio waves; visible light and the wavelengths used for photosynthesis occupy only a narrow band of the spectrum.

b. Range of the electromagnetic spectrum

The shortest, most energetic wavelengths

Most of the radiation that reaches Earth's surface is in this range.

Heat that escapes into space from Earth's surface is in this range.

The longest, lowest-energy wavelengths

| Gamma rays | X-rays | Ultraviolet radiation | Near-infrared radiation | Infrared radiation | Microwaves | Radio waves |

Visible light

Wavelength of visible light (nm)

Photon is absorbed by an excitable electron that moves from a relatively low energy level to a higher energy level.

Photon

Electron at ground state

Electron at excited state

Low energy level

High energy level

Either   Or   Or

Electron-accepting molecule

Pigment molecule

The electron returns to its ground state by emitting a less energetic photon (fluorescence) or releasing energy as heat.

The high-energy electron is accepted by an electron-accepting molecule, the primary acceptor.

The electron returns to its ground state, and the energy released transfers to a neighboring pigment molecule, a process called inductive resonance.

Figure 9.5
Alternative effects of light absorbed by a pigment molecule.

mann's experiment described in the introduction to this chapter, is the combination of wavelengths *not used* by the plants in photosynthesis.

Light is absorbed in a pigment molecule by excitable electrons occupying certain energy levels (shells) in the atoms (see Section 2.2). When not absorbing light, these electrons are at a relatively low energy level known as the *ground state.* If an electron in the pigment absorbs the energy of a photon, it jumps to a higher energy level farther from the atomic nucleus called the *excited state* **(Figure 9.5).** The difference in energy level between the ground state and the excited state is equivalent to the energy of the photon of light that was absorbed.

One of three events then occurs, depending on the atom and other molecules in the vicinity. The electron may return to its ground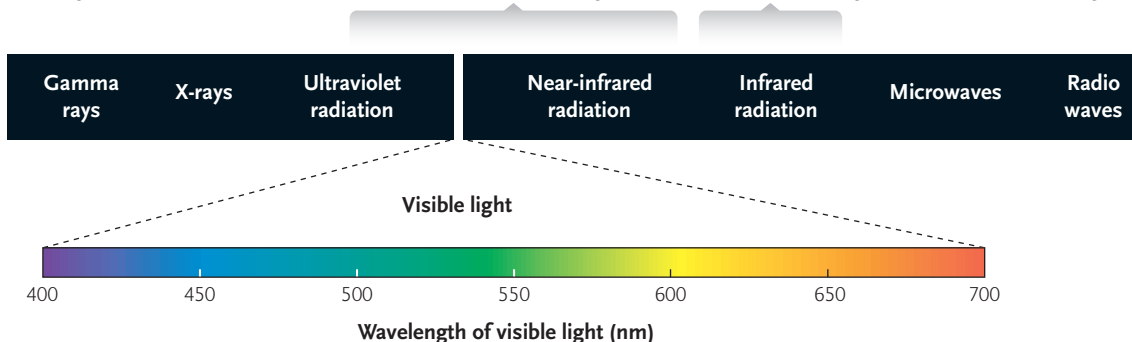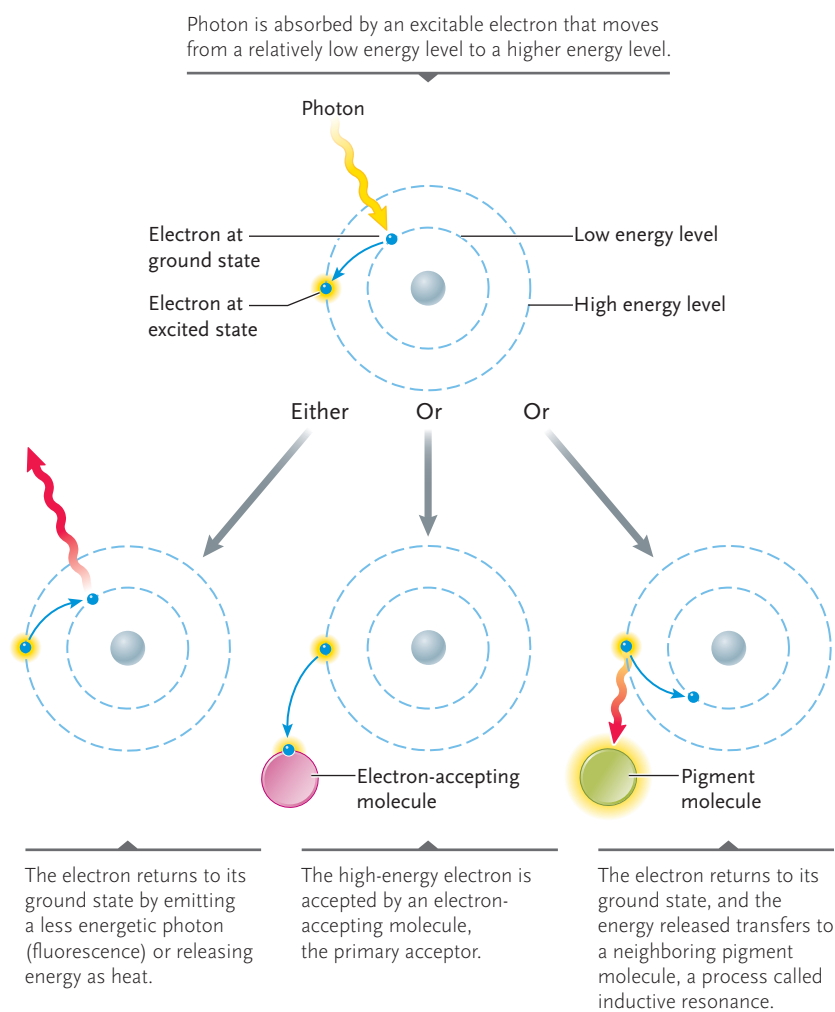 state, releasing its energy either as heat or as an emission of light of a longer wavelength than the absorbed light, a process called *fluorescence.* Alternatively, the high-energy electron is transferred from the pigment molecule to a nearby electron-accepting molecule called a *primary acceptor.* In green algae and plants, chlorophyll is the

pigment molecule from which excited electrons transfer to stable orbitals in acceptor molecules. In the transfer, chlorophyll is oxidized because it loses an electron, and the primary acceptor is reduced because it gains an electron. In the third way, the energy of the excited electron, but not the electron itself, is transferred to a neighboring pigment molecule, a process called *inductive resonance.* This transfer excites the second molecule, while the first molecule returns to its ground state. Very little energy is lost in this energy transfer.

Chlorophylls and Carotenoids Cooperate in Light Absorption

Chlorophylls are the major photosynthetic pigments in plants, green algae, and cyanobacteria. They absorb photons and transfer excited electrons to stable orbitals in primary acceptors. Closely related molecules, the *bacteriochlorophylls,* carry out the same functions in other photosynthetic bacteria. Carotenoids absorb light energy and pass it on to the chlorophylls by inductive resonance in both eukaryotes and bacteria. Chlorophylls and carotenoids are bound to proteins in photosynthetic membranes.

Molecules of the chlorophyll family **(Figure 9.6a)** have a carbon ring structure, to which is attached a long, hydrophobic side chain. A magnesium atom is bound at the center of the ring structure. The most important kind of chlorophyll is chlorophyll *a,* which is found in plants, green algae, and cyanobacteria. A second kind, chlorophyll *b,* is found only in plants and green algae. Chlorophyll *a* and chlorophyll *b* differ only in one side group attached to a carbon of the ring structure (shown in Figure 9.6a).

A chlorophyll molecule contains a network of electrons capable of absorbing light (shaded in orange in Figure 9.6a). The amount of light absorbed at each wavelength is represented by a curve called an **absorption spectrum**, in which the height of the curve at any wavelength indicates the amount of light absorbed. **Figure 9.7a** shows the absorption spectra for chlorophylls *a* and *b*.

The carotenoids are built on a long backbone that typically contains 40 carbon atoms **(Figure 9.6b).** Carotenoids expand the range of wavelengths used for photosynthesis because they absorb different wavelengths than chlorophyll does. Carotenoids transmit or reflect other wavelengths in combinations that appear yellow, orange, red, or brown, depending on the type of carotenoid. The carotenoids contribute to the red, orange, and yellow colors of vegetables and fruits and to the brilliant colors of autumn leaves, in which the green color is lost when the chlorophylls break down.

The light absorbed by the carotenoids and chlorophylls, acting in combination, drives the reactions

a. Chlorophyll structure
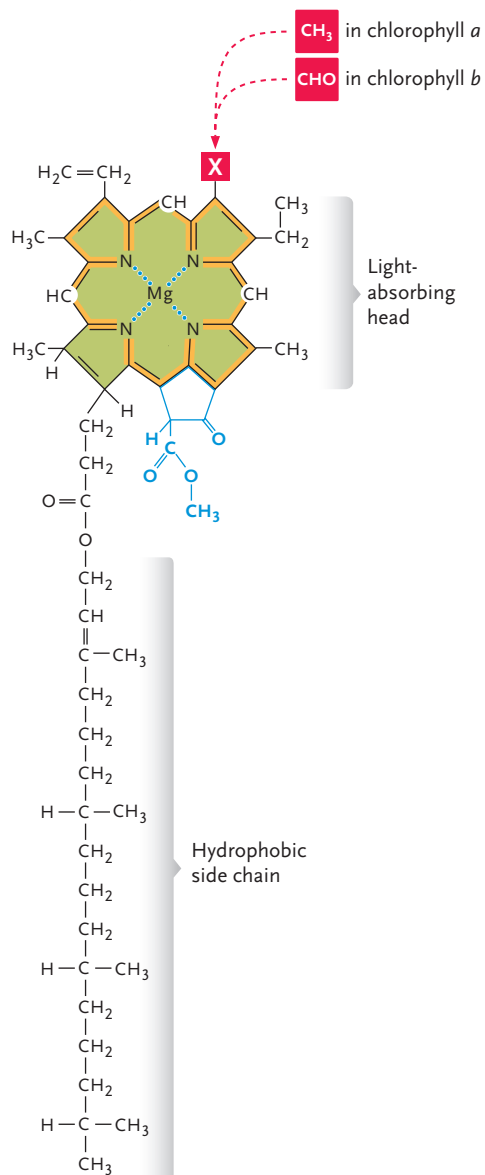
b. Carotenoid structure

Figure 9.6
Pigment molecules used in photosynthesis. **(a)** Chlorophylls *a* and *b*, which differ only in the side group attached at the X. Light-absorbing electrons are distributed among the bonds shaded in orange. The chlorophylls are similar in structure to the cytochromes, which occur in both the chloroplast and mitochondrial electron transfer systems. **(b)** Carotenoids. Th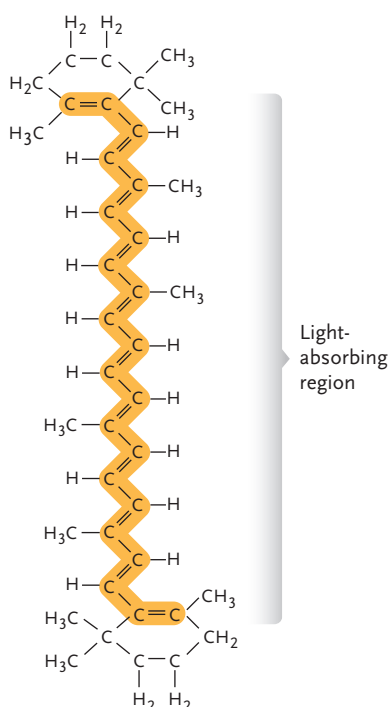e electrons absorbing light are distributed in a series of alternating double and single bonds in the backbone of these pigments.

of photosynthesis. Plotting the effectiveness of light at each wavelength in driving photosynthesis produces a graph called the **action spectrum** of photosynthesis (**Figure 9.7b** shows the action spectrum of higher plants). The action spectrum is usually determined by measuring the amount of O_2 released by photosynthesis at different wavelengths of visible light, as Engelmann did indirectly in the experiment described in the introduction to this chapter (compare Figures 9.1 and 9.7b).

