# 7 where it starts—photosynthesis

#### Sunlight and Survival

Think about the last bit of apple, lettuce, chicken, pizza, or any other food you put in your mouth. Where did it come from? Look past the refrigerator, the market or restaurant, and the farm. Look to plants, the starting point for nearly all of the food—the carbon-based compounds—you eat.

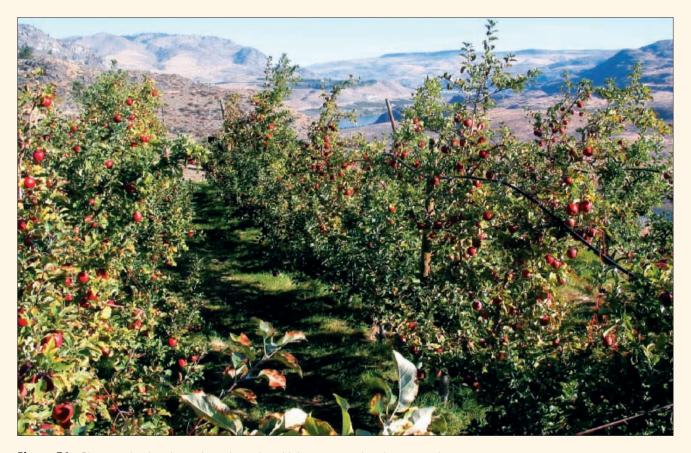
Plants are among the **autotrophs**, or "self-nourishing" organisms. Autotrophs get energy and carbon from the physical environment and use it to make their own food. Most bacteria, many protists, and all fungi and animals are like you; they cannot obtain energy and carbon from the physical environment. They are **heterotrophs**, which feed on autotrophs, one another, and organic wastes. *Hetero*– means other, as in "being nourished by others."

Plants are a type of *photo*autotroph. By the process of **photosynthesis**, they make sugars and other compounds by using sunlight as an energy source and carbon dioxide as their source of carbon. Each year, plants around the

world produce 220 billion tons of sugar, enough to make 300 quadrillion sugar cubes. That is a LOT of sugar. They also release great amounts of oxygen (Figure 7.1).

It wasn't always this way. The first prokaryotic cells on Earth were *chemo*autotrophs. Like the existing archaeans, they did not have the enzymes for complicated metabolic magic. They extracted energy and carbon from simple organic and inorganic compounds, such as methane and hydrogen sulfide, that happened to be around. Both gases were part of the chemical brew that made up the early atmosphere. Carbon dioxide also was present, but it takes special enzymes to harness it. There was little free oxygen.

Things did not change much for about a billion years. Then light-sensitive molecules evolved in a few lineages, which became the first *photo*autotrophs. Life had tapped into an immense supply of energy. Not long afterward, parts of the photosynthetic machinery became modified



**Figure 7.1** Photosynthesis—the main pathway by which energy and carbon enter the web of life. This orchard of photosynthetic autotrophs is producing apples and oxygen at the Jerzy Boyz organic farm in Chelan, Washington.

### IMPACTS, ISSUES

in some photoautotrophs. Water molecules could now be split apart as a source of electrons for the reactions, and supplies of water were essentially unlimited. Over time, oxygen atoms released from uncountable water molecules diffused out of uncountable numbers of cells —and the world of life would never be the same.

Free oxygen reacts fast with metals, including metal ions that help enzymes. The reactions release free radicals which, as you know, are toxic to cells. So oxygen that had accumulated in the atmosphere put selection pressure on prokaryotic populations all over the world. Prokaryotes that could not neutralize toxic oxygen radicals vanished or were marginalized in muddy sediments, deep water, and other anaerobic (oxygen-free) habitats.

As you will read in this chapter, pathways that could detoxify the oxygen radicals evolved in some lineages. One pathway, aerobic respiration, lets cells *use* oxygen's reactive properties in highly beneficial ways.

Another bonus for life: As oxygen accumulated high in the atmosphere, many atoms combined to form ozone  $(O_3)$ . An ozone layer formed and became a shield against lethal ultraviolet radiation from the sun. Life could now move out of the deep ocean, out from mud, out from under rocks, and diversify under the open sky.

As you read this chapter on photosynthesis, keep in mind that its emergence and its continuity are big reasons why *you* can exist, and read this book, and think about what it takes to stay alive.



## How Would You Vote?

The oxygen in Earth's atmosphere is a sure indicator that photosynthetic organisms flourish here. New technologies will allow astronomers in search of life to measure the oxygen content of the atmosphere of planets too far away for us to visit. Should public funds be used to continue this research? See BiologyNow for details, then vote online.

## Key Concepts

#### THE RAINBOW CATCHERS

A one-way flow of energy through the world of life starts after chlorophylls and other pigments absorb wavelengths of visible light from the sun's rays. In plants, some bacteria, and many protists, that energy ultimately drives the synthesis of glucose and other carbohydrates. Sections 7.1, 7.2

#### OVERVIEW OF PHOTOSYNTHESIS

In plant cells and many protists, photosynthesis proceeds through two stages inside organelles called chloroplasts. At a membrane system in the chloroplast, the sun's energy is first converted to chemical energy. Then carbohydrates are synthesized in the chloroplast's semifluid matrix. Section 7.3

#### MAKING ATP AND NADPH

In the first stage of photosynthesis, sunlight energy becomes converted to chemical bond energy in ATP. NADPH forms, and free oxygen escapes into the air. Sections 7.4, 7.5

#### MAKING SUGARS

The second stage is the "synthesis" part of photosynthesis. Enzymes assemble sugars from atoms of carbon and oxygen obtained from carbon dioxide. The reactions use the ATP and NADPH that formed in the first stage of photosynthesis. The ATP delivers energy, and the NADPH delivers electrons and hydrogens to the reaction sites. Sections 7.6, 7.7

#### GLOBAL IMPACTS OF AUTOTROPHS

The emergence of the world's main energy-releasing pathway, aerobic respiration, was an evolutionary consequence of photosynthesis—the world's main energy-acquiring pathway. Collectively, photoautotrophs and chemoautotrophs make the food that sustains all of life. They also have enormous impact on the global climate. Section 7.8



Before considering the chemical basis of photosynthesis, you may wish to review the nature of electron energy levels (Section 2.3), particularly how photons and electrons interact. You will be using your knowledge of carbohydrate structure (3.4), chloroplasts (4.8), active transport proteins (5.2, 5.4), and concentration gradients (5.3).

Remember the concepts of energy flow and the underlying organization of life (6.1 and 6.2)? They help explain how energy flows through photosynthesis reactions. You also will expand your understanding of how cells harvest energy through the operation of electron transfer chains (6.5).

THE RAINBOW CATCHERS

## 7.1

LINKS TO SECTIONS

2.3, 6.1, 6.2

## Sunlight as an Energy Source

Remember how energy flows in one direction through the world of life? In nearly all cases, the flow starts when photoautotrophs intercept energy, in the form of wavelengths of visible light, from the sun.

#### PROPERTIES OF LIGHT

An understanding of photosynthesis requires a bit of knowledge of the properties of energy that radiates from the sun. That energy undulates across space in a manner analogous to the waves moving across a sea. The term **wavelength** refers to the horizontal distance between the crests of every two successive waves of radiant energy.

Although energy travels in waves, it has a particlelike quality. When absorbed, it can be measured as if it were organized in discrete packets, or **photons**. A photon consists of a fixed amount of energy. The least energetic photons travel in longer wavelengths, and the most energetic ones travel in shorter wavelengths.

