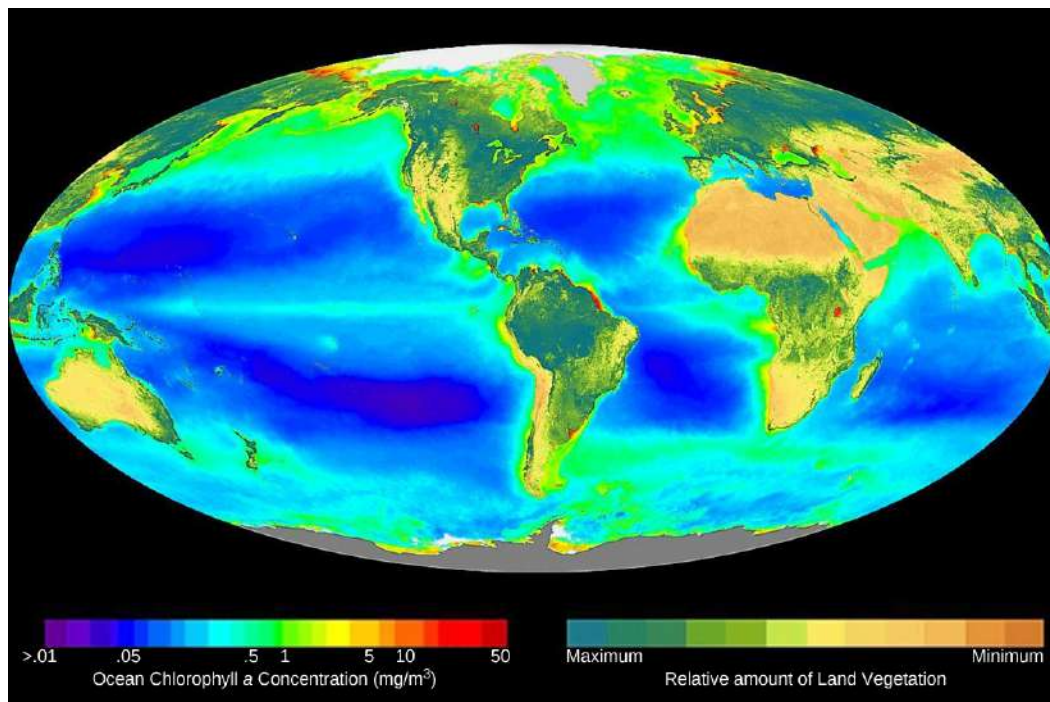


# 8 | PHOTOSYNTHESIS



**Figure 8.1** This world map shows Earth's distribution of photosynthesis as seen via chlorophyll a concentrations. On land, this is evident via terrestrial plants, and in oceanic zones, via phytoplankton. (credit: modification of work by SeaWiFS Project, NASA/Goddard Space Flight Center and ORBIMAGE)

## Chapter Outline

**8.1: Overview of Photosynthesis**

**8.2: The Light-Dependent Reaction of Photosynthesis**

**8.3: Using Light to Make Organic Molecules**

## Introduction

All biological processes require energy. To get this energy, many organisms access stored energy by eating, that is, by ingesting other organisms. But where does the stored energy in food originate? Almost all of this energy can be traced back to photosynthesis.

Photosynthetic organisms are the basis for almost all of the food webs on the planet. For example, the Indian River Lagoon, a 156 mile mixture of fresh and salt water along the eastern coast of Florida, depends on its sea grass for the survival of its marine life. Unfortunately, when certain algal phytoplankton species grow in overabundance, it destroys the sea grass. Scientists conducted a 16 year study of algal blooms and found that extreme climate conditions, such as cold weather and low rainfall, change which particular species of phytoplankton is more likely to bloom, resulting in a die-off of sea grass, decrease in other marine life, and changes in salinity. The research study can be found [here \(http://openstaxcollege.org/l/32algae\)](http://openstaxcollege.org/l/32algae).

## 8.1 | Overview of Photosynthesis

In this section, you will explore the following questions:

- What is the relevance of photosynthesis to living organisms?
- What are the main cellular structures involved in photosynthesis?
- What are the substrates and products of photosynthesis?

### Connection for AP<sup>®</sup> Courses

As we learned in Chapter 7, all living organisms, from simple bacteria to complex plants and animals, require free energy to carry out cellular processes, such as growth and reproduction. Organisms use various strategies to capture, store, transform, and transfer free energy, including photosynthesis. Photosynthesis allows organisms to access enormous amounts of free energy from the sun and transform it to the chemical energy of sugars. Although all organisms carry out some form of cellular respiration, only certain organisms, called photoautotrophs, can perform photosynthesis. Examples of photoautotrophs include plants, algae, some unicellular eukaryotes, and cyanobacteria. They require the presence of chlorophyll, a specialized pigment that absorbs certain wavelengths of the visible light spectrum to harness free energy from the sun. Photosynthesis is a process where components of water and carbon dioxide are used to assemble carbohydrate molecules and where oxygen waste products are released into the atmosphere. In eukaryotes, the reactions of photosynthesis occur in chloroplasts; in prokaryotes, such as cyanobacteria, the reactions are less localized and occur within membranes and in the cytoplasm. (The structural features of the chloroplast that participate in photosynthesis will be explored in more detail later in The Light-Dependent Reactions of Photosynthesis and Using Light Energy to Make Organic Molecules.) Although photosynthesis and cellular respiration evolved as independent processes—with photosynthesis creating an oxidizing atmosphere early in Earth's history—today they are interdependent. As we studied in Cellular Respiration, aerobic cellular respiration taps into the oxidizing ability of oxygen to synthesize the organic compounds that are used to power cellular processes.

Information presented and the examples highlighted in the section support concepts and learning objectives outlined in Big Idea 1 and Big Idea 2 of the AP<sup>®</sup> Biology Curriculum Framework, as shown in the table. The learning objectives listed in the Curriculum Framework provide a transparent foundation for the AP<sup>®</sup> Biology course, an inquiry-based laboratory experience, instructional activities, and AP<sup>®</sup> exam questions. A learning objective merges required content with one or more of the seven science practices.

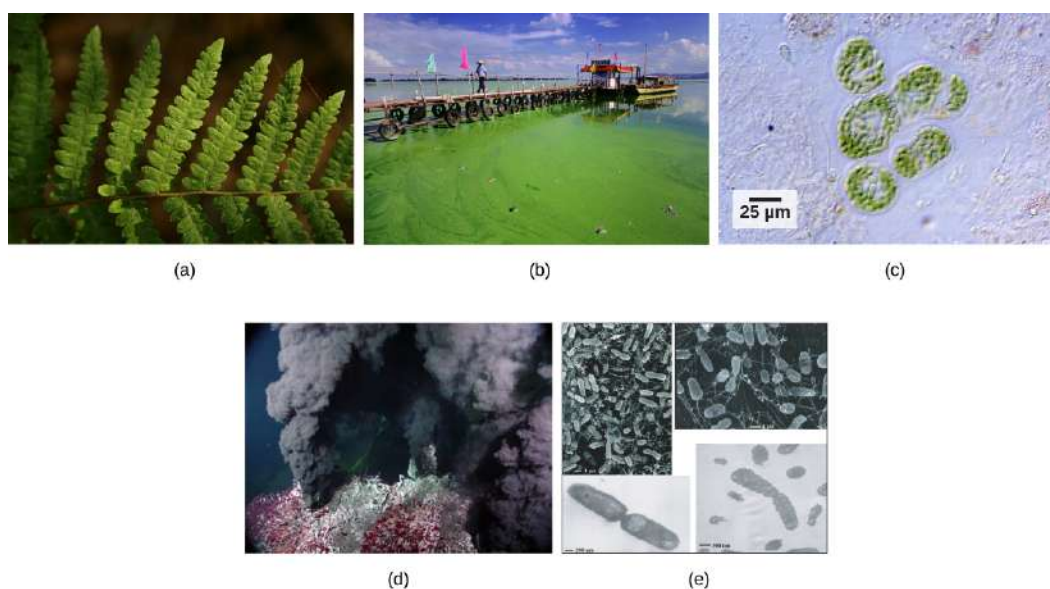
<b>Big Idea 1</b>	The process of evolution drives the diversity and unity of life.
<b>Enduring Understanding 1.B</b>	Organisms are linked by lines of descent from common ancestry.
<b>Essential Knowledge</b>	<b>1.B.1</b> Structural and functional evidence supports the relatedness of all domains, with organisms shared many conserved core processes.
<b>Science Practice</b>	<b>6.1</b> The student can justify claims with evidence.
<b>Learning Objective</b>	<b>1.15</b> The student is able to describe specific examples of conserved core biological processes and features shared by all domains or within one domain of life, and how these shared, conserved core processes and features support the concept of common ancestry for all organisms.
<b>Big Idea 2</b>	Biological systems utilize free energy and molecular building blocks to grow, to reproduce, and to maintain dynamic homeostasis.
<b>Enduring Understanding 2.A</b>	Growth, reproduction and maintenance of living systems require free energy and matter.

<b>Essential Knowledge</b>	<b>2.A.2</b> Organisms use various strategies to capture and store free energy for use in biological processes.
<b>Science Practice</b>	<b>1.4</b> The student can use representations and models to analyze situations or solve problems qualitatively and quantitatively.
<b>Science Practice</b>	<b>3.1</b> The student can pose scientific questions.
<b>Learning Objective</b>	<b>2.4</b> The student is able to use representations to pose scientific questions about what mechanisms and structural features allow organisms to capture, store, and use free energy.
<b>Essential Knowledge</b>	<b>2.A.2</b> Organisms use various strategies to capture and store free energy for use in biological processes.
<b>Science Practice</b>	<b>6.2</b> The student can construct explanations of phenomena based on evidence produced through scientific practices.
<b>Learning Objective</b>	<b>2.5</b> The student is able to construct explanations of the mechanisms and structural features of cells that allow organisms to capture, store, or use free energy.

## Importance of Photosynthesis

Photosynthesis is essential to all life on earth; both plants and animals depend on it. It is the only biological process that can capture energy that originates in outer space (sunlight) and convert it into chemical compounds (carbohydrates) that every organism uses to power its metabolism. In brief, the energy of sunlight is captured and used to energize electrons, whose energy is then stored in the covalent bonds of sugar molecules. How long lasting and stable are those covalent bonds? The energy extracted today by the burning of coal and petroleum products represents sunlight energy captured and stored by photosynthesis almost 200 million years ago.

Plants, algae, and a group of bacteria called cyanobacteria are the only organisms capable of performing photosynthesis (**Figure 8.2**). Because they use light to manufacture their own food, they are called **photoautotrophs** (literally, “self-feeders using light”). Other organisms, such as animals, fungi, and most other bacteria, are termed **heterotrophs** (“other feeders”), because they must rely on the sugars produced by photosynthetic organisms for their energy needs. A third very interesting group of bacteria synthesize sugars, not by using sunlight’s energy, but by extracting energy from inorganic chemical compounds; hence, they are referred to as **chemoautotrophs**.



**Figure 8.2** Photoautotrophs including (a) plants, (b) algae, and (c) cyanobacteria synthesize their organic compounds via photosynthesis using sunlight as an energy source. Cyanobacteria and planktonic algae can grow over enormous areas in water, at times completely covering the surface. In a (d) deep sea vent, chemoautotrophs, such as these (e) thermophilic bacteria, capture energy from inorganic compounds to produce organic compounds. The ecosystem surrounding the vents has a diverse array of animals, such as tubeworms, crustaceans, and octopi that derive energy from the bacteria. (credit a: modification of work by Steve Hillebrand, U.S. Fish and Wildlife Service; credit b: modification of work by "eutrophication&hypoxia"/Flickr; credit c: modification of work by NASA; credit d: University of Washington, NOAA; credit e: modification of work by Mark Amend, West Coast and Polar Regions Undersea Research Center, UAF, NOAA)

The importance of photosynthesis is not just that it can capture sunlight's energy. A lizard sunning itself on a cold day can use the sun's energy to warm up. Photosynthesis is vital because it evolved as a way to store the energy in solar radiation (the "photo-" part) as energy in the carbon-carbon bonds of carbohydrate molecules (the "-synthesis" part). Those carbohydrates are the energy source that heterotrophs use to power the synthesis of ATP via respiration. Therefore, photosynthesis powers 99 percent of Earth's ecosystems. When a top predator, such as a wolf, preys on a deer (**Figure 8.3**), the wolf is at the end of an energy path that went from nuclear reactions on the surface of the sun, to light, to photosynthesis, to vegetation, to deer, and finally to wolf.



**Figure 8.3** The energy stored in carbohydrate molecules from photosynthesis passes through the food chain. The predator that eats these deer receives a portion of the energy that originated in the photosynthetic vegetation that the deer consumed. (credit: modification of work by Steve VanRiper, U.S. Fish and Wildlife Service)

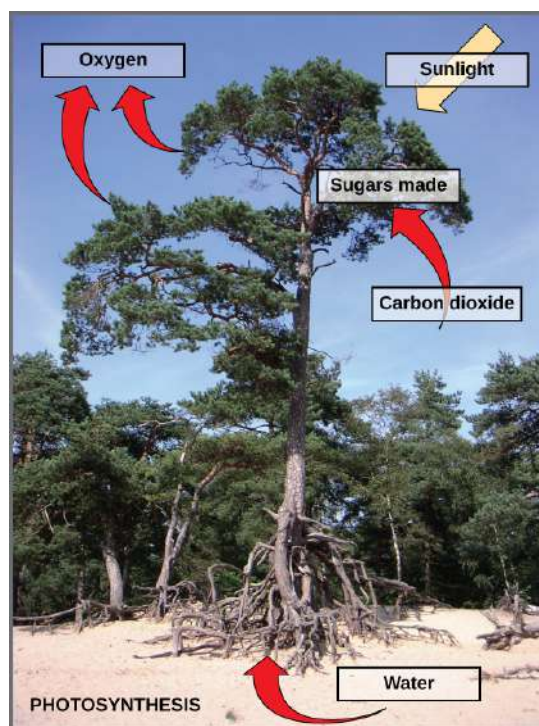
## science practices CONNECTION for AP® Courses

### Think About It

- Why do scientists think that photosynthesis evolved before aerobic cellular respiration?
- Why do carnivores, such as lions, depend on photosynthesis to survive? What evidence supports the claim that photosynthesis and cellular respiration are interdependent processes?