In all eukaryotes, a specialized chlorophyll *a* molecule passes excited electrons to stable orbitals in the primary acceptor. Other chlorophyll molecules, along with carotenoids, act as *accessory pigments* that pass their energy to chlorophyll *a*. Light energy absorbed by the entire collection of chlorophyll and carotenoid molecules in chloroplasts is passed by inductive reso-

nance to the specialized chlorophyll *a* molecules that are directly involved in transforming light into chemical energy.

The Photosynthetic Pigments Are Organized into Photosystems in Chloroplasts

The light-absorbing pigments are organized with proteins and other molecules into large complexes called **photosystems (Figure 9.8),** which are embedded in thylakoid membranes and stromal lamellae. The photosystems are the sites at which light is absorbed and converted into chemical energy.

Plants, green algae, and cyanobacteria have two types of these complexes, called **photosystems I** and **II,** which carry out different parts of the light-dependent reactions. Each consists of two closely associated components: an **antenna complex** (also called a *light-harvesting complex*), and a **reaction center.**

The antenna complex contains an aggregate of many chlorophyll pigments and a number of carotenoid pigments. The chlorophyll molecules are anchored in the complex by being bound to specific membrane proteins. In this form, they are efficiently arranged to optimize the capture of light energy.

The reaction center contains a pair of specialized chlorophyll *a* molecules complexed with proteins. The specialized chlorophyll *a* at the reaction center of pho-

a. The absorption spectra of chlorophylls *a* and *b* and carotenoids
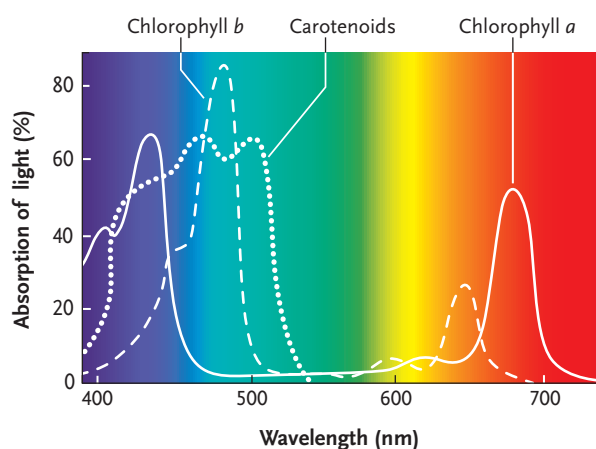
b. The action spectrum in higher plants, representing the combined effects of chlorophylls and carotenoids
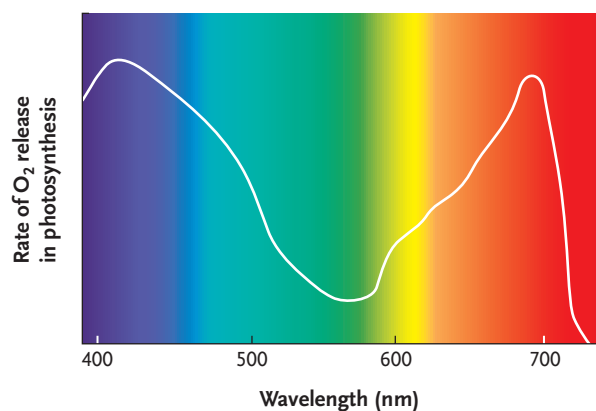
The peaks in the action spectrum are typically broader than those for the individual pigments, reflecting both their combined effects and changes in the absorption spectra of individual pigments by their combination with proteins in chloroplasts.

Figure 9.7
The absorption spectra of the photosynthetic pigments **(a)** and the action spectrum of photosynthesis **(b)** in higher plants. The absorption spectra in **(a)** were made from pigments that were extracted from cells and purified.

Figure 9.8
Major components of a photosystem: a group of pigments forming an antenna complex (light-harvesting complex) and a reaction center. Some components of the electron transfer system are located within the photosystems. Light energy absorbed anywhere in the antenna complex is conducted by inductive resonance to specialized chlorophyll *a* molecules in the reaction center. The absorbed light is converted to chemical energy when an excited electron is transferred to a stable orbital in a primary acceptor, also in the reaction center. High-energy electrons are conducted out of the photosystem by the components of the electron transfer system. The blue arrows show the path of energy flow.

tosystem I is called *P700* (P = pigment) because it absorbs light optimally at a wavelength of 700 nm. The reaction center of photosystem II contains a different specialized chlorophyll *a, P680,* which absorbs light optimally at a wavelength of 680 nm. P700 and P680 are structurally identical to other chlorophyll *a* molecules; their specific light absorption patterns result from interactions with particular proteins in the photosystems.

Light energy in the form of photons is absorbed by the pigment molecules of the antenna complex. This absorbed light energy reaches P700 and P680 in the reaction center by inductive resonance. On arrival, the energy is captured quickly in the form of an excited electron passed to a stable orbital in a primary acceptor molecule. That electron is passed to

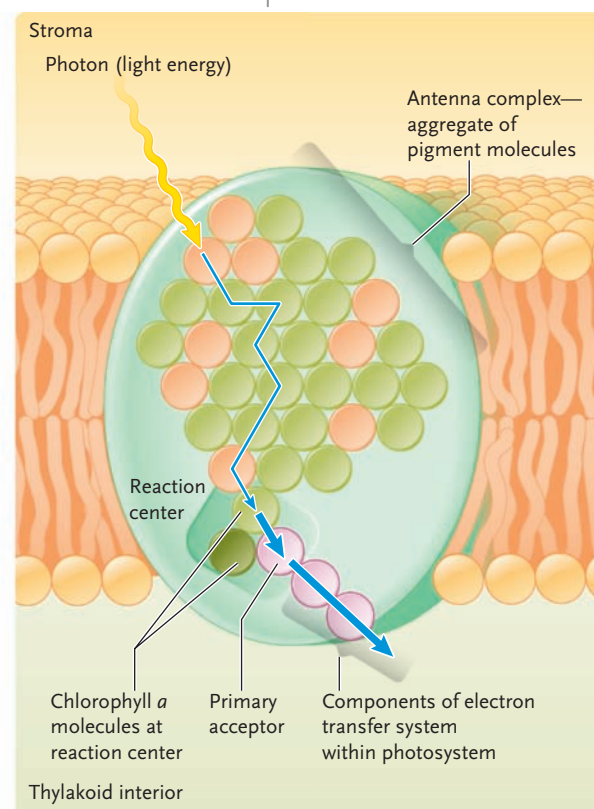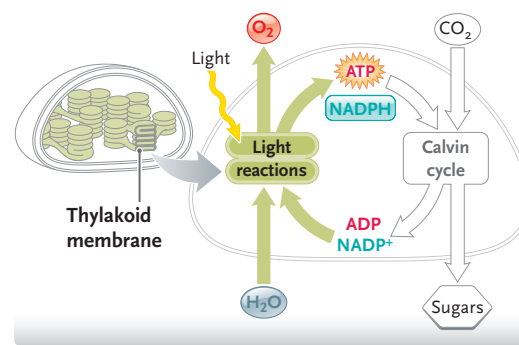the electron transfer system, which has some components within the photosystems and other components separate.

The electron transfer system within a photosystem carries electrons away from the primary acceptor. Photosystem II, in addition, is closely linked to a group of

enzymes that carries out the initial reaction splitting water into electrons, protons, and oxygen.

Electrons Flow from Water to Photosystem II to Photosystem I to NADP$^+$ Leading to the Synthesis of NADPH and ATP

In the second main process of the light-dependent reactions, the electrons obtained from the splitting of water (two electrons per molecule of water; see Section 9.1) are used for the synthesis of NADPH and ATP. These electrons, which were pushed to higher levels by the energy from light, pass through an electron transfer system consisting of a series of electron carriers that are alternately reduced and oxidized as they pick up and release electrons in sequence. The electron carriers are embedded in a thylakoid membrane in eukaryotes and in the plasma membrane in prokaryotes.

As in all electron transfer systems, the electron carriers of the photosynthetic system consist of nonprotein organic groups that pick up and release the electrons traveling through the system. The carriers include the same types that act in mitochondrial electron transfer—cytochromes, quinones, and iron-sulfur centers (discussed in Section 8.4). Most of the carriers are organized with proteins into larger complexes, which are distributed among the thylakoid membranes and stromal lamellae of chloroplasts.

The electron carriers of photosynthesis are arranged in a chain first deduced by Robert Hill and Fay Bendall of Cambridge University **(Figure 9.9).** Electrons from water first flow through photosystem II, becoming excited to a higher energy level in P680 through energy absorbed from light. The electrons then flow "downhill" in energy level through an electron transfer system connecting photosystems II and I. (Note: Photosystem I is so named because it was discovered first; the systems were given their numbers before their order of use in the pathway was worked out.) The electron transfer system consists of a pool of molecules of the electron carrier plastoquinone, a cytochrome complex, and the protein plastocyanin. The electrons release free energy at each transfer from a donor to an acceptor molecule as they pass through the system; some of this energy is used to create a gradient of H$^+$ across the membrane. The gradient provides the energy source for ATP synthesis, just as it does in mitochondria.

The electrons then pass to photosystem I, where they are excited a second time in P700 through energy absorbed from light. The high-energy electrons enter a short electron transfer system leading to the final acceptor of the chloroplast system, NADP$^+$. The enzyme NADP$^+$ reductase reduces NADP$^+$ to NADPH, using two electrons and two protons from the surrounding water solution and releasing one proton.

This pathway is frequently called **noncyclic electron flow** because electrons travel in a one-way direction from H$_2$O to NADP$^+$; it is sometimes called the *Z scheme* because of the sawtooth changes in electron energy level.

NADPH has the same primary role in all eukaryotes—to deliver high-energy electrons to synthetic reactions that require a reduction. In photosynthesis, the reaction requiring a reduction, the fixation of CO$_2$, takes place in the second stage of photosynthesis, the light-independent reactions.

Figure 9.10 shows how the electron transfer and ATP synthesis systems for the light-dependent reactions are organized in the thylakoid membrane. Let us follow the noncyclic electron pathway using this figure.

1. **Excitation in P680.** Electrons entering the pathway from the water-splitting reaction system associated with photosystem II are accepted one at a time by a P680 chlorophyll *a* in the reaction center of photosystem II. As P680 accepts the electrons, they are raised to the excited state, using energy passed to the reaction center from the light-absorbing pigment molecules in the antenna complex. The excited electrons are immediately transferred to the primary acceptor of photosystem II, which is a modified form of chlorophyll *a* without magnesium.

2. **Movement to the Plastoquinone Pool.** From the primary acceptor the electrons flow through a short chain of carriers within the photosystem and then transfer to a *plastoquinone,* which forms the first carrier of the electron transfer system linking photosystem II to photosystem I. The plastoquinones, analogous in structure and function to the ubiquinones of the mitochondrial electron system (shown in Figure 8.14), form a "pool" of molecules within the thylakoid membranes.

