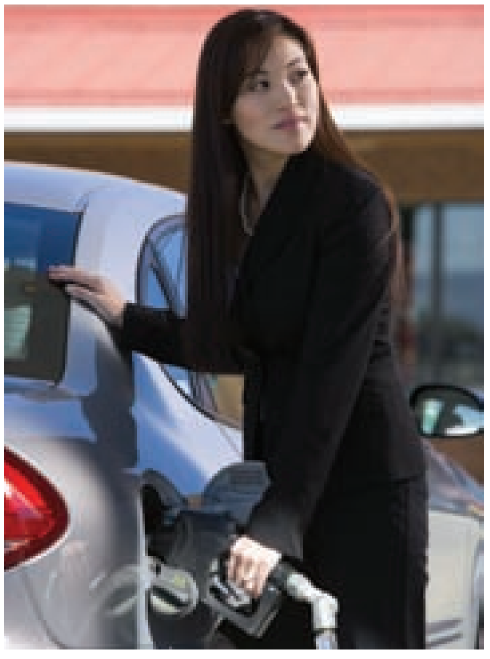
CHAPTER 7

Biochemical Pathways—Photosynthesis



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Designer Bacteria—Future Source of Biofuels?

Genetically Modified to Generate Fuel.

A team of scientists has transferred cellulose-making genes from one kind of bacterium to another. The photosynthetic bacteria receiving the genes, cyanobacteria, are able to capture and use sunlight energy to grow and reproduce. The added genes give them a new trait (i.e., the ability to manufacture large amounts of cellulose, sucrose and glucose). Because cyanobacteria (formerly known as blue-green algae) can also capture atmospheric nitrogen (N_2), they can be grown without costly, petroleum-based fertilizer.

The cellulose that is secreted is in a relatively pure, gel-like form that is easily broken down to glucose that can be fermented to produce ethanol and other biofuels. The biggest expense in making biofuels from cellulose is in using enzymes and mechanical methods to break cellulose down to fermentable sugars.

Genetically modified cyanobacteria could have several advantages in the production of biofuels. They can be grown in sunlit industrial facilities on nonagricultural lands and can grow in salty water that is unsuitable for other uses. This could reduce the amount of agricultural land needed to grow corn that is being fermented to biofuels. There are social and financial pressures to use more corn, sugar cane, and other food crops for nonfood uses throughout the world, thus reducing the amount of food crops. For example, Brazil is being pressured to cut more of the Amazon rainforest in order to grow more sugarcane to meet growing world energy needs.

- **How does photosynthesis trap light energy?**
- **What happens in photosynthetic organisms that results in the production of organic compounds?**
- **Should our government provide the same agricultural support payments to those who grow cyanobacteria as it pays to corn farmers?**

Background Check

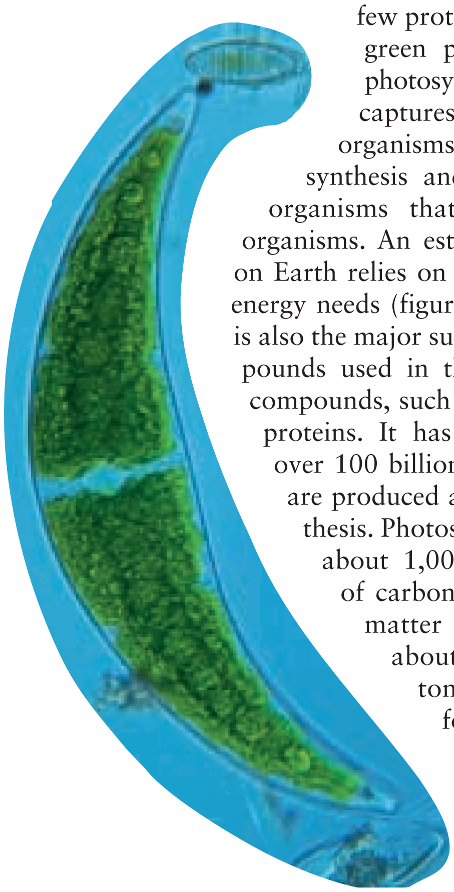
Concepts you should already know to get the most out of this chapter:

- The energy levels and position of electrons encircling an atom (chapter 2)
- The basic structure and function of chloroplasts and the types of cell in which they are located (chapter 4)
- How enzymes work in conjunction with ATP, electron transport, and a proton pump (chapter 5)
- The differences between autotrophs and heterotrophs (chapter 6)

7.1 Photosynthesis and Life

Although there are hundreds of different chemical reactions taking place within organisms, this chapter will focus on the reactions involved in the processes of photosynthesis. Recall from chapter 4 that, in photosynthesis, organisms such as green plants, algae, and certain bacteria trap radiant energy from sunlight. They are then able to convert it into the energy of chemical bonds in large molecules, such as carbohydrates. Organisms that are able to make energy-containing organic molecules from inorganic raw materials are called autotrophs. Those that use light as their energy source are more specifically called *photosynthetic* autotrophs or photoautotrophs.

Among prokaryotes, there are many bacteria capable of carrying out photosynthesis. For example, the cyanobacteria described in the opening article are all capable of manufacturing organic compounds using light energy.



Among the eukaryotes, a few protozoa and all algae and green plants are capable of photosynthesis. Photosynthesis captures energy for use by the organisms that carry out photosynthesis and provides energy to organisms that eat photosynthetic organisms. An estimated 99.9% of life on Earth relies on photosynthesis for its energy needs (figure 7.1). Photosynthesis is also the major supplier of organic compounds used in the synthesis of other compounds, such as carbohydrates and proteins. It has been estimated that over 100 billion metric tons of sugar are produced annually by photosynthesis. Photosynthesis also converts about 1,000 billion metric tons of carbon dioxide into organic matter each year, yielding about 700 billion metric tons of oxygen. It is for these reasons that a basic understanding of this biochemical pathway is important (How Science Works 7.1).

7.1 CONCEPT REVIEW

1. What are photosynthetic autotrophs?
2. How do photosynthetic organisms benefit heterotrophs?

7.2 An Overview of Photosynthesis

Ultimately, the energy to power all organisms comes from the sun. An important molecule in the process of harvesting sunlight is **chlorophyll,** a green pigment that absorbs light energy. Through photosynthesis, light energy is transformed to chemical-bond energy in the form of ATP. ATP is then used to produce complex organic molecules, such as glucose. It is from these organic molecules that organisms obtain energy through the process of cellular respiration. Recall from chapter 4 that, in algae and the leaves of green plants, photosynthesis occurs in cells that contain organelles called chloroplasts. Chloroplasts have two distinct regions within them: the grana and the stroma. **Grana** consist of stacks of individual membranous sacs, called **thylakoids,** that contain chlorophyll. The **stroma** are the spaces between membranes (figure 7.2).

The following equation summarizes the chemical reactions photosynthetic organisms use to make ATP and organic molecules:

$$\text{light energy} + \text{carbon dioxide} + \text{water} \rightarrow \text{glucose} + \text{oxygen}$$
$$\text{light energy} + 6\,CO_2 + 6\,H_2O \rightarrow C_6H_{12}O_6 + 6\,O_2$$

There are three distinct events in the photosynthetic pathway:

1. **Light-capturing events.** In eukaryotic cells, photosynthesis takes place within chloroplasts. Each chloroplast is surrounded by membranes and contains chlorophyll, along with other photosynthetic pigments. Chlorophyll and the other pigments absorb specific wavelengths of light. When specific amounts of light are absorbed by the photosynthetic pigments, electrons become "excited." With this added energy, these excited electrons can enter into the chemical reactions responsible for the production of ATP. These reactions take place within the grana of the chloroplast.
2. **Light-dependent reactions.** Light-dependent reactions use the excited electrons produced by the light-capturing

(a) (b) (c)

FIGURE 7.1 Our Green Planet
From space you can see that Earth is a green-blue planet. The green results from photosynthetic pigments found in countless organisms on land and in the blue waters. It is the pigments used in the process of photosynthesis that generate the organic molecules needed to sustain life. Should this biochemical process be disrupted for any reason (e.g., climate change), there would be a great reduction in the food supply to all living things.

HOW SCIENCE WORKS 7.1

Solution to Global Energy Crisis Found in Photosynthesis?

The most important chemical reaction on Earth, photosynthesis, is thought to have been around about 3 billion years. There has been plenty of time for this metabolic process to evolve into a highly efficient method of capturing light energy. Terrestrial and aquatic plants and algae are little solar cells that convert light into usable energy. They use this energy to manufacture organic molecules from carbon dioxide and water.

Photosynthetic organisms capture an estimated 10 times the global energy used by humans annually. Scientists and inventors have long recognized the value in being able to develop materials that mimic the light-capturing events of photosynthesis. The overall efficiency of photosynthesis is between 3–6% of total solar radiation that reaches the earth. Recently the National Energy Renewable Laboratory (NREL) verified that new organic-based photovoltaic solar cells have demonstrated 6% efficiency. They are constructed of a new family of photo-active polymers—polycarbazoles. Developers see their achievement as a major breakthrough and are hoping to develop solar cells with efficiencies in excess of 10%.