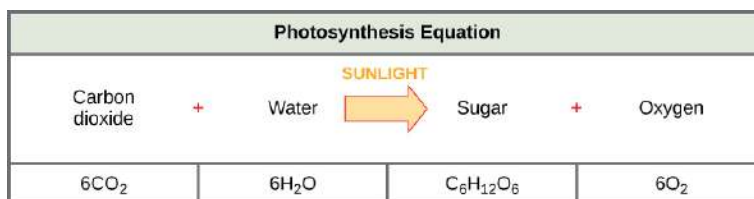
## Main Structures and Summary of Photosynthesis

Photosynthesis is a multi-step process that requires sunlight, carbon dioxide (which is low in energy), and water as substrates (**Figure 8.4**). After the process is complete, it releases oxygen and produces glyceraldehyde-3-phosphate (GA3P), simple carbohydrate molecules (which are high in energy) that can subsequently be converted into glucose, sucrose, or any of dozens of other sugar molecules. These sugar molecules contain energy and the energized carbon that all living things need to survive.



**Figure 8.4** Photosynthesis uses solar energy, carbon dioxide, and water to produce energy-storing carbohydrates. Oxygen is generated as a waste product of photosynthesis.

The following is the chemical equation for photosynthesis (**Figure 8.5**):



**Figure 8.5** The basic equation for photosynthesis is deceptively simple. In reality, the process takes place in many steps involving intermediate reactants and products. Glucose, the primary energy source in cells, is made from two three-carbon GA3Ps.

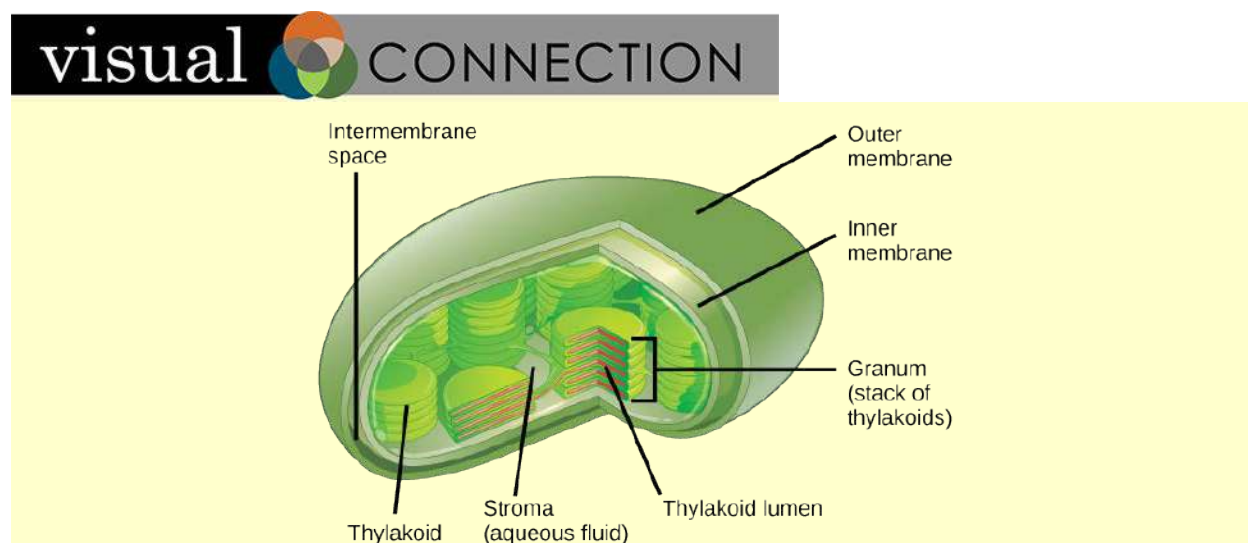
Although the equation looks simple, the many steps that take place during photosynthesis are actually quite complex. Before



learning the details of how photoautotrophs turn sunlight into food, it is important to become familiar with the structures involved.

In plants, photosynthesis generally takes place in leaves, which consist of several layers of cells. The process of photosynthesis occurs in a middle layer called the **mesophyll**. The gas exchange of carbon dioxide and oxygen occurs through small, regulated openings called **stomata** (singular: stoma), which also play roles in the regulation of gas exchange and water balance. The stomata are typically located on the underside of the leaf, which helps to minimize water loss. Each stoma is flanked by guard cells that regulate the opening and closing of the stomata by swelling or shrinking in response to osmotic changes.

In all autotrophic eukaryotes, photosynthesis takes place inside an organelle called a **chloroplast**. For plants, chloroplast-containing cells exist in the mesophyll. Chloroplasts have a double membrane envelope (composed of an outer membrane and an inner membrane). Within the chloroplast are stacked, disc-shaped structures called **thylakoids**. Embedded in the thylakoid membrane is chlorophyll, a **pigment** (molecule that absorbs light) responsible for the initial interaction between light and plant material, and numerous proteins that make up the electron transport chain. The thylakoid membrane encloses an internal space called the **thylakoid lumen**. As shown in **Figure 8.6**, a stack of thylakoids is called a **granum**, and the liquid-filled space surrounding the granum is called **stroma** or “bed” (not to be confused with stoma or “mouth,” an opening on the leaf epidermis).



**Figure 8.6** Photosynthesis takes place in chloroplasts, which have an outer membrane and an inner membrane. Stacks of thylakoids called grana form a third membrane layer.

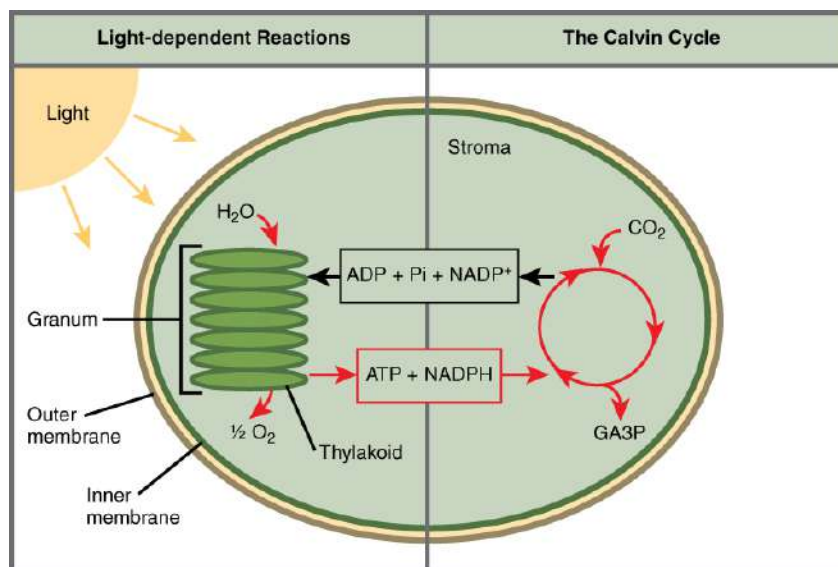
On a hot, dry day, plants close their stomata to conserve water. What impact will this have on photosynthesis?

- Rate of photosynthesis will be inhibited as the level of carbon dioxide decreases.
- Rate of photosynthesis will be inhibited as the level of oxygen decreases.
- The rate of photosynthesis will increase as the level of carbon dioxide increases.
- Rate of photosynthesis will increase as the level of oxygen increases.

## The Two Parts of Photosynthesis

Photosynthesis takes place in two sequential stages: the light-dependent reactions and the light independent-reactions. In the **light-dependent reactions**, energy from sunlight is absorbed by chlorophyll and that energy is converted into stored chemical energy. In the **light-independent reactions**, the chemical energy harvested during the light-dependent reactions drives the assembly of sugar molecules from carbon dioxide. Therefore, although the light-independent reactions do not use light as a reactant, they require the products of the light-dependent reactions to function. In addition, several enzymes of the light-independent reactions are activated by light. The light-dependent reactions utilize certain molecules to temporarily store the energy: These are referred to as energy carriers. The energy carriers that move energy from light-dependent reactions to light-independent reactions can be thought of as “full” because they are rich in energy. After the energy is

released, the “empty” energy carriers return to the light-dependent reaction to obtain more energy. **Figure 8.7** illustrates the components inside the chloroplast where the light-dependent and light-independent reactions take place.



**Figure 8.7** Photosynthesis takes place in two stages: light dependent reactions and the Calvin cycle. Light-dependent reactions, which take place in the thylakoid membrane, use light energy to make ATP and NADPH. The Calvin cycle, which takes place in the stroma, uses energy derived from these compounds to make GA3P from  $CO_2$ .



Click the [link \(http://openstaxcollege.org/l/photosynthesis\)](http://openstaxcollege.org/l/photosynthesis) to learn more about photosynthesis.

Explain how the light reactions and light independent reactions (Calvin cycle) of photosynthesis are interdependent on each other.

- The light reactions produces ATP and NADPH, which are then used in the Calvin cycle.
- The light reactions produces  $NADP^+$  and ADP, which are then used in the Calvin cycle.
- The light reactions uses NADPH and ATP, which are produced by the Calvin cycle.
- The light reactions produce only NADPH, which is produced by the Calvin cycle.

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### Photosynthesis at the Grocery Store



**Figure 8.8** Foods that humans consume originate from photosynthesis. (credit: Associação Brasileira de Supermercados)

Major grocery stores in the United States are organized into departments, such as dairy, meats, produce, bread, cereals, and so forth. Each aisle (**Figure 8.8**) contains hundreds, if not thousands, of different products for customers to buy and consume.

Although there is a large variety, each item links back to photosynthesis. Meats and dairy link, because the animals were fed plant-based foods. The breads, cereals, and pastas come largely from starchy grains, which are the seeds of photosynthesis-dependent plants. What about desserts and drinks? All of these products contain sugar—sucrose is a plant product, a disaccharide, a carbohydrate molecule, which is built directly from photosynthesis. Moreover, many items are less obviously derived from plants: For instance, paper goods are generally plant products, and many plastics (abundant as products and packaging) are derived from algae. Virtually every spice and flavoring in the spice aisle was produced by a plant as a leaf, root, bark, flower, fruit, or stem. Ultimately, photosynthesis connects to every meal and every food a person consumes.

Where would photosynthetic organisms likely be placed on a food web within most ecosystems?

- at the base
- near the top
- in the middle, but generally closer to the top
- in the middle, but generally closer to the base

## 8.2 | The Light-Dependent Reaction of Photosynthesis

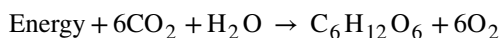
In this section, you will explore the following questions:

- How do plants absorb energy from sunlight?
- What are the differences between short and long wavelengths of light? What wavelengths are used in photosynthesis?
- How and where does photosynthesis occur within a plant?



## Connection for AP<sup>®</sup> Courses

Photosynthesis consists of two stages: the light-dependent reactions and the light-independent reactions or Calvin cycle. The light-dependent reactions occur when light is available. The overall equation for photosynthesis shows that it is a redox reaction; carbon dioxide is reduced and water is oxidized to produce oxygen:



The light-dependent reactions occur in the thylakoid membranes of chloroplasts, whereas the Calvin cycle occurs in the stroma of chloroplasts. Embedded in the thylakoid membranes are two photosystems (PS I and PS II), which are complexes of pigments that capture solar energy. Chlorophylls *a* and *b* absorb violet, blue, and red wavelengths from the visible light spectrum and reflect green. The carotenoid pigments absorb violet-blue-green light and reflect yellow-to-orange light. Environmental factors such as day length and temperature influence which pigments are predominant at certain times of the year. Although the two photosystems run simultaneously, it is easier to explore them separately. Let's begin with photosystem II.

A photon of light strikes the antenna pigments of PS II to initiate photosynthesis. In the noncyclic pathway, PS II captures photons at a slightly higher energy level than PS I. (Remember that shorter wavelengths of light carry more energy.) The absorbed energy travels to the reaction center of the antenna pigment that contains chlorophyll *a* and boosts chlorophyll *a* electrons to a higher energy level. The electrons are accepted by a primary electron acceptor protein and then pass to the electron transport chain also embedded in the thylakoid membrane. The energy absorbed in PS II is enough to oxidize (split) water, releasing oxygen into the atmosphere; the electrons released from the oxidation of water replace the electrons that were boosted from the reaction center chlorophyll. As the electrons from the reaction center chlorophyll pass through the series of electron carrier proteins, hydrogen ions ( $\text{H}^+$ ) are pumped across the membrane via chemiosmosis into the interior of the thylakoid. (If this sounds familiar, it should. We studied chemiosmosis in our exploration of cellular respiration in Cellular Respiration.) This action builds up a high concentration of  $\text{H}^+$  ions, and as they flow through ATP synthase, molecules of ATP are formed. These molecules of ATP will be used to provide free energy for the synthesis of carbohydrate in the Calvin cycle, the second stage of photosynthesis. The electron transport chain connects PS II and PS I. Similar to the events occurring in PS II, this second photosystem absorbs a second photon of light, resulting in the formation of a molecule of NADPH from  $\text{NADP}^+$ . The energy carried in NADPH also is used to power the chemical reactions of the Calvin cycle.

Information presented and the examples highlighted in the section support concepts and learning objectives outlined in Big Idea 2 of the AP<sup>®</sup> Biology Curriculum Framework, as shown in the table. The learning objectives listed in the Curriculum Framework provide a transparent foundation for the AP<sup>®</sup> Biology course, an inquiry-based laboratory experience, instructional activities, and AP<sup>®</sup> exam questions. A learning objective merges required content with one or more of the seven science practices.

