

CASE STUDY Colors of Fall

Taking a walk in the woods in the fall when the leaves are turning colors can be an enjoyable and relaxing form of exercise. Interestingly, the same process that causes leaves to change colors in the fall is also involved in the ripening of fruits such as apples and pears—and the end product of the process may have health benefits as well! Leaves contain several types of pigments, including the green chlorophylls and the yellow to red carotenoids. These pigments absorb the solar energy that the plant utilizes to carry out photosynthesis. In the fall when lower temperatures signal a change in the seasons, the supply of water and nutrients to the leaves declines and chlorophyll begins to degrade. Now, the carotenoids, which were formerly masked by chlorophyll, become visible allowing us to enjoy the change of color. The breakdown of chlorophyll provides us with colorful woodlands and can also give us a healthy dose of antioxidants when we eat fruits.

Researchers have discovered that when a fruit ripens and its skin changes color, chlorophyll is degraded in the same manner as in leaves. This produces antioxidants that become concentrated in the skin. Antioxidants stabilize free radicals, dangerous molecules that otherwise damage the DNA and proteins of a cell. Several health problems, including cancer and heart disease, are thought to be promoted by the accumulation of free radicals. In this chapter, we will see how pigments are involved in the process of photosynthesis. The solar energy that is captured by the pigments is used by the plant to make its food. It is this food that will be used to sustain the plant and the organisms that feed on the plant.

As you read through the chapter, think about the following questions:

1. Which pigments provide the maximum efficiency for a plant as it conducts photosynthesis?
2. Why do leaves appear green in the spring and summer and then turn to red or yellow in the fall?

Photosynthesis

8

CHAPTER OUTLINE

- 8.1** Overview of Photosynthesis
- 8.2** Plants as Solar Energy Converters
- 8.3** Plants as Carbon Dioxide Fixers
- 8.4** Alternative Pathways for Photosynthesis
- 8.5** Photosynthesis versus Cellular Respiration

BEFORE YOU BEGIN

Before beginning this chapter, take a few moments to review the following discussions:

Section 3.3 Which cellular structures are necessary for photosynthesis?

Figure 6.1 How does energy flow in biological systems?

Section 6.3 What role do enzymes play in regulating metabolic processes?

8.1 Overview of Photosynthesis

Learning Outcomes

Upon completion of this section, you should be able to

1. Compare and contrast autotrophs and heterotrophs.
2. Explain the role of photosynthesis for all organisms on Earth.
3. Recognize the overall chemical equation for photosynthesis.
4. Describe the process of photosynthesis in terms of two sets of reactions that take place in a chloroplast.

Photosynthesis converts solar energy into the chemical energy of a carbohydrate. Photosynthetic organisms, including plants, algae, and cyanobacteria, are called **autotrophs** because they produce their own food (Fig. 8.1). Each year, photosynthesizing organisms produce between 100 and 200 billion metric tons of carbohydrates. No wonder photosynthetic organisms are able to sustain themselves and all other organisms on Earth.

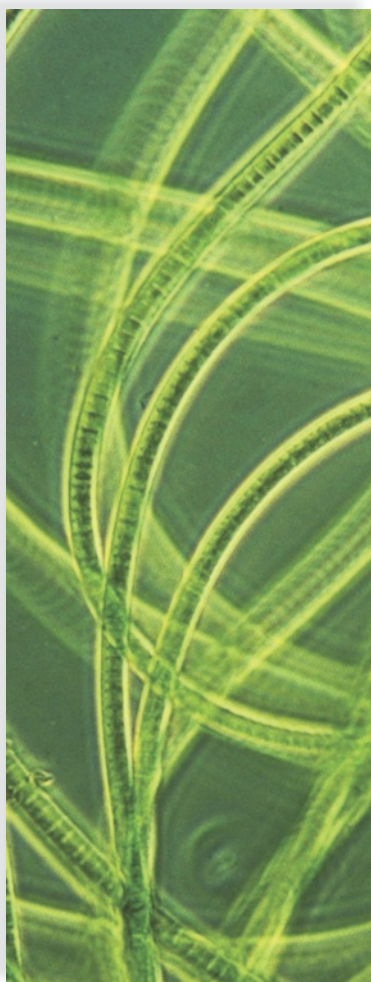
With some exceptions, it is possible to trace the majority of food chains back to plants and algae. In other words, producers,

which have the ability to synthesize carbohydrates, feed not only themselves but also consumers, which must take in pre-formed organic molecules. Collectively, consumers are called **heterotrophs**. Both autotrophs and heterotrophs use organic molecules produced by photosynthesis as a source of building blocks for growth and repair and as a source of chemical energy for cellular work.

Pigments allow photosynthetic organisms to capture solar energy, which acts as the “fuel” that makes photosynthesis possible. Most photosynthetic organisms contain **chlorophyll**, the pigment that gives them a green color. However, the green of chlorophyll can be masked by other pigments. The **carotenoids** give photosynthesizing cells a yellow to red color. In addition, the *phycobilins* give red algae their red color and cyanobacteria a bluish color.

Flowering Plants as Photosynthesizers

Although many different organisms can photosynthesize, we will focus our discussion on the flowering plants. Portions of the plant, particularly the leaves, contain chlorophyll and other pigments that enable the plant to carry on photosynthesis. The leaf of a flowering



a. *Oscillatoria*



40× b. Kelp



c. Sequoias

Figure 8.1 Photosynthetic organisms.

Photosynthetic organisms include (a) cyanobacteria such as *Oscillatoria*, which are a type of bacterium; (b) algae such as kelp, which typically live in water and can range in size from microscopic to macroscopic; and (c) plants such as the sequoia, which typically live on land.

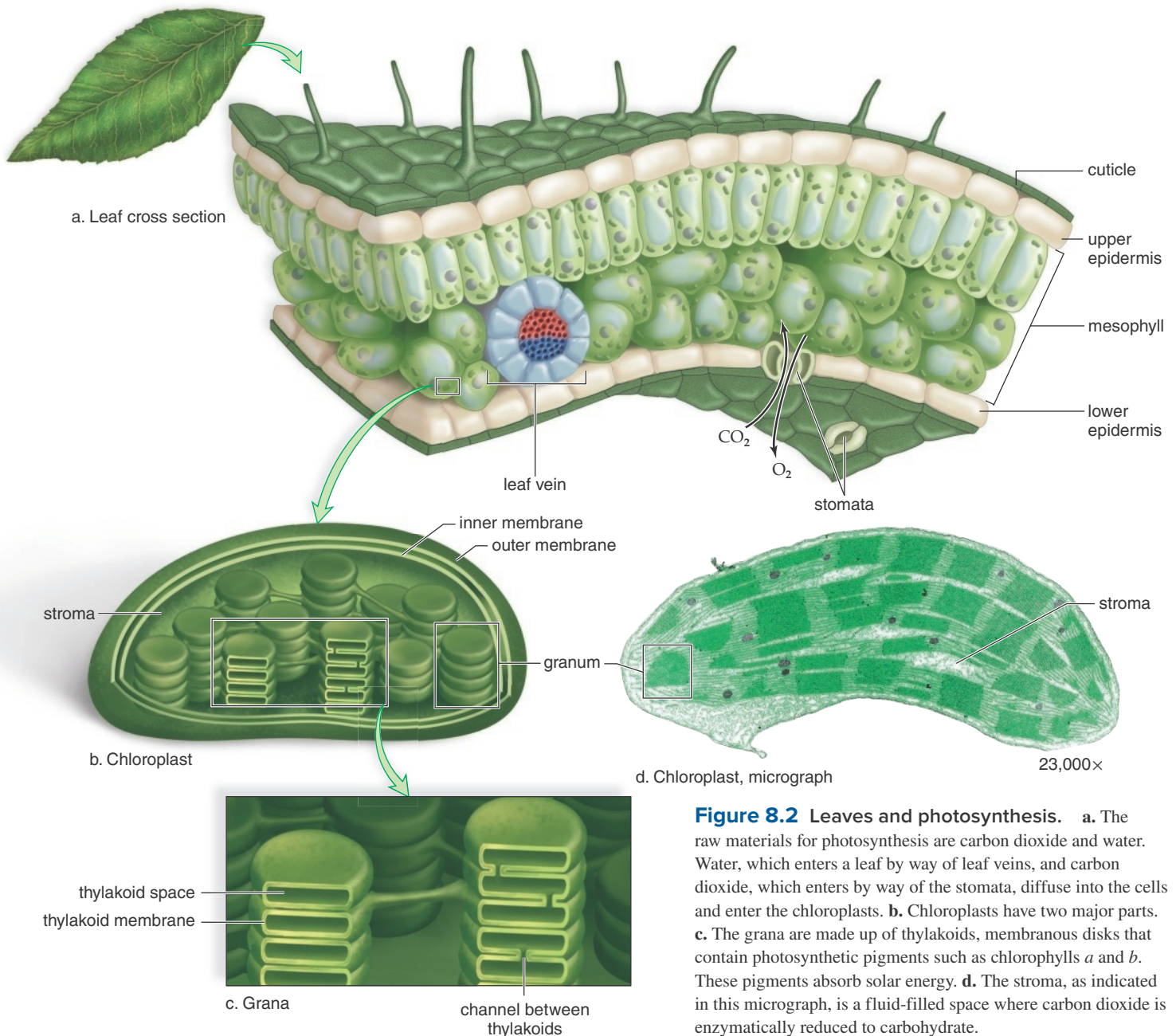


Figure 8.2 Leaves and photosynthesis. **a.** The raw materials for photosynthesis are carbon dioxide and water. Water, which enters a leaf by way of leaf veins, and carbon dioxide, which enters by way of the stomata, diffuse into the cells and enter the chloroplasts. **b.** Chloroplasts have two major parts. **c.** The grana are made up of thylakoids, membranous disks that contain photosynthetic pigments such as chlorophylls *a* and *b*. These pigments absorb solar energy. **d.** The stroma, as indicated in this micrograph, is a fluid-filled space where carbon dioxide is enzymatically reduced to carbohydrate.

plant contains mesophyll tissue, which contains cells that are specialized for photosynthesis (Fig. 8.2*a*). The raw materials for photosynthesis are water and carbon dioxide. The roots of a plant absorb water, which then moves through vascular tissue up the stem to a leaf by way of the leaf veins. Carbon dioxide in the air enters a leaf through small openings called **stomata** (sing., stoma) that are surrounded by guard cells. After entering a leaf, carbon dioxide and water diffuse into the cells and enter the chloroplasts (Fig. 8.2*b, d*), the organelles that carry on photosynthesis.