These cells have the ability to capture light energy and, at the same time, be used in many a variety of situations. Flexible plastic, leaf-like sheets can be attached to cell phones, clothing, awnings, roofs, toys, and windows to provide power to many kinds of electronic devices.

Solar-powered fan helmet being tried by a traffic policeman

events. Light-dependent reactions are also known as *light reactions*. During these reactions, excited electrons from the light-capturing events are used to produce ATP. As a by-product, hydrogen and oxygen are also produced. The oxygen from the water is released to the environment as O_2 molecules. The hydrogens are transferred to the electron carrier coenzyme $NADP^+$ to produce NADPH. ($NADP^+$ is similar to NAD^+, which was discussed in chapter 5.) These reactions also take place in the grana of the chloroplast. However, the NADPH and ATP leave the grana and enter the stroma, where the light-independent reactions take place.

3. **Light-independent reactions.** These reactions are also known as *dark reactions,* because light is not needed for them to occur. During these reactions, ATP and NADPH from the light-dependent reactions are used to attach CO_2 to a 5-carbon molecule, already present in the cell, to manufacture new, larger organic molecules. Ultimately, glucose ($C_6H_{12}O_6$) is produced. These light-independent reactions take place in the stroma in either the light or dark, as long as ATP and NADPH are available from the light-dependent stage. When the ATP and NADPH give up their energy and hydrogens, they turn back into ADP and $NADP^+$. The ADP and the $NADP^+$ are recycled back to the light-dependent reactions to be used over again.

The process of photosynthesis can be summarized as follows. During the light-capturing events, *light energy* is captured by chlorophyll and other pigments, resulting in excited electrons. The energy of these excited electrons is used during the light-dependent reactions to disassociate *water* molecules into hydrogen and oxygen, and the *oxygen* is released. Also during the light-dependent reactions, ATP is produced and $NADP^+$ picks up hydrogen released from water to form NADPH. During the light-independent reactions, ATP and NADPH are used to help combine *carbon dioxide* with a 5-carbon molecule, so that ultimately organic molecules, such as *glucose,* are produced (figure 7.3).

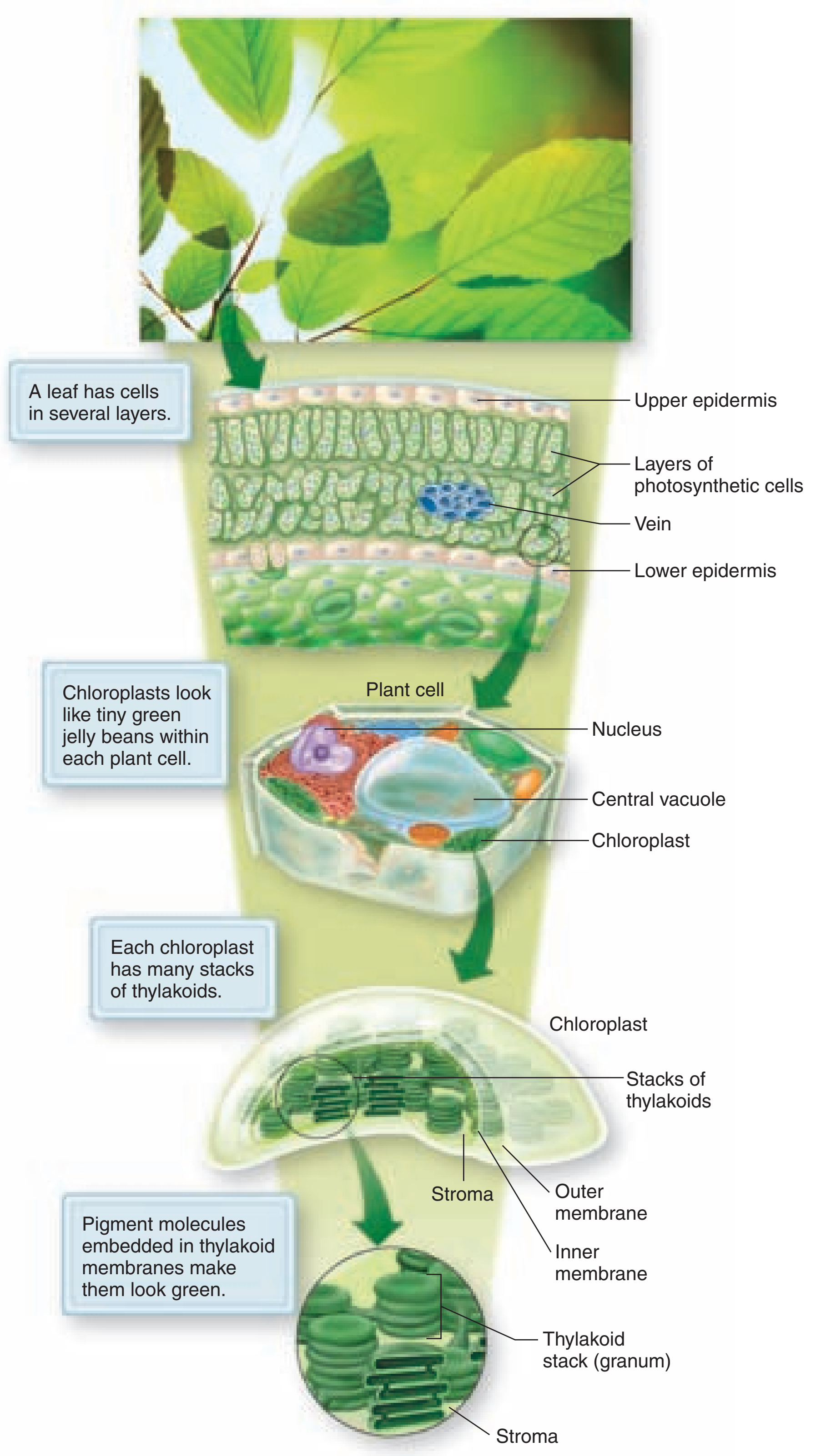


FIGURE 7.2 The Structure of a Chloroplast, the Site of Photosynthesis
Plant cells contain chloroplasts that enable them to store light energy as chemical energy. It is the chloroplasts that contain chlorophyll and that are the site of photosynthesis. The chlorophyll molecules are actually located within membranous sacs called thylakoids. A stack of *thylakoids* is known as a *granum*.

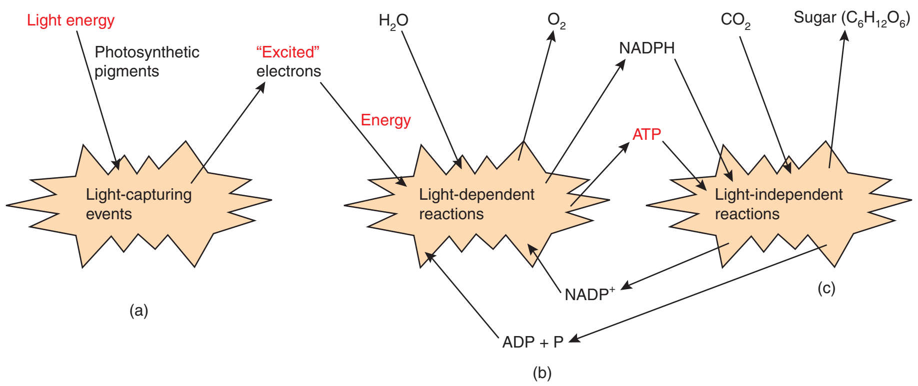


FIGURE 7.3 Photosynthesis: Overview
Photosynthesis is a complex biochemical pathway in plants, algae, and certain bacteria. This illustrates the three parts of the process: *(a)* the light-capturing events, *(b)* the light-dependent reactions, and *(c)* the light-independent reactions. The end products of the light-dependent reactions, NADPH and ATP, are necessary to run the light-independent reactions and are regenerated as $NADP^+$, ADP, and P. Water and carbon dioxide are supplied from the environment. Oxygen is released to the environment and sugar is manufactured for use by the plant.

7.2 CONCEPT REVIEW

3. Photosynthesis is a biochemical pathway that involves three kinds of activities. Name these and explain how they are related to each other.
4. Which cellular organelle is involved in the process of photosynthesis?

7.3 The Metabolic Pathways of Photosynthesis

It is a good idea to begin with the simplest description and add layers of understanding as you go to additional levels. Therefore, this discussion of photosynthesis is divided into two levels:

1. a fundamental description, and
2. a detailed description.

Ask your instructor which level is required for your course of study.