3. **H$^+$ Pumping by Plastoquinones and the Cytochrome Complex.** Electrons then pass from the plastoquinones to the next carrier, the *cytochrome complex,* in a structure that is closely related to complex III of the mitochondrial electron transfer system. As it accepts and releases electrons, the cytochrome complex pumps H$^+$ from the stroma into the thylakoid lumen. Those protons drive ATP synthesis (see step 7).

4. **Shuttling by Plastocyanin.** From the cytochrome complex, electrons pass to the mobile carrier *plastocyanin,* which shuttles electrons between the cytochrome complex and photosystem I.

5. **The Second Excitation in P700.** Electrons pass from plastocyanin to a P700 chlorophyll *a* in the reaction center of photosystem I, where they are excited to high energy levels again by absorbing more light energy. The excited electrons are transferred from P700 to the primary acceptor of this
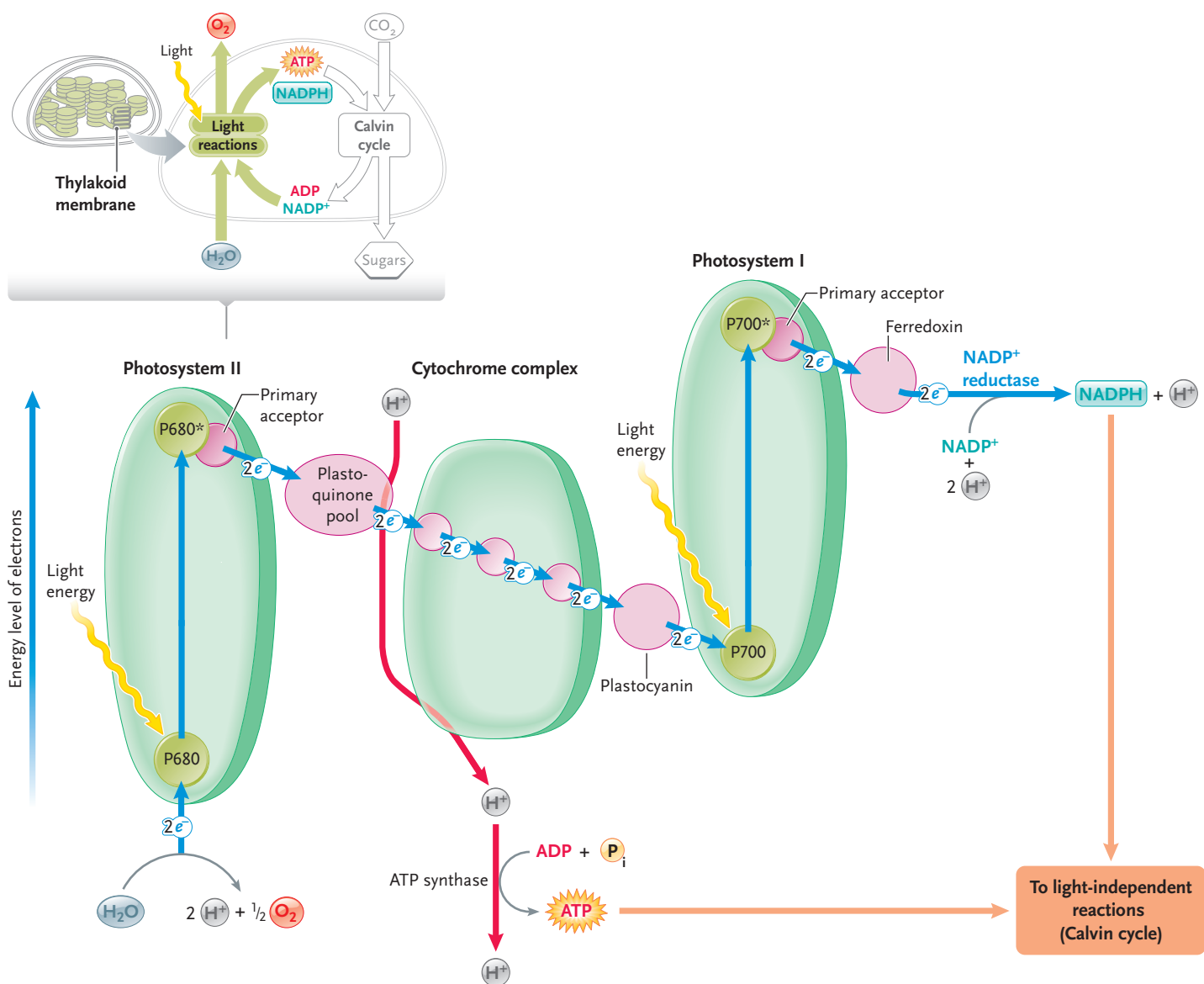
Figure 9.9

The pathway of the light-dependent reactions, noncyclic electron flow. Electrons (e^- in the figure) derived from water absorb light energy in photosystem II and, after transfer to a primary acceptor, travel through the electron transfer system to reach photosystem I. As they travel, some of their energy is tapped off to drive ATP synthesis. In photosystem I, the electrons absorb a second boost of energy and then, after transfer to a primary acceptor, are delivered to the final electron acceptor, $NADP^+$. As $NADP^+$ accepts the electrons, it combines with two protons to form NADPH and a proton. The asterisks indicate the excited forms of P680 and P700.

photosystem, formed by another specialized chlorophyll *a* molecule.

6. **Transfer to $NADP^+$ by Ferredoxin.** After passage through a short sequence of carriers within photosystem I, the electrons are transferred to *ferredoxin,* an iron-sulfur protein that acts as another mobile electron carrier of the pathway. The ferredoxin transfers the electrons, still at very high energy levels, to $NADP^+$, the final acceptor of the noncyclic pathway. $NADP^+$ is reduced to NADPH by $NADP^+$ reductase.

7. **ATP Synthesis.** Proton pumping by the plastoquinones and the cytochrome complex, as described in step 3, creates a concentration gradient of H^+ with the high concentration within the thylakoid lumen and the low concentration in the stroma. The gradient is enhanced by the addition of two protons to the lumen for each water molecule split, and by the removal of one proton from the stroma for each NADPH molecule synthesized. Because protons carry a positive charge, an electrical gradient forms across the thylakoid mem-
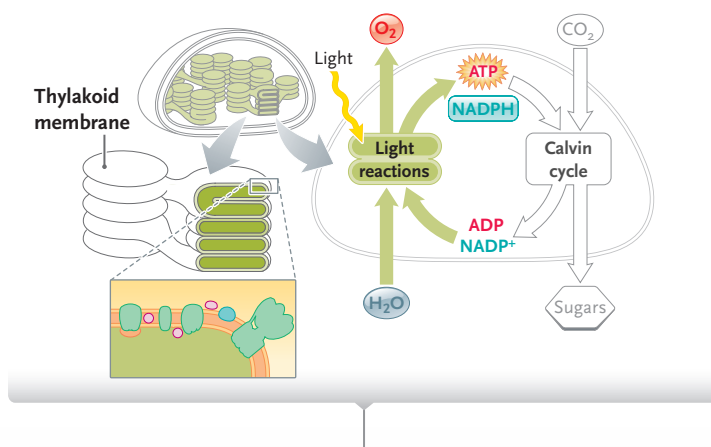
Figure 9.10

The components of the electron transfer and ATP synthesis systems in the thylakoid membrane, illustrating the synthesis of NADPH and ATP by the noncyclic electron flow pathway. The electron transfer system is organized into four complexes and two individual electron carriers. Photosystems II and I, both of which are embedded in the membrane, form two of the complexes. One of the remaining complexes is the membrane-embedded cytochrome complex. The other is ferredoxin, which is on the stromal surface of the membrane alongside the membrane-embedded NADP$^+$ reductase, which catalyzes the reduction of NADP$^+$ to NADPH. Plastoquinone is dissolved as a pool of molecules in the thylakoid membrane interior; plastocyanin is located on the membrane surface facing the thylakoid lumen. The enzyme for ATP synthesis by chemiosmosis, ATP synthase, is embedded in the same membrane.
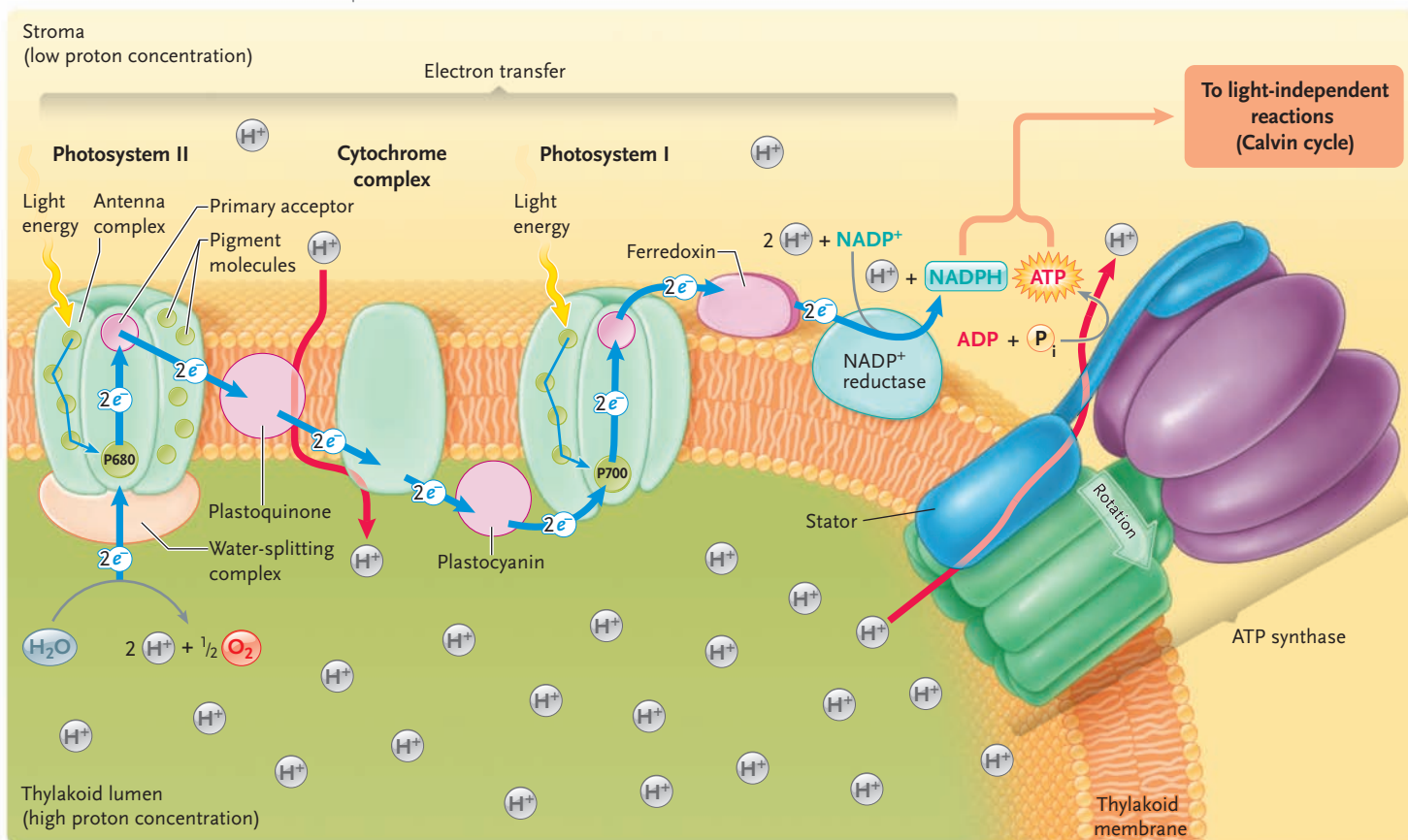
brane, with the lumen more positively charged than the stroma. The combination of a proton gradient and a voltage gradient across the membrane produces stored energy known as the *proton-motive force* (also discussed in Section 8.4), which contributes energy for ATP synthesis by ATP synthase. Just as for the mitochondrial ATP synthase, the chloroplast enzyme is embedded in the same membranes as the electron transfer system. Protons flow through a membrane channel from the thylakoid lumen to the stroma along their concentration gradient (see Figure 9.10). Free energy is released as H$^+$ moves through the channel, and it powers synthesis of ATP from ADP and P$_i$ by

the ATP synthase. This process of using an H$^+$ gradient to power ATP synthesis, called *chemiosmosis,* is the same as that used for ATP synthesis in mitochondria (see Section 8.4).