Photoautotrophs only capture light of wavelengths between 380 and 750 nanometers. Humans and other organisms see light of these wavelengths as different colors, from deep violet through blue, green, yellow, orange, and red. Figure 7.2 shows where the spectrum of visible light fits in the **electromagnetic spectrum** the range of all wavelengths of radiant energy, from shortest (gamma rays) to longest (radio waves).

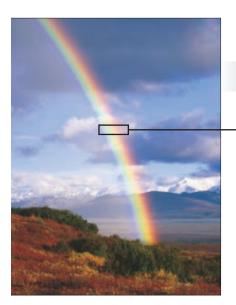
Shorter wavelengths are energetic enough to alter or break chemical bonds in DNA and proteins. That is why UV (ultraviolet) light, x-rays, and gamma rays are a threat to all organisms. That is why early life evolved away from sunlight—deep in the ocean, or in sediments, or under rocks. Life did not move onto dry land until after the ozone layer formed high above Earth. The ozone layer absorbs much of the dangerous UV light (Sections 48.1 and 48.2).

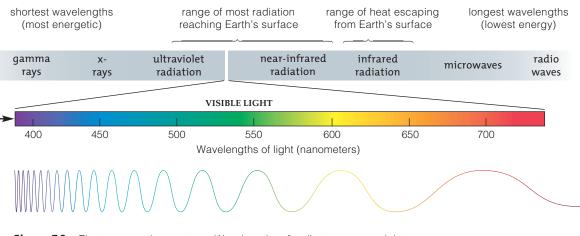
Visible light of all wavelengths combined appears white. White light separates into its individual colors when it passes through a prism or water droplets in moisture-laden air. The prism or droplets bend light of longer wavelengths (yellow to red) more than they bend shorter wavelengths (violet to blue), the result being the band of colors we see in rainbows.

#### FROM SUNLIGHT TO PHOTOSYNTHESIS

**Pigments** are a class of molecules that absorb photons in particular wavelengths only. Certain kinds are the molecular bridges from sunlight to photosynthesis.

Photons that a specific pigment does not absorb are reflected by it or continue traveling right on through it. Chlorophyll a, the major pigment in all but one group of photoautotrophs, absorbs violet and red light. It reflects green and yellow light, which is why plant parts with an abundance of chlorophylls appear green. Accessory pigments harvest additional wavelengths. The most common accessory pigment, chlorophyll b, reflects green and blue light. Carotenoids reflect red, orange, and yellow light. Besides their photosynthetic role, carotenoids impart color to many flowers, fruits, and vegetables. Xanthophylls reflect yellow, brown, blue or purple light. The anthocyanins reflect red and purple light, as they do in cherries and many flowers. In many deciduous plants, chlorophylls in green leaves mask accessory pigments until autumn (Figure 7.3*a*).





**Figure 7.2** Electromagnetic spectrum. Wavelengths of radiant energy undulate across space and are measured in nanometers. About 2.5 million nanometers are equal to one inch. Visible light is a very small part of the spectrum, which includes all electromagnetic waves. The shorter the wavelength, the higher the energy.



The **phycobilins** reflect red or blue-green light. Red algae and cyanobacteria have notable amounts of these accessory pigments. A few bacteria of ancient lineages have unique pigments. Purple bacteriorhodopsin is the main kind in the archaean *Halobacterium halobium*.

Collectively, different photosynthetic pigments can absorb nearly all wavelengths across the spectrum of visible light. What happens next? You have to zoom into a pigment for the answer. As Figure 7.3*b*,*c* shows, a pigment molecule has at least one array of atoms in which single covalent bonds alternate with double covalent bonds. Remember electron orbitals (Section 2.3)? Electrons of these atoms share one orbital that spans the entire array. That array lets the pigment act like an antenna for receiving photon energy.

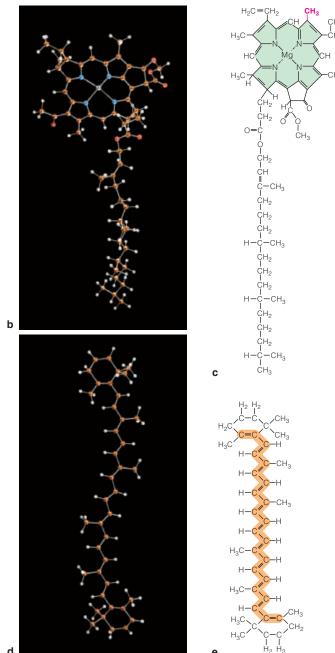
Each pigment absorbs light of specific wavelengths, which correspond to photon energy. Energy inputs, remember, boost electrons to higher energy levels. A photon is absorbed by a pigment only if it has exactly enough energy to boost an electron of the pigment's antenna region to a higher energy level.

An excited electron returns to a lower energy level almost immediately and emits its extra energy as heat or as a photon. As you will see shortly, that energy bounces back and forth like a fast volleyball among a team of photosynthetic pigments. It quickly reaches the team captain—a special chlorophyll that can *give up* excited electrons and so start the reactions.

Radiation from the sun travels in waves, which differ in length and energy content. We perceive visible light of different wavelengths as different colors and measure their energy content in packets called photons.

In plants, chlorophyll a and accessory pigments absorb specific wavelengths of visible light. They are molecular bridges between the sun's energy and photosynthesis.

Pigment molecules absorb photons at their arrays of alternating single and double covalent bonds. The arrays let the pigments act like energy-receiving antennas.



**Figure 7.3** (a) Evidence of pigments in the changing leaves of autumn. In bright green leaves, photosynthetic cells continuously make chlorophyll, which masks accessory pigments. In autumn, chlorophyll synthesis lags behind its breakdown in many species. Accessory pigments then show through and give leaves characteristic red, orange, and yellow fall colors.

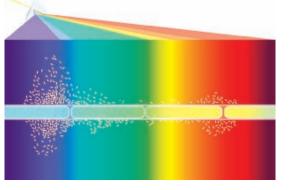
Ball-and-stick models and structural formulas for  $(\mathbf{b}, \mathbf{c})$  chlorophyll *a* and  $(\mathbf{d}, \mathbf{e})$  beta-carotene. The light-catching region of each pigment is tinted the specific color of light it transmits. Each pigment has a hydrocarbon backbone that readily dissolves in the lipid bilayer of cell membranes.

Chlorophylls *a* and *b* differ only in one functional group at the position shaded *red* ( $-CH_3$  for chlorophyll *a* and  $-COO^-$  for chlorophyll *b*). The light-catching portion is the flattened ring structure, which is similar to a heme (Section 3.1). It holds a magnesium atom instead of iron.

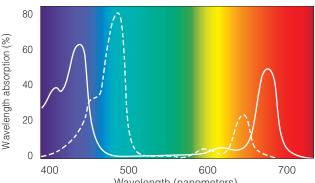


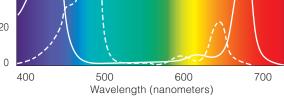


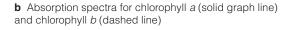
### Harvesting the Rainbow

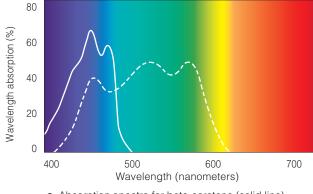


a Outcome of Engelmann's experiment









**c** Absorption spectra for beta-carotene (solid line) and one of the phycobilins (dashed line)

Figure 7.4 Animated! (a) One of the early photosynthesis experiments. W. T. Engelmann directed a ray of sunlight-broken into its component colors by a crystal prism-across a water droplet on a microscope slide. The droplet held an algal strand (Cladophora) and aerobic bacterial cells. As shown here, nearly all of the cells gathered under violet and red light, the most efficient wavelengths for photosynthesis.