Fundamental Description

Light-Capturing Events

Light energy is used to drive photosynthesis during the light-capturing events. Visible light is a combination of many different wavelengths of light, seen as different colors. Some of these colors appear when white light is separated into its colors to form a rainbow. The colors of the electromagnetic spectrum that provide the energy for photosynthesis are correlated with different kinds of light-energy-absorbing pigments. The green chlorophylls are the most familiar and abundant. There are several types of this pigment. The two most common types are chlorophyll *a* and chlorophyll *b*. Both absorb strongly in the red and blue portions of the electromagnetic spectrum, although in slightly different portions of the spectrum (figure 7.4).

Carotenoids in tomato

Chlorophylls reflect green light. That is why we see chlorophyll-containing plants as predominantly green. Other pigments common in plants are called **accessory pigments.** These include the *carotenoids* (yellow, red, and orange). They absorb mostly blue and blue-green light while reflecting the oranges and yellows. The presence of these pigments is generally masked by the presence of chlorophyll, but in the fall, when chlorophyll disintegrates, the reds, oranges, and yellows show through. Accessory pigments are also responsible for the brilliant colors of vegetables, such as carrots, tomatoes, eggplant, and peppers. Photosynthetic bacteria and various species of algae have other kinds of accessory pigments not found in plants. Having a combination of different pigments, each of which absorbs a portion of the light spectrum hitting it, allows the organism to capture much of the visible light that falls on it.

Any cell with chloroplasts can carry on photosynthesis. However, in most plants, leaves are specialized for photosynthesis and contain cells that have high numbers of chloroplasts (figure 7.5).

Chloroplasts are membrane-enclosed organelles that contain many thin, flattened sacs that contain chlorophyll. These chlorophyll-containing sacs are called *thylakoids* and a number of these thylakoids stacked together is known as a *granum*. In addition to chlorophyll, the thylakoids contain accessory pigments, electron-transport molecules, and enzymes. Recall that the fluid-filled spaces between the grana are called the stroma of

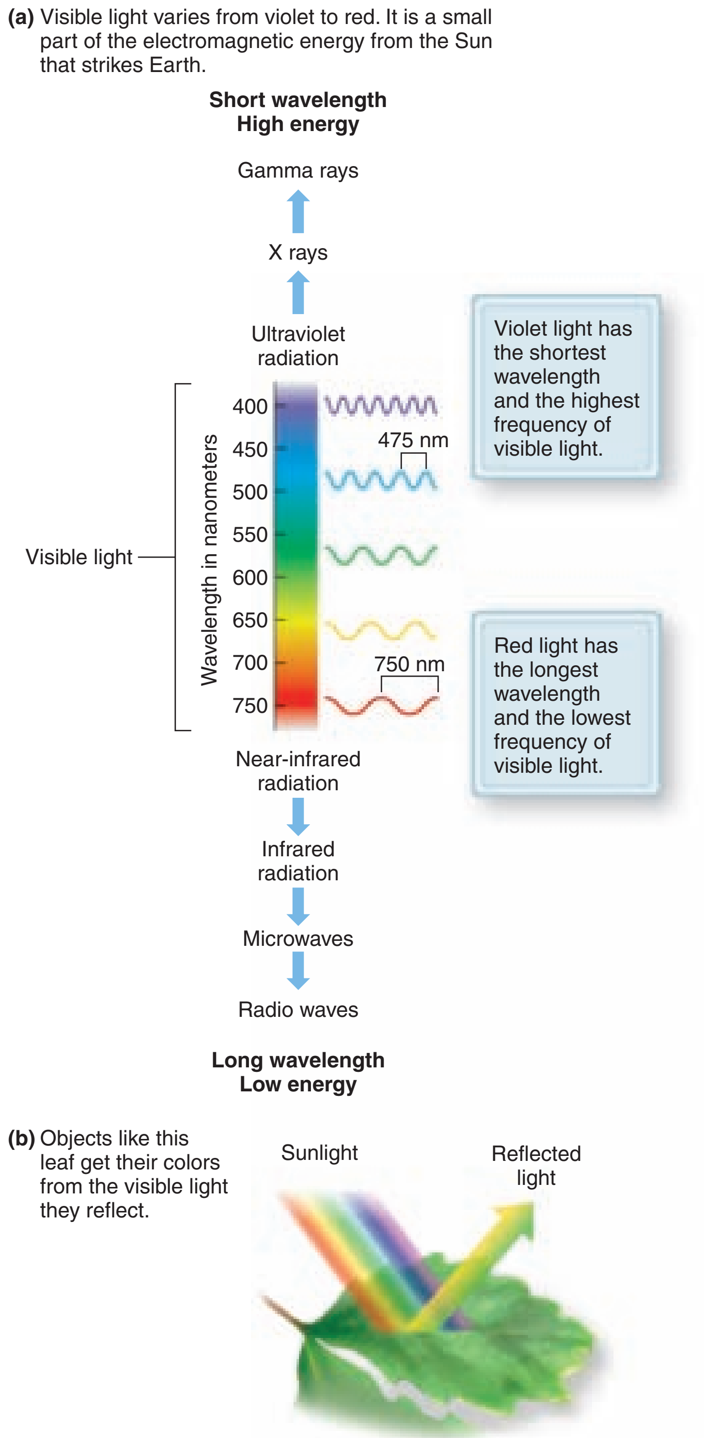


FIGURE 7.4 The Electromagnetic Spectrum, Visible Light, and Chlorophyll
Light is a form of electromagnetic energy that can be thought of as occurring in waves. Chlorophyll absorbs light most strongly in the blue and red portion of the electromagnetic spectrum but poorly in the green portions. The shorter the wavelength, the more energy it contains. Humans are capable of seeing only waves that are between about 400 and 740 nanometers (nm) long.

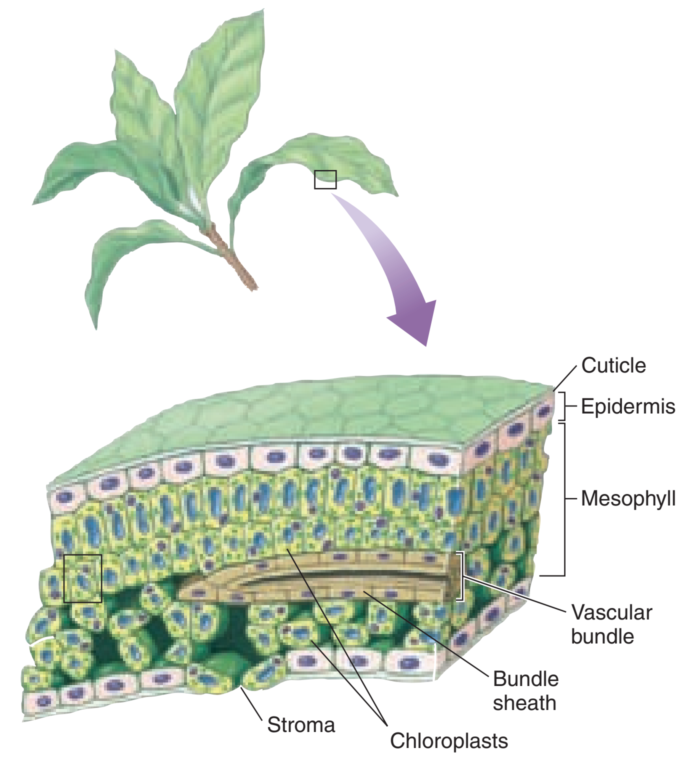


FIGURE 7.5 Photosynthesis and the Structure of a Plant Leaf
Plant leaves are composed of layers of cells that contain chloroplasts, which contain chlorophyll.

the chloroplast. The structure of the chloroplast is directly related to both the light-capturing and the energy-conversion steps of photosynthesis. In the light-capturing events, the pigments (e.g., chlorophyll), which are embedded in the membranes of the thylakoids, capture light energy and some of the electrons of pigments become excited. The chlorophylls and other pigments involved in trapping sunlight energy and storing it are arranged into clusters called **photosystems.** By clustering the pigments, photosystems serve as energy-gathering, or energy-concentrating, mechanisms that allow light to be collected more efficiently and excite electrons to higher energy levels.

A Fundamental Summary of Light-Capturing Events

photons of light energy → excited electrons from chlorophyll

Light-Dependent Reactions

The light-dependent reactions of photosynthesis also take place in the thylakoid membranes inside the chloroplast. The excited electrons from the light-capturing events are passed to protein molecules in the thylakoid membrane. The electrons are passed through a series of electron-transport steps, which result in protons being pumped into the cavity of the thylakoid. When the protons pass back out through the membrane to the outside of the thylakoid, ATP is produced. This is very similar to the reactions that happen in the electron-transport system (ETS) of aerobic cellular respiration. In addition, the chlorophyll that just lost its electrons to the chloroplast's electron-transport system regains electrons from water molecules. This results in the production of hydrogen ions, electrons, and oxygen gas. The next light-capturing event will excite this new electron and send it along the electron-transport system. As electrons finish moving through the electron-transport system, the coenzyme $NADP^+$ picks up the electrons and is reduced to NADPH. The hydrogen ions attach because, when $NADP^+$ accepts electrons, it becomes negatively charged ($NADP^-$). The positively charged H^+ are attracted to the negatively charged $NADP^-$. The oxygen remaining from the splitting of water molecules is released into the atmosphere, or it can be used by the cell in aerobic cellular respiration, which takes place in the mitochondria of plant cells. The ATP and NADPH molecules move from the grana, where the light-dependent reactions take place, to the stroma, where the light-independent reactions take place.