The overall yield of the noncyclic electron flow pathway is one molecule of NADPH and one molecule of ATP for each pair of electrons produced from the splitting of water. The synthesis of ATP coupled to the transfer of electrons energized by photons of light is called **photophosphorylation.** This process is analogous to oxidative phosphorylation in mitochondria (see Section 8.4), except that in chloroplasts light provides the energy for establishing the proton gradient.
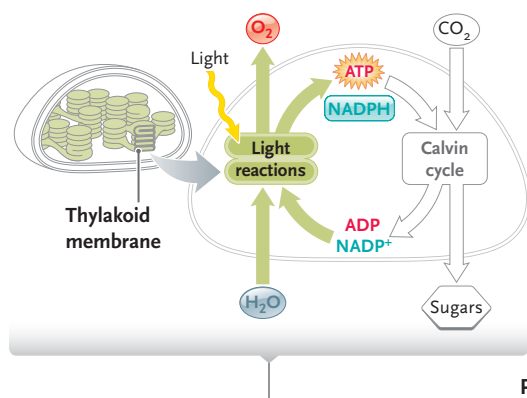
Figure 9.11

Cyclic electron flow around photosystem I. Electrons move in a circular pathway from ferredoxin back to the cytochrome complex, then to plastocyanin, through photosystem I, and back to ferredoxin again. The cycle pumps additional H^+ each time electrons flow through the cytochrome complex. The H^+ drive ATP synthesis as described for the noncyclic flow pathway.
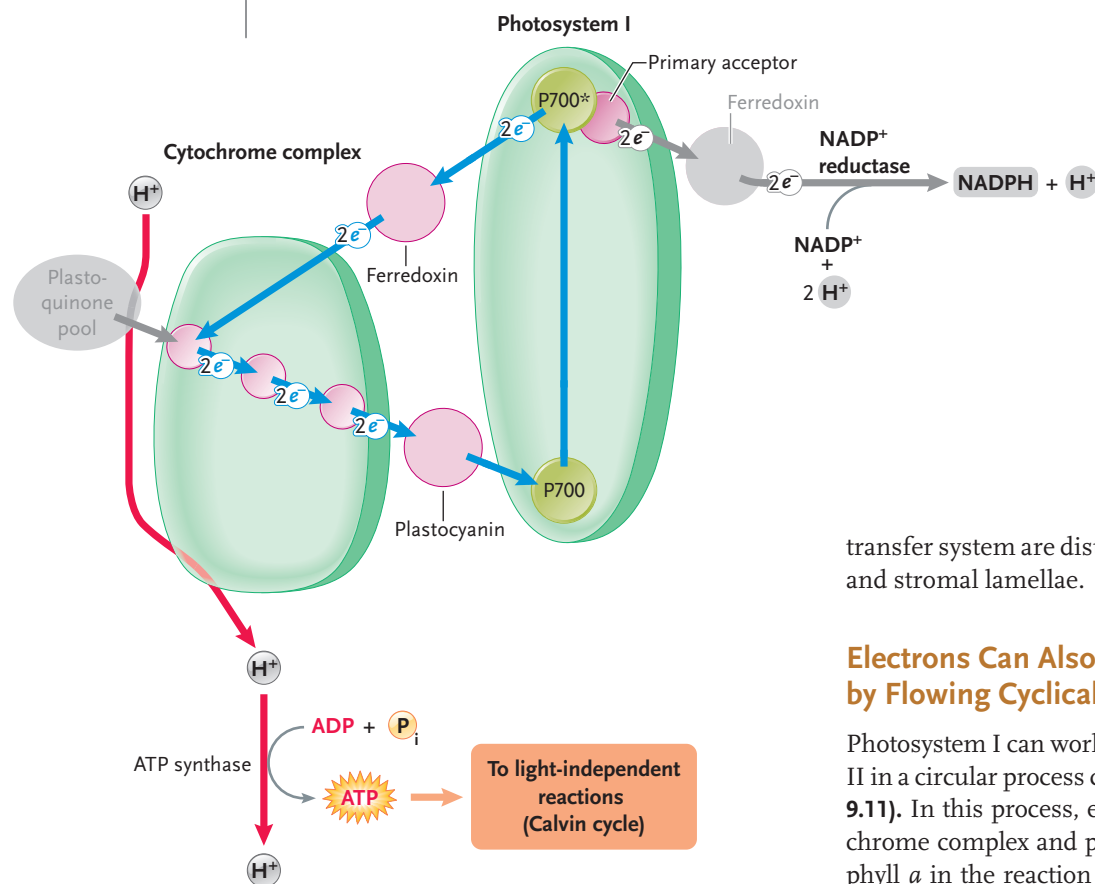
transfer system are distributed among both thylakoids and stromal lamellae.

Electrons Can Also Drive ATP Synthesis by Flowing Cyclically around Photosystem I

Photosystem I can work independently of photosystem II in a circular process called **cyclic electron flow (Figure 9.11).** In this process, electrons pass through the cytochrome complex and plastocyanin to the P700 chlorophyll *a* in the reaction center of photosystem I where they are excited by light energy. The electrons then flow from photosystem I to ferredoxin, but rather than being used for $NADP^+$ reduction by $NADP^+$ reductase, they flow back to the cytochrome complex. The electrons again pass to plastocyanin and on to photosystem I where they receive another energy boost, and so the cycle continues. Each time electrons flow around the cycle, more H^+ is pumped across the thylakoid membranes, driving ATP synthesis in the way already described. The net result of cyclic electron flow is that the energy absorbed from light is converted into the chemical energy of ATP *without* reduction of $NADP^+$ to NADPH.

The cyclic electron flow pathway is an important part of photosynthesis. The light-independent reactions require more ATP molecules than NADPH molecules, and the additional ATP molecules are provided by cyclic electron flow. Other energy-requiring reactions in the chloroplast also depend on ATP produced by cyclic electron flow.

Comparing the noncyclic pathway with the mitochondrial electron transfer system (shown in Figure 8.14) reveals that the pathway from the plastoquinones through plastocyanin in chloroplasts is essentially the same as the pathway from the ubiquinones through cytochrome *c* in mitochondria. The similarities between the two pathways indicate that the electron transfer system is a very ancient evolutionary development that became adapted to both photosynthesis and oxidative phosphorylation.

The elements of the noncyclic pathway are not located in fixed, organized assemblies as Figure 9.10 might suggest. Instead, photosystem II is located almost exclusively in thylakoid membranes, in regions where one thylakoid membrane is fused to the next in the stacks of grana; photosystem I is located primarily in stromal lamellae. Other components of the electron

Experiments with Chloroplasts Helped Confirm the Synthesis of ATP by Chemiosmosis

Our present understanding of the connection between electron transfer and ATP synthesis was first proposed for mitochondria in Mitchell's chemiosmotic hypothesis (discussed in Section 8.4). Several experiments have shown that the same mechanism operates in chloroplasts.

One of these experiments was carried out in 1966 by Andre T. Jagendorf and Ernest Uribe at Johns Hopkins University **(Figure 9.12).** The two scientists placed a solution containing intact chloroplasts (isolated from cells by cell fractionation: see Figure 8.5) in darkness, thereby eliminating light absorption and electron transfer as a source of energy for photosynthesis. They next created a surplus of H^+ inside the chloroplasts by adding an organic acid to the solution, which lowered the pH of the solution inside the stroma and thylakoids to pH 4. The chloroplasts, still in darkness, were then transferred to a second solution at a basic pH (pH 8). This process created an H^+ gradient, high inside the thylakoid lumen and low in the stroma. As H^+ moved from the thylakoid lumen to the stroma in response to the gradient, ATP was synthesized in the chloroplasts. Because the darkness eliminated electron transfer as an energy source, the observed ATP synthesis could have been powered only by the H^+ gradient.

Our description of photosynthesis to this point shows how the light-dependent reactions generate NADPH and ATP, which provide the reducing power and chemical energy required to produce organic molecules from CO_2. The next section follows NADPH and ATP through the light-independent reactions and shows how the organic molecules are produced.

STUDY BREAK

1. What is the difference between the chlorophyll *a* molecules in the antenna complexes and the chlorophyll *a* molecules in the reaction centers of the photosystems?
2. How is NADPH made in the noncyclic electron flow pathway?
3. What is the difference between the noncyclic electron flow pathway and the cyclic electron flow pathway?

9.3 The Light-Independent Reactions of Photosynthesis

The electrons carried from the light-dependent reactions by NADPH retain much of the energy absorbed from sunlight. These electrons provide the reducing

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Figure 9.12 Experimental Research

Demonstration That an H^+ Gradient Drives ATP Synthesis in Chloroplasts

QUESTION: Does chemiosmosis power ATP synthesis by a proton gradient in chloroplasts?

EXPERIMENT: Jagendorf and Uribe placed chloroplasts in darkness in an acidic medium, which allowed H^+ to penetrate inside, including into the thylakoid lumen.
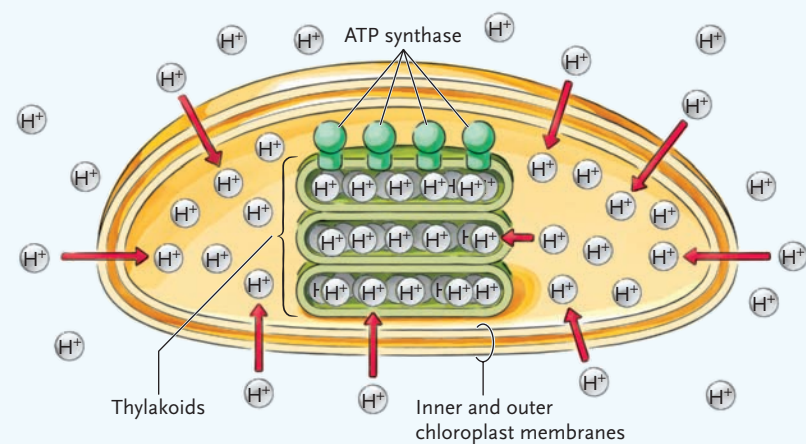
The chloroplasts were then placed in a medium at a basic pH, causing H^+ to move out of the thylakoid lumen in response to the gradient.
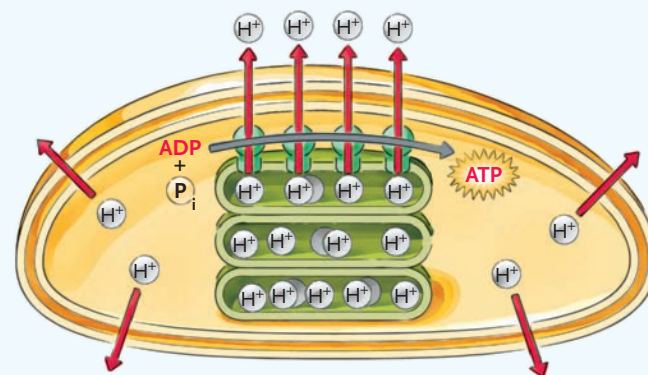
RESULT: ATP was synthesized by the chloroplast.