A double membrane surrounds a chloroplast and its fluid-filled interior, which is called the *stroma*. A different membrane system within the stroma forms flattened sacs called *thylakoids* (Fig. 8.2*c*). In some places, thylakoids are stacked to form *grana* (sing., granum), which were named because they looked like piles

of seeds to early microscopists. The space of each thylakoid is connected to the space of every other thylakoid within a chloroplast, thereby forming a continuous inner compartment within the chloroplast called the thylakoid space.

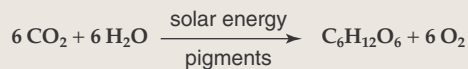
Chlorophyll and other pigments that are part of a thylakoid membrane are capable of absorbing solar energy. This is the energy that drives photosynthesis. The stroma, filled with enzymes, is where carbon dioxide is first attached to an organic compound and is then reduced to a carbohydrate. Therefore, it is proper to associate the absorption of solar energy with the thylakoid membranes making up the grana, and to associate the reduction of carbon dioxide to a carbohydrate with the stroma of a chloroplast.

Humans, and indeed nearly all organisms, release carbon dioxide into the air as a waste product from metabolic processes

such as cellular respiration. This is some of the same carbon dioxide that enters a leaf through the stomata and is converted to carbohydrate. Carbohydrate, in the form of glucose, is the chief energy source for most organisms.

Photosynthetic Reaction

For convenience, the overall equation for photosynthesis is sometimes simplified in this manner:



This equation shows glucose and oxygen as the products of photosynthesis.

The oxygen given off by photosynthesis comes from water. This was proven experimentally by exposing plants first to CO_2 and then to H_2O that contained an isotope of oxygen called heavy oxygen (^{18}O). Only when heavy oxygen was a part of water did this isotope appear in O_2 given off by the plant. Therefore, O_2 released by chloroplasts comes from H_2O , not from CO_2 .

The overall equation tells us that during photosynthesis, H_2O is oxidized and CO_2 is reduced to form a carbohydrate. Reduction of any molecule requires energy. During photosynthesis this energy is ultimately provided by the sun.

The overall chemical equation for photosynthesis tells us why plants are so important to our lives. Plants provide us with food in the form of carbohydrates, and much of the oxygen that we breathe and use for cellular respiration.

Two Sets of Reactions

The word photosynthesis suggests that the process requires two sets of reactions: *photo*, which means light, refers to the reactions that capture solar energy, and *synthesis* refers to the reactions that produce carbohydrate.

The two sets of reactions are called the **light reactions** (light-dependent reactions) and the **Calvin cycle reactions** (light-independent reactions) (Fig. 8.3). We will see that the light reactions release oxygen and provide the molecules that allow the Calvin cycle reactions to reduce carbon dioxide to a carbohydrate. The coenzyme **NADP⁺ (nicotinamide adenine dinucleotide phosphate)** carries hydrogen atoms from the light reactions to the Calvin cycle reactions. When NADP⁺ accepts hydrogen atoms, it becomes NADPH. Also, ATP carries energy from the light reactions to the Calvin cycle reactions.

The light reactions are sometimes called the light-dependent reactions because they cannot occur unless light is present. The Calvin cycle reactions are sometimes called the light-independent reactions because they will occur whether light is present or not.

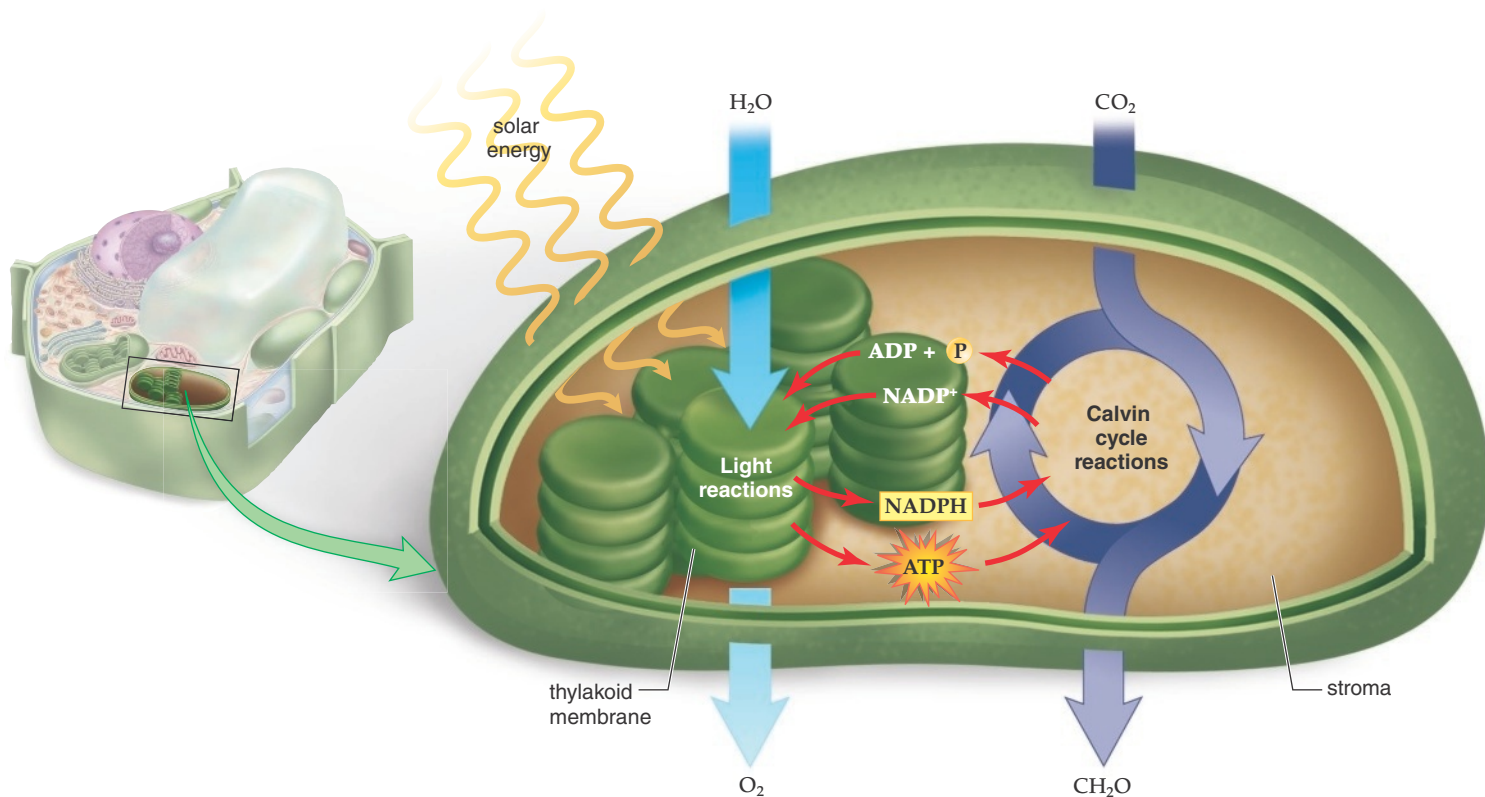


Figure 8.3 Overview of photosynthesis. The process of photosynthesis consists of the light reactions and the Calvin cycle reactions. The light reactions, which produce ATP and NADPH, occur in the thylakoid membrane. These molecules are used in the Calvin cycle reactions in the stroma to reduce carbon dioxide to a carbohydrate.

Check Your Progress 8.1

1. Recognize the primary source of energy for carbohydrate production in plants.
2. Identify the major components in the structure of a chloroplast.
3. Identify the overall equation for photosynthesis.
4. Describe the two sets of reactions involved in photosynthesis.

8.2 Plants as Solar Energy Converters**Learning Outcomes**

Upon completion of this section, you should be able to

1. Identify the photosynthetic pigments required to absorb the various wavelengths of light necessary for photosynthesis.
2. Explain the role of the noncyclic electron pathway and the cyclic electron pathway.
3. Describe the organization of the thylakoid and how this organization is critical to the production of ATP during photosynthesis.

During the light reactions, the various pigments within the thylakoid membranes absorb solar energy. Solar energy (radiant energy from the sun) can be described in terms of its wavelength and its energy content. Figure 8.4 lists the different types of radiant energy, from the shortest wavelength, gamma rays, to the longest, radio waves. White, or *visible*, light is only a small portion of this spectrum.

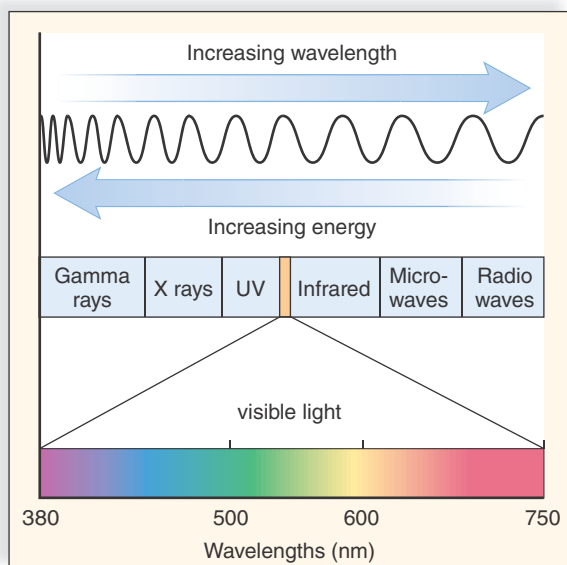


Figure 8.4 The electromagnetic spectrum. The electromagnetic spectrum extends from the very short wavelengths of gamma rays through the very long wavelengths of radio waves. Visible light, which drives photosynthesis, is expanded to show its component colors. Each color varies in its wavelength and energy content.

Visible Light

Visible light itself contains various wavelengths of light. When it is passed through a prism, we see all the different colors that make up visible light. The sensory areas of our brains identify these wavelengths as distinct colors. The colors in visible light range from violet (the shortest wavelength) to indigo, blue, green, yellow, orange, and red (the longest wavelength). The energy content is highest for violet light and lowest for red light.

Only about 42% of the solar radiation that hits Earth's atmosphere ever reaches the surface of Earth, and most of this radiation is within the visible-light range. Higher-energy wavelengths are screened out by the ozone layer in the atmosphere, and lower-energy wavelengths are screened out by water vapor and carbon dioxide (CO₂) before they reach the Earth's surface. Both the organic molecules within organisms and certain life processes, such as vision and photosynthesis, are adapted to the solar radiation that is most prevalent in the environment.

The pigments found within most types of photosynthesizing cells, the chlorophylls *a* and *b* and the carotenoids, are capable of absorbing various portions of visible light. The absorption spectrum for these pigments is shown in Figure 8.5. Both chlorophyll *a* and chlorophyll *b* absorb violet, indigo, blue, and red light better than the light of other colors. Because green light is reflected and only minimally absorbed, leaves appear green to us. The yellow or orange carotenoids are able to absorb light in the violet-blue-green range. These pigments and others become noticeable in the fall when chlorophyll breaks down and the other pigments are uncovered. Photosynthesis begins when the pigments within thylakoid membranes absorb solar energy.

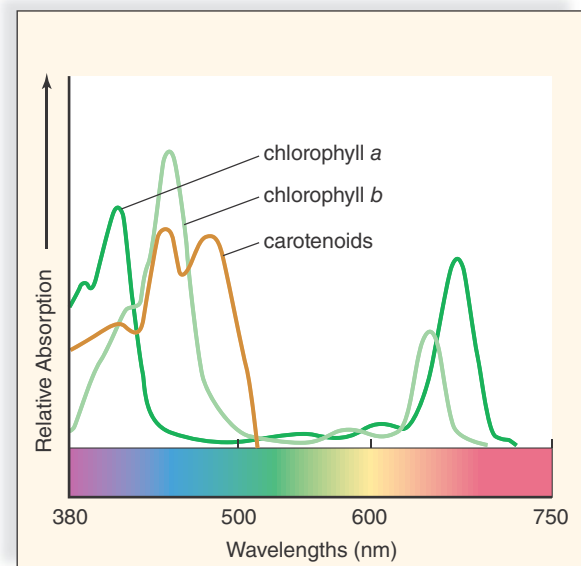


Figure 8.5 Photosynthetic pigments and photosynthesis.

The photosynthetic pigments in chlorophylls *a* and *b* and the carotenoids absorb certain wavelengths within visible light. This is their absorption spectrum. Notice that they do not absorb green light. That is why the leaves of plants appear green to us. You observe the color that is not absorbed by the leaf.

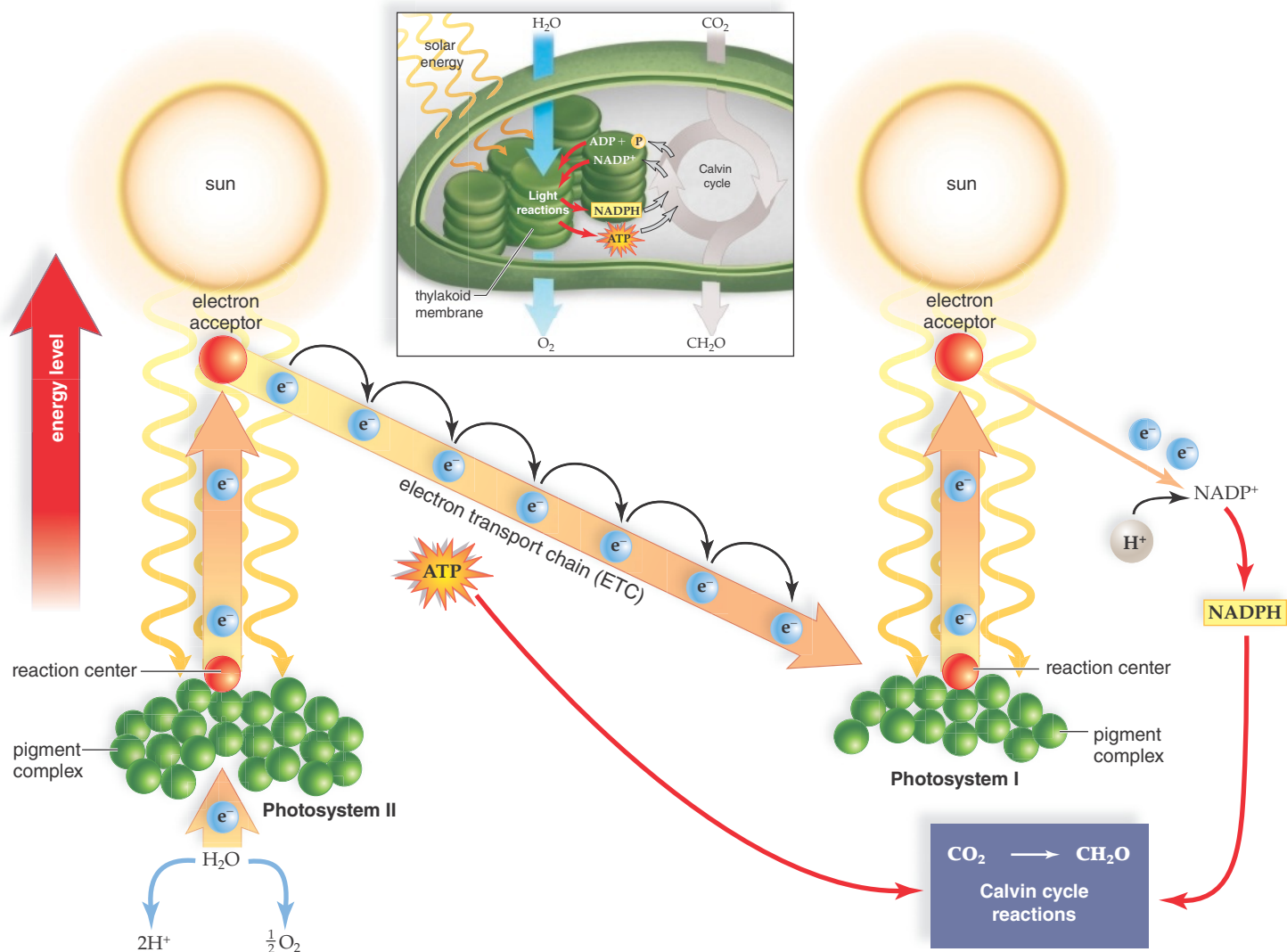


Figure 8.6 Noncyclic electron pathway: Electrons move from water to NADP⁺. Energized electrons (taken from water, which splits, releasing oxygen) leave photosystem II and pass down an electron transport chain, leading to the formation of ATP. Energized electrons (replaced by photosystem II) leave photosystem I and pass to NADP⁺, which then combines with H⁺, becoming NADPH.

Light Reactions

The light reactions that occur in the thylakoid membrane consist of two electron pathways called the noncyclic electron pathway and the cyclic electron pathway. Both electron pathways produce ATP, but only the noncyclic pathway also produces NADPH.

Noncyclic Electron Pathway

The **noncyclic electron pathway** is so named because the electron flow can be traced from water to a molecule of NADP⁺ (Fig. 8.6). This pathway uses two photosystems, called photosystem I (PS I) and photosystem II (PS II). The photosystems are named for the order in which they were discovered, not for the order in which they participate in the photosynthetic process. A **photosystem** consists of a pigment complex (molecules of chlorophyll *a*, chlorophyll *b*, and the carotenoids) and an electron acceptor within the thylakoid membrane. The pigment complex serves as an “antenna” for gathering solar energy.

The noncyclic pathway begins with photosystem II. The pigment complex absorbs solar energy, which is then passed from one pigment molecule to another until it is concentrated in a particular pair of chlorophyll *a* molecules called the *reaction center*. Electrons (e⁻) in the reaction center chlorophyll become so energized that they escape from the reaction center and move to a nearby electron acceptor.

Photosystem II would disintegrate without replacement electrons. These replacement electrons are provided by water, which splits, releasing oxygen to the atmosphere. Many organisms, including plants and even ourselves, use this oxygen. The hydrogen ions (H⁺) stay in the thylakoid space and contribute to the formation of a hydrogen ion gradient. As shown in the overall chemical reaction for photosynthesis, water is used up and oxygen is produced.

The electron acceptor that received the energized electrons from the reaction center will send the electrons down a series of carriers that pass electrons from one to the other, known as the electron transport chain. As the electrons pass from one carrier to

the next, the energy that is released is used to move hydrogen ions (H^+) from the stroma into the thylakoid space, forming a hydrogen ion gradient. When these hydrogen ions flow down their electrochemical gradient through **ATP synthase** complexes, ATP production occurs, as will be described shortly. Notice that this ATP will be used in the Calvin cycle reactions in the stroma to reduce carbon dioxide to a carbohydrate.

Similarly, when the photosystem I pigment complex absorbs solar energy, energized electrons leave its reaction center and are captured by a different electron acceptor. After going through the electron transport chain, the electrons from photosystem II are now low-energy electrons. These electrons are used to replace those lost by photosystem I. The electron acceptor in photosystem I passes its electrons to $NADP^+$ molecules. Each $NADP^+$ accepts two electrons

and an H^+ to become a reduced form of the molecule—that is, NADPH. This NADPH will also be used by the Calvin cycle reactions in the stroma to reduce carbon dioxide to a carbohydrate.

The Organization of the Thylakoid Membrane

The following molecular complexes are present in the thylakoid membrane and are involved in the noncyclic electron pathway (Fig. 8.7):

- Photosystem II, which consists of a pigment complex and an electron acceptor molecule, receives electrons from water, which splits, releasing oxygen.
- The electron transport chain carries electrons from photosystem II to photosystem I, and pumps H^+ from the stroma into the thylakoid space.

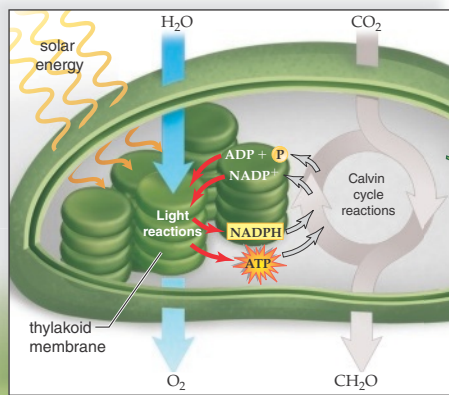
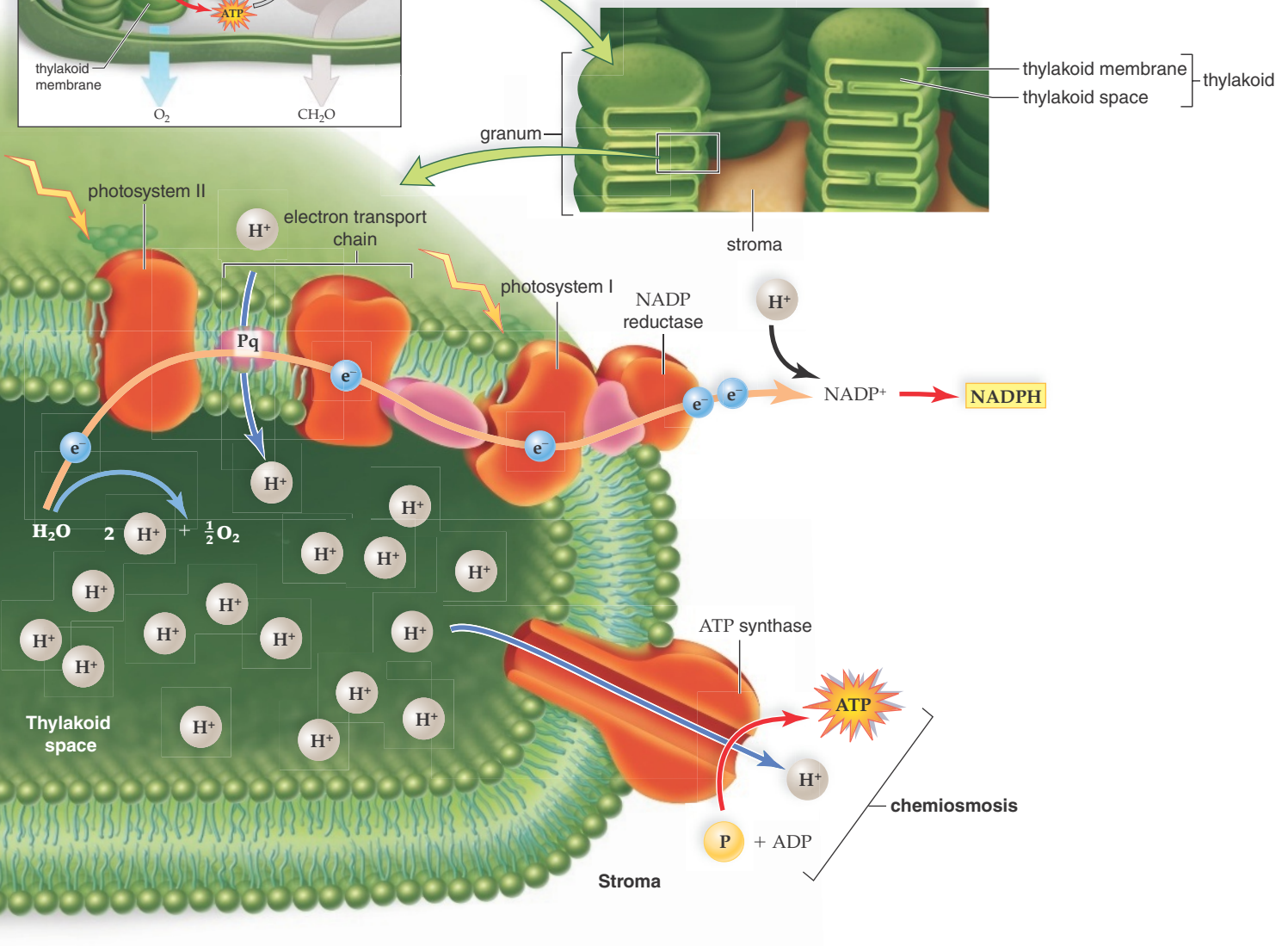


Figure 8.7 Organization of a thylakoid. Each thylakoid membrane within a granum produces NADPH and ATP. Electrons move through photosystem II, photosystem I, and electron transport chains within the thylakoid membrane. Electrons pass to $NADP^+$, after which it becomes NADPH. A carrier at the start of the electron transport chain pumps hydrogen ions from the stroma into the thylakoid space. When hydrogen ions flow back out of the space into the stroma through the ATP synthase complex, ATP is produced from $ADP + P$.



- Photosystem I, which also consists of a pigment complex and an electron acceptor molecule, is adjacent to NADP reductase, which reduces NADP^+ to NADPH.
- The ATP synthase complex crosses the thylakoid membrane and contains an interior channel and a protruding ATP synthase, an enzyme that joins $\text{ADP} + \text{P}$.

Cyclic Electron Pathway

Under some environmental conditions, such as high oxygen levels, NADPH levels may accumulate in the cell, and therefore photosynthetic cells may enter the **cyclic electron pathway** (Fig. 8.8). This pathway is also found in many prokaryotic cells. It differs from the noncyclic reactions in that the electrons are recycled back to photosystem I. The pathway begins when the photosystem I

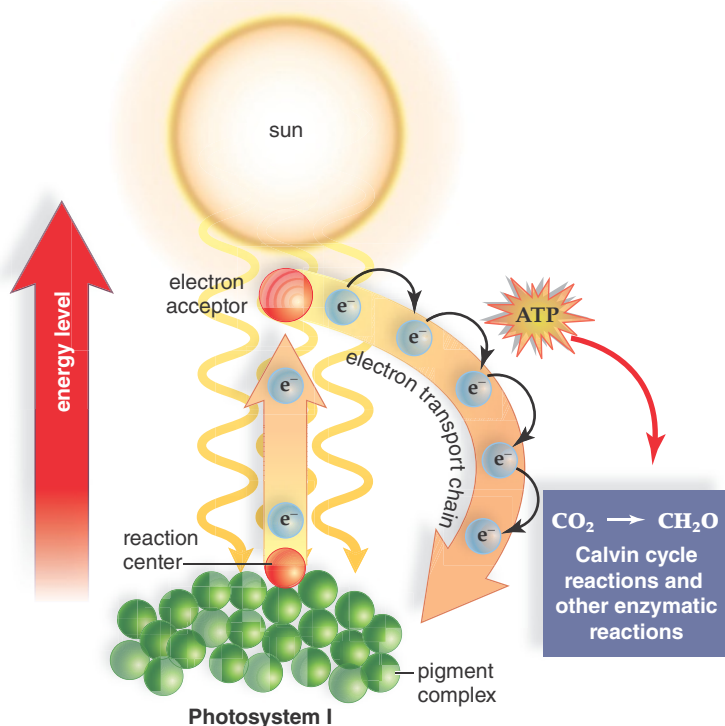
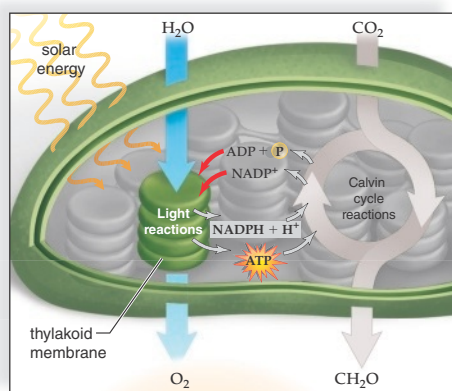


Figure 8.8 Cyclic electron pathway: Electrons leave and return to photosystem I. Energized electrons leave the photosystem I reaction center and are taken up by an electron acceptor, which passes them down an electron transport chain before they return to photosystem I. Only ATP production occurs as a result of this pathway.

pigment complex absorbs solar energy that is passed from one pigment to the next until it becomes concentrated in a reaction center. As with photosystem II, electrons (e^-) become so energized that they escape from the reaction center and move to nearby electron acceptor molecules.

This time, instead of the electrons moving on to NADP^+ , energized electrons (e^-) taken up by an electron acceptor are sent down an electron transport chain. As the electrons pass from one carrier to the next, their energy becomes stored as a hydrogen (H^+) gradient. Again, the flow of hydrogen ions down their electrochemical gradient through ATP synthase complexes produces ATP.

The spent electrons return to photosystem I after the electron transport chain. This is how photosystem I receives replacement electrons and why this electron pathway is called cyclic. It is also why the cyclic pathway produces ATP but does not produce NADPH.

ATP Production

The thylakoid space acts as a reservoir for hydrogen ions (H^+). Each time oxygen is removed from water, two H^+ remain in the thylakoid space. As the electrons move from carrier to carrier along the electron transport chain, the electrons give up energy, which is used to pump H^+ from the stroma into the thylakoid space. This is like pumping water into a reservoir. The end result is that there are more H^+ in the thylakoid space than in the stroma. Because H^+ is charged, this is an electrochemical gradient. Not only are there more hydrogen ions, but there are more positive charges within the thylakoid space than the stroma. When a channel is opened in the ATP synthase complex, H^+ flows from the thylakoid space into the stroma, just like water flowing out of the reservoir. The flow of H^+ from high to low concentration across the thylakoid membrane provides the energy that allows the ATP synthase enzyme to enzymatically produce ATP from $\text{ADP} + \text{P}$. This method of producing ATP is called chemiosmosis because ATP production is tied to the establishment of an H^+ gradient.