A Fundamental Summary of the Light-Dependent Reactions

$$\text{excited electrons} + H_2O + ADP + NADP^+ \rightarrow ATP + NADPH + O_2$$

Light-Independent Reactions

The ATP and NADPH provide energy, electrons and hydrogens needed to build large, organic molecules. The light-independent reactions are a series of oxidation-reduction reactions, which combine hydrogen from water (carried by NADPH) with carbon dioxide from the atmosphere to form simple organic molecules, such as sugar. As CO_2 diffuses into the chloroplasts, the enzyme **Ribulose-1,5-bisphosphate carboxylase oxygenase** (**RuBisCO**) speeds the combining of the CO_2 with an already present 5-carbon sugar, **ribulose.** NADPH then donates its hydrogens and electrons to complete the reduction of the molecule. The resulting 6-carbon molecule is immediately split into two 3-carbon molecules of **glyceraldehyde-3-phosphate.** Some of the glyceraldehyde-3-phosphate molecules are converted through another series of reactions into ribulose. Thus, these reactions constitute a cycle, in which carbon dioxide and hydrogens are added and glyceraldehyde-3-phosphate and the original 5-carbon ribulose are produced. The plant can use surplus glyceraldehyde-3-phosphate for the synthesis of glucose. The plant can also use glyceraldehyde-3-phosphate to construct a wide variety of other organic molecules (e.g., proteins, nucleic acids), provided there are a few additional raw materials, such as minerals and nitrogen-containing molecules (figure 7.6).

A Fundamental Summary of the Light-Independent Reactions

$$ATP + NADPH + \text{ribulose} + CO_2$$
$$\downarrow$$
$$ADP + NADP^+ + \text{complex organic molecule} + \text{ribulose}$$

Detailed Description

Light-Capturing Events

The energy of light comes in discrete packages, called *photons.* Photons of light having different wavelengths have different amounts of energy. A photon of red light has a different amount of energy than a photon of blue light. Pigments of different kinds are able to absorb photons of certain wavelengths of light. Chlorophyll absorbs red and blue light best and reflects green light. When a chlorophyll molecule is struck by and absorbs a photon of the correct wavelength, its electrons become excited to a higher energy level. This electron is replaced when chlorophyll takes an electron from a water molecule. The excited electron goes on to form ATP. The reactions that result in the production of ATP and the splitting of water take place in the thylakoids of chloroplasts. There are many different molecules involved, and most are embedded in the membrane of the thylakoid. The various molecules involved in these reactions are referred to as *photosystems.* A photosystem is composed of (1) an *antenna complex,* (2) a *reaction center,* and (3) other enzymes necessary to store the light energy as ATP and NADPH.

The antenna complex is a network of hundreds of chlorophyll and accessory pigment molecules, whose role is to capture photons of light energy and transfer the energy to a specialized portion of the photosystem known as the reaction center. When light shines on the antenna complex and strikes a chlorophyll molecule, an electron becomes excited. The energy of the excited electron is passed from one pigment to another through the antenna complex network. This series of excitations continues until the combined energies from several excitations are transferred to the reaction center, which consists of a complex of chlorophyll *a* and protein molecules. An electron is excited and passed to a primary electron acceptor molecule, oxidizing the chlorophyll and reducing the acceptor. Ultimately, the oxidized chlorophyll then has its electron replaced with another electron from a different electron donor. Exactly where this replacement electron comes from is the basis on which two different photosystems have been identified—photosystem I and photosystem II, which will be discussed in the next section.

Summary of Detailed Description of the Light-Capturing Reactions

1. They take place in the thylakoids of the chloroplast.
2. Chlorophyll and other pigments of the antenna complex capture light energy and produce excited electrons.
3. The energy is transferred to the reaction center.
4. Excited electrons from the reaction center are transferred to a primary electron acceptor molecule.

Light-Dependent Reactions

Both photosystems I and II have antenna complexes and reaction centers and provide excited electrons to primary electron acceptors. However, each has slightly different enzymes and

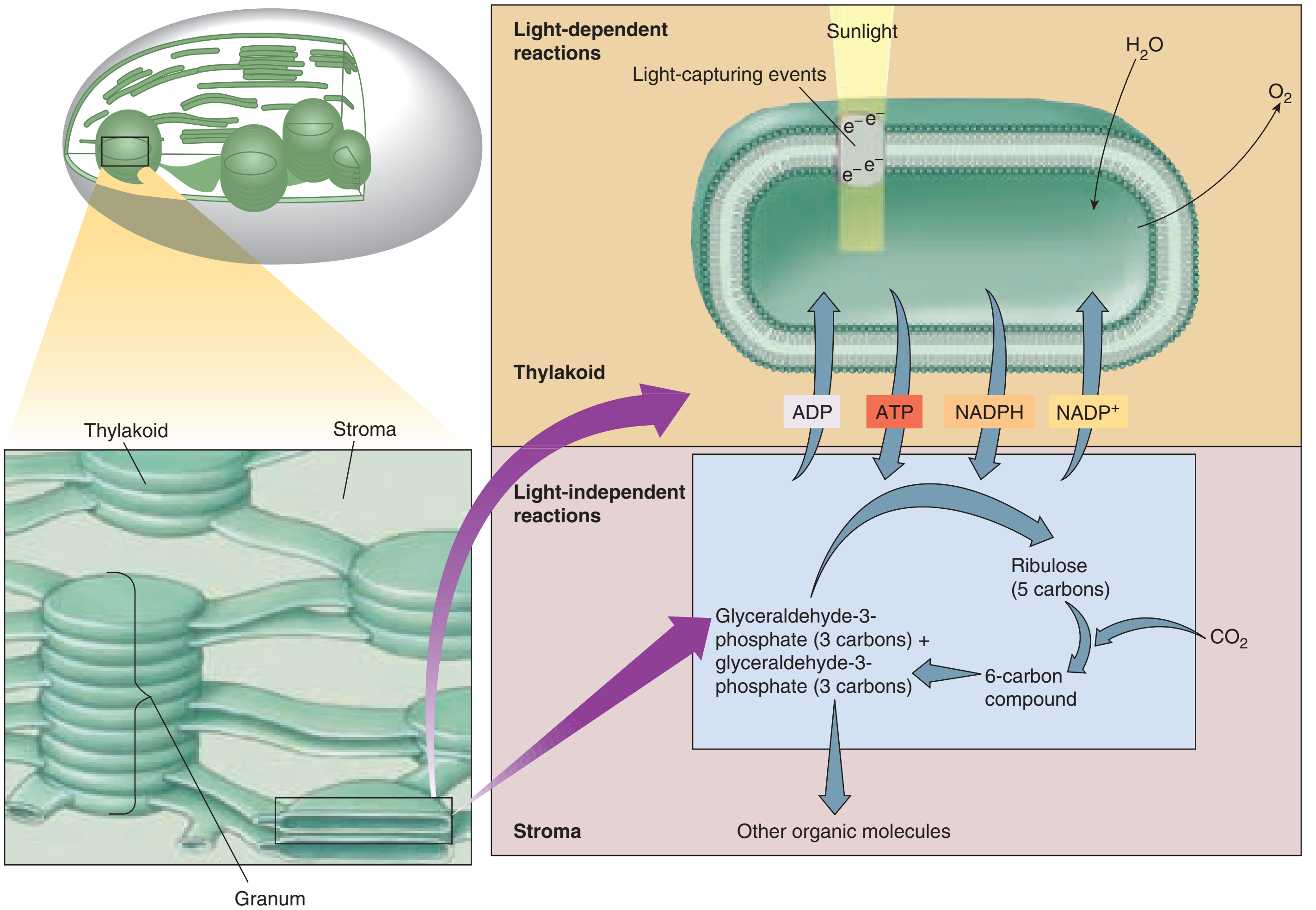


FIGURE 7.6 Photosynthesis: Fundamental Description
The process of photosynthesis involves light-capturing events by chlorophyll and other pigments. The excited electrons are used in the light-dependent reactions to split water, releasing hydrogens and oxygen. The hydrogens are picked up by $NADP^+$ to form NADPH and the oxygen is released. Excited electrons are also used to produce ATP. The ATP and NADPH leave the thylakoid and enter the stroma of the chloroplast, where they are used in the light-independent reactions to incorporate carbon dioxide into organic molecules. During the light-independent reactions, carbon dioxide is added to a 5-carbon ribulose molecule to form a 6-carbon compound, which splits into glyceraldehyde-3-phosphate. Some of the glyceraldehyde-3-phosphate is used to regenerate ribulose and some is used to make other organic molecules. The ADP and $NADP^+$ released from the light-independent reactions stage return to the thylakoid to be used in the synthesis of ATP and NADPH again. Therefore, each stage is dependent on the other.