CONCLUSION: Because chloroplasts in darkness cannot use electron transfer as an energy source, chemiosmosis must power ATP synthesis by an H^+ gradient.

---

power required to fix CO_2 into carbohydrates and other organic molecules in the light-independent reactions. Additional energy for the light-independent reactions is supplied by the ATP generated in the light-dependent reactions. The reactions using NADPH and ATP to fix CO_2 occur in a circuit known as the **Calvin cycle,** named for its discoverer, Melvin

Basic Research: Two-Dimensional Paper Chromatography and the Calvin Cycle

The first significant progress in unraveling the light-independent reactions was made in the 1940s, when newly developed radioactive compounds became available to biochemists. One substance, CO_2 labeled with the radioactive carbon isotope [14]C (discussed in the *Focus on Research* in Chapter 2), was critical to this research.

Beginning in 1945, Melvin Calvin, Andrew A. Benson, and their colleagues at the University of California, Berkeley, combined ^{14}C-labeled CO_2 with a widely used technique called *two-dimensional paper chromatography* to trace the pathways of the light-independent reactions in a green alga, *Chlorella*. The researchers exposed actively photosynthesizing *Chlorella* cells to the labeled carbon dioxide. Then, at various times, cells were removed and placed in hot alcohol, which instantly stopped all the photosynthetic reactions of the algae. Radioactive carbohydrates were then extracted from the cells and, to identify them chemically, a drop of the extract was placed at one corner of a piece of paper and dried. The paper was placed with its edge touching a solvent (step 1 in the figure); Calvin used a water solution of butyl alcohol and propionic acid for this step. The compounds in the dried spot dissolved and were carried upward by the solvent through the paper (step 2 in the figure), at rates that var-

ied according to their molecular size and solubility. This line of spots was the first dimension of the two-dimensional technique.

The paper was then dried, turned 90º, and touched to a second solvent (Calvin used a water solution of phenol for this part of the experiment). As this solvent moved through the paper, the compounds again migrated upward from the spots produced by the first dimension, but at rates that were different from their mobility in the first solvent (step 3 in the figure). This step, the second dimension of the two-dimensional technique, separated molecules that, although different, had produced a single spot in the first solvent because they had migrated at the same rate. After all the molecules had migrated through the second dimension, the individual spots were identified by comparing their locations with the positions of spots made by known molecules when the "knowns" were run through the same procedure.

In a final step, the dried paper was covered with a sheet of photographic film. The radioactive compounds exposed spots on the film (step 4 in the figure), which was developed and compared with the spots on the paper to identify compounds that were radioactive. By comparing the labeled compounds revealed by the two-dimensional chromatography tech-

nique in extracts prepared from *Chlorella* cells under different conditions, Calvin and his colleagues were able to reconstruct the reactions of the Calvin cycle.

In carbohydrate extracts made within a few seconds after the cells were exposed to the labeled CO_2, most of the radioactivity was found in 3PGA, indicating that it is one of the earliest products of photosynthesis. In extracts made after longer periods of exposure to the label, radioactivity showed up in G3P and in more complex substances including a variety of six-carbon sugars, sucrose, and starch.

In other experiments, Calvin reduced the amount of CO_2 available to the *Chlorella* cells so that photosynthesis worked slowly even in bright light. Under these conditions, RuBP accumulated in the cells, suggesting that it is the first substance to react with CO_2 in the light-independent reactions, and that it accumulates if CO_2 is in short supply. By similar methods, most of the intermediate compounds between CO_2 and six-carbon sugars were identified.

Using this information, Calvin and his colleagues pieced together the light-independent reactions of photosynthesis and showed that they formed a continuous cycle. Melvin Calvin was awarded a Nobel Prize in 1961 for his work on the assimilation of carbon dioxide in plants.

Turn paper 90°

1 A drop of solution containing extracted molecules is placed at the corner of a piece of chromatography paper. The edge of the paper is placed in a solvent.

2 The solvent rises in the paper and separates the extracted molecules into a vertical row of spots. This is the first dimension of the technique.

3 The paper is turned 90° and placed in the second solvent. As this solvent rises in the paper, it separates different molecules in the first row into vertical rows of spots. This is the second dimension of the technique.

4 A photographic film is placed over the paper. Radioactive molecules expose the film in spots over their locations in the paper. Developing the film reveals the locations of the radioactive spots.

Calvin. *Focus on Research* describes the experiments Calvin and his colleagues used to elucidate the light-independent reactions.

The Calvin Cycle Uses NADPH, ATP, and CO_2 to Generate Carbohydrates

The light-independent reactions of the Calvin cycle use CO_2, ATP, and NADPH as inputs. As products, the cycle releases ADP; $NADP^+$; the three-carbon carbohydrate molecule glyceraldehyde-3-phosphate (G3P), already familiar as part of glycolysis; and inorganic phosphate (outlined in **Figure 9.13a**). The Calvin cycle takes place entirely in the chloroplast stroma.

Figure 9.13a focuses primarily on tracking the carbon atoms through the cycle. In phase 1 of the cycle, *carbon fixation,* a carbon atom from CO_2 is added to ribulose 1,5-bisphosphate (RuBP), a five-carbon sugar, to produce two three-carbon molecules of 3-phosphoglycerate (3PGA). In phase 2, *reduction,* reactions using NADPH and ATP from the light-dependent reactions convert 3PGA into G3P, another three-carbon molecule. After several rounds of the Calvin cycle, two molecules of G3P leave the cycle and are used to form the products of the cycle, the six-carbon sugar glucose and other organic compounds. In phase 3, *regeneration,* some G3P molecules are used to produce the five-carbon RuBP with the help of energy from ATP. The cycle then begins again.

Now let us consider the reactions in more detail. **Figure 9.13b** shows the chemical structures, reactions, and enzymes of the cycle. The key reaction of the cycle is the first, carbon fixation, in which CO_2 combines with RuBP, forming a transient six-carbon molecule that is cleaved to form 3PGA. This reaction, which fixes CO_2 into organic form, is catalyzed by the key enzyme of the Calvin cycle, **RuBP carboxylase/ oxygenase** (abbreviated as **rubisco**). In the next two reactions (reactions 2 and 3 in Figure 9.13b, shown in two parallel paths because two molecules of 3PGA are being processed), the three-carbon molecules are raised in energy level by the addition of phosphate groups transferred from ATP and electrons from NADPH (the ATP and NADPH are products of the light-dependent reactions). The G3P generated by reaction 3 is the carbohydrate product of the Calvin cycle.

Most of the G3P produced by the reactions is used to regenerate the RuBP entering in the first reaction of the cycle. However, some G3P is released as a net product; it serves as the primary building block for reactions producing glucose and many other organic molecules in chloroplasts.

The G3P used to regenerate RuBP enters a complex series of reactions (reaction series 4 in Figure 9.13b) that yields the five-carbon sugar ribulose 5-phosphate. In the final reaction of the cycle (reaction 5), a phosphate group is transferred from ATP to regenerate the RuBP used in the first reaction, and the cycle is ready to turn again.

Three Turns of the Calvin Cycle Are Needed to Make One Net G3P Molecule

If the Calvin cycle is run through one turn, the cycle cannot turn again if a molecule of G3P is taken away. The remaining G3P, with three carbons in its structure, cannot supply the five carbons needed to regenerate the RuBP molecule required for another turn. In fact, the cycle must run through *three* turns before enough G3P molecules are made so that one can be released.

Here's how it works. Three turns of the Calvin cycle produce six molecules of G3P (totaling 18 carbons) and use three molecules of RuBP (totaling 15 carbons) and three molecules of CO_2 (totaling three carbons). Of the six G3P molecules, five (totaling 15 carbons) go back into the cycle to regenerate the three RuBP molecules (15 carbons) used in the three turns. Thus, the cycle can generate one surplus molecule of G3P (three carbons) after three turns. The leftover G3P is free to enter reaction pathways that yield glucose, sucrose, starch, and other complex organic substances.

Another way to look at it is to consider that one turn of the Calvin cycle takes up one molecule of CO_2 and generates one (CH_2O) unit of carbohydrate. On this basis, you can understand that three turns are required to make enough (CH_2O) units to assemble one surplus molecule of G3P. Providing enough (CH_2O) units to make a six-carbon carbohydrate such as glucose requires six turns of the cycle.

This approach allows us to total all the inputs and outputs of the Calvin cycle. For each turn of the cycle, 2 ATP and 2 NADPH are used in reactions 2 and 3, and one additional ATP is used in reaction 5, for a total of 3 ATP and 2 NADPH for each turn. Although one of the phosphates derived from ATP is attached to G3P, this phosphate is eventually released when G3P is converted into other substances. As net reactants and products, one complete turn of the cycle therefore includes:

$$CO_2 + 2\ NADPH + 3\ ATP \rightarrow$$
$$(CH_2O) + 2\ NADP^+ + 3\ ADP + 3\ P_i$$
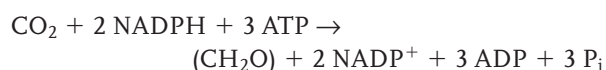
Rubisco Is the Key Enzyme of the World's Food Economy

Rubisco, the enzyme that catalyzes the first reaction of the Calvin cycle, is unique to photosynthetic organisms. By catalyzing CO_2 fixation, it provides the source of organic molecules for most of the world's organisms—the enzyme converts about 100 billion tons of CO_2 into carbohydrates annually. There are so many rubisco mole-

a. Overall phases of the Calvin Cycle

Phase 1 Fixation of CO_2

Phase 2 Reduction and sugar production

Phase 3 Regeneration of RuBP

Calvin Cycle

RuBP

2 molecules of 3PGA

2 molecules of G3P

Organic compounds (glucose)

ADP

ATP

ATP

ADP

2 NADPH

2 NADP⁺

2 P_i

CO_2
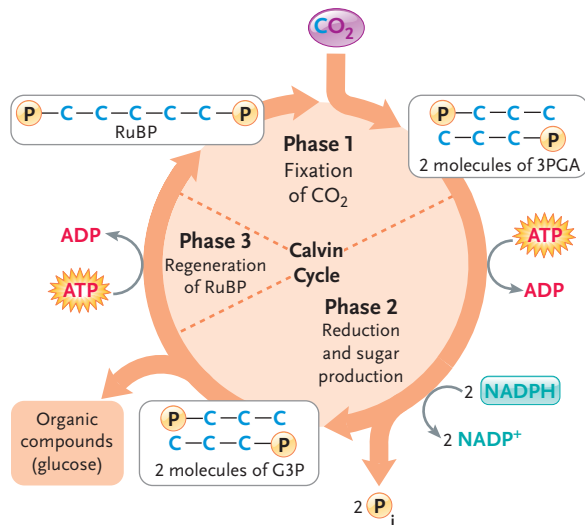
Figure 9.13

The Calvin cycle. **(a)** Overview of the three phases of the Calvin cycle. The figure tracks the carbon atoms in the molecules in the cycle. **(b)** Reactions and enzymes of the Calvin cycle (the enzymes are printed in rust). Reaction 1 first produces an unstable, six-carbon intermediate (not shown), which splits almost immediately into two molecules of 3PGA, the substance detected by the labeling experiments as the first product of the light-independent reactions.

Light

Light reactions

Calvin cycle

Chloroplast stroma

O_2

CO_2

ATP

NADPH

ADP

NADP⁺

H_2O

Sugars

b. Reactions and enzymes of the Calvin Cycle

5 Another phosphate is transferred from ATP to ribulose 5-phosphate to produce RuBP. This reaction regenerates the RuBP used in reaction 1, and the cycle is ready to turn again.