(**b**,**c**) Later research revealed that all photosynthetic pigments combined absorb most wavelengths in the spectrum of visible light with remarkable efficiency. These graphs show absorption spectra for only four of many pigments: chlorophylls a and b, beta-carotene, and a phycobilin.

Different kinds of photosynthetic pigments work together. How efficient are these pigments at harvesting light of different wavelengths in the sun's rays?

At one time, people thought that plants used substances in soil to make food. By 1882, a few chemists had an idea that plants use sunlight, water, and something in the air. The botanist Wilhelm Theodor Engelmann wondered: What parts of sunlight do plants favor? He already knew that photosynthesis releases free oxygen. He came up with a hypothesis. If photosynthesis involves certain colors of light, then photosynthesizers will release more or less oxygen in response to different colors.

Engelmann also knew that certain bacteria use oxygen during aerobic respiration, and he predicted that they would gather in places where a photosynthetic organism was releasing the most oxygen. He directed a spectrum of visible light across a drop of water that contained bacterial cells (Figure 7.4*a*). The droplet also contained a strand of Cladophora, a photosynthetic alga (Figure 7.5).

Most of the bacterial cells gathered where violet and red light fell across the algal strand. More free oxygen had to be diffusing away from parts of the strand that were illuminated by the violet and red light—a sign that those colors are best at driving photosynthesis.

Engelmann did identify the wavelengths. But molecular biology was far in the future, so he did not know about the pigments that absorb the light.

Today, an **absorption spectrum** conveys how efficiently a given pigment absorbs light of different wavelengths. As Figure 7.4b shows, chlorophylls are best at absorbing red and violet light, but they transmit much of the yellow and green light. What if you combined absorption spectra for chlorophylls and all of the accessory pigments, including those in Figure 7.4*b*,*c*? You would see that, collectively, they respond to almost the full spectrum of wavelengths from the sun. They are efficient at what they do.

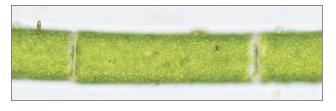


Figure 7.5 Light micrograph of the type of cells making up one algal strand.

OVERVIEW OF PHOTOSYNTHESIS

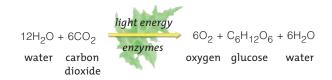
## 7.3 Overview of Photosynthesis Reactions

Plants do something you never will do. They can make their own food from no more than light, water, and carbon dioxide.

Photosynthesis proceeds in two reaction stages. In the first stage—the **light-dependent reactions**—sunlight energy is converted to chemical bond energy of ATP. Water molecules are split, and typically the coenzyme NADP<sup>+</sup> accepts the released hydrogen and electrons, thus becoming NADPH. The oxygen atoms released from water molecules escape into the surroundings.

The second stage, the **light-independent reactions**, runs on energy delivered by ATP. That energy drives the synthesis of glucose and other carbohydrates. The building blocks are the hydrogen atoms and electrons from NADPH, as well as carbon and oxygen atoms stripped from carbon dioxide and water.

Photosynthesis is often summarized this way:

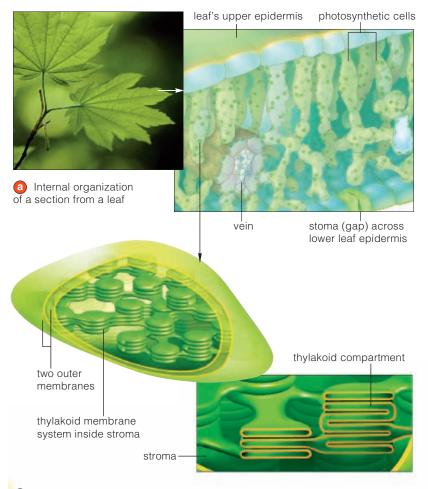


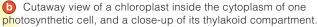
We will focus on what goes on inside **chloroplasts**, the organelles of photosynthesis in plants and many protists. A chloroplast has two outer membranes that enclose a semifluid matrix called the **stroma**. A third membrane—the **thylakoid membrane**—is folded up inside the stroma. In many cells, it looks like stacks of flattened sacs (thylakoids) connected by channels. But the space inside all the sacs and channels forms one continuous compartment, as in Figure 7.6b. Sugars are synthesized outside the compartment, in the stroma.

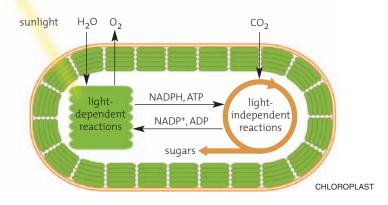
As you will see in the next section, the thylakoid membrane is studded with pigments. Most pigments are packed together as light-harvesting complexes. A number of **photosystems**, or reaction centers, also are embedded in the membrane, and each is surrounded by hundreds of light-harvesting complexes that pass on energy to it. With enough energy, its electrons get excited. That excitation sets in motion the first stage of reactions, as sketched out in Figure 7.6*c*.

In the first stage of photosynthesis, sunlight energy drives ATP and NADPH formation, and oxygen is released. In chloroplasts, this stage occurs at the thylakoid membrane.

The second stage proceeds in the stroma of chloroplasts. Energy from ATP drives the synthesis of sugars from water and carbon dioxide.







• Two stages of photosynthesis. The first stage depends on inputs of sunlight. It occurs at the thylakoid membrane system. ATP and NADPH form; free oxygen diffuses away. In the second stage, enzymes in the stroma catalyze the assembly of sugars. Energy from ATP starts the reactions. Building blocks are hydrogen atoms and electrons (from NADPH) and carbon atoms (from carbon dioxide).

**Figure 7.6** *Animated!* Zooming in on sites of photosynthesis inside the leaf of a typical plant.

MAKING ATP AND NADPH

## 7.4 Light-Dependent Reactions

LINKS TO SECTIONS 5.2, 6.5 In the first stage of photosynthesis, photons absorbed at photosystems drive ATP formation. Water molecules are split. Their oxygen diffuses away, but the coenzyme NADP<sup>+</sup> picks up the released electrons and hydrogen.

#### WHAT HAPPENS TO THE ABSORBED ENERGY?

Visualize a lone photon as it collides with a pigment molecule. One of the pigment's electrons can absorb that photon's energy, which boosts the electron to a higher energy level. If nothing else were to happen, the electron would drop back to its unexcited state and lose the extra energy as a photon or as heat.

In the thylakoid membrane, however, energy that excited electrons give up is kept in play. Embedded in the membrane are many hundreds of light-harvesting complexes: circular clusterings of pigments and other proteins (Figure 7.7*a*). The pigments in light-harvesting complexes do not waste absorbed photons. Instead, their electrons hold on to photon energy by passing it back and forth, like a volleyball.

Energy released from one complex gets passed to another, which passes it on to another, and so on until the energy reaches a photosystem. Chloroplasts have two kinds of photosystems, *type I* and *type II*. The two have slightly different chlorophyll *a* molecules. Each contains other molecules, including different pigments. Hundreds of light-harvesting complexes surround it.

Look back on Figure 7.3, which shows the structure of chlorophyll. Two molecules of chlorophyll *a* are at the center of a photosystem. Their flat rings face each other so closely that the electrons in *both* rings are destabilized. When light-harvesting complexes pass on photon energy to a photosystem, electrons are popped right off of that special pair of chlorophylls.

The freed electrons immediately enter an electron transfer chain positioned next to the photosystem. As

you know, **electron transfer chains** are components of cell membranes. Each is an orderly array of enzymes, coenzymes, and other proteins that transfer electrons step-by-step (Section 6.5). *The entry of electrons from a photosystem into an electron transfer chain is the first step in the light-dependent reactions*—in the conversion of photon energy to chemical energy for photosynthesis.

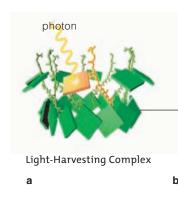
#### MAKING ATP AND NADPH

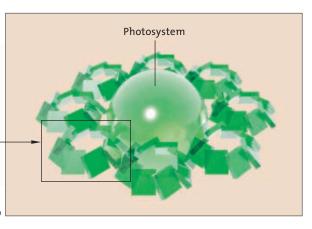
Figure 7.8 tracks electrons from a type II photosystem on through an electron transfer chain in the thylakoid membrane. As certain components of the chain accept and donate the electrons, they pick up hydrogen ions (H<sup>+</sup>) from the stroma and release them into the inner thylakoid compartment. They do so again and again. Soon, concentration and electric gradients are built up across the membrane, and the combined force of the gradients attracts H<sup>+</sup> back toward the stroma.

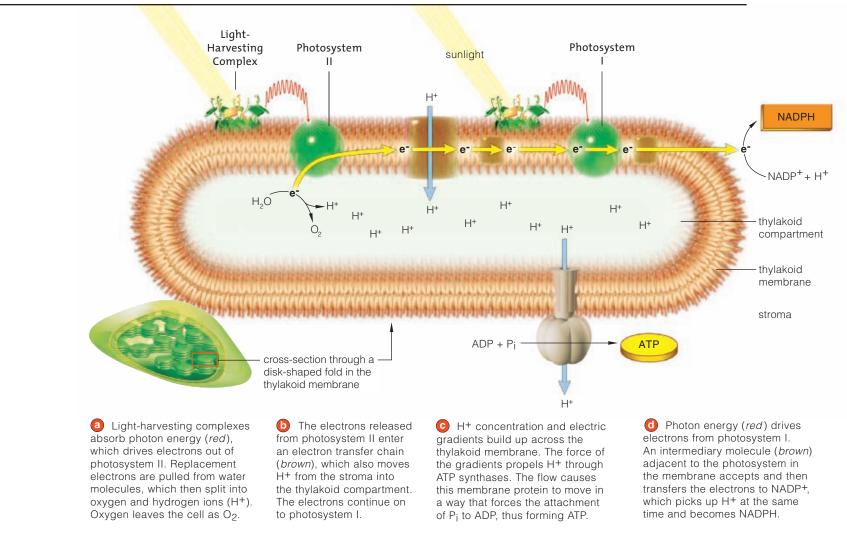
But H<sup>+</sup> cannot diffuse across the membrane's lipid bilayer. It can cross only through channels inside **ATP synthases**, a type of transport protein you read about in Section 5.2. In this case, the knoblike portion of the protein projects into the stroma. Ion flow through the channel makes the knob turn, which forces inorganic phosphate to become attached to an ADP molecule. In this way, ATP forms in the stroma.

As long as electrons flow through transfer chains, the cell can keep on producing ATP. But how are the electrons from photosystem II replaced? By a process called *photolysis*, new electrons are pulled away from water molecules, which then dissociate into hydrogen ions and molecular oxygen. The free oxygen diffuses out of the chloroplast, then out of the cell and into the surroundings. Hydrogen ions remain in the thylakoid compartment. They contribute to the concentration and electric gradients that drive ATP formation.

Figure 7.7 (a) Ringlike array of pigment molecules that intercept rays of sunlight coming from any direction. (b) One of the many photosystems (represented as a *green* sphere) embedded in a chloroplast's thylakoid membrane. Each photosystem collects energy from hundreds of light-harvesting complexes that surround it; only eight complexes are shown here.







**Figure 7.8** *Animated!* How ATP and NADPH form during the first stage of photosynthesis. The drawing represents a cross-section through one of the disk-shaped folds of the thylakoid membrane. This entire sequence is called the *noncyclic* pathway of photosynthesis, because electrons that originally left photosystem II are not cycled back to it. They end up in NADPH.

But where do the electrons end up? After they pass through the electron transfer chain, they enter a type I photosystem where the light-harvesting complexes are volleying energy to a special pair of chlorophylls at the reaction center. The chlorophylls release electrons, which an intermediary molecule transfers to NADP<sup>+</sup>. When this coenzyme accepts the electrons, it attracts hydrogen ions and thereby becomes NADPH.

We have been describing the *noncyclic* pathway of ATP formation in chloroplasts, so named because the electrons that leave photosystem II do not get cycled back to it; they end up in NADPH.

When too much NADPH forms, it accumulates in the stroma, so the photosystem II pathway backs up. At such times, photosystem I may run independently so that cells can continue to make ATP. It is a *cyclic* pathway of ATP formation, because the electrons that leave photosystem I get cycled back to it. Before they return, they pass through an electron transfer chain that moves H<sup>+</sup> into the thylakoid compartment. The resulting H<sup>+</sup> gradients drive ATP formation, but no NADPH forms in this shorter pathway.

Two kinds of photosystems, type I and type II, are embedded in the thylakoid membrane. Hundreds of light-harvesting complexes surround and transfer photon energy to each one.

In a noncyclic pathway of photosynthesis, photon energy forces electrons out of photosystem II and on to an electron transfer chain, which sets up H<sup>+</sup> gradients that drive ATP formation. Electrons continue on through photosystem I and end up in a reduced coenzyme, NADPH.

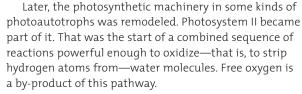
ATP also can form by a cyclic pathway, in which electrons leave photosystem I and are cycled back to it. However, NADPH cannot form by this pathway. MAKING ATP AND NADPH

## Energy Flow in Photosynthesis

LINKS TO SECTIONS 6.1–6.3 One of the recurring themes in biology is that organisms convert one form of energy to another in highly controlled ways. The energy exchanges during the light-dependent reactions, outlined in Figure 7.9, are a classic example.

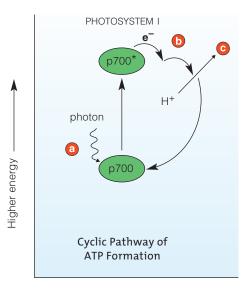
The preceding section focused on a photosynthetic pathway that starts at photosystem II and ends with the formation of ATP and NADPH. However, a simpler pathway that was less energy efficient preceded it. When photoautotrophs first evolved, remember, they were anaerobic. Their lightdependent pathway of photosynthesis yielded ATP alone, and it still operates today.

Again, this set of reactions is said to be cyclic because excited electrons flow out of photosystem I, through an electron transfer chain, then back to photosystem I.



Remember, the combined pathway is noncyclic; the electrons that leave photosystem II are not returned to it. They end up in NADPH, which delivers them to the sugar factories in the stroma.

Today, some bacteria have only photosystem I. Others have only photosystem II. Cyanobacteria, plants, and all photosynthetic protists have photosystems of both types and carry out both cyclic and noncyclic pathways. Which pathway dominates depends on conditions at the time.



 Photosystem I receives photon energy from a light-harvesting complex. It loses an electron.

• The electron passes from one molecule to another in an electron transfer chain that is embedded in the thylakoid membrane. It loses a little energy with each transfer, and ends up being reused by photosystem I (thus the pathway is considered "cyclic").

• Molecules in the transfer chain carry H<sup>+</sup> across the thylakoid membrane into the inner compartment. Hydrogen ions accumulating in the compartment create an electrochemical gradient across the membrane that drives ATP synthesis, as shown in Figure 7.8.

PHOTOSYSTEM I NADPH p700 PHOTOSYSTEM II NADP + + H+ p680 photon 3  $H^+$ p700 photon **a** p680 2H<sub>2</sub>O Noncyclic Pathway of ATP and NADPH Formation  $4H^{+} + O_{2}$ 

Photosystem II receives photon energy from a light-harvesting complex, then loses an electron. The electron moves through a different electron transfer chain. It loses a little energy with each transfer and ends up at photosystem I.

D Photosystem I receives photon energy from a light-harvesting complex, then loses an electron. Released electrons and hydrogen ions are used in the formation of NADPH from NADP<sup>+</sup>.

As in the cyclic pathway, operation of the electron transfer chain pulls hydrogen ions into the thylakoid compartment. In this case, hydrogens released from dissociated water molecules also enter the compartment. The H<sup>+</sup> concentration and electric gradient across the membrane are tapped for ATP formation (Figure 7.8).

G Electrons lost from photosystem I are replaced by the electrons lost from photosystem II. Electrons lost from photosystem II are replaced by electrons obtained from water. (Photolysis pulls water molecules apart into electrons, H<sup>+</sup>, and O<sub>2</sub>.)

**Figure 7.9** *Animated!* Using energy in the light-dependent reactions. The pair of chlorophyll *a* molecules at the center of photosystem I is designated p700. The pair in photosystem II is designated p680. The pairs respond most efficiently to wavelengths of 700 and 680 nanometers, respectively.

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MAKING SUGARS

## 7.6

## 6 Light-Independent Reactions: The Sugar Factory

In the chloroplast's stroma, cyclic, enzyme-mediated reactions build sugars from hydrogen, carbon, and oxygen. These lightindependent reactions run on energy that became conserved in ATP during the first stage of photosynthesis. NADPH that formed in the first stage donates the hydrogen and electrons. Plants get the carbon and oxygen from carbon dioxide ( $CO_2$ ) in the air; algae get them from  $CO_2$  dissolved in water.

The light-independent reactions proceed from carbon fixation, to PGAL formation, then RuBP regeneration. In **carbon fixation**, a carbon atom from  $CO_2$  becomes attached to an organic compound. **Rubisco** (ribulose bisphosphate carboxylase/oxygenase) mediates this step in most plants. When it transfers the carbon to five-carbon RuBP (ribulose biphosphate), it opens the sugar factory—a series of enzyme-mediated reactions called the **Calvin–Benson cycle** (Figure 7.10).

The six-carbon intermediate that forms is unstable and splits at once into two PGA (phosphoglycerate) molecules, each with a three-carbon backbone (Figure 7.10*a*). Next, ATP energy and the reducing power of NADPH convert each PGA to a different three-carbon compound, PGAL (phosphoglyceraldehyde, or G3P). How? ATP transfers a phosphate group to each PGA, and NADPH donates hydrogen and electrons to it.

Glucose, remember, has six carbon atoms. Six CO<sub>2</sub> must be fixed and twelve PGAL must form to produce one glucose molecule and also to keep the Calvin–Benson cycle running. Two PGAL combine to form one six-carbon glucose molecule with a phosphate group attached. The other ten PGAL undergo internal rearrangements in ways that regenerate RuBP (Figure 7.10*c*–*f*).

Most of the glucose is converted at once to sucrose or starch by other pathways that conclude the lightindependent reactions. Sucrose is a transportable form of carbohydrate in plants. Excess glucose is converted to starch and briefly stored, as starch grains, in the stroma. Starch is converted to sucrose for export to leaves, stems, and roots. Plants can use photosynthetic products and intermediates as energy sources and as building blocks for all required organic compounds.

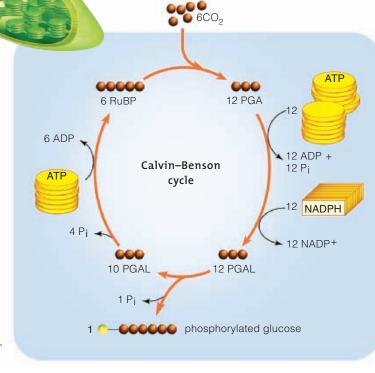
Driven by ATP energy, the light-independent reactions make sugars with hydrogen and electrons from NADPH, and with carbon and oxygen from carbon dioxide.



Remember, it takes six turns of the Calvin– Benson cycle (six carbon atoms) to produce one glucose molecule.

Ten of the PGAL get phosphate groups from ATP. In terms of energy, this primes them for an uphill run—for synthesis reactions that regenerate RuBP.

G The phosphorylated glucose enters reactions that form carbohydrate products—mainly sucrose, starch, and cellulose.



CO<sub>2</sub> in air spaces inside a leaf diffuses into a photosynthetic cell. Six times, rubisco attaches a carbon atom of CO<sub>2</sub> to the RuBP that starts the Calvin–Benson cycle. Each time, the resulting intermediate splits to form two PGA molecules, for a total of twelve PGA.

Each PGA molecule gets a phosphate group from ATP, plus hydrogen and electrons from NADPH. The resulting intermediate, PGAL, is thus primed for reaction.

• Two of the twelve PGAL molecules combine to form one molecule of glucose with an attached phosphate group.

**Figure 7.10** *Animated!* Light-independent reactions of photosynthesis. The sketch is a summary of all six turns of the Calvin–Benson cycle and its product, one glucose molecule. *Brown* circles signify carbon atoms. Appendix VII details the reaction steps

MAKING SUGARS

7.7

## Different Plants, Different Carbon-Fixing Pathways

If sunlight intensity, air temperature, rainfall, and soil composition never varied, photosynthesis might be the same in all plants. But environments differ, and so do details of photosynthesis, as you can see by comparing what happens on hot, dry days when water is scarce.

#### C4 VERSUS C3 PLANTS

All plant surfaces exposed to air have a waxy, waterconserving cuticle. The only way for gases to diffuse into or out of a plant is at **stomata** (singular, stoma). These are tiny openings across the surface of leaves and green stems (Figure 7.11*a*). Stomata close on hot, dry days. Water stays inside the plant, but the CO<sub>2</sub> required for photosynthesis cannot diffuse in, and the O<sub>2</sub> by-product of photosynthesis cannot diffuse out.

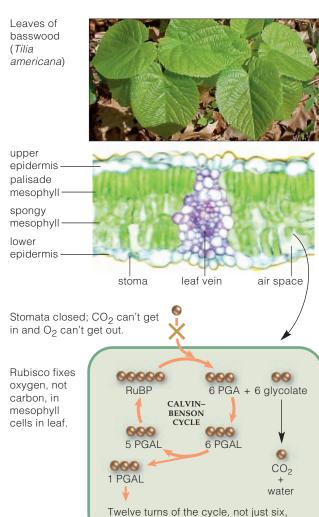
That is why basswood, beans, peas, and many other plants do not grow well in hot, dry climates without steady irrigation. We call them **C3 plants**, because the *three*-carbon PGA is the first stable intermediate of the Calvin–Benson cycle. When their stomata are closed and the photosynthetic reactions are running, oxygen builds up in leaves and triggers a process that lowers a plant's sugar-making capacity. Remember rubisco, the enzyme that fixes carbon for the Calvin–Benson cycle? When O<sub>2</sub> levels rise, *photorespiration* dominates; rubisco attaches oxygen—not carbon—to RuBP. This reaction yields one molecule of PGA instead of two. The lower yield slows sugar production and growth of the plant. Compare Figure 7.11*a* with Figure 7.10.

C4 plants, such as corn, also close stomata on hot, dry days. But the CO<sub>2</sub> level does not decline as much because these plants fix carbon twice, in two types of photosynthetic cells (Figure 7.11*b*). In *mesophyll* cells, a four-carbon molecule, oxaloacetate, forms when CO<sub>2</sub> donates a carbon to PEP. The enzyme catalyzing this step will not use oxygen no matter how much there is. Oxaloacetate is converted to malate, which moves into *bundle-sheath cells* through plasmodesmata. The malate releases CO<sub>2</sub>, which enters the Calvin–Benson cycle.

The C4 cycle keeps the CO<sub>2</sub> level near rubisco high enough to stop photorespiration. It requires one more ATP than the C3 cycle. However, less water is lost and more sugar can be made on hot, bright, dry days.

Photorespiration hampers the growth of many C3 plants. So why hasn't natural selection eliminated it? Rubisco evolved when the atmosphere held little  $O_2$  and a great deal of  $CO_2$ . Perhaps the gene coding for rubisco's structure cannot mutate without disruptive effects on rubisco's primary role—carbon fixation.

Over the past 50 to 60 million years, the C4 cycle evolved independently in many lineages. Before then,



(a) Carbon fixation in C3 plants during hot, dry weather, when there is too little  $CO_2$  and too much  $O_2$  in leaves.

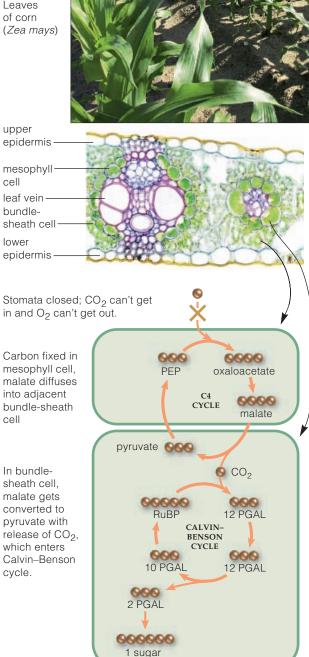
to make one 6-carbon sugar

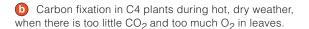
**Figure 7.11** Comparison of carbon-fixing adaptations in three kinds of plants that evolved in different environments.

(a) The Calvin–Benson cycle, which also is called the C3 cycle, is common in evergreens and many nonwoody plants of temperate zones, such as basswood and bluegrass.
(b) A C4 cycle is common in grasses, corn, and other plants that evolved in the tropics and that fix CO<sub>2</sub> twice. (c) Prickly pear (*Opuntia*), a CAM plant. These plants, which open stomata and fix carbon at night, include orchids, pineapples, and many succulents besides cacti.

atmospheric  $CO_2$  levels were higher, so C3 plants had the selective advantage in hot climates. Which cycle will be most adaptive in the future? The  $CO_2$  levels have been rising for decades and may double in the next fifty years. If so, C3 plants will yet again be at an advantage—and many vital crop plants may benefit.

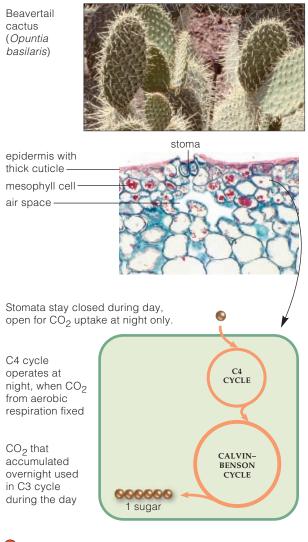
Leaves of corn (Zea mays)





#### CAM PLANTS

We see a carbon-fixing adaptation to desert conditions in a cactus. This plant, a type of succulent, has juicy, water-storing tissues and thick surface layers that limit loss of water. It is one of many CAM plants (short for Crassulacean Acid Metabolism). A cactus will not open stomata on hot days; it opens them and fixes CO2 at



Carbon fixation in CAM plants, adapted to hot, dry climates.

night, when mesophyll cells use a C4 cycle. Each cell stores malate and other organic acids until the next day, when stomata close. Malate releases CO<sub>2</sub>, which the cell uses in the Calvin–Benson cycle (Figure 7.11c).

Some CAM plants survive prolonged drought by keeping stomata shut even at night. They fix CO<sub>2</sub> from aerobic respiration. Not much forms, but it is enough to maintain low metabolic rates and very slow growth. Try growing cacti in mild climates, and you will see that they compete poorly with C3 and C4 plants.

C3 plants, C4 plants, and CAM plants respond differently to hot, dry conditions. At such times, stomata close to conserve water, and so photosynthetic cells must deal with too much oxygen and not enough carbon dioxide in leaves.

GLOBAL IMPACTS OF AUTOTROPHS

## 7.8 Autotrophs and the Biosphere

We conclude this chapter by reflecting on the mindboggling numbers of single-celled and multicelled photosynthesizers and other autotrophs. We find them on land and in the water provinces, and they profoundly influence the biosphere.

#### THE ENERGY CONNECTION

This chapter opened with a brief look at the origin of photosynthesis and its impact on the world of life. All organisms require ongoing supplies of energy and carbon-based compounds for growth and survival. Autotrophs get them from the physical environment. Energy-rich carbon compounds become concentrated in single-celled kinds and in the tissues of multicelled kinds. In this way, autotrophs become concentrated stores of food tempting to heterotrophs.

Autotrophs are more than carbon-rich food baskets for the biosphere. Early practitioners of the noncyclic pathway of photosynthesis enriched the atmosphere with oxygen, and their descendants still replenish it.

Early photoautotrophs lived when iron and other metals were abundant both above and below the seas. As fast as oxygen was released, it swiftly latched onto (oxidized) the metals. Over time, it rusted them out, as evidenced by the bands of red iron deposits on the seafloor. Once that happened, oxygen bubbled out of vast populations of photoautotrophs, unimpeded.

In a wink of geologic time, maybe a few hundred thousand years, oxygen levels rose in the seas and the sky. Most anaerobic species had no means of adapting to the change, and they perished in a mass extinction. Other chemoautotrophs that could not tolerate oxygen endured in seafloor sediments, hot springs, and other anaerobic habitats. Some still live near hydrothermal vents, where superheated water spews out from big fissures in the seafloor. Archaeans near the vents get hydrogen and electrons from hydrogen sulfide in the mineral-rich water. Chemoautotrophs live in oxygenfree soils, where they extract energy from nitrogenrich wastes and remains of other organisms.

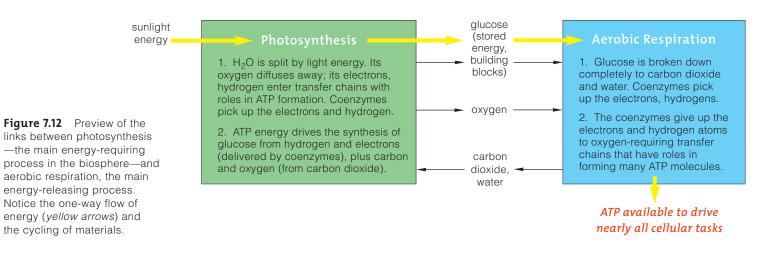
However, among some ancient species of bacteria, metabolic pathways became modified in ways that detoxified oxygen. Later on, a pathway that released energy from organic compounds became modified in ways that allowed it to *use* oxygen as a final electron acceptor. As a direct outcome of the selection pressure exerted by oxygen—a by-product of photosynthesis aerobic respiration had evolved (Figure 7.12).

#### PASTURES OF THE SEAS

Today, aerobic species are all around us. Each spring, the renewed growth of photoautotrophs is evident as trees leaf out and fields turn green. At the same time, uncountable numbers of single-celled species drifting through the ocean's surface waters make a seasonal response. You can't see them without a microscope. In some regions, a cup of seawater may hold 24 million cells of one species, and that number does not include any other aquatic species suspended in the cup.

Collectively, these cells are the "pastures of the seas." Most are bacteria and protists that ultimately feed nearly all other marine species. Their primary productivity is the start of vast aquatic food webs.

Imagine zooming in on a small patch of "pasture" in an Antarctic sea. There, tiny shrimplike crustaceans are feeding on even tinier photosynthesizers. Dense concentrations of these crustaceans, or krill, are food for other animals, such as fishes, penguins, seabirds, and immense blue whales. A single, mature whale is straining four tons of krill from the water. Before they



themselves became food for the whale, the four tons' worth of krill had munched their way through 1,200 tons of the pasture!

The pastures "bloom" in spring, when the seawater becomes warmer and greatly enriched with nutrients that currents churn up from the deep. The conditions favor huge increases in population sizes.

Until NASA gathered data from space satellites, we had no idea of the size and distribution of these marine pastures. Figure 7.13*a* shows the near-absence of photosynthetic activity one winter in the Atlantic Ocean. Figure 7.13*b* shows a springtime bloom that stretched from North Carolina all the way past Spain!

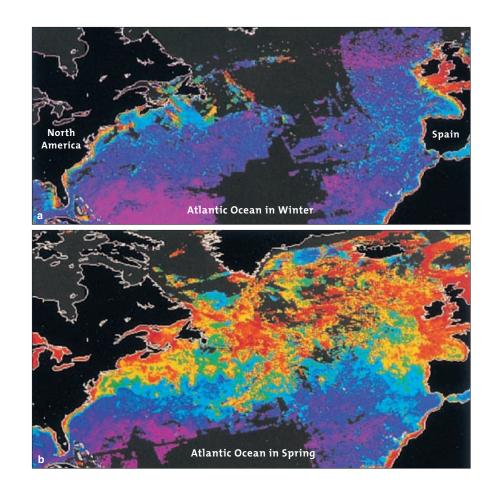
Collectively, these cells affect the global climate, because they deal with staggering numbers of gaseous reactant and product molecules. For instance, they sponge up nearly half of the carbon dioxide used in carbon fixation. Without them, atmospheric carbon dioxide would accumulate more rapidly and possibly accelerate global warming (Sections 47.9 and 47.10).

Although drastic global change is a real possibility, human activities release more carbon dioxide to the atmosphere than photoautotrophs can take up. Such activities include burning fossil fuels and setting fire to vast tracts of forests to clear land for farming.

There is more. Each day, tons of industrial wastes, raw sewage, and fertilizers in runoff from croplands enter the ocean and change its chemical composition. How long can we expect the marine photoautotrophs to function in this chemical brew? The answer may affect your life in more ways than one. It may affect populations and ecosystems throughout the world.

In sum, autotrophs exist in tremendous numbers. They nourish themselves and all other living things, and they are major players in the cycling of oxygen, nitrogen, phosphorus, and other elements all through the biosphere. Later chapters focus on their impact on the environment. In this unit, we turn next to major pathways by which all cells release the chemical bond energy that is stored in glucose and other biological molecules—the legacy of autotrophs everywhere.

Energy flow and the cycling of carbon and other nutrients through the biosphere starts with autotrophs.



**Figure 7.13** Two satellite images that convey the sheer magnitude of photosynthetic activity during springtime in the surface waters of the North Atlantic Ocean. Sensors in equipment launched with the satellite recorded concentrations of chlorophyll, which were greatest in regions coded *red*.

Take a deep breath while looking at these images. You just took in free oxygen that originated with some photoautotroph, somewhere in the world. Poison the autotrophs and how long will oxygen-dependent heterotrophs last?

#### http://biology.brookscole.com/starr11

#### Summary

**Section 7.1** Photosynthesis runs on energy obtained when pigment molecules absorb wavelengths of visible light from the sun. Chlorophyll *a*, the main pigment, is best at absorbing violet and red wavelengths. Diverse photosynthetic pigments are accessory pigments. They form light-harvesting complexes that capture photons of particular wavelengths. Photons not captured are reflected as the characteristic color of each pigment.

**Section 7.2** Collectively, photosynthetic pigments absorb most of the full range of wavelengths in the spectrum of visible light with impressive efficiency.

**Section 7.3** Photosynthesis has two stages: light-dependent and light-independent reactions. Figure 7.14 and the following equation summarize the process:

12H<sub>2</sub>O + 6CO<sub>2</sub> water carbon dioxide

In chloroplasts, the light-dependent reactions occur at a thylakoid membrane that forms a single compartment in the semifluid interior (stroma).

#### Biology **S**Now

*View the sites where photosynthesis takes place with the animation on BiologyNow.* 

**Sections 7.4, 7.5** Accessory pigments arrayed in clusters in the thylakoid membrane absorb photons and pass energy to many photosystems. Light-dependent

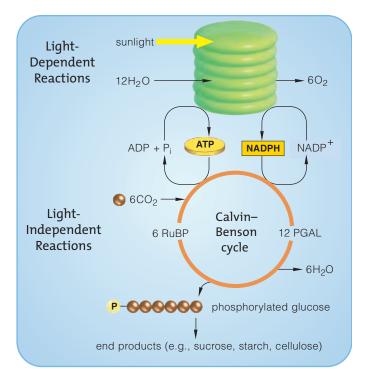


Figure 7.14 Visual summary of photosynthesis.

reactions use electrons released from photosystems in a noncyclic or a cyclic pathway of ATP formation.

In the noncyclic pathway, electrons are released from photosystem II and enter an electron transfer chain. Their flow through the chain causes hydrogen ions to accumulate in the thylakoid compartment. They flow on to photosystem I where photon absorption also causes the release of electrons. An intermediary molecule next to photosystem I accepts the electrons and transfers them to NADP<sup>+</sup>, which attracts hydrogen ions (H<sup>+</sup>) at the same time and becomes a reduced coenzyme, NADPH.

The electrons lost from photosystem II are replaced by way of photolysis—a reaction that pulls electrons from water molecules, with the release of  $H^+$  and  $O_2$ .

In the cyclic pathway, electrons from photosystem I enter an electron transfer chain, then are cycled back to the same photosystem. NADPH does not form.

In both pathways, the H<sup>+</sup> buildup in the thylakoid compartment forms concentration and electric gradients across the thylakoid membrane. H<sup>+</sup> flows in response to the gradients, through ATP synthases. The flow causes P<sub>i</sub> to be attached to ADP in the stroma, forming ATP.

#### Biology 🔊 Now

*Review the pathways by which light energy is used to form ATP with the animation on BiologyNow.* 

**Section 7.6** The light-independent reactions proceed in the stroma. In C3 plants, the enzyme rubisco attaches carbon from  $CO_2$  to RuBP to start the Calvin–Benson cycle. In this cyclic pathway, energy from ATP, carbon and oxygen from  $CO_2$ , and hydrogen and electrons from NADPH are used to make phosphorylated glucose, which quickly enters reactions that form the products of photosynthesis (mainly sucrose, cellulose, and starch). It takes six turns of the Calvin–Benson cycle to fix the six  $CO_2$  required to make one glucose molecule.

Biology 🔊 Now

Read the InfoTrac article "Robust Plants' Secret? Rubisco Activase!" Marcia Wood, Agricultural Research, November 2002.

**Section 7.7** Environments differ, and so do details of sugar production. On hot, dry days, plants conserve water by closing stomata, but  $O_2$  from photosynthesis cannot escape. In C3 plants, high  $O_2$ /low  $CO_2$  levels cause the enzyme rubisco to use  $O_2$  in an alternate pathway that does not make as much sugar. In C4 plants, carbon fixation occurs in one cell type, and the carbon enters the Calvin–Benson cycle in a different cell type. CAM plants close stomata in the day and fix carbon at night.

#### Biology

Read the InfoTrac article "Light of Our Lives," Norman Miller, Geographical, January 2001.

**Section 7.8** Photoautotrophs and chemoautotrophs produce the food that sustains themselves and all other organisms. Also, staggering numbers of diverse aerobic and anaerobic autotrophs live in the seas as well as on land. They have impact on the global cycling of oxygen, carbon, nitrogen, and other substances, and the global climate. Human activities are having impact on them.



Figure 7.15 Leaves of Elodea, an aquatic plant.

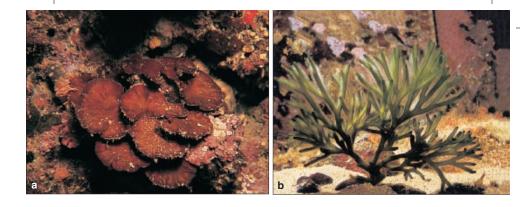


Figure 7.16 (a) Red alga from a tropical reef. (b) Coastal green alga (Codium)

 Self-Quiz
 Answers in Appendix II

 1. Photosynthetic autotrophs use \_\_\_\_\_\_ from the air as a carbon source and \_\_\_\_\_\_ as their energy source.

Chlorophyll *a* absorbs violet and red light, and it reflects light of \_\_\_\_\_\_ and \_\_\_\_\_ wavelengths.
 a. violet; red
 c. green only

b. yellow; green d. white; orange

- Light-*dependent* reactions in plants occur at the \_\_\_\_\_\_
   a. thylakoid membrane c. stroma
   b. plasma membrane d. cytoplasm
- 4. In the light-*dependent* reactions, \_\_\_\_\_\_.
  a. carbon dioxide is fixed c. CO<sub>2</sub> accepts electrons
  b. ATP and NADPH form d. sugars form

5. What accumulates inside the thylakoid compartment during the light-*dependent* reactions?

- a. glucose b. RuBP c. hydrogen ions d. CO<sub>2</sub>
- When a photosystem absorbs light, \_\_\_\_\_\_\_
   a. sugar phosphates are produced
   b. electrons are transferred to ATP
   c. RuBP accepts electrons
   d. light-dependent reactions begin
- 7. Light-*independent* reactions proceed in the \_\_\_\_\_. a. cytoplasm b. plasma membrane c. stroma
- The Calvin–Benson cycle starts when \_\_\_\_\_\_
   a. light is available
   b. carbon dioxide is attached to RuBP
   c. electrons leave photosystem II
- 9. What substance is *not* part of the Calvin–Benson cycle? a. ATP d. carotenoids

a. AIP	a. carotene
b. NADPH	e. O <sub>2</sub>
c. RuBP	f. CÕ <sub>2</sub>

- 10. Match each event with its most suitable description. \_\_\_\_\_ ATP formation only \_\_\_\_\_ a. rubisco required
  - \_\_\_\_\_ CO<sub>2</sub> fixation \_\_\_\_\_ PGAL formation

b. ATP, NADPH required c. electrons cycled back to photosystem II

Additional questions are available on Biology SNow™

#### Critical Thinking

1. About 200 years ago, Jan Baptista van Helmont did experiments on the nature of photosynthesis. He wanted to know where growing plants get the materials necessary for increases in size. He planted a tree seedling weighing 5 pounds in a barrel filled with 200 pounds of soil. He watered the tree regularly. Five years passed. Then van Helmont weighed the tree and the soil. The tree weighed 169 pounds, 3 ounces. The soil weighed 199 pounds, 14 ounces. Because the tree gained so much weight and the soil lost so little, he concluded the tree had gained all of its additional weight by absorbing water he had added to the barrel. Given what you know about biological molecules, why was he misguided? Knowing what you do about photosynthesis, what really happened?

2. A cat eats a bird, which earlier ate a caterpillar that chewed on a weed. Which organisms are autotrophs? Which are the heterotrophs?

3. Imagine walking through a garden of red, white, and blue petunias. Explain each of the colors in terms of which wavelengths of light the flower is absorbing.

4. Krishna exposes pea plants to a carbon radioisotope  $({}^{14}CO_2)$ , which they absorb. In which compound will the labeled carbon appear first if the plants are C3? C4?

5. While gazing into an aquarium, you observe bubbling from an aquatic plant (Figure 7.15). What is happening?

6. Only about eight classes of pigment molecules are known, but this limited group gets around in the world. For example, photoautotrophs make carotenoids, which move through food webs, as when tiny aquatic snails graze on green algae and then flamingos eat the snails. Flamingos modify the ingested carotenoids. Their cells split beta-carotene to form two molecules of vitamin A. This vitamin is the precursor of retinol, a visual pigment that transduces light into electric signals in eyes. Betacarotene gets dissolved in fat reservoirs under the skin. Cells that give rise to bright pink feathers take it up.

Select a similar organism and do some research to identify sources for pigments that color its surfaces.

7. Most pigments respond to only part of the rainbow of visible light. If acquiring energy is so vital, then why doesn't each kind of photosynthetic pigment absorb the whole spectrum? *Why isn't each one black*?

If early photoautotrophs evolved in the seas, then so did their pigments. Ultraviolet and red wavelengths do not penetrate water as deeply as green and blue wavelengths do. Possibly natural selection favored the evolution of different pigments at different depths. Many relatives of the red alga in Figure 7.16*a* live deep in the sea. Some are nearly black. Green algae, such as the one in Figure 7.16*b*, live in shallow water. Their chlorophylls absorb red wavelengths, and accessory pigments harvest others. Some accessory pigments also function as shields against ultraviolet radiation.

Speculate on how natural selection may have favored the evolution of different pigments at different depths, starting at hydrothermal vents. You might start at Richard Monasterky's article in *Science News* (September 7, 1996) on Cindy Lee Dover's work at hydrothermal vents.