other proteins associated with it, so each does a slightly different job. In actuality, photosystem II occurs first and feeds its excited electrons to photosystem I (figure 7.7). One special feature of photosystem II is that there is an enzyme in the thylakoid membrane responsible for splitting water molecules ($H_2O \rightarrow 2\ H + O$). The oxygen is released as O_2 and the electrons of the hydrogens are used to replace the electrons that had been lost by the chlorophyll. The remaining hydrogen ions (protons) are released to participate in other reactions. Thus, in a sense, the light energy trapped by the antenna complex is used to split water into H and O. The excited electrons from photosystem II are sent through a series of electron-transport reactions, in which they give up some of their energy. This is similar to the electron-transport system of aerobic cellular respiration. After passing through the electron-transport system, the electrons are accepted by chlorophyll molecules in photosystem I. While the electron-transport activity is happening, protons are pumped from the stroma into the space inside the thylakoid. Eventually, these protons move back across the membrane. When they do, ATPase is used to produce ATP (ADP is phosphorylated to produce ATP). Thus, a second result of this process is that the energy of sunlight has been used to produce ATP.

The connection between photosystem II and photosystem I involves the transfer of electrons from photosystem II to photosystem I. These electrons are important because photons (from sunlight) are exciting electrons in the reaction center of photosystem I and the electrons from photosystem II replace those lost from photosystem I.

In photosystem I, light is trapped and the energy is absorbed in the same manner as in photosystem II. However, this system does not have the enzyme involved in splitting water; therefore, no O_2 is released from photosystem I. The high-energy electrons

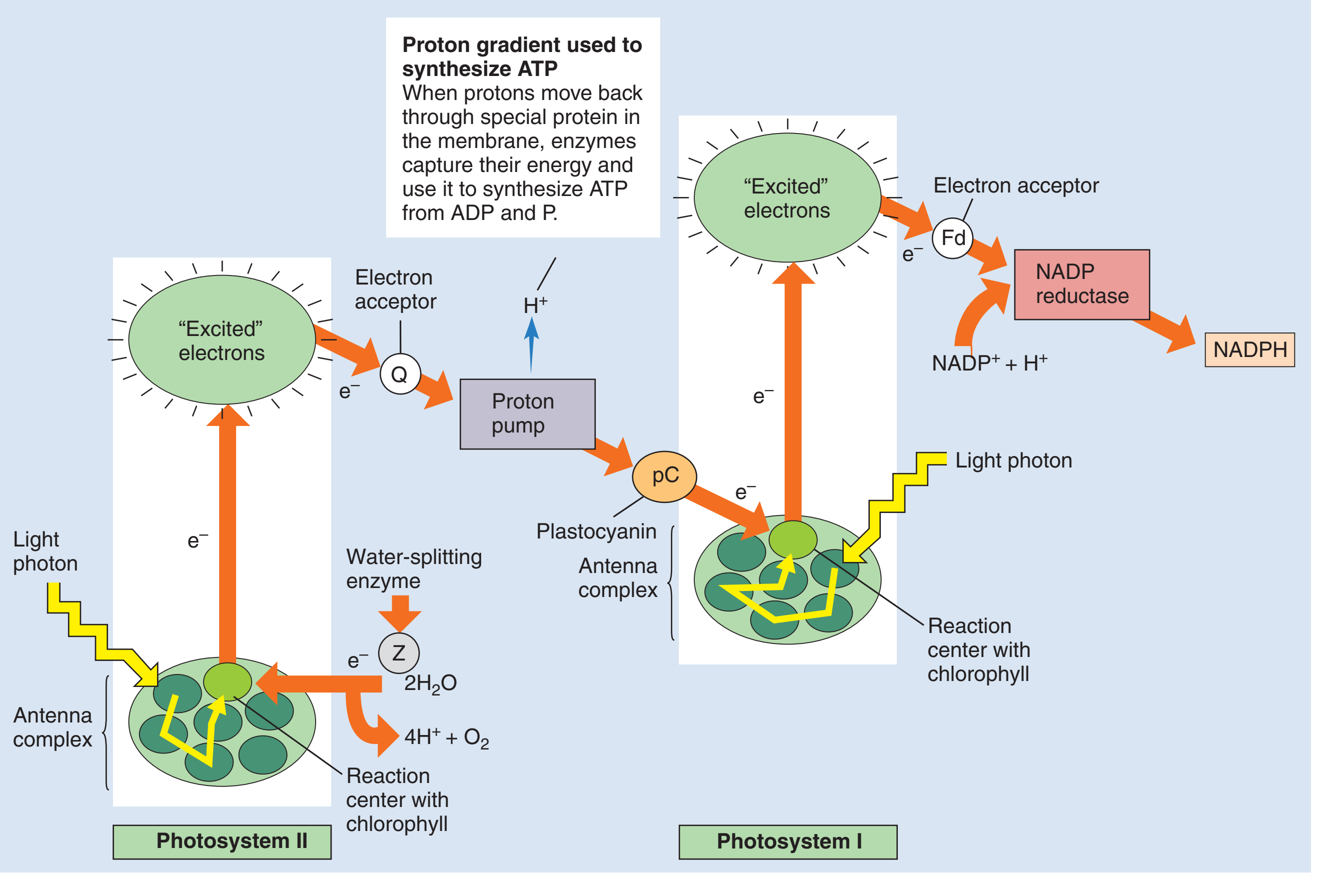


FIGURE 7.7 **Photosystems II and I and How They Interact: Detailed Description**
Although light energy strikes and is absorbed by both photosystem II and I, what happens and how they interconnect are not the same. Notice that the electrons released from photosystem II end up in the chlorophyll molecules of photosystem I. The electrons that replace those "excited" out of the reaction center in photosystem II come from water.

leaving the reaction center of photosystem I make their way through a different series of oxidation-reduction reactions. During these reactions, the electrons are picked up by $NADP^+$, which is reduced to NADPH (review figure 7.7). Thus, the primary result of photosystem I is the production of NADPH.

Summary of Detailed Description of the Light-Dependent Reactions of Photosynthesis

1. They take place in the thylakoids of the chloroplast.
2. Excited electrons from photosystem II are passed through an electron-transport chain and ultimately enter photosystem I.
3. The electron-transport system is used to establish a proton gradient, which produces ATP.
4. Excited electrons from photosystem I are transferred to $NADP^+$ to form NADPH.
5. In photosystem II, an enzyme splits water into hydrogen and oxygen. The oxygen is released as O_2.
6. Electrons from the hydrogen of water replace the electrons lost by chlorophyll in photosystem II.

Light-Independent Reactions

The light-independent reactions take place within the stroma of the chloroplast. The materials needed for the light-independent reactions are ATP, NADPH, CO_2, and a 5-carbon starter molecule called *ribulose*. The first two ingredients (ATP and NADPH) are made available from the light-dependent reactions, photosystems II and I. The carbon dioxide molecules come from the atmosphere, and the ribulose starter molecule is already present in the stroma of the chloroplast from previous reactions.

Carbon dioxide is said to undergo *carbon fixation* through the **Calvin cycle** (named after its discoverer, Melvin Calvin). In the Calvin cycle, ATP and NADPH from the light-dependent reactions are used, along with carbon dioxide, to synthesize larger, organic molecules. As with most metabolic pathways, the synthesis of organic molecules during the light-independent reactions requires the activity of several enzymes to facilitate the many steps in the process. The fixation of carbon begins with carbon dioxide combining with the 5-carbon molecule ribulose to form an unstable 6-carbon molecule. This reaction is carried out by the enzyme Ribulose-1,5-bisphosphate carboxylase oxygenase (RuBisCO), reportedly the most abundant enzyme on the planet. The