1 Ribulose 1,5-bisphosphate (RuBP) reacts with CO_2, producing two molecules of 3PGA. This reaction converts CO_2 into organic form.

2 A phosphate group from ATP is added to each of the two 3PGA molecules, producing two molecules of 1,3-bisphosphoglycerate. The reaction raises the energy content of the products to a level high enough to enter the next reaction of the cycle.

3 The two molecules of 1,3-bisphosphoglycerate are reduced by electrons carried by NADPH. One phosphate is removed from each reactant at the same time, yielding two molecules of G3P.

4 Some of the G3P produced by reaction 3 enters a series of reactions yielding ribulose 5-phosphate.

Calvin Cycle

Ribulose 1,5-bisphosphate (RuBP)

RuBP carboxylase

3-Phosphoglycerate (3PGA)

3-Phosphoglycerate kinase

1,3-Bisphosphoglycerate

1,3-Bisphosphoglycerate kinase

Glyceraldehyde-3-phosphate (G3P)

Ribulose 5-phosphate

Ribulose 5-phosphate kinase

Complex reactions regenerating ribulose 5-phosphate

Some net G3P

To reactions synthesizing sugars and other organic compounds

CO_2

ATP

ADP

NADPH

NADP⁺

P_i

Small but Pushy

We noted that all the active sites of rubisco appear to be on the large polypeptide subunit of the enzyme. Even so, 99% of the enzyme's catalytic activity is lost if the small subunit is removed. What does the small subunit do?

Betsy A. Reed and F. Robert Tabita of The Ohio State University set out to answer this question using molecular techniques. They hypothesized that the structure of a specific region of the small subunit was critical to its function. To test this hypothesis, the investigators used DNA cloning techniques (described in Chapter 18) to produce five versions of the small subunit, each with a different amino acid substituted for the normal one at five different positions in the protein, and examined the effects of the substitutions on enzyme activity. One of the modified small subunits, which had glutamine substituted for arginine at position 88

in the small subunit amino acid sequence, was unable to assemble with the large subunit to form a complete enzyme complex, showing that the arginine in position 88 is essential for normal enzyme assembly.

The four remaining versions of the small subunit assembled normally with large subunits. Each complete rubisco complex was placed in a test tube system containing RuBP and other factors required for the initial reaction of the Calvin cycle. The altered versions of the enzyme were all able to recognize and bind their substrate—RuBP, CO_2, or O_2—as ably as the normal enzyme. Therefore, these four alterations induced in the small subunit had no effect on the specificity of the enzyme.

The investigators next checked the rates at which the enzymes catalyzed CO_2 fixation. Three of the four altered

enzymes ran the first reaction of the Calvin cycle at only 35% of the rate of the normal enzyme. The most active worked only about half as fast as the normal enzyme. In other words, the small subunit has a very significant effect on the enzyme's rate of catalysis. The effect is critically important when considered in the context of the comparatively slow reaction rate of the normal enzyme. The enzyme's multiple form—eight copies of each subunit, massed together, all doing the same thing—and the very large amount of the enzyme packed into leaves compensate for the slow rate. Evidently, the small subunit evolved as yet another way to compensate for the enzyme's slow action, by pushing the large subunit to do its job faster. It may do so by altering the three-dimensional folding of the large subunit into patterns that increase its catalytic rate.

cules in chloroplasts that the enzyme may make up 50% or more of the total protein of plant leaves. As such, it is also the world's most abundant protein, estimated to total some 40 million tons worldwide, equivalent to about 10 kg for every human.

Rubisco has essentially the same overall structure in almost all photosynthetic organisms: eight copies each of a large and a small polypeptide, joined together in a 16-subunit structure. The large subunit contains all of the known binding sites for substrates, including CO_2 and RuBP. Although the small subunit has no active sites, it is still essential for efficient operation of the enzyme. *Insights from the Molecular Revolution* describes a recent effort to determine the molecular functions of the small subunit.

Rubisco is also the key regulatory site of the Calvin cycle. The enzyme is stimulated by both NADPH and ATP; as long as these substances are available from the light-dependent reactions, the enzyme is active and the light-independent reactions proceed. During the daytime, when sunlight powers the light-dependent reactions, the abundant NADPH and ATP supplies keep the Calvin cycle running; in darkness, when NADPH and ATP become unavailable, the enzyme is inhibited and the Calvin cycle slows or stops. Similar controls based on the avail-

ability of ATP and NADPH also regulate the enzymes that catalyze other reactions of the Calvin cycle, including reactions 2 and 3 in Figure 9.13b.

G3P Is the Starting Point for Synthesis of Many Other Organic Molecules

The net G3P formed in the Calvin cycle is the starting point for production of a wide variety of organic molecules. More complex carbohydrates such as glucose and other monosaccharides are made from G3P by reactions that, in effect, reverse the first half of glycolysis. Once produced, the monosaccharides enter biochemical pathways that make disaccharides such as sucrose, polysaccharides such as starches and cellulose, and other complex carbohydrates of cell walls. Other pathways manufacture amino acids, fatty acids and lipids, proteins, and nucleic acids. The reactions forming these products occur both within chloroplasts and in the surrounding cytosol and nucleus.

Sucrose, a disaccharide consisting of glucose linked to fructose, is the main form in which the products of photosynthesis circulate from cell to cell in higher plants. Organic nutrients are stored in most higher plants as sucrose or starch, or as a combination of the two in proportions that depend on the plant spe-

cies. Sugar cane and sugar beets, which contain stored sucrose in high concentrations, are the main sources of the sucrose we use as table sugar.

STUDY BREAK

1. What is the reaction that rubisco catalyzes? Why is rubisco the key enzyme for producing the world's food, and how it is the key regulatory site of the Calvin cycle?
2. How many molecules of carbon dioxide must enter the Calvin cycle for the plant to produce a sugar containing 12 carbon atoms? How many ATP and NADPH molecules would be required to make that molecule?

9.4 Photorespiration and the C_4 Cycle

Oxygen can compete with carbon dioxide for the active site of rubisco. When oxygen binds to the active site, rubisco acts as an *oxygenase* instead of a carboxylase. As an oxygenase, it catalyzes a reaction in which O_2 instead of CO_2 is added to RuBP. The products of the reaction are toxic and cannot be used by plants for synthesis of carbohydrates. Instead, the products are eliminated by pathways that *release* CO_2. Because O_2 is taken up by rubisco's oxygenase activity, and CO_2 is released at later steps, the entire process is known as **photorespiration.**

Photorespiration reduces the efficiency of energy use in photosynthesis and impairs the growth of many plants, including some of the crop plants that provide food for our population. However, many plants have evolved ways of dealing with photorespiration, including a preliminary reaction series known as the **C_4 cycle,** which allows CO_2 to be fixed by a different carboxylase

that is unaffected by high oxygen concentrations. This adaptation is combined with other adaptations that restrict rubisco's carboxylase activity to conditions where oxygen concentration remains low.

The Oxygenase Activity of Rubisco Leads to the Formation of a Toxic Molecule

Figure 9.14 shows the result of the oxygenase activity of rubisco. First, the reaction converts RuBP into one molecule of 3PGA and one molecule of a two-carbon substance, phosphoglycolate. No carbon is fixed during this reaction, and energy must then be used to salvage the carbons from phosphoglycolate. The pathway for the latter process begins with the removal of the phosphate group from phosphoglycolate, producing *glycolate,* a toxic substance that is eliminated by oxidation inside microbodies (microbodies are discussed in Section 5.3). The products of this oxidation enter reaction pathways that yield CO_2. Thus, as an overall pathway, photorespiration uses O_2 and releases CO_2.

The balance of the carboxylase and oxygenase activities of rubisco depends on the relative concentrations of O_2 and CO_2 inside leaves and other structures carrying out photosynthesis. As O_2 concentration rises and CO_2 concentration falls, the oxygenase activity of rubisco increases proportionately.

Why does rubisco have the oxygenase activity? One possibility is that the enzyme evolved before the water-splitting reaction of photosynthesis appeared, at a time when the atmosphere was rich in CO_2 and low in O_2. Under these conditions, there would be no selection against the oxygenase activity of the enzyme.

Elevated Temperatures Increase the Level of Photorespiration in Many Plants

Oxygen concentration rises in leaves, and CO_2 concentration falls, when photosynthesis proceeds at high rates, as it does on hot, sunny days. Other physiological responses of plants to hot weather also tend to tip the O_2/CO_2 balance in the direction of O_2. As photosynthesis proceeds during the day, plants open their stomata to release the O_2 made in photosynthesis and to let in CO_2. However, opening the stomata also releases water, leading to dehydration of the plants during hot weather. As the stomata close in response to the water loss, O_2 builds up and CO_2 concentration falls in the leaves, increasing the oxygenase activity of RuBP carboxylase and the rate of photorespiration.

Unfortunately, many economically important crop plants are among those seriously impaired by high photorespiration rates at elevated temperatures—rice, barley, wheat, soybeans, tomatoes, and potatoes, to name a few. The detrimental effects of photorespiration on these plants can be estimated by growing them at elevated temperatures in hothouses contain-
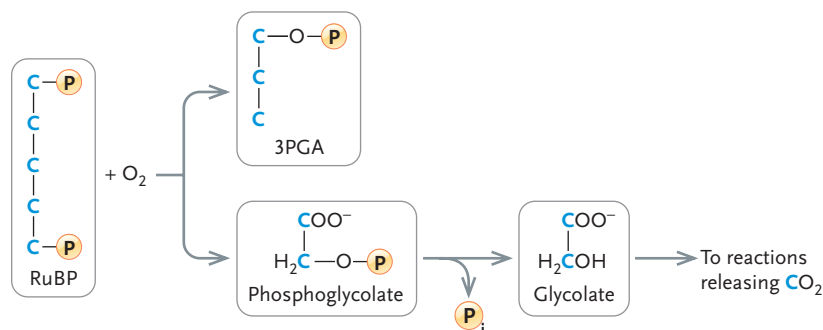

Figure 9.14

Photorespiration, an alternative pathway for rubisco in which, in the presence of oxygen, the oxygenase activity of the enzyme produces glycolate. Glycolate, a toxic product, is eliminated by reactions that convert carbon back to inorganic form as CO_2.

ing CO_2 in high concentrations. Under these conditions, which curtail photorespiration, some of the crops grow as much as five times faster (as measured by dry weight) than they do at the CO_2 concentrations of the atmosphere.

The C_4 Cycle Circumvents Photorespiration by Using a Carboxylase That Has No Oxygenase Activity

In the C_4 cycle **(Figure 9.15),** CO_2 initially combines with a three-carbon molecule, *phosphoenolpyruvate (PEP),* producing the four-carbon intermediate oxaloacetate. The reaction is catalyzed by the critical enzyme of the C_4 cycle, *PEP carboxylase*. The C_4 cycle gets its name because its first product is a four-carbon molecule rather than a three-carbon molecule as in the Calvin cycle (the Calvin cycle is often called the C_3 cycle to make this distinction). Oxaloacetate is then reduced to *malate,* a four-carbon acid, by electrons transferred from NADPH.

With some variations in intermediates and products, the C_4 cycle takes place in several groups of plants, including important cereal crops such as corn.

The C_4 cycle runs when O_2 concentrations are high. PEP carboxylase has no activity as an oxygenase, and is therefore unaffected when O_2 concentrations are high in leaves. Later, at a location or time when O_2 concentrations are low, the malate produced by the C_4 cycle is oxidized to a three-carbon product, pyruvate, with release of CO_2:

$$\text{malate} + \text{NADP}^+ \rightarrow \text{pyruvate} + \text{NADPH} + CO_2$$
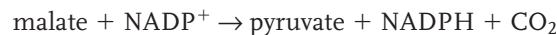
The CO_2 then enters the Calvin cycle for fixation by rubisco into G3P and other products of the light-independent reactions. Because O_2 concentrations are low and CO_2 concentrations are high, the oxygenase activity of rubisco is limited, and the Calvin cycle proceeds normally.