Check Your Progress 8.2

1. Explain why leaves appear green.
2. Compare the production of NADPH to ATP in noncyclic photosynthesis.
3. Identify which part of a thylakoid will contain the photosystems, electron transport chain, and the ATP synthase complex.
4. Describe why the H^+ gradient across a thylakoid membrane is referred to as a storage of energy.

8.3 Plants as Carbon Dioxide Fixers

Learning Outcomes

Upon completion of this section, you should be able to

1. Describe the three phases of the Calvin cycle.
2. Explain how the products of the Calvin cycle are used to form the other molecules found in plants.

The Calvin cycle reactions take place after the light reactions. This is a series of reactions that produce a carbohydrate before returning to the starting point (Fig. 8.9). The cycle is named for Melvin Calvin, who, with colleagues, used the radioactive isotope ^{14}C as a tracer to discover the reactions making up the cycle.

This series of reactions uses atmospheric carbon dioxide to produce a carbohydrate. Humans and most other organisms take in oxygen from the atmosphere and release carbon dioxide. The Calvin cycle includes (1) carbon dioxide fixation; (2) carbon

dioxide reduction; and (3) regeneration of RuBP (ribulose-1,5-bisphosphate), the starting material of the cycle.

Fixation of Carbon Dioxide

Carbon dioxide fixation is the first step of the Calvin cycle. During this reaction, three molecules of carbon dioxide from the atmosphere are attached to three molecules of RuBP, a 5-carbon molecule. The result is three 6-carbon molecules. Each 6-carbon

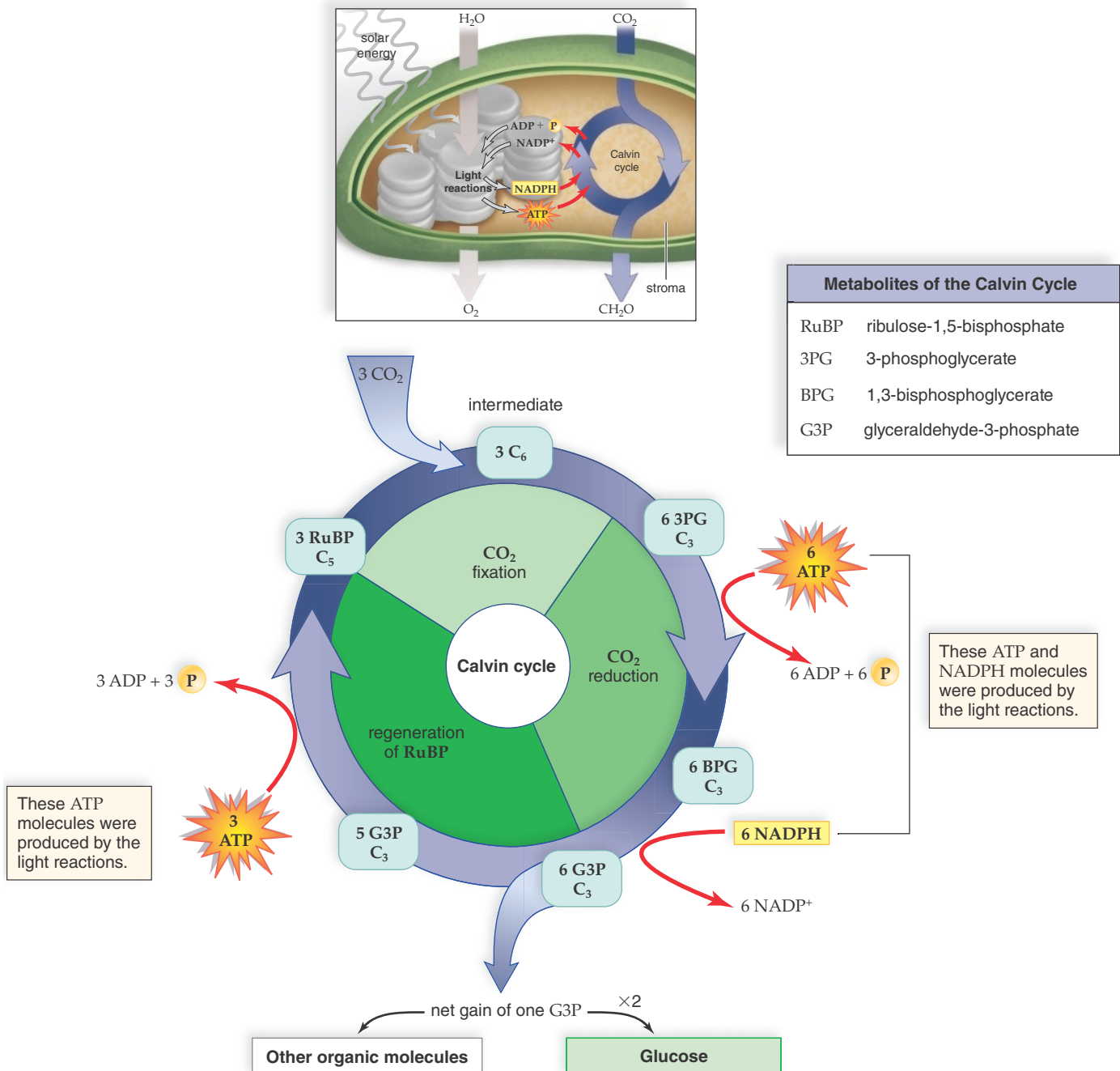


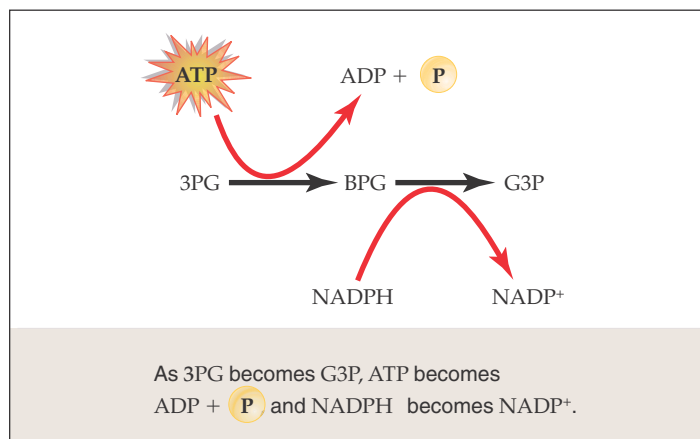
Figure 8.9 The Calvin cycle reactions. The Calvin cycle is divided into three portions: CO_2 fixation, CO_2 reduction, and regeneration of RuBP. Because five G3P are needed to re-form three RuBP, it takes three turns of the cycle to have a net gain of one G3P. Two G3P molecules are needed to form glucose.

molecule then splits in half, forming a total of six 3-carbon molecules. This first 3-carbon molecule is called 3-phosphoglycerate or 3PG.

The enzyme that speeds this reaction, called **RuBP carboxylase**, is a protein that makes up about 20% to 50% of the protein content in chloroplasts. The reason for its abundance may be that it is unusually slow (it processes only a few molecules of substrate per second compared to thousands per second for a typical enzyme), and so there has to be a lot of it to keep the Calvin cycle going.

Reduction of Carbon Dioxide

Each of two 3PG molecules undergoes reduction to G3P in two steps. The first step converts 3PG into 1,3-bisphosphoglycerate (BPG) using ATP, and the second reaction converts BPG into glyceraldehyde-3-phosphate (G3P) using NADPH.



This sequence of reactions uses ATP and NADPH from the light reactions. These reactions also result in the reduction of

SCIENCE IN YOUR LIFE ► ECOLOGY

Diesel Power from Algae

Algae are at the base of many food chains. But researchers are now using algae to produce a variety of different fuel types. Solazyme, a San Francisco-based company, has discovered the methods necessary to produce crude oil from various plant-based sugars with the help of microalgae (Fig. 8A). The process they have developed does not depend on the photosynthetic ability of the algae. It uses genetically modified algae grown in large vats. Instead of being exposed to sunlight, the algae are fed sugar that they convert into various types of oil. Different types of algae produce different types of oil. Because the algae are grown in the dark, the genes for photosynthesis have been switched off. With these genes turned off, the algae actually make more oil.

Algae-based biofuels are considered “green” fuels. These fuels can be used for a variety of purposes, but one of the more common is the production of biodiesel that can be used in cars and mass transportation systems. Some of the benefits of Solazyme-based fuels over traditional petroleum-based fuels are that they meet industry standards and can be used with factory-standard diesel engines without any type of modifications. Not just automobiles may be powered by these biofuels. In 2010, Solazyme delivered 80,000 liters of marine diesel and jet fuel to the U.S. Navy that was derived from algae-based production. In 2011, a United Airways jet conducted the first commercial flight powered by biofuels.

The oils produced by the algae are not only used for the production of fuel, but may



Figure 8A Production of biodiesel from algae. The algae in these containers have the ability to produce a form of oil that can be used as a fuel.

also be used to manufacture cosmetics and food additives.

With the increasing concern over the effects of global climate change on the world’s populations and ecosystems, many governments (both local and national) and private industries are looking to use biofuels as an alternative “green-energy” source. Currently, demand still outpaces the production abilities of the companies, but advances in technology

and techniques will increasingly make biofuels an attractive alternate energy source.

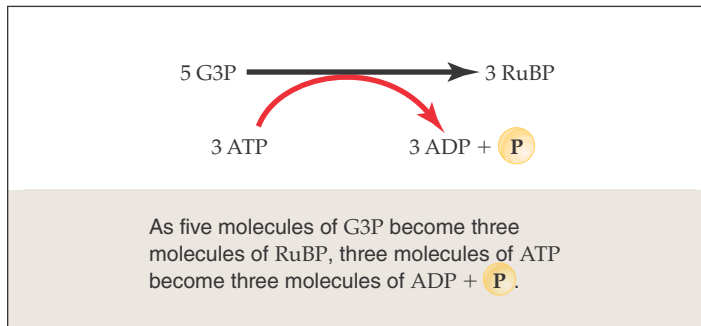
Questions to Consider

1. Why would growing algae help reduce the carbon footprint of a city or town?
2. Fossil fuels are still relatively cheap to extract and produce. What technology advances do you think are needed to make biodiesel cheaper to produce?

carbon dioxide to a carbohydrate because $R\text{—CO}_2$ has become $R\text{—CH}_2\text{O}$. Energy and electrons are needed for this reduction reaction, and they are supplied by ATP and NADPH.

Regeneration of RuBP

Notice that the Calvin cycle reactions in Figure 8.9 are multiplied by three because it takes three turns of the Calvin cycle to allow one G3P to exit. For every three turns of the Calvin cycle, five molecules of G3P are used to re-form three molecules of RuBP and the cycle continues. Notice that 5×3 (carbons in G3P) = 3×5 (carbons in RuBP):



This reaction also uses some of the ATP produced by the light reactions.

The Importance of the Calvin Cycle

G3P (glyceraldehyde-3-phosphate) is the product of the Calvin cycle that can be converted to other molecules a plant needs. Compared to animal cells, algae and plants have enormous biochemical capabilities. They use G3P for glucose, sucrose, starch, cellulose, fatty acid, and amino acid synthesis.

Glucose phosphate is one of the organic molecules that results from G3P metabolism. Glucose is the molecule that plants and animals most often metabolize to produce the ATP molecules they require for their energy needs.

Glucose phosphate can be combined with fructose (and the phosphate removed) to form sucrose, the molecule plants use to transport carbohydrates from one part of the plant to the other.

Glucose phosphate is also the starting point for the synthesis of starch and cellulose. Starch is the storage form of glucose. Some starch is stored in chloroplasts, but most starch is stored in roots. Cellulose is a structural component of plant cell walls and becomes fiber in our diet because we are unable to digest it.

A plant can use the hydrocarbon skeleton of G3P to form fatty acids and glycerol, which are combined in plant oils, such as corn oil, sunflower oil, or olive oil—commonly used in cooking. As described in the Ecology feature, “Diesel Power from Algae,” these oils are being used as a new source of fuel called biodiesel. Also, when nitrogen is added to the hydrocarbon skeleton derived from G3P, amino acids are formed.

Check Your Progress 8.3

1. Describe how carbon dioxide is fixed and then reduced to a carbohydrate.
2. Illustrate why it takes three turns of the Calvin cycle to produce one glucose molecule.
3. Explain why G3P is an important molecule in plant metabolism.

8.4 Alternative Pathways for Photosynthesis

Learning Outcomes

Upon completion of this section, you should be able to

1. Contrast C_3 , C_4 , and CAM photosynthesis.
2. Explain how different photosynthetic modes allow plants to adapt to a particular environment.

Plants are able to live under all sorts of environmental conditions, and one reason is that various modes of photosynthesis have evolved (Fig. 8.10).

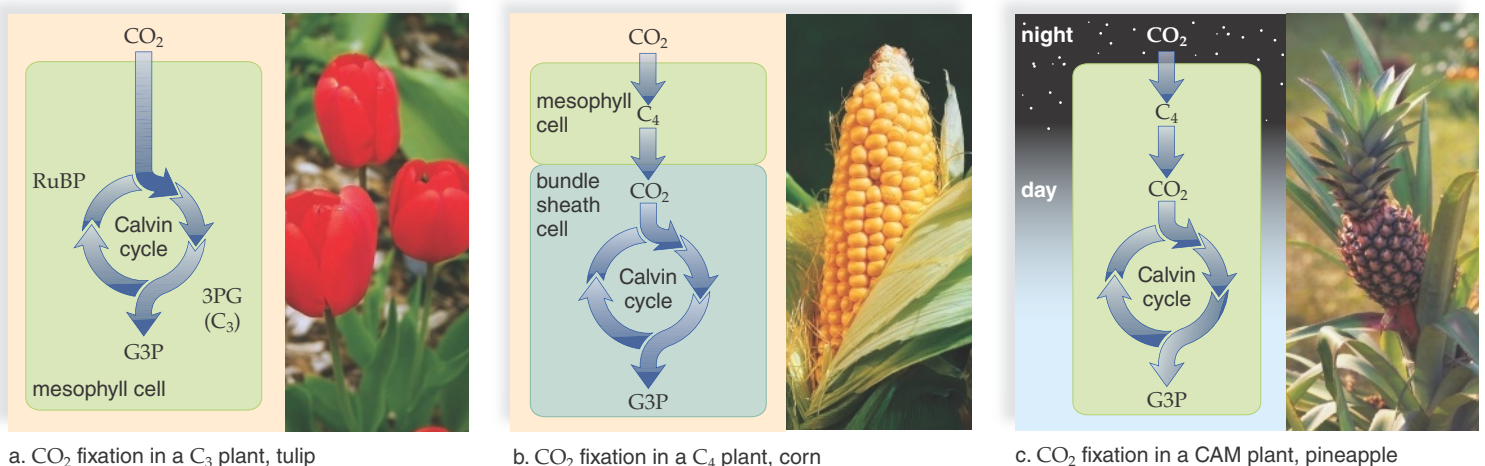


Figure 8.10 Alternative pathways for photosynthesis. Photosynthesis can be categorized according to how, where, and when CO_2 fixation occurs. **a.** In C_3 plants, CO_2 is taken up by the Calvin cycle directly in mesophyll cells. **b.** C_4 plants form a C_4 molecule in mesophyll cells prior to releasing CO_2 to the Calvin cycle in bundle sheath cells. **c.** CAM plants fix CO_2 at night, forming a C_4 molecule.

C₃ Photosynthesis

The leaves of C₃ plants have a particular structure and a different means of fixing CO₂ compared with C₄ plants. In C₃ plants, such as wheat, rice, and oats, mesophyll cells are in parallel layers. The bundle sheath cells around the plant veins do not contain chloroplasts (Fig. 8.11a). This structure exposes the cells containing the Calvin cycle to the incoming CO₂. CO₂ is fixed by RuBP carboxylase of the Calvin cycle, and the first detectable molecule following fixation is a 3-carbon molecule (see Fig. 8.9). Unfortunately, RuBP carboxylase can not only bind CO₂, it can also bind with O₂. When the enzyme binds oxygen, it undergoes a nonproductive, wasteful reaction called photorespiration because it uses oxygen and releases carbon dioxide. Photorespiration makes C₃ photosynthesis an inefficient way to produce carbohydrate when oxygen concentrations rise in the leaf space. This can happen when drought conditions occur because this type of weather leads to the closing of stomata in order to conserve water.

C₄ Photosynthesis

In C₄ plants, such as sugarcane and corn, the mesophyll cells are arranged in concentric rings around the bundle sheath cells, which also contain chloroplasts (Fig. 8.11b). In the mesophyll cells, CO₂ is initially fixed by forming a 4-carbon molecule. The

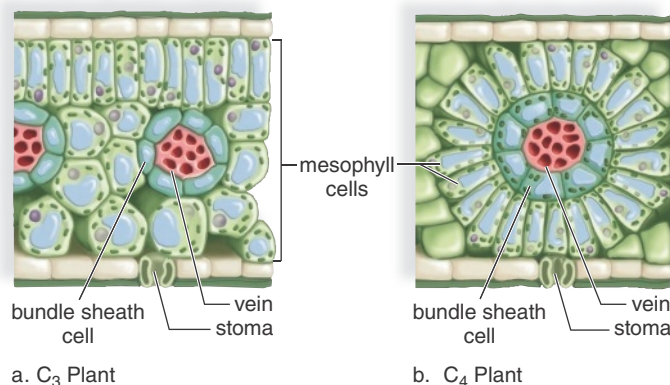


Figure 8.11 C₃ and C₄ plant leaf cell arrangement. **a.** C₃ plants contain mesophyll cells in parallel layers. The bundle sheath cells do not contain chloroplasts. **b.** C₄ plants contain mesophyll cells arranged in concentric rings around chlorophyll containing bundle sheath cells.

formation of this molecule accounts for the terms C₄ plant and C₄ photosynthesis. The 4-carbon molecule releases CO₂ to the Calvin cycle and carbohydrate production follows.

Because of the need to transport molecules from where CO₂ is fixed to where the Calvin cycle is located, it would appear that the

SCIENCE IN YOUR LIFE ► ECOLOGY

The New Rice

According to international government leaders who met in Japan in July of 2008, a global food crisis is developing. The world's population continues to grow, and grain is being diverted for biofuels and to feed livestock. The world's farmers are not keeping up with the demand for wheat, sorghum, maize, and rice. But according to the International Rice Research Institute (IRRI) in Los Baños, Philippines, two-thirds of the world's poorest people subsist primarily on rice (Fig. 8B). So a shortage of rice affects world hunger more than the other grains. More rice is being consumed than grown, and world rice stockpiles have been declining since 2001. In order to keep up with demand, the world must grow 50 million tons more rice per year than it did in 2005. This requires an increase globally of 1.2% per year.

Several environmental factors are causing these declines, including global climate change and regional flooding. For example, most varieties of rice will die if they are submerged for three or more days. However, one variety, called flood resistant (FR), could survive even if submerged for three weeks. A single gene, called the *Sub1A* gene, appeared to confer a significant degree of submergence tolerance to the FR variety. IRRI scientists were able to



Figure 8B Rice to feed the world.

Rice provides food for two-thirds of the world's poorest people. New technologies may increase the production of rice.

introduce the gene into commercial rice strains via hybridization, and four varieties are currently in field trials.

China plants approximately 57% of its rice crop in hybrid varieties. Hybrid rice produces approximately 20% more per acre than the traditional inbred varieties. The hybrids

developed by the Chinese are best suited for growth in the tropics and are not effective in temperate zones. In addition, the rice lacks in flavor compared to the inbred varieties.

One of the more long-term research programs with rice is trying to convert rice from a C₃ into a C₄ plant! C₄ plants are 50% more efficient at turning sunlight into food than C₃ plants. There are two aspects of a C₄ plant that would need to be introduced into rice. The first would be the actual enzymes involved in fixing carbon dioxide. The second would be the leaf anatomy of the mesophyll and bundle sheath cells. Researchers have succeeded in introducing the appropriate enzymes from maize, a C₄ plant, into rice plants. Without the proper leaf anatomy, however, there is no guarantee the cloned enzymes will increase the efficiency of photosynthesis.

Questions to Consider

1. If the poorest people in the world go hungry due to the lack of grain, how much difference would it make to solving world hunger if you reduced your meat and fuel consumption?
2. Are genetically modified organisms the only way to feed the world's growing population?

C_4 pathway would be little utilized among plants. However, when the weather is hot and dry, C_4 plants have an advantage. This is because when the stomata close in order to conserve water and oxygen increases in leaf air space, RuBP carboxylase is not exposed to this oxygen in C_4 plants and photorespiration does not occur. Instead, in C_4 plants, the carbon dioxide is delivered to the Calvin cycle, which is located in bundle sheath cells that are sheltered from the leaf air spaces.

When the weather is moderate, C_3 plants ordinarily have the advantage, but when the weather becomes hot and dry, C_4 plants have the advantage, and we can expect them to predominate. In the early summer, C_3 plants such as Kentucky bluegrass and creeping bent grass predominate in lawns in the cooler parts of the United States, but by mid-summer, crabgrass, a C_4 plant, begins to take over.

CAM Photosynthesis

Another alternative pathway, called the CAM pathway (Fig. 8.10c), has also evolved because of environmental pressures. CAM stands for crassulacean-acid metabolism. Crassulaceae is a family of flowering succulent plants that live in warm, arid regions of the world. CAM photosynthesis is prevalent among most succulent plants that grow in desert environments, including the cacti, but it is now known to occur in a variety of other plants.

While the C_4 pathway separates components of photosynthesis by location, the CAM pathway separates them in time. CAM plants fix CO_2 into a 4-carbon molecule at night, when they can keep their stomata open without losing much water. The 4-carbon molecule is stored in large vacuoles in their mesophyll cells until the next day. During the day, the 4-carbon molecule releases the CO_2 to the Calvin cycle within the same cell.

Plants are capable of fixing carbon by more than one pathway. These pathways appear to be the result of adaptation to different climates.

Check Your Progress 8.4

1. Identify various plants that use a method of photosynthesis other than C_3 photosynthesis.
2. Explain why C_4 photosynthesis is advantageous in hot, dry conditions.

8.5 Photosynthesis Versus Cellular Respiration

Learning Outcomes

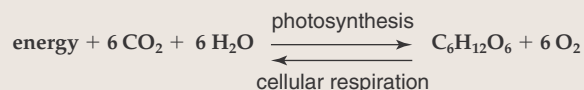
Upon completion of this section, you should be able to

1. Compare the overall chemical equation for photosynthesis and cellular respiration.
2. Describe the similarities and differences between cellular respiration and photosynthesis.

Both plant and animal cells carry on cellular respiration, but animal cells cannot photosynthesize. Plants, algae, and cyanobacteria are capable of photosynthesis. The organelle for cellular

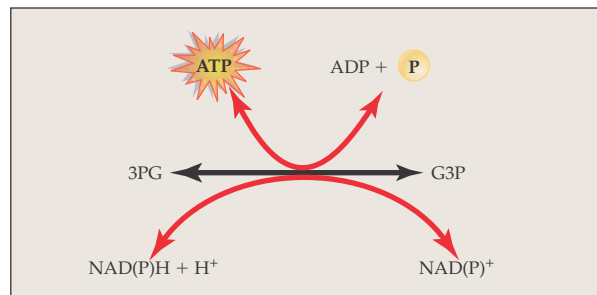
respiration is the mitochondrion, whereas the organelle for photosynthesis is the chloroplast. Note that in some bacteria, such as the cyanobacteria, photosynthesis occurs without chloroplasts—this is because these bacteria do have thylakoid-like structures in the cell. Photosynthesis is the formation of glucose, whereas cellular respiration is the breaking down of glucose. Figure 8.12 compares the two processes.

The following overall chemical equation for photosynthesis is the opposite of that for cellular respiration. The reaction in the forward direction represents photosynthesis, and the word *energy* stands for solar energy. The reaction in the opposite direction represents cellular respiration, and the word *energy* then stands for ATP:



Both photosynthesis and cellular respiration are metabolic pathways within cells, and therefore consist of a series of reactions that the overall equation does not indicate. Both pathways, which use an electron transport chain located in membranes, produce ATP by chemiosmosis. Both also use an electron carrier; photosynthesis uses $NADP^+$, and cellular respiration uses NAD^+ .

Both pathways utilize the following reaction, but in opposite directions. For photosynthesis, read the reaction from left to right; for cellular respiration, read the reaction from right to left:



Both photosynthesis and cellular respiration occur in plant cells. In plants, both processes occur during the daylight hours, whereas only cellular respiration occurs at night. During daylight hours, the rate of photosynthesis exceeds the rate of cellular respiration, resulting in a net increase and storage of glucose. The stored glucose is used for cellular metabolism, which continues during the night.

Check Your Progress 8.5

1. Explain the similarities, and differences, between cellular respiration and photosynthesis. Use the chemical equation for these reactions in your answer.
2. Explain why a plant cell must contain both chloroplasts and mitochondria.

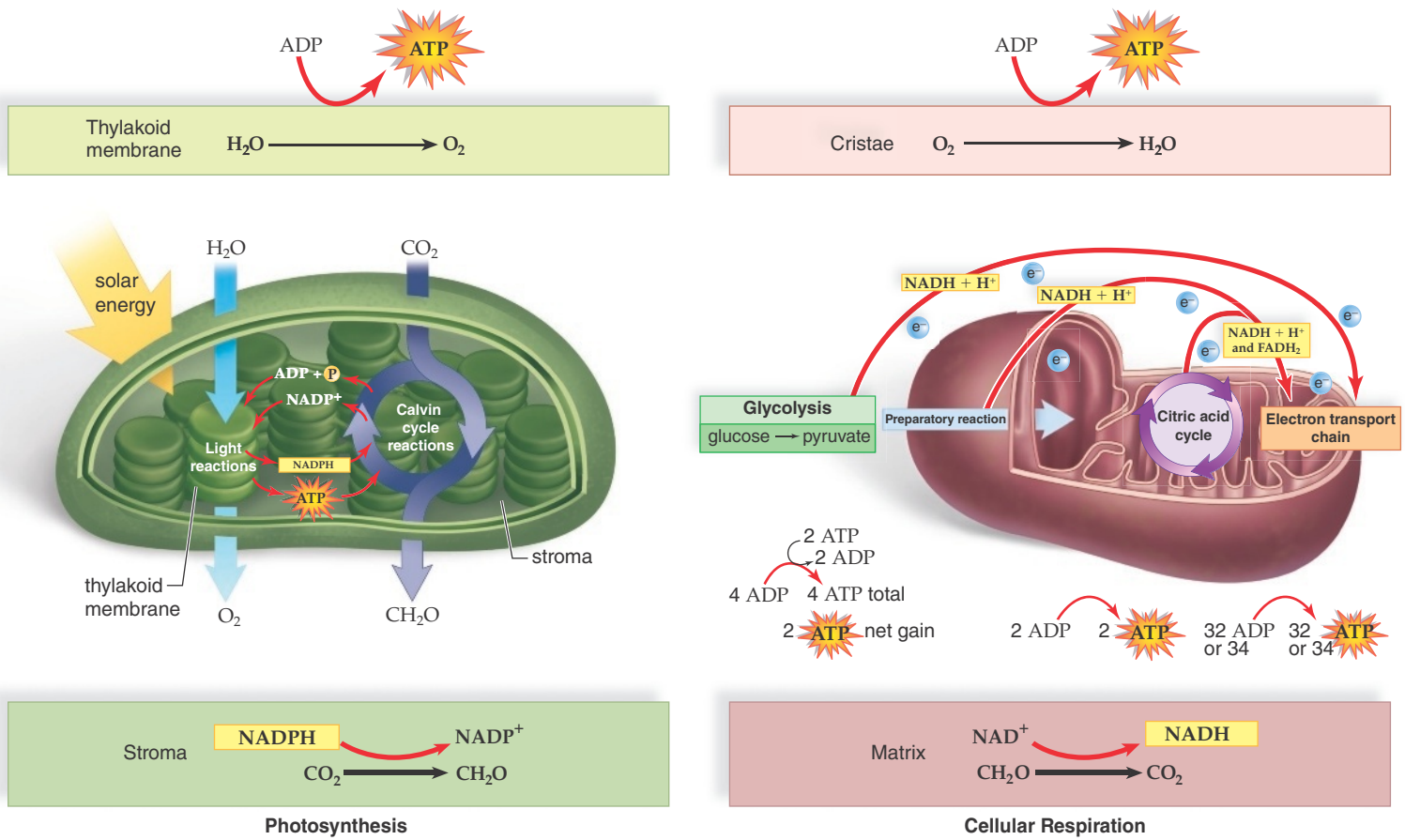


Figure 8.12 Photosynthesis versus cellular respiration. Both photosynthesis and cellular respiration have an electron transport chain located within membranes, where ATP is produced. Both processes have enzyme-catalyzed reactions located within the fluid interior of respective organelles. In photosynthesis, hydrogen atoms are donated by NADPH + H⁺ when CO₂ is reduced in the stroma of a chloroplast. During cellular respiration, NADH forms when glucose is oxidized in the cytoplasm and glucose breakdown products are oxidized in the matrix of a mitochondrion.

Conclusion

Throughout the summer and fall every year, plants undergo a wide variety of color changes. During the summer, leaves and fruits are typically green due to the large amounts of chlorophyll present in them. As the season progresses, the chlorophyll degrades and the carotenoids, yellow to red pigments, become more visible. It is this wide range of pigments that enables the plants of the world to absorb the necessary solar energy to run photosynthesis. Once the solar energy is absorbed, a series of chemical reactions are set in place that will ultimately produce

oxygen and glucose. The consumers of the world require this oxygen and glucose to run cellular respiration.




The additional benefit that scientists have discovered is that the degradation of chlorophyll in the skin of fruits results in the production of antioxidants. It is thought that antioxidants help stabilize free radicals, the molecules that can damage DNA and lead to cancer. Photosynthesis not only supplies the oxygen and glucose necessary for consumers, but it also has health benefits for us as well.

MEDIA STUDY TOOLS

<http://connect.mheducation.com>

Maximize your study time with McGraw-Hill SmartBook®, the first adaptive textbook.



 Animations	 3D Animations	 Tutorials
8.2 Electron Transport System and ATP Synthesis • Proton Pump	8.1 Photosynthesis: Structure of a Chloroplast 8.2 Photosynthesis: Properties of Light • Photosynthesis: Light-Dependent Reactions 8.3 Photosynthesis: Calvin Cycle	8.2 Noncyclic Photosynthesis 8.3 Calvin Cycle

SUMMARIZE

8.1 Overview of Photosynthesis

- **Photosynthesis** is absolutely essential for the continuance of life because by this process **autotrophs**, such as plants, manufacture the food needed for all life, including the **heterotrophs**, to survive.
- Chloroplasts carry on photosynthesis. During photosynthesis, solar energy is converted to chemical energy within carbohydrates. A chloroplast contains two main portions: the stroma and membranous grana made up of thylakoid sacs. **Chlorophyll** and other pigments like the **carotenoids** that are located within the thylakoid membrane absorb solar energy, and enzymes in the fluid-filled stroma reduce CO_2 . CO_2 enters the leaf through small openings called **stomata**.
- The overall equation for photosynthesis is $6 \text{CO}_2 + 6 \text{H}_2\text{O} \rightarrow \text{C}_6\text{H}_{12}\text{O}_6 + 6 \text{O}_2$. Photosynthesis consists of two reactions: the **light reactions** and the **Calvin cycle reactions**. The Calvin cycle reactions, located in the stroma, use **NADP⁺ (nicotinamide adenine dinucleotide phosphate)** and ATP to reduce carbon dioxide. These molecules are produced by the light reactions located in the thylakoid membranes of the grana, after chlorophyll captures the energy of sunlight.

8.2 Plants as Solar Energy Converters

- Photosynthesis uses solar energy in the visible-light range. Chlorophylls *a* and *b* and the carotenoids largely absorb violet, indigo, blue, and red wavelengths and reflect green wavelengths. This causes leaves to appear green to us.
- Photosynthesis begins when pigment complexes within **photosystem I** and photosystem II absorb radiant energy. In the **noncyclic electron pathway**, electrons are energized in photosystem II before they enter an electron transport chain. Electrons from H_2O replace those lost in photosystem II. As the electrons pass through the electron transport chain, they help establish a hydrogen ion gradient. The electrons energized in photosystem I pass to **NADP⁺**, which becomes NADPH. Electrons from the electron transport chain replace those lost by photosystem I.
- In the **cyclic electron pathway** of the light reactions, electrons energized by the sun leave photosystem I and enter an electron transport chain that produces a hydrogen ion gradient. Then the energy-spent electrons return to photosystem I.

- The hydrogen ion gradient across the thylakoid membrane is used to synthesize ATP using an **ATP synthase** enzyme complex.

8.3 Plants as Carbon Dioxide Fixers

- The ATP and NADPH made in thylakoid membranes pass into the stroma, where carbon dioxide is reduced during the Calvin cycle reactions.
- **Carbon dioxide fixation** attaches CO_2 to a 5-carbon molecule named RuBP by the enzyme **RuBP carboxylase**. The resulting 6-carbon molecule splits into two molecules of 3-carbons, each called 3PG. ATP and NADPH from the light reactions are then used to reduce 3PG to G3P.
- G3P is used to synthesize various molecules, including carbohydrates such as glucose.

8.4 Alternative Pathways for Photosynthesis

- In **C₃ plants**, the first molecule observed following carbon dioxide fixation is a 3-carbon molecule. The structure of these plants allows RuBP carboxylase to bind with oxygen during photorespiration.
- Plants utilizing **C₄ photosynthesis** have a different construction than plants using **C₃ photosynthesis**. **C₄ plants** fix CO_2 in mesophyll cells and then deliver the CO_2 to the Calvin cycle in bundle sheath cells. Now, O_2 cannot compete for the active site of RuBP carboxylase when stomata are closed due to hot and dry weather. This represents a partitioning of pathways in space: carbon dioxide fixation occurs in mesophyll cells, and the Calvin cycle occurs in bundle sheath cells.
- **CAM plants** fix carbon dioxide at night when their stomata remain open. This represents a partitioning of pathways in time: carbon dioxide fixation occurs at night, and the Calvin cycle occurs during the day.

8.5 Photosynthesis versus Cellular Respiration

- Both photosynthesis and cellular respiration utilize an electron transport chain and ATP synthesis. However, photosynthesis reduces CO_2 to a carbohydrate. The oxidation of H_2O releases O_2 . Cellular respiration oxidizes carbohydrate, and CO_2 is given off. Oxygen is reduced to water.

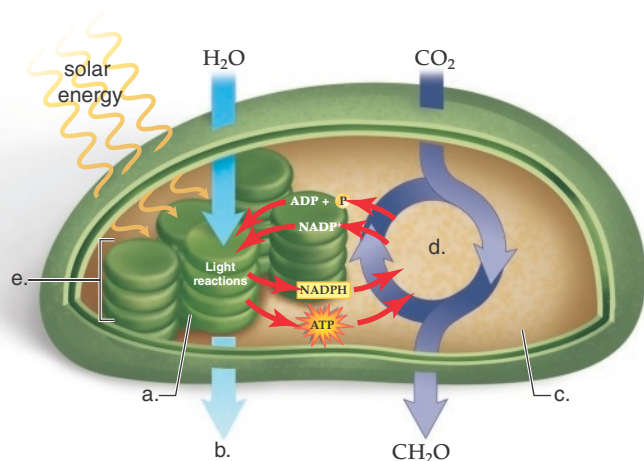
ASSESS

Testing Yourself

Choose the best answer for each question.

8.1 Overview of Photosynthesis

1. Label each of the items in the diagram below:



2. The function of light reactions is to

- obtain CO_2 .
- make carbohydrate.
- convert light energy into a usable form of chemical energy.
- regenerate RuBP.

3. The Calvin cycle reactions

- produce carbohydrate.
- convert one form of chemical energy into a different form of chemical energy.
- regenerate more RuBP.
- use the products of the light reactions.
- All of these are correct.

8.2 Plants as Solar Energy Converters

4. The final acceptor of electrons during the light reactions of the noncyclic electron pathway is

- PS I.
- PS II.
- ATP.
- NADP^+ .
- water.

5. The oxygen given off by photosynthesis comes from

- H_2O .
- CO_2 .
- glucose.
- RuBP.

6. The noncyclic electron pathway, but not the cyclic pathway, generates

- 3PG.
- chlorophyll.
- ATP.
- NADPH.

8.3 Plants as Carbon Dioxide Fixers

7. The ATP and NADPH from the light reactions are used to

- split water.
- cause RuBP carboxylase to fix CO_2 .
- re-form the photosystems.
- cause electrons to move along their pathways.
- convert 3PG to G3P.

8. In the absence of sunlight, plants are not able to engage in the Calvin cycle due to a lack of

- ATP.
- oxygen.
- NADPH.
- Both a and c are correct.

8.4 Alternative Pathways for Photosynthesis

9. CAM photosynthesis

- is the same as C_4 photosynthesis.
- is an adaptation to cold environments in the Southern Hemisphere.
- is prevalent in desert plants that close their stomata during the day.
- occurs in plants that live in marshy areas.
- stands for “chloroplasts and mitochondria.”

10. C_4 photosynthesis

- is the same as C_3 photosynthesis, because it takes place in chloroplasts.
- occurs in plants whose bundle sheath cells contain chloroplasts.
- takes place in plants such as wheat, rice, and oats.
- is an advantage when the weather is hot and dry.
- Both b and d are correct.

8.5 Photosynthesis versus Cellular Respiration

11. Cellular respiration and photosynthesis both

- use oxygen.
- produce carbon dioxide.
- contain an electron transport chain.
- occur in the chloroplast.

12. Which of the following does not occur in photosynthesis?

- reduction of CO_2
- oxidation of water
- reduction of oxygen
- All of these are correct.

ENGAGE

BioNOW

Want to know how this science is relevant to your life? Check out the BioNow videos below:

- Energy Part I: Energy Transfers
- Energy Part II: Photosynthesis
- Energy Part III: Cellular Respiration

Thinking Critically

- How do broad, thin leaves provide an advantage for photosynthesis?
- Artificial leaves are beginning to be developed by biotechnology companies. Outline the basic characteristics that an artificial leaf would need to have to manufacture a sugar.
- In the 17th century a Belgian doctor, Jan Baptista van Helmont, planted a small willow tree in a pot of soil. He weighed the tree and the soil. The tree was watered for 5 years and weighed 74.4 kg more than when he began, but the soil had only lost 57 g of mass. Explain what accounts for the plant's increase in biomass.

PHOTO CREDITS

Opener(trees): © Don Johnston/Getty Images; opener(fruit): © Evelyn Jo Johnson; 8.1a: © Sinclair Stammers/Getty Images; 8.1b: © Chuck Davis/Stone/Getty Images; 8.1c: © Dynamic Graphics Group/Creatas/Alamy RF; 8.2d: © Science Source; 8A: © Agencja Fotograficzna; 8.10a: © Evelyn Jo Johnson; 8.10b: © David Frazier/Corbis RF; 8.10c: © Pictal/Age fotostock RF; 8B: © Doable/A.collection/Getty Images.