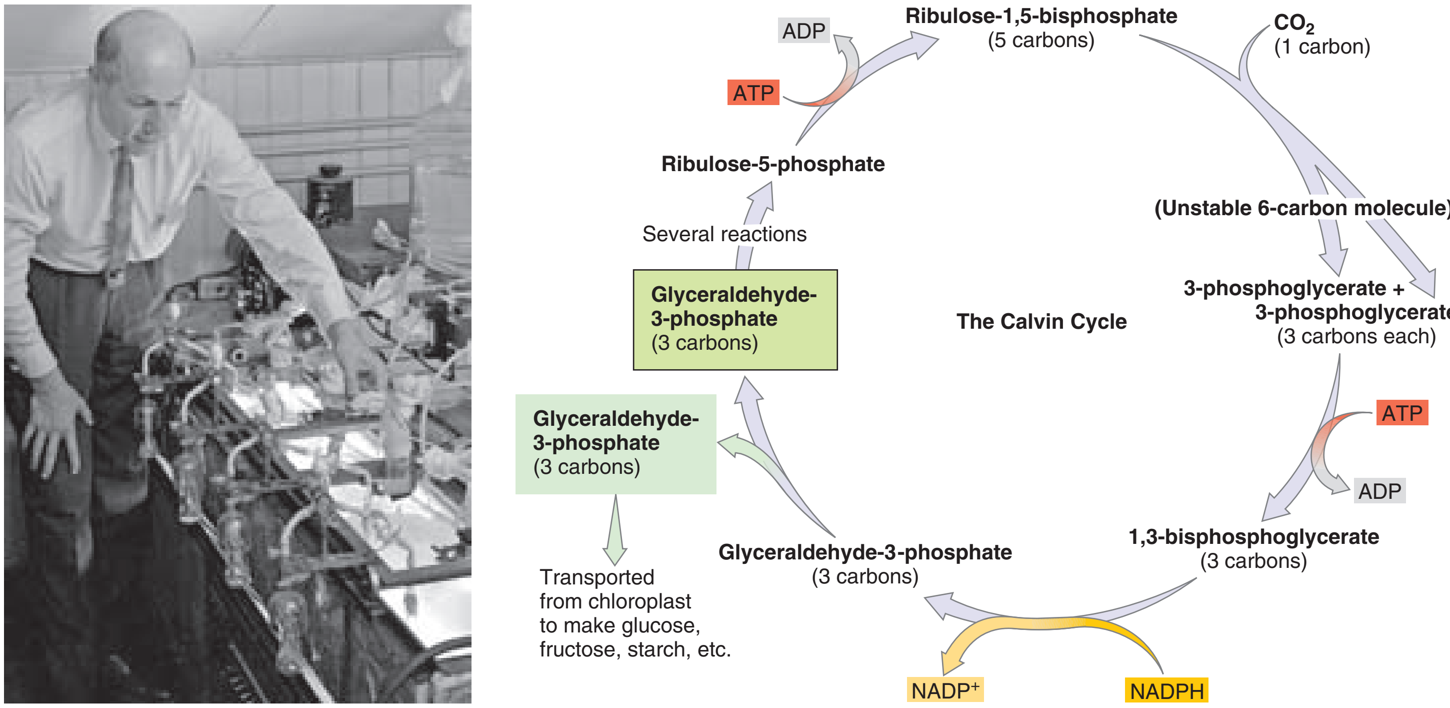


FIGURE 7.8 The Calvin Cycle: Detailed Description
During the Calvin cycle, ATP and NADPH from the light-dependent reactions are used to attach CO_2 to the 5-carbon ribulose molecule. The 6-carbon molecule formed immediately breaks down into two 3-carbon molecules. Some of the glyceraldehyde-3-phosphate formed is used to produce glucose and other, more complex organic molecules. In order to accumulate enough carbon to make a new glucose molecule, the cycle must turn six times. The remaining glyceraldehyde-3-phosphate is used to regenerate the 5-carbon ribulose to start the process again.

newly formed 6-carbon molecule immediately breaks down into two 3-carbon molecules, each of which then undergoes a series of reactions involving a transfer of energy from ATP and a transfer of hydrogen from NADPH. The result of this series of reactions is two glyceraldehyde-3-phosphate molecules. Because glyceraldehyde-3-phosphate contains 3 carbons and is formed as the first stable compound in this type of photosynthesis, this is sometimes referred to as the C3 photosynthetic pathway. Some of the glyceraldehyde-3-phosphate is used to synthesize glucose and other organic molecules, and some is used to regenerate the 5-carbon ribulose molecule, so this pathway is a cycle (figure 7.8). Outlooks 7.1 describes some other forms of photosynthesis that do not use the C3 pathway.

Summary of Detailed Description of the Reactions of the Light-Independent Events

1. They take place in the stroma of chloroplasts:

$$\text{CO}_2 + \text{ATP} + \text{NADPH} + \text{5-carbon starter (ribulose)}$$
$$\downarrow$$
$$\text{glyceraldehyde-3-phosphate} + \text{NADP}^+ + \text{ADP} + \text{P}$$

2. ATP and NADPH from the light-dependent reactions leave the grana and enter the stroma.
3. The energy of ATP is used in the Calvin cycle to combine carbon dioxide to a 5-carbon starter molecule (ribulose) to form a 6-carbon molecule.
4. The 6-carbon molecule immediately divides into two 3-carbon molecules of glyceraldehyde-3-phosphate.
5. Hydrogens from NADPH are transferred to molecules in the Calvin cycle.
6. The 5-carbon ribulose is regenerated.
7. ADP and $NADP^+$ are returned to the light-dependent reactions.

OUTLOOKS 7.1

The Evolution of Photosynthesis

It is amazing that the processes of photosynthesis in prokaryotes and eukaryotes are so similar. The evolution of photosynthesis goes back over 3 billion years, when all life on Earth was prokaryotic and occurred in organisms that were aquatic. (There were no terrestrial organisms at the time.) Today, some bacteria perform a kind of photosynthesis that does not result in the release of oxygen. In general, these bacteria produce ATP but do not break down water to produce oxygen. Perhaps these are the descendents of the first organisms to carry out a photosynthetic process, and oxygen-releasing photosynthesis developed from these earlier forms of photosynthesis.

Evidence from the fossil record shows that, beginning approximately 2.4 billion years ago, oxygen was present in the atmosphere. Eukaryotic organisms had not yet developed, so the organisms responsible for producing this oxygen would have been prokaryotic. Today, many kinds of cyanobacteria perform photosynthesis in essentially the same way as plants, although they use a somewhat different kind of chlorophyll. As a matter of fact, it is assumed that the chloroplasts of eukaryotes are evolved from photosynthetic bacteria. Initially, the first eukaryotes to perform photosynthesis would have been various kinds of algae. Today, certain kinds of algae (red algae, brown algae, green algae) have specific kinds of chlorophylls and other accessory pigments different from the others. Because the group known as the green algae has the same chlorophylls as plants, it is assumed that plants are derived from this aquatic group.

The evolution of photosynthesis did not stop once plants came on the scene, however. Most plants perform photosynthesis in the manner described in this chapter. Light energy is used to generate ATP and NADPH, which are used in the Calvin cycle to incorporate carbon dioxide into glyceraldehyde-3-phosphate. Because the primary product of this form of photosynthesis is a 3-carbon molecule of glyceraldehyde-3-phosphate, it is often called C3 photosynthesis. Among plants, there are two interesting variations of photosynthesis, which use the same basic process but add interesting twists.

Ripe barley crop–C3

Corn–C4

Jade plant–CAM

C4 photosynthesis is common in plants like grasses, such as corn (maize), crabgrass, and sugarcane that are typically subjected to high light levels. In these plants, carbon dioxide does not directly enter the Calvin cycle. Instead, the fixation of carbon is carried out in two steps, and two kinds of cells participate. It appears that this adaptation allows plants to trap carbon dioxide more efficiently from the atmosphere under high light conditions. Specialized cells in the leaf capture carbon dioxide and convert a 3-carbon compound to a 4-carbon compound. This 4-carbon compound then releases the carbon dioxide to other cells, which use it in the normal Calvin cycle typical of the light-independent reactions. Because a 4-carbon molecule is formed to "store" carbon, this process is known as C4 photosynthesis.

Another variation of photosynthesis is known as Crassulacean acid metabolism (CAM), because this mechanism was first discovered in members of the plant family, Crassulaceae. (A common example, *Crassula*, is known as the jade plant.) CAM photosynthesis is a modification of the basic process of photosynthesis that allows photosynthesis to occur in arid environments while reducing the potential for water loss. In order for plants to take up carbon dioxide, small holes in the leaves (stomata) must be open to allow carbon dioxide to enter. However, relative humidity is low during the day and plants would tend to lose water if their stomates were open. CAM photosynthesis works as follows: During the night, the stomates open and carbon dioxide can enter the leaf. The chloroplasts trap the carbon dioxide by binding it to an organic molecule, similar to what happens in C4 plants. The next morning, when it is light (and drier), the stomates close. During the day, the chloroplasts can capture light and run the light-dependent reactions. They then use the carbon stored the previous night to do the light-independent reactions.

Glyceraldehyde-3-Phosphate: The Product of Photosynthesis

The 3-carbon glyceraldehyde-3-phosphate is the actual product of the process of photosynthesis. However, many textbooks show the generalized equation for photosynthesis as

$$6\ CO_2 + 6\ H_2O + \text{light} \rightarrow C_6H_{12}O_6 + 6\ O_2$$

making it appear as if a 6-carbon sugar (hexose) were the end product. The reason a hexose ($C_6H_{12}O_6$) is usually listed as the end product is simply because, in the past, the simple sugars were easier to detect than was glyceraldehyde-3-phosphate.