The pyruvate returns to the C_4 cycle, where it is converted to PEP at the expense of one molecule of

1 When O_2 concentration is high, CO_2 combines with PEP to produce oxaloacetate. Energy to drive the reaction is derived from the phosphate group removed from PEP.

2 Oxaloacetate is reduced to malate by electrons transferred from NADP$^+$.

4 Pyruvate is phosphorylated to produce PEP at the expense of one molecule of ATP converted to AMP, regenerating the PEP used in the first step of the cycle.

3 When O_2 concentration is low, malate is oxidized to pyruvate, with release of CO_2. The released CO_2 enters the Calvin cycle.

Figure 9.15
The C_4 cycle and its integration with the Calvin cycle. Enzymes are printed in rust. Each turn of the cycle, which delivers one molecule of CO_2 to the Calvin cycle, proceeds at the expense of two phosphate groups removed from ATP.

ATP converted to AMP. Because two phosphates are removed from ATP for each turn of the C_4 cycle, making each molecule of glucose by the combined activities of the C_4 and Calvin pathways requires an additional 12 ATP.

In spite of the extra penalty paid in ATP, the ability to bypass photorespiration gives plants using the C_4/Calvin cycle combination an advantage in warmer climates over plants with only the Calvin cycle. The crossover point lies at about 30°C. Above this temperature, C_4 plants become significantly more efficient than Calvin-limited plants; below 30°C, the additional ATP used by C_4 plants makes Calvin-limited species more efficient in spite of photorespiration.

The 30°C crossover point gives C_4 plants an advantage in the tropics and in temperate regions with high summer temperatures, such as the southern and central United States. In colder areas, Calvin plants have the advantage. For example, in Florida 80% of all native species are C_4 plants, compared with 0% in Manitoba, Canada.

The C_4 pathway occurs in at least 16 different families of flowering plants (angiosperms; discussed in Chapter 27). Some of the families are only distantly related, suggesting that the C_4 pathway may have developed independently several times in the evolution of higher plants.

Some Plants Circumvent Photorespiration by Running the C_4 and Calvin Cycles in Different Locations

Some C_4 plants run the Calvin and C_4 cycles at the same time, but in locations with differing CO_2 and O_2 concentrations. In corn, the C_4 cycle occurs in *mesophyll* cells, which lie close to the surface of leaves and stems, where O_2 is abundant **(Figures 9.16a and b).** The malate product of the C_4 cycle diffuses from the meso-
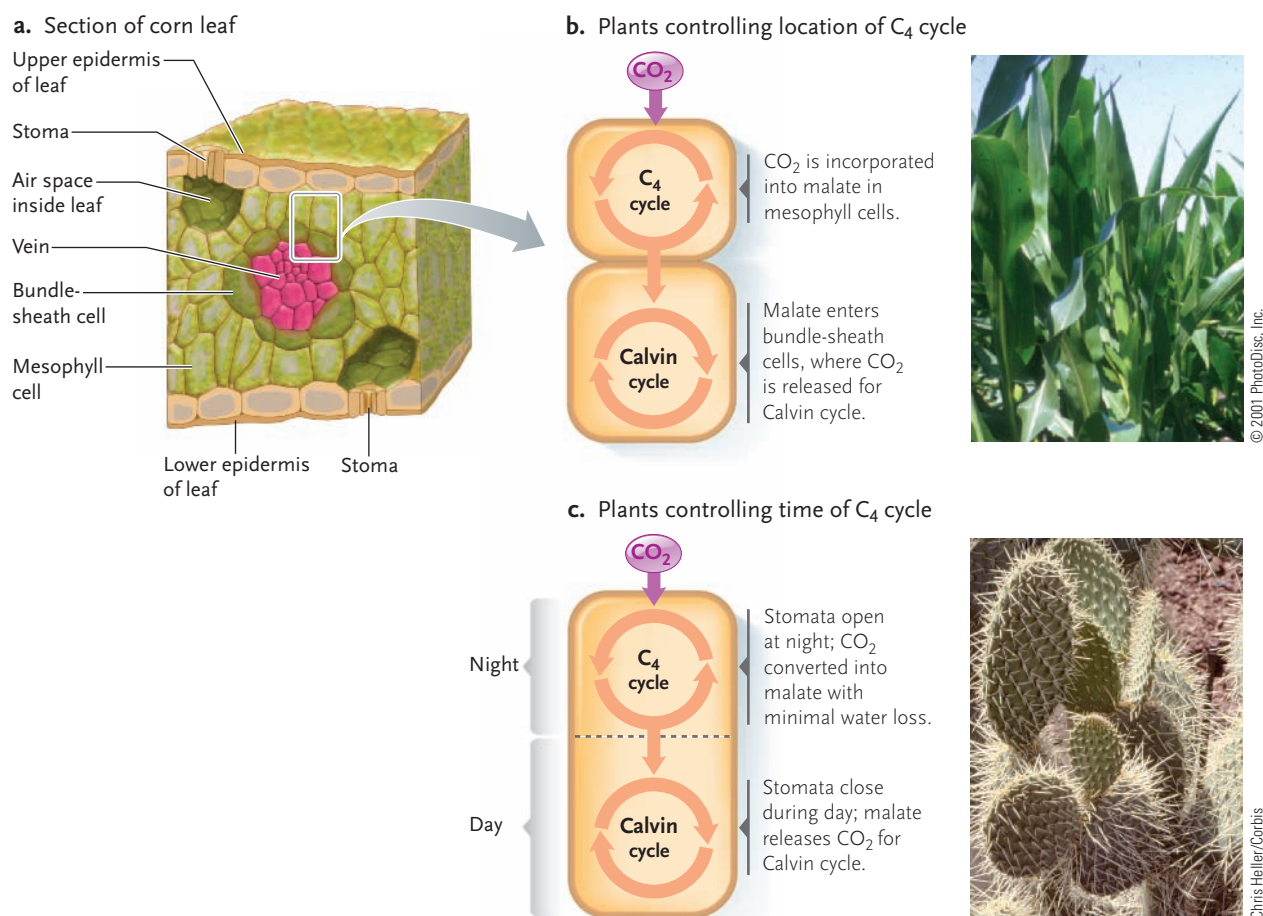

a. Section of corn leaf

Upper epidermis of leaf

Stoma

Air space inside leaf

Vein

Bundle-sheath cell

Mesophyll cell

Lower epidermis of leaf   Stoma

b. Plants controlling location of C_4 cycle

CO_2

C_4 cycle — CO_2 is incorporated into malate in mesophyll cells.

Calvin cycle — Malate enters bundle-sheath cells, where CO_2 is released for Calvin cycle.

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c. Plants controlling time of C_4 cycle

CO_2

Night — C_4 cycle — Stomata open at night; CO_2 converted into malate with minimal water loss.

Day — Calvin cycle — Stomata close during day; malate releases CO_2 for Calvin cycle.

Chris Heller/Corbis

Figure 9.16

Coordination of the C_4 and Calvin cycles to minimize photorespiration. **(a)** and **(b)** Some C_4 plants separate the two cycles into different locations internally, as in the corn leaf shown in this diagram. The mesophyll cells (lighter green), which are closer to the leaf surfaces, carry out the C_4 cycle in a relatively O_2-rich environment. The bundle-sheath cells (darker green), which are cut off from O_2 by the surrounding layer of mesophyll cells, carry out the Calvin cycle. **(c)** Other C_4 plants carry out the two cycles at different times, as in the beavertail cactus *(Opuntia basilaris)* in the photo.

Photosynthesis is considered by many to be the most important biological process on Earth. In particular, directly or indirectly (through herbivorous animals), photosynthesis provides all of our food requirements. Research on photosynthesis therefore is of high importance and is likely to have significant benefit for humankind. For example, a complete understanding of the chemistry of photosynthesis, the regulation of the process, and the genes that encode the components of the process could be applicable to other endeavors of human interest, such as solar energy conversion and the development of therapeutic drugs.

From research on agricultural crops, we have learned that photosynthesis is not a very efficient process. Estimates are that only 1% to 2% of the solar energy that strikes the planet's surface is converted to new photosynthetic products. Research is being done to learn enough about photosynthesis so that crop plants can be engineered to be more efficient. An area of particular relevance here is photorespiration, which reduces the efficiency of energy use in photosynthesis. Hopefully, research will give us a better understanding of the biochemical control of photorespiration and provide clues about breeding new, more energy-efficient plants.

Let us consider two specific avenues of research.

How is the efficiency of photosynthesis regulated?

The laboratory of David Kramer at Washington State University is interested in the energetics and control of photosynthesis, the electron transfer reactions, the coupling of electron transfer reactions to ATP synthesis, and photosynthesis in extreme environments.

As you have learned, energy conversion by the chloroplast involves the capture of light energy and the channeling of that energy through an electron transfer system with the eventual synthesis of NADPH and ATP. At high concentrations, many of the intermediates produced in this energy conversion can potentially destroy the photosynthetic apparatus, a phenomenon called photoinhibition. To prevent such damage, the effi-ciency of some of the photosystem components is reduced by the release of some of the energy as heat. Increased heat lowers the efficiency of photosynthesis, however. Evidence from a range of studies indicates that the balance between protection against photoinhibition and photosynthetic efficiency is important in enabling plants to acclimate to environmental changes. Kramer's group is doing research to develop an understanding of the structure and function of ATP synthase and the cytochrome complex, and the effects of these components on the proton-motive force, which is known to play a pivotal role in balancing photoinhibition and photosynthetic efficiency. The results will illuminate how the specific mechanisms of photosynthesis determine plant growth and survival. In addition, the technology developed as part of the research may lead to applications in plant breeding and farming, providing farmers with a means to assess the physiological states of the plants they are growing and, therefore, to modify the conditions for optimal growth.

How are chloroplast thylakoid membrane-protein complexes assembled?

Research by Andrew Webber's group at Arizona State University is directed to understanding the formation of chloroplast thylakoid membrane-protein complexes. Those complexes are key to the process of photosynthesis, yet their assembly is not understood. Using molecular biology and biochemistry techniques, Webber's group is studying how the synthesis of chloroplast proteins, some of which are encoded by genes in the chloroplast and others of which are encoded by genes in the nucleus, is coordinated and regulated. The researchers are also using molecular techniques to change specific amino acids in the chloroplast proteins with the aim of elucidating how those amino acids are involved in assembly and functioning of the complexes. The results will add more detailed knowledge about the structure and function of components that are key to the process of photosynthesis.

Peter J. Russell

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phyll cells to *bundle sheath cells,* located in deeper tissues where O_2 is less abundant. In these cells, in which the Calvin cycle operates, the malate enters chloroplasts and is converted to pyruvate and CO_2. Because O_2 concentration is low, and CO_2 concentration is high because of its release by malate breakdown, the oxygenase activity of rubisco is inhibited and carboxylase activity is promoted. The pyruvate produced by malate oxidation returns to the mesophyll cells to enter another turn of the C_4 cycle.

Several tropical and temperate crop plants in addition to corn, including sugar cane, sorghum, and some pasture grasses, use the C_4 cycle to control the location of initial CO_2 fixation in leaf cells. Unfortunately, many highly successful weed pests, such as Bermuda grass and crabgrass, also use the same adaptation to compete successfully with lawn grasses and crops in warm climates.