<b>Big Idea 2</b>	Biological systems utilize free energy and molecular building blocks to grow, to reproduce, and to maintain dynamic homeostasis.
<b>Enduring Understanding 2.A</b>	Growth, reproduction and maintenance of living systems require free energy and matter.
<b>Essential Knowledge</b>	<b>2.A.2</b> The light-independent reactions of photosynthesis in eukaryotes involve a series of reactions that capture free energy present in light.
<b>Science Practice</b>	<b>1.4</b> The student can use representations and models to analyze situations or solve problems qualitatively and quantitatively.
<b>Science Practice</b>	<b>3.1</b> The student can pose scientific questions.
<b>Learning Objective</b>	<b>2.4</b> The student is able to use representations to pose scientific questions about what mechanisms and structural features allow organisms to capture, store, and use free energy.
<b>Essential Knowledge</b>	<b>2.A.2</b> The light-independent reactions of photosynthesis in eukaryotes involve a series of reactions that capture free energy present in light.
<b>Science Practice</b>	<b>6.2</b> The student can construct explanations of phenomena based on evidence produced through scientific practices.

<b>Learning Objective</b>	<b>2.5</b> The student is able to construct explanations of the mechanisms and structural features of cells that allow organisms to capture, store, or use free energy.
<b>Big Idea 4</b>	Biological systems interact, and these systems and their interactions possess complex properties.
<b>Enduring Understanding 4.A</b>	Interactions within biological systems lead to complex properties.
<b>Essential Knowledge</b>	<b>4.A.2</b> Chloroplasts are specialized organelles that capture energy through photosynthesis.
<b>Science Practice</b>	<b>6.4</b> The student can make claims and predictions about natural phenomena based on scientific theories and models.
<b>Learning Objective</b>	<b>4.4</b> The student is able to make a prediction about the interactions of subcellular organelles.
<b>Essential Knowledge</b>	<b>4.A.2</b> Chloroplasts are specialized organelles that capture energy through photosynthesis.
<b>Science Practice</b>	<b>6.2</b> The student can construct explanations of phenomena based on evidence produced through scientific practices.
<b>Learning Objective</b>	<b>4.5</b> The student is able to construct explanations based on scientific evidence as to how interactions of subcellular structures provide essential functions.
<b>Essential Knowledge</b>	<b>4.A.2</b> Chloroplasts are specialized organelles that capture energy through photosynthesis.
<b>Science Practice</b>	<b>1.4</b> The student can use representations and models to analyze situations or solve problems qualitatively and quantitatively.
<b>Learning Objective</b>	<b>4.6</b> The student is able to use representations and models to analyze situations qualitatively to describe how interactions of subcellular structures, which possess specialized functions, provide essential functions.

The Science Practice Challenge Questions contain additional test questions for this section that will help you prepare for the AP exam. These questions address the following standards:

[APLO 2.5][APLO 2.16][APLO 2.18][APLO 1.9][APLO 1.32][APLO 4.14][APLO 2.2][APLO 2.3][APLO 2.23][APLO 1.15][APLO 1.29]

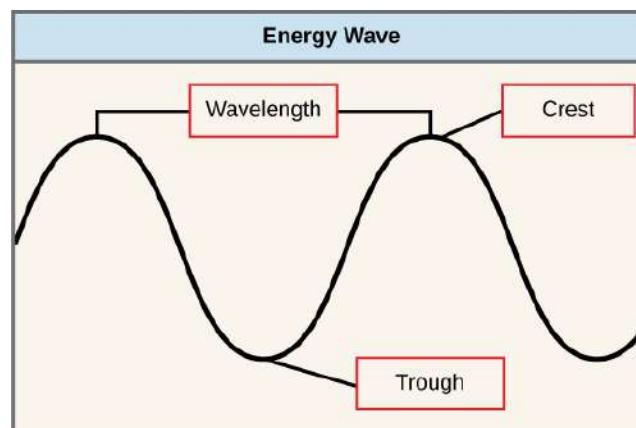
How can light be used to make food? When a person turns on a lamp, electrical energy becomes light energy. Like all other forms of kinetic energy, light can travel, change form, and be harnessed to do work. In the case of photosynthesis, light energy is converted into chemical energy, which photoautotrophs use to build carbohydrate molecules (**Figure 8.9**). However, autotrophs only use a few specific components of sunlight.



**Figure 8.9** Photoautotrophs can capture light energy from the sun, converting it into the chemical energy used to build food molecules. (credit: Gerry Atwell)

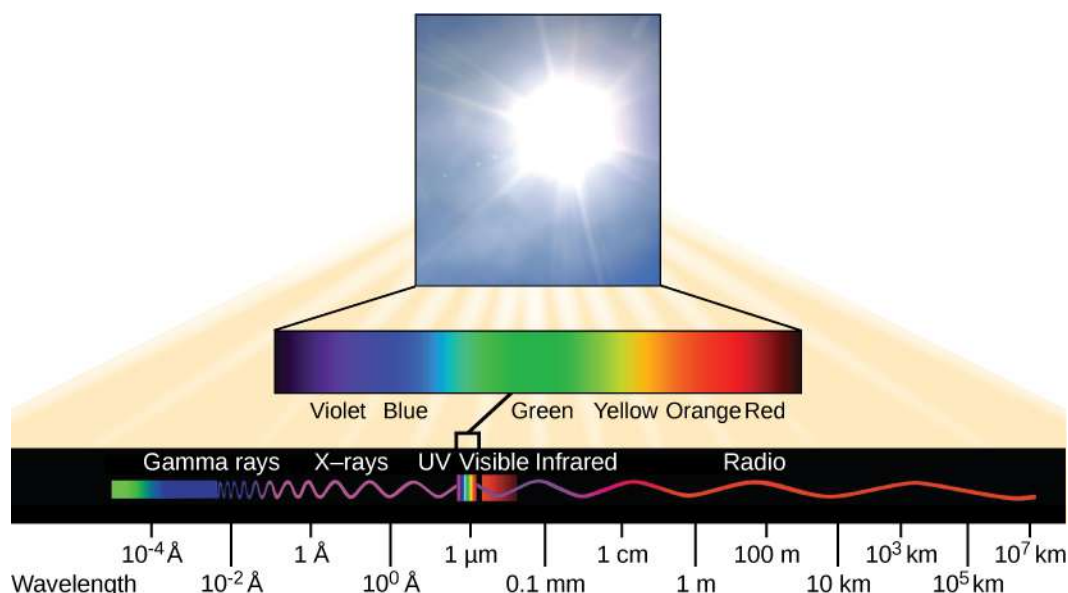
## What Is Light Energy?

The sun emits an enormous amount of electromagnetic radiation (solar energy). Humans can see only a fraction of this energy, which portion is therefore referred to as “visible light.” The manner in which solar energy travels is described as waves. Scientists can determine the amount of energy of a wave by measuring its **wavelength**, the distance between consecutive points of a wave. A single wave is measured from two consecutive points, such as from crest to crest or from trough to trough (**Figure 8.10**).



**Figure 8.10** The wavelength of a single wave is the distance between two consecutive points of similar position (two crests or two troughs) along the wave.

Visible light constitutes only one of many types of electromagnetic radiation emitted from the sun and other stars. Scientists differentiate the various types of radiant energy from the sun within the electromagnetic spectrum. The **electromagnetic spectrum** is the range of all possible frequencies of radiation (**Figure 8.11**). The difference between wavelengths relates to the amount of energy carried by them.



**Figure 8.11** The sun emits energy in the form of electromagnetic radiation. This radiation exists at different wavelengths, each of which has its own characteristic energy. All electromagnetic radiation, including visible light, is characterized by its wavelength.

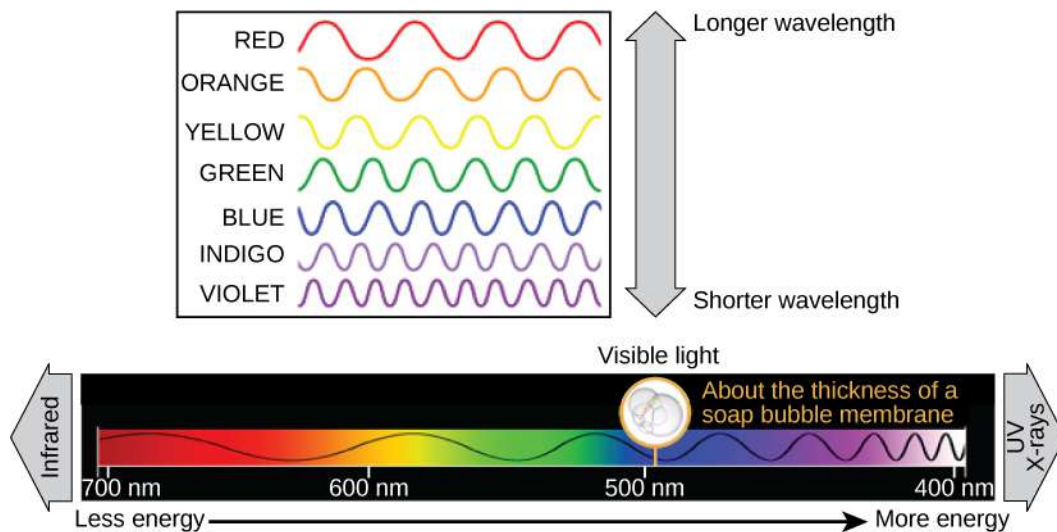
Each type of electromagnetic radiation travels at a particular wavelength. The longer the wavelength (or the more stretched out it appears in the diagram), the less energy is carried. Short, tight waves carry the most energy. This may seem illogical, but think of it in terms of a piece of moving a heavy rope. It takes little effort by a person to move a rope in long, wide waves. To make a rope move in short, tight waves, a person would need to apply significantly more energy.

The electromagnetic spectrum (**Figure 8.11**) shows several types of electromagnetic radiation originating from the sun, including X-rays and ultraviolet (UV) rays. The higher-energy waves can penetrate tissues and damage cells and DNA, explaining why both X-rays and UV rays can be harmful to living organisms.

## Absorption of Light

Light energy initiates the process of photosynthesis when pigments absorb the light. Organic pigments, whether in the human retina or the chloroplast thylakoid, have a narrow range of energy levels that they can absorb. Energy levels lower than those represented by red light are insufficient to raise an orbital electron to a populatable, excited (quantum) state. Energy levels higher than those in blue light will physically tear the molecules apart, called bleaching. So retinal pigments can only “see” (absorb) 700 nm to 400 nm light, which is therefore called visible light. For the same reasons, plants pigment molecules absorb only light in the wavelength range of 700 nm to 400 nm; plant physiologists refer to this range for plants as photosynthetically active radiation.

The visible light seen by humans as white light actually exists in a rainbow of colors. Certain objects, such as a prism or a drop of water, disperse white light to reveal the colors to the human eye. The visible light portion of the electromagnetic spectrum shows the rainbow of colors, with violet and blue having shorter wavelengths, and therefore higher energy. At the other end of the spectrum toward red, the wavelengths are longer and have lower energy (**Figure 8.12**).



**Figure 8.12** The colors of visible light do not carry the same amount of energy. Violet has the shortest wavelength and therefore carries the most energy, whereas red has the longest wavelength and carries the least amount of energy. (credit: modification of work by NASA)

## Understanding Pigments

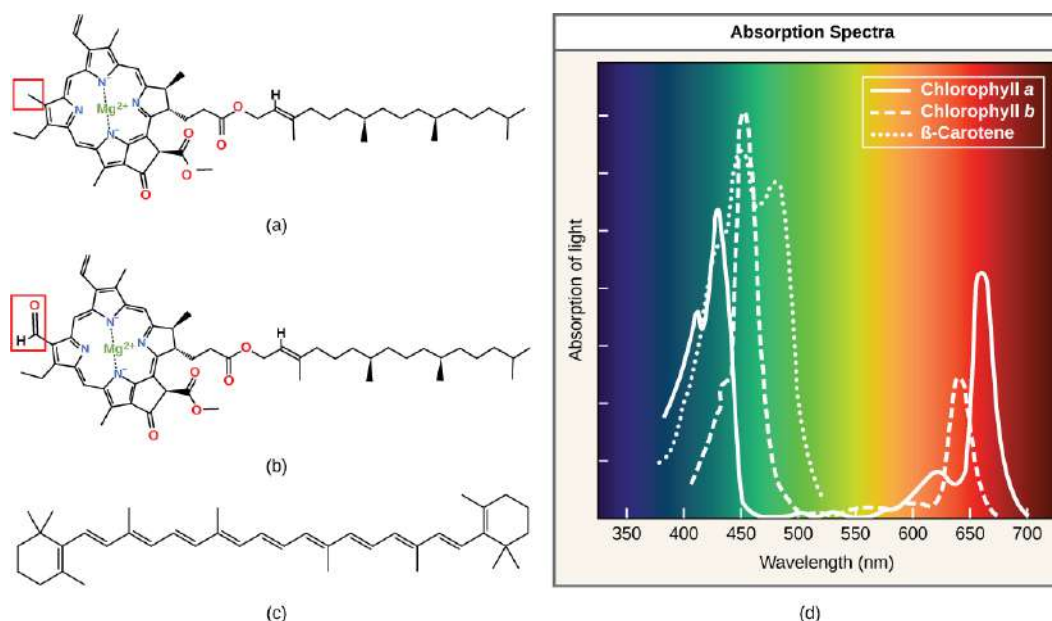
Different kinds of pigments exist, and each absorbs only certain wavelengths (colors) of visible light. Pigments reflect or transmit the wavelengths they cannot absorb, making them appear in the corresponding color.

Chlorophylls and carotenoids are the two major classes of photosynthetic pigments found in plants and algae; each class has multiple types of pigment molecules. There are five major chlorophylls: *a*, *b*, *c* and *d* and a related molecule found in prokaryotes called bacteriochlorophyll. **Chlorophyll *a*** and **chlorophyll *b*** are found in higher plant chloroplasts and will be the focus of the following discussion.

With dozens of different forms, carotenoids are a much larger group of pigments. The carotenoids found in fruit—such as the red of tomato (lycopene), the yellow of corn seeds (zeaxanthin), or the orange of an orange peel ( $\beta$ -carotene)—are used as advertisements to attract seed dispersers. In photosynthesis, **carotenoids** function as photosynthetic pigments that are very efficient molecules for the disposal of excess energy. When a leaf is exposed to full sun, the light-dependent reactions are required to process an enormous amount of energy; if that energy is not handled properly, it can do significant damage. Therefore, many carotenoids reside in the thylakoid membrane, absorb excess energy, and safely dissipate that energy as heat.

Each type of pigment can be identified by the specific pattern of wavelengths it absorbs from visible light, which is the **absorption spectrum**. The graph in **Figure 8.13** shows the absorption spectra for chlorophyll *a*, chlorophyll *b*, and a type of carotenoid pigment called  $\beta$ -carotene (which absorbs blue and green light). Notice how each pigment has a distinct set of peaks and troughs, revealing a highly specific pattern of absorption. Chlorophyll *a* absorbs wavelengths from either end of the visible spectrum (blue and red), but not green. Because green is reflected or transmitted, chlorophyll appears green. Carotenoids absorb in the short-wavelength blue region, and reflect the longer yellow, red, and orange wavelengths.





**Figure 8.13** (a) Chlorophyll a, (b) chlorophyll b, and (c)  $\beta$ -carotene are hydrophobic organic pigments found in the thylakoid membrane. Chlorophyll a and b, which are identical except for the part indicated in the red box, are responsible for the green color of leaves.  $\beta$ -carotene is responsible for the orange color in carrots. Each pigment has (d) a unique absorbance spectrum.

Many photosynthetic organisms have a mixture of pigments; using them, the organism can absorb energy from a wider range of wavelengths. Not all photosynthetic organisms have full access to sunlight. Some organisms grow underwater where light intensity and quality decrease and change with depth. Other organisms grow in competition for light. Plants on the rainforest floor must be able to absorb any bit of light that comes through, because the taller trees absorb most of the sunlight and scatter the remaining solar radiation (**Figure 8.14**).



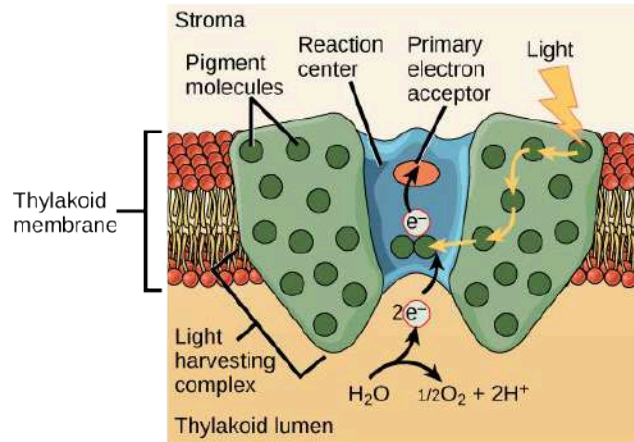
**Figure 8.14** Plants that commonly grow in the shade have adapted to low levels of light by changing the relative concentrations of their chlorophyll pigments. (credit: Jason Hollinger)

When studying a photosynthetic organism, scientists can determine the types of pigments present by generating absorption spectra. An instrument called a **spectrophotometer** can differentiate which wavelengths of light a substance can absorb. Spectrophotometers measure transmitted light and compute from it the absorption. By extracting pigments from leaves and placing these samples into a spectrophotometer, scientists can identify which wavelengths of light an organism can absorb. Additional methods for the identification of plant pigments include various types of chromatography that separate the pigments by their relative affinities to solid and mobile phases.

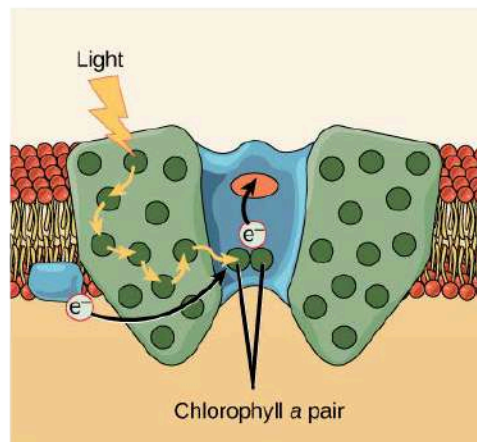
## How Light-Dependent Reactions Work

The overall function of light-dependent reactions is to convert solar energy into chemical energy in the form of NADPH and ATP. This chemical energy supports the light-independent reactions and fuels the assembly of sugar molecules. The light-dependent reactions are depicted in **Figure 8.15**. Protein complexes and pigment molecules work together to produce NADPH and ATP.

(a) Photosystem II (P680)



(b) Photosystem I (P700)

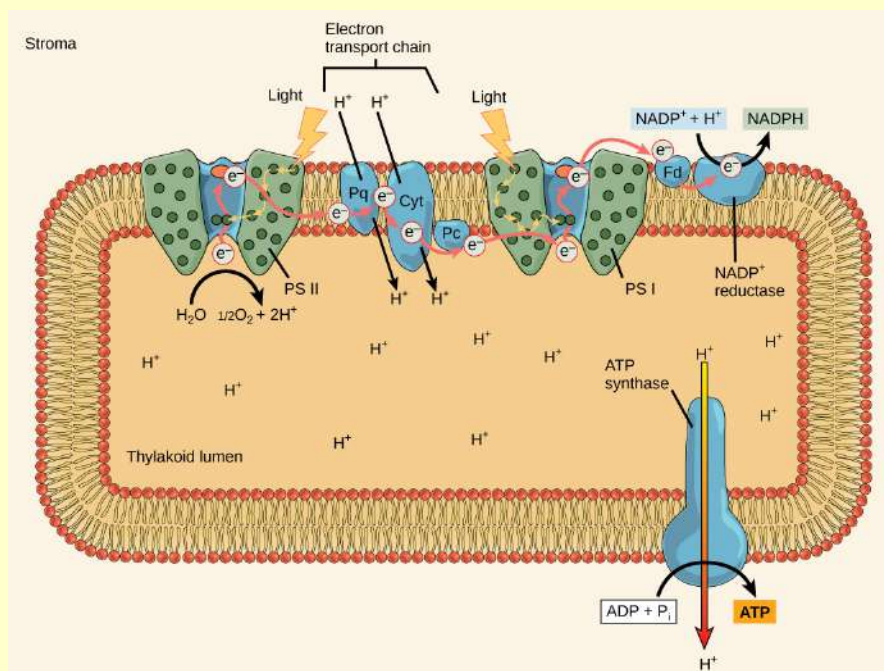


**Figure 8.15** A photosystem consists of a light-harvesting complex and a reaction center. Pigments in the light-harvesting complex pass light energy to two special chlorophyll *a* molecules in the reaction center. The light excites an electron from the chlorophyll *a* pair, which passes to the primary electron acceptor. The excited electron must then be replaced. In (a) photosystem II, the electron comes from the splitting of water, which releases oxygen as a waste product. In (b) photosystem I, the electron comes from the chloroplast electron transport chain discussed below.

The actual step that converts light energy into chemical energy takes place in a multiprotein complex called a **photosystem**, two types of which are found embedded in the thylakoid membrane, **photosystem II** (PSII) and **photosystem I** (PSI) (**Figure 8.16**). The two complexes differ on the basis of what they oxidize (that is, the source of the low-energy electron supply) and what they reduce (the place to which they deliver their energized electrons).

Both photosystems have the same basic structure; a number of **antenna proteins** to which the chlorophyll molecules are bound surround the **reaction center** where the photochemistry takes place. Each photosystem is serviced by the **light-harvesting complex**, which passes energy from sunlight to the reaction center; it consists of multiple antenna proteins that contain a mixture of 300–400 chlorophyll *a* and *b* molecules as well as other pigments like carotenoids. The absorption of a single **photon** or distinct quantity or “packet” of light by any of the chlorophylls pushes that molecule into an excited state. In short, the light energy has now been captured by biological molecules but is not stored in any useful form yet. The energy is transferred from chlorophyll to chlorophyll until eventually (after about a millionth of a second), it is delivered to the reaction center. Up to this point, only energy has been transferred between molecules, not electrons.

# visual CONNECTION



**Figure 8.16** In the photosystem II (PSII) reaction center, energy from sunlight is used to extract electrons from water. The electrons travel through the chloroplast electron transport chain to photosystem I (PSI), which reduces  $\text{NADP}^+$  to  $\text{NADPH}$ . The electron transport chain moves protons across the thylakoid membrane into the lumen. At the same time, splitting of water adds protons to the lumen, and reduction of  $\text{NADPH}$  removes protons from the stroma. The net result is a low pH in the thylakoid lumen, and a high pH in the stroma. ATP synthase uses this electrochemical gradient to make ATP.

What is the external source of the electrons that ultimately pass through photosynthetic electron transport chains?

- carbon dioxide
- $\text{NADPH}$
- oxygen
- water

The reaction center contains a pair of chlorophyll *a* molecules with a special property. Those two chlorophylls can undergo oxidation upon excitation; they can actually give up an electron in a process called a **photoact**. It is at this step in the reaction center, this step in photosynthesis, that light energy is converted into an excited electron. All of the subsequent steps involve getting that electron onto the energy carrier  $\text{NADPH}$  for delivery to the Calvin cycle where the electron is deposited onto carbon for long-term storage in the form of a carbohydrate. PSII and PSI are two major components of the photosynthetic **electron transport chain**, which also includes the **cytochrome complex**. The cytochrome complex, an enzyme composed of two protein complexes, transfers the electrons from the carrier molecule plastoquinone (Pq) to the protein plastocyanin (Pc), thus enabling both the transfer of protons across the thylakoid membrane and the transfer of electrons from PSII to PSI.

The reaction center of PSII (called **P680**) delivers its high-energy electrons, one at the time, to the **primary electron acceptor**, and through the electron transport chain (Pq to cytochrome complex to plastocyanine) to PSI. P680's missing electron is replaced by extracting a low-energy electron from water; thus, water is split and PSII is re-reduced after every photoact. Splitting one  $\text{H}_2\text{O}$  molecule releases two electrons, two hydrogen atoms, and one atom of oxygen. Splitting two molecules is required to form one molecule of diatomic  $\text{O}_2$  gas. About 10 percent of the oxygen is used by mitochondria in the leaf to support oxidative phosphorylation. The remainder escapes to the atmosphere where it is used by aerobic organisms to support respiration.

As electrons move through the proteins that reside between PSII and PSI, they lose energy. That energy is used to move hydrogen atoms from the stromal side of the membrane to the thylakoid lumen. Those hydrogen atoms, plus the ones produced by splitting water, accumulate in the thylakoid lumen and will be used to synthesize ATP in a later step. Because the electrons have lost energy prior to their arrival at PSI, they must be re-energized by PSI, hence, another photon is absorbed by the PSI antenna. That energy is relayed to the PSI reaction center (called **P700**). P700 is oxidized and sends a high-energy electron to  $\text{NADP}^+$  to form NADPH. Thus, PSII captures the energy to create proton gradients to make ATP, and PSI captures the energy to reduce  $\text{NADP}^+$  into NADPH. The two photosystems work in concert, in part, to guarantee that the production of NADPH will roughly equal the production of ATP. Other mechanisms exist to fine tune that ratio to exactly match the chloroplast's constantly changing energy needs.

## Generating an Energy Carrier: ATP

As in the intermembrane space of the mitochondria during cellular respiration, the buildup of hydrogen ions inside the thylakoid lumen creates a concentration gradient. The passive diffusion of hydrogen ions from high concentration (in the thylakoid lumen) to low concentration (in the stroma) is harnessed to create ATP, just as in the electron transport chain of cellular respiration. The ions build up energy because of diffusion and because they all have the same electrical charge, repelling each other.

To release this energy, hydrogen ions will rush through any opening, similar to water jetting through a hole in a dam. In the thylakoid, that opening is a passage through a specialized protein channel called the ATP synthase. The energy released by the hydrogen ion stream allows ATP synthase to attach a third phosphate group to ADP, which forms a molecule of ATP (**Figure 8.16**). The flow of hydrogen ions through ATP synthase is called chemiosmosis because the ions move from an area of high to an area of low concentration through a semi-permeable structure.



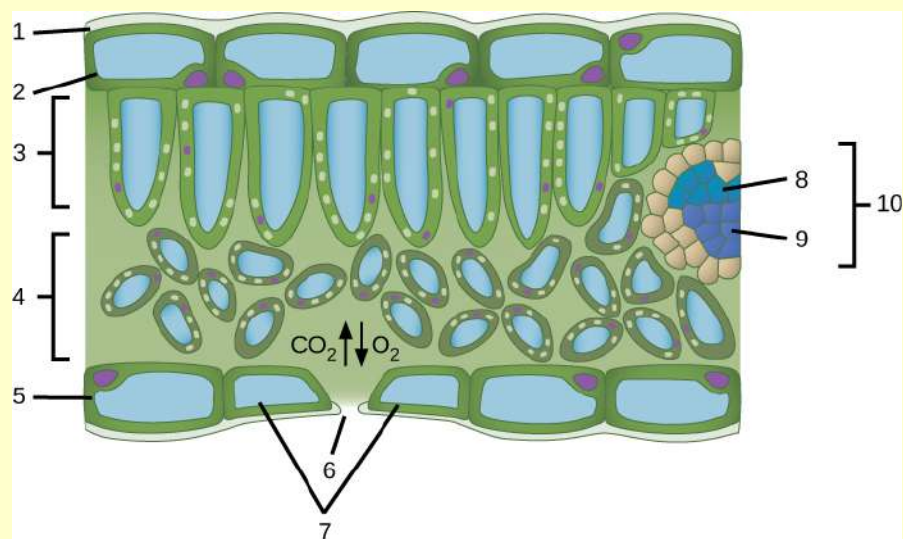
Visit this **site** ([http://openstaxcollege.org/l/light\\_reactions](http://openstaxcollege.org/l/light_reactions)) and click through the animation to view the process of photosynthesis within a leaf.

What role do electrons play in the formation of NADPH?

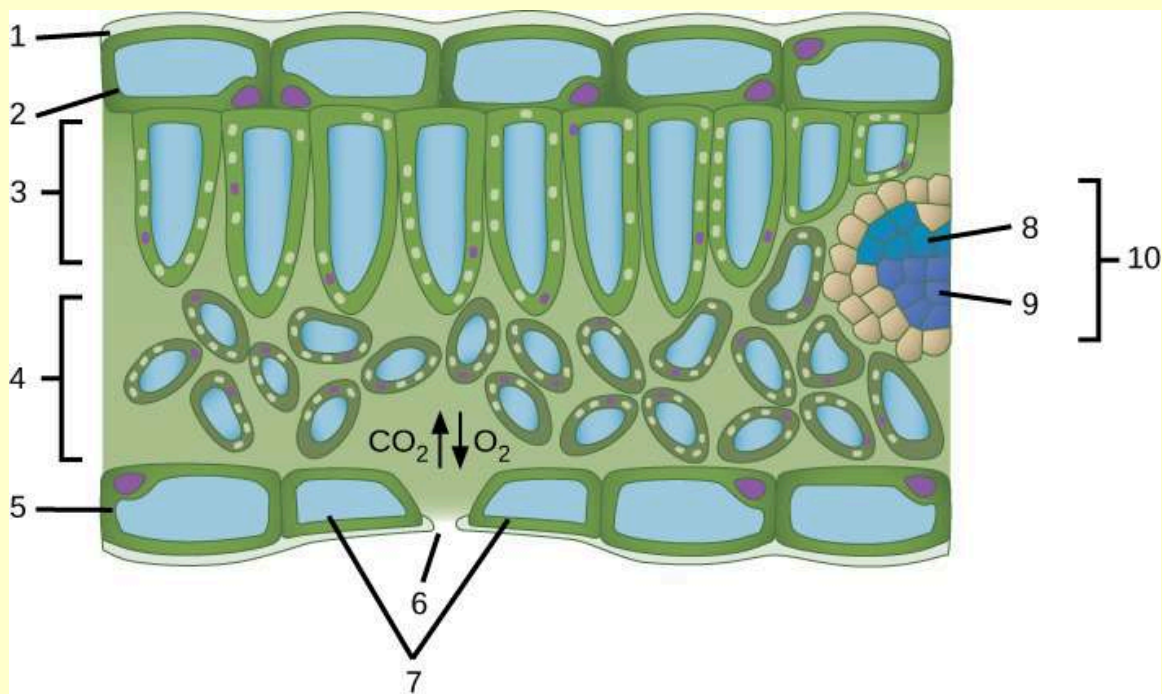
- Electrons from PS I cause the reduction of NADPH to  $\text{NADP}^+$  .
- Electrons from PSII cause the reduction of  $\text{NADP}^+$  to NADPH.
- Electrons from PS I cause the reduction of  $\text{NADP}^+$  to NADPH.
- Electrons are gained which causes the oxidation of  $\text{NADP}^+$  .



## everyday CONNECTION for AP<sup>®</sup> Courses



**Figure 8.17** The anatomy of a leaf. The cuticle and epidermis are the outer layers of the leaf and protect it from drying out. Chloroplasts are found in the mesophyll cells and are where photosynthesis occurs. Gas is exchanged through pores called stomata, which are opened and closed by the guard cells. Legend: 1) cuticle 2) upper epidermis 3) palisade mesophyll 4) spongy mesophyll 5) lower epidermis 6) stoma 7) guard cells 8) xylem 9) phloem 10) vascular bundle.



If the stomata were sealed, what would happen to oxygen ( $O_2$ ) and carbon dioxide ( $CO_2$ ) levels in a photosynthesizing leaf?

- $O_2$  levels would increase and  $CO_2$  levels would decrease.
- $CO_2$  levels would increase and  $O_2$  levels would decrease.



- c.  $O_2$  and  $CO_2$  levels would both decrease.
- d.  $O_2$  and  $CO_2$  levels would both increase.

## science practices CONNECTION for AP<sup>®</sup> Courses

### Think About It

On a hot, dry day, plants close their stomata to conserve water. Predict the impact of this on photosynthesis and justify your prediction.

## 8.3 | Using Light to Make Organic Molecules

In this section, you will explore the following questions:

- What are the reactions in the Calvin cycle described as the light-independent reactions?
- Why does the term “carbon fixation” describe the products of the Calvin cycle?
- What is the role of photosynthesis in the energy cycle of all living organisms?

### Connection for AP<sup>®</sup> Courses

The free energy stored in ATP and NADPH produced in the light-dependent reactions is used to power the chemical reactions of the light-independent reactions or Calvin cycle, which can occur during both the day and night. In the Calvin cycle, an enzyme called ribulose biphosphate carboxylase (RuBisCO), catalyzes a reaction with  $CO_2$  and another molecule called ribulose biphosphate (RuBP) that is regenerated from a previous Calvin cycle. After a series of chemical reactions, the carbon from carbon dioxide in the atmosphere is “fixed” into carbohydrates, specifically a three-carbon molecule called glyceraldehydes-3-phosphate (G3P). (Again, count the carbons as we explore the Calvin cycle.) After three turns of the cycle, a three-carbon molecule of G3P leaves the cycle to become part of a carbohydrate molecule. The remaining G3P molecules stay in the cycle to be regenerated into RuBP, which is then ready to react with more incoming  $CO_2$ . In other words, the cell generates a stockpile of G3P to be assembled into organic molecules, including carbohydrates. Each step of the Calvin cycle is catalyzed by specific enzymes. (You do not have to memorize the reactions of the Calvin cycle; however, if provided with a diagram of the cycle, you should be able to interpret it.) Some plants evolved chemical modifications to more efficiently trap  $CO_2$  if environmental conditions limit its availability. For example, when it’s hot outside, plants tend to keep their stomata closed to prevent excessive water loss; when the outside temperature cools, stomata open and plants take in  $CO_2$  and use a more efficient system to feed it into the Calvin cycle.

As we explored in Overview of Photosynthesis, photosynthesis forms an energy link with cellular respiration. Plants need both photosynthesis and respiration in order to conduct metabolic processes during both light and dark times. Therefore, plant cells contain both chloroplasts and mitochondria.

Information presented and the examples highlighted in the section, support concepts and learning objectives outlined in Big Idea 2 of the AP<sup>®</sup> Biology Curriculum Framework, as shown in the table. The learning objectives listed in the Curriculum Framework provide a transparent foundation for the AP<sup>®</sup> Biology course, an inquiry-based laboratory experience, instructional activities, and AP<sup>®</sup> exam questions. A learning objective merges required content with one or more of the seven science practices.

<b>Big Idea 2</b>	Biological systems utilize free energy and molecular building blocks to grow, to reproduce, and to maintain dynamic homeostasis.
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<b>Enduring Understanding 2.A</b>	Growth, reproduction and maintenance of living systems require free energy and matter.
<b>Essential Knowledge</b>	<b>2.A.2</b> Light energy captured in photosynthesis is stored in carbohydrates produced during the Calvin cycle.
<b>Science Practice</b>	<b>1.4</b> The student can use representations and models to analyze situations or solve problems qualitatively and quantitatively.
<b>Learning Objective</b>	<b>2.4</b> The student is able to use representations to pose scientific questions about what mechanisms and structural features allow organisms to capture, store, and use free energy.
<b>Essential Knowledge</b>	<b>2.A.2</b> Light energy captured in photosynthesis is stored in carbohydrates produced during the Calvin cycle
<b>Science Practice</b>	<b>6.2</b> The student can construct explanations of phenomena based on evidence produced through scientific practices.
<b>Learning Objective</b>	<b>2.5</b> The student is able to construct explanations of the mechanisms and structural features of cells that allow organisms to capture, store, or use free energy.

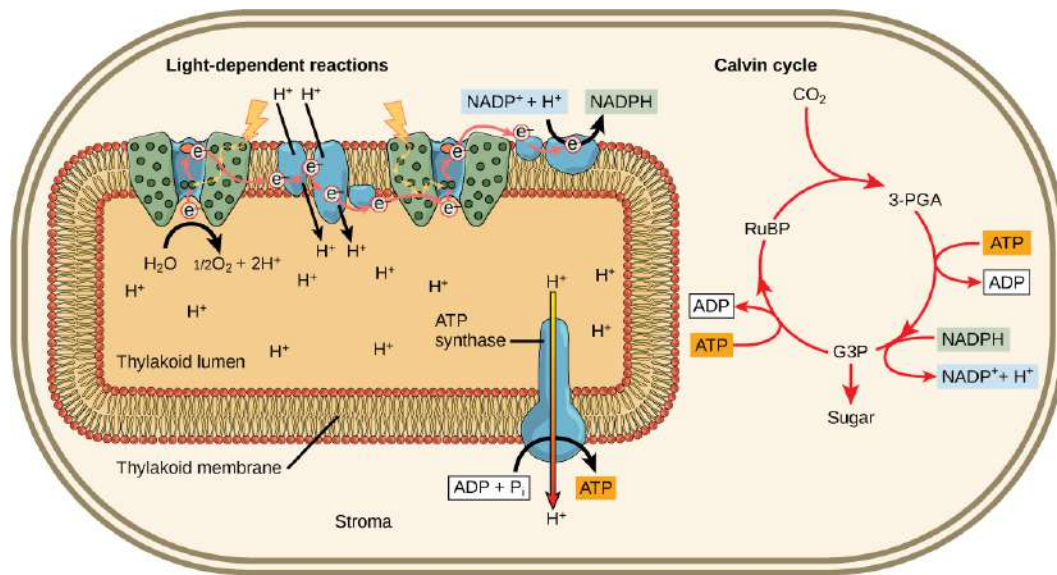
The Science Practice Challenge Questions contain additional test questions for this section that will help you prepare for the AP exam. These questions address the following standards:

[APLO 2.5][APLO 2.11][APLO 4.17]

## The Calvin Cycle

After the energy from the sun is converted into chemical energy and temporarily stored in ATP and NADPH molecules, the cell has the fuel needed to build carbohydrate molecules for long-term energy storage. The products of the light-dependent reactions, ATP and NADPH, have lifespans in the range of millionths of seconds, whereas the products of the light-independent reactions (carbohydrates and other forms of reduced carbon) can survive for hundreds of millions of years. The carbohydrate molecules made will have a backbone of carbon atoms. Where does the carbon come from? It comes from carbon dioxide, the gas that is a waste product of respiration in microbes, fungi, plants, and animals.

In plants, carbon dioxide (CO<sub>2</sub>) enters the leaves through stomata, where it diffuses over short distances through intercellular spaces until it reaches the mesophyll cells. Once in the mesophyll cells, CO<sub>2</sub> diffuses into the stroma of the chloroplast—the site of light-independent reactions of photosynthesis. These reactions actually have several names associated with them. Another term, the **Calvin cycle**, is named for the man who discovered it, and because these reactions function as a cycle. Others call it the Calvin-Benson cycle to include the name of another scientist involved in its discovery. The most outdated name is dark reactions, because light is not directly required (**Figure 8.18**). However, the term dark reaction can be misleading because it implies incorrectly that the reaction only occurs at night or is independent of light, which is why most scientists and instructors no longer use it.



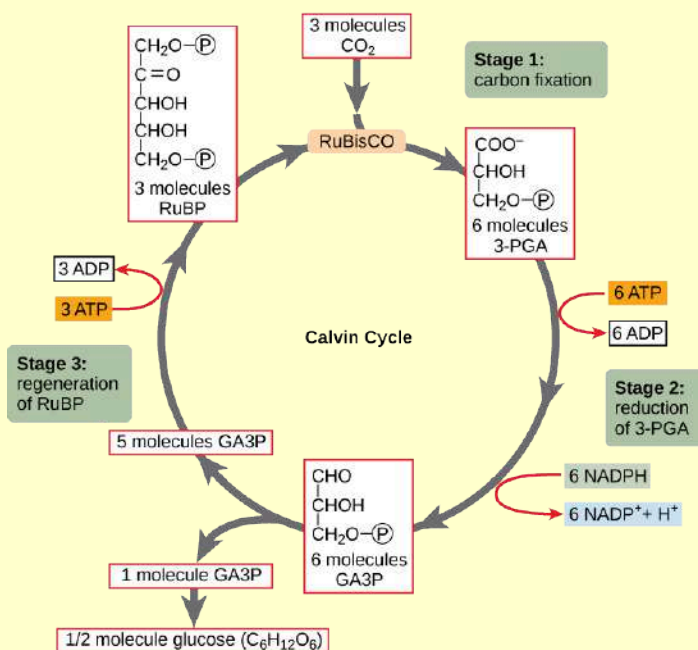
**Figure 8.18** Light reactions harness energy from the sun to produce chemical bonds, ATP, and NADPH. These energy-carrying molecules are made in the stroma where carbon fixation takes place.

The light-independent reactions of the Calvin cycle can be organized into three basic stages: fixation, reduction, and regeneration.

### Stage 1: Fixation

In the stroma, in addition to  $\text{CO}_2$ , two other components are present to initiate the light-independent reactions: an enzyme called ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO), and three molecules of ribulose bisphosphate (RuBP), as shown in **Figure 8.19**. RuBP has five atoms of carbon, flanked by two phosphates.

# visual CONNECTION



**Figure 8.19** The Calvin cycle has three stages. In stage 1, the enzyme RuBisCO incorporates carbon dioxide into an organic molecule, 3-PGA. In stage 2, the organic molecule is reduced using electrons supplied by NADPH. In stage 3, RuBP, the molecule that starts the cycle, is regenerated so that the cycle can continue. Only one carbon dioxide molecule is incorporated at a time, so the cycle must be completed three times to produce a single three-carbon GA3P molecule, and six times to produce a six-carbon glucose molecule.

Which of the following statements is true?

- In photosynthesis, oxygen, carbon dioxide, ATP and NADPH are reactants. GA3P and water are products.
- In photosynthesis, chlorophyll, water and carbon dioxide are reactants. GA3P and oxygen are products.
- In photosynthesis, water, carbon dioxide, ATP and NADPH are reactants. RuBP and oxygen are products.
- In photosynthesis, water and carbon dioxide are reactants. GA3P and oxygen are products.

RuBisCO catalyzes a reaction between  $\text{CO}_2$  and RuBP. For each  $\text{CO}_2$  molecule that reacts with one RuBP, two molecules of another compound (3-PGA) form. PGA has three carbons and one phosphate. Each turn of the cycle involves only one RuBP and one carbon dioxide and forms two molecules of 3-PGA. The number of carbon atoms remains the same, as the atoms move to form new bonds during the reactions (3 atoms from  $3\text{CO}_2 + 15$  atoms from  $3\text{RuBP} = 18$  atoms in 3 atoms of 3-PGA). This process is called **carbon fixation**, because  $\text{CO}_2$  is “fixed” from an inorganic form into organic molecules.

## Stage 2: Reduction

ATP and NADPH are used to convert the six molecules of 3-PGA into six molecules of a chemical called glyceraldehyde 3-phosphate (G3P). That is a reduction reaction because it involves the gain of electrons by 3-PGA. Recall that a **reduction** is the gain of an electron by an atom or molecule. Six molecules of both ATP and NADPH are used. For ATP, energy is released with the loss of the terminal phosphate atom, converting it into ADP; for NADPH, both energy and a hydrogen atom are lost, converting it into  $\text{NADP}^+$ . Both of these molecules return to the nearby light-dependent reactions to be reused and reenergized.

## Stage 3: Regeneration

Interestingly, at this point, only one of the G3P molecules leaves the Calvin cycle and is sent to the cytoplasm to contribute to the formation of other compounds needed by the plant. Because the G3P exported from the chloroplast has three carbon atoms, it takes three “turns” of the Calvin cycle to fix enough net carbon to export one G3P. But each turn makes two G3Ps, thus three turns make six G3Ps. One is exported while the remaining five G3P molecules remain in the cycle and are used

to regenerate RuBP, which enables the system to prepare for more  $\text{CO}_2$  to be fixed. Three more molecules of ATP are used in these regeneration reactions.



This [link \(http://openstaxcollege.org/l/calvin\\_cycle\)](http://openstaxcollege.org/l/calvin_cycle) leads to an animation of the Calvin cycle. Click stage 1, stage 2, and then stage 3 to see G3P and ATP regenerate to form RuBP.

Explain why the process of producing glucose in plants is a cycle.

- Three RuBP molecules get converted to three G3P, and two G3P molecules with the help of three ATPs are converted back to three molecules of RuBP.
- Three RuBP molecules get converted to six G3P, and five G3P molecules with the help of three ATPs are converted back to three molecules of RuBP.
- Three RuBP molecules get converted to five G3P, and three G3P molecules with the help of three ATPs are converted back to three molecules of RuBP.
- Three RuBP molecules get converted to six G3P, and five G3P molecules with the help of five ATPs are converted back to three molecules of RuBP.



## e<sup>l</sup>olution CONNECTION



**Figure 8.20** The harsh conditions of the desert have led plants like these cacti to evolve variations of the light-independent reactions of photosynthesis. These variations increase the efficiency of water usage, helping to conserve water and energy. (credit: Piotr Wojtkowski)

Which of the following events is associated with the development of oxygenic photosynthesis?

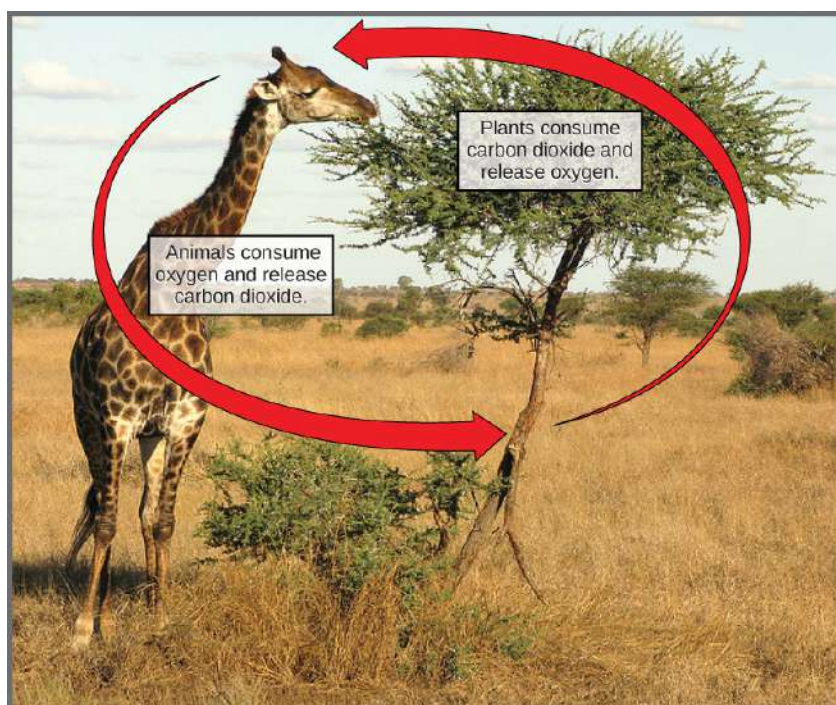
- a. Photosynthetic organisms began to use NADPH and ATP as an energy source.
- b. Photosynthetic organisms evolved from single-celled bacteria into multicellular plants.
- c. Photosynthetic organisms began to use two photosystems instead of one.
- d. Photosynthetic organisms began to use light reactions as well as dark reactions.

## The Energy Cycle

Whether the organism is a bacterium, plant, or animal, all living things access energy by breaking down carbohydrate molecules. But if plants make carbohydrate molecules, why would they need to break them down, especially when it has been shown that the gas organisms release as a “waste product” ( $\text{CO}_2$ ) acts as a substrate for the formation of more food in photosynthesis? Remember, living things need energy to perform life functions. In addition, an organism can either make its own food or eat another organism—either way, the food still needs to be broken down. Finally, in the process of breaking down food, called cellular respiration, heterotrophs release needed energy and produce “waste” in the form of  $\text{CO}_2$  gas.

In nature, there is no such thing as waste. Every single atom of matter and energy is conserved, recycling over and over infinitely. Substances change form or move from one type of molecule to another, but their constituent atoms never disappear. (**Figure 1.21** is an illustrative example of this process.)

$\text{CO}_2$  is no more a form of waste than oxygen is wasteful to photosynthesis. Both are byproducts of reactions that move on to other reactions. Photosynthesis absorbs light energy to build carbohydrates in chloroplasts, and aerobic cellular respiration releases energy by using oxygen to metabolize carbohydrates in the cytoplasm and mitochondria. Both processes use electron transport chains to capture the energy necessary to drive other reactions. These two powerhouse processes, photosynthesis and cellular respiration, function in biological, cyclical harmony to allow organisms to access life-sustaining energy that originates millions of miles away in a burning star humans call the sun.



**Figure 8.21** Photosynthesis consumes carbon dioxide and produces oxygen. Aerobic respiration consumes oxygen and produces carbon dioxide. These two processes play an important role in the carbon cycle. (credit: modification of work by Stuart Bassil)

## everyday CONNECTION for AP<sup>®</sup> Courses

Photosynthesis and aerobic respiration are interrelated in important ways. During photosynthesis, plants take in carbon dioxide and water. The water molecule is split, the oxygen is released into the atmosphere, and the carbon dioxide is used to build carbohydrates. During aerobic respiration, organisms take in water and oxygen for respiration and produce carbon dioxide.

The Earth did not contain oxygen in its atmosphere throughout much of its history, even after life on Earth had already begun. It did, however, contain carbon dioxide. What does this suggest about when photosynthetic organisms evolved, relative to non-photosynthetic organisms, and why?

- Photosynthetic organisms evolved before non-photosynthetic organisms because no oxygen was present in the atmosphere when life began.
- Photosynthetic organisms evolved after non-photosynthetic organisms because no oxygen was present in the atmosphere when life began.
- Non-photosynthetic organisms evolved before photosynthetic organisms because no oxygen was present in the atmosphere when life began.
- Photosynthetic organisms evolved before non-photosynthetic organisms because no oxygen was present in the atmosphere when life began.

## science practices CONNECTION for AP<sup>®</sup> Courses

### Activity

Create a model or diagram to show the links between photosynthesis and cellular respiration.

### Think About It

What cellular features and processes are similar in both respiration and photosynthesis?

## KEY TERMS

**absorption spectrum** range of wavelengths of electromagnetic radiation absorbed by a given substance

**antenna protein** pigment molecule that directly absorbs light and transfers the energy absorbed to other pigment molecules

**Calvin cycle** light-independent reactions of photosynthesis that convert carbon dioxide from the atmosphere into carbohydrates using the energy and reducing power of ATP and NADPH

**carbon fixation** process of converting inorganic CO<sub>2</sub> gas into organic compounds

**carotenoid** photosynthetic pigment that functions to dispose of excess energy

**chemoautotroph** organism that can build organic molecules using energy derived from inorganic chemicals instead of sunlight

**chlorophyll a** form of chlorophyll that absorbs violet-blue and red light and consequently has a bluish-green color; the only pigment molecule that performs the photochemistry by getting excited and losing an electron to the electron transport chain

**chlorophyll b** accessory pigment that absorbs blue and red-orange light and consequently has a yellowish-green tint

**chloroplast** organelle in which photosynthesis takes place

**cytochrome complex** group of reversibly oxidizable and reducible proteins that forms part of the electron transport chain between photosystem II and photosystem I

**electromagnetic spectrum** range of all possible frequencies of radiation

**electron transport chain** group of proteins between PSII and PSI that pass energized electrons and use the energy released by the electrons to move hydrogen ions against their concentration gradient into the thylakoid lumen

**granum** stack of thylakoids located inside a chloroplast

**heterotroph** organism that consumes organic substances or other organisms for food

**light harvesting complex** complex that passes energy from sunlight to the reaction center in each photosystem; it consists of multiple antenna proteins that contain a mixture of 300–400 chlorophyll *a* and *b* molecules as well as other pigments like carotenoids

**light-dependent reaction** first stage of photosynthesis where certain wavelengths of the visible light are absorbed to form two energy-carrying molecules (ATP and NADPH)

**light-independent reaction** second stage of photosynthesis, though which carbon dioxide is used to build carbohydrate molecules using energy from ATP and NADPH

**mesophyll** middle layer of chlorophyll-rich cells in a leaf

**P680** reaction center of photosystem II

**P700** reaction center of photosystem I

**photoact** ejection of an electron from a reaction center using the energy of an absorbed photon

**photoautotroph** organism capable of producing its own organic compounds from sunlight

**photon** distinct quantity or “packet” of light energy

**photosystem** group of proteins, chlorophyll, and other pigments that are used in the light-dependent reactions of photosynthesis to absorb light energy and convert it into chemical energy

**photosystem I** integral pigment and protein complex in thylakoid membranes that uses light energy to transport electrons

from plastocyanin to  $\text{NADP}^+$  (which becomes reduced to NADPH in the process)

**photosystem II** integral protein and pigment complex in thylakoid membranes that transports electrons from water to the electron transport chain; oxygen is a product of PSII

**pigment** molecule that is capable of absorbing certain wavelengths of light and reflecting others (which accounts for its color)

**primary electron acceptor** pigment or other organic molecule in the reaction center that accepts an energized electron from the reaction center

**reaction center** complex of chlorophyll molecules and other organic molecules that is assembled around a special pair of chlorophyll molecules and a primary electron acceptor; capable of undergoing oxidation and reduction

**reduction** gain of electron(s) by an atom or molecule

**spectrophotometer** instrument that can measure transmitted light and compute the absorption

**stoma** opening that regulates gas exchange and water evaporation between leaves and the environment, typically situated on the underside of leaves

**stroma** fluid-filled space surrounding the grana inside a chloroplast where the light-independent reactions of photosynthesis take place

**thylakoid** disc-shaped, membrane-bound structure inside a chloroplast where the light-dependent reactions of photosynthesis take place; stacks of thylakoids are called grana

**thylakoid lumen** aqueous space bound by a thylakoid membrane where protons accumulate during light-driven electron transport

**wavelength** distance between consecutive points of equal position (two crests or two troughs) of a wave in a graphic representation; inversely proportional to the energy of the radiation

## CHAPTER SUMMARY

### 8.1 Overview of Photosynthesis

The process of photosynthesis transformed life on Earth. By harnessing energy from the sun, the evolution of photosynthesis allowed living things access to enormous amounts of energy. Because of photosynthesis, living things gained access to sufficient energy that allowed them to build new structures and achieve the biodiversity evident today.

Only certain organisms, called photoautotrophs, can perform photosynthesis; they require the presence of chlorophyll, a specialized pigment that absorbs certain portions of the visible spectrum and can capture energy from sunlight. Photosynthesis uses carbon dioxide and water to assemble carbohydrate molecules and release oxygen as a waste product into the atmosphere. Eukaryotic autotrophs, such as plants and algae, have organelles called chloroplasts in which photosynthesis takes place, and starch accumulates. In prokaryotes, such as cyanobacteria, the process is less localized and occurs within folded membranes, extensions of the plasma membrane, and in the cytoplasm.

### 8.2 The Light-Dependent Reaction of Photosynthesis

The pigments of the first part of photosynthesis, the light-dependent reactions, absorb energy from sunlight. A photon strikes the antenna pigments of photosystem II to initiate photosynthesis. The energy travels to the reaction center that contains chlorophyll *a* and then to the electron transport chain, which pumps hydrogen ions into the thylakoid interior. This action builds up a high concentration of ions. The ions flow through ATP synthase via chemiosmosis to form molecules of ATP, which are used for the formation of sugar molecules in the second stage of photosynthesis. Photosystem I absorbs a second photon, which results in the formation of an NADPH molecule, another energy and reducing power carrier for the light-independent reactions.

### 8.3 Using Light to Make Organic Molecules

Using the energy carriers formed in the first steps of photosynthesis, the light-independent reactions, or the Calvin cycle, take in  $\text{CO}_2$  from the environment. An enzyme, RuBisCO, catalyzes a reaction with  $\text{CO}_2$  and another molecule, RuBP.



After three cycles, a three-carbon molecule of G3P leaves the cycle to become part of a carbohydrate molecule. The remaining G3P molecules stay in the cycle to be regenerated into RuBP, which is then ready to react with more  $\text{CO}_2$ . Photosynthesis forms an energy cycle with the process of cellular respiration. Plants need both photosynthesis and respiration for their ability to function in both the light and dark, and to be able to interconvert essential metabolites. Therefore, plants contain both chloroplasts and mitochondria.

## REVIEW QUESTIONS

- Which of the following components is not used by both plants and cyanobacteria to carry out photosynthesis?
  - carbon dioxide
  - chlorophyll
  - chloroplasts
  - water
- Why are chemoautotrophs not considered the same as photoautotrophs if they both extract energy and make sugars?
  - Chemoautotrophs use wavelengths of light not available to photoautotrophs.
  - Chemoautotrophs extract energy from inorganic chemical compounds.
  - Photoautotrophs prefer the blue side of the visible light spectrum.
  - Photoautotrophs make glucose, while chemoautotrophs make galactose.
- In which compartment of the plant cell do the light-independent reactions of photosynthesis take place?
  - mesophyll
  - outer membrane
  - stroma
  - thylakoid
- What is a part of grana?
  - the Calvin cycle
  - the inner membrane
  - stroma
  - thylakoids
- What are two major products of photosynthesis?
  - chlorophyll and oxygen
  - oxygen and carbon dioxide
  - sugars/carbohydrates and oxygen
  - sugars/carbohydrates and carbon dioxide
- What is the primary energy source for cells?
  - glucose
  - starch
  - sucrose
  - triglycerides
- Which portion of the electromagnetic radiation originating from the sun is harmful to living tissues?
  - blue
  - green
  - infrared
  - ultraviolet
- The amount of energy in a wave can be measured using what trait?
  - color intensity
  - distance from trough to crest
  - the amount of sugar produced
  - wavelength
- What portion of the electromagnetic radiation emitted by the sun has the least energy?
  - gamma
  - infrared
  - radio
  - X-rays
- What is the function of carotenoids in photosynthesis?
  - They supplement chlorophyll absorption.
  - They are visible in the fall during leaf color changes.
  - They absorb excess energy and dissipate it as heat.
  - They limit chlorophyll absorption.
- Which of the following structures is not a component of a photosystem?
  - antenna molecule
  - ATP synthase
  - primary electron acceptor
  - reaction center
- Which complex is not involved in producing the electromotive force of ATP synthesis?
  - ATP synthase
  - cytochrome complex
  - Photosystem I
  - Photosystem II
- What can be calculated from a wavelength

measurement of light?

- a. a specific portion of the visible spectrum
- b. color intensity
- c. the amount of energy of a wave of light
- d. the distance from trough to crest of the wave

**14.** Which molecule must enter the Calvin cycle continually for the light-independent reactions to take place?

- a.  $\text{CO}_2$
- b. RuBisCO
- c. RuBP
- d. 3-PGA

**15.** Which order of molecular conversions is correct for the Calvin cycle?

- a.  $\text{RuBP} + \text{G3P} \rightarrow 3\text{-PGA} \rightarrow \text{sugar}$
- b.  $\text{RuBisCO} \rightarrow \text{CO}_2 \rightarrow \text{RuBP} \rightarrow \text{G3P}$
- c.  $\text{RuBP} + \text{CO}_2 \rightarrow [\text{RuBisCO}]3\text{-PGA} \rightarrow \text{G3P}$
- d.  $\text{CO}_2 \rightarrow 3\text{-PGA} \rightarrow \text{RuBP} \rightarrow \text{G3P}$

**16.** Which statement correctly describes carbon fixation?

- a. the conversion of  $\text{CO}_2$  into an organic compound
- b. the use of RuBisCO to form 3-PGA
- c. the production of carbohydrate molecules from G3P
- d. the use of ATP and NADPH to reduce  $\text{CO}_2$

**17.** Which substance catalyzes carbon fixation?

- a. 3-PGA
- b. NADPH
- c. RuBisCO
- d. RuBP

**18.** Which pathway is used by both plants and animals?

- a. carbon fixation
- b. cellular respiration
- c. photosystem II
- d. photosynthesis

**19.** Which of the following organisms is a heterotroph?

- a. Cyanobacterium
- b. intestinal bacteria
- c. kelp
- d. pond algae

**20.** What is the role of ribulose-1,5-bisphosphate, abbreviated RuBisCO, in photosynthesis?

- a. It catalyzes the reaction between  $\text{CO}_2$  and ribulose bisphosphate (RuBP).
- b. It catalyzes the reaction that produces glyceraldehyde-3-phosphate (G3P).
- c. It catalyzes the reaction that regenerates RuBP.
- d. It catalyzes the reaction utilizing ATP and NADPH.

**21.** What is the product of the Calvin cycle?

- a. Glucose
- b. Glyceraldehyde-3-Phosphate
- c. Phosphoglycerate (PGA)
- d. sucrose

## CRITICAL THINKING QUESTIONS

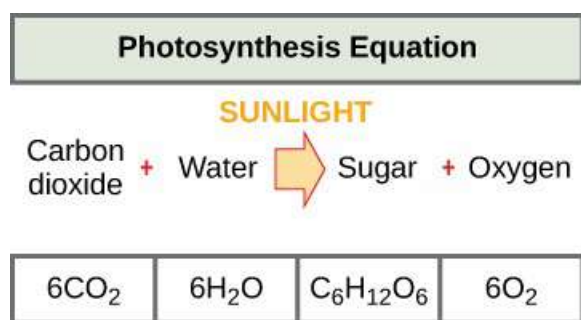
**22.** What are the roles of ATP and NADPH in photosynthesis?

- a. ATP and NADPH are forms of chemical energy produced from the light dependent reactions to be used in the light independent reactions that produce sugars.
- b. ATP and NADPH are forms of chemical energy produced from the light independent reactions, to be used in the light dependent reactions that produce sugars.
- c. ATP and NADPH are forms of chemical energy produced from the light dependent reactions to be used in the light independent reactions that produce proteins.
- d. ATP and NADPH are forms of chemical energy produced from the light dependent reactions to be used in the light independent reactions that use sugars as reactants.

23. What is the overall outcome of the light reactions in photosynthesis?

- NADPH and ATP molecules are produced during the light reactions and are used to power the light independent reactions.
- NADPH and ATP molecules are produced during the light reactions, which are used to power the light dependent reactions.
- Sugar and ATP are produced during the light reactions, which are used to power the light independent reactions.
- Carbon dioxide and NADPH are produced during the light reactions, which are used to power the light dependent reactions.

24.



How does the equation relate to both photosynthesis and cellular respiration?

- Photosynthesis utilizes energy to build carbohydrates while cellular respiration metabolizes carbohydrates.
- Photosynthesis utilizes energy to metabolize carbohydrates while cellular respiration builds carbohydrates.
- Photosynthesis and cellular respiration both utilize carbon dioxide and water to produce carbohydrates.
- Photosynthesis and cellular respiration both metabolize carbohydrates to produce carbon dioxide and water.

25. How is the energy from the sun transported within chloroplasts?

- When photons strike photosystem (PS) II, pigments pass the light energy to chlorophyll a molecules that excite an electron, which is then passed to the electron transport chain. The cytochrome complex transfers protons across the thylakoid membrane and transfers electrons from PS-II to PS-I. The products of the light dependent reaction are used to power the Calvin cycle to produce glucose.
- When photons strike photosystem (PS) I, pigments pass the light energy to chlorophyll molecules that excite electrons, which is then passed to the electron transport chain. The cytochrome complex then transfers protons across the thylakoid membrane and transfers electrons from PS-II to PS-I. The products of the light dependent reaction are used to power the Calvin cycle to produce glucose.
- When photons strike photosystem (PS) II, pigments pass the light energy to chlorophyll molecules that in turn excite electrons, which are then passed to the electron transport chain. The cytochrome complex transfers protons across the thylakoid membrane and transfers electrons from PS-I to PS-II. The products of the light dependent reaction are used to power the Calvin cycle to produce glucose.
- When photons strike photosystem (PS) II, pigments pass the light energy to chlorophyll molecules that excite electrons, which is then passed to the electron transport chain. The cytochrome complex transfers protons across the thylakoid membrane and transfers electrons from PS II to PS I. The products of the light independent reaction are used to power the Calvin cycle to produce glucose.

26. Explain why X-rays and ultraviolet light wavelengths are dangerous to living tissues.

- UV and X-rays are high energy waves that penetrate the tissues and damage cells.
- UV and X-rays are low energy waves that penetrate the tissues and damage cells.
- UV and X-rays cannot penetrate tissues and thus damage the cells.
- UV and X-rays can penetrate tissues and thus do not damage the cells.

27. If a plant were to be exposed to only red light, would photosynthesis be possible?

- Photosynthesis does not take place.
- The rate of photosynthesis increases sharply.
- The rate of photosynthesis decreases drastically.
- The rate of photosynthesis decreases and then increases.

**28.** Describe the electron transfer pathway from photosystem II to photosystem I in the light-dependent reactions.

- After splitting water in PS-II, high energy electrons are delivered through the chloroplast electron transport chain to PS-I.
- After splitting water in PS-I, high energy electrons are delivered through the chloroplast electron transport chain to PS-II.
- After the photosynthesis reaction, the released products like glucose help in the transfer of electrons from PS-II to PS-I.
- After the completion of the light dependent reactions, the electrons are transferred from PS-II to PS-I.

**29.** What will happen to a plant leaf that loses  $\text{CO}_2$  too quickly?

- no effect on the rate of photosynthesis
- Photosynthesis will slow down or stop possibly.
- Photosynthesis will increase exponentially.
- Photosynthesis will decrease and then increase.

**30.** Carbon, in the form of  $\text{CO}_2$ , must be taken from the atmosphere and attached to an existing organic molecule in the Calvin cycle. Therefore, the carbon is bound to the molecule. The products of the cycle only occur because of the added carbon. What are the products of the Calvin cycle and what is regenerated?

- The product of the Calvin cycle is glyceraldehyde-3 phosphate and RuBP is regenerated.
- The product of the Calvin cycle is glyceraldehyde-3 phosphate and RuBisCO is regenerated.
- The product of the Calvin cycle is a 3-PGA molecule and glyceraldehyde-3 phosphate is regenerated.
- The product of the Calvin cycle is glyceraldehyde-3 phosphate and oxygen is regenerated.

**31.** How do desert plants prevent water loss from the heat, which would compromise photosynthesis?

- by using CAM photosynthesis and by closing stomatal pores during the night
- by using CAM photosynthesis and by opening of stomatal pores during the night
- by using CAM photosynthesis and by keeping stomatal pores closed at all times
- by bypassing CAM photosynthesis and by keeping stomatal pores closed at night

**32.** Why are carnivores, such as lions, dependent on photosynthesis to survive?

- because the prey of lions are generally herbivores which depend on heterotrophs
- because the prey of lions are generally smaller carnivorous animals which depend on non-photosynthetic organisms
- because the prey of lions are generally herbivores which depend on autotrophs
- because the prey of lions are generally omnivores that depend only on autotrophs.

**33.** Why does it take three turns of the Calvin cycle to produce G3P, the initial product of photosynthesis?

- To fix enough carbon to export one G3P molecule.
- To fix enough oxygen to export one G3P molecule.
- To produce RuBisCO as an end product.
- To produce ATP and NADPH for fixation of G3P.

## TEST PREP FOR AP® COURSES

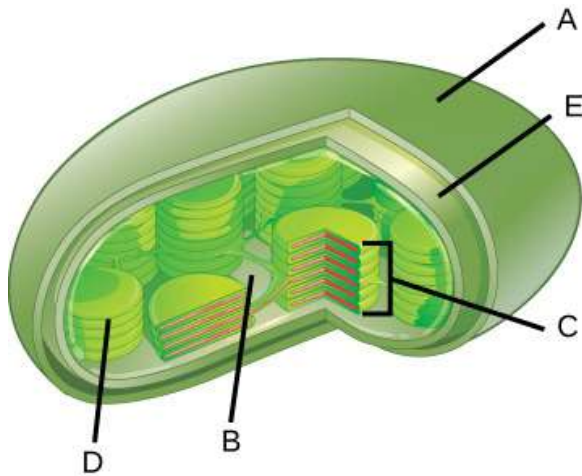
**34.** Photosynthesis and cellular respiration are found throughout the eukaryotic world. They are complementary to each other because they each use products of the other process. What do the two pathways share?

- chloroplasts and mitochondria
- Photosystems I and II
- the cytochrome complex
- thylakoids

**35.** What evidence exists that the evolution of photosynthesis and cellular respiration support the concept that there is a common ancestry for all organisms?

- a. All organisms perform cellular respiration, using oxygen and glucose, which are produced by photosynthesis.
- b. All organisms perform cellular respiration using carbon dioxide and glucose, which are produced by photosynthesis.
- c. All organisms perform cellular respiration using oxygen and lipids, which are produced by photosynthesis.
- d. All organisms perform cellular respiration using carbon dioxide and lipids, which are produced by photosynthesis.

36.



Correctly label the indicated parts of a chloroplast.

- a. A. stroma, B. outer membrane, C. granum, D. thylakoid, E. inner membrane
- b. A. outer membrane, B. stroma, C. granum, D. thylakoid, E. inner membrane
- c. A. outer membrane, B. stroma, C. granum, D. inner membrane, E. thylakoid
- d. A. stroma, B. outer membrane, C. inner membrane, D. granum, E. thylakoid

37. What cellular features and processes are similar in both photosynthesis and cellular respiration?

- a. Both processes are contained in organelles with single membranes, and both use a version of the cytochrome complex.
- b. Both processes are contained in organelles with double membranes, and neither use a version of the cytochrome complex.
- c. Both processes are contained in organelles with double membranes, and use a version of the cytochrome complex.
- d. Both processes are contained in organelles with single membranes, and neither use a version of the cytochrome complex.

38. Why do the light-dependent reactions of photosynthesis take place in the thylakoid?

- a. Photosystem I is anchored to the membrane, but not photosystem II.
- b. The cytochrome complex requires a membrane for chemiosmosis to occur.
- c. The light-dependent reactions depend on the presence of carbon dioxide.
- d. Light energy is absorbed by the thylakoid membrane.

39. Metabolic pathways both produce and use energy to perform their reactions. How does the Calvin cycle help to harness, store, and use energy in its pathway?

- a. The Calvin cycle harnesses energy in the form of 6 ATP and 6 NADPH that are used to produce Fructose-3- phosphate (F3P) molecules. These store the energy captured from photosynthesis. The cycle uses this energy to regenerate RuBP.
- b. The Calvin cycle harnesses energy in the form of 6 ATP and 6 NADPH that are used to produce Glyceraldehyde-3- phosphate (GA3P) molecules. These store the energy captured from photosynthesis. The cycle uses this energy to regenerate RuBP.
- c. The Calvin cycle harnesses energy in the form of 3 ATP and 3 NADPH that are used to produce Glyceraldehyde-3- phosphate (GA3P) molecules. These store the energy captured from photosynthesis. The cycle uses this energy to regenerate the RuBP.
- d. The Calvin cycle harnesses energy in the form of 6 ATP and 3 NADPH that are used to produce Glyceraldehyde-3- phosphate (GA3P) molecules. These store energy captured from photosynthesis. The cycle uses this energy to regenerate RuBP.

40. Based on **Figure 8.18**, which would most likely cause a plant to run out of NADP?

- a. missing the ATP synthase enzyme
- b. exposure to light
- c. A lack of water would prevent  $H^+$  and  $NADP^+$  from forming NADPH
- d. not enough  $CO_2$

41. As temperatures increase, gases such as  $CO_2$  diffuse faster. As a result, plant leaves will lose  $CO_2$  at a faster rate than normal. If the amount of light impacting on the leaf and the amount of water available is adequate, predict how this loss of gas will affect photosynthesis in the leaf.



- a. Loss of gases, mainly  $\text{CO}_2$ , will not affect photosynthesis in the leaf, as adequate amounts of water and light are still present which will let the Calvin cycle run smoothly.
  - b. Loss of gases, mainly  $\text{CO}_2$ , will affect photosynthesis in the leaf, as the Calvin cycle will become faster to compensate for the loss.
  - c. Loss of gases, mainly  $\text{CO}_2$ , will not affect photosynthesis in the leaf, as stored reservoirs of  $\text{CO}_2$  in the leaf can be utilized in such times.
  - d. Loss of gases, mainly  $\text{CO}_2$ , will affect photosynthesis in the leaf, as the Calvin cycle will slow down and possibly stop because of inadequate carbon to fix in the system.
42. How do the cytochrome complex components involved in photosynthesis contribute to the electron transport chain?
- a. Photosystem I excites the electron as it moves down the electron transport chain into Photosystem II.
  - b. Plastoquinone and plastocyanine perform redox reactions that allow the electron to move down the electron transport chain into Photosystem I.
  - c. ATP synthase “de-excites” the electron as it moves down the electron transport chain into Photosystem I.
  - d. RuBisCO excites the electron as it moves down the electron transport chain into Photosystem II.
43. Discuss how membranes in chloroplasts contribute to the organelles’ essential functions.
- a. The inner membrane contains the chemicals needed for the Calvin cycle and also components of the light dependent reactions. The thylakoid membrane contains photosystems I and II, as well as the enzyme  $\text{NAD}^+$  reductase.
  - b. The inner membrane contains only the chemicals needed for the Calvin cycle. The thylakoid membrane contains components of the light dependent reactions, photosystems I and II, and the enzyme  $\text{NAD}^+$  reductase.
  - c. The inner membrane contains components of the light dependent reactions as well as photosystems I and II. The thylakoid membrane contains the chemicals needed for the Calvin cycle and also the enzyme  $\text{NAD}^+$  reductase.
  - d. The inner membrane contains the chemicals needed for the Calvin cycle, components of the light dependent reactions and photosystems I and II. The thylakoid membrane contains the enzyme  $\text{NAD}^+$  reductase.
44. If the absorption spectrum of photosynthetic pigments was restricted to the green portion of the spectrum, which pigment or pigments would be affected the least?
- a. carotenoids
  - b. chlorophyll a
  - c. chlorophyll b
  - d. chlorophyll c
45. Describe the passage of energy from light until it is captured in the primary electron acceptor.
- a. Chlorophyll molecules in the photosystems are excited and pass the energy to the primary electron acceptor where the energy is used to excite electrons from the splitting of water.
  - b. Chlorophyll a molecules in the photosystems are excited and pass the energy to the primary electron acceptor where the energy is used to excite electrons from the splitting of water.
  - c. Chlorophyll b molecules in the photosystems are excited and pass the energy to the primary electron acceptor where the energy is used to excite electrons from the splitting of water.
  - d. Chlorophyll molecules in the photosystems absorb light and get excited in the primary electron acceptor from where the energy is used to excite electrons from the splitting of water.

## SCIENCE PRACTICE CHALLENGE QUESTIONS

46. On a hot, dry day, plants close their stomata to conserve water. **Explain** the connection between the oxidation of water in photosystem II of the light-dependent reactions and the synthesis of glyceraldehyde-3-phosphate

(G3PA) in the light-independent reactions. **Predict** the effect of closed stomata on the synthesis of G3PA and **justify** the prediction.

47. The emergence of photosynthetic organisms is recorded in layers of sedimentary rock known as a banded iron formation. Dark-colored and iron-rich bands composed of hematite ( $\text{Fe}_2\text{O}_3$ ) and magnetite ( $\text{Fe}_3\text{O}_4$ ) only a few millimeters thick alternate with light-colored and iron-poor shale or chert. Hematite and magnetite can form precipitates from water that has a high concentration of dissolved oxygen. Shale and chert can form under conditions that have high concentrations of carbonates ( $\text{CO}_3^{2-}$ ). These banded iron formations appeared 3.7 billion years ago (and became less common 1.8 billion years ago). **Justify the claim** that these sedimentary rock formations reveal early Earth conditions.

48. The following diagram summarizes the light reactions of photosynthesis.

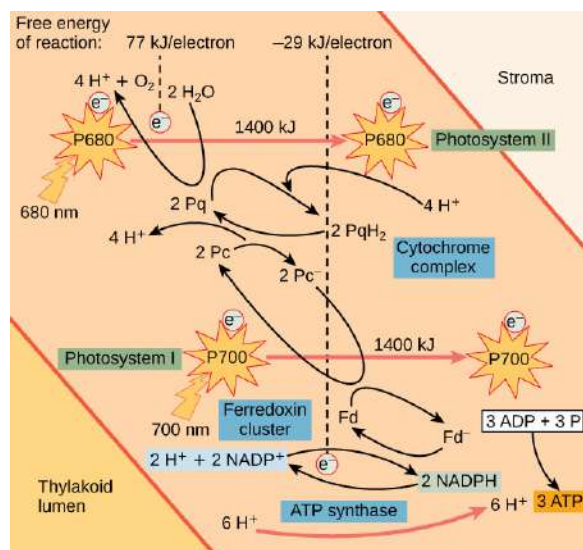
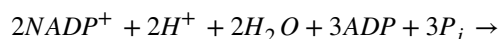


Figure 8.22

The diagram shows light-dependent reactions of photosynthesis, including the reaction centers, electron transport chains, and the overall reactions within each of these. The free energy per electron is shown for the oxidation-reduction reactions. The free change of the captured radiant energy is shown.



- In the *overall* mass balance equation for the light reactions shown above, **identify** the source of electrons for the synthesis of NADPH.
- Calculate** the number of electrons transferred in this reaction.
- Using the free energies per electron displayed, **calculate** the free energy change of the light-dependent reactions.
- Given that the free energy change for the hydrolysis of ATP is -31.5 kJ/mole and the free energy change for the formation of NADPH from  $\text{NADP}^+$  is 18 kJ/mole, **calculate** the total production of free energy for the light reactions.
- Using this definition of energy efficiency, **calculate** the efficiency of the light reaction of photosynthesis: energy efficiency = free energy produced/energy input.

49. Algae can be used for food and fuel. To maximize profit from algae production under artificial light, researchers proposed an experiment to determine the dependence of the efficiency of the process used to grow the algae on light intensity ("brightness") that will be purchased from the electric company.

The algae will be grown on a flat sheet that will be continuously washed with dissolved carbon dioxide and nutrients. Light-emitting diodes (LEDs) will be used to illuminate the growth sheet. Photodiodes placed above and below the sheet will be used to detect light transmitted through and reflected from the algal mat. The intensity of light can be varied, and the algae can be removed, filtered, and dried. The amount of stored energy in the algal mats can be determined by calorimetry.

- Identify** a useful definition of efficiency for this study and **justify** your choice.
- Frequencies of light emitted by the LEDs will not be variables but must be specified for the construction of the apparatus. **Identify** the frequencies of light that should be used in the experiment and justify your choice.
- Evaluate the claim** that the experiment is based on the assumption that there is an upper limit on the intensity of light used to support growth of algae. **Predict** a possible effect on algal growth if light with too great an intensity is used and **justify** the prediction.
- Design an experiment** by describing a procedure that can be used to determine the relationship between light intensity and efficiency.

50. The classical theory of evolution is based on a gradual transformation, the accumulation of many random mutations that are selected. The biological evidence for evolution is overwhelming, particularly when one considers what has not changed: core conserved characteristics.

A. **Describe** three conserved characteristics common to both chloroplasts and mitochondria.

Some hypotheses that have been proposed to account for biological diversity are saltatory, involving sudden changes, rather than gradualist. In defense of the classical gradualist theory of evolution, nearly all biologists in the late 1960s rejected the theory of endosymbiosis as presented by Lynn Margulis in 1967.

B. Suppose that you want to disprove the theory of endosymbiosis.

**Explain** how the following evidence could disprove the theory:

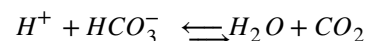
- a “transitional species” with cellular features that are intermediate cells with and without mitochondria
- a “transitional organelle” with some features, such as compartmentalized metabolic processes, but not other features, such as DNA

**Explain** how the following evidence supports the theory of endosymbiosis:

- bacteria live within your intestines, but you still have a separate identity
- no one has directly observed the fusion of two organisms in which a single organism results

**51.** Discovering the carbon-fixation reactions (or light-independent reactions) of photosynthesis earned Melvin Calvin a Nobel Prize in 1961. The isolation and identification of the products of algae exposed to  $^{14}\text{C}$  revealed the path of carbon in photosynthesis.  $^{14}\text{C}$  was fed to the algal culture in the form of bicarbonate ion ( $\text{HCO}_3^-$ ). To agitate the culture, air, which contains  $\text{CO}_2$ , was bubbled through the system, so there were two sources of carbon.

Since Calvin’s experiment, research has focused on the way carbon from a solution containing bicarbonate ions is absorbed by algae. In aqueous solution, the bicarbonate anion ( $\text{HCO}_3^-$ ) is in equilibrium with dissolved  $\text{CO}_2$  as shown in the equation below:



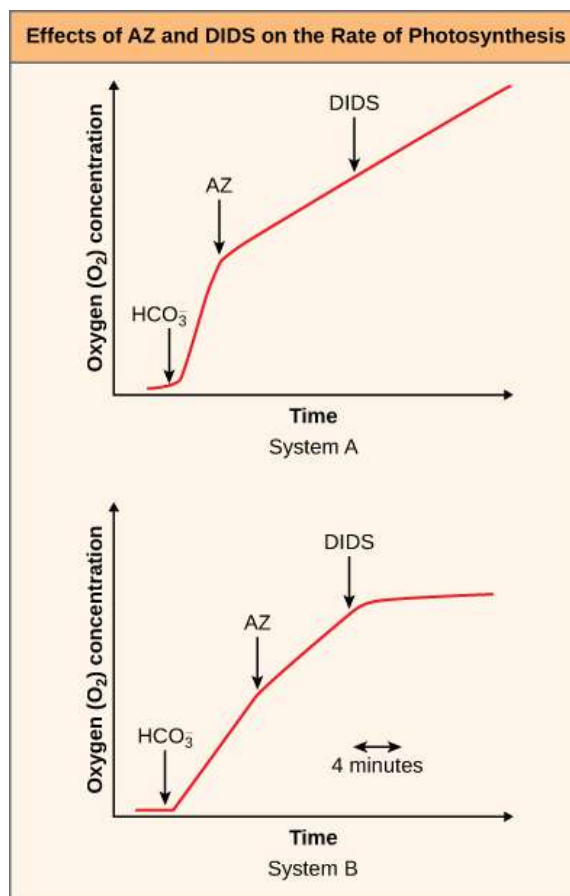
In a later experiment, Larsson and Axelsson (1999) used acetazolamide (AZ), a carbonate anhydrase inhibitor, to inhibit enzymes that convert bicarbonate into carbon dioxide. They also used disulfonate (DIDS), an inhibitor of the transport of anions, such as the bicarbonate ion, through the plasma membrane.

A. **Pose a scientific** question that can be pursued with AZ and DIDS in terms of the path of carbon in photosynthesis.

B. The plasma membrane is permeable to the nonpolar, uncharged carbon dioxide molecule. However, the concentration of carbon dioxide in solution can be very

small. **Explain** how the enzyme carbonate anhydrase can increase the availability of carbon dioxide to the cell.

C. Larsson and Axelsson conducted experiments in which the growth medium was fixed at two different pH levels and determined the effects of AZ and DIDS on the rate of photosynthesis by measuring oxygen concentrations at various times. The results are shown in the two graphs below. The arrows indicate the time points during which  $\text{HCO}_3^-$ , AZ, and DIDS were added to each system.



**Figure 8.23** This figure displays the effects of AZ and DIDS on the rate of photosynthesis of two systems, system A and system B, in a line graph. The line graph plots the oxygen concentration over time.

In which system, A or B, is there a strong reliance on the bicarbonate ion as the mechanism of carbon uptake by the cell? **Justify** your answer using the data.

D. If both systems are dosed with the same concentrations of bicarbonate ion, in which system, A or B, is the pH higher? **Justify** your answer using the data and the bicarbonate-carbon dioxide equilibrium equation.