Several things can happen to glyceraldehyde-3-phosphate. If a plant goes through photosynthesis and produces 12 glyceraldehyde-3-phosphates, 10 of the 12 are rearranged by a series of complex chemical reactions to regenerate the 5-carbon ribulose needed to operate the light-independent reactions stage. The other two glyceraldehyde-3-phosphates can be considered profit from the process. The excess glyceraldehyde-3-phosphate molecules are frequently changed into a hexose. So, the scientists who first examined photosynthesis chemically thought that sugar was the end product. It was only later that they realized that glyceraldehyde-3-phosphate is the true end product of photosynthesis.

Cells can do a number of things with glyceraldehyde-3-phosphate, in addition to manufacturing hexose (figure 7.9). Many other organic molecules can be constructed using glyceraldehyde-3-phosphate. Glyceraldehyde-3-phosphate can be converted to glucose molecules, which can be combined to form complex carbohydrates, such as starch for energy storage or cellulose for cell wall construction. In addition, other simple sugars can be used as building blocks for ATP, RNA, DNA, and other carbohydrate-containing materials.

The cell can also convert the glyceraldehyde-3-phosphate into lipids, such as oils for storage, phospholipids for cell membranes, or steroids for cell membranes. The glyceraldehyde-3-phosphate can serve as the carbon skeleton for the construction of the amino acids needed to form proteins. Almost any molecule that a green plant can manufacture begins with this glyceraldehyde-3-phosphate molecule. Finally, glyceraldehyde-3-phosphate can be broken down during cellular respiration. Cellular respiration releases the chemical-bond energy from glyceraldehyde-3-phosphate and other organic molecules and converts it into the energy of ATP. This conversion of chemical-bond energy enables the plant cell and the cells of all organisms to do things that require energy, such as grow and move materials (Outlooks 7.2).

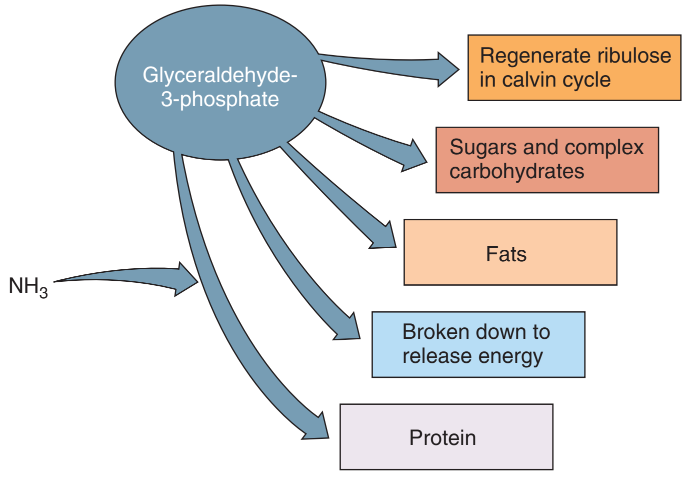


FIGURE 7.9 Uses for Glyceraldehyde-3-Phosphate
The glyceraldehyde-3-phosphate that is produced as the end product of photosynthesis has a variety of uses. The plant cell can make simple sugars, complex carbohydrates, or even the original 5-carbon starter from it. The glyceraldehyde-3-phosphate can also serve as an ingredient of lipids and amino acids (proteins). In addition, it is a major source of metabolic energy provided from aerobic respiration in the mitochondria of plant cells.

7.3 CONCEPT REVIEW

5. How do photosystem I and photosystem II differ in the kinds of reactions that take place?
6. What does an antenna complex do? How is it related to the reaction center?
7. What role is played by the compound Ribulose-1,5-bisphosphate carboxylase oxygenase (RuBisCo)?
8. What role is played by the compound glyceraldehyde-3-phosphate?
9. Describe how photosystem II interacts with photosystem I.
10. What is the value of a plant to have more than one kind of photosynthetic pigment?

7.4 Other Aspects of Plant Metabolism

Photosynthetic organisms are able to manufacture organic molecules from inorganic molecules. Once they have the basic carbon skeleton, they can manufacture a variety of other complex molecules for their own needs—fats, proteins, and complex carbohydrates are some of the more common. However, plants produce a wide variety of other molecules for specific purposes. Among the molecules they produce are compounds that are toxic to animals that use plants as food. Many of these compounds have been discovered to be useful as medicines. Digitalis from the foxglove plant causes the hearts of animals that eat the plant to malfunction (figure 7.10). However, it can be used as a medicine in humans who have certain heart ailments. Molecules that paralyze animals have been used in medicine to treat specific ailments and relax muscles, so that surgery is easier to perform. Still others have been used as natural insecticides.

OUTLOOKS 7.2

Even More Ways to Photosynthesize

Having gone through the information on photosynthesis, you might have thought that this was the only way for this biochemical pathway to take place. However, there are many prokaryotes capable of carrying out photosynthesis using alternative pathways. These Bacteria and Archaea have light-capturing pigments, but they are not the same as plant chlorophylls or the accessory pigments. The range of light absorption differs, allowing many of these Bacteria and Archaea to live in places unfriendly to plants. Some forms of photosynthetic bacteria do not release oxygen, but rather release other by-products such as H_2, H_2S, S, or organic compounds. Table 7.1 compares some of the most important differences between eukaryotic and prokaryotic photosynthesis.

TABLE 7.1 Different Types of Photosynthesis

Property	Eukaryotic	Prokaryotic—Cyanobacteria	Prokaryotic—Green and Purple Bacteria
Photosystem pigments	Chlorophyll *a*, *b*, and accessory pigments	Chlorophyll *a* and phycocyanin (blue-green pigment)	Combinations of bacteriochlorophylls *a*, *b*, *c*, *d*, or *e* absorb different wavelengths of light and some absorb infrared light.
Thylakoid system	Present	Present	Absent—pigments are found in vesicles called chlorosomes, or they are simply attached to plasma membrane.
Photosystem II	Present	Present	Absent
Source of electrons	H_2O	H_2O	H_2, H_2S, S, or a variety of organic molecules
O_2 production pattern	Oxygenic—release O_2	Oxygenic	Anoxygenic—do not release O_2 May release S, other organic compounds other than that used as the source of electrons
Primary products of energy conversion	ATP + NADPH	ATP + NADPH	ATP
Carbon source	CO_2	CO_2	Organic and/or CO_2
Example	Maple tree—*Acer*	*Anabaena* *Ocillatoria* *Nostoc*	Green sulfur bacterium—*Chlorobium* Green nonsulfur bacterium—*Chloroflexus* Purple sulfur bacterium—*Chromatium* Purple nonsulfur bacterium—*Rhodospirillum*

Vitamins are another important group of organic molecules derived from plants. Vitamins are organic molecules that we cannot manufacture but must have in small amounts to maintain good health. The vitamins we get from plants are manufactured by them for their own purposes. By definition, they are not vitamins to the plant, because the plant makes them for its own use. However, because we cannot make them, we rely on plants to synthesize these important molecules for us, and we consume them when we eat foods containing them.

7.4 CONCEPT REVIEW

11. Is vitamin C a vitamin for an orange tree?

7.5 Interrelationships Between Autotrophs and Heterotrophs

The differences between autotrophs and heterotrophs were described in chapter 6. Autotrophs are able to capture energy to manufacture new organic molecules from inorganic molecules. Heterotrophs must have organic molecules as starting points. *However, it is important for you to recognize that all organisms must do some form of respiration.* Plants and other autotrophs obtain energy from food molecules, in the same manner as animals and other heterotrophs—by processing organic molecules through the respiratory pathways. This means that plants, like animals, require oxygen for the ETS portion of aerobic cellular respiration.

(a) (b) (c)

FIGURE 7.10 Foxglove, *Cannabis*, and Coffee Plants
(a) Foxglove, *Digitalis purpurea*, produces the compound cardenolide digitoxin, a valuable medicine in the treatment of heart disease. The drug containing this compound is known as digitalis. *(b) Cannabis sativais*, the source of marijuana, has been show to be effective in the treatment of pain, nausea, and vomiting, and acts as an antispasmodic and anticonvulsant. *(c)* The plant *Coffea arabica* is one source of the compound caffeine and has been shown to reduce the risk of diabetes and Parkinson's disease.

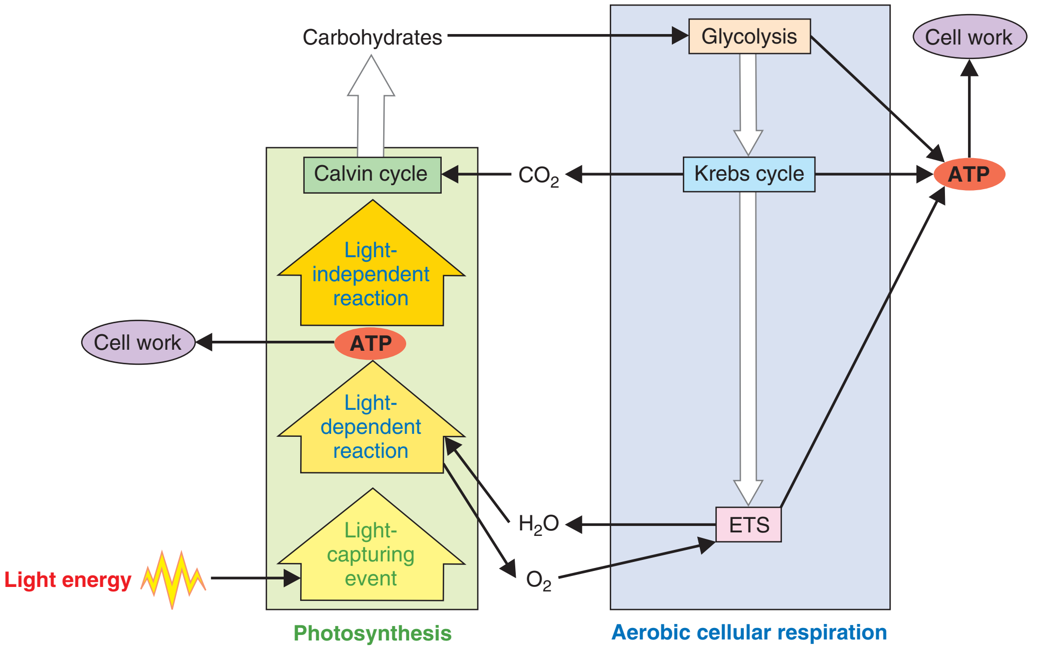


FIGURE 7.11 The Interdependence of Photosynthesis and Aerobic Cellular Respiration
Although both autotrophs and heterotrophs carry out cellular respiration, the photosynthetic process that is unique to photosynthetic autotrophs provides essential nutrients for both processes. Photosynthesis captures light energy, which is ultimately transferred to heterotrophs in the form of carbohydrates and other organic compounds. Photosynthesis also generates O_2, which is used in aerobic cellular respiration. The ATP generated by cellular respiration in both heterotrophs (e.g., animals) and autotrophs (e.g., plants) is used to power their many metabolic processes. In return, cellular respiration supplies two of the most important basic ingredients of photosynthesis, CO_2 and H_2O.

Many people believe that plants only give off oxygen and never require it. Actually, plants do give off oxygen in the light-dependent reactions of photosynthesis, but in aerobic cellular respiration they use oxygen, as does any other organism that uses aerobic respiration. During their life spans, green plants give off more oxygen to the atmosphere than they take in for use in respiration. The surplus oxygen given off is the source of oxygen for aerobic cellular respiration in both plants and animals. Animals are dependent on plants not only for oxygen but ultimately for the organic molecules necessary to construct their bodies and maintain their metabolism (figure 7.11).

Thus, animals supply the raw materials—CO_2, H_2O, and nitrogen—needed by plants, and plants supply the raw materials—sugar, oxygen, amino acids, fats, and vitamins—needed by animals. This constant cycling is essential to life on Earth. As long as the Sun shines and plants and animals remain in balance, the food cycles of all living organisms will continue to work properly.

7.5 CONCEPT REVIEW

12. Even though animals do not photosynthesize, they rely on the Sun for their energy. Why is this so?
13. What is an autotroph? Give an example.
14. Photosynthetic organisms are responsible for producing what kinds of materials?
15. Draw your own simple diagram that illustrates how photosynthesis and respiration are interrelated.

Summary

Sunlight supplies the essential initial energy for making the large organic molecules necessary to maintain the forms of life we know. Photosynthesis is the process by which plants, algae, and some bacteria use the energy from sunlight to produce organic compounds. In the light-capturing events of photosynthesis, plants use chemicals, such as chlorophyll, to trap the energy of sunlight using photosystems. During the light-dependent reactions, they manufacture a source of chemical energy, ATP, and a source of hydrogen, NADPH. Atmospheric oxygen is released in this stage. In the light-independent reactions of photosynthesis, the ATP energy is used in a series of reactions (the Calvin cycle) to join the hydrogen from the NADPH to a molecule of carbon dioxide and form a simple carbohydrate, glyceraldehyde-3-phosphate. In subsequent reactions, plants use the glyceraldehyde-3-phosphate as a source of energy and raw materials to make complex carbohydrates, fats, and other organic molecules. Table 7.2 summarizes the process of photosynthesis.

Key Terms

Use the interactive flash cards on the ***Concepts in Biology, 14/e*** *website to help you learn the meaning of these terms.*

accessory pigments 139
Calvin cycle 143
chlorophyll 136
glyceraldehyde-3-phosphate 141
grana 136
light-capturing events 136
light-dependent reactions 136
light-independent reactions 138
photosystems 140
ribulose 141
Ribulose-1,5-bisphosphate carboxylase oxygenase (RuBisCO) 141
stroma 136
thylakoids 136

Basic Review

1. Which of the following is *not* able to carry out photosynthesis?
   a. algae
   b. cyanobacteria
   c. frogs
   d. broccoli
2. A _______ consists of stacks of membranous sacs containing chlorophyll.
   a. granum
   b. stroma
   c. mitochondrion
   d. cell wall
3. During the ______ reactions, ATP and NADPH are used to help combine carbon dioxide with a 5-carbon molecule, so that ultimately organic molecules, such as glucose, are produced.
   a. light-independent
   b. light-dependent
   c. Watson cycle
   d. Krebs cycle

TABLE 7.2 Summary of Photosynthesis

Process	Where in the Chloroplast It Occurs	Reactants	Products
Light-energy trapping events	In the chlorophyll molecules and accessory pigments of the thylakoids	Chlorophylls	Excited electrons
Light-dependent reactions	In the thylakoids of the grana	Water, ADP, $NADP^+$	Oxygen, ATP, NADPH
Light-independent reactions	Stroma	Carbon dioxide, ribulose, ATP, NADPH	Glyceraldehyde-3-phosphate, ribulose, ADP, $NADP^+$

4. Pigments other than the green chlorophylls that are commonly found in plants are collectively known as ______. These include the carotenoids.
   a. chlorophylls
   b. hemoglobins
   c. accessory pigments
   d. thylakoids
5. This enzyme speeds the combining of CO_2 with an already present 5-carbon ribulose.
   a. DNAase
   b. ribose
   c. Ribulose-1,5-bisphosphate carboxylase oxygenase (RuBisCO)
   d. phosphorylase
6. Carbon dioxide undergoes carbon fixation, which occurs in the
   a. Calvin cycle.
   b. Krebs cycle.
   c. light-dependent reactions.
   d. photosystem I.
7. The chlorophylls and other pigments involved in trapping sunlight energy and storing it are arranged into clusters called
   a. chloroplasts.
   b. photosystems.
   c. cristae.
   d. thylakoids.
8. Light energy comes in discrete packages called
   a. $NADP^+$.
   b. lumina.
   c. photons.
   d. brilliance units.
9. The electrons released from photosystem ______ end up in the chlorophyll molecules of photosystem ______.
   a. I, II
   b. A, B
   c. B, A
   d. II, I
10. ______ are sacs containing chlorophylls, accessory pigments, electron-transport molecules, and enzymes.
    a. Thylakoids
    b. Mitochondria
    c. Photosystems
    d. Ribosomes
11. Which kind of organisms use respiration to generate ATP?
    a. plants
    b. animals
    c. algae
    d. all of the above
12. Plants, like animals, require ______ for the ETS portion of aerobic cellular respiration.
    a. silicone
    b. hydrogen
    c. nitrogen
    d. oxygen
13. ______ are an important group of organic molecules derived from plants. These are organic molecules that we cannot manufacture but must have in small amounts.
    a. Accessory pigments
    b. Vitamins
    c. Nitrogenous compounds
    d. Minerals
14. These prokaryotic organisms are capable of manufacturing organic compounds using light energy.
    a. algae
    b. protozoa
    c. cyanobacteria
    d. tomatoes
15. Chlorophyll-containing organisms look green because they reflect ______-colored light.
    a. green
    b. red
    c. yellow
    d. white

Answers
1. c 2. a 3. a 4. c 5. c 6. a 7. b 8. c 9. d 10. a 11. d 12. d 13. b 14. c 15. a

Thinking Critically

From a Metabolic Point of View
Both plants and animals carry on metabolism. From a metabolic point of view, which of the two is the more complex organism? Include in your answer the following topics:

1. Cell structure
2. Biochemical pathways
3. Enzymes
4. Organic molecules
5. Photosynthetic autotrophy and heterotrophy