Other Plants Control Photorespiration by Running the C_4 and Calvin Cycles at Different Times

Instead of running the Calvin and C_4 cycles simultaneously in different locations, some C_4 plants run the cycles at different times to circumvent photorespiration. The plants in this group include many with thick, succulent leaves or stems such as the cactus shown in **Figure 9.16c.** These plants are known collectively as **CAM plants,** named for *crassulacean acid metabolism,* from the Crassulaceae family in which the CAM adaptation was first observed.

CAM plants typically live in regions that are hot and dry during the day and cool at night. Their fleshy leaves or stems have a low surface-to-volume ratio, and their stomata are reduced in number. Further, the stomata open only at night, when they release O_2 that

accumulates from photosynthesis during the day and allow CO_2 to enter the leaves. The entering CO_2 is fixed by the C_4 pathway into malate, which accumulates throughout the night and is stored in large cell vacuoles.

Daylight initiates the second phase of the strategy. As the sun comes up and the temperature rises, the stomata close, reducing water loss and cutting off the exchange of gases with the atmosphere. Malate diffuses from cell vacuoles into the cytosol, where it is oxidized to pyruvate, and CO_2 is released in high concentration. The high CO_2 concentration favors the carboxylase activity of rubisco carboxylase, allowing the Calvin cycle to proceed at maximum efficiency with little loss of organic carbon from photorespiration. The pyruvate produced by malate breakdown accumulates during the day; as night falls, it enters the C_4 reactions converting it back to malate. During the night, oxygen is released by the plants, and more CO_2 enters.

Reduction of water loss by closure of the stomata during the hot daylight hours has the added benefit of making CAM plants highly resistant to dehydration.

As a result, CAM species can tolerate extreme daytime heat and dryness.

In this chapter, you have seen how photosynthesis supplies the organic molecules used as fuels by almost all the organisms of the world. It is a story of electron flow: electrons, pushed to high energy levels by the absorption of light energy, are added to CO_2, which is fixed into carbohydrates and other fuel molecules. The high-energy electrons are then removed from the fuel molecules by the oxidative reactions of cellular respiration, which use the released energy to power the activities of life. Among the most significant of these activities are cell growth and division, the subjects of the next chapter.

STUDY BREAK

1. When does photorespiration occur? What are the reactions of photorespiration, and what are the energetic consequences of the process?
2. How do C_4 plants circumvent photorespiration?

Review

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9.1 Photosynthesis: An Overview

• In photosynthesis, plants, algae, and photosynthetic prokaryotes use the energy of sunlight to drive synthesis of organic molecules from simple inorganic raw materials. The organic molecules are used by the photosynthesizers themselves as fuels; they also form the primary energy source for heterotrophs.

• The two overall stages of photosynthesis are the light-dependent and light-independent reactions. In eukaryotes, both stages take place inside chloroplasts (Figures 9.2 and 9.3).

• Photosynthesizers use the energy of sunlight to push electrons to elevated energy levels. In eukaryotes and many prokaryotes, water is split as the source of the electrons for this process, and oxygen is released to the environment as a by-product.

• The high-energy electrons provide an indirect energy source for ATP synthesis and also for CO_2 fixation, in which CO_2 is fixed into organic substances by the addition of both electrons and protons.

Animation: Photosynthesis overview

Animation: Sites of photosynthesis

9.2 The Light-Dependent Reactions of Photosynthesis

• In the light-dependent reactions of photosynthesis, light is converted to chemical energy when electrons, excited by absorption of light in a pigment molecule, are passed from the pigment to a stable orbital in a primary acceptor molecule (Figure 9.5).

• Chlorophylls and carotenoids, the photon-absorbing pigments in eukaryotes and cyanobacteria, together absorb light energy at

a range of wavelengths, enabling a wide spectrum of light to be used in photosynthesis (Figures 9.6 and 9.7).

• In organisms that split water as their electron source, the pigments are organized with proteins into two photosystems. Specialized forms of chlorophyll *a* pass excited electrons to primary acceptor molecules in the photosystems (Figure 9.8).

• Electrons obtained from splitting water are used for the synthesis of NADPH and ATP. In the noncyclic electron flow pathway, electrons first flow through photosytem II, becoming excited there to a higher energy level, and then pass through an electron transfer system to photosystem I releasing energy that is used to create an H^+ gradient across the membrane. The gradient is used by ATP synthase to drive synthesis of ATP. The net products of the light-dependent reactions are ATP, NADPH, and oxygen (Figures 9.9 and 9.10).

• Electrons can also flow cyclically around photosystem I and the electron transfer system, building the H^+ concentration and allowing extra ATP to be produced, but no NADPH (Figure 9.11).

Interaction: Wavelengths of light

Animation: Noncyclic pathway of electron flow

9.3 The Light-Independent Reactions of Photosynthesis

• In the light-independent reactions of photosynthesis, CO_2 is reduced and converted into organic substances by the addition of electrons and hydrogen carried by the NADPH produced in the light-dependent reactions. ATP, also derived from the light-dependent reactions, provides additional energy. The key enzyme of the light-independent reactions is rubisco (RuBP carboxylase/oxygenase), which catalyzes the reaction that combines CO_2 into organic compounds (Figure 9.13).

- In the process, NADPH is oxidized to $NADP^+$, and ATP is hydrolyzed to ADP and phosphate. These products of the light-independent reactions cycle back as inputs to the light-dependent reactions.
- The Calvin cycle produces surplus molecules of G3P, which are the starting point for synthesis of glucose, sucrose, starches, and other organic molecules. The light-independent reactions take place in the chloroplast stroma in eukaryotes and in the cytoplasm of photosynthetic bacteria.

  Animation: Calvin cycle

9.4 Photorespiration and the C_4 Cycle

- When oxygen concentrations are high relative to CO_2 concentrations, rubisco acts as an oxygenase, catalyzing the combination of RuBP with O_2 rather than CO_2 and forming toxic products that cannot be used in photosynthesis. The toxic products are eliminated by reactions that release carbon as CO_2, greatly reducing the efficiency of photosynthesis. The entire process is called photorespiration because it uses oxygen and releases CO_2 (Figure 9.14).
- Some plants have evolved the C_4 pathway, a supplemental system that bypasses the oxygenase activity of rubisco. In the pathway, initial fixation of CO_2 is catalyzed by a carboxylase that has no oxygenase activity, in specific locations or at times within the plant when oxygen is overabundant. In later steps, the CO_2 is released in relatively oxygen-free regions or times for final fixation in the reactions using RuBP in the Calvin cycle (Figures 9.15 and 9.16).

  Animation: C_3-C_4 comparison

Questions

Self-Test Questions

1. An organism exists for long periods by using only CO_2 and H_2O. It could be classified as a (an):
   a. herbivore.
   b. carnivore.
   c. decomposer.
   d. autotroph.
   e. heterotroph.

2. During the light-dependent reactions:
   a. CO_2 is fixed.
   b. NADPH and ATP are synthesized using electrons derived from splitting water.
   c. glucose is synthesized.
   d. water is split and the electrons generated are used for glucose synthesis.
   e. photosystem I is unlinked from photosystem II.

3. Which of the following is a correct step in the light-dependent reactions of the Z system?
   a. Light is absorbed at P700, and electrons flow through a pathway to the NADPH acceptor.
   b. Electrons flow from photosystem II to water.
   c. $NADP^+$ is oxidized to NADPH as it accepts electrons.
   d. Water is degraded to activate P680.
   e. Electrons pass through a thylakoid membrane to create energy to pump H^+ through the cytochrome complex.

4. The light-dependent reactions of photosynthesis resemble aerobic respiration as both:
   a. synthesize NADPH.
   b. synthesize NADH.
   c. require electron transfer systems to synthesize ATP.
   d. require oxygen as the final electron acceptor.
   e. have the same initial energy source.

5. The molecules that link the light-dependent and light-independent reactions are:
   a. ADP and H_2O.
   b. RuBP and CO_2.
   c. cytochromes and water.
   d. G3P and RuBP.
   e. ATP and NADPH.

6. You bite into a spinach leaf. Which one of the following is true?
   a. You are getting 50% of the protein in the leaf in the form of ribulose 1,5-bisphosphate carboxylase.
   b. The major pigment you are ingesting is a carotenoid.
   c. The water in the leaf is a product of the light-independent reactions.
   d. Any energy from the leaf you can use directly is in the form of ATP.
   e. The spinach most likely was grown in an area with a low CO_2 concentration.

7. The molecule produced by the light-dependent reactions that is used for the synthesis of glucose and other organic molecules is:
   a. ADP.
   b. G3P.
   c. CO_2.
   d. $NADP^+$.
   e. NADPH.

8. Which of the following statements about the C_4 cycle is *incorrect*?
   a. CO_2 initially combines with PEP.
   b. PEP carboxylase catalyzes a reaction to produce oxaloacetate.
   c. Oxaloacetate transfers electrons from NADPH and is reduced to malate.
   d. Less ATP is used to run the C_4 cycle than the C_3 cycle.
   e. The cycle runs when O_2 concentration is high.

9. In one turn of the Calvin cycle, one molecule of CO_2 generates:
   a. 6 ATP.
   b. 6 NADH.
   c. 6 ATP and 6 NADPH.
   d. one (CH_2O) unit of carbohydrate.
   e. one molecule of glucose.

10. All of the following are adaptations that assist C_4 plants in surviving in hot dry regions *except:*
    a. closing stomata.
    b. using crassulacean acid metabolism.
    c. increasing their rate of photorespiration.
    d. running cycles at different times.
    e. running cycles at different positions in the cell.

Questions for Discussion

1. Suppose a garden in your neighborhood is filled with red, white, and blue petunias. Explain the floral colors in terms of which wavelengths of light are absorbed and reflected by the petals.

2. About 200 years ago, Jan Baptista van Helmont tried to determine the source of raw materials for plant growth. To do so, he planted a young tree weighing 5 pounds in a barrel filled with 200 pounds of soil. He watered the tree regularly. After 5 years, he again weighed the tree and the soil. At that time the tree weighed 169 pounds, 3 ounces, and the soil weighed

199 pounds, 14 ounces. Because the tree's weight had increased so much, and the soil's weight had remained about the same, he concluded that the tree gained weight as a result of the water he had added to the barrel. Criticize his conclusion in terms of the information you have learned from this chapter.

3. Like other accessory pigments, the carotenoids extend the range of wavelengths absorbed in photosynthesis. They also protect plants from a potentially lethal process known as *photooxidation*. This process begins when excitation energy in chlorophylls drives the conversion of oxygen into free radicals, substances that can damage organic compounds and kill cells. When plants that cannot produce carotenoids are grown in light, they bleach white and die. Given this observation, what molecules in the plants are likely to be destroyed by photooxidation?

4. What molecules would you have to provide a plant, theoretically speaking, for it to make glucose in the dark?

Experimental Analysis

Space travelers of the future land on a planet in a distant galaxy, where they find populations of a carbon-based life form. The beings on this planet are of a vibrantly purple color. The travelers sus-

pect that the beings secure the energy necessary for survival by a process similar to photosynthesis on Earth. How might they go about testing this conclusion?

Evolution Link

If global warming raises the temperature of our climate significantly, will C_3 plants or C_4 plants be favored by natural selection? How will global warming change the geographical distributions of plants?

How Would You Vote?

The oxygen in Earth's atmosphere is a sure indicator that photosynthetic organisms flourish here. New technologies will allow astronomers in search of life to measure the oxygen content of the atmosphere of planets too far away for us to visit. Should public funds be used to continue this research? Go to www .thomsonedu.com/login to investigate both sides of the issue and